Horizontale und vertikale Konnektivität in Fließgewässern und Seen – Ökologische Funktionen und anthropogene Überformung

Habilitationsschrift

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Die Welt ist wie ein Strom, der in seinem Bette fortläuft,
bald hier, bald da zufällig Sandbänke ansetzt
und von diesen wieder zu einem anderen Wege genötigt wird.

Johann Wolfgang von Goethe (1749-1832)
Aus: F. W. Riemer, Mitteilungen über Goethe, 1807

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1. Einleitung

1.1 Wissenschaftliches Interesse an der ökologischen Konnektivität von Gewässern

Die feste Landoberfläche der Erde ist nur auf wenigen Prozent der Fläche von Binnengewässern bedeckt, davon auf 1,9% von Süßwasserseen > 1 ha, entsprechend einer Fläche von ca. 2,80 Millionen km^2 (LEHNER & DÖLL 2004), und nur auf 0,24% von Fließgewässern mit einem mittlerem Abfluss > 1 m^3/s, entsprechend einer Fläche von ca. 360 000 km^2 (LEHNER et al. 2011). Die Fließgewässer erstrecken sich allerdings über eine Gesamtlänge von 7,56 Millionen Kilometern, entsprechend dem 189-fachen des Erdumfangs. Bei Einbeziehung der kleineren Fließgewässer würde diese Längenabschätzung noch um ein Mehrfaches steigen.

Trotz ihres geringen Anteils an der Landoberfläche haben Gewässer nicht nur vermutlich in der Evolution des Menschen (z.B. VERHAEGEN et al. 2007, NIEMITZ 2010) sondern auch bei der Entwicklung der menschlichen Zivilisation eine Schlüsselrolle gespielt, da Flusslandschaften und Seeufer dem Menschen eine Reihe grundlegender Ökosystemleistungen zur Verfügung stellen (MILLENIUM ECOSYSTEM ASSESSMENT 2003). Auch heute lebt mehr als die Hälfte der Weltbevölkerung in einer Entfernung von weniger als 3 km vom nächsten Binnengewässer, und nur 10% leben weiter als 10 km davon entfernt (KUMMU et al. 2011).

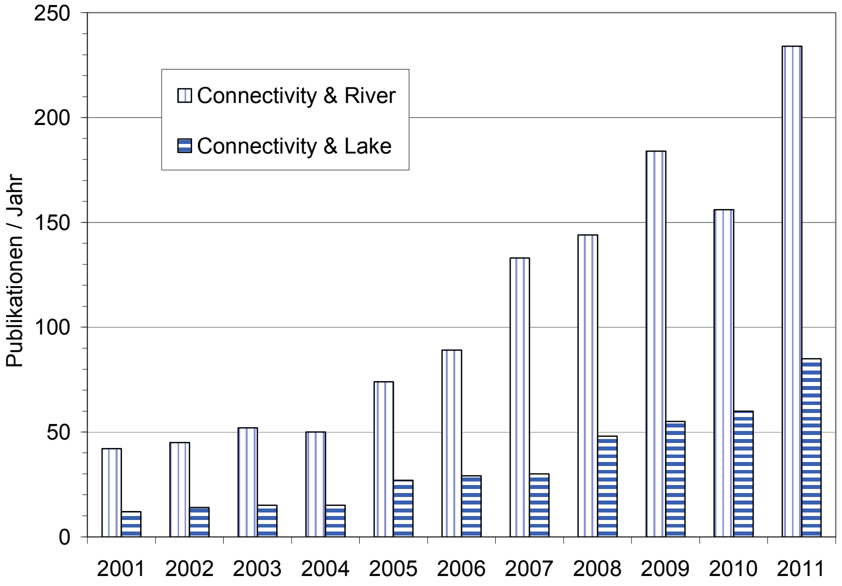
Die wissenschaftliche Untersuchung von Binnengewässern hat seit den Anfängen ihren Schwerpunkt in der Planktologie von Seen, die bereits zu Anfang des 20. Jahrhunderts in mehreren Ländern intensiv untersucht wurde (SCHWOERBEL & BRENDELBERGER 2005). Das dort erkannte Ineinandergreifen von Produktions- und Destruktionsprozessen veranlasste AUGUST THIENEMANN, Seen als weitgehend homogene und abgeschlossene Systeme anzusehen, deren Komponenten durch Wechselwirkungen eng miteinander verbunden sind (THIENEMANN 1925). In der weiteren Entwicklung der limnologischen Wissenschaft wurde zunehmend zu hypothesengeleiteten Untersuchungsansätzen übergegangen, die das Verständnis der Struktur und Funktion limnischer Systeme in den folgenden Jahrzehnten wesentlich vertieft haben.

Entsprechend der „Logik der Forschung“ (POPPER 1935) wird durch solche kompetitive, hypothesengeleitete Herangehensweise eine Wissenschaft einerseits mit hohem Erkenntnisgewinn weiterentwickelt. Andererseits besteht dabei jedoch kein Anspruch, dass die getesteten Theorien die Naturphänomene real abbilden, da einerseits die induktive Theoriebildung durch zeitbedingte Paradigmen und methodische Restriktionen beschränkt sein kann, und andererseits ihre Gültigkeit durch Experimente deduktiv nur widerlegt, aber nicht verallgemeinernd bestätigt werden können. Werden solche Beschränkungen der Theoriebildung überwunden, kann es in der Wissenschaft zu „Revolutionen“ (KUHN 1962) kommen.

So wurde erst gegen Ende des 20. Jahrhunderts in der Landschaftsökologie das Konzept der ökologischen Konnektivität von Lebensräumen entwickelt (MERRIAM 1984). Es bezog sich ursprünglich auf die Möglichkeit von Organismen, von einem Ressourcenfleck zu einem anderen zu gelangen ("*the degree to which the landscape facilitates or impedes movement among resource patches*", TAYLOR et al. 1993, 2006, TISCHENDORF & FAHRIG 2000). Der Begriff wird aber auch allgemeiner verwendet, etwa im Sinne von *„connectivity is the measure of how* *connected or spatially continuous a corridor, network, or matrix is*" (Forman 1995) und wird auch auf Stoffluxe ohne Interaktion mit Konsumenten angewendet (Moran et al. 1999, Massicotte & Frenette 2011). Ökologische Konnektivität in einem Landschaftsausschnitt kann quantifiziert werden z.B. mittels der Analogie des Stromkreislaufs (McRae et al. 2008).

Seit der Entwicklung des Konzepts der Konnektivität wurde mithilfe der nun bestehenden Möglichkeiten zur Untersuchung ökologischer Funktionen und Stofffluxe in Gewässern nachgewiesen, dass die Intensität der ökologischen Konnektivität von Komponenten innerhalb von Ökosystemen stark variieren kann, und andererseits die Konnektivität mit benachbarten Ökosystemen deutlich intensiver ist als bisher angenommen. Dies gilt insbesondere für die Fließgewässer als relativ „offene" Gewässerökosysteme (z.B. Stanford & Ward 1993), aber auch für Seen (Schindler et al. 1996, Polis et al. 1997, Pusch et al. 1998, Amoros & Bornette 2002, Schindler & Scheuerell 2002, Vadeboncoeur et al. 2002, Vander Zanden & Vadeboncoeur 2002, Naiman et al. 2005). Insbesondere die Stabilisotopenmethode zur Aufklärung von Nahrungsnetzen erbrachte hierbei überraschende neue Befunde. Die Anzahl der wissenschaftlichen Publikationen zur Konnektivität von Flüssen und Seen nahm seither stark zu (Abb. 1).

Abb. 1: Jährliche Anzahl der erschienenen wissenschaftlichen Publikationen zu den Stichwortkombinationen „connectivity & river" sowie „connectivity & lake" über die vergangenen 10 Jahre (Quelle: ISI Web of Science).



Ökosysteme sind per definitionem Ausschnitte der belebten Natur, an denen sich in der zeitlichen Dimension die Zyklen der Nährstoffkreisläufe über die Verbindungen der Nahrungsnetze mit der Ontogenese der dort lebenden Organismen vielfach verschränken, wobei die Art und Ausdehnung der Kontaktflächen zwischen Nährstoffkreisläufen mit den Lebenszyklen auf längere Sicht einer gerichteten Veränderung durch die Evolution unterliegen. Dabei werden in Gewässern Nährstoffe wegen der gering ausgebildeten pflanzlichen Stützstoffe und der in Lösung besseren Verfügbarkeit schneller rezykliert als im terrestrischen Bereich (Shurin et al. 2006). Die Nährstoffkreisläufe sind allerdings unvollkommen, da Anteil davon ständig durch permanente Sedimentation oder Auswaschung verloren gehen (Odum 1959).

Daher hängt die Persistenz von aquatischen Lebensgemeinschaften vom ständigen Eintrag von anorganischen Nährstoffen aus dem terrestrischen Umland ab (vgl. Howarth et al. 1996, BEHRENDT & BACHOR 1998). Durch diese horizontale Konnektivität erhalten Gewässerökosysteme auch erhebliche Einträge von partikulärem und gelöstem organischem Material aus den Einzugsgebieten, die die schnelle Dynamik der organischen Ressourcen in Gewässern stabilisieren (HUXEL & MCCANN 1998, TAKIMOTO et al. 2002, ROONEY et al. 2006). In Fließgewässern sind die Zyklen dabei zu Spiralen ausgezogen (NEWBOLD et al. 1981, 1982, 1983, ELWOOD et al. 1983, SPEAKER et al. 1984, MULHOLLAND et al. 1990, STREAM SOLUTE WORKSHOP 1990, RUNKEL et al. 2002), die sich durch die Überlagerung des unidirektionalen Transports mit der Strömung mit der temporären Fixierung der Nährstoffe im Benthal ergeben. Die vertikale Konnektivität durch die benthisch-pelagische Kopplung (GRAF 1992) bestimmt dabei die Spiralenlänge und damit auch die Intensität der Stoffumsetzungen in Fließgewässern.

Somit werden die ökologischen Funktionen von Gewässerökosystemen wesentlich durch deren horizontale und vertikale ökologische Konnektivität bestimmt. Diese Bedeutung der Konnektivität konnte im Rahmen der dieser Habilitationsschrift zugrunde liegenden Publikationen vielfach auch quantitativ dargestellt werden. In diesen Publikationen wurden wesentliche Ökosystemkompartimente und Stofffluxe in den zwei Flachlandflüssen Spree (6. Größenordnung nach STRAHLER 1957) und Elbe (8. Größenordnung) sowie im Litoral nordostdeutscher Seen untersucht. Die zugrunde liegenden Forschungsvorhaben waren jeweils in integrativer Weise konzipiert, dass die energetische oder stoffliche Konnektivität mehrerer Ökosystemkomponenten und die sie bestimmenden ökologischen Faktoren erfasst wurden (vgl. STREIT 1995; z.B. Abb. 2).

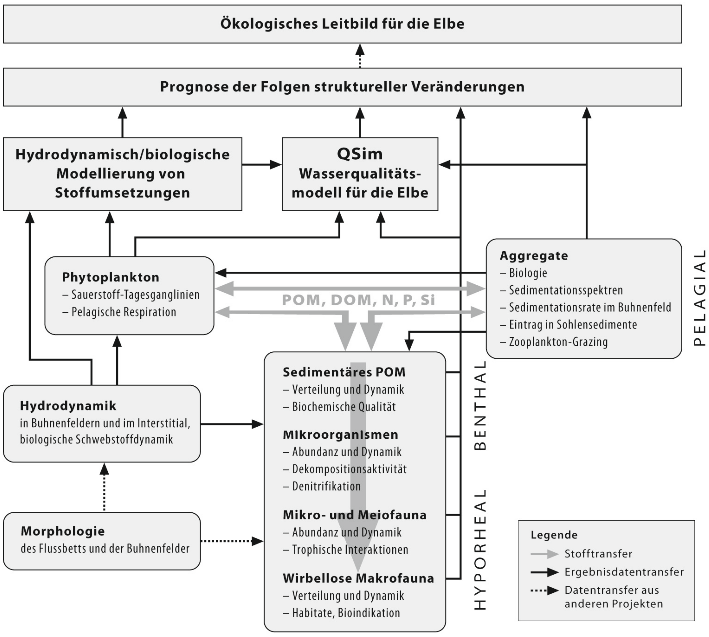


Abb. 2: Fachliche Organisation des multidisziplinären, vom Habilitanden konzipierten und geleiteten Verbundprojekts *„Strukturgebundener Stoffumsatz und Habitatstruktur in der Elbe“ innerhalb des BMBF-Forschungsprogramms „Elbe-Ökologie“*. Die Felduntersuchungen zu Organismen und Prozessen im Hyporheal (sowie Parafluvial), zentralen und litoralen Benthal sowie im Pelagial dienten nicht nur der fachspezifischen Auswertung, sondern auch zur (Weiter-)Entwicklung von Modellierungsansätzen und eines ökologischen Leitbilds der Elbe.

Ökologische Funktionen im Benthal größerer Fließgewässer wie Spree oder Elbe sind wissenschaftlich wenig untersucht, da die methodische Schwierigkeit besteht, das in erheblicher Wassertiefe – bei starker Überströmung – liegende Benthal und Hyporheal verlässlich zu beproben. Diese methodische Hürde wurde – soweit erforderlich – durch den Einsatz von Tauchern (dSpree) bzw. eines Taucherschachtschiffs (Elbe) gelöst. Die Ergebnisse wurden in zwei Monographien jeweils synoptisch dargestellt (KÖHLER et al. 2002, PUSCH & FISCHER 2006).

1.2 Vertikale Konnektivität in Fließgewässern

Aufgrund des ständigen unidirektionalen Wassertransports ist der Durchsatz von biologischen Ressourcen durch Fließgewässersysteme besonders hoch. Die Ausbildung der Biozönosen hängt somit entscheidend von der vertikalen Konnektivität, insbesondere der pelagisch-benthischen Kopplung zwischen dem strömenden Freiwasser und dem relativ ortsstabilen Benthal ab (NEWBOLD et al. 1982). Die Analyse der Fracht und Nutzung von organischem Material in einem Fließgewässerabschnitt erlaubt somit grundlegende Einblicke in die Funktionalität eines Fließgewässerökosystems (FISHER 1977, PUSCH & SCHWOERBEL 1994, WEBSTER & MEYER 1997, PUSCH 1996) bzw. dessen funktionale Veränderung durch anthropogene Belastungen (z.B. VITOUSEK et al. 1997). Da Ressourcen, die von Biozönosen im Oberlauf genutzt werden, zunächst nicht zu den stromab lebenden Biozönosen transportiert werden und von diesen genutzt werden können, beeinflusst die vertikale Konnektivität auch die longitudinale Konnektivität zwischen Flussabschnitten innerhalb eines Flusssystems (VANNOTE et al. 1980), sowie die Bedeutung von Diskontinuitäten darin (WARD & STANFORD 1983).

Die vertikale Konnektivität kann experimentell annähernd bestimmt werden durch Zugabe limitierender Stoffe (Additionsexperimente) evtl. zusammen mit nicht reaktiven Tracern, wodurch örtlich, quantitativ und qualitativ gut definierte Stoffquellen erzeugt werden, deren Retention und gegebenenfalls weitere Nutzung durch das Nahrungsnetz dann quantitativ verfolgt werden kann (PAYN et al. 2005). Die vertikale Konnektivität zwischen Pelagial und Benthal wurde somit für Fließgewässer mittels der „Nährstoffspiralenkonzept“ theoretisch gefasst und parameterisiert (*Spiralling concept*; WEBSTER & PATTEN 1979, NEWBOLD et al. 1981, 1992, ELWOOD et al. 1983). Gemäß dieser Theorie interagieren in Fließgewässersystemen das fließende Wasser als die Tranportphase und das Benthal als die feste Phase in charakteristischer Weise (HARVEY & WAGNER 2000), indem suspendiert oder gelöst transportierte Teilchen durch diverse Retentionsvorgänge mit einer bestimmten Wahrscheinlichkeit und Rate im Benthal zurückgehalten und damit aus dem fließenden Wasser entfernt werden (BEHRENDT & OPITZ 1999, KRONVANG et al. 1999). Im Benthal können diese Teilchen biologischen Umsetzungen unterliegen, in jedem Fall besteht wieder eine gewisse Wahrscheinlichkeit und Rate, dass die Teilchen resuspendiert und mit der fließenden Welle weitertransporiert werden (NEWBOLD et al. 1992).

Die für weniger stark durchströmte Ökosysteme postulierten Zyklen insbesondere der anorganischen Makronährstoffe Stickstoff und Phosphor werden hier somit durch Überlagerung mit zeitweiligen Transportphasen in der fließenden Welle zu charakteristischen Spiralen auseinander gezogen. Eine Spiralenumdrehung entspricht dabei einem Zyklus der Assimilation und Ausscheidung durch Organismen einschließlich des Aufenthalts des Stoffteilchens in unbelebten Kompartimenten des Ökosystems. Die Zeitdauer, während der ein Stoffteilchen als Teil einem Organismus’ verbleibt, wird als Umsatzzeit („turnover time“) bezeichnet, und die gegebenenfalls (im Falle von Plankton oder anderen driftenden Organismen) dabei zurückgelegte Fließlänge als Umsatzlänge („turnover length“). Die Umsatzlänge wird dabei wesentlich durch die Fließgeschwindigkeit und die Retentionseffizienz des betrachteten Fließgewässerabschnitts bestimmt und kann in weiten Bereichen schwanken (Minshall et al. 1983).

In ihrem Transportverhalten, ihrer Retentionseffizienz und in ihrer Umsatzzeit unterscheiden sich die biologischen Makronährstoffe C, N und P – soweit untersucht – oftmals erheblich. Obwohl die Umsatzraten oft miteinander gekoppelt sind (z. B. Wallace et al. 1999), müssen daher die Nährstoffspiralen für jedes Element getrennt untersucht werden (z.B. Hall et al. 2003). Dieses unterschiedliche Retentionsverhalten kann z.B. anthropogene Ungleichgewichte in der Verfügbarkeit der Makronährstoffe C, N und P (vgl. z.B. Carpenter et al. 1998, Caraco & Cole 1999, Haggard et al. 2001, 2005, Doyle et al. 2003, Gücker et al. 2004) erzeugen, verstärken oder verringern. Gemäß dem Konzept der „ökologischen Stöchiometrie“ (Sterner & Elser 2002) können solche Ungleichgewichte in der Verfügbarkeit biologischer Nährstoffe, insbesondere das stöchiometrische Verhältnis der darin enthaltenen Elemente, wesentlich die Lebensstrategien und das Verhalten der Organismen sowie ebenso auch Stofffuxe und die Struktur von Nahrungsnetzen bestimmen (Bernhardt & Likens 2002, Dodds et al. 2002, Woodward & Hildrew 2002).

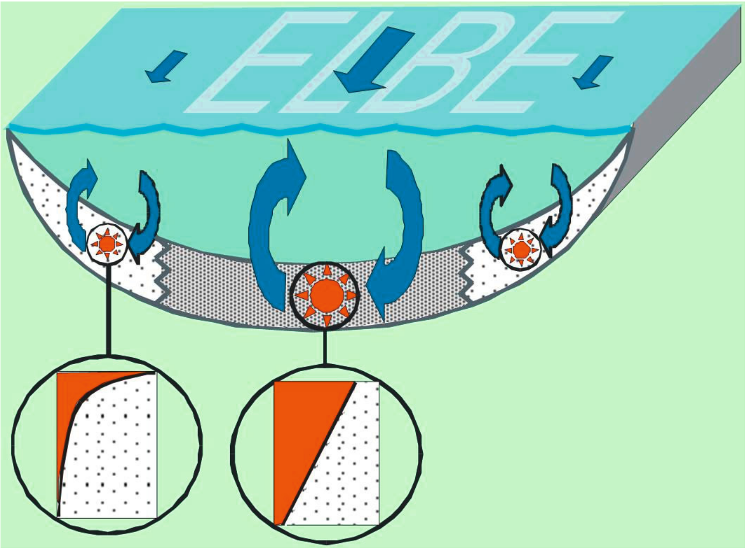


Abb. 3: Schematische Darstellung der ökologischen Funktion zentraler Flusssedimente als “Leber des Flusses”, am Beispiel der Elbe. Die mobilen Sedimente im zentralen Teil des Flussbetts eines frei fließenden Flusses sind mit dem fließenden Wasser durch relativ engen hydrologischen Austausch verbunden, wodurch bis zu einer relativ großen Tiefe mit gelöster Sauerstoff und partikuläres und gelöstes organisches Material eingetragen werden. Dadurch wird eine hohe mikrobielle Aktivität (großes Strahlensymbol) bis in große Sedimenttiefe ermöglicht, die mit der Sedimenttiefe etwa linear abnimmt (vergrößertes Bild unten rechts). Im Gegensatz dazu sind ufernahe Sedimente nur in geringem Umfang mit der Wassersäule verbunden, und zeigen eine deutlich geringere mikrobielle Aktivität (kleines Strahlensymbol), da diese von der Sedimentoberfläche abwärts steil abnimmt (vergrößertes Bild unten links). Die aus der vertikalen Integration der Aktivität der zentralen Flusssedimente sich ergebende erhebliche Umsatzaktivität kann somit als „Leberfunktion“ innerhalb der Stoffumsetzungen eines Flussökosystems angesehen werden (aus Fischer & Pusch 2005).

Die Frage, ob Organismen in Flüssen ihr Mikrohabitat auch wegen einer bestimmten stöchiometrischen Zusammensetzung der (aus der fließenden Welle zurückgehaltenen) Nahrungsressourcen wählen, ist allerdings noch völlig offen.

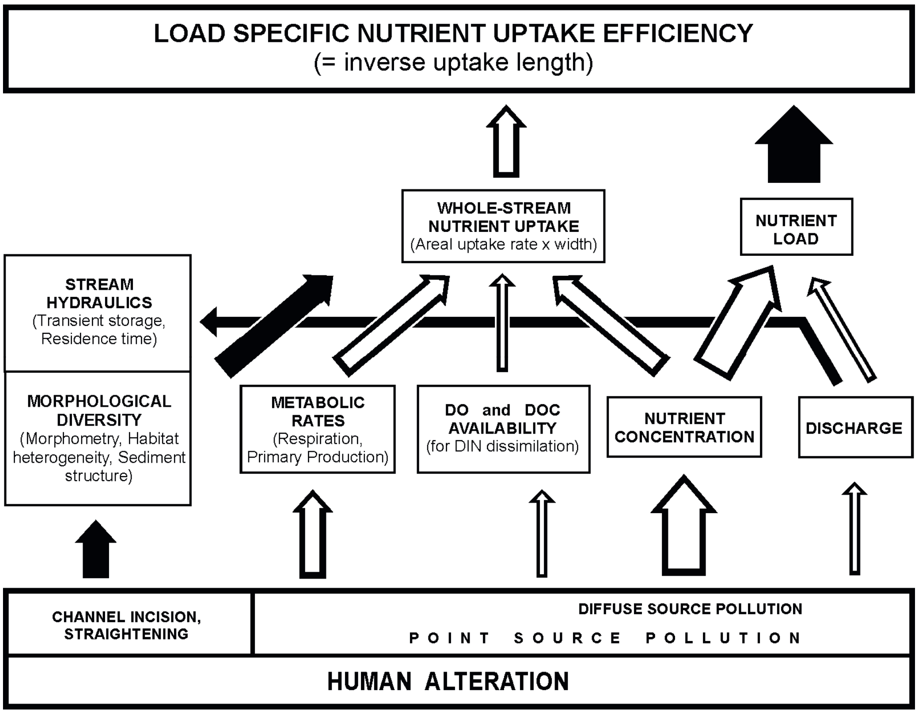
Weiterhin ist für Bäche gezeigt worden, dass verschiedene Strukturelemente (*patches*) im hierarchischen morphologischen Mosaik eines Bach- oder Flussbetts (Frissell et al. 1986, Pringle et al. 1988, Palmer et al. 1997) sich in Bezug auf die Retentionseffizienz unterscheiden (Fisher et al. 1998). Diese sind entsprechend konzeptionell als ‘*functional process zones*’ bezeichnet worden (Thorp et al. 2005)(Abb. 3).

Ihre qualitativen und quantitativen Eigenschaften werden in starkem Maße und auf mehreren Skalenebenen durch das hydromorphologische Geschehen beeinflusst, wie im Modell der „*Hierarchical patch dynamics*" in Fließgewässern dargestellt (PRINGLE et al. 1988, TOWNSEND 1989, WU & LOUCKS 1995, STANFORD et al. 2005). Der Umfang der Funktionalität von Fließgewässern wird somit ebenso durch intrinsische „Störungen" bestimmt wie ihr Grad der Biodiversität (RESH et al. 1988, HILDREW & GILLER 1993, LAKE 2000). Dieser Zusammenhang ist hinsichtlich der Diversität durch das „*intermediate disturbance model*" beschrieben worden (CONNELL 1978, WARD & STANFORD 1983, WARD & TOCKNER 2001).

Die Quantifizierung des in der marinen Ökologie entwickelten Prinzips der benthisch-pelagischen Kopplung (GRAF 1992) in Fließgewässern durch Messungen organismischer Filtrationsraten (z.B. WOTTON et al. 1996, 1998, PUSCH et al. 2001, BÄRLOCHER & BRENDELBERGER 2004) sowie das Nährstoffspiralenkonzept hat das Verständnis des Transportverhaltens, der Nahrungsnetze und des Stoffaubbaus in Fließgewässern wesentlich vertieft und erleichtert (z.B. MULHOLLAND et al. 2002). Leider wurden Nährstoffspiralen bisher fast ausschließlich in kleinen Bächen untersucht (z.B. MUNN & MEYER 1990, VALETT et al. 1996, 2002, INWOOD et al. 2005), so dass über Trends entlang des Längskontinuums nur wenig bekannt ist (JOHNSON et al. 1995, THORP et al. 2005).

Im Rahmen der der vorliegenden Habilitationsschrift wurden wesentliche Erkenntnisse hinsichtlich der Wirkung der Flussmorphologie auf die benthisch-pelagische Kopplung in Flachlandfließgewässern erbracht, die wiederum einen Schlüsselprozess darstellt für die Retention von in der fließenden Welle transportierten Stoffen, und damit letztlich für die Produktivität eines Flussabschnitts. Die Ergebnisse zeigten, dass die untersuchten Flachlandbäche hoher flächenbezogene Retentionsraten (U) aufwiesen, aber dennoch die mittlere Spiralenlänge aufgrund der wesentlich höheren Nährstofffracht hier wesentlich länger war als in naturnahen Bächen. Da somit die Nährstoffretention insgesamt wenig effektiv war, wurden sehr lange Nährstoffaufnahmelängen (S_W, i.e. das Inverse der Retentionseffizienz) bestimmt. Im Gegensatz zu Befunden an naturnahen Bächen (GÜCKER & BOËCHAT 2004) hing in diesen Bächen die flächenbezogene Nährstoffaufnahmerate weder vom Wasserdurchfluss noch von der Gewässermorphologie (Anteil an Totzonen) ab. Allerdings waren die jahreszeitlichen Durchflussschwankungen auch relativ gering. Stattdessen war die Retentionsrate mit der Intensität der im Gewässer ablaufenden Umsetzungen des organischen Kohlenstoffs gekoppelt, nämlich durch die Primärproduktion aquatischer Makrophyten und durch den mikrobiellen Abbau von gelöstem organischem Material (dissolved organic matter, DOM), das durch die Kläranlagen eingetragen wurde. Aus dem stöchiometrischen Verhältnis der Aufnahmeraten von Stickstoff und Phosphor konnte geschlossen werden, dass der Stickstoff nicht nur assimilativ von der Gewässerbiozönose aufgenommen wurde, sondern auch dissimilativ auf dem Wege der Nitrifikation (bei Ammonium) und Denitrifikation eliminiert wurde. Aus diesen Ergebnissen konnte ein mechanistisches Modell der Steuerung der Nährstoffretention in anthropogen belasteten Bächen abgeleitet werden (Abb. 4).

Abb. 4: Mechanistisches Modell der Steuerung der Nährstoffretention in Fließgewässern. Weiße Pfeile: fördernde Wirkung; schwarze Pfeile: hemmende Wirkung



1.3 Horizontale Konnektivität von Fließgewässern

Die enge Konnektivität von Fließgewässern mit umgebenden Lebensräumen ist bereits in den 1970er Jahren erkannt und dargestellt worden (FISHER & LIKENS 1973, HYNES 1975, VANNOTE et al. 1980, MINSHALL et al. 1983, WARD 1989, WARD & STANFORD 1995, ARSCOTT et al. 2002). Die biologische Struktur und Funktionalität in einem bestimmten Fließgewässerabschnitt werden somit nicht nur wesentlich durch seine Position innerhalb des Längskontinuums geprägt, sondern auch durch die umgebenden terrestrischen Biome. Das in die Oberläufe von Fließgewässern eingetragene allochthone organische Material (z. B. MARIDET et al. 1995) wird dort trotz intensiver Nutzung (WALLACE et al. 1997) aufgrund der großen Mengen und der hydrologischen Dynamik nicht vollständig abgebaut, sondern als eine Form von „Leckage" (*leakage*) auch in erheblichen Mengen stromab exportiert, so dass letztlich Biozönosen im gesamten Fließgewässerkontinuum von den Exporten der Oberläufe profitieren (PROCHAZKA et al. 1991, GOMI et al. 2002). Ähnliches gilt für die in organischem Material enthaltenen anderen potenziell limitierenden Nährstoffe, die bei jedem biologischen Abbauschritt vorzugsweise entzogen werden. So wurde auch für Pflanzennährstoffe angenommen, dass innerhalb der Flussgebiete kleine naturnahe Bäche mit ihren Retentionsleistungen (z.B. MARTÍ & SABATER 1996, MARTÍ et al. 2004)entscheidend die Nährstoffexporte in stromabwärts gelegene Flüsse, Seen und Ästuare steuern (ALEXANDER et al. 2000, PETERSON et al. 2001).

Im Zuge der folgenden abiotischen und biologischen Zerkleinerung des partikulären organischen Materials (POM) allochthoner Herkunft im Allgemeinen immer refraktärer, d.h. für weitere biologische Bearbeitung (*processing*) unzugänglicher. Da der beschriebenen biologischen Bearbeitung der Transport mit der fließenden Welle überlagert ist, ergibt sich daraus, dass in größeren Fließgewässern Detritus eine immer schlechtere ernährungsphysiologische Qualität aufweisen sollte, etwa hinsichtlich des C/N-Werts (vgl. HEDGES et al. 1994, MASSICOTTE &

FRENETTE 2011). Gemäß des River Continuum Concepts (RCC)(VANNOTE et al. 1980) werden in den Fließgewässer-Mittelläufen größere Mengen organischen Materials autochthon produziert, vor allem durch Phytobenthos. Dieses autochthone organsche Material wird schneller biologisch abgebaut als das allochthone, da es durchschnittlich eine deutlich bessere ernährungsphysiologische Qualität aufweist (WEBSTER & BENFIELD 1986, ENRÍQUEZ et al. 1993, ROYER & MINSHALL 1997). Gemäß diesen Vorstellungen sollten den Lebensgemeinschaften der großen Flüsse vor allem refraktärer Detritus als Nahrungsgrundlage zur Verfügung stehen (VANNOTE et al. 1980, NAIMAN et al. 1987). Ergänzt wird diese schlecht nutzbare Nahrungsressource lediglich durch Einträge allochthonen organischen Materials aus den Auen (SEDELL et al. 1989), vor allem bei Hochwasser, wie im Hochwasserpulskonzept (*flood pulse concept*, FPC) beschrieben (JUNK et al. 1989).

Die beschriebenen charakteristischen Zusammenhänge der Stoffeinträge, -transporte und Stoffumsetzungen wurden zuerst im *River Continuum Concept* (RCC, VANNOTE et al. 1980) zusammengefasst. Dieses ist bis heute das wichtigste Konzept ökologischer Forschung in Fließgewässern geblieben, da es als einziges Fließgewässermodell physische Gewässerstruktur, Nahrungsressourcen und funktionelle Eigenschaften der biologischen Besiedlung (Ernährungstypen) innerhalb des gesamten Gewässernetzes verknüpft (THORP et al. 2005). Die darin aufgestellten Thesen zur Längszonierung in Fließgewässersystemen wurden im Zuge nachfolgender Forschungen teilweise kritisiert, modifiziert und weiter ausgearbeitet (WARD & STANFORD 1983, MINSHALL et al. 1983, STATZNER & HIGLER 1985, SEDELL et al., 1989, WARD 1989).

Allerdings gibt es seit den 1990er Jahren Untersuchungen, die das vom RCC und FPC gezeichnete Bild der Kohlenstoffquellen innerhalb eines Fließgewässerkontinuums stark modifizieren. So wurde etwa gezeigt, dass auch in Oberläufen, die durch Uferbäume nicht vollständig beschattet werden, das Nahrungsnetz überwiegend auf autochthoner Algenproduktion beruhen kann, wobei die autotrophe Komponente zum Mittellauf hin noch weiter an Bedeutung gewinnt (FINLAY 2001, DELONG & THORP 2006). Die Mittel- und Unterläufe von bestimmten Flusstypen weisen oft ein dichtes Phytoplankton auf (KÖHLER 1994, REYNOLDS & DESCY 1996), das eine wertvolle potentielle Nahrungsquelle für das Nahrungsnetz in solchen Flussabschnitten darstellt. Allerdings wird die autochthone Primärproduktion in den Mittelläufen anderer Flusstypen von benthischen Makrophyten bestimmt (vgl. ODUM 1956, LAMBERTI & STEINMAN 1997), die auf direktem Weg nur in geringem Umfang von aquatischen Organismen aufgenommen werden (CARPENETER & LODGE 1986).

Das Flussproduktionsmodell (*riverine productivity model*) behauptet, dass sich die Nahrungsquellen der mikrobiellen Schleife (*microbial loop*) und des metazoischen Nahrungsnetzes in großen Flüssen deutlich unterscheiden. Dabei soll die metazoische Biomasseproduktion überwiegend auf autochthoner Produktion beruhen (THORP & DELONG 1994, 2002, DELONG & THORP 2006, siehe auch HAMILTON et al. 1992, FORSBERG et al. 1993, LEWIS et al. 2001 zu tropischen Flüssen). Diese Annahme beruht auf dem u. a. mittels Analysen der natürlichen C- und N-Isotope gewonnenen Befund, dass in großen Flüssen transportiertes partikuläres organisches Material (POM) überwiegend autochthonen Ursprungs ist (THORP et al. 1998; DELONG et al. 2001 KENDALL et al. 2001), auch das aus Flussauen eingetragene (THORP et al. 1998, SCHIEMER et al. 2001, HEIN et al., 2003). Selbst wenn allochthoner Detritus von Metazoen aufgenommen wird, werden die Inhaltsstoffe enthaltener Algen zu einem wesentlich höheren Anteil assimiliert (ARAUJO-LIMA 1986).

Allerdings konzentrierten sich Studien zur Funktionalität von Fließgewässerökosystemen auf kleine naturnahe Bäche, während nur wenige Arbeiten Fließgewässerunterläufe betrachteten (z.B. NAIMAN et al. 1987, MINSHALL et al. 1992). Die funktionelle Ökologie von Flüssen sowie von anthropogen überformten Fließgewässern, also die in diesen Ökosystemen ablaufenden Prozesse und Wechselbeziehungen zu den Organismen, ist daher erst in jüngerer Zeit systematisch untersucht wurden (Thorp et al. 1994, 1998, 2002, FISCHER & PUSCH 2001, PAETZOLD et al. 2005, WILCZEK et al. 2005, WANTZEN & JUNK 2006, KENNEDY & TURNER 2011). In der vorliegenden Habilitationsschrift wird die horizontale Konnektivität von Flachlandflüssen am Beispiel von Spree und Elbe auf verschiedenen analytischen Ebenen dargestellt. Es werden Zusammenhänge zwischen Konnektivität und den ablaufenden ökologischen Funktionen aufgezeigt, sowie auch hinsichtlich örtlicher Schwerpunkte, Saisonalität und Intensität. Die Bilanzierung von ökologischen Funktionen, das Verständnis ihrer hierarchischen und horizontalen Verknüpfungen mit anderen Umweltfaktoren und Prozessen ist ohne Betrachtung der ökologischen Konnektivität nicht möglich.

Es liegen ist heute somit zunehmend evident, dass die horizontale Konnektivität von Fließgewässern mit ihren Flussauen die Ausprägung wichtiger ökosystemarer Dienstleistungen wie Hochwasserretention, Erhalt der Biodiversität und Selbstreinigung des Gewässers wesentlich bestimmt, und Flussauen somit wesentliche Komponenten von Flussökosystemen darstellen (NAIMAN & DECAMPS 1997, PUSCH et al. 1998, TOCKNER et al. 2002, PUSCH & FISCHER 2006,). Flussauen leisten ökologische Funktionen als Pufferzonen und Retentionsgebiete, die die Stoffdurchflüsse zwischen den terrestrischen und aquatischen Schnittstellen ebenso wie zwischen Ober- und Unterläufen der Flüsse regulieren (LOWRANCE et al 1985, PINAY & LABROUE 1986, KNAUER & MANDER 1989; AMBUS 1990, COOPER 1990; JANSSON et al 1998, VAN DER PEIJL & VERHOEVEN et al. 2000, HEIN 2010). Diese Stofffluxe in longitudinaler, horizontal-transversaler und vertikaler Richtung unterscheiden sich deutlich zwischen Niedrig- und Hochwassersituationen (PUSCH et al. 1998, Abb. 5).

Nährstoffretention in flussnahen Auen erfolgt zumeist über Sedimentation (bei Phosphor) und Denitrifikation (bei Stickstoff), sowie auch auf längere Sicht über Nährstoffaufnahme durch die Vegetation. Diese Prozesse und die sie steuernden hydrogeomorphologischen Faktoren (z.B. Überflutung) bestimmen daher, ob eine spezifische Flussaue als ein Nährstoffsenke oder eine Nährstoffquelle fungiert (VYMAZAL 1999, VERHOEVEN et al. 2006). Um somit die Rate der Nährstoffretention in einer Aue vorhersagen zu können, müssen lokale Umweltparameter in Betracht gezogen werden, vor allem jene, die die hydrologische Konnektivität der Retentionsgebiete an den Fluss charakterisieren (FISCHER at al. 2005, GÜCKER & Pusch 2006, TICKNER et al 2004). Am Beispiel der Donau wurde die Nährstoffretention in Flussauen abgeschätzt für die Stickstoffreduktion als 100 – 150 kg N ha^{-1} a^{-1}, und für Phosphor 10 – 20 kg P ha^{-1} a^{-1} (TICKNER et al. 2004).

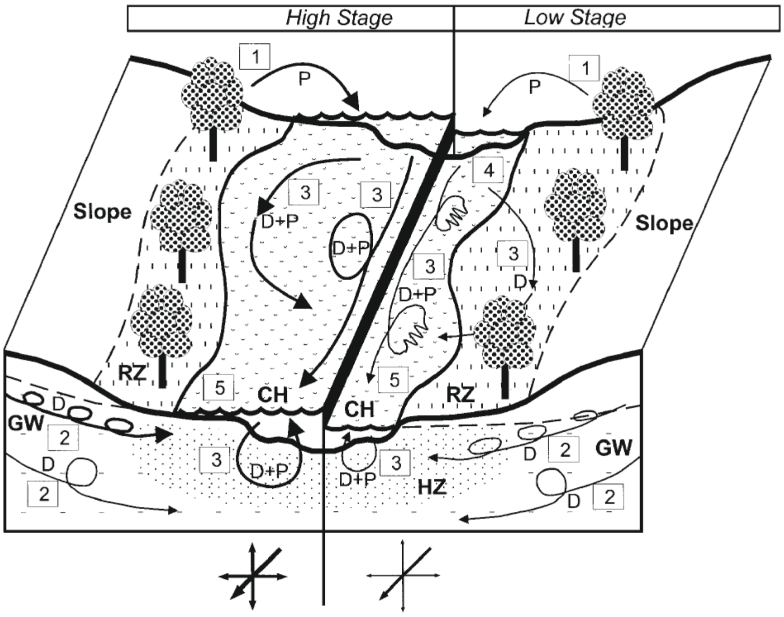


Abb. 5: Schema einer Uferzone (RZ) eines Fließgewässers bei geringem (rechts) und hohem (links) Wasserstand mit Fluxen organischen Kohlenstoffs (aus PUSCH et al. 1998). P=partikuläres organisches Material, D=gelöstes organisches Material, CH=Fließgerinne, GW=Grundwasser, HZ=Hyporheische Zone. Die in drei Dimensionen stattfindenden Stofffluxe unterschiedlichen Umfangs sind durch Pfeile unterschiedlicher Stärke dargestellt, die durch die Pfeilgruppen im Vordergrund für die zwei hydrologischen Situationen zusammengefasst werden. Die Zahlen stehen für: 1, 2=oberflächlicher bzw. unterirdischer Eintrag allochthoner organischer Substanz, 3=Umlagerung innerhalb des Fließgerinnes und in der Aue, 4=autochthone Primärproduktion im Fließgewässer, 5=Metabolisierung während der Aufenthaltszeit organischen Materials im Fließgewässer oder der Aue

Folglich werden aus wasserwirtschaftlicher Sicht sowohl die zielgerichtete Nutzung von existierenden Feuchtgebieten zur Wasserreinigung als auch die funktionelle Wiederherstellung von degenerierten Auen durch ihre erneute Anbindung an den Hauptfluss in Betracht gezogen, um erhöhte Anforderungen an die Wasserqualität zu erfüllen, sowie auch um die Lebensbedingungen für die Menschen zu verbessern, die in der Nähe von flussnahen Flussauen von den ökosystemaren Dienstleistungen abhängig sind (ZEDLER & KERCHER 2005, HEIN 2010).

Die Evaluierung von Restaurierungsprojekten, in denen frühere Flussauen wieder an die Hauptflussläufe angebunden wurden, haben deren Erfolge sowohl auf die Biodiversität als auch auf die ökosystemaren Dienstleistungen wie Nährstoffretention gezeigt (SCHIEMER & RECKENDORFER 2004, TRÉMOLIÈRES et al. 2008), und ein Gesamtökosystem-Experiment, das Flussauen anlegte, die pulsierender Flusswasserführung ausgesetzt sind, zeigte klare ebenso Effekte auf die Vegetationsstruktur und den Nährstoffkreislauf (z.B. MITSCH et al 2005).

Da die meisten Flussauen jedoch mehrfachen Nutzungen unterliegen, müsssen bei Renaturierungsaktivitäten Strategien gefunden werden, die alle ökosystemaren Dienstleistungen optimieren, die typischerweise in den Flussauen vorhanden sind (PALMER et al. 2005, BONDAR et al. 2007, TOCKNER 2007, TOCKNER et al. 2010).

1.4 Horizontale Konnektivität von Seen

Erst seit kurzem hat sich sich Erkenntnis durchgesetzt, dass auch in Seen Benthal und Litoral einen großen Teil zur gesamten Bioproduktion bei tragen (COVICH et al. 1999, VANDER ZANDEN & VADEBONCOEUR 2002, VADEBONCOEUR et al 2002, STRAYER & FINLAY 2010). In Seen beruht die hohe Produktivität der Uferzone teils darauf, dass Nährstoffeinträge aus dem terrestrischen Umfeld zuerst dort aufgefangen werden können (STRAYER & FINLAY 2010). Die Produktivität der terrestrischen Uferzone profitiert wiederum erheblich von der guten Verfügbarkeit von Wasser, sowie vom Transfer von Nährstoffen aus dem See über emergierende Insekten (VANDER ZANDEN et al. 2004, RAIKOW et al. 2011). Die durch diese Wechselwirkungen entstehende horizontale aquatisch-terrestrische Konnektivität der ökologischen Funktionen und Strukturen ist in verschiedenen Seentypen unterschiedlich ausgeprägt, abhängig u.a. von deren Trophiezustand, Uferentwicklung, Ufergefälle und jahreszeitlichen Wasserstandsschwankungen (z.B. DOLSON et al. 2009). Allerdings wurde das Litoral zumeist jeweils als Ganzes (als black box) betrachtet. Die erkennbare unterschiedliche Strukturierung des Litorals in eine verschiedene Anzahl von stratifizierbaren Habitaten, vertikale Beziehungen innerhalb des Tiefengradients des Litorals, und die Zuordnung entsprechender ökologischer Eigenschaften wurde erst im Rahmen der vorliegenden Habilitationsschrift dargestellt.

1.5 Ökologische Bedeutung von Konnektivität

Insgesamt trägt die vertikale oder horizontale Konnektivität zur Stabilisierung der beteiligten Ökosysteme bei (HUXEL & MCCANN 1998, TAKIMOTO et al. 2002, ROONEY et al. 2006): Sie ermöglicht den Austausch von Pflanzennährstoffen, von toter Biomasse, die als Energieträger fungiert, sowie von migrierenden lebender Organismen. Diese ökologische Konnektivität gleicht tendenziell die Wirkungen jahreszeitlicher Dynamiken sowie externer Störungen auf die Nahrungsnetze aus, indem Ressourcen des jeweils anderen Lebensraums zur Verfügung stehen (POST et al. 2000, NOWLIN et al. 2008) und Migrationskorridore in andere Teillebensräume verfügbar sind (vgl. BRUNKE et al. 2001). Insbesondere der Eintrag von Detritus aus der terrestrischen Sphäre stabilisiert die Nahrungsverfügbarkeit in aquatischen Systemen (WETZEL 1995, 2001). Darüber hinaus wird die Produktivität erhöht, da oftmals der aquatische Lebensraum organische Nahrungsressourcen zu Zeitpunkten erhält, in denen die aquatische Bioproduktion gering ist, und da terrestrische Lebensräume vom Import von Nährstoffen aus den Gewässern profitieren. Die oft wechselseitig unterstützende Funktion der Konnektivität für Ressourcenbereitstellung zwischen Wasserkörper und Sediment bzw. terrestrischem Umfeld (FISHER et al. 2004) gründet sich auf systembedingt unterschiedliche abiotische Bedingungen in diesen Kompartimenten: Im terrestrischen Bereich findet wegen oftmaliger Trockenheit der Abbau organischen Materials nur relativ langsam statt, ähnlich wie in tieferen Sedimenten aufgrund von Sauerstoffmangel, so dass hier eine erhebliche temporären Speicherung organischen Materials kommt (SHURIN et al. 2006). Hingegen finden im Wasserkörper sowie in den oberflächlichen Biofilmen auf Sedimenten schnelle dissimilative Stoffumsetzungen statt, die zu einem effizienten Recycling von Substanzen und damit zur schnellen Wiederbereitstellung von Pflanzennährstoffen führen (z.B. MINSHALL et al. 1992). Die intensive Verzahnung von Wasserkörper, Sedimenten sowie Ufer-und Auenlebensräumen infolge von Schwankungen des Wasserspiegels in Flüssen und Seeen infolge von Hochwässern und Trockenperioden, sowie durch die Umlagerung von Sedimenten in Flüssen führt daher zu charakteristischen Spitzen bestimmter metabolischer Ökosystemfunktionen (WILCZEK et al. 2005, WANTZEN & JUNK 2006) im Jahresverlauf, die zudem mit den Sukzessionsabläufen der Organismengemeinschaften interagieren.

1.6 Bedeutung von Konnektivität für die Gewässerbewirtschaftung

Diese Ergebnisse können bei der Bewirtschaftung von Gewässern dahingehend genutzt werden, dass die Gewährleistung horizontaler und vertikaler Konnektivität in der Regel mit räumlich komplexeren, diverseren, zeitlich und strukturell resilienteren sowie leistungsfähigeren Ökosystemen einhergeht, die somit intensiver und sicherer nachhaltig genutzt werden können (BRADSHAW 1996, ARTHINGTON et al. 2006, WOOLSEY et al. 2007, TOCKNER et al 2008, 2011). Eine Reihe diese Zusammenhänge mit angewandten Fragestellungen wurden im Rahmen der vorliegenden Habilitationsschrift durch Labor- und Feldexperimente sowie durch gezielte Feldmessungen von Parametern funktionaler Zusammenhänge wie Stoffretention, Enzymaktivität und Isotopenzusammensetzung in ausgewählten Gewässerteilen in quantitativer Weise dargestellt.

Die Nutzung einer kleinen Auswahl von Ökosystemleistungen der Flüsse und Seen durch den Menschen und Beschränkung ihrer Konnektivität hat vielfach zu starken Verlusten bei anderen Ökosystemleistungen geführt (HYNES 1974, PUSCH et al. 1998, MALMQVIST & RUNDLE 2002, PUSCH & FISCHER 2006, SONDERGAARD & JEPPESEN 2007, TOCKNER et al 2008, PUSCH et al. 2009). Die Zusammenhänge zwischen menschlichen Eingriffen, Veränderungen der Umweltbedingungen und Auswirkungen auf Organismen und Prozesse im Flussökosystem sind in Tab. 1 am Beispiel eines schiffbaren Flusses (Elbe) dargestellt. Adaptives Gewässermanagement sollte daher die Entwicklung einer neuen Multifunktionalität der Gewässer anstreben, und somit vor allem die verkümmerten ökologischen Dienstleistungen unterstützen (CARPENTER et al. 2006).

Das Prinzip eines eines integrierten Gewässermanagements eröffnet neue Perspektiven, ökologische Konnektivität wieder zu entwickeln (RAHAMAN et al. 2005), insbesondere wenn der Nutzungsdruck auf Teilbereiche der Landschaft im Rahmen des sozioökonomischen Wandels sinkt. Da die Bewirtschaftung der Gewässer in der dicht besiedelten Kulturlandschaft oftmals kaum veränderbaren Zwängen sowie unumkehrbaren Veränderungen unterliegt (BERNHARDT & PALMER 2007), müssen Ökosystemleistungen gegebenenfalls durch abiotische und biologische Strukturen erbracht werden, die deutlich von den ursprünglichen abweichen (LORENZ et al. 1997, BRISMAR 2002, BISHOP et al. 2009, TOCKNER et al. im Druck). Der nachhaltige Erfolg solcher Revitalisierungsprojekte wird erhöht, wenn man die Gewässer der Kulturlandschaften als gekoppelte sozial-ökologische Systeme begreift und alle relevanten gesellschaftlichen

Interessen und Entwicklungen bereits bei der Konzeption mit einbezieht (Carpenter et al. 2009). Von wissenschaftlicher Seite kann die Untersuchung, Entwicklung und Implementierung von Strategien zum integrierten Management solcher komplexer sozial-ökologischer Systeme unterstützt werden, indem die Ökosystemleistungen bewertet und gegebenenfalls monetarisiert werden, indem Indikatoren für ihre Ausprägung erstellt werden, und indem inter- und transdisziplinäre Verbundprojekte durchgeführt werden, die in von allen Beteiligten akzeptierte Entscheidungsgrundlagen münden (Carpenter et al. 2006).

Tab. 1: Auswirkungen wichtiger Eingriffe des Menschen auf Stoffdynamik und Habitatstruktur im Flussökosystem der Elbe (aus Pusch & Fischer 2006), ohne Berücksichtigung von Spurenstoffeinträgen, Fischerei, Auswirkungen in der Aue, u. a.. Die wasserbaulicher Maßnahmen (Bau und Unterhaltung von Buhnen und Längswerken) dienen größtenteils der Erleichterung der Schifffahrt. * = gemäß Nestmann & Büchele (2002), ** Eisvogel, Uferschwalbe, Bienenfresser, Solitärbienen, *** = zusammengefasst von Kausch (1996).

Eingriff	**Veränderung der Umweltbedingungen**	**Auswirkungen auf Organismen und Prozesse im Flussökosystem**
Bau von Staustufen	Pufferung des Abflussregimes	Verringerung der Durchflussdynamik
	Erhöhung der Wasseraufenthaltszeit	Starker Eintrag von Planktonorganismen
	Unterbrechung des Längskontinuums	Behinderung von Fischwanderungen und des Geschiebetriebs
Einleitung von Abwässern *(zumeist geklärt) und diffuse Nährstoffeinträge aus der Landwirtschaft*	Eintrag von organischen Stoffen	Verschlechterung der Sauerstoffverhältnisse im Sediment durch den dortigen Stoffabbau
	Eintrag der Pflanzennährstoffe Stickstoff und Phosphor	Starke Erhöhung des Phytoplanktongehalts (Sekundärverschmutzung), dadurch zunächst starke Sauerstoffübersättigung, beim Abbau starke Sauerstoffzehrung führt.
Flussbegradigung	Erhöhung des Gefälles, der Fließgeschwindigkeit und der Tiefenerosion	Verlust an Habitatfläche und -vielfalt, besonders an dynamischen Habitaten, Verringerung der Grundwasserstände
Buhnen und Längswerke *(Bau und Unterhaltung in der Standardform mit durchgehenden Buhnen auf Mittelwasserniveau)*	Einengung des Stroms mit nachfolgender Tiefenerosion	Erhöht Sedimenttransport, führt zu kürzeren und höheren Transportkörpern *
		Wasserstandsverfall führt zur Abkopplung von Altarmen vom Hauptstrom für Fische
		Starke Verkleinerung der Siedlungsflächen des Zoobenthos, da diese weitgehend im Uferbereich leben; dadurch starke Verringerung des Aufkommens an Fischnährtieren.
	Verkleinerung der Spiegelbreite durch voranschreitende Verlandung der Buhnenfelder	Fehlender seitlicher Sedimenteintrag trägt zur Tiefenerosion bei
	Unterbindung von Flussdynamik im Uferbereich	Keine steilen Erosionsufer mit überhängenden und fallenden Bäumen, den flusstypischen Habitaten für höhlenbrütende Arten**, Jungfische und xylobionte Wirbellose
	Morphologische Uniformierung des Uferbereichs	Fehlen von ufernahen Nebengerinnen mit kleinräumiger Sedimentdynamik und Tiefenvarianz, dadurch teilweise Entwertung der Uferhabitate für Wirbellose und Jungfische
	Einbringung großer Mengen von (Schlacke-) Steinen	Unnatürliches Siedlungssubstrat mit Dominanz von Neozoen; evtl. Schwermetallfreisetzung

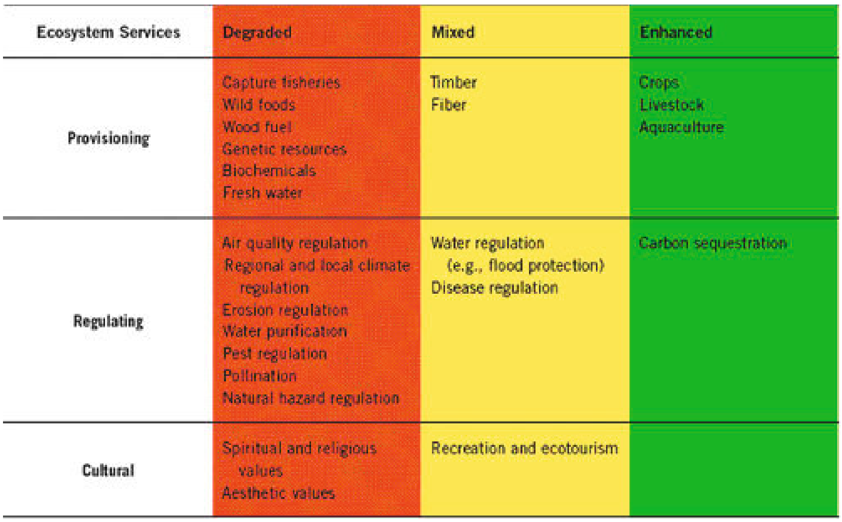
	Erhöhung der Wasseraufenthaltszeit im Uferbereich	Geringe Erhöhung des Planktongehalts der Elbe um weniger als 5 %, dadurch leichter Rückgang der Nährstoffkonzentration im Hauptstrom. Sedimentation und zum Teil dauerhafte Ablagerung von Schwebstoffen sowie daran gebundenen Schadstoffen
Regelquerschnitt der Stromsohle *(und seine Unterhaltung)*	Abtrag von Untiefen (Transportkörpern)	Verringerung der benthisch-pelagischen Kopplung, Reduzierung der Selbstreinigungsprozesse
	Verfüllung von Kolken und Entfernung von Totholz	Beseitigung von Fischunterständen, damit Verringerung der Bestände und Artenvielfalt von Fischen*** und Zoobenthos
Schifffahrt *(insbesondere Großschifffahrt)*	Bei Schiffsdurchfahrt plötzliche hohe Sohlschubspannungen in Buhnenfeldern (unnatürliches Störungsregime)	Remobilisierung und Verfrachtung von Sediment, Trübung des Flusswassers
		Schädigung und Verdriftung von Zoobenthos, Stranden von Jungfischen

1.7 Konnektivität und Ökosystem-Dienstleistungen

Der Begriff der Ökosystem-Dienstleistungen wurde implizit von mehreren Autoren während der 2. Hälfte des 20. Jahrhunderts entwickelt, als deutlich wurde, dass die natürlichen Lebensgrundlagen der menschlichen Zivilisation bedroht sein könnten (Gómez-Baggethun 2009, Groß 2011). Die Dienstleistungen wurden als solche erstmals im Jahr 1977 in einem Artikel in *Science* thematisiert (Westman 1977). Die Wortkombination „ecosystem services“ wurde als solche erstmals von Ehrlich & Ehrlich (1981) verwendet. Die Entwicklung des Begriffs der Ökosystem-Dienstleistungen stand dabei in inhaltlicher Verbindung zur Entwicklung des Begriffs der Nachhaltigkeit. Dieser war ursprünglich im 18. Jahrhundert mit der Etablierung systematischer Forstwirtschaft in Deutschland begründet worden (Groß 2011). Der Begriff der Nachhaltigkeit wurde im Jahre 1972 von D.L. Meadows im Bericht *Die Grenzen des Wachstums* an den Club of Rome (Meadmes et al. 1972) erstmals auf die allgemeine Entwicklung des Globus angewendet, und im Jahre 1987 von der UN-Weltkommission für Umwelt und Entwicklung (sog. Brundtland-Kommission) grundlegend definiert als *Entwicklung zukunftsfähig zu machen, heißt, dass die gegenwärtige Generation ihre Bedürfnisse befriedigt, ohne die Fähigkeit der zukünftigen Generation zu gefährden, ihre eigenen Bedürfnisse befriedigen zu können*. Die darin implizierte Erkenntnis der Bedeutung der natürlichen Ressourcen für die weitere Entwicklung der Menschheit wurde anschließend von De Groot (1987) und Costanza (1991) als Werkzeug erkannt, die seit dem 19. Jahrhundert getrennt entwickelten Wissenschaften der Ökologie und Ökonomie angesichts der erkennbaren, ökologisch bedingten Endlichkeit ökonomischen Wachstums wieder zu verknüpfen. Die faktisch unabweisbare grundlegende Einbettung der Ökonomie in ökologische Rahmenbedingungen wurde durch die weitere Konkretisierung (Daily 1997, De Groot et al. 2002) des Konzepts der Ökosystem-Dienstleistungen greifbar gemacht und dadurch in weiten Kreisen popularisiert (Daily et al. 2009, De Groot et al. 2010).

Die politische Wirksamkeit des Konzepts der Ökosystem-Dienstleistungen wurde im weiteren durch das Erscheinen des Millenium Ecosystem Assessment Report (MA 2005) wesentlich erhöht (Gómez-Baggethun 2009), in dem direkte und indirekte Ökosystem-Dienstleistungen in Kulturdienstleistungen (wie Erholung und ästhetisches Vergnügen z.B. durch Korallenriffe oder

Mineralquellen), Unterstützungsdienstleistungen (wie Bodenbildung, Photosynthese oder Nährstoffkreislauf), Versorgungsdienstleistungen (wie Nahrungsmittel, Wasser, Faserstoffe, Holz oder Öl) und Regulierungsdienstleistungen (wie die Regulierung von Klima, Überflutungen, Krankheiten oder Wasserqualität) systematisiert und konkret benannt wurden (DE GROOT et al. 2010). Im Millenium Ecosystem Assessment Report wurden außerdem auch der Degradationszustand der Ökosystem-Dienstleistungen untersucht (Abb. 6), und Verbindungen zur weltweiten Bekämpfung der Armut hergestellt (MA 2005).



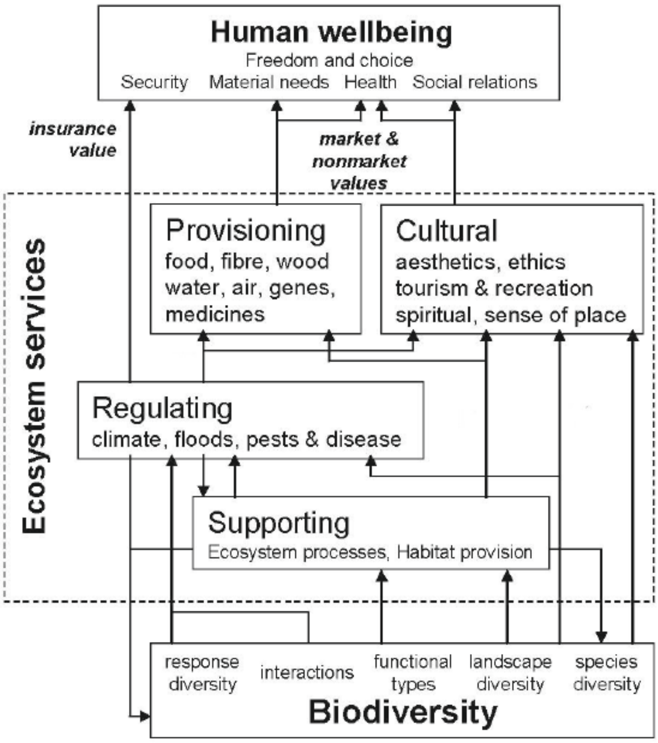
Ecosystem Services	Degraded	Mixed	Enhanced
Provisioning	Capture fisheries Wild foods Wood fuel Genetic resources Biochemicals Fresh water	Timber Fiber	Crops Livestock Aquaculture
Regulating	Air quality regulation Regional and local climate regulation Erosion regulation Water purification Pest regulation Pollination Natural hazard regulation	Water regulation (e.g., flood protection) Disease regulation	Carbon sequestration
Cultural	Spiritual and religious values Aesthetic values	Recreation and ecotourism	

Abb. 6: Zustand (anthopogene Degradation versus Förderung) wichtiger Ökosystem-Dienstleistungen gemäß Millenium Ecosystem Assessment Report (MA 2005)

Im Millenium Ecosystem Assessment Report wird auch explizit davon ausgegangen, dass viele Ökosystem-Dienstleistungen durch Mitwirkung von Lebewesen bereitgestellt werden, und diese Leistungen durch verringerte Biodiversität beeinträchtigt werden könnten (MA 2005) Abb. 6). Als Folge genießen Untersuchungen von Einflussfaktoren auf Ökosystem-Diensteistungen große wissenschaftliche Aufmerksamkeit (DAILY et al. 2009, GÓMEZ-BAGGETHUN 2009). Da die Hälfte der Weltbevölkerung in einer Entfernung von weniger als 3 km vom nächsten Binnengewässer lebt, wird vermutlich ein großer Teil der beanspruchten Ökosystem-Dienstleistungen aus Gewässerlandschaften genutzt. Die meisten der in Abb. 6 aufgeführten Ökosystem-Dienstleistungen stehen jedoch nur noch in reduziertem Umfang zur Verfügung, wenn die longitudinale, horizontal-transversale oder die vertikale Konnektivität der Gewässer gekappt wird, insbesondere die Bioproduktion von Fisch, Wild, Holz, gentischer Vielfalt und Trinkwasser, die regulierenden Funktionen hinsichtlich Hochwasser, Erosion und Selbstreinigung, sowie die spirituellen und ästhetischen Werte einschließlich Erholung und Tourismus. Daher stellt der Erhalt der Konnektivität eine notwendige Vorausetzung nicht nur für den Erhalt der hohen Biodiversität von Binnengewässern (BALIAN et al. 2007, TAYLOR et al 2006) sondern auch eine hohe Verfügbarkeit von Ökosystem-Dienstleistungen in Flusskorridoren dar.

Das Konzept der Ökosystem-Dienstleistungen ermöglicht grundsätzlich ihre Monetarisierung und Internalisierung, d.h. die Konzeption von Zahlungen durch die Nutzer dieser Dienstleistungen nach dem Verursacher-Prinzip. Dadurch sollen die durch die (Über-)Nutzung der zunächst kostenlosen Ökosystem-Dienstleistungen entstehenden Nachteile und Kosten für die anderen Mitglieder der Gesellschaft kompensiert werden (z.B. GÓMEZ-BAGGETHUN 2009), einschließlich der Mitigation der Nutzungsfolgen, um die Tragödie der Allmende (HARDIN 1968) zu vermeiden. Allerdings sind einige Ökosystem-Dienstleistungen, insbesondere großräumig auftretende, regulierende und kulturelle Dienstleistungen oder solche, die in Zukunft erheblich Wert gewinnen könnten, nur schwer quantifizierbar, wie etwa der Nutzen der genetischen Ressourcen einer hohen Biodiversität (DE GROOT et al. 2010).

Abb. 7: Verknüpfungen zwischen der Biodiversität, Kategorien ökosystemarer Dienstleistungen und dem menschlichen Wohlergehen (aus NATIONALES KOMITEE [2011], nach SCHOLES et al. [2010], basierend auf MA [2005]). Die Pfeile stellen ein Wechselwirkungsnetzwerk von Interaktionen dar, dessen Quantifizierung in verschiedenen Ökosystem-Typen und Regionen noch weitgehend fehlt.



Seit dem Erscheinen des Millenium Ecosystem Assessment Report wird immer deutlicher, dass die Anwendung des Konzepts der Ökosystem-Dienstleistungen noch an wesentlichen Kenntnislücken leidet, insbesondere hinsichtlich ihrer ökonomischen Bewertung, der Identifikation des tatsächlichen oder potenziellen Nutzerkreises, sowie hinsichtlich der Umsetzung zusammen mit Akteuren (CARPENTER et al. 2006, 2009, TEEB 2010, Abb. 7). *Allgemein zeichnet sich ab, dass die größte Herausforderung in einer integrativen Forschung zu sehen ist, die sich etwa den Trade-Offs zwischen der Nutzung verschiedener Ökosystemdienstleistungen widmet* (NATIONALES KOMITEE 2011). Um die politischen Wirksamkeit des Konzepts der ökosystemaren Dienst-eistungen zu erhöhen, fehlt es bislang noch an einem gesellschaftlichen Rahmen, innerhalb dessen der gesellschaftliche Nutzen dieser Dienstleistungen in politische Entscheidungen (DAILY et al. 2009) oder schließlich in konkrete Landschaftsplanung (DE GROOT et al. 2010) Eingang finden könnte. Darüber hinaus stellen die Verfügbarkeit, die Nutzbarkeit und der Nutzen der ökosystemaren Dienstleistungen keine feste Größe dar, sondern diese sind in ein komplexes ökologisch-ökonomisch-politisches Wirkungsnetz eingebunden (NORGAARD 2010).

2. Übersicht über die der Habilitationsschrift zugrunde liegenden Manuskripte

Die kumulative Habilitationsschrift *Horizontale und vertikale Konnektivität in Flüssen und Seen – Ökologische Funktionen und anthropogene Überformung* basiert auf einem Kapitel in einer internationalen Monographie sowie auf insgesamt 24 internationalen referierten Zeitschriftenartikeln mit einem durchschnittlichen Impaktfaktor der Zeitschriften von 3,02 (Stand 2010).

Die der kumulativen Habilitation zugrunde liegenden Publikationen enthalten keine Ergebnisse meiner Dissertation aus dem Jahr 1993 mit dem Titel *„Heterotropher Stoffumsatz und faunistische Besiedlung des hyporheischen Interstitials eines Mittelgebirgsbachs (Steina, Schwarzwald)"*. Die Publikationen enthalten – bis auf zwei Review-Artikel und ein Buchkapitel – Ergebnisse aus selbst konzipierten, eingeworbenen und fachlich betreuten Drittmittelprojekten. Dabei wurde den in den betreffenden Projekten arbeitenden Doktoranden und Nachwuchswissenschaftlern in der Regel die Erstautorenschaft eingeräumt.

Diese Publikationen werden folgenden Themenfeldern zugeordnet, und deren Beiträge dazu in entsprechenden Einleitungskapiteln erläutert werden:

A) Konnektivität als strukturierender Habitatfaktor des Makrozoobenthos in Fließgewässern und Seen

B) Longitudinale Spiralen – Stoffretention in Fließgewässern

C) Benthisch-pelagische Kopplung als Schlüsselfaktor für mikrobielle Stoffumsetzungen in Flüssen

D) Vom Einzugsgebiet zum Mikrohabitat – anthropogene Kaskadenwirkungen auf Gewässer

A. Publikationen zum Themenfeld *„Konnektivität als strukturierender Habitatfaktor des Makrozoobenthos in Fließgewässern und Seen"*

1. *Garcia, X.-F., Schnauder, I.,* ***Pusch, M.T.*** (im Druck): How does the complex hydromorphology of river meanders contribute to benthic invertebrate diversity in rivers? *Hydrobiologia*
2. *Schwalb, A.,* ***Pusch, M.T***. (2007): Horizontal and vertical movements of unionid mussels (Bivalvia: Unionidae) in a lowland river. *Journal of the North American Benthological Society 26: 261–272*
3. *Brauns, M., Gücker, B., Wagner, C., Garcia, X.-F., Walz, N.,* ***Pusch, M.T.*** (2011): Human lakeshore development alters the structure and trophic basis of littoral food webs. *Journal of Applied Ecology 48: 916–925*
4. *Donohue I., Jackson A.L.,* ***Pusch M.T.,*** *Irvine K.* (2009): Nutrient enrichment homogenizes lake benthic assemblages at local and regional scales. *Ecology 90: 3470-3477*
5. *Gabel, F, Garcia, X.-F. , Brauns, M., Sukhodolov, A., Leszinski, M.,* ***Pusch, M.T.*** (2008): Resistance to ship-induced waves of benthic invertebrates in various littoral habitats. *Freshwater Biology 53, 1567–1578*
6. *Brauns, M., Garcia, X.F.,* ***Pusch, M.T.*** (2008): Potential effects of water level fluctuations on littoral invertebrates in lowland lakes. *Hydrobiologia 613: 5-12*

7. *Brauns, M., Garcia, X.-F., Walz, N.,* ***Pusch, M.T.*** (2007): Effects of human shoreline development on littoral invertebrates in lowland lakes. *Journal of Applied Ecology, 44, 1138-1144*
8. *Brauns, M., Garcia, X.-F.,* ***Pusch, M.T.****, Walz, N.* (2007): Eulittoral macroinvertebrate communities of lowland lakes: discrimination among trophic states. *Freshwater Biology 52: 1022-1032*

B. Publikationen zum Themenfeld „*Longitudinale Spiralen – Stoffretention in Fließgewässern*“

9. *Gücker, B****, Pusch, MT.*** (2006): Regulation of nutrient uptake in eutrophic lowland streams. *Limnology and Oceanography: 1443-1453*
10. *Fischer, H., Sachse, A., Steinberg, C.,* **Pusch, M.** (2002): Differential retention and utilization of dissolved organic carbon (DOC) by bacteria in river sediments. *Limnology and Oceanography 47: 1702-1711*
11. *Wanner, S.C.,* **Pusch, M.** (2000): Use of fluorescently labelled Lycopodium spores as a tracer for suspended particles in a lowland river. *Journal of the North American Benthological Society* 19: 648-658
12. ***Pusch, M.,*** *Fiebig, D., Brettar, I., Eisenmann, H., Ellis, B.K., Kaplan, L.A., Lock, M. A., Naegeli, M. W. & W. Traunspurger* (1998): The role of micro-organisms in the ecological connectivity of running waters. *Freshwater Biology* 40: 453-494.

C. Publikationen zum Themenfeld „*Benthisch-pelagische Kopplung als Schlüsselfaktor für mikrobielle Stoffumsetzungen in Flüssen*“

13. *Wilczek, S., Fischer, H.,* ***Pusch, M.T.*** (2005): Regulation and seasonal dynamics of extracellular enzyme activities in the sediments of a large lowland river. *Microbial Ecology 50, 253–267*
14. *Fischer, H., Kloep, F. Wilczek, S. &* ***Pusch, M.T.*** (2005): A river's liver – microbial processes within the hyporheic zone of a large lowland river. *Biogeochemistry 76: 349–371*
15. *Craft, J.A., Stanford, J.A.,* ***Pusch, M.*** (2002): Microbial Respiration within a Flood-plain Aquifer of a Large Gravel-bed River. *Freshwater Biology 47: 251-262*
16. *Fischer, H.,* ***Pusch, M.*** (2001): Comparison of bacterial production in sediments, epiphyton and the pelagic zone of a lowland river. *Freshwater Biology* 46: 1335-1348
17. *Fischer, H****., Pusch, M.*** (1999): Use of the [14C]leucine incorporation technique to measure bacterial production in river sediments and epiphyton. *Applied Environmental Microbiology* 65: 4411-4418

D. Publikationen zum Themenfeld „*Vom Einzugsgebiet zum Mikrohabitat – anthropogene Kaskadenwirkungen auf Gewässer*“

18. ***Pusch, M.****, Andersen, H.E., Bäthe, J., Behrendt, H., Fischer, H., Friberg, N., Gancarczyk, A., Hoffmann, C.C., Hachoł, J., Kronvang, B., Nowacki, F., Peder-sen, M.L., Sandin, L., Schöll, F., Scholten, M., Stendera, S., Svendsen. L.M., Wnuk-Gławdel, E., Wolter, C. (*2009): Rivers of the Central Highlands and Plains. *In: Tockner, K., Uehlinger, U. and Robinson, C. T. (Eds): Rivers of Europe. Elsevier, London, 525-576*

19. *Brunke, M., A. Hoffmann,* ***Pusch, M.*** (2001): Use of mesohabitat-specific relationships between flow velocity and discharge to assess invertebrate minimum flow requirements. *Regulated Rivers: Research and Management* 17: 667-676
20. ***Pusch, M.,*** *Hoffmann, A.* (2000): Conservation concept for a river ecosystem (River Spree, Germany) impacted by flow abstraction in a large post-mining area. *Landscape and Urban Planning* 51: 165-176

Die **Eigenanteile** an den Publikationen sind in der folgenden Tabelle dargestellt. Von den 25 aufgelisteten Publikationen wurden 23 überwiegend selbst initiiert, d.h. wären ohne meine Initiative sicher nicht erstellt worden. Oftmals wurden den in den selbst eingeworbenen Drittmittelprojekten beschäftigten DoktorandInnen oder Jungwissenschaftlern, die vom Habilitanden in der Datenerhebungsphase konzeptionell und methodisch intensiv fachlich betreut worden waren, in der Publikationsphase der Projekte die Erstautorenschaft eingeräumt.

<table>
<tr><th rowspan="3">Lfd Nr.</th><th colspan="5">Publikation (Impactfaktor der Zeitschrift, Stand 2010)</th></tr>
<tr><th colspan="3">Eigenanteil bei</th><th rowspan="2">Rolle des Erstautors</th><th rowspan="2">Rolle der übrigen Koautoren (Doktoranden und Projektwissenschaftler = wiss. Mitarbeiter in selbst konzipierten, eingeworbenen und betreuten Drittmittelprojekten)</th></tr>
<tr><th>Konzeption der Forschung</th><th>Datenerhebung</th><th>Manuskripterstellung</th></tr>
<tr><td rowspan="2">1.</td><td colspan="5">Garcia, X.-F., Schnauder, I., Pusch, M.T. (im Druck): How does the complex hydromorphology of river meanders contribute to benthic invertebrate diversity in rivers? Hydrobiologia (1,964)</td></tr>
<tr><td>80%</td><td>0%</td><td>30%</td><td>Projektwissenschaftler</td><td>Projektwissenschaftler</td></tr>
<tr><td rowspan="2">2.</td><td colspan="5">Schwalb, A., Pusch, M.T. (2007): Horizontal and vertical movements of unionid mussels (Bivalvia: Unionidae) in a lowland river. Journal of the North American Benthological Society 26: 261-272 (2,974)</td></tr>
<tr><td>90%</td><td>10%</td><td>60%</td><td>Diplomandin</td><td></td></tr>
<tr><td rowspan="2">3</td><td colspan="5">Brauns, M., Gücker, B., Wagner, C., Garcia, X.-F., Walz, N., Pusch, M.T. (2011): Human lakeshore development alters the structure and trophic basis of littoral food webs. Journal of Applied Ecology 48: 916–925 (4,970)</td></tr>
<tr><td>70%</td><td>5%</td><td>40%</td><td>Doktorand</td><td>Datenerhebung, Teilbeiträge</td></tr>
<tr><td rowspan="2">4.</td><td colspan="5">Donohue I., Jackson A.L., Pusch M.T., Irvine K. (2009): Nutrient enrichment homogenizes lake benthic assemblages at local and regional scales. Ecology 90: 3470-3477 (5,073)</td></tr>
<tr><td>50%</td><td>0%</td><td>20%</td><td>Projektwissenschaftler</td><td>Datenanalyse, Hauptbetreuung</td></tr>
<tr><td rowspan="2">5.</td><td colspan="5">Gabel, F, Garcia, X.-F. , Brauns, M., Sukhodolov, A., Leszinski, M., Pusch, M.T. (2008): Resistance to ship-induced waves of benthic invertebrates in various littoral habitats. Freshwater Biology 53, 1567-1578 (3,082)</td></tr>
<tr><td>50%</td><td>0%</td><td>40%</td><td>Doktorandin</td><td>Datenerhebung, Kobetreuung, Teilbeiträge</td></tr>
<tr><td rowspan="2">6.</td><td colspan="5">Brauns, M., Garcia, X.F., Pusch, M.T. (2008): Potential effects of water level fluctuations on littoral invertebrates in lowland lakes. Hydrobiologia 613: 5-12 (1,964)</td></tr>
<tr><td>40%</td><td>0%</td><td>40%</td><td>Doktorand</td><td>Datenerhebung</td></tr>
<tr><td rowspan="2">7.</td><td colspan="5">Brauns, M., Garcia, X.-F., Walz, N., Pusch, M.T. (2007): Effects of human shoreline development on littoral invertebrates in lowland lakes. Journal of Applied Ecology, 44, 1138-1144 (4,970)</td></tr>
<tr><td>80%</td><td>0%</td><td>50%</td><td>Doktorand</td><td>Datenerhebung, Kobetreuung</td></tr>
<tr><td rowspan="2">8.</td><td colspan="5">Brauns, M., Garcia, X.-F., Pusch, M.T., Walz, N. (2007): Eulittoral macroinvertebrate communities of lowland lakes: discrimination among trophic states. Freshwater Biology 52: 1022-1032 (3,082)</td></tr>
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<tr><td>9.</td><td colspan="5">Gücker, B, Pusch, MT. (2006): Regulation of nutrient uptake in eutrophic lowland streams. Limnology and Oceanography: 1443-1453 (3,385)</td></tr>
</table>

	90%	5%	40%	Doktorand	
10.	Fischer, H., Sachse, A., Steinberg, C., Pusch, M. (2002): Differential retention and utilization of dissolved organic carbon (DOC) by bacteria in river sediments. Limnology and Oceanography 47: 1702-1711 (3,385)				
	50%	5%	40%	Doktorand	Datenanalyse, Fachbeitrag
11.	Wanner, S.C., Pusch, M. (2000): Use of fluorescently labelled Lycopodium spores as a tracer for suspended particles in a lowland river. Journal of the North American Benthological Society 19: 648-658 (2,974)				
	80%	10%	40%	Doktorandin	
12.	Pusch, M., Fiebig, D., Brettar, I., Eisenmann, H., Ellis, B.K., Kaplan, L.A., Lock, M. A., Naegeli, M. W., W. Traunspurger (1998): The role of micro-organisms in the ecological connectivity of running waters. Freshwater Biology 40: 453-494 (3,082)				
	60%	30%	40%	Fachkollegen	Teilbeiträge
13.	Wilczek, S., Fischer, H., Pusch, M.T. (2005): Regulation and seasonal dynamics of extracellular enzyme activities in the sediments of a large lowland river. Microbial Ecology 50, 253-267 (2,875)				
	90%	5%	50%	Doktorandin	Projektwissenschaftler
14.	Fischer, H., Kloep, F. Wilczek, S., Pusch, M.T. (2005): A river's liver - microbial processes within the hyporheic zone of a large lowland river. Biogeochemistry 76: 349-371 (2,674)				
	80%	20%	40%	Projektwissenschaftler	Fachbeitrag, Doktorandin
15.	Craft, J.A., Stanford, J.A., Pusch, M. (2002): Microbial Respiration within a Flood-plain Aquifer of a Large Gravel-bed River. Freshwater Biology 47: 251-262 (3,082)				
	70%	20%	40%	externer Doktorand	Fachbeitrag
16.	Fischer, H., Pusch, M. (2001): Comparison of bacterial production in sediments, epiphyton and the pelagic zone of a lowland river. Freshwater Biology 46: 1335-1348 (3,082)				
	50%	5%	50%	Doktorand	
17.	Fischer, H., Pusch, M. (1999): Use of the [14C]leucine incorporation technique to measure bacterial production in river sediments and epiphyton. Applied Environmental Microbiology 65: 4411-4418 (3,778)				
	50%	5%	40%	Doktorand	
18.	Pusch, M., Andersen, H.E., Bäthe, J., Behrendt, H., Fischer, H., Friberg, N., Gancarczyk, A., Hoffmann, C.C., Hachol, J., Kronvang, B., Nowacki, F., Pedersen, M.L., Sandin, L., Schöll, F., Scholten, M., Stendera, S., Svendsen. L.M., Wnuk-Glawdel, E., Wolter, C. (2009.): Rivers of the Central Highlands and Plains. In: Tockner, K., Uehlinger, U. and Robinson, C. T. (Eds): Rivers of Europe. Elsevier, London, 525-576				
	70%	50%	70%		Teilbeiträge
19.	Brunke, M., A. Hoffmann, Pusch, M. (2001): Use of mesohabitat-specific relationships between flow velocity and discharge to assess invertebrate minimum flow requirements. Regulated Rivers: Research and Management 17: 667-676 (1,822)				
	80%	10%	50%	Projektwissenschaftler	Datenerhebung
20.	Pusch, M., Hoffmann, A. (2000): Conservation concept for a river ecosystem (River Spree, Germany) impacted by flow abstraction in a large post-mining area. Landscape and Urban Planning 51: 165-176 (2,004)				
	100%	50%	80%		Datenerhebung

3. Sonderdrucke der Manuskripte

3.1 Garcia, X.-F., Schnauder, I., **Pusch, M.T.** (im Druck): How does the complex hydro-morphology of river meanders contribute to benthic invertebrate diversity in rivers? *Hydrobiologia*

Hydrobiologia
DOI 10.1007/s10750-011-0905-z

HABITAT COMPLEXITY

Review paper

Complex hydromorphology of meanders can support benthic invertebrate diversity in rivers

X.-F. Garcia · I. Schnauder · M. T. Pusch

Received: 3 May 2011 / Accepted: 25 September 2011

Abstract In freshwater environments, high biodiversity is commonly associated with habitat heterogeneity. River bends and meanders are particularly complex morphodynamic elements of watercourses. However, the specific spatio-temporal interactions between hydromorphology and the resident biota have scarcely been studied. This article reviews the relationships between hydraulic processes, and morphological units that are typical for meanders, and analyzes the concomitant spatial and temporal dynamics of habitats suitable for aquatic invertebrates. Flow in river bends is characterized by significant cross-stream velocities, which modify primary flow patterns, and create helical flow trajectories. Consequently, boundary shear stresses at the river-bed are altered, so that complex erosion, transport, and accumulation processes characteristically shape bed and bank morphology. The diversity of substrate types and complex bathymetry in meanders provide a large variety of habitat conditions for benthic invertebrates within a relatively small spatial domain, which are connected via hydraulic pathways. Periodic reversal of hydromorphological processes between low and high flow, and seasonal growth of aquatic macrophytes creates spatio-temporal dynamics at the meso- and microhabitat scales. Such habitat dynamics increases benthic invertebrate diversity to the extent it is consistent with spatio-temporal scales of invertebrate mobility and life cycle. Furthermore, the presence of flow refugia, and hydraulic dead zones in meanders is essential to sustain species richness. This study concludes that meanders are highly complex morphodynamic elements that exhibit several self-regulating principles supporting invertebrate diversity and resilience in fluvial ecosystems.

Keywords River bends · Flow dynamics · Habitat heterogeneity · Flow refugia · Ecosystem resilience · River restoration

Guest editors: K. E. Kovalenko & S. M. Thomaz /
The importance of habitat complexity in waterscapes

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Introduction

The functional linkage between habitat heterogeneity and biodiversity has been observed in several types of ecosystems, including terrestrial (Galley et al., 2009 Jannsen et al., 2009), marine (Yanezarancibia et al., 1988; Hull et al., 2001), and freshwater environments (Harper et al., 1997; Williams et al., 2005). In addition, the relationship is observed at a hierarchical spatial scale, which exhibits distinct hydromorphological habitat and biotic characteristics. At large scales, the correlation is exemplified by the presence of dynamic floodplains, where morphological diversity in floodplains significantly increases biodiversity in river corridors (Johnston & Naiman, 1987; Pringle et al., 1988; Harper et al., 1997). Gray et al. (2006) also reported an increase in invertebrate diversity due to the presence of braided channels, spring-sources, spring creeks, or connectivity to groundwater zones. At intermediate spatial scales, river systems can be divided into several hydromorphological units, nested within river systems. The units, resulting from the interaction between hydraulic and morphological processes, provide distinctive habitats for biota (Frissell et al., 1986; Poole, 2002). At smaller spatial scales, the composition and characteristics of river sediments govern habitat heterogeneity, which influence the distribution and diversity of benthic invertebrates (Dahl & Greenberg, 1996; Lamouroux et al., 2004; Merigoux & Doledec, 2004). Three key features are important in characterizing particle size: (i) mean sediment particle size; (ii) variance of particle size; a wide variance may result in clogging of interstitial spaces provided by large particles; and (iii) the development of organic substrate coverings, e.g., biofilm, mud, or macrophytes. Downes et al. (1998) indicated that high diversity of habitats at large, intermediate, and local spatial scales support increased abundance and species richness of benthic invertebrates. However, attempts to establish direct mechanistic relationships that explain invertebrate diversity based on habitat variability have to date rarely been undertaken.

The effect of habitat heterogeneity on overall benthic invertebrate and fish biodiversity has been approached in empirical and analytical studies. Field studies have clearly established a positive relationship between invertebrate richness and abundance, and the structural complexity of habitats found in complex three-dimensional environments (e.g., woody debris, tree roots, or macrophytes) (Scealy et al., 2007; Schmude et al., 1998; Thomaz et al., 2008; Hansen et al., 2010). Stream habitat models have been developed based on statistical relationships between basic physical habitat characteristics, and the probability of species presence, according to species known ecological preferences for flow conditions or substrate characteristics [Lamouroux et al., 1992; Gore et al., 1994; Harby et al., 2004, CASIMIR (see Bloesch et al., 2005)]. However, in these studies, the physical factors acting on the organisms investigated have rarely been systematically measured at organism location. Therefore, the results do not facilitate the establishment of quantitative mechanistic relationships between the physical parameters and biotic communities. In addition, the models are generally restricted to predict a single species presence, and most models are developed for fish taxa. Moreover, the influence of spatial arrangements of the habitat patch within the habitat mosaic has scarcely been considered. Similarly, the influence of temporal variation on invertebrate diversity under varied habitat conditions due to seasonality and flow dynamics has seldom been assessed. Hence, integrative approaches to establish and understand mechanistic relationships between fluvial hydromorphology and invertebrate diversity are still lacking.

Habitat diversification is a common practice used in river restoration efforts to improve the ecological status of streams and rivers. Restoration success is monitored using the species richness metric, because the validity of the “habitat heterogeneity—biodiversity” principle is widely recognized. However, success cannot always be demonstrated because stressors affecting the stream reach have been inadequately quantified prior to restoration (Jähnig et al., 2010; Palmer et al., 2010). Furthermore, re-colonization of target species is often hampered, either by lack of source populations, or by disruption of habitat connectivity (Kail & Hering, 2005). An inter-disciplinary eco-geomorphological approach to analyze linkages between physical environment and biotic diversity would be especially valuable for rivers, which exhibit higher aquatic diversity along their meandering reaches compared to straight sections (Nakano & Nakamura, 2006). In addition, this approach shows high potential to improve the effectiveness of river restoration measures, which often re-establish a meandering morphology, but frequently fail to improve aquatic diversity (Bernhardt et al., 2005; Palmer & Bernhardt, 2006).

Re-meandering is a favored restoration approach. Most rivers exhibited much higher sinuosity prior to historic straightening and channelization, depending on geomorphic river type (Rosgen, 1996). Meandering is indicative of a natural river state, characterized by intense sediment transport, and the presence of habitat variability within a relatively small spatial domain. However, efforts to re-establish meandering are often unsustainable in certain river types, because meanders are largely a shaped and maintained due to and sediment transport regime. Morphodynamic processes in meanders are reversed periodically due to changing flow conditions (Keller, 1971; MacWilliams et al., 2006; Thompson, 2010). Consequently, even if river meanders and their characteristic biotic assemblages appear stable during low flow, their ecological functioning will be more appropriately understood when viewed as a dynamic equilibrium resulting from the relationship between physical and biotic processes.

In this article, we review and discuss how major hydraulic and morphological processes that occur in meanders may result in high habitat spatial heterogeneity and temporal dynamics, resulting in diverse and resilient assemblages of benthic invertebrates. We focused on processes occurring at meso- and microhabitat spatial scales along longitudinal and transverse hydraulic pathways, which were evaluated based on our own observations from meandering lowland rivers (Schnauder & Sukhodolov, 2011; Sukhodolov, 2011). The article is divided into four sections. The "Hydromorphologic processes in meanders" section describes the specific hydro-morphological processes occurring in meanders. The "Spatio-temporal dynamics of habitats and biodiversity in meanders" section discusses the mechanistic interactions between hydromorphological processes, habitat dynamics, and benthic invertebrates distributed at various spatial and temporal scales. The "Conclusion" section synthesizes the mechanistic relationships between hydromorphology, habitat variability and invertebrate diversity emphasized in this interdisciplinary functional analysis of river meanders, and discusses the potential applications in river restoration involving channel re-meanderings. In the final "Perspectives" section, we outline directions for future research.

Hydro-morphologic processes in meanders

Bathymetry and flow patterns

River meanders are characterized by a diverse bathymetry, which is the product of their characteristic three-dimensional flow patterns. Typically, meander cross-section transitions from near symmetry in the straight cross-over sections above riffles, to pronounced depth asymmetry across pool transects (Fig. 1). Near the 'apex', a pool is scoured adjacent to the outer bank, with a point bar formed by finer sediment near the inner bank. Further downstream, cross-sectional bathymetric profiles gradually approach the symmetrical shape of the riffle section, and depth decreases. Velocities are higher above riffles, and typically coarser grained sediments are deposited than in the pools. Sediment scoured from the pool at high flows is deposited in the shallower zones of the downstream riffle, and point bar. However, coarse sediments are also often found in the pools, but originate from eroded and drowned bank material, rather than sediment transport along the meander.

The characteristic flow pattern in meander bends relates to the significant cross-stream secondary flow, associated with (i) pronounced lateral gradients in the water level; (ii) energy losses due to dissipation from turbulence; and (iii) streamwise or primary flow pattern modifications, which further alter the shear stress distribution along the river-bed and banks. Spiral trajectories or 'helical flow' develop, advecting fluid with higher velocity from the channel center in a lateral direction toward the outer bank, and vertically downward (Thomson, 1876; Rozovskii, 1957; Bathurst et al., 1979). In meanders, the degree of helicity peaks downstream from the point of greatest channel curvature, where near-bed velocity gradients, and bed shear stresses increase, leading to maximum pool scouring.

In many cases, primary and secondary flow patterns in river bends are affected by additional mechanisms,

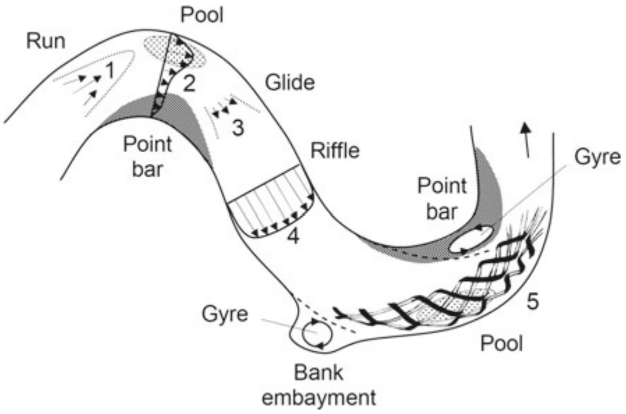


Fig. 1 Schematic of meander and flow patterns: *1* converging flow above a run; *2* pool velocity profile; *3* diverging flow above a glide; *4* riffle velocity profile; *5* helical flow pattern with two counter-rotating cells

which mainly depend on channel curvature and bed topography. Among them, potential vortex effects increase flow velocity at the inner bank, which may elicit strong impacts on secondary flow. In tightly curving bends, horizontal flow separation creates recirculation zones near the inner and outer banks (Leeder & Bridges, 1975; Ferguson et al., 2003). These effects promote sediment deposition at river margins, which may result in the formation of shallow bank-benches (Woodyer, 1975; Hickin, 1978). Bank irregularities or larger embayments are often stepping stones for the formation of recirculation zones bordered by horizontal shear layers. Turbulence production and dissipation of kinetic energy is enhanced in the shear layers, and increases the overall hydraulic roughness of the bend. Thorne et al. (1984) reported that shear layers along the banks cause further distortion to the primary and secondary flow, and shift peak velocities and stresses away from the banks, providing ‘buffer zones’ that protect the banks from erosion. Similar modifications are the result of multi-cellular secondary flow patterns found downstream of short riffle sections, where helicity from the upstream bend persists, and relocates the center of the secondary flow cell of the downstream bend (Chacinski & Francis, 1952; Wilson, 1973; Thorne & Hey, 1979). Furthermore, Dietrich & Smith (1983) demonstrated that shallowing topography and increased roughness effects over the point bar promoted unidirectional cross-streamwise flow toward the center of the channel which they termed ‘topographical steering’. Large-amplitude meanders may be sufficiently long to develop multiple pool-riffle sequences (Frothingham & Rhoads, 2003). In very tight bends, a shift of fast velocities from the channel center to the convex bank may occur, which leads to circular pool formation characterized by almost symmetrical pool cross-sections (Alford et al., 1982; Andrle, 1994).

The boundary shear stress acting on the meander bed and banks depends on the local velocity gradients. Typically, the maximum bed shear stress zone is near the inner bank at the upstream part of the bend, stretching toward the outer bank near the bend apex. Low stress areas are located in the lee of the point bar toward the pool, and at the outer bank in the entrance section (Dietrich et al., 1979). Sediment transport rate and particle size generally correspond to a bed shear stress pattern, e.g., the highest transport rates and coarsest grains are found in the line of maximum shear stress. Bedforms, such as ripples or small sand-waves, migrate through the bend in a downstream direction, but the orientation may locally differ from the main flow. If wave crests are not perpendicular to the main flow, the crests affect the local direction of bedload transport (Dietrich et al., 1979). Micro-scale flow in troughs between waves may entrain and transport sediment particles parallel to the wave crests. Dietrich et al. (1979) provided field evidence showing that transport was directed toward the point bar in the first two thirds of the bend, preventing sediments from entering the pool. At the downstream end of the point bar, trough currents transported the sediment away from the point bar toward the next bar downstream. These processes can undergo spatio-temporal changes due to processes such as discharge fluctuations, and the seasonal cycle of macrophyte growth.

Dynamics of riffle-pool units

Riffle-pool units not only occur in conjunction with meanders, but also in straight reaches, and have long been recognized as a primary channel unit type in fluvial geomorphology (Hawkins et al., 1993). The spacing between pools is more or less regular, and equates to 5–7 times channel width, even in disturbed channelized sections, or following introduction of woody debris (Gregory et al., 1994; Knighton, 1998). Stream ecologists further divide riffle-pool sequences into subcategories to refine the scale of their physical and biological functions (Hawkins et al., 1993). Common classifications distinguish between the transition from riffle to pool termed ‘run’, and from pool to riffle termed ‘glide’ (Fig. 2). The bed material is coarsest in runs, followed by riffles, glides, and pools, suggesting the presence of grain size sorting mechanisms at the local scale. Riffles and pools persist with varying discharge, and maintain their position within the bend. The ‘velocity reversal hypothesis’ provides a relatively simple explanation for riffle and pool sustainability (Keller, 1971). At low flow, the water surface slope is steeper above riffles, but with increasing discharge, the pool slope increases at a faster rate. This leads to pool scouring at high flows, and accumulation of eroded sediments on downstream riffles. At low flow, processes are reversed as pools refill with eroded sediments from the riffles, and re-establish the ‘initial’ bathymetry. Several field studies supported the flow reversal hypothesis, however, other studies generated incongruent data or were inconclusive (reviewed in Thompson, 2010). Recent studies revealed that the flow structure in riffle-pool sequences is often highly three-dimensional, so that shear stresses acting on the bed may vary considerably, even within the same cross-section. Flow along the run was observed to converge into a jet-like structure or 'turbulent run' (Caamaño et al., 2010; Rhoads & Massey, 2011). The accelerated fluid mass then plunges into the pool, and scours the zone where it impacts the stream-bed (Schnauder & Sukhodolov, 2011). Flow decelerates into the pool, and expands above the glide due to shallowing and widening bathymetry (Thompson et al., 1998). At the margins of jet-like flow, horizontal shear layers develop in association with large turbulent structures (Schnauder & Sukhodolov, 2011). Lab and field studies indicated the persistence of such jet-like flows independent of discharge or water level stage (Thompson et al., 1998; Caamaño et al., 2010). However, discharge and pool geometry can exhibit a significant effect on the magnitude, shape, and jet alignment (Lisle, 1987; Thompson et al., 1998). Caamaño et al. (2010) observed that at low flows, jets in a bend were oriented toward the inner bank facilitating point bar formation, but moved toward the outer bank at high flows and scoured the pools. To some extent, this supports Keller's (1971) principal tenet that a reversal of morphodynamic processes is the crucial factor for the persistence of riffle-pool units.

Recirculation zones

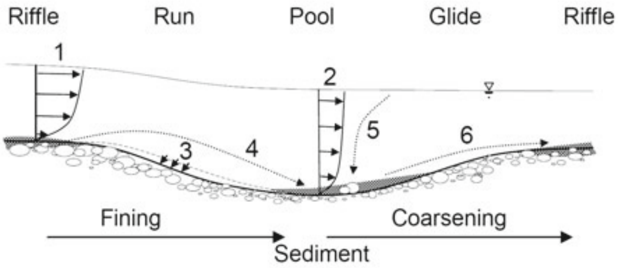


Fig. 2 Schematic of a riffle-pool sequence at low flow: *1* accelerating flow with high near-bed gradients; *2* decelerating flow above a pool; *3* regressive run erosion; *4* pool refilling; *5* accumulation of individual coarser grains due to bank erosion; *6* pool scouring and riffle deposition at high flows (velocity reversal)

Recirculation zones provide shelter from high velocities and shear stress, and promote accumulation of fine sediments and woody debris. Near-bank recirculation zones are typically occupied by a large stationary eddy or 'gyre', with a vertical rotation axis (Fig. 1). On a smaller river depth scale, there are also vertical recirculation zones with horizontal rotation axes, e.g., in the wake behind macrophyte patches, or other flow obstructions, including large boulders or woody debris deposited on the bed. Recirculations are related to flow separation from channel boundaries, forced by obstacles, or abrupt changes in bank lines, e.g., in tight bends where flow separates from the inner or outer banks. For this type of bend, Hickin (1978) suggested the ratio between the curvature radius and channel width was equal or less than two. Channel expansion and widening of the pool section are required for flow separation and recirculation zone development (Page & Nanson, 1982). Size depends on discharge stage, roughness condition, bank curvature, and topography. For example, point bar erosion may significantly enlarge outer bank recirculations (Ferguson et al., 2003). Field observations further suggested that pronounced deepening from riffle to pool shifts the separation zones further upstream, and counteracts the effects associated with channel widening (Leeder & Bridges, 1975). Other factors affecting separation zones include curvature and cross-sectional shape of the upstream section, and remnant helicity created in the upstream bend (Hodskinson & Ferguson, 1998). The hydrodynamics of recirculation zones and potential effects on meander morphology and development are best explained from groyne field analogs. Groyne fields are embayments occupied by single or multiple gyres, often developed along navigational rivers in order to prevent bank erosion and maintain minimal water depth for ships in the middle of the channel. Velocities are lowest in the gyre center, and increase toward the margins. Low velocities promote fine sediment accumulation, resulting in the thickest layer of deposited fines in the gyre center, which decreases toward the banks and the main flow. Suspended sediment composition changes during passage through the recirculation zone, because the heaviest particles precipitate out of the water column, and resuspension and bioproduction tend to enrich the water column with small organic particles (Sukhodolov et al., 2002). Larger non-suspended sediment fractions are transported near the bed ('bedload'), which enter the recirculation zones at the downstream end, and follow the direction of the gyre, where the formation of bedforms, like small sand-waves, is promoted

(Yossef & de Vriend, 2010). This process leads to sorting of particle size from coarse fractions at the entrance to finer fractions in the inner recirculation zone. Typically, sedimentation in recirculation zones is most pronounced at high flows, when suspended sediment and bedload concentrations are elevated. In general, recirculations are persistent features in meanders, although variation in discharge affects the gyre flow velocity, and the location of flow separation, which in turn may modify the spatial extent of the zone.

Structure and dynamics of banks

The banks of river meanders are shaped by the following factors: (i) the flow pattern, and the associated local boundary shear stress; (ii) mechanic properties of the soil (e.g., cohesiveness, and pore water content); (iii) differences between the groundwater and river water levels; and (iv) riparian vegetation, which may play stabilizing or destabilizing roles (Gray & Leiser, 1982). Typically, three different 'classes' of meander banks are easily distinguishable from visual observations: (a) the outer steep bank in the pool vicinity; (b) the inner mildly sloping bank merging with the point bar; and (c) the straight and symmetric banks along the riffle transects. Boundary shear stress is highest at the outer bank, leading to bank erosion, which is the fundamental requirement for meander formation and migration. Cohesive sediments form steep banks partially restrained by roots, which are often undercut and have diverse modes of erosion, for example slip failure of entire blocks of sediment (Biedenharn et al., 1997). Such blocks slip into the water and form a compact sediment deposit, which may resist erosion for a long time, protecting the banks, and creating diverse flow structures. Non-cohesive banks fail when they are close to the angle of repose, e.g., when granular material on the slope face is on the verge of sliding and progressive undercutting of the bank is initiated. The eroded material accumulates in cones and fans at the toe of the bank, and is efficiently transported downstream during higher flows. However, if the bank material is non-uniform with a variety of different grain sizes, the largest grains often resist erosion, and remain in the pools. Where large root balls or boulders protect the outer bank, the flow scours the adjacent areas and creates horizontal embayments (see Sect. 1.2). Roots and boulders protrude into the flow and act as obstructions, which cause high velocity gradients and stresses, but may also promote flow separation and buffer layers protecting the banks. Rough banks cause a shift of peak velocities toward the channel center, and reduce the strength of secondary circulation (Thorne & Furbish, 1995). Consequently, the primary bank erosion mechanism is counteracted. Point bars are formed as deposits of finer sediments at the bend inner banks, adjacent to pools. These are low energy environments, characterized by low-flow, stagnant water, or recirculation zones (see Sect. 1.2). Point bars are typically gently sloping, and small changes in water level cause relatively large areas to be wetted or dried. Emergent point bars are often colonized by riparian vegetation at low flow. Point bars form due to near-bed sediment transport from the pool toward the inner bank induced by helical flow. Grain size sorting is initiated by the transverse sloping bed, which causes different grain sizes to move in different directions (Parker & Andrews, 1985). Coarser fractions are deposited at the upstream and toe parts of the bar, whereas gradual fining acts toward the downstream end and the inner bank, often promoting smaller patches of bedforms.

The riffle banks are comparable to straight-river reaches with shallow flows. Their cross-sectional shape is often parabolic, indicating equilibrium between boundary shear stresses and resistance of the bed and bank material. Boundary shear stresses acting on straight banks are lower than those at the outer bank of pool transects, and bank erosion is typically insignificant with morphological changes restricted to the main channel bed.

Influence of aquatic vegetation

Flow structure and morphodynamics are subject to seasonal modifications in case of aquatic vegetation growth (Fig. 3). On a reach scale, aquatic vegetation significantly increases the roughness of a stream, and elevates the water level compared to unvegetated conditions. In winter, and at locations devoid of vegetation, vertical velocity profiles are typically logarithmic, with maximum velocity gradients and shear stresses at bed-level. Vegetation patches block flow, and divert it around and above their canopy. As a result, velocities decrease substantially within the vegetation patch, but increase in surrounding open areas. Within vegetation patches, reduced velocities

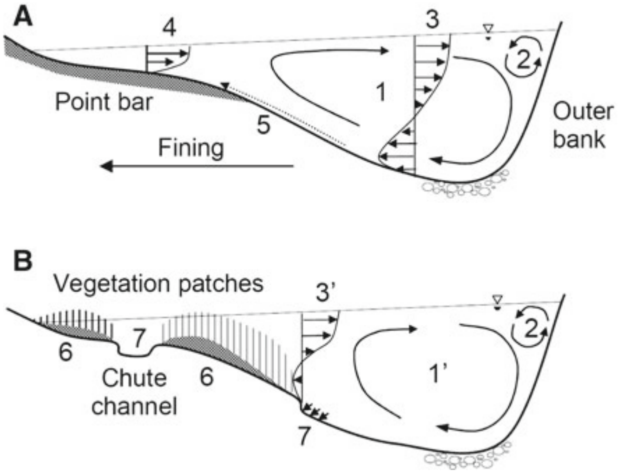


Fig. 3 Schematic of a pool cross-section: (**A**) unvegetated, and (**B**) point bar colonized with vegetation. *1* primary-secondary flow cell, and its modification by vegetation (1′); *2* outer bank secondary flow cell; *3* cross-streamwise velocity profile (modified by vegetation 3′); *4* unidirectional flow (topographic steering); *5* bedload transport; *6* fine sediment accumulation; *7* local erosion

and stresses promote accumulation of fine sediments with high nutrient content (Sand-Jensen & Mebus, 1996; Cotton et al., 2006). In contrast, remaining open areas between vegetation stands tend to erode, and are modified into chute channels (Wolfert et al., 2001; Schnauder & Sukhodolov, 2011). The magnitude of lateral sediment redistribution depends primarily on seasonal changes in discharge, as well as macrophyte biomass, density, and distribution. In lowland rivers, deposition may require relatively high macrophyte densities, which only occurs over a 2–3 week peak growth period during the summer (Kleeberg et al., 2010). As plants decay, the accumulated particulate matter will gradually be resuspended with increasing bed shear stresses during higher winter discharges. Even a small increase in stresses may lead to significant resuspension and entrainment of fine sediments into the water column (Kleeberg et al., 2010). Morphological changes induced by macrophytes during unvegetated periods of the year are therefore reversed. Pools in meanders are often sufficiently deep to significantly reduce light attenuation, and limit establishment of submerged vegetation (Wolfert et al., 2001; Schnauder & Sukhodolov, 2011). Secondary flow is then laterally confined within open areas, and distorted where bed and banks are covered by vegetation. Interactions between macrophytes, flow, and morphology have been a vital field of research in ecohydraulics for a decade, and a substantial gain in knowledge may be expected within the next few years.

Case studies

Similar hydro-morphological processes occur in most river meanders, however, each meander exhibits different hydro-morphological characteristics, and site-specific dominance of different processes involve diverse habitat conditions for invertebrates. Table 1 illustrates the uniqueness of meanders using an example of four European lowland rivers (Tollense, Spree, Mulde, and Ledra rivers) differing in hydro-morphological characteristics. The four rivers distribute along a gradient of increasing water surface slope and associated bed material coarseness in the following sequence: Tollense, Mulde, Spree, and Ledra. The Tollense and Ledra rivers are characterized by tight bends and strong secondary flow on the contrary to the mildy curved Spree and Mulde rivers. The ratio of pool to riffle depths is high at Tollense and Spree and low at Ledra and Mulde.

Spatio-temporal dynamics of habitats and biodiversity in meanders

Key factors determining aquatic habitats for invertebrates

Aquatic biota has adapted to use different meander morphological units (described in the previous section) as specific habitats. In ecological terminology, aquatic habitats are the living environment of aquatic organisms that consist of relatively homogeneous depth and flow, bounded by sharp gradients (Hawkins et al., 1993). For benthic invertebrates, habitat conditions are defined by two key factors: the substrate (e.g., hard or soft substrate, sediment particle size, and the presence of vegetation), and hydraulic conditions (e.g., mean current velocity, turbulence characteristics, and boundary shear stress). Freshwater ecologists have long recognized these two components as major factors explaining species distribution (Bournaud, 1963; Williams & Hynes, 1974; Rabeni & Minshall, 1977; Reice, 1980; Rae, 1985). However, of these two factors, hydraulics is the primary characteristic shaping aquatic habitat for invertebrates, since it influences

Table 1 Hydro-morphological characteristics of four lowland meanders from the Tollense, Spree, and Mulde rivers (North-East Germany), and the Ledra River (North-East Italy)

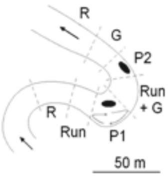
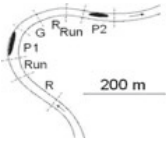
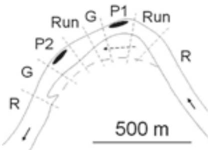
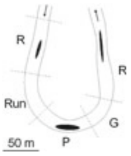
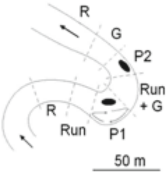
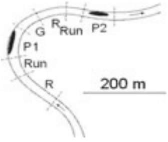
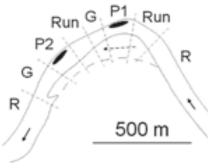
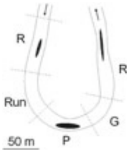
River	Tollense	Spree	Mulde	Ledra
				
Geological setting	Glacial sandy deposits, peat	Young glacio-fluvial sandy deposits	Older glacio-fluvial sandy deposits	Young glacio-fluvial mixed-size deposits at Alpine piedmont
Discharge Regulation	Regulated, constant water levels throughout the year	Regulated, daily fluctuations (<bankful), episodic overbank flows	Regulated, high dynamics of medium floods below bankful. Overbank flows	Regulated, small fluctuations (<bankful), overbank flows (1–2 per winter)
Length of meander × channel width	60 m × 19 m	380 m × 32 m	700 m × 60 m (low flow)	300 m × 15 m
Bathymetry	P1: circular pool, P2: bend pool, Run + G: transitional glide-run	P1: primary pool, P2: secondary pool	P1: primary pool (low flow); P2: second pool (flood stage)	R: riffles elongated with small pools (straight units)
Curvature	Tight	Mild, large amplitude	Mild	Tight
Point bar	Small, vegetated, recirculating flow, fine deposits	Small (bank protection), sand deposits	Large, riparian vegetation, floodplain pools	Stagnant, dead wood (CWD) deposits, fine matter accumulation
Riffle (R)	Vegetated, chute channel	Sandy, bedforms	Coarse sand, uniform depth	Coarse sediments, secondary pools
Pool (P)	Fine sediment deposition at medium/low flows, erosion at high flows	Gravel and coarse sands	Large boulders slipped from banks, depth >6 m, low light attenuation	Shallow, boulders
Recirculations	Large outer bank recirculation	Outer bank flow separation	Outer bank embayments (remnant groynes, deadwood)	Outer bank embayments (riparian vegetation, boulders)
Primary flow	Pronounced jet-like flow and bend flow, submergence of high velocity fluid	Bend flow pattern, submergence of high velocity fluid at outer bank	Strong acceleration by channel narrowing at the apex	High velocity fluid is buffered away from the bank
Secondary flow	In second half of the bend	Pronounced helicity at apex, outer bank secondary flow cell	Locally strong cross-flow, but helicity not fully developed	Pronounced helicity at apex, outer bank secondary flow cell
Flow velocity in riffle (cm/s)	20–50	20–60	50–100	120–150
Flow velocity in pool (cm/s)	5–20	10–40	100–180	80–100
Substrate	Mean 0.3 mm, peat, sand, mud, subfossile gastropod shells	Mean 0.6 mm, sand-gravel, banks with rip-rap	Mean 10 mm, sand, gravel, outer bank with rip-rap	Mean 25 mm, fine sediments up to boulders (300 mm), rip-rap at outer banks (1000 cm)

Table 1 continued

River	Tollense	Spree	Mulde	Ledra
				
Sediment dynamics	Accumulation and erosion of fine sediments related to vegetation growth cycle	Sand bedload transport, small bedforms (dunes, ripples), some fines	Sand bedload transport	Armoured bed with large boulders
Vegetation	Pronounced aquatic and riparian (reed belts)	Riparian trees, algae and biofilm	Insignificant, point bar with riparian pioneer vegetation	Dense riparian trees, aquatic mosses

substrate characteristics. The hydraulic boundary layer above the substrate comprises most benthic invertebrate habitat, which does not exceed a few millimeters in height (Ambühl, 1960). The boundary layer, which is determined by near-bed flow and roughness, defines the strength of lift and drag forces acting on benthic invertebrates (Statzner, 1988), in addition to habitat conditions in the interstitial space of subsurface sediments (Ingendahl et al., 2009). Hydraulic characteristics also determine the following factors in providing suitable aquatic habitat: (i) sediment particle size distribution; (ii) sediment movement and bedload transport; (iii) accumulation and resuspension of fine particulate organic matter; and (iv) growth of biofilm and submerged macrophytes.

The concept of meso- and microhabitats

At the scale of hydro-morphological units, areas exhibiting similar environmental characteristics visually discernible from other areas are called 'mesohabitats' (Pardo & Armitage, 1997). Each mesohabitat is colonized by species having similar ecological requirements and tolerances, including hydraulic conditions, substrate structure, dissolved oxygen (DO) concentrations, and food resources (Brunke et al., 2002). Therefore, functionally homogeneous biotic assemblages should colonize a mesohabitat which exhibit clear differences, relative to assemblages supported by other mesohabitats. However, these assemblages are undergoing continuous turnover due to the migration and drift of organisms, because individual organisms/species only recognize their local microhabitat conditions. As long as the microhabitat conditions remain within the range of ecological tolerance of the species, individuals will stay in the habitat. Otherwise, individuals will migrate and actively search for better conditions. Hence, characterization of microhabitat conditions has been recognized as another promising approach to explain benthic invertebrate distribution, because it better embraces variance in species ecological requirements, and diversity of individual behavior (Hart & Finelli, 1999; Lancaster et al., 2009).

Temporal scales in habitat dynamics

As described in the "Hydro-morphologic processes in meanders" section, river meanders involve marked temporal changes in habitat conditions, triggered by changes in flow conditions and seasonal growth of macrophytes. Typically, morphological changes lag behind changes in hydraulic conditions. Moreover, flow variation is continuous, whereas changes in substrate characteristics respond to well-defined thresholds. Consequently, current (i.e., immediate) features characterize a habitat, as well as long-term and seasonal dynamics. Therefore, the composition of any biotic assemblage inhabiting a given mesohabitat is not only determined by current living conditions, but by natural disturbance regimes. If a single key habitat variable surpasses a threshold value (above or below), the microhabitat will no longer be in the ecological tolerance range for the species. This is illustrated by the crayfish *Orconectes propinquus* that is unable to feed on filamentous algae beyond its flow velocity tolerance limits (Hart, 1992). Alternatively, low flow velocity reduces capture and ingestion of suspended particles by filter feeders (Malmqvist & Sackmann, 1996). However, this rule is non-linear, because despite the primary control by hydraulic forces, habitat preferences for a benthic invertebrate are not only determined by the habitat conditions *sensu stricto* (e.g., substrate and flow conditions), but are also influenced by other interacting factors, such as food availability, food quality, or DO concentration. For example, Quinn & Hickey (1994) reported that under hydraulic stress conditions, invertebrates showed increased survivorship when food resources and DO conditions were not limiting. Moreover, the use of preferential habitat is influenced by intra- and inter-specific interactions, such as colonization density and predator presence. Hence, the composition of invertebrate assemblages results from changes in habitat conditions occurring at different temporal scales, ranging from seasonal to daily modifications. Meanders with known complex morphodynamics are therefore likely to exhibit a major impact on invertebrate diversity.

Linkages between habitat heterogeneity and biodiversity

A positive correlation between biodiversity and habitat heterogeneity and complexity is generally recognized (Downing, 1991; Huston, 1994). In freshwater ecosystems, this often refers to heterogeneity of mesohabitats or geomorphologic units, as the mosaic of water body types (e.g., main and secondary channels, backwaters…) in alluvial plains (Johnston & Naiman, 1987; Pringle et al., 1988), or the presence of complex habitats, such as dead wood accumulation or macrophyte patches (Benke et al., 1984; Schneider & Winemiller, 2008; Thomaz et al., 2008). In support of hydraulics as one of the two influential habitat factors, high aquatic biodiversity and productivity has also been associated with variability in flow conditions. Cardinale et al. (2005) demonstrated, based on a survey of 83 streams, that a positive relationship between species richness and the net production of biomass only occurs in streams characterized by highly variable discharge regimes. Indeed, in the absence of flow variability, biotic diversity would clearly be lower, with dominance by a single competitively superior taxon in the extreme case, as shown experimentally by Cardinale & Palmer (2002). Mechanistically, flow variation triggers local and temporary species turnover by constantly changing local habitat conditions. The resulting species dynamic equilibrium leads to an increase in diversity, as proposed by the intermediate disturbance hypothesis (IDH) (Connell, 1978; Townsend et al., 1997; Weithoff et al., 2001; Roxburgh et al., 2004; Johst & Huth, 2005). In contrast, extreme disturbance events such as floods lead to catastrophic drift, which not only removes most resident fauna, but also reduces species diversity (Poff & Ward, 1989; Townsend & Hildrew, 1994; see also Lepori and Hjerdt, 2006). Alternatively, the persistence of certain specialist species may depend on the occurrence of such rare events.

Mesohabitat conditions in meanders at intermediate flows

As described in the "Hydro-morphologic processes in meanders" section, meanders support a mosaic of geomorphological units exhibiting various environmental conditions. The principal geomorphic units are riffles, runs, glides, and pools adjacent to the outer banks, point bars, straight banks at the cross-over stretch, and recirculation zones. Unique combinations of depth, mean velocity, velocity gradients, bed shear stresses, and substrate characterize these units (Harrison et al., 2011). At medium flow, and assuming stationary conditions, habitat suitability for benthic invertebrate species can be deduced from the characteristic environments (Table 2).

Riffles and runs are typified by high velocity, high bed shear stress, and coarse substrate, but differ in flow characteristics, as runs generally exhibit three-dimensional flows. These mesohabitat units, with harsh flow conditions but intense re-oxygenation rates, are usually colonized by rheophilic species that rely either on seston filtration (filter feeders) or phototrophic biofilm grazing (scrapers) (Pedersen & Friberg, 2007; Heino, 2009). Streams with a coarse cobble substratum are dominated by rheophilic species that rely on CPOM (coarse particulate organic matter) trapped between the cobbles (shredders). If sediments remain stable during the summer, aquatic macrophytes develop, benefitting from high sunlight penetration at the stream bottom in these shallow sections (Wolfert

Table 2 Characteristics of geomorphic units at medium stable flow including a reversal of hydro-morphological process during peak flow, typical dominant invertebrate species, and feeding guilds

	Riffle	Run	Pool	Glide	Point bar	Outer bank	Straight bank	Recirculation
Depth	Low	Medium	High	Medium	Low	High	Medium	Medium
Flow velocity	High	High	Low	Low	Low-stagnant	Medium–high	Medium–low	Gradient at low level
Bed shear stress (low & medium flow)	High (uniform 2D)	Highest (jet 3D)	Lowest	Low	Low	Medium–high	Medium–low	Very low
Grain size	Coarse, armouring	Coarsest	Medium but with coarsest grains	Medium, Deposition of larger grains	Fine	Eroded, coarse	Medium	Very fine
Hydromorphologic process during low and medium flow	Scouring	Scouring, regressive erosion	Deposition (refilling)	Deposition armouring of largest grains	Deposition	Neutral–moderate erosion	Neutral	Accumulation of fines particles
Hydromorphologic process at high flow	Strong, deposits of material eroded from pools	Medium effect	Scouring	Medium	Stabilisation	Erosion, bank retreat	Moderate erosion	Stable
DO availability in benthic boundary layer[a]	Not limiting	Not limiting	Limiting	Not limiting	Limiting	Not limiting	Not limiting	Limiting
FPOM accumulation[b]	Low	Low	Medium to high	Medium	High	Trapped in vegetation or low	Trapped in vegetation or low	High
CPOM accumulation[b]	Low	Low	Medium to high	Medium	High	Trapped in vegetation or low	Trapped in vegetation or low	High
Typical species guild	Rheophilic	Rheophilic	Limnophilic	Rheophilic Limnophilic	Limnophilic Rheophilic Semi-terrestrial	Limnophilic Rheophilic	Limnophilic Rheophilic	Limnophilic
Typical feeding guild	Filter feeder Scraper	Filter feeder Scraper	Shredder Gatherer	Shredder Gatherer	Gatherer Shredder	Scraper Shredder Gatherer Filter feeder	Scraper Shredder Gatherer Filter feeder	Gatherer

In most cases, differences in vertical velocity gradients and shear stresses were not considered due to the difficulties in field determination (Dittrich & Schmedtje, 2006)

[a] Can be summer limited in all geomorphic units before sunrise if the river supports extensive submerged vegetation

[b] Dependent on sediment size, i.e., coarser sediments have higher trapping efficiency

et al., 2001). Macrophyte development results in a biodiversity peak due to diverse habitat conditions along pronounced lateral and vertical, and trapped organic material from the margin toward the center of the macrophyte patch. In comparison, invertebrate diversity is significantly lower in submerged macrophyte patches located in pools, due to the absence of high-flow microhabitats at the patch margin (Helesic & Sedlak, 1995).

In contrast to riffles and runs, pools, glides, recirculation zones, and point bars are characterized by lower velocity and bed shear stress, as well as finer sediments. Therefore, DO concentration in the top-sediment layer, where most benthic invertebrates are located, can be a limiting factor due to high biological oxygen demand by sediments with high organic content. Lotic invertebrates feeding on fine sediments (collectors/gatherers), or CPOM (shredders) comprise a large proportion of the invertebrate assemblage in these mesohabitat units. In pools and recirculation zones, sedimentation processes dominate, including deposition of CWD (Coarse Woody Debris). Meander sections with recirculation zones are especially efficient in trapping CWD, and consequently reduce CWD travel distances in rivers (James & Henderson, 2005). CWD deposition in pools or recirculation zones further increases substrate complexity in an environment dominated by soft sediments. Trapped dead wood is colonized by biofilm, and provides habitat for specialized xylophagous species that are either closely dependent on the presence of wood, or feed on wood directly (e.g., the caddisfly larvae *Lype pheopa*, or the midge larvae *Stenochironomus* sp.) (Anderson, 1982; Pereira et al., 1982; Schulte et al., 2003). Schneider and Winemiller (2008) report that CWD accumulations form important habitat for invertebrates because they offer flow refugia and organic matter trapped in a three-dimensional structure, increasing invertebrate abundance and diversity.

Point bars are shallow depositional areas, which are transitionally inundated at higher flows and subject to wetting and drying processes with changing water levels. Because the bars alternately offer terrestrial, wet and aquatic habitats, different specialized communities, associated with a range of moisture and vegetation characteristics, alternate in point bars habitats according to water level fluctuations (Sendstadt et al., 1977).

Outer banks of meanders are often artificially stabilized in order to prevent erosion. Embankments made by rip-rap stones offer habitats with three-dimensional structure, which are physically very stable and may protect invertebrates against fish predation or harsh hydraulic conditions. These habitats also offer abundant food resources, as stable stone surfaces facilitate undisturbed growth of phototrophic biofilm, and CPOM and FPOM (Fine Particulate Organic Matter) is trapped in crevices between stones; habitats of this nature generally host diverse assemblages (Shields et al., 1995; Schmude et al., 1998). A river restoration case study by Nakano & Nakamura (2006) revealed that hydraulic conditions were moderate in meander littoral habitats compared to straight reaches, which likely increased invertebrate densities and species richness.

It is not clear if erosional or depositional mesohabitat units exhibit higher benthic invertebrate diversity. Reid et al. (2010) found that accumulation zones exhibit higher diversity and abundance of benthic invertebrates, as well as greater abundance of sensitive species, compared to erosive patches of a streambed. However, Crosa et al. (2002) reported an opposite trend in high gradient streams. In an alluvial gravel stream, pools were more diverse, however, riffles supported an increased abundance of benthic invertebrates (Brown & Brussock, 1991). The inconsistency may be due to local substrate differences, hydraulic conditions, river size, and biogeographical context.

The higher number of mesohabitat types in the meander increases the number of available ecological niches, and consequently, the overall species richness. Moreover, the spatial proximity of these mesohabitat units (which are linked by primary and secondary flow pathways), allows easy migration among habitats in the mosaic. The mosaic of habitat conditions enables the establishment of species populations, which shift habitats during larval growth, e.g., as the individuals become increasingly sensitive to hydraulic stress with increasing body size (Hildrew et al., 2007). In case of accidental drift, individuals can be trapped in one of several sedimentation zones, from which they can easily recolonize initial areas by upstream migration (Lancaster et al., 1996). Hence, meanders are expected to exhibit high resilience of benthic invertebrate populations due to availability and connectivity of contrasted mesohabitats.

Microhabitats in meanders

Microhabitats are generally nested within mesohabitats, and correspond either to transition zones between mesohabitat units, or to hydromorphological heterogeneities inside the mesohabitat.

Microhabitats are more directly dependent on short term water level fluctuations than mesohabitats. The dynamic nature of microhabitats has been described as the patch dynamic concept (Pickett & Thompson, 1978; Townsend, 1989) which states that patches of habitat created and constantly modified by natural disturbance regimes are essential to maintain biodiversity. Microhabitat dynamics is probably more important for invertebrate distributions, because its time scale matches that of an invertebrate life cycle, while changes in mesohabitats occur at time scales exceeding individual life cycles (Lancaster & Belyea, 1997).

Microhabitats are numerous and diverse in meanders, e.g., small size recirculation zones occur locally behind macrophyte patches, large roughness elements (boulders or CWD) or along the bank due to bank irregularities. Owing to water level fluctuations, these structures evolve rapidly by growing, disappearing, or changing their location. The recirculation zone itself is not homogeneous, as low flow occurs in the center of the gyre and increases toward the margins, accompanied by differential grain size sorting. This creates a gradient in microhabitat conditions favourable for species species of different body sizes, with different sediment size and/or oxygen requirements. Similarly, transition zones between habitats are known to favor biodiversity, because transitions are rarely abrupt but constitute a gradient of environmental conditions (Ward et al., 1999). For example, a gradient of decreasing velocity and increasing POM deposition occurs toward the center of a macrophyte patch, allowing colonization by both rheophilic and lentic species.

Microhabitats significantly increase biodiversity because they provide a wide range of environmental conditions suitable to cover the specific ecological requirements of various species. For example, Brooks et al. (2005) and Davy-Bowker et al. (2006) demonstrated that small-scale differences in hydraulic conditions inside riffles influence the spatial distribution of benthic invertebrates by providing contrasting environmental conditions. Microhabitats exist in straight reaches as well as in meanders, however, the hydro-morphological complexity of meanders generates much more transition zones, and increases local heterogeneity compared to that in straight reaches, increasing the potential for biodiversity.

Flow refugia in meanders

Flow refugia are habitats subjected to low hydraulic stress even during high flow events; and organisms inhabiting the refugia are minimally affected by harsh hydraulic conditions (Winterbottom et al., 1997; Imbert & Perry, 1999; Rempel et al., 1999). The role of refugia for benthic invertebrates has been well-documented for various streams and rivers. For example, higher local invertebrate densities were observed in stream bottom patches identified as flow refugia after periods of high and fluctuating flow, while density in other patch types was reduced (Lancaster & Hildrew, 1993a). In the Upper Mississippi River, unionids were determined to exploit areas of low boundary shear stress during high flow (Steuer et al., 2008; Zigler et al., 2008). Winterbottom et al. (1997) made similar observations in a small English stream, where benthic invertebrates colonized exposed refugium cages only during periods of high flow.

Flow refugia have been identified at all spatial scales. At the stream corridor scale, flow refugia may consist of backwaters, inundated floodplain areas, or deep pools (Giberson & Caissie, 1998; Rempel et al., 1999; Negishi et al., 2002). Consistently, Negishi et al. (2002) recorded increases in invertebrate densities and species richness in backwaters and inundated habitats during high flow. Similarly, depths where maximum invertebrate densities and species richness were detected changed from 1.5 m at low flow to 0.5 and 0.2 m at peak flow in a large gravel-bed river (Rempel et al., 1999). At the micro-scale, flow refugia are even more important in protecting invertebrates from high hydraulic shear stress, especially for sensitive species with low mobility (Lancaster & Belyea, 1997, Lancaster, 2000). Nearby small-scale flow refugia can be detected by flow-sensitive invertebrate organs, and can be reached by the organisms within a short-time period, whereas macroscale dead zones, including newly wetted areas at stream margins or deep pools can only be reached by drift, depending on hydraulic pathways and sedimentation conditions.

Microscale flow refugia may be created by hydraulic or geomorphological mechanisms. They may appear in regions of recirculating flow like wake zones or eddies, which Way et al. (1995) demonstrated to be preferentially colonized by certain species, e.g., caddisfly *Hydropsyche orris*. Microscale flow refugia may also be found in crevices on the surface of large stable stones (Matthaei et al., 2000), accumulations of dead wood (Palmer et al., 1996), or artificial embankments that include rip-rap structures. As a consequence, these habitats, providing a large range of habitat conditions at microscale, harbor high numbers of invertebrate species differing in flow velocity requirements (Growns, & Davis, 1994).

Gore et al. (1994) described a patchy change in near-substrate hydraulic conditions with increasing discharge in terms of both spatial and temporal dimensions. Three types of local hydraulic modifications during high flow can be identified: (i) patches where shear stress increases for a short duration only, then returns to its initial level; (ii) patches where shear stress increases briefly, then decreases but stays higher than its initial level; and (iii) patches where shear stress remains high during the entire flow peak duration. These differences emphasize the complexity of spatio-temporal interactions between flow and river-bed, and support the formation of flow refugia even in areas exposed to high flow.

Studies have shown that flow refugia significantly reduce the loss of invertebrate populations during high flows. Therefore, refugia have an influence on the structure of biotic assemblages, and even ecosystem functioning (Sedell et al., 1990). Consequently, invertebrates maintained in refugia facilitate a more rapid re-colonization of stream reaches that were scoured and mostly deprived of their biota during high flows (Fuller et al., 2010). Flow refugia are seen as a key factor structuring the micro-distribution of invertebrate populations, especially for those subjected to daily changes in flow conditions (Sedell et al., 1990; Strayer, 1999; Fuller et al., 2010). Therefore, flow refugia enable the persistence of species that would otherwise be unable to resist hydraulic stress (Townsend et al., 1997a, b), leading to increases in faunal diversity. Furthermore, flow refugia may act as a selective filter. Several authors have shown that the ability to use refugia varies among species, as a function of interactions between the size of refugia, and the body size and mobility of species (Mobes-Hansen, & Waringer, 1998; Lancaster, 1999). Alternatively, flow refugia can enable predation during high flows, as prey and predators use the same refugium and are in close proximity (Felten et al., 2008). Thus, flow refugia in meanders influence the structure of biotic assemblages both directly and indirectly via the modulation of biological interactions.

Rivers exhibit varying potential for flow refugia due to geomorphic differences (Lancaster & Hildrew, 1993b), within or outside meanders. Regrettably, we are not aware of any studies on the characteristic physical and hydraulic features of meanders leading to the origin of flow refugia for benthic invertebrates. However, based on information described above for the origins of flow refugia, it can be expected that the heterogeneity and proximity of mesohabitat units (e.g., pools, recirculation zones, and vegetated banks) will favor the availability of flow refugia during high flow, because hydraulic dead zones are proximate and easy for invertebrate individuals to reach by active migration, or by intentional or passive drift. In straight-river reaches, biofilm and aquatic vegetation, as well as bedforms, i.e., dunes or riffles, also offer varying flow conditions, including areas of low shear stress, which can serve as local flow refugia. However, zones with recirculating flow constitute a typical feature of meanders. These features are relatively stable at different discharge levels, and therefore provide functional transient storage for invertebrates drifted away during high flows. Furthermore, increased retention efficiency occurs in meanders due to the influence of transversal flow on drift trajectories, which gain importance during high flows, effectively connecting retentive channel compartments with the sites for invertebrate drift, even from areas a significant distance upstream of the meander.

Conclusion

Several lines of evidence indicate that meanders exhibit complex hydrodynamics that favor high biodiversity. However, comprehensive field studies that provide direct confirmation are still lacking. Complex interactions among channel morphology, three-dimensional flow paths, and transported sediments foster a diverse mosaic of geomorphic units. These units contain meso- and microhabitats with numerous combinations of depth, flow velocity, turbulence, sediment particle size, sediment turnover frequency, and availability of organic matter that can be exploited by benthic invertebrates. Invertebrate species diversity is also favored by the presence of habitats with a complex three-dimensional structure, including woody debris or macrophytes, which are often found growing in the shallow parts of the meander. Temporal variability of meso- or microhabitat conditions is especially marked in meanders due to the reversal in hydro-morphologic processes during increasing or decreasing flow. Sediments and particulate organic matter are redistributed based on flow conditions during high flow, shaping habitat conditions for extended periods of time when flow is low. Hence, habitat dynamics in meanders results from a complex interaction between flow and substrate along spatially and temporally nested gradients.

Meanders support a diversity of geomorphic units, which form a mosaic of closely neighboring habitats that are linked by primary and secondary flow pathways. The implication of such closeness is important for benthic invertebrates considering their small size; this mosaic allows active migration among habitats if a more suitable ecological niche is necessary following small-scale habitat modification or recovery from incidental dislodgement. The complex and diverse mosaic habitat structure, including several habitat types that serve as flow refugia, occur within a relatively small spatial domain and constitute the key meander characteristic. These meander habitat features provide high potential for biodiversity hot spots, as well as increased biota resilience toward natural or anthropogenic disturbances.

Consequently, re-creation of meander bends is an ideal measure for river restorations that have been straightened in the past. Re-meandering of rivers already constitutes one of the most widely used approaches for river restoration (Kondolf, 2006). However, in many of these restoration projects, embankments fix the margins of the restored meander. While fixation of river channels is necessary in urban settings, it should and can be avoided elsewhere. Lateral erosion and the resulting meander migration is a key mechanism for maintaining sediment supply and redistribution. This temporal variability of meanders is of key importance for habitat diversity, and subsequently biodiversity. Re-meandering has been shown to increase species richness in comparison to nearby straightened reaches, especially due to the presence of trapped dead wood and macrophyte patches (Lorenz et al., 2009). However, few studies showed such a positive effect of re-meandering on invertebrate diversity or species abundance. Indeed, most restoration studies have not demonstrated any biodiversity differences before or after restoration. This might be explained by unfavorable environmental conditions in the surrounding restored stream sections, which were located in farmland or suburban areas (Biggs et al., 1998; Friberg et al., 1998; Nakano & Nakamura, 2008). In large urban or agricultural catchments, the remaining populations of sensitive species may be small or extirpated. In such cases, species recolonization following habitat improvement/restoration may be delayed for a considerable amount of time. In recent studies evaluating restoration success, unfavorable environmental conditions in sites neighboring restored areas have been identified as the primary problem responsible for unsuccessful restorations (Jähnig et al., 2010; Palmer et al., 2010). Under unfavorable conditions, enhancements of in-stream channel habitats must be accompanied by efforts to mitigate other stressors, such as altered hydrology or degraded water quality. It is not appropriate to focus only on one aspect of a restoration issue, e.g., channel re-configuration and other stressors affecting biota must be addressed simultaneously. Kail & Hering (2009) found the geomorphic integrity of adjacent reaches influenced the local ecological status, with near-natural reaches having a positive effect, and heavily degraded reaches a negative effect. This illustrates the link between different spatial scales, and emphasizes the need to maintain this bridge to succeed in river restoration. As clearly indicated, re-meandering favors a variety of habitats at macro- and micro-spatial scales, connected by complex flow pathways. Meandering will also mitigate, in the short-term, an existing incision trend in the riverbed, and help to re-establish the river's natural transport rate of sediment bed load. Consequently, re-meandering should be a preferential measure to enhance or preserve biodiversity of river reaches.

Perspectives

Spatio-temporal interactions between hydro-morphology and biota are complex and scale-dependent. Consequently, the various mechanisms leading to high biodiversity are a challenge to disentangle. Although the mechanisms acting at large spatial and temporal scales are relatively well-identified, small-scale habitat heterogeneity and dynamics, as well as the influence on invertebrate individuals remains poorly understood. Hence, there is an urgent need to quantify mechanistic relationships between habitat and biota at the local scale to understand how physical attributes influence population dynamics at larger spatial scales. Considering the strong relationship between invertebrate assemblages and flow dynamics, and the various species response patterns based on body shape and behavioral traits, we suggest that future research should use inter-disciplinary and integrative approaches to analyze the relationships between physical structure and biotic diversity. The need for a close collaboration between specialists in hydrology, geomorphology, and ecology has already been stressed, particularly in river restoration (Palmer & Bernhardt, 2006). Moreover, predictive modeling should integrate the range of species response patterns to flow variability and predict biotic assemblage dynamics, rather than single species occurrences.

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3.2 Schwalb, A., **Pusch, M.T.** (2007): Horizontal and vertical movements of unionid mussels (Bivalvia: Unionidae) in a lowland river. *Journal of the North American Benthological Society* 26: 261–272

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Horizontal and vertical movements of unionid mussels in a lowland river

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Abstract. Abstract.Freshwater mussels are important constituents of freshwater ecosystems, yet much of their basic biology remains to be examined. The behavior of 3 species of unionid mussels (*Unio tumidus*, *Unio pictorum*, and *Anodonta anatina*) was examined in the lowland River Spree (Germany). Mussels were marked individually, and their positions on the sediment surface and depth below the sediment surface were recorded weekly between May and October 2004. The average rate of horizontal movement was 11 ± 15 cm/wk (mean ± 1 SD). The direction of the movements seemed erratic; however, a significant net shoreward displacement of ~17 cm, possibly caused by rising water levels, was observed during the study. A surprisingly high percentage of the mussels (74 ± 7%) was burrowed entirely in the sediment to depths as great as 20 cm during the summer. Smaller mussels and individuals not infested by the zebra mussel, *Dreissena polymorpha*, burrowed deeper in the sediments than larger or infested mussels. Burrowing reduced infestation densities in a laboratory experiment. Significantly more *U. tumidus* individuals were found on the sediment surface during the reproductive period in early summer than in late summer, suggesting that reproductive activity may influence burrowing. Burrowing was significantly related to current velocity (discharge), day length, and water temperature (multiple linear regression, $R^2 = 0.74$, $p < 0.001$), but current velocity appeared to be the dominant factor driving vertical movements ($R^2 = 0.53$, $p < 0.01$). We propose that movement behaviors are important adaptations of unionid mussel populations to the flow and food conditions in rivers. Movement behavior also may help unionids escape predators and control infestation by *D. polymorpha*.

Key words: freshwater mussels, Unionidae, behavior, locomotion, vertical distribution, discharge, sediment, *Unio tumidus*, *Dreissena polymorpha*.

Mussels are an important component of freshwater ecosystems. They constitute up to 90% of benthic invertebrate biomass (Ökland 1963, Negus 1966, Pusch et al. 2002) and influence aquatic ecosystems in many ways. As suspension feeders, freshwater mussels are an important link coupling the pelagic and benthic zones because they clear suspended particles from the water column, thereby decreasing phytoplankton biomass (Welker and Walz 1998, Ackerman et al. 2001, Pusch et al. 2001). Freshwater mussels redirect nutrients and organic matter from the pelagic to the benthic food web through biodeposition of feces and pseudofeces. Exposed shells at the sediment surface provide habitat for epizoic and epiphytic organisms and for many invertebrate species, which can reach high densities in mussel beds (Brunke et al. 2002). In addition, mussel burrowing activities cause bioturbation of sediments, which increases the O_2 content of the sediment and influences the release of sediment-borne nutrients to the water column. Burrowing also may protect unionids from infestation by epizoic *Dreissena polymorpha* (Pallas) and remove already attached *D. polymorpha* (Nichols and Wilcox 1997, Burlakova et al. 2000). However, we lack detailed knowledge of these sediment-related processes, and this lack is a significant gap in our understanding of the functional role of unionid mussels in aquatic systems (Vaughn and Hakenkamp 2001).

Mussels traditionally have been viewed as sessile animals, despite the observation of tracks created by unionid mussels moving horizontally on the sediment surface. It was believed that mussels would move only to avoid adverse conditions such as exposure to air during low water levels and cold winter temperatures (Mentzen 1926, Engel 1990). However, studies have suggested a connection between aggregations of mussels and reproduction (e.g., Pichocki 1969, Amyot

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and Downing 1998). For example, *Anodonta* sp. individuals move closer together during the summer spawning season (Burla et al. 1974). Recent studies have documented seasonal migration in both the vertical (Amyot and Downing 1991, 1997, Balfour and Smock 1995, Watters et al. 2001, Perles et al. 2003) and horizontal directions (Amyot and Downing 1997, 1998). Adults apparently migrate vertically and emerge at the sediment surface during the reproductive period (Balfour and Smock 1995, Watters et al. 2001), whereas juvenile mussels (<3 y) always remain within the sediment (Balfour and Smock 1995). Horizontal movements also might bring animals of the opposite sex closer together during spawning (Amyot and Downing 1998). Aggregations are important for reproduction because the sperm of dioecious species (Wächtler et al. 2001) are released into the water by males and taken up by females. Fertilization of the eggs and development to a parasitic larval stage (glochidium) take place in the suprabranchial chambers of females. Spawning may occur several times per season in European *Unio* species (Hochwald and Bauer 1990), and *Anodonta cygnea* (Linnaeus) specifically releases a portion of glochidia when a potential host fish species is nearby (Bauer 2001). Thus, adult mussels must move to the sediment surface—at least with the posterior part of their valves—for sexual reproduction and larval release into the surface water.

Studies of movements of unionid mussels may provide important clues for understanding their functional role in aquatic ecosystems. Environmental factors, such as temperature and day length, influence seasonal variation in vertical and horizontal movements of unionid mussels (Amyot and Downing 1997, Watters et al. 2001, Perles et al. 2003) and are likely to have the same effects on mussels in both lentic and lotic systems. However, other factors, such as discharge, are specific to lotic systems. Discharge and velocity can be highly variable in streams, exposing mussels to different flow velocities and bottom shear stress, and might affect burrowing behavior (Di Maio and Corkum 1995, Strayer 1999). Most recent studies concerning vertical or horizontal movements of unionids were conducted in lakes (Amyot and Downing 1991, 1997, Saarinen and Taskinen 2003), creeks (Balfour and Smock 1995), or artificial systems (Watters et al. 2001, Perles et al. 2003 [in part]). To the best of our knowledge, no study has examined horizontal movements of unionid mussels in a lowland river. The purposes of our study were to quantify horizontal movements of unionid mussels in the lowland River Spree and to examine how environmental factors influenced the vertical movements of the most abundant species, *Unio tumidus* (Philipsson).

Methods

Study area

Field observations were conducted in the River Spree, a lowland river in northern Germany, that originates in the Lusatian mountains (Saxony, Germany) and flows for 380 km through several shallow lakes to its confluence with the River Havel in Berlin (Welker and Walz 1998). The study reach was part of a 6th-order river section called the Müggelspree, chosen for its high density of unionid mussels (up to 350 ind./m^2; Pusch et al. 2002, this study), which is linked to high seston concentrations and the absence of catastrophic floods. The study site was 45 km east of Berlin, ~400 to 500 m downstream of the Große Tränke weir near the city of Fürstenwalde (lat 52°22′20″N, long 13°59′54″E). As a result of channelization in the early 20th century, the river channel is roughly trapezoidal in profile, with a mean width of 27 m (18–40 m) and water depths ranging between 0.7 and 2.3 m. River discharge varied between 2.5 m^3/s in summer and 21.2 m^3/s in winter 2004. Water depth is strongly influenced by massive macrophyte growth in downstream reaches and, therefore, varies partially independently of discharge. The sediment consists almost exclusively of sand (mean particle size [D_{50}] = 0.42 ± 0.12 mm). In some locations, the sediment contains a hard layer of bog-iron ore, i.e., sand glued together by Fe(III)-hydroxide/oxyhydrate, which is created by precipitation processes when anaerobic ground water entering the river reaches oxygenated river sediments. The Müggelspree is considered eutrophic. Total N concentrations ranged between 0.7 and 1.9 mg/L, total P ranged between 74 and 187 µg/L, and chlorophyll *a* concentrations ranged between 14 and 82 µg/L in 2004. The Müggelspree holds small to moderate populations of otter (*Lutra lutra*) and the nonindigenous species muskrat (*Ondatra zibethicus*) and mink (*Mustela vison*), all of which are potential predators of unionid mussels.

Horizontal and vertical movements

Horizontal and vertical movements of mussels were studied simultaneously in a 3 × 3-m permanently marked study area (area A) >3.5 m from shore. Water depth varied between 0.5 to 1 m (early May) and 1.5 to 2 m (mid-July). Area A was divided into nine 1-m^2 quadrats marked only by short metal stakes, so that mussels could move freely. Mussels on the sediment surface were mapped weekly between 8 May and 4

September and on 2 October 2004. During sampling, a 1-m^2 aluminum frame, subdivided into 25 × 25-cm subquadrats, was placed temporarily over each of the nine 1-m^2 quadrats with the help of a professional SCUBA diver. The grid was used to determine the position of all mussels visible at the sediment surface and was removed after mapping was completed.

All mussels on the sediment surface in area A were labeled individually using numbered plastic labels (Dymo®) that were glued to the posterior part of a valve. Shell length of each mussel was measured (±1 mm) using calipers, species was determined, and individuals were returned to the 25 × 25-cm subquadrat where they were found. On each subsequent sampling date, any unmarked mussels were measured, identified to species, and labeled. The identification numbers of recovered mussels were recorded, and all individuals were returned to their original location. Additional sampling was done on 21 August to determine if labeled mussels had moved from the study area ($\leq$2 m) or had burrowed into the sediment in the study area (1 subquadrat was sampled). On 2 October, all mussels were removed from the sediment to determine the total (labeled and newly encountered individuals) number of mussels within the study area.

The distance traveled by a mussel between encounters was taken as the shortest distance between the centers of the subquadrats in which a mussel was found. The total number of mussels visible on the sediment surface on each sampling date and the total number of individuals within the study area on 2 October were used to calculate the percentages of burrowed mussels during the study period, assuming that the number of mussels in the study area remained constant. The average length of time during which mussels disappeared and were assumed to have burrowed into the substrate was calculated based on data from 35 individuals found in the center 1 × 1-m quadrat of the study area between 8 May and 12 June. This conservative estimate ensured that any disappearance was the result of burrowing rather than of migration from the study area.

Vertical distribution of mussels in the sediment

The vertical distribution of mussels in the sediment was examined in ten 1-m^2 quadrats within a 9 × 3-m area (area B) that was more densely populated than area A. Area B was 5.5 m from shore and ~100 m upstream of area A. Quadrats were chosen randomly within area B; no quadrat was sampled twice. Seven quadrats were sampled in early summer (8 June–7 August 2004) during the reproductive period of the most abundant species (*U. tumidus*), and the 3 remaining quadrats were examined in late summer (28 August–4 September). In quadrats sampled in June, mussels on the sediment surface and burrowed mussels were identified and measured. In quadrats sampled between July and September, the depth of each individual in the sediment (0–5, 5–10, 10–15, or 15–20 cm) was recorded. Unionids were identified to species and measured (shell length), the number of epizoic *D. polymorpha*) per mussel was recorded, and the mussels were returned to the sediment. All mussels found in the upper sediment layer (0–5-cm depth) were defined as epibenthic (surface-dwelling) mussels.

Laboratory experiments

Unio tumidus and *D. polymorpha* were collected in the littoral zone of Lake Dämeritz (lat 52°25′14″N, long 13°43′53″E), which is part of the River Spree. All individuals were transported to the laboratory within 1 h of collection in cooled plastic boxes filled with water and were placed in aerated aquaria or plastic tanks with a sediment layer that allowed mussels to burrow. Experiments were carried out within 1 wk after collecting the mussels. Mussels were fed once a day with dried and ground nettles (Neudorff Ltd., Emmerthal, Germany), which is easily accepted by unionid mussels as food and is commercially available with a constant composition.

Experiment 1 was designed to investigate the influence of mussel size (shell length = body length) on burrowing depth. Twenty large (>6 cm) and 20 small (<5 cm) *U. tumidus* were distributed evenly in a plastic tank (180 L) with their anterior ends placed gently in a 10-cm layer of sandy sediment. The posterior ends of large individuals were marked to permit differentiation from small individuals when they were partially burrowed. The tank was aerated continuously and kept outdoors (temperature 10–20°C). The burrowing depth of all mussels was recorded as the proportion (0–25, 25–75, 75–100, or >100%) of the valve length buried after 24 and 48 h. Differences in the burrowing depth of the 2 groups were examined using a χ^2 test.

Experiment 2 was designed to investigate the influence of *D. polymorpha* infestation on burrowing depth of unionids. Forty *U. tumidus* (6.9 ± 0.6 cm) were distributed among 6 aquaria. Twenty mussels were labeled individually, and *D. polymorpha* were allowed to attach to their valves over a period of 24 to 48 h (cf. Haag et al. 1993), resulting in a mean infestation density of 16 ± 7 (mean ± SD) *D. polymorpha* ind./*U. tumidus* ind. This infestation density was much higher than the mean infestation density found in the field (1 ± 2 *D. polymorpha* ind./*U.*

tumidus ind.; $n = 1803$). All mussels were put in a plastic tank (180 L) as described above. The burrowing depth of all mussels was recorded after 24 and 96 h.

Statistical analyses

χ^2 tests were used to compare differences in the number of mussels at different burrowing depths (experiments 1 and 2) and to compare the number of individuals that moved toward vs away from the shore (River Spree). For all other analyses, the Kolmogorov–Smirnov and Shapiro–Wilk test for smaller sample sizes ($n < 20$) were used to determine whether the data were normally distributed. If data were not normally distributed, nonparametric tests were used (e.g., Spearman rank correlation instead of Pearson correlation). The horizontal distances moved were compared among species with a Kruskal–Wallis test. A Wilcoxon test was used to compare infestation densities of *D. polymorpha* between adjacent depth layers because the data were not independent. Mann–Whitney tests were used to determine whether 1) the percentage of mussels on the sediment surface differed between early and late summer, and 2) the lengths of burrowed mussels differed between the 0–5-cm sediment layer and deeper layers. Stepwise multiple linear regression analysis was used to examine the relationship between surface densities of mussels and water temperature, day length, discharge, and water level.

Results

Horizontal movements

Densities of unionid mussels in areas A and B ranged from 22 to 289 ind./m^2. In area B, *U. tumidus* had the highest mean density (156 ± 79 ind./m^2, mean ± SD), and densities of *Unio pictorum* (Linnaeus) and *Anodonta anatina* (Linnaeus) were lower (18 ± 9 and 11 ± 6 ind./m^2, respectively).

A total of 759 mussels was labeled. Of these labeled mussels, 544 (72%; *U. tumidus*: $n = 428$, *U. pictorum*: $n = 26$, *A. anatina*: $n = 90$) were encountered at least twice, i.e., recaptured at least once (Table 1), so that the distance they had moved could be calculated. Fourteen labeled mussels were later found dead, but only 4 of those had not been recaptured alive at least once. Mussel movement rate varied between 0 and 226 cm/wk and averaged 11 ± 15 cm/wk ($n = 544$). Approximately 90% of the mussels moved between 0 and 25 cm/wk, and some individuals (19%) always were found in the same 25 × 25-cm subquadrat. No significant differences in the distances moved were found among species (Kruskal–Wallis-test, $H = 4.3$, $p > 0.05$, df $= 2$), size classes ($H = 5.0$, $p > 0.05$, df $= 4$), or months ($H = 1.9$, $p > 0.05$, df $= 4$) because of high variability among individuals. However, mean distance moved increased slightly (from 8 cm to 11 cm/wk or 1.5–2 body lengths) between May and October. Mean movement rate was significantly related to temperature and increased by 0.5 ± 0.07 cm/°C ($R^2 = 0.95$, $p < 0.01$; Fig. 1).

The direction of the horizontal movements of mussels seemed erratic. Mussels frequently turned back in the direction from which they came and crossed subquadrats twice (Fig. 2). However, mean displacement was 17 cm shoreward over the entire study period, and significantly more mussels moved toward the shore than away from the shore ($\chi^2_1 = 38$, $p < 0.01$, $n = 333$). No significant upstream or downstream movement was detected.

Labeled mussels were found as far as 2 m outside the boundary of area A and were found burrowed in the sediment within the study area (based on 1 subquadrat sampled) on 21 August. On average, 40 ± 13% of the mussels found on the surface on one sampling date appeared on the surface within the study area on the subsequent sampling date. Given that 90% of the mussels moved <25 cm/wk, it is likely that ~½ of the mussels burrowed every week. In many cases, mussels disappeared for several weeks (3 ± 2 wk, $n = 35$).

Vertical movements and environmental factors

Mean unionid density on the sediment surface of area A was 17 ± 8 (range = 4–27 ind./m^2; Fig. 3A), whereas the estimated percentage of burrowed mussels was 43 ± 26% (range = 20–92%; Fig. 3B). The highest surface densities (>20 ind./m^2) were found between early June and mid-August, but these peaks were interrupted by a sharp decline between 10 July and 17 July, when surface density decreased from 24 to 11 ind./m^2 (Fig. 3A). The lowest surface densities were found in early May and from the end of August to early October (the end of the study period). Many marked mussels (396/759 marked individuals) were found burrowed in the sediment in early October (Fig. 3B).

Discharge varied considerably during the study period (range = 2.5–13.9 m^3/s). The greatest flows occurred in May and September (Fig. 3C). Water temperature increased from 15 to 23°C between May and August and decreased again to a low of 13°C in October (Fig. 3D). The sudden decrease in mussel surface density in July (Fig. 3A) was paralleled by an increase in river discharge (from 5.2 to 9.1 m^3/s; Fig. 3C), and by a slight decreases in water temperature (from 19.7 to 18.8°C; Fig. 3D) and day length (from 16.5

TABLE 1. The number of newly marked and recaptured individuals in area A of the River Spree in 2004, and the frequency of subsequent recaptures for individuals marked on a sampling date.

	No. of individuals		No. of times a mussel was recaptured														
Date	Recaptured	Newly marked	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14
8 May	0	63	0	5	3	8	12	3	8	10	5	3	3	0	0	2	1
22 May	26	79	11	6	5	9	13	5	12	9	2	4	1	1	0	1	
29 May	72	93	13	11	16	18	12	7	8	4	1	2	1				
5 June	109	87	16	21	16	14	8	4	3	5							
12 June	124	68	8	13	13	8	9	5	9	1	1	0	1				
19 June	136	57	9	12	13	9	6	6	1	1							
26 June	176	64	27	18	4	8	1	3	3								
3 July	192	40	10	11	8	7	3	0	1								
10 July	179	39	15	11	4	4	3	1	1								
17 July	76	20	13	4	2	1	0	0									
24 July	122	30	12	9	6	2	0	1									
7 August	186	39	25	11	2	0	1										
14 August	189	40	25	10	4	1											
21 August	157	21	17	3	1												
28 August	64	9	7	2													
4 September	31	6	3	3													
2 October	31	4[a]															
Total		759[a]	211	150	97	89	68	35	46	30	9	9	6	1	0	3	1

[a] Does not include 177 burrowed individuals

to 16.2 h; Fig. 3E). A stepwise multiple linear regression (corrected $R^2 = 0.74$, $p < 0.001$) showed that the dynamics in surface densities of mussels during the study period could be largely explained by discharge (b [slope] $= -1.6 \pm 0.5$ [SE], $p < 0.01$), day length ($b = 2.4 \pm 0.01$, $p < 0.01$), and water temperature ($b = 1.0 \pm 0$, $p < 0.05$) (compare Fig. 3A with Figs 3C–E). Note that regression results are valid only within the ranges of water temperature (13.5–23.2°C) and day length (12.0–16.8 h) observed during the study period. Discharge alone explained 53% of the variation in mussel density ($R^2 = 0.53$, $p < 0.01$; Fig. 4), but water level was rejected as an additional predictor because it was correlated with discharge (Spearman $r = 0.63$, $p < 0.01$; Figs 3C, F).

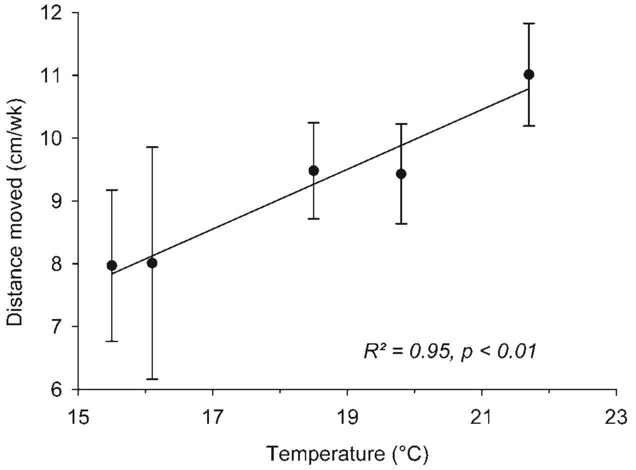


FIG. 1. Linear regression for mean (±1 SE) distance moved/mo as a function of mean monthly temperature. $n = 96$ (May), 539 (June), 555 (July), 590 (August), and 62 (September and October).

Vertical distribution in the sediment

River Spree.—A total of 1803 individuals (1516 *U. tumidus*, 182 *U. pictorum*, 105 *A. anatina*) was found in area B, and 74 ± 7% (range = 61–84% in individual 1-m^2 plots) of the mussels were found completely burrowed. Individuals of all 3 species were found as far as 20 cm below the sediment surface. Most mussels (70 ± 16%) were found within the first 10 cm below the sediment surface. Nearly ½ of the mussels (45 ± 18%; $n = 7$ quadrats) were in the 5–10-cm depth layer, whereas 25 ± 7% were in the 0–5-cm depth layer, 17 ± 8% were in the 10–15-cm depth layer, and 13 ± 12% were in the 15–20-cm depth layer.

The percentage of burrowed *U. tumidus* individuals varied seasonally. In area A, surface densities were highest from June to mid-August (mean = 22 ind./m^2) and lower in May (12 ind./m^2) and from late August to October (9 ind./m^2). In area B, significantly higher percentages were observed on the sediment surface from June to early August (30 ± 8%) than from late August to early September (16 ± 3%) (Mann–Whitney test for small sample size, $U = 6$, $p < 0.05$, $n = 10$).

Vertical distribution varied with size class (Fig. 5). On average, mussels of all species in the 0–5-cm

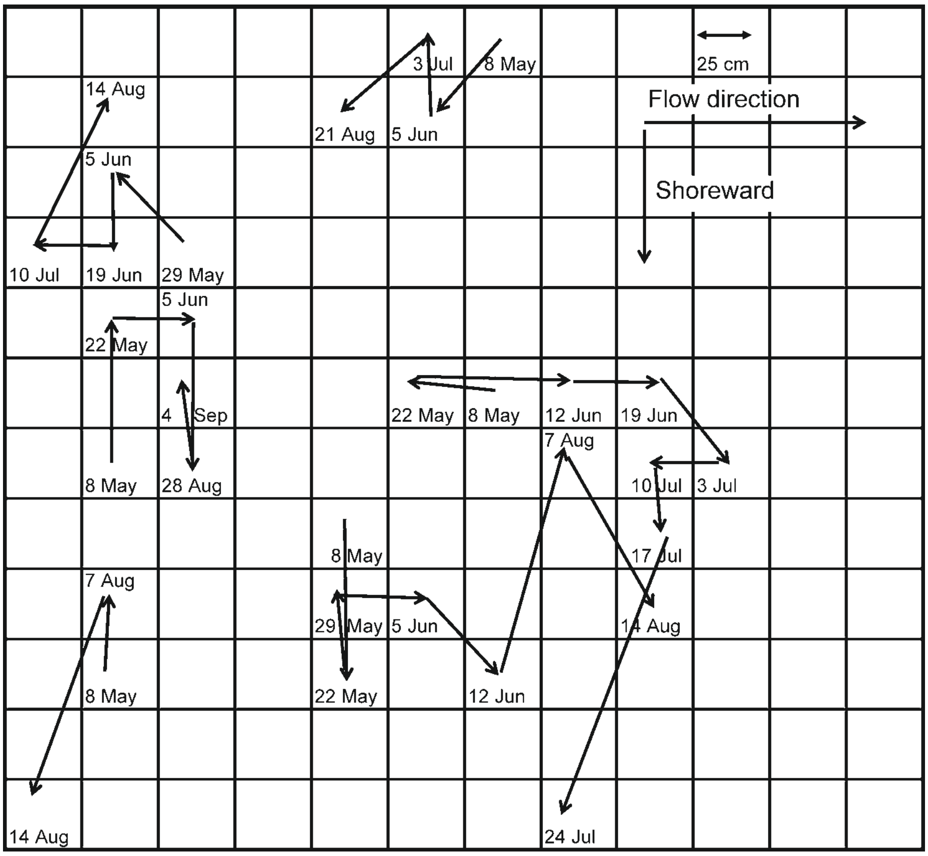


FIG. 2. Examples of movement patterns of 6 individuals (*Unio* sp. and *Anodonta anatina*) during the study period. Changes in positions are shown with the respective recording dates.

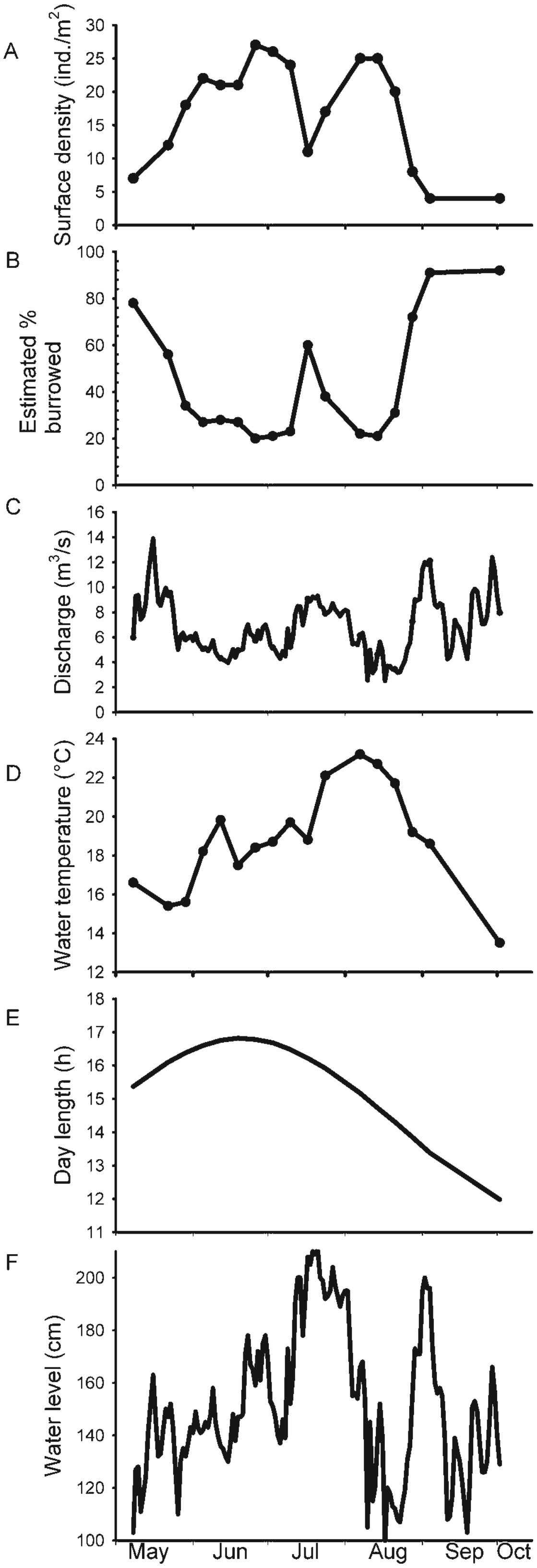
sediment layer were ~1 cm larger than mussels in the deeper sediment layers (Mann–Whitney test, $z = 13.6$, $p < 0.01$, $n = 1459$). The percentage of all individuals in the >5-cm size class that was in the 0–5-cm depth layer (38 ± 6%) was significantly larger than the percentages of all individuals in the <3-cm and 3–5-cm size classes that were in the 0–5-cm depth layer (Wilcoxon test, $z = 2.2$ and 2.4, $p < 0.05$, $n = 7$). No significant differences in the vertical distributions of individuals within size classes were found in the 5–20-cm depth layers (Fig. 5).

Experiment 1.—Burrowing depth differed between mussels in small and large size classes. Large mussels (>6 cm) burrowed deeper than small (<5 cm) mussels. All mussels burrowed ≥25% of their valve length after 48 h. Eight large and 0 small mussels burrowed 25–75% of their valve length, 9 large and 8 small individuals burrowed 75–100% of their valve length, and 3 large and 12 small individuals burrowed >100% of their valve length in the sediment. The differences in burrowing depths were significant (after 24 h: $\chi^2_2 = 8.8$, $p = 0.01$; after 48 h: $\chi^2_2 = 13.5$, $p < 0.01$; $n = 40$). Significantly more small than large mussels were completely burrowed (χ^2 test with continuity correction; after 24 h: $\chi^2_1 = 6.4$, $p = 0.01$; after 48 h: $\chi^2_1 = 6.8$, $p < 0.01$; $n = 40$).

Dreissena polymorpha infestation density

River Spree.—*Dreissena polymorpha* infestation density was generally low (*U. tumidus*: mean = 1 ± 2 *D. polymorpha* ind./unionid ind., range = 0–15, $n = 1514$; *U. pictorum*: mean = 1 ± 1, range = 0–6, $n = 182$; *A. anatina*: mean = 2 ± 4, range = 0–26, $n = 105$). Fifty to 66% of the individuals of all 3 species were not infested by zebra mussels. Infestation density tended to be lower on mussels in the 5–20-cm depth layers than on mussels in the 0–5-cm depth layer. Infestation density on *U. tumidus* individuals in the 3.0–4.9-cm and 5.0–6.9-cm size classes was significantly greater in the 0–5-cm depth layer than in the 5–20-cm depth layers (Wilcoxon test, $z = 2.4$ and 2.0, $p < 0.05$, $n = 7$; Fig. 6).

Experiment 2.—Burrowing depth did not differ between mussels with or without epizoic *D. polymorpha* after 24 h and 96 h (χ^2 test with continuity correction, $\chi^2_1 = 1.8$, $p = 0.2$, $n = 40$). However, fewer



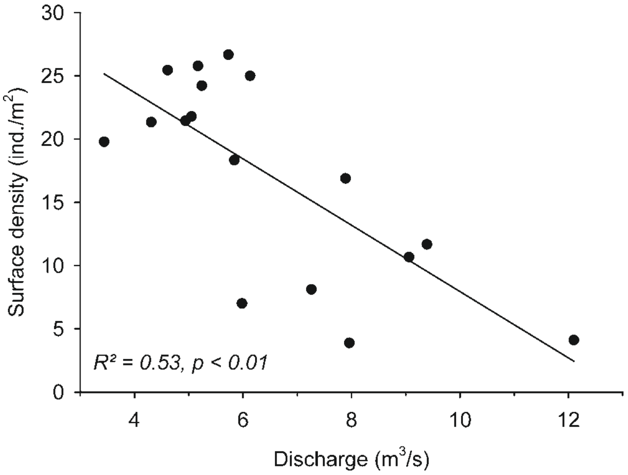


Fig. 4. Linear regression for surface density of unionid mussels and discharge ($y = -2.6x + 34$).

mussels with than without epizoic *D. polymorpha* (4 vs 9 ind.) were completely burrowed after 24 and 96 h. Infestation density was negatively correlated with burrowing depth (Spearman $r = 0.85$, $p < 0.01$), i.e., the lower the infestation density, the deeper unionid mussels were burrowed. Mean infestation density decreased from 16 ± 7 *D. polymorpha* ind./*U. tumidus* ind. at the beginning of the experiment to 9 ± 6 *D. polymorpha* ind./*U. tumidus* ind. at the end of the experiment.

Discussion

Vertical distribution and vertical movements

All mussels found in the 0–5-cm depth layer were defined as epibenthic, but juvenile mussels in this layer probably were burrowed rather than on the sediment surface. Juvenile unionid mussels remain burrowed in the sediment for the first 2 to 4 y of life (e.g., Hochwald and Bauer 1990). Adult mussels also burrow in the sediment (e.g., Amyot and Downing 1991). In particular, high percentages of burrowed adult mussels typically are found during winter months (Amyot and Downing 1991, Balfour and Smock 1995). The estimated percentage of burrowed mussels (juveniles and adults) in area A in the River Spree in the summer was

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Fig. 3. Density of unionid mussels on the sediment surface of area A (A), estimated percentage of burrowed mussels (B), discharge (C), water temperature (D), day length (E), and water level (F) during the study period. The percentage of burrowed mussels was estimated based on surface density and the total number of mussels in area A at the end of the study period.

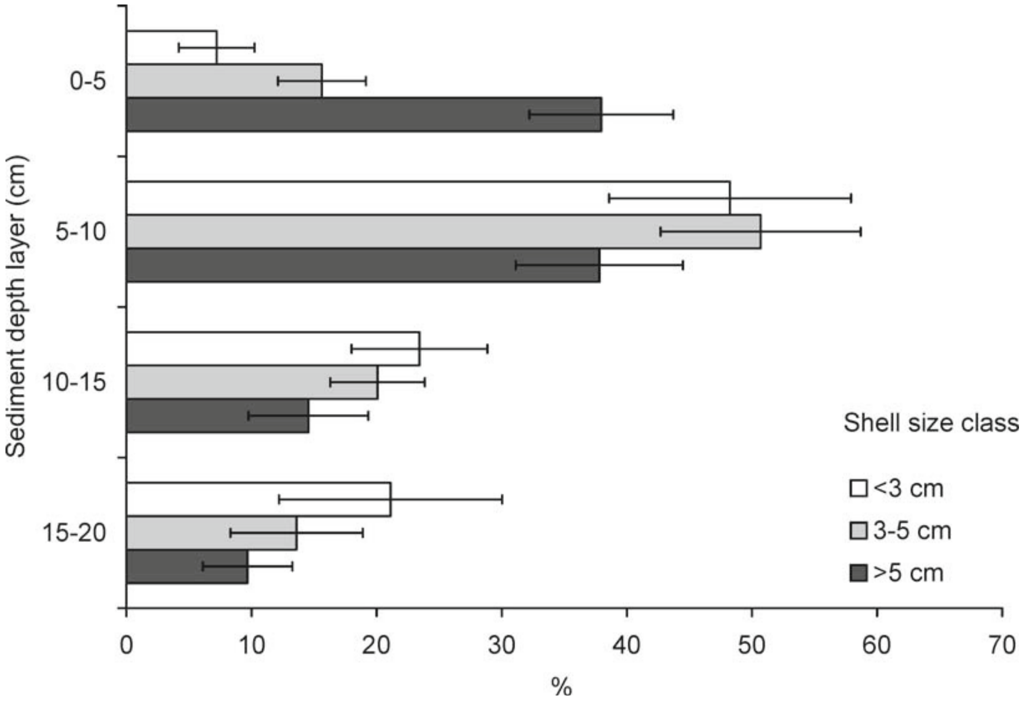

FIG. 5. Vertical distribution of *Unio tumidus* in several shell-length categories. Columns represent the mean (±1 SE, $n = 7$ quadrats) percentages of each size category (relative to the total number of individuals in the size category) found in each sediment depth layer.

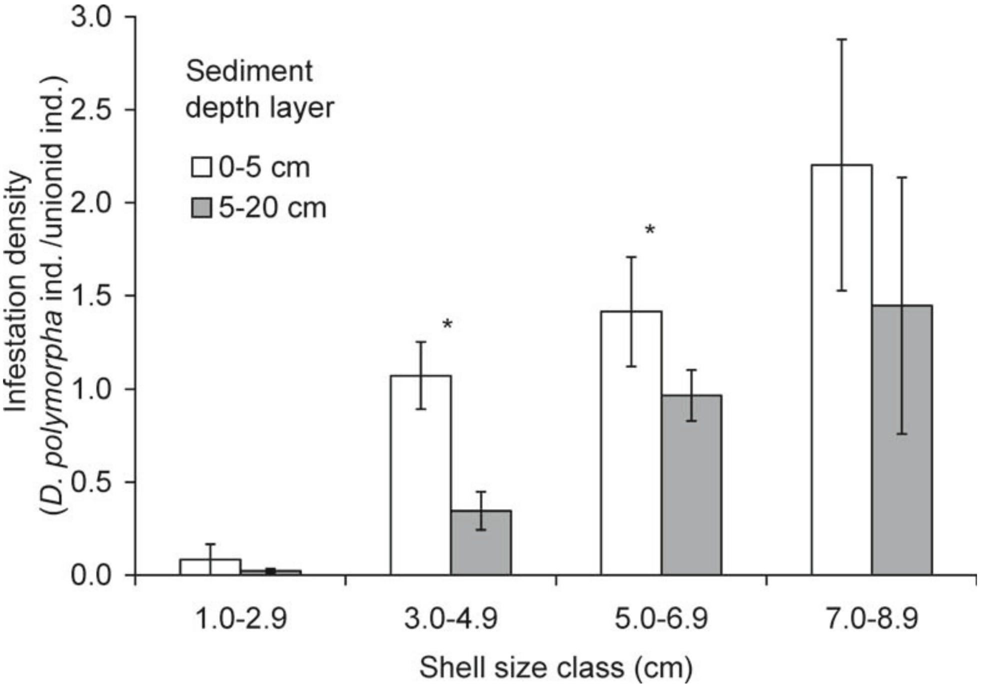

FIG. 6. Mean (±1 SE, $n = 7$) number of epizootic *Dreissena polymorpha/Unio tumidus* individual in shell-size categories in 2 sediment depth layers in the River Spree. * = significant differences between sediment depths (Wilcoxon test, $p < 0.05$, $n = 7$).

43 ± 26%, and the percentage of burrowed mussels found in area B was 74% ± 7%. The percentage of burrowed mussels in area B was surprisingly high, but agrees with earlier estimates of ~80% from a different section of the River Spree during the summer (Pusch et al. 2002). Thus, a major part of the unionid population was not visible at the sediment surface, and this result should be considered when planning or implementing conservation strategies (i.e., relocation efforts). Specifically, surveys may strongly underestimate actual population sizes and, thus, may fail to protect endangered or threatened species (cf. Smith et al. 2001).

No mussels were found >20 cm below the sediment surface. A hard layer of Fe(III)-hydroxide/oxyhydrate found in one 1-m^2 plot at ~10 cm sediment depth might have prevented mussels from burrowing deeper. However, the lower limit of the mussels' vertical distribution is probably a consequence of low dissolved O_2 (DO) concentration in deeper sediment layers. *Unio crassus* was found as much as 30 to 35 cm below the sediment surface in sediments with relatively high DO concentration (21–25% saturation 30 cm below the sediment surface) in 2 streams in northern Germany (Engel 1990). However, in the Müggelspree, DO decreases to ~30% saturation 7 cm below the sediment surface (Gücker and Fischer 2003) and to 7% saturation 20 to 30 cm below the sediment surface even in mid-channel sediments (ANS, personal observation). The low DO concentration at greater sediment depth in the Müggelspree may also explain the significantly lower infestation density on *U. tumidus* (of sizes 3.0–6.9 cm) in deeper (5–20 cm) sediment layers than in the upper sediment layer (0–5 cm). *Dreissena polymorpha* has poor tolerance for low DO concentrations (Nichols and Wilcox 1997). Other explanations for the lower infestation density of *D. polymorpha* on unionids that are deeper in the sediments are possible (Nichols and Wilcox 1997, Karatayev et al. 1997), but it seems clear that *D. polymorpha* does not strongly affect the unionid population (including their burrowing activity) in the River Spree.

The vertical distribution of unionid mussels differed with mussel size. Significantly more large (>5 cm) than small (<5 cm) individuals were found in the upper sediment layer (0–5-cm depth) in the river, and this pattern was reflected in the higher burrowing activity of small than large mussels in experiment 2. The laboratory results suggest that the differences in the vertical distribution between small and large mussels observed in the field were the result of variations in behavior rather than of passive burial by shifting sediments. The differences in vertical distribution between size classes also may reflect differences between the juvenile stage, which is characterized by permanent burial in sediment, and the adult stage, which is characterized by alternating periods of burrowing and surfacing related to reproduction.

The large number of mussels found in the sediment in early October in area A indicates that, at least at that time, most mussels that were not visible on the sediment surface had burrowed in the sediment rather than moved outside of the study area. This result is in agreement with other studies that have shown that unionid mussels emerge at the sediment surface in spring and burrow again before winter, with the specific timing influenced by local climate conditions (Amyot and Downing 1991, 1997, Balfour and Smock 1995). Vertical movements in the River Spree, as indicated by changes in mussel density on the sediment surface, were influenced by discharge, day length, and water temperature, which together explained 74% of the variation in mussel density. In other studies, water temperature (Amyot and Downing 1997), day length (Perles et al. 2003), or an inseparable combination of these 2 variables (Watters et al. 2001) were listed as the primary factor determining burrowing. Hence, the proximal control of vertical migration is not fully understood.

In the River Spree, water temperature per se was not a proximal factor controlling mussel behavior. However, changes in water temperature appeared to be important because the highest (early June) and the lowest (early September) surface densities of unionids were observed at similar water temperatures (18.2°C and 18.6°C, respectively). In contrast, discharge appeared to be the most important factor affecting burrowing activity. The sudden decrease in surface density associated with high discharge in July is not likely to be explained by any other variable considered in our study. Our observations support the hypothesis that mussels may circumvent dislodgement during extreme flows by burrowing deeper into the sediment (Di Maio and Corkum 1995), and our results suggest that flow velocity may be the dominant factor driving vertical movements of riverine unionid populations.

Horizontal movements

Horizontal movements were detected only if mussels moved from one subquadrat (25 × 25 cm) to another and, therefore, distance moved was underestimated by the spatial resolution of our observational method. The longest distance moved by a unionid mussel in our study was 226 cm/wk. Thus, unionid mussels are capable of moving long distances (i.e., ~40 body lengths) in a relatively short time, a result that agrees with the presence of long tracks that have been observed in the sandy sediment of the River Spree, especially during low water levels in summer (ANS, personal observation). Long tracks also have been observed in several lakes (maximum mean length of crawling tracks = 1.9 ± 2 m; Saarinen and Taskinen 2003). Nevertheless, the mean distance moved within the River Spree population was only 11 cm/wk, and many mussels did not move at all. We are not aware of any comparable data for river-dwelling mussels. However, *Elliptio complanata* moved ~5.6 cm/wk in a 1st-order stream (Balfour and Smock 1995) and 4.2 cm/wk in an oligotrophic lake (Amyot and Downing 1997), whereas *Anodonta* sp. moved between 15 and 45 cm/wk in Lake Zürich (Burla 1971; Table 2). Thus, the horizontal distances moved in the River Spree deviate little from the distances reported for different unionid species in other aquatic systems. However, there are evident differences in the horizontal movement distances among genera, especially when normalized by body length (Table 2). Collectively, these results indicate that unionids can move considerable distances (e.g., 2 body lengths/wk; our study) during the summer months. Little to no movement has been reported in winter (Burla 1971).

The unionid population in the River Spree showed a slight net shoreward movement. The shoreward movement does not appear to have been part of a seasonal horizontal migration, as has been found in other studies (Burla 1971, Engel 1990), because a change in the net direction of the mussels' movements was not noted until the end of the study period. The shoreward movement might have been related to a change in water level. At the beginning of the study (early May), the water level was extremely low. The mussels might have moved toward deeper mid-river areas and returned to the abandoned shallower areas as the water level rose until mid-July. Similar behavior has been observed in *Anodonta grandis* and other species, which migrate on the shore in response to seasonal changes in the water level to avoid prolonged emersion (Mentzen 1926, White [1979] as cited in McMahon 1991).

Mussels moved throughout our study, including during times without major changes in water levels. Such horizontal movements might be related to feeding, e.g., mussels might move to gain greater access to benthic food and to areas that have not been depleted of food. The movement itself could be part of the feeding mechanism (McMahon 1991), e.g., food could be ingested through a focused water current into the anterior portion of unionids, as suggested by Nichols et al. (2005). If a form of pedal feeding occurs

TABLE 2. Compilation of published data on the horizontal movement rates of unionid mussels. BL = body length.

Species	Location	Sampling interval	Mean distance moved (cm/wk)	Mean distance moved (BL/wk)[a]	Study area	Spatial resolution	No. of individuals	Study
Elliptio complanata	1st-order stream; Virginia, USA	1 mo	5.6[b]	0.4	76 1-m² plots	0.01 m²	84	Balfour and Smock 1995
E. complanata	Oligotrophic lake; Quebec, Canada	1–2 wk	4.2	0.3	40 m²	Exact position	527	Amyot and Downing 1997
Unio pictorum	Lowland river; River Spree, Germany	1–2 wk	13	1.4	9 m²	0.0625 m²	26	This study
Unio tumidus	Lowland river; River Spree, Germany	1–2 wk	10	1.3	9 m²	0.0625 m²	428	This study
Anodonta sp.	Mesotrophic lake; Lake Zürich, Switzerland	1 mo	~15–45[c]	1.0–3.1[d]	100 m²	0.25 m²	89[e]	Burla 1971, Burla et al. 1974
Anodonta anatina	Lowland river; River Spree, Germany	1–2 wk	15	1.6	9 m²	0.0625 m²	90	This study

[a] Maximum body length found in literature was used because mean body lengths were not available for all studies

[b] Calculated from mean distance moved/y

[c] Estimated from fig. 9 in Burla (1971)

[d] Calculated based on mean maximum body length of *A. anatina* and *Anodonta cygnea*

[e] 55 of 144 individuals died during the study

in unionids in the River Spree, this mechanism could explain the highly erratic horizontal movements we observed. It might also explain how the unionids were able to meet their nutritional needs even at very low seston concentrations (Pusch et al. 2002).

Biological consequences of movement behaviors

The percentage of the population on the sediment surface increased and, therefore, the surface density of *U. tumidus* population increased during the reproductive period (June to mid-August). Aggregation, which can be caused by mussels moving closer together, can increase reproductive success (Burla et al. 1974, Amyot and Downing 1997). Similar changes in vertical distribution have been observed for unionids in other lotic and lentic systems (Balfour and Smock 1995, Watters et al. 2001).

Unionids in the River Spree burrowed and reemerged several times during their surface stay in summer. In contrast, *Lampsilis siliquoidea* individuals did not return to the surface in the same year once they were completely burrowed in the sediment (Perles et al. 2003). The pattern of burrowing and return to the surface observed in the River Spree might indicate that separate surface stays are used for egg fertilization and glochidia release, or that multiple clutches of glochidia are produced, as was observed for *U. crassus* (Hochwald and Bauer 1990). Stream conditions might help to disperse sperm, so that the need for aggregation is lower in lotic systems than in lentic systems. During their reproductive period, *U. crassus* individuals were more frequently found in the middle of the stream, where higher flow velocities might have increased fertilization efficiency, than near the banks of the stream (Engel 1990).

Living burrowed within the sediment for long periods may reduce unionids' risks of adverse biological interactions. For example, unionids are preyed on by muskrat, mink, and otter, and empty shells of unionids can be occasionally observed at predator feeding sites (Diggins and Stewart 2000). In addition, *D. polymorpha* cannot colonize unionid shells when the unionids are burrowed, and experiment 2 showed that burrowing reduces the number of epizoic *D. polymorpha* on unionid individuals already infested. However, living burrowed for long periods during summer prevents intake of food resources that are suspended in the water column (Pusch et al. 2001).

In conclusion, we propose that movement behavior is an important adaptation of unionid mussel populations to the flow conditions in rivers. Movement enables unionids to react to the regular disturbances that occur as a result of changing flow conditions and water levels, and movement may help unionids to escape predators and control *D. polymorpha* infestation. Moreover, conditions in the sediment are as important as water quality for the biology and conservation of these organisms because unionids spend most of their lives in the sediment.

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Human lakeshore development alters the structure and trophic basis of littoral food webs

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Summary

1. Shoreline development and the associated loss of littoral habitats represent a pervasive alteration of the ecological integrity of lakes and have been identified as major drivers for the loss of littoral biodiversity world-wide. Little is known about the effects of shoreline development on the structure of, and energy transfer in, littoral food webs, even though this information is urgently needed for management and mitigation measures.
2. We measured macroinvertebrate biomass and analysed potential food resources using stable isotopes (δ^{13}C, δ^{15}N) and mixing models to compare the complexity and the trophic base of littoral food webs between undeveloped and developed shorelines in three North German lowland lakes.
3. The lower diversity of littoral habitats found at developed shorelines was associated with lower diversity of food resources and consumers. Consequently, the number of trophic links in food webs at developed shorelines was up to one order of magnitude lower as compared with undeveloped shorelines.
4. Mixing model analysis showed that consumer biomass at undeveloped shorelines was mainly derived from fine particulate organic matter (FPOM) and coarse particulate organic matter of terrestrial origin (CPOM). The contribution of CPOM to consumer biomass was twofold lower at developed shorelines, and consumer biomass was mainly derived from FPOM and suspended particulate organic matter.
5. *Synthesis and application*. Shoreline development impacts the flow of organic matter within littoral food webs primarily through the reduction in littoral habitat diversity. These effects are exacerbated by clearcutting of the riparian vegetation, which disrupts cross-boundary couplings between the riparian and the littoral zone. Lakeshore conservation should focus on preserving the structural integrity of the littoral zone, while restoration of coarse woody debris, reed and root habitats can be a cost-efficient measure to improve degraded lakeshores. The local effects of shoreline development demonstrated in this study might lead to whole-lake effects, but future studies are needed to derive thresholds at which shoreline development has consequences for the structure and functioning of the entire ecosystem.

Key-words: aquatic-terrestrial coupling, coarse woody debris, habitat loss, macroinvertebrates, retaining walls, riparian clearcutting, SIAR

Introduction

Human modifications of lakeshores and changes in riparian land use constitute an increasing threat to the ecological integrity of lakes world-wide (Schnaiberg *et al.* 2002; Carpenter *et al.* 2007). For example, housing density around lakes in Wisconsin (USA) has increased more than fivefold over the last 60 years (Gonzales-Abraham *et al.* 2007). Similar trends are apparent in Central Europe, where housing density at Lake Constance (Germany) has more than doubled since 1960

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(Schmieder 2004). It is expected that human use of lakes and lakeshores will continue and will extend into areas that are currently unimpaired (Peterson *et al.* 2003).

Aside from inputs of nutrients, shoreline development affects the littoral zone mainly through the alteration and loss of littoral habitats. The organic matter content of littoral habitats can be substantially lower at developed than at undeveloped shorelines, and macrophytes are often absent at developed shorelines (Elias & Meyer 2003; Francis *et al.* 2007). Such effects on littoral habitat diversity are intensified by clear-cutting of the riparian vegetation, resulting in a reduction in habitat provided by coarse woody debris (CWD) (Christensen *et al.* 1996) and submerged tree roots (Brauns *et al.* 2007). Thereby, human impacts on the structure of the littoral zone can have considerable consequences for littoral biotic communities such as strong reductions in species richness and production of littoral fish communities (Jennings *et al.* 1999; Schindler, Geib & Williams 2000). Similarly, macroinvertebrate species richness decreases with increasing intensity of shoreline development, and macroinvertebrate community composition is altered at highly developed shorelines (Brauns *et al.* 2007; Rosenberger *et al.* 2008). Human disturbances that affect species diversity may have consequences that go beyond impacts on community structure because littoral species constitute a functionally important part of the lake food web. Hence, alterations of littoral biodiversity following habitat loss might disrupt species interactions, thereby altering food web structure.

The decline of habitat heterogeneity following shoreline development may also have impacts on the diversity and quantity of food resources for littoral food webs. For example, the loss of CWD and macrophytes may be associated with a reduction in surface areas for the growth of periphyton that contributes substantially to whole-lake primary production and constitutes an important food resource for littoral consumers (Vadeboncoeur, Vander Zanden & Lodge 2002). Moreover, the littoral is not only spatially but also energetically coupled to the riparian zone via terrestrial inputs of dissolved and particulate organic matter. As a consequence, terrestrial subsidies can contribute up to 70% to the biomass of littoral consumers (Cole *et al.* 2006; Solomon *et al.* 2008). However, the terrestrial–aquatic coupling depends on the integrity of the riparian vegetation and may be strongly disrupted by removal of the riparian vegetation, as is often found along developed shorelines (France, Culbert & Peters 1996). Overall, human shoreline development may have the potential to drastically alter the structure and trophic basis of littoral food webs but empirical evidence as to what extent shoreline development can have such functional consequences is largely lacking.

In this study, we used the stable isotope composition of consumers and potential food resources, mixing model analysis and estimates of macroinvertebrate biomass to quantify the effects of shoreline development on the structure and trophic basis of littoral food webs of three North German lowland lakes. Specifically, we tested the hypothesis that lower habitat diversity at developed shorelines is associated with lower species richness and thus food web complexity. Furthermore, we hypothesised that shoreline development alters the trophic basis of macroinvertebrate food webs by reducing the diversity of food resources.

Materials and methods

SAMPLING AND SAMPLE PREPARATION

The study was conducted at three North German lowland lakes that differ in trophic status and have widely differing proportions of developed shorelines (Table 1). Within each lake, we established a 100m long sampling site at an undeveloped shoreline, a retaining wall and a recreational beach, respectively. Sampling sites within each lake were located at a distance of *c.* 500 m from each other to ensure that effects of natural environmental variables (e.g. wind exposure) are comparable. Shoreline development at the studied lakes was associated with the absence of riparian vegetation at the retaining walls of Lake Grienericksee and Lake Unteruckersee. The remaining developed shorelines exhibited riparian vegetation less dense as compared with undeveloped shorelines.

In October 2005, macroinvertebrates were sampled from each habitat present at each shoreline type (water depth $< 1{\cdot}2$ m). At undeveloped shorelines, macroinvertebrates were sampled from CWD, reed, sand, stones and submerged tree roots, except for the undeveloped shoreline at Lake Langer See, which lacks a stone habitat. At retaining walls, macroinvertebrate were sampled from concrete walls, sand and stones. At beaches, macroinvertebrates were sampled from sand only, as no other habitats were present. The habitat-specific sampling is described elsewhere (Brauns *et al.* 2007). Briefly, we collected samples from CWD and stones by brushing off macroinvertebrates. Reed and roots were sampled with a hand net. Sand was sampled using a Surber sampler modified for lentic conditions (area 0·05 m^2, 250-μm mesh). Concrete walls were sampled by scraping a defined area using a special scrape net (250-μm mesh; Hydrobios, Kiel, Germany). The sampled area of each habitat was restricted to 0·2 m^2. The areal coverage of the sampled habitats was estimated using a tape measure.

In the laboratory, habitat-specific samples were processed by sorting, counting and identifying macroinvertebrates to the lowest

Table 1. Geographical location, surface area, total phosphorus concentration (TP, mean annual concentration in 2005), shoreline length (L_{shore}) and the percentage of undeveloped shorelines, retaining walls and recreational beaches on total shoreline length at the studied lakes

	Geographical location					Shoreline type (%)		
	Latitude	Longitude	Area (km^2)	TP (μg L^{-1})	L_{shore} (km)	Undeveloped	Retaining wall	Beach
Grienericksee	53°06′22″	12°53′12″	2·7	115	6·4	76	21	3
Langer See	52°24′32″	13°36′50″	2·5	161	18·3	35	61	4
Unteruckersee	53°16′41″	13°51′51″	10·4	30	16·7	91	8	1

feasible taxonomic level (see Table S1 in Supporting Information). Macroinvertebrates were then kept individually for 24 h in filtered lake water to allow for gut clearance. Molluscs were removed from their shells, and macroinvertebrates were dried at 60 °C until constant weight. Dry weight of each species was determined by weighing 5–100 individuals per habitat-specific sample to the nearest 0·01 mg. Individual weights were used to calculate species-specific biomass.

For stable isotope analysis, we sampled all potential food resources present at each shoreline type. Coarse particulate organic matter of terrestrial origin (CPOM), i.e. decaying leaves from riparian trees and herbaceous riparian vegetation, was collected by hand. Fine particulate organic matter (FPOM) from reed stands and sand was sampled using a sediment corer (Uwitec, Mondsee, Austria). The upper 1 cm of each core was extracted and stored separately in acid-washed boxes. CPOM and FPOM samples were examined under a microscope, and invertebrates were removed. Suspended particulate organic matter (SPOM) was sampled by filtering lake water through precombusted Whatman GF/F filters. Periphyton was brushed from CWD, concrete, reed, submerged roots and stones into lake water filtered through Whatman GF/F filters. In the laboratory, periphyton samples were processed by removing detritus and invertebrates under 20× magnification using forceps. We were unable to obtain sufficient amounts of periphyton from submerged roots; we therefore used stable isotope values of periphyton from CWD from the same sampling site assuming that signatures are comparable. After processing, resource samples were dried at 60 °C until constant weight was reached.

STABLE ISOTOPE ANALYSIS

To prepare samples for stable isotope analysis, macroinvertebrates and food resources were ground with mortar and pestle, and Crustacea were acid treated to remove inorganic carbon (Yamamuro & Kayanne 1995). Each macroinvertebrate sample for stable isotope analysis consisted of several individuals from the same habitat to obtain sufficient material for analysis. Samples from unionids corresponded to single individuals.

Two subsamples of each species (~500 μg) and food resource (2–21 mg) from each habitat were loaded into tin capsules. Carbon (C) and nitrogen (N) content and stable isotopes of C and N were analysed on a Carlo Erba NC2500 elemental analyser connected to a Finnigan MAT Delta Plus mass spectrometer at Cornell University's Stable Isotope Facility. Stable isotope data are expressed as the relative difference between ratios of samples and standards (PeeDee Belemnite for δ^{13}C, atmospheric N for δ^{15}N):

$$\delta R(‰) = [(R_{\mathrm{SAMPLE}}/R_{\mathrm{STANDARD}}) - 1] \times 10^3 \qquad \text{eqn 1}$$

where $R = {}^{13}\mathrm{C}/{}^{12}\mathrm{C}$ or ${}^{15}\mathrm{N}/{}^{14}\mathrm{N}$.

Analytical precision (SD from in-house standards) from multiple runs was 0·08‰ for δ^{13}C and 0·14‰ for δ^{15}N.

MIXING MODELS AND FOOD WEBS

The contribution of food resources to consumer diet was estimated using their δ^{13}C and δ^{15}N values and mixing model analysis. We analysed stable isotope data separately for each habitat, which allowed us to constrain the number of potential food resources to those that were accessible to a given species in its habitat (Table S1). The habitat-specific analysis did not allow the determination of the degree of distinctness of resource isotopic signatures within a habitat. However, we tested whether isotopic signatures of resources significantly differed across sites using *t*-tests and ANOVA followed by Scheffé's *post hoc* test (PASW version 17; SPSS Inc., Chicago, IL, USA). We assumed that if food resources were distinct at the site scale, they should be distinct at the habitat scale too. This assumption is corroborated by previous studies demonstrating that the spatial variability of isotopic signatures is smaller within than among sampling sites (Jennings *et al.* 1997; Syväranta, Hämäläinen & Jones 2006).

The contribution of food resources to consumer diet was determined using the SIAR software (Version 4.0.2). SIAR is based on a Bayesian approach that estimates probability distributions of resource contributions to a consumer diet by accounting for all uncertainties of the input data (Parnell *et al.* 2010). Because consumer data were unreplicated at the habitat scale, we used the SIAR function 'siarsolomcmcv4' that does not include a residual error term (Parnell *et al.* 2010) and is analogous to the mixing model proposed by Moore & Semmens (2008). We accounted for trophic fractionation using fractionation factors and uncertainties published in Post (2002), i.e. 0·4 ± 1·3‰ for δ^{13}C and 3·4 ± 1·0‰ for δ^{15}N. For running the mixing models, the appropriate number of iterations (up to 1×10^7) was chosen according to SIAR's convergence diagnostic. From the resulting up to 33 200 dietary proportions, we calculated the mean and variance.

SIAR was also used to estimate the contribution of resources to the biomass of secondary consumers. For that, we estimated consumer trophic position by relating their δ^{13}C and δ^{15}N values to a site-specific trophic baseline derived from stable isotope values of all non-predatory macroinvertebrates (Vander Zanden & Rasmussen 1999). We then used SIAR to estimate the contribution of potential macroinvertebrate prey to the biomass of secondary consumers. Based on estimated contributions of food resources to prey biomass, we used ratio calculation to estimate the resource contribution to secondary consumer biomass.

To compare resource contributions among shoreline types and lakes, we first calculated macroinvertebrate biomass of each site by weighting individual biomasses with the proportional coverage of each habitat. We then calculated the sum of the contributions of the individual resource items to weighted consumer biomass for the resource categories: CPOM, FPOM, periphyton, and SPOM. This calculation is subjected to error propagation as each dietary estimate has an individual uncertainty. Hence, we calculated a global standard deviation for each resource category contribution by summing the variances of the estimates for each resource item.

An initial inspection of the data revealed that contributions of SPOM to consumer biomass were more than threefold higher at Lake Langer See and more than twofold higher at Lake Unteruckersee than at Lake Grienericksee (data not shown). This was mainly because of the invasive mussel *Dreissena polymorpha* (Pallas) that contributed on average 42% to total biomass at the undeveloped shoreline of Lake Langer See and 8% at Lake Unteruckersee but was absent from Lake Grienericksee. Hence, we removed *D. polymorpha* from the food web analyses to allow for a better comparison among lakes.

Macroinvertebrate food webs were constructed for each shoreline type and lake based on information on the trophic position of consumers and the resource contribution to their biomass.

STATISTICAL ANALYSIS

Habitat diversity was calculated using the areal proportions of the habitats at each site and the Shannon–Weaver index. We used correlation analysis (Spearman's ρ, PASW version 17; SPSS Inc.) to test for relationships between habitat diversity and consumer biomass, number of trophic links, number of available food resources and number of consumers in the food webs.

We conducted an exploratory analysis on the effects of shoreline development on the whole-littoral scale. Therefore, we estimated whole-littoral macroinvertebrate biomass by calculating the weighted average biomass based on the proportion of undeveloped and developed shorelines (Table 1). We then calculated the difference of relative whole-littoral biomass to a whole-littoral biomass with no shoreline development to compare effects among lakes.

Results

ISOTOPE SIGNATURES

Stable isotope biplots revealed sufficient separation between most food resources to be included into mixing model analysis. CPOM resources were significantly different in δ^{13}C from FPOM (ANOVA, Scheffé's *post hoc* test, $P = 0{\cdot}030, n = 20$) and from periphyton (Scheffé's *post hoc* test, $P = 0{\cdot}029$, $n = 21$) but not from SPOM (Scheffé's *post hoc* test, $P = 0{\cdot}810$, $n = 11$). The δ^{15}N values of CPOM resources differed significantly from all other resources (ANOVA, Scheffé's *post hoc* test, $P = 0{\cdot}003$ at the lowest). FPOM from reed stands differed significantly in δ^{13}C from FPOM from sand (*t*-test, $t = 2{\cdot}52$, $P = 0{\cdot}046$, $n = 12$) but not in δ^{15}N (*t*-test, $t = 0{\cdot}02$, $P = 0{\cdot}988$, $n = 12$). FPOM signatures from reed and sand overlapped at the beach at Lake Unteruckersee (Fig. 1) and were pooled for mixing model analysis.

Carbon isotope values of periphyton from CWD and reed differed significantly from that of concrete and stones (*t*-test, $t = 2{\cdot}35$, $P = 0{\cdot}034$, $n = 11$) (Fig. 1). Stable isotope values of periphyton from CWD overlapped with those from reed at the undeveloped shoreline of Lake Grienericksee. However, our habitat-specific approach enabled a separate analysis for both resources because it is unlikely that consumers from CWD have fed on periphyton from reed.

FOOD WEB STRUCTURE

Weighted consumer biomass did not significantly decrease with decreasing habitat diversity (Fig. 2a). There was a signifi-

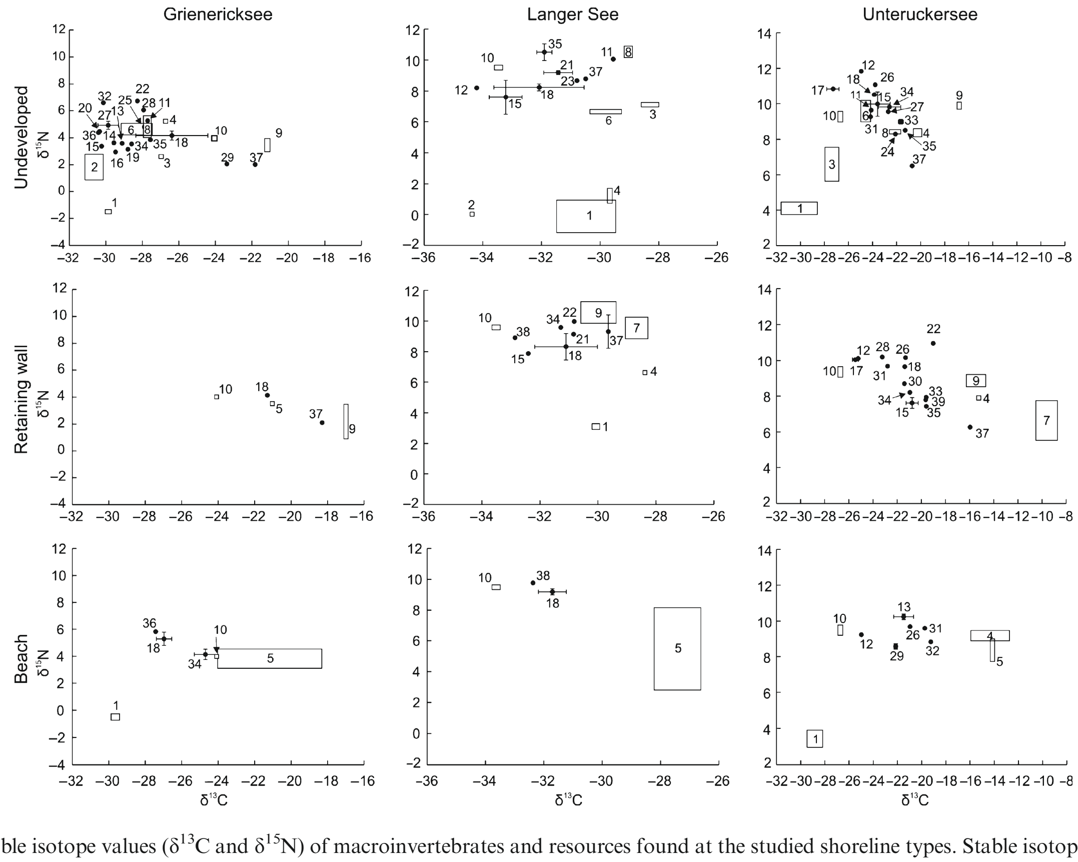

Fig. 1. Stable isotope values (δ^{13}C and δ^{15}N) of macroinvertebrates and resources found at the studied shoreline types. Stable isotope values of potential resources (mean) are shown as boxes delineated by ± 1 SD, and values of macroinvertebrates are given as mean (± 1 SD) if species occurred on more than one habitat. Resources (circles) are the following: Terrestrial coarse particulate organic matter from (1) alder leaves and (2) herbaceous riparian vegetation; fine particulate organic matter (3) in reed stands, (4) on sand, and (5) from submerged macrophytes; Periphyton on (6) coarse woody debris, (7) concrete, (8) reed and (9) stones; and (10) suspended particulate organic matter. Species are as follows: (11) *Acroloxus lacustris*, (12) *Anodonta cygnea*, (13) *Asellus aquaticus*, (14) *Bithynia leachi*, (15) *B. tentaculata*, (16) *Caenis* sp., (17) *Chelicorophium curvispinum*, (18) Chironominae, (19) *Cloeon dipterum*, (20) *Dikerogammarus haemobaphes*, (21) *D. villosus*, (22) *Erpobdella octoculata*, (23) *Gyraulus albus*, (24) *Haliplus* sp., (25) *Lype phaeopa*, (26) *Molanna angustata*, (27) *Mystacides niger/longicornis*, (28) Oligochaeta, (29) *Oulimnius* sp., (30) *Physa fontinalis*, (31) *Pisidium* sp., (32) *Platambus maculatus*, (33) *Pontogammarus robustoides*, (34) *Potamopyrgus antipodarum*, (35) *Radix balthica*, (36) *Sphaerium corneum*, (37) *Tinodes waeneri*, (38) *Unio tumidus* and (39) *Valvata piscinalis*.

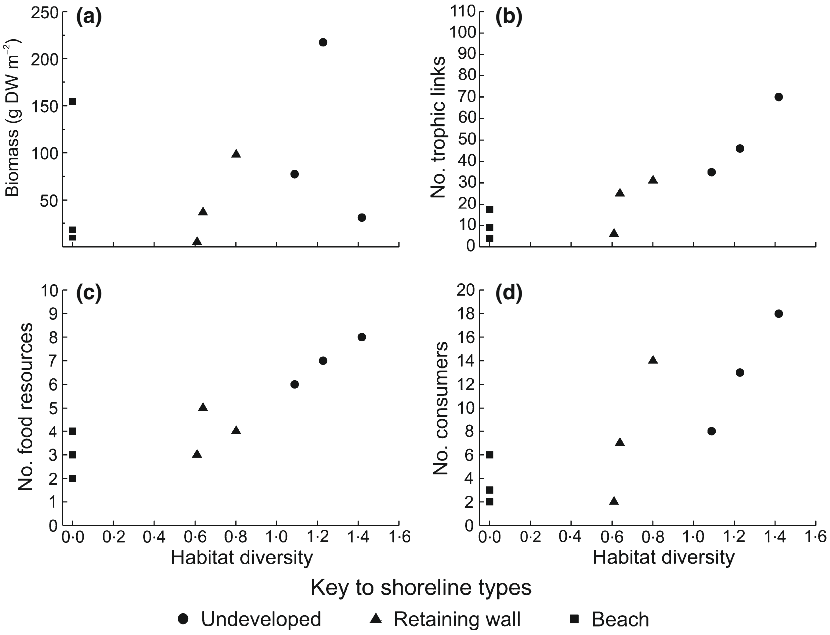

Fig. 2. Relationship between habitat diversity and (a) weighted macroinvertebrate consumer biomass (g DW m^{-2}), (b) number of trophic links, (c) number of available food resources and (d) number of consumers.

cant decrease in number of trophic links (Spearman's $\rho = 0{\cdot}92$, $P = 0{\cdot}001$, $n = 9$, Fig. 2b), number of available food resources (Spearman's $\rho = 0{\cdot}89$, $P = 0{\cdot}001$, $n = 9$, Fig. 2c) and macroinvertebrate consumer richness (Spearman's $\rho = 0{\cdot}85$, $P = 0{\cdot}004$, $n = 9$, Fig. 2d) with decreasing habitat diversity. Accordingly, the number of trophic links was highest at undeveloped shorelines (Fig. 2b) and on average twofold lower at retaining walls and fivefold lower at beaches. The substantial reduction in trophic complexity was particularly apparent at Lake Grienericksee, where the food web at the undeveloped shoreline had 70 trophic links and three trophic levels, while the food web at the retaining wall and beach had only six and nine trophic links, respectively (Fig. 3). These differences between developed and undeveloped shorelines were mostly the result of the absence of CWD, reed and roots from developed shorelines. At undeveloped shorelines, CWD, reed and roots together contributed on average 56% to total weighted biomass, 58% to macroinvertebrate consumer richness and 60% to total number of trophic links (Table 2).

The number of secondary consumers was highest at retaining walls, followed by undeveloped shorelines, whereas secondary consumers were absent at beaches (Fig. 3). Secondary consumers were represented by the leech *Erpobdella octoculata* (Linnaeus) that occurred at undeveloped shorelines and at retaining walls, and by the diving beetle *Platambus maculatus* (Linnaeus) that was restricted to the root habitat at the undeveloped shoreline of Lake Grienericksee (Fig. 3).

At the lake scale, shoreline development resulted in a clear decrease in whole-littoral macroinvertebrate biomass compared with a hypothetical whole-littoral biomass with no shoreline development. At Lakes Unteruckersee, Grienericksee and Langer See, where 9%, 24% and 65% of the shoreline have been developed, respectively, whole-littoral macroinvertebrate biomass was estimated to reach 95%, 80% and 64%, respectively, of the theoretical whole-lake biomass that would be expected without any shoreline development.

TROPHIC BASIS OF FOOD WEBS

Food webs at undeveloped shorelines were mainly based on FPOM and terrestrial CPOM, together contributing 74% to total weighted macroinvertebrate biomass (Fig. 4). Major differences in the trophic basis of food webs between developed and undeveloped shorelines were found in the contribution of CPOM, which was twofold lower at retaining walls and beaches than at undeveloped shorelines. At developed shorelines, food webs were mainly based on FPOM and SPOM that together contributed 80% to total weighted macroinvertebrate biomass (Fig. 4). Differences between retaining walls and beaches were marginal except for periphyton that did not contribute to biomass at beaches probably because of the lack of solid habitats suitable for periphyton growth (Fig. 4).

We found considerable variation in resource contributions with shoreline type and lake. At the undeveloped shoreline of Lake Grienericksee, the biomass of trophic level 2 and 3 was mainly derived from CPOM and FPOM (Table 3). At the retaining wall, trophic level 2 biomass was mainly derived from SPOM, to a lesser extent from FPOM, and CPOM was absent (Table 3).

At the undeveloped shoreline of Langer See, the food web was mainly based on terrestrial CPOM and to a lesser extent on SPOM and periphyton (Table 3). At the retaining wall, contributions of CPOM and SPOM were comparable to those at the undeveloped shoreline. At the beach food web, the

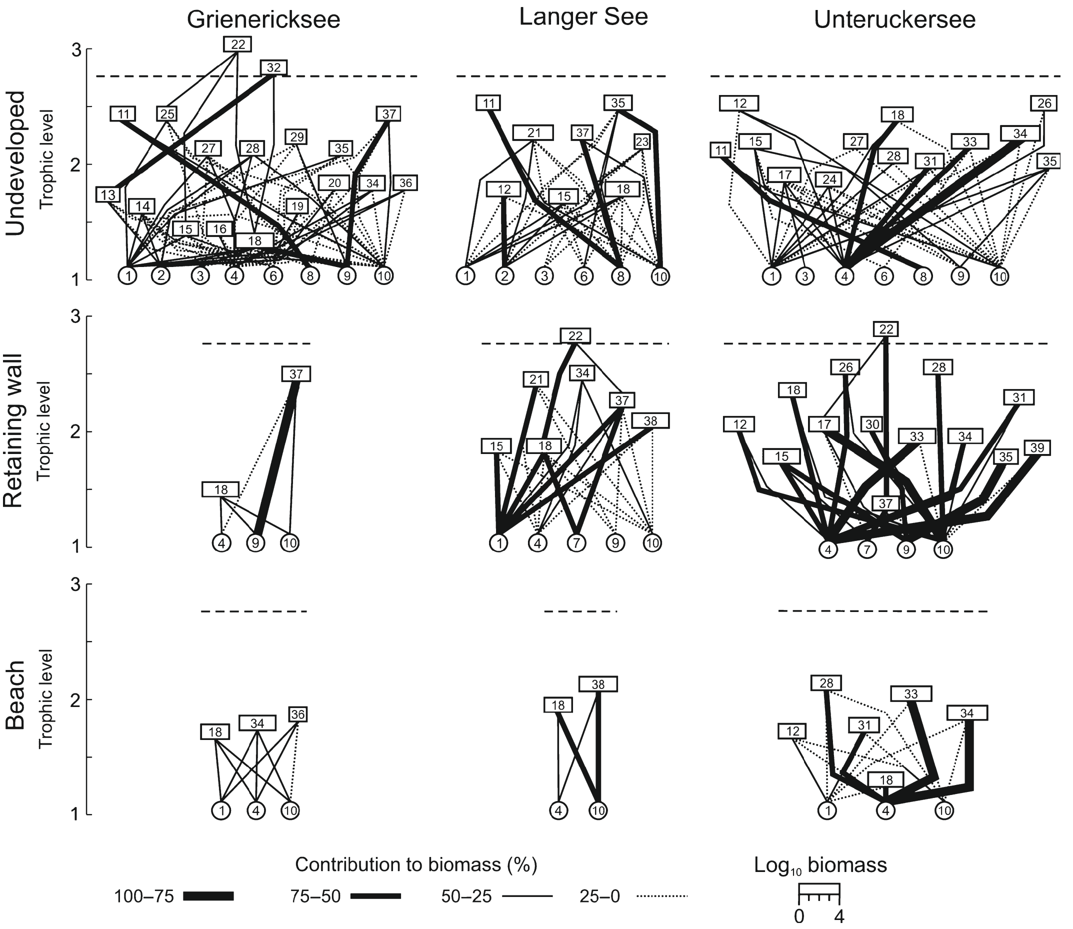

Fig. 3. Macroinvertebrate food webs of undeveloped and developed shorelines at the studied lakes. The width of consumer boxes is proportional to their weighted $\log_{10}$ biomass (mg DW m^{-2}). Trophic links are depicted by lines, whose thickness corresponds to the percentage contribution of resources to consumer biomass. If a species was recorded on more than one habitat, means for biomass and biomass contribution are given. The vertical position of food resources and macroinvertebrates represents their trophic level. Food resources were assigned to trophic level one, and the trophic level of macroinvertebrate consumers was calculated after Vander Zanden & Rasmussen (1999). The dashed line depicts the distinction between primary and secondary consumers. See Fig. 1 for codes to resources and species.

Table 2. Percentage contribution of individual habitats to total weighted biomass, total consumer richness and total number of trophic links at undeveloped shorelines

	Grienericksee			Langer See			Unteruckersee		
	Biomass	Consumer richness	Trophic links	Biomass	Consumer richness	Trophic links	Biomass	Consumer richness	Trophic links
Coarse woody debris	19	17	24	17	20	20	1	9	7
Reed	45	17	14	14	40	43	0	14	11
Roots	6	25	28	57	25	27	8	9	7
Sand	26	25	18	11	15	10	79	45	47
Stones	4	17	16	–	–	–	12	23	28

majority of macroinvertebrate biomass was derived from SPOM because CPOM and periphyton were absent.

At undeveloped shoreline of Lake Unteruckersee, consumer biomass was mainly derived from FPOM (Table 3). Marginal differences in resource contributions were found between the retaining wall and the undeveloped shoreline except for CPOM that was absent at the retaining wall.

Discussion

Previous research has shown that human development of lakeshores and the associated reduction in littoral habitat diversity has profound effects on the composition and biodiversity of littoral communities (Schindler, Geib & Williams 2000; Brauns *et al.* 2007). In this study, we demonstrated that shoreline

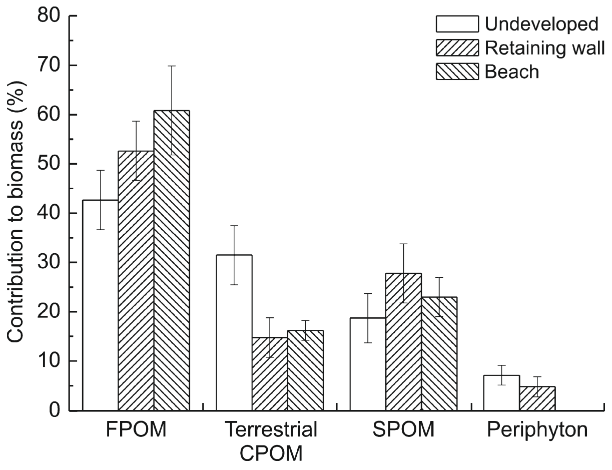

Fig. 4. Percentage contribution of food resources to total macroinvertebrate biomass at undeveloped shorelines, retaining walls and beaches across the three studied lakes. For each proportional contribution, the overall uncertainty (±1 SD) is given as the sum of uncertainties of each individual mixing model run. Contributions to biomass were calculated excluding the invasive *Dreissena polymorpha* (Bivalvia) to allow for comparisons among lakes.

development not only affects the structure of littoral communities but also their functioning, which was evident in substantial differences in the structure and the transfer of organic matter through macroinvertebrate food webs of undeveloped and developed shorelines.

In accordance with our first hypothesis, food web structure in terms of trophic links declined with decreasing habitat diversity, reflecting significant relationships between shoreline morphology and both species richness and number of available food resources. The lower trophic complexity of food webs at developed shorelines was mainly because of the absence of CWD, reed and submerged tree roots. These habitats contributed substantially to food web complexity as well as to consumer richness at undeveloped shorelines. The remaining habitats at developed shorelines could not compensate for the absence of CWD, reed and submerged tree roots. An exception was the sand habitat at the undeveloped shoreline at Lake Unteruckersee that alone contributed 79% to total weighted biomass (Table 2). However, modifications of the sand habitat of the recreational beach at Lake Unteruckersee, in particular the physical impairment via human trampling, were associated with a decline of total weighted biomass and food web complexity compared with the undeveloped shoreline (Fig. 3).

The simplification of food webs at trophic level 3 was particularly apparent at beaches, because macroinvertebrate predators were absent from the studied beach food webs. Retaining walls harboured predator populations even though food web complexity was lower compared with undeveloped shorelines. In our study, predatory *E. octoculata* and *P. maculatus* were only found at undeveloped shorelines and retaining walls. *Platambus maculatus* commonly inhabits spatially complex habitats, such as tree roots (Hendrich 2003), and is indeed among the first species to become extinct if such habitats are lost from the littoral zone. In contrast, *E. octoculata* is a habitat

Table 3. Percentage contribution of food resources to total weighted macroinvertebrate biomass at undeveloped shorelines, retaining walls and beaches. The trophic level (TL) of macroinvertebrates was calculated following Vander Zanden & Rasmussen (1999) and rounded to integers. For each contribution, the uncertainty (±1 SD) is given as the sum of uncertainties of individual mixing model runs. Contributions were calculated excluding invasive *Dreissena polymorpha* (Bivalvia) to allow for comparisons among lakes (– = food resource not present)

	Grienericksee				Langer See				Unteruckersee			
	Undeveloped		Retaining wall	Beach	Undeveloped	Retaining wall		Beach	Undeveloped	Retaining wall		Beach
	TL 2	TL 3	TL 2	TL 2	TL 2	TL 2	TL 3	TL 2	TL 2	TL 2	TL 3	TL 2
Fine particulate organic matter	25 ± 6	24 ± 5	33 ± 7	30 ± 7	2 ± 1	17 ± 6	23 ± 2	32 ± 7	64 ± 10	69 ± 7	0	78 ± 10
Periphyton	14 ± 4	18 ± 5	22 ± 4	–	19 ± 6	2 ± 1	8 ± 1	–	1 ± 0	2 ± 1	55 ± 7	–
Suspended particulate organic matter	25 ± 5	20 ± 7	45 ± 6	31 ± 6	20 ± 4	14 ± 5	5 ± 8	68 ± 7	17 ± 5	29 ± 7	45 ± 0	3 ± 2
Terrestrial coarse particulate organic matter	36 ± 4	38 ± 0	–	39 ± 4	60 ± 7	66 ± 6	64 ± 0	–	18 ± 5	–	–	19 ± 2

generalist (Mann 1953) that may persist as long as solid habitats remain. This observation does not entirely follow the prediction that species at higher trophic levels are among the first to disappear as a result of habitat loss (Ryall & Fahrig 2006). Instead, our results indicate that there is no overall response of littoral macroinvertebrate predators to habitat loss, but that their extinction threshold is determined by the degree of species-specific habitat specialisation.

According to hypothesis 2, we found differences in the trophic basis of littoral food webs not only between lakes but also between shoreline types. Major differences were observed for contributions of terrestrial CPOM, as CPOM contributed half as much to weighted consumer biomass at developed than at undeveloped shorelines. The lower significance of terrestrial CPOM was probably the result of the removal or thinning of the riparian vegetation at developed shorelines. Consequently, CPOM was absent at three of six developed shorelines and scarce at the remaining sites (Table 3). These results support earlier findings that terrestrially derived organic matter is an important subsidy for littoral communities at undeveloped shorelines (Solomon *et al.* 2008; Weidel *et al.* 2008). However, our results demonstrate that human shoreline development adversely affects this energetic coupling between the littoral and the riparian zone by disrupting flows of organic matter across the aquatic–terrestrial boundary.

The alteration of the trophic basis of macroinvertebrate food webs was also reflected in differing contributions of periphyton to consumer biomass. Periphyton contributions did not differ between retaining walls and undeveloped shorelines but periphyton did not contribute to macroinvertebrate biomass at beaches. The absence of periphyton at beaches may be the result of the loss of solid habitats enabling periphyton growth, because CWD, reed and stones were lacking at beaches. This result may partially be biased because of our inability to discriminate benthic FPOM into epipsammic algae and detritus. However, we think that epipsammic algae marginally contributed to consumer biomass as we did not observe conspicuous algal mats or a distinct epipsammic periphyton during sampling. Periphyton growth may have been restricted by sediment instability caused by wind-induced waves that are characteristic for the investigated lakes with their large surface area. This assumption is corroborated by a study in a lake of similar morphology (Lake Erken, Sweden), where epipsammic algae contributed only 0·1–1·5% to total FPOM standing stocks (Hillebrand & Kahlert 2002). Moreover, the physical disturbance by human trampling at recreational beaches may have prevented a notable growth of epipsammic periphyton in the studied lakes.

In addition to differences between shoreline types, there was considerable natural variation in consumer resource use at undeveloped shorelines of the studied lakes (Table 2). This may be because of differences in macroinvertebrate community composition between lakes and an associated differing consumer feeding ecology. For example, the macroinvertebrate community of Lake Grienericksee was dominated by indigenous species, whereas Lake Langer See and Unteruckersee exhibited communities dominated by the nonindigenous amphipods *Dikerogammarus villosus* (Sowinsky) and *Pontogammarus robustoides* Sars and the snail *Potamopyrgus antipodarum* (Grey) (Table S1). Previous studies have shown that nonindigenous species can have different feeding strategies than their native counterparts (Statzner, Bonada & Doledec 2008). This may explain the high contribution of FPOM to consumer biomass at the undeveloped shoreline of Lake Unteruckersee. Alternatively, indigenous consumers encountered at the undeveloped shorelines that were studied may have more flexible feeding strategies than commonly assumed. For example, terrestrial CPOM had the highest contribution to the biomass of the snail *Bithynia tentaculata* (Linnaeus) at Lake Grienericksee (46%), whereas FPOM had the highest contribution to the biomass of this species at Lake Unteruckersee (63%). Similarly, SPOM contributed most to the biomass of the snail *Radix balthica* (Linnaeus) at Lake Langer See (60%), whereas terrestrial CPOM had the highest contribution to the biomass of this species at Lake Unteruckersee (44%). These differences in feeding ecology may be because of differences in the quantitative availability of food resources at undeveloped shorelines and may have forced omnivorous consumers to adjust their diet to the local resource availabilities. Despite the natural variation in consumer resource use among lakes, human shoreline development had evident effects on the trophic base of the studied food webs suggesting that the results of the present study are robust and may be applicable to a wider variety of lake types.

The adverse effects on macroinvertebrate biomass that were demonstrated at the site scale may also lead to impacts at the whole-littoral scale. An exploratory analysis indicated that whole-littoral macroinvertebrate biomass may substantially decrease with increasing percentage of shoreline development. At Langer See, the lake exhibiting the highest percentage of shoreline development, estimated whole-littoral macroinvertebrate biomass was 36% lower than expected without shoreline development. It is unclear to what extent potential whole-littoral impacts on macroinvertebrate biomass may affect fish because mass-balanced food web studies for lakes subjected to shoreline development are largely lacking. In a whole-lake CWD manipulation experiment, Sass *et al.* (2006) removed 75% of the CWD from Little Rock Lake (WI, USA) to simulate the loss of CWD associated with residential shoreline development. While there were no changes in macroinvertebrate community composition and density (Helmus & Sass 2008), largemouth bass *Micropterus salmoides* (Lacépède) had lower growth rates and yellow perch *Perca flavescens* (Mitchill) declined in population density (Sass *et al.* 2006). This suggests that the removal of CWD following moderate shoreline development may not exert effects on fish because of reductions in benthic prey but rather by the reduction in the physical shelter provided by littoral CWD. In our lakes however, reductions in littoral habitat diversity were considerably higher in comparison with the study cited above because in addition to the absence of CWD, reed and submerged tree roots were also absent at developed shorelines. These habitats contributed on average 56% to total weighted biomass at undeveloped shorelines and their absence at developed shorelines may be the cause for the lower whole-littoral biomass at the highly developed Lake Langer See. Such substantial reductions of prey biomass as well as littoral structure may be severe enough to directly affect fish biomass because retaining walls and beaches represent the dominant shoreline types in highly developed lakes (Sly 1991; Schindler, Geib & Williams 2000).

IMPLICATIONS FOR SHORELINE MANAGEMENT

We have demonstrated that shoreline development adversely affects the structure of the littoral zone and is associated with a lower diversity of food resources and lower consumer species diversity. Hence, food webs at developed shorelines had an up to one order of magnitude lower complexity because of the substantially lower number of trophic links between macroinvertebrate consumers and food resources. Moreover, clear-cutting or thinning of the riparian vegetation at developed shorelines diminished the supply of terrestrial organic matter to littoral food webs suggesting that human shoreline development decouples the littoral from the riparian zone. These results reveal that ecological effects of human activities in the littoral zone may go beyond simple alterations of littoral communities and have the potential to drastically alter the structure of, and the energy transfer in, littoral food webs.

Our limited understanding of food web effects and whole-lake impacts of human activities in the littoral zone currently hampers the identification of effective measures for the restoration of lakes subjected to intensive shoreline development. Hence, we advocate integrative approaches to the assessment of shoreline development by quantifying fish and benthic secondary production, as well as matter fluxes between trophic compartments under different development scenarios. Such comprehensive ecosystem function analysis would allow for the determination of thresholds at which shoreline development severely affects biomass production and the organic matter transfer within food webs.

Our habitat-specific results provide a first approach to cost-efficient restoration measures. Shorelines affected by erosion control structures such as retaining walls could be restored by replacing these structures with more appropriate stake palisades in front of lake shores. Such measures have been successfully implemented at Lake Constance (Germany), where a double palisade of stakes was installed in front of the shoreline to protect the reed belt against erosion (Ostendorp *et al.* 1995). Furthermore, littoral habitat diversity behind the stake palisade could be increased by restoring reed stands and planting of native riparian trees to allow for the supply of CWD and submerged root habitats. In cases of retaining walls that cannot be replaced, the establishment of reed stands should be fostered by protecting the upper littoral zone from lake-side disturbances, such as boating. The energetic coupling of littoral food webs to the riparian zone evidenced in our study suggests that the riparian vegetation should be conserved or restored at shorelines developed by retaining walls. Here, our data show that impacts of retaining walls on the trophic base of littoral food webs may be less severe as long as the riparian vegetation is not impacted.

An ecologically meaningful restoration of recreational beaches is unlikely because of their persistent use, but it is highly recommended to restrict their spatial extent to keep whole-lake impacts as low as possible. However, we strongly advocate that lakeshore conservation and impact mitigation strategies should primarily focus on conserving the structural integrity of the littoral zone.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Mean proportional contribution of food resources to the diet of macroinvertebrate consumers found at each habitat.

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Nutrient enrichment homogenizes lake benthic assemblages at local and regional scales

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Abstract. The compositional heterogeneity of biotic assemblages among sites, or β-diversity, regulates the relationship between local and regional species diversity across scales. Recent work has suggested that increased harshness of environmental conditions tends to reduce β-diversity by decreasing the importance of stochastic processes in structuring assemblages. We investigated the effect of nutrient enrichment on the compositional heterogeneity of lake benthic invertebrate assemblages in Ireland at both local (within-lake) and regional (among-lake) scales. At local scales, we found that the compositional heterogeneity of benthic assemblages was related inversely to the extent of nutrient enrichment (as indicated by measurements of water column total phosphorus, total nitrogen, and chlorophyll *a*), after effects of lake morphology (i.e., surface area, connectivity, and depth of sampling) and alkalinity were accounted for. At regional scales, we found that nutrient-rich lakes had significantly more homogenous benthic assemblages than nutrient-poor lakes, over and above the effect of alkalinity and across a similar range of lake morphologies. These findings have profound implications for global aquatic biodiversity, as the homogenization of benthic assemblages at both local and regional scales may have important and unpredictable effects on whole aquatic ecosystems, with potentially considerable ecological and evolutionary consequences.

Key words: disturbance; diversity; eutrophication; homogenization; invertebrate; Ireland; productivity; variability.

INTRODUCTION

The compositional heterogeneity of biotic assemblages among sites, or β-diversity, regulates the relationship between local and regional species diversity across scales (Whittaker 1972, Cornell and Lawton 1992, Lande 1996, Loreau 2000). β-diversity is itself a function of heterogeneity in both environmental conditions and species niches, of which the latter define the mechanisms by which species respond to environmental heterogeneity (Loreau 2000). Widespread anthropogenic homogenization of taxonomic, genetic and functional diversity, either indirectly through homogenization of environmental conditions (Balata et al. 2007, Brauns et al. 2007*b*, Passy and Blanchet 2007, Poff et al. 2007), or directly via alteration of biotic assemblages (Rahel 2002, Olden and Poff 2004, Olden and Rooney 2006, Chase 2007, Chalcraft et al. 2008) have, therefore, profound implications for ecology, evolution, and global biological diversity (Olden et al. 2004).

The compositional heterogeneity of biotic assemblages among sites has been correlated positively with productivity (Chase and Leibold 2002, Chase and Ryberg 2004). It has, however, been demonstrated (Chalcraft et al. 2008) that anthropogenic nutrient enrichment can both increase and decrease the β-diversity of terrestrial grasslands, depending upon initial site productivity. Recently, Chase (2007) demonstrated that increased harshness of environmental conditions tends to reduce compositional heterogeneity among sites by decreasing the importance of stochastic processes in structuring assemblages. Moreover, anthropogenic enrichment of ecosystems with nutrients frequently increases the harshness of environmental conditions for biota indirectly by, for example, reducing availability of resources such as light and oxygen and modifying habitat structure, food webs, predation pressure and other interspecific interactions (e.g., Cadotte et al. 2006, Fukami et al. 2006, Brauns et al. 2007*a*, Declerck et al. 2007). This suggests that reductions in β-diversity may be expected wherever nutrient enrichment increases the harshness of environmental conditions for biota, irrespective of changes in productivity.

Cultural eutrophication from nutrient enrichment comprises a globally important anthropogenic impact on aquatic ecosystems (Smith et al. 2006, Schindler and Vallentyne 2008). In spite of this, current understanding of its effects on benthic assemblages remains poor,

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particularly in lakes. This owes largely to their high spatiotemporal variability at scales among and within both lakes and habitats (White and Irvine 2003, Stoffels et al. 2005, Brauns et al. 2007*a*). The negative effects of nutrient enrichment are, however, arguably manifested most strongly in the benthic zone owing to decreased oxygen availability (Charlton 1980) and reduction of phytobenthic production (Vadeboncoeur et al. 2003, Chandra et al. 2005) and structural complexity (Scheffer et al. 1993, Egertson et al. 2004). We tested the hypothesis that nutrient enrichment homogenizes lake benthic assemblages by analyzing data from both littoral and profundal/sublittoral invertebrate assemblages extracted from a national lakes database for Ireland. Further, as spatial scale can affect the nature of productivity–biodiversity relationships (Chase and Leibold 2002, Chase and Ryberg 2004), and productivity is generally related strongly to nutrient concentrations (Schindler 1978, Smith 1979), we also examined whether relationships between the extent of nutrient enrichment and the compositional heterogeneity of benthic assemblages varied between local (within-lake) and regional (among-lake) scales.

METHODS

Sampling and laboratory analyses

Littoral invertebrates were collected by kick sampling in stony substrates (gravels, pebbles, or cobbles without obvious macrophyte presence) for 30 seconds with a 1-mm mesh pond net for the analysis at within-lake scales, and for 2 minutes with a 670-μm mesh pond net for the analysis among lakes. Two hundred and four littoral invertebrate taxa were collected and identified to the lowest practicable taxonomic level (60% to species and 31% to genus, with the remainder identified to family, except for Hydrachnidia, Lepidoptera, Oligochaeta, Ostracoda, and Turbellaria). Profundal/sublittoral invertebrates (range of water depths sampled 1.1–71.9 m; Appendices A and B) were sampled with an Ekman grab (sampling area 0.0225 m^2) and passed through a 500-μm mesh. Ninety seven profundal/sublittoral invertebrate taxa were found, of which 26% were identified to species (including Oligochaeta and Hirudinea), 53% to genus (including Chironomidae), and the remainder to family except for Hydrachnidia, Nematoda, Ostracoda, and Turbellaria.

Concurrent measures of water column total phosphorus (TP), total nitrogen (TN), chlorophyll *a*, and alkalinity (quantified following Eisenreich et al. 1975, Standing Committee of Analysts 1980, Clesceri et al. 1998, Grasshoff et al. 1999) were made on every sampling occasion. Lakes exposed to minimal anthropogenic disturbance in Ireland have been shown consistently to be oligotrophic (Leira et al. 2006). This supports the assertion that lakes of higher trophy analyzed here have undergone anthropogenic nutrient enrichment, particularly since the mid-1970s.

Data analyses

Data from six samples of littoral invertebrates from each of 25 lakes and three samples of profundal/sublittoral invertebrates from each of 12 lakes (Appendix A), sampled as described above, were extracted from an Irish lakes database and used to quantify the compositional heterogeneity of benthic assemblages (see *Statistical methods*) within lakes. The samples were taken from a number of locations throughout each lake between 1996 and 2002 on sampling occasions distributed throughout the year (Appendix A). Sampling of profundal/sublittoral assemblages was, however, limited to the period between March and September. Owing to availability of data, it was not possible to disentangle the individual contributions of spatial and temporal variability. The data were instead used to estimate total spatiotemporal heterogeneity in the composition of benthic assemblages. In cases where in excess of six samples of littoral invertebrates (21 out of 25 lakes) or three of profundal/sublittoral invertebrates (10 out of 12 lakes) were available from a particular lake, samples included in the analyses were selected randomly from the pool of those available (mean number of available littoral samples per lake [±SD] = 8.6 ± 2.3, range = 6–15; mean number of available profundal/sublittoral samples per lake = 5.6 ± 2.4, range = 3–11).

Data from single samples of both littoral and profundal/sublittoral invertebrate assemblages, collected between 1996 and 2005 from, respectively, 40 and 52 lakes (Appendix B) distributed throughout Ireland were also extracted from the database and used to quantify compositional heterogeneity at among-lake scales. These samples were extracted from the database on the basis of their concurrent water chemistry fulfilling criteria for either oligotrophic (nutrient-poor) or eutrophic (nutrient-rich) status; lakes classified as oligotrophic (littoral, $n = 20$; profundal/sublittoral, $n = 26$) had both TP and chlorophyll *a* concentrations less than 10 and 2.5 μg/L, respectively, at the time of sampling. Those with concentrations of greater than, respectively, 35 and 8 μg/L were classified as eutrophic (littoral, $n = 20$; profundal/sublittoral, $n = 26$), following Organisation for Economic Cooperation and Development (1982). Owing to subsequent analytical requirements for equal numbers of lakes in each trophic group, lakes included in the analyses from the group with greater numbers of samples were selected randomly from those available (littoral, 46 oligotrophic lakes available; profundal/sublittoral, 37 oligotrophic lakes available). In cases where in excess of one sample fulfilling the water chemistry criteria was available from any particular lake (littoral, 7 out of 40 lakes; profundal/sublittoral, 4 out of 52 lakes), the sample included in the analyses was selected randomly from the pool of those available.

Statistical methods

Global relative multivariate dispersion (calculated following Warwick and Clarke 1993, Clarke and

Warwick 2001) was used as a holistic measure of compositional heterogeneity (Anderson et al. 2006) both within and among lakes. All multivariate analyses of biotic data were based on Bray-Curtis similarity matrices (Bray and Curtis 1957) and were calculated from $\log(x + 1)$-transformed abundances in the case of profundal/sublittoral data and proportional abundances in the case of the littoral invertebrate data, the latter owing to the nonquantitative nature of kick sampling. Multivariate dispersion, which is not confounded with estimates of α- or γ-diversity (Lande 1996), comprises a relative multivariate measure of variability in different groups of samples and is calculated by comparing ranked distance/similarity measures within and among groups in a similarity matrix. This was calculated independently for littoral and profundal/sublittoral assemblages.

Multiple regression (linear first-order main effects with normal errors) was used to test the significance and nature of relationships between multivariate dispersion within lakes and each of three measures of nutrient enrichment: mean water column concentrations of TP, TN, and chlorophyll *a*. The significance of each measure of nutrient enrichment was determined in separate multiple regression analyses. Owing to the fact that water column alkalinity, surface area, and connectivity of lakes are all likely to influence strongly the composition and taxonomic richness of their biotic assemblages (Nilsson and Nilsson 1978, Browne 1981, Dodson 1992, Chase and Ryberg 2004, Smith et al. 2005), these factors were offered as independent variables to the multiple regression analyses in conjunction with each measure of nutrient enrichment in the maximal model. We used the number of lakes connected directly to the sampled lakes as our measure of lake connectivity. In addition, the mean depth of sampling was incorporated into the analyses of profundal/sublittoral invertebrates. Step-wise model selection was performed based on Akaike's information criterion (AIC_c), corrected to account for small sample size biases (Burnham and Anderson 2004), using forward and backward selection to identify the minimum adequate model (Whittingham et al. 2006). Significance of the effects of the various measures of nutrient enrichment on compositional heterogeneity at within-lake scales was then quantified by its contribution to model fit determined by AIC_c. Each of TP, TN, chlorophyll *a*, and lake surface area were $\log_{10}$-transformed to normalize distributions prior to analysis.

A combination of permutational analysis of multivariate dispersions (PERMDISP; Anderson 2006) and permutational multivariate analysis of variance (PERMANOVA; Anderson 2001, McArdle and Anderson 2001) was used to test whether the compositional heterogeneity of littoral or profundal/sublittoral invertebrate assemblages varied between nutrient-poor and nutrient-rich lakes (i.e., at among-lake scales). PERMDISP comprises a distance-based test of the homogeneity of multivariate dispersions among groups of a single factor, comprising essentially a multivariate extension of Levene's test (Levene 1960). Although similar ranges in alkalinity, surface area, connectivity, and depth of sampling were present in both trophic groups (Appendix B), ($\log_{10}$-transformed) alkalinity was significantly higher in the eutrophic lakes in both the littoral (*t* test; $t_{38.8} = 4.28$, $P \leq 0.0001$) and profundal/sublittoral ($t_{37.9} = 5.92$, $P \leq 0.0001$) analyses, reflecting geographical association between intensive grassland agriculture in Ireland and alkaline soils. Consequently, to disentangle the possible confounding effects of alkalinity and trophic status on compositional heterogeneity, we categorized lakes into three alkalinity groups (low alkalinity, <20 mg $CaCO_3$/L; moderate alkalinity, 20–100 mg $CaCO_3$/L; high alkalinity, >100 mg $CaCO_3$/L) following the Irish lake classification scheme (EPA 2005) under the EU Water Framework Directive (2000/60/EC). PERMDISP was then used to calculate the distances between samples and their trophic group centroids separately for each alkalinity group. Similar to standard PERMDISP analyses, PERMANOVA was then used to compare these distances, except we used a two-factor PERMANOVA design, with 9999 permutations of the residuals under a reduced model, as recommended by Anderson (2005), with trophic status (fixed factor, two levels) crossed with alkalinity group (fixed factor, three levels). This model design was also used to examine whether the spatial distances among lakes differed significantly between the nutrient-rich and nutrient-poor lakes used in the among-lake analysis. Among-lake distances were calculated as the Euclidian distances among the eastings and northings of lake midpoints. Taxa that were contributing most to the dissimilarities between nutrient-poor and nutrient-rich lakes were identified using similarity percentages (SIMPER) analyses (Clarke and Warwick 2001) with alkalinity and trophic status incorporated as independent variables. All multivariate analyses were done with PRIMER Version 6.1 (PRIMER-E Ltd., Plymouth, UK). Finally, in order to test whether changes in the compositional heterogeneity of benthic assemblages were a result of reductions in the frequency of occurrence of intolerant taxa (see Chase 2007) and, hence, less sporadic occurrences of taxa in nutrient-enriched lakes, we conducted independent-samples *t* tests (without assuming equal variances; Welsh 1947) comparing the frequency of occurrence of taxa in nutrient-poor and nutrient-rich lakes. This was done at among-lake scales for both littoral and profundal/sublittoral assemblages. An α significance level of 0.05 was used for all analyses.

RESULTS

Each of our covariates measuring nutrient enrichment were retained in the models best describing multivariate dispersion of both littoral and profundal/sublittoral invertebrate assemblages at the within-lake scale (Table

1). Further, these relationships were inverse in every case (Table 1, Fig. 1). Comparison of AIC_c values indicate that the model containing chlorophyll *a*, alkalinity, connectivity, and surface area best explained the data for littoral assemblage heterogeneity, whereas a model containing TN and surface area was best for profundal/sublittoral assemblages.

At among-lake scales, the composition of both littoral and profundal/sublittoral invertebrate assemblages was significantly (Table 2) less heterogeneous (Fig. 2) in nutrient-rich than nutrient-poor lakes, while there was no effect of water column alkalinity and no significant interaction between trophic status and alkalinity. Further, the relative variability of the distances among lakes was not affected by trophic status (Appendix C). *Asellus aquaticus*, *Gammarus* sp., and oligochaete worms were found to be the three taxa from littoral samples contributing most to the dissimilarity between nutrient-poor and nutrient-rich lakes while the two oligochaete taxa *Limnodrilus* sp. and *Potamothrix hammoniensis* together with the Chaoboridae contributed most to this dissimilarity for the profundal/sublittoral zone (Appendix D). The oligochaetes were also consistently more abundant in the nutrient-rich lakes. There was, however, no difference in the frequency of occurrence of taxa between nutrient-poor and nutrient-rich lakes (*t* test; littoral, $t_{150.25} = 0.08$, $P = 0.94$; profundal/sublittoral, $t_{63.77} = 1.2$, $P = 0.24$); of the littoral taxa observed in at least one of the nutrient-poor lakes, each was observed in 4.72 ± 1.01 (mean ± 95% CI) of the nutrient-poor lakes, while of those sampled from nutrient-rich lakes, each was sampled from 4.78 ± 1.2 of the nutrient-rich lakes. Similarly, each profundal/sublittoral taxon found in at least one of the nutrient-poor lakes was found in 4.64 ± 1.21 of the nutrient-poor lakes, while for those found in nutrient-rich lakes, each was sampled from 6.19 ± 2.3 of the nutrient-rich lakes.

Table 1. Results of multiple regression analyses with multivariate dispersion within lakes as the dependent variable for two benthic zones (littoral and profundal/sublittoral).

Independent variable	*B* (2.5%, 97.5% CI)	AIC_c (null model)
Littoral zone ($n = 25$)		
a)		
$\log_{10}$(area)†	−0.31 (−0.50, −0.12)	
Alkalinity	−0.00 (−0.00, 0.00)	
Connectivity	removed	
$\log_{10}$(TP)‡	−0.47 (−0.73, −0.21)	5.97 (24.47)
b)		
$\log_{10}$(area) †	−0.35 (−0.57, −0.12)	
Alkalinity	removed	
Connectivity	removed	
$\log_{10}$(TN) §	−0.52 (−0.92, −0.12)	10.22 (24.47)
c)		
$\log_{10}$(area)	−0.30 (−0.48, −0.01)	
Alkalinity	−0.00 (−0.00, −0.00)	
Connectivity	−0.04 (−0.07, −0.00)	
$\log_{10}$(chlorophyll *a*)	−0.48 (−0.68, −0.03)	1.84 (24.47)
Profundal/sublittoral zone ($n = 12$)		
d)		
$\log_{10}$(area)	−0.54 (−0.94, −0.13)	
Alkalinity	removed	
Sample depth	removed	
Connectivity	removed	
$\log_{10}$(TP)	−0.68 (−1.1, −0.27)	10.12 (15.86)
e)		
$\log_{10}$(area)	−0.50 (−0.87, −0.13)	
Alkalinity	removed	
Sample depth	removed	
Connectivity	removed	
$\log_{10}$(TN)	−1.10 (−1.67, −0.54)	7.84 (15.86)
f)		
$\log_{10}$(area)	−0.41 (−0.83, 0.00)	
Alkalinity	removed	
Sample depth	removed	
Connectivity	removed	
$\log_{10}$(chlorophyll *a*)	−0.64 (−1.04, 0.00)	10.64 (15.86)

Notes: The maximal model included all covariates as listed for models specifically including total phosphorus (TP; a and d), total nitrogen (TN; b and e) and chlorophyll *a* (c and f) as independent covariates. Results for the minimal adequate models based on AIC_c are presented. Parameter estimates are given by *B* with 2.5% and 97.5% confidence intervals in parentheses. The AIC_c value for the corresponding null model (i.e., with the overall mean as the only model parameter) is also given in parentheses for comparison. Area was measured in hectares, alkalinity in mg $CaCO_3$/L, sample depth in m, TP in μg/L, TN in mg/L, and chlorophyll *a* in μg/L. Connectivity was measured as the number of lakes connected directly to the sampled lakes.

Discussion

Our results indicate strongly that nutrient enrichment homogenizes the composition of lake benthic assemblages. The fact that similar results were obtained from independent analyses of both littoral and profundal/sublittoral invertebrate assemblages within and among lakes suggests that this pattern occurs throughout the benthic zone of lakes at both local and regional scales. Two mechanisms could account for these patterns. First, if nutrient enrichment promotes homogenization of habitat structure, increased compositional similarity of biotic assemblages is likely to occur among sites at both local and regional scales (Chase and Leibold 2002). Habitat heterogeneity is recognized as one of the most important mechanisms generating β-diversity (Connor and McCoy 1979, Loreau 2000), and empirical field surveys have shown that decreased habitat heterogeneity owing to anthropogenic disturbance can reduce β-diversity significantly (Passy and Blanchet 2007). Although we did not quantify habitat heterogeneity directly, increased homogeneity of habitats both within and among lakes with increasing trophy, owing to blanketing of the lakebed with organic sediments and reduction of structural heterogeneity from macrophytes (Scheffer et al. 1993, Egertson et al. 2004), may have contributed to the observed homogenization of benthic assemblages. Similarly, decreased importance of trophic heterogeneity within and among benthic habitats owing to greater reliance on open-water productivity with increasing extent of nutrient enrichment (Vadeboncoeur et al. 2003, Chandra et al. 2005) could also lead to reduced heterogeneity of benthic communities. The

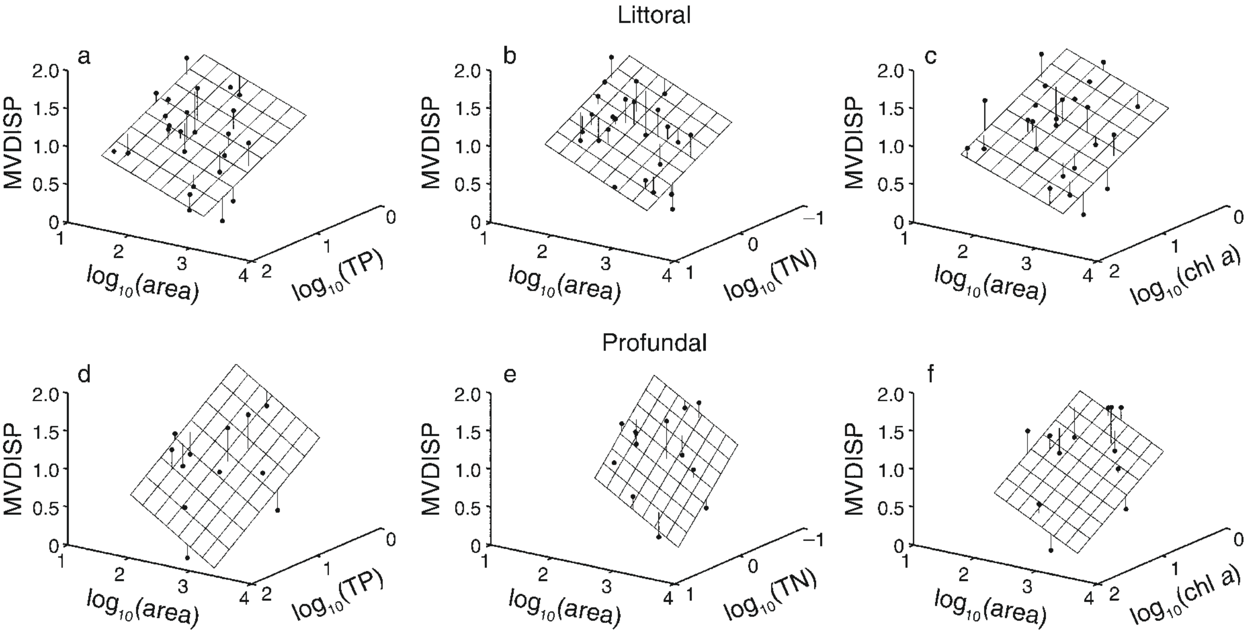

FIG. 1. Raw data (dots) with the fitted model (grid) detailed on Table 1 showing multivariate dispersion (MVDISP, a unitless measure) within lakes as a function of lake surface area and (a, d) TP, (b, e) TN, and (c, f) chlorophyll *a* for both littoral and profundal/sublittoral invertebrate assemblages. Stem lines join the raw data points to the fitted model surface indicating their relative position. Axes for the measures of nutrient enrichment are plotted in reverse direction. Models (a) and (c) contained additional covariates (see Table 1 for details), which were fixed at their mean value for the purposes of graphical representation.

important contribution of oligochaete worms, which normally exhibit a general preference for fine organic-rich sediments, to the dissimilarity between nutrient-poor and nutrient-rich lakes, coupled with their increased abundance in nutrient-rich lakes, supports these assertions.

Second, recent work by Chase (2007) suggests that harsh "ecological filters," such as those resulting from strong anthropogenic disturbance, reduce the importance of stochastic processes in structuring biotic communities and, hence, reduce the compositional heterogeneity of biotic assemblages among sites. This process is driven by niche selection resulting in the exclusion of intolerant taxa and could occur independently of alterations to habitat heterogeneity (cf. Loreau 2000). The fact that there was no difference in the frequency of occurrence of taxa between nutrient-poor and nutrient-rich lakes suggests strongly, however, that this mechanism was not a significant driver of the patterns observed here.

In contrast to our results, Chase and coworkers (Chase and Leibold 2002, Chase and Ryberg 2004) found positive associations between periphyton productivity and the compositional heterogeneity of whole biotic assemblages (including fish, amphibians, benthic and free-swimming invertebrates, plants, and algae) in ponds located along a natural gradient in productivity. This indicates that the effects of relatively recent anthropogenic nutrient enrichment on β-diversity may differ from those of more natural variability in productivity. Recent work by Chalcraft et al. (2008), which found that initial site productivity determines

TABLE 2. Results of PERMANOVA analyses examining the effects of lake water column alkalinity and trophic status on the compositional heterogeneity of littoral and profundal/sublittoral invertebrate assemblages at among-lake scales.

Source	df	Sum of squares	Mean square	Pseudo *F*	*P*
Littoral					
Alkalinity (Alk)	2	24.25	12.12	0.45	0.64
Trophic status (TS)	1	870.32	870.32	32.5	≤0.0001
Alk × TS	2	17.79	8.89	0.33	0.71
Residual	34	910.41	26.78		
Total	39	2245.1			
Profundal/sublittoral					
Alkalinity	2	199.22	99.61	1.23	0.3
Trophic status	1	1666.9	1666.9	20.56	≤0.0001
Alk × TS	2	468.29	234.14	2.89	0.07
Residual	46	3730.4	81.1		
Total	51	9131.6			

whether compositional heterogeneity increases or decreases with nutrient enrichment provides a potential mechanism for these contrasting findings. Whereas the gradual natural eutrophication of ponds over relatively long timescales supports the assembly of communities comprised of species adapted to increasingly productive conditions, the rapid increases in productivity caused by anthropogenic nutrient enrichment likely induce unfavorable conditions for biotic assemblages in situ, and may, therefore, affect compositional heterogeneity in entirely different ways.

Empirical surveys (Chase 2003, Chase and Ryberg 2004), experimental (Forbes and Chase 2002, Cadotte and Fukami 2005), and theoretical (Hastings and Gavrilets 1999, Mouquet and Loreau 2002, 2003, Loreau et al. 2003) work has shown that greater dispersal or connectivity among localities reduces β-diversity by homogenizing metacommunities. The inverse effect of lake area on the compositional heterogeneity of benthic communities within lakes observed in our study concurs with this (cf. Loreau 2000). That our results reveal a greater importance of lake area compared with connectivity among lakes in mediating β-diversity at within-lake scales likely reflects greater connectivity among metacommunities within, compared with among, lakes. In spite of this, we found that nutrient-rich lakes contained significantly less heterogeneous benthic assemblages than nutrient-poor lakes, across a large range of lake sizes and connectivities and over and above the effect of water column alkalinity, which concurs with our results from independent analyses at within-lake scales. Our results have, therefore, profound implications for the conservation and management of global aquatic biodiversity, owing to the primacy of nutrient enrichment as one of the most pervasive anthropogenic impacts on aquatic ecosystems worldwide (Smith et al. 2006, Schindler and Vallentyne 2008) and because the problem is expected to increase considerably in coming decades (Tilman 1999). Benthic assemblages provide important roles in aquatic food-webs and in the sequestration and recycling of materials (Underwood 1991, Schindler and Scheuerell 2002, Lohrer et al. 2004), which attests to their importance to overall ecosystem functioning. Homogenization of benthic assemblages at both local and regional scales may, therefore, have important and unpredictable effects on whole aquatic ecosystems at the regional scale, with potentially considerable ecological and evolutionary consequences (Olden et al. 2004). Moreover, the compositional homogenization of biotic assemblages at both local and regional scales suggests that studies done at local scales alone underestimate the effects of anthropogenic nutrient enrichment significantly.

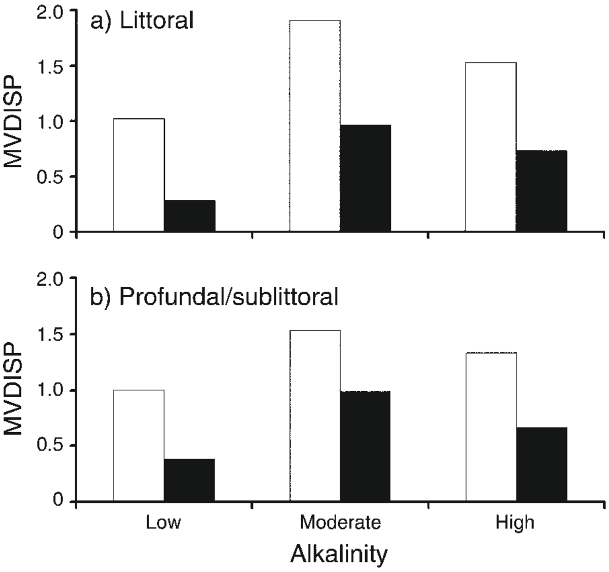

FIG. 2. Multivariate dispersion values of (a) littoral and (b) profundal/sublittoral invertebrate assemblages calculated at among-lake scales for the nutrient-poor (open bars) and nutrient-rich (solid bars) lakes in each alkalinity group.

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APPENDIX A

Lake morphology, water chemistry, mean number of taxa per sample, and the total number of taxa found for the analysis of the compositional heterogeneity of invertebrate assemblages within lakes (*Ecological Archives* E090-241-A1).

APPENDIX B

Morphology and concurrent water chemistry of the lakes used to investigate the compositional heterogeneity of invertebrate assemblages at among-lake scales (*Ecological Archives* E090-241-A2).

APPENDIX C

Results of PERMANOVA analyses examining the effects of lake alkalinity and trophic status on the relative variability of the spatial distances among lakes sampled for invertebrates (*Ecological Archives* E090-241-A3).

APPENDIX D

Results of SIMPER analyses identifying the five taxa contributing most to the dissimilarity between nutrient-poor and nutrient-rich lakes and indicating the relative changes in the abundance of each taxon in lakes of differing trophic status (*Ecological Archives* E090-241-A4).

3.5 Gabel, F, Garcia, X.-F. , Brauns, M., Sukhodolov, A., Leszinski, M., **Pusch, M.T.** (2008): Resistance to ship-induced waves of benthic invertebrates in various littoral habitats. *Freshwater Biology* 53, 1567–1578

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Resistance to ship-induced waves of benthic invertebrates in various littoral habitats

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SUMMARY

1. Ship-induced waves disturb benthic invertebrate assemblages colonizing littoral zones of lakes and rivers. However, the impact of ship-induced waves on invertebrates has rarely been quantified, and the influencing factors have not been addressed.
2. In an experimental wave tank, five benthic invertebrate species, *Bithynia tentaculata, Calopteryx splendens*, *Dikerogammarus villosus*, *Gammarus roeseli* and *Laccophilus hyalinus*, were exposed to waves of increasing shear stress (0.43–2.19 N m^{-2}). Mean number of detached individuals was recorded for five littoral habitats [coarse woody debris (CWD), reeds, sand, stones and tree roots], representing different levels of structural complexity as quantified by their fractal dimensions (FD).
3. Results showed that detachment of invertebrates was significantly related to shear stress in all habitats except tree roots. Detachments averaged for the five species were significantly lower in habitats with a high degree of structural complexity, decreasing in the habitat sequence: sand, CWD, stones, reeds and tree roots.
4. Consistent with their different morphologies and methods of attachment to substrates, the five species displayed differences in their response to hydraulic stress that were dependent on habitat.
5. The increasing sheltering effect of structural habitat complexity was mirrored by increasing dissipation of the kinetic energy of waves; i.e. the FD of the habitat was positively correlated with shear stress reduction due to the flow resistance of the habitat.
6. Network habitats such as tree roots provided the best sheltering conditions against hydraulic disturbance, because they combined good refuge availability for all studied invertebrate species and maximal dissipation of kinetic wave energy. Consequently, persistent anthropogenic impacts, such as lakeshore modification or long-term exposure to ship-induced waves, which cause disappearance of complex littoral habitats such as tree roots or dense reed belts, will drastically increase the adverse effects of boating and ship traffic on littoral invertebrate assemblages.

Keywords: fractal analysis, inland navigation, invertebrate detachment, shear stress, structural habitat complexity

Introduction

Wind-induced waves are a key determinant of habitat conditions at wind-exposed shores of lakes. Wind exposure maintains stony bottoms by preventing sediment accumulation (Brodersen, 1995; James *et al.*, 1998; Tolonen *et al.*, 2001), which generally favours high diversity and abundance of benthic invertebrates (Cardinale, Burton & Brady, 1997; Abdallah & Barton, 2003). Ship-induced waves produced by freight barges, passenger ships and recreational boats constitute a major additional hydraulic disturbance for invertebrates in the littoral zones of lakes, rivers and

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canals used as inland waterways. Although organisms at wind-exposed shores may be adapted to a regime of strong hydrodynamic forces, ship-induced waves are characterized by strong amplitudes and short-term increase of flow velocity (Bhowmik & Mazumder, 1990; Rodriguez *et al.*, 2002) and boat wakes can introduce waves to otherwise sheltered habitats where organisms are poorly adapted to hydrodynamic forces.

Very few published studies have documented the impact of ship-induced waves on shore assemblages. Studies of estuarine invertebrates have indicated that hydrodynamics regime and not sediment characteristics drive differences between invertebrate assemblages of wash and no-wash zones (Bishop, 2004, 2007; Bishop & Chapman, 2004). Bishop (2003, 2005) found lower abundances of gastropods and amphipods on sea grass blades exposed to ship-induced waves, and suggested that invertebrates were detached by the flapping of the blades as wave propagates. In the littoral zone of navigable rivers, ship-induced waves evidently constitute a major impact on macroinvertebrate communities (Brunke *et al.*, 2002; Garcia, Brauns & Pusch, 2006) and on young fish (Holland, 1986; Wolter & Vilcinskas, 1997; Arlinghaus *et al.*, 2002; Wolter & Arlinghaus, 2003). Mainly, organisms are expected to be relocated, but also to suffer from mechanical injuries caused by shear stress, increased expenditure of metabolic energy for swimming, oxygen depletion due to sediment resuspension and increased risk of predation.

However, little is known about potential thresholds in the response of littoral invertebrates to anthropogenic wave disturbances of increasing shear stress, or about the interaction with habitat properties. In particular, the factors influencing the extent to which invertebrates are detached by waves in specific littoral habitats have never been addressed. The only published evidence comes from a related case with stream invertebrates exposed to continuous flow in flume experiments, which demonstrated that current-induced drift of lotic invertebrate species increased with increasing flow velocities (Borchardt, 1993; Imbert & Perry, 2000), and that the proportion of drifting individuals decreased when woody debris was added to a sand habitat (Borchardt, 1993).

As the global navigation network constantly expands (see Revenga *et al.*, 2000), and recreational boating increases, quantitative information about the impacts of ship-induced waves is urgently needed to develop scientifically-based recommendations for shoreline management in navigable waterbodies. We therefore investigated the resistance of invertebrates to ship-induced waves in relation to the structural complexity of littoral habitats. Five benthic macroinvertebrate species, representing a spectrum of body morphologies and attachment strategies, were successively exposed to waves of increasing shear stress in five habitats exhibiting different structural complexity. We hypothesized that (i) the proportion of detached individuals depends on the level of shear stress associated with the wave; (ii) the proportion of detached individuals also depends on species-specific adaptations to certain habitats and (iii) the number of detached individuals decreases with greater habitat structural complexity.

Methods

Experimental system

Experiments were conducted in an experimental wave tank 3.0 m long, 0.80 m wide and 0.60 m deep made of 10 mm thick Perspex panels (Fig. 1). Waves of different shear stress were produced with a flap wave maker (Dean & Dalrymple, 1984), by varying the water level in the wave tank and the weights used to move the flap-plate.

In the observation area, two removable plastic trays each of 0.115 m^2 area and filled with sand, were placed side by side, in which the various habitats were exposed to waves. At the far end of the tank a slope with an angle of 20 ° and a discharge basin covered by a net were added to prevent reflection of the waves against the tank wall. The net collected invertebrates that were flushed from the observation area by the wave. Sand was glued on the plates 40 cm in front and behind the habitat trays to avoid any hydraulic perturbations in the study area due to changes in roughness along the wave route.

Hydrodynamic characteristics of the waves were measured by electronic devices installed in front of the habitat trays on the right side of the tank. Wave height was recorded with an acoustic wave sensor (UltraLab USS2001300, 20 Hz recording, General Acoustics, Kiel, Germany) located 50 cm above the water level. Flow velocity was recorded using an Acoustic Doppler velocimeter (Micro ADV 16 MHz,

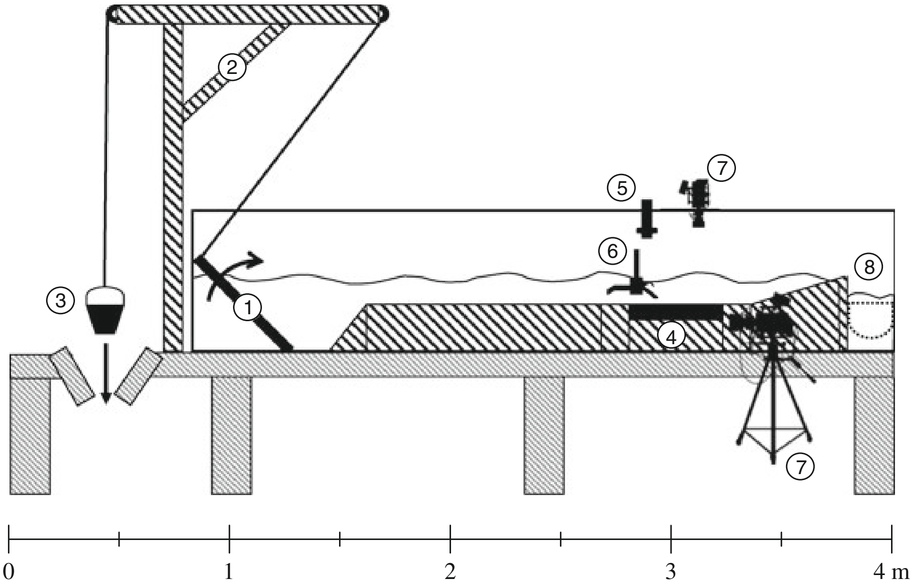

Fig. 1 Sketch of the experimental wave tank. Wave maker system: flap-plate (1), gibbet (2), bucket with varying weight (3). Observation area: removable habitat trays (4), acoustic wave sensor (5), acoustic Doppler velocimeter (6), video camera (7) and discharge basin with net (8).

50 Hz recording; Sontek, San Diego, CA, U.S.A.) with the sampling volume positioned 1 cm above the flow bed. This location was the closest location to the bottom allowed by the technical characteristics of the ADV for measurements of flow velocities faced by invertebrate species. We assumed that bottom boundary layer is thinner than the body height of the flattest invertebrate species studied so that flow velocities measured by the ADV are those really faced by invertebrates. The proportion of benthic invertebrates disturbed by the experimental waves was assessed by counting the number of individuals detached from the habitat, using video records from two cameras located on the top and on the right side of the study area (Fig. 1).

Shear stress calculation

The bottom shear stress τ (N m^{-2}) caused by the wave at the location of the habitat trays was calculated as:

$$\tau = \frac{0.5 f \rho U_b^2}{10}$$

where ρ is the density of water (1 g cm^{-3}), U_b (cm s^{-1}) is maximum wave orbital velocity (measured by the ADV) and f is the wave friction factor. The null values recorded for the vertical and lateral components of the maximum wave orbital velocity indicated that the flow in the wave tank was unidirectional. In addition, Reynolds numbers for the experimental flow calculated as:

$$\mathrm{Re} = \frac{ul}{v}$$

where u is the maximum wave velocity behind the different habitats (maximum 43 cm s^{-1}), l is the wave amplitude (Dyer, 1986) (maximum 4 cm) and v is water viscosity (*c.* 0.01 cm^2 s^{-1}), were about 10^4, which is one order of magnitude lower than the critical value reported by Jensen (1989) for turbulent flows on smooth beds. Hence, shear stress at the front of the habitat tray was mainly produced by mean flow since according to calculated Reynolds numbers, no significant turbulences were generated. Consequently, the wave friction factor was calculated according to the formula given by Dyer (1986) for laminar flow:

$$f = 2\sqrt{\frac{v}{U_b A_b}}$$

where A_b (cm) is the maximum bottom wave amplitude (measured by the acoustic wave sensor).

Flow conditions in the wave tank

Single waves (soliton) were generated in the wave tank to simulate the first wave of a characteristic ship-induced wave train hitting the habitats. In natural conditions, the first wave of a characteristic ship-induced wave train is expected to have the greatest effects on invertebrates because of its highest amplitude and sudden appearance. We thus used solitons since they are technically easier to produce in an experimental wave tank than a wave train. Using combinations of eight different weights and two water levels, waves of 10 different shear stress levels were produced in the experimental wave tank. Resulting shear stress values at the location of the habitat trays ranged from 0.45 to 2.19 N m^{-2} (Table 1), and were significantly different from each other (ANOVA with Scheffé *post hoc* test, $n = 100$, lowest significance level: $P = 0.023$; Table 1). The observed coefficient of variation for all combinations was low, ranging from 0.36% to 2.17% (Table 1), indicating that a given combination of weight and water level generated waves with similar hydraulic characteristics.

The waves produced in the wave tank (wave heights ranging from 1.5 to 8 cm and maximum orbital velocities from 11 to 50 cm s^{-1}) were comparable with wave characteristics induced by small private boats (wave heights 4.5–8.8 cm, maximum orbital velocities of 21–44 cm s^{-1}) as measured on Lake Langer See and the River Spree, Berlin, Germany (D. Franke, unpubl. data).

To assess the spatial homogeneity of the hydraulic conditions at location of the habitat trays, 10 repeated measurements of wave characteristics were conducted on both the left and right sides of the tank for two different shear stress levels (0.43 and 1.37 N m^{-2}). No significant differences in maximum wave orbital velocities, wave heights or calculated shear stress values were found between the two sides (ANOVA, $n = 10$ per test, $P > 0.05$ for all tests). Consequently, all experiments were conducted with the electronic devices fixed on the right side of the wave tank. Similarly, no significant differences in flow velocities were found at different depths along the vertical profile (measured each subsequent centimetre from 1.0 to 8.0 cm above the flow bed for 10 replicated waves of 1.37 N m^{-2}, ANOVA with Scheffé *post hoc* test, $n = 90$, $P > 0.05$), indicating that the flow generated by the waves in the experimental wave tank was vertically uniform above bottom boundary layer and that the measurement point of 1 cm distance to the bottom is representative for the flow.

Habitat trays

Five habitats [coarse woody debris (CWD), reeds, sand, stones and tree roots] commonly found in the littoral zone of north-east German lakes were used for the experiments. Structural elements used in the simulations of the five habitats were collected from regional lakes, and arranged in the removable trays on a 2 cm thick layer of sand, respecting design and densities observed under natural conditions. The CWD habitat tray consisted of two flat pieces of ridged bark of about 400 cm^2 each. The reed [*Phragmites australis* (Cav.) ex. Trin. Steud.] habitat

Table 1 Flow conditions in the wave tank

Weight (kg)	Water depth (cm)	Wave height (cm)	Wave velocity (cm s^{-1})	Shear stress (N m^{-2})	*P*-value	CV (%)
8	15	1.50 ± 0.02	11.18 ± 0.06	0.432 ± 0.002	<0.001	2.17
10	15	2.50 ± 0.03	19.29 ± 0.11	0.751 ± 0.003	<0.001	1.55
12	15	3.64 ± 0.03	28.16 ± 0.01	1.111 ± 0.004	<0.001	1.13
14	15	4.85 ± 0.03	33.74 ± 0.09	1.254 ± 0.004	<0.001	1.50
16	15	6.45 ± 0.04	39.32 ± 0.11	1.369 ± 0.004	<0.001	1.00
18	15	6.92 ± 0.04	42.37 ± 0.10	1.483 ± 0.003	0.013	0.81
20	15	7.42 ± 0.04	45.22 ± 0.10	1.579 ± 0.002	0.023	0.39
22	15	7.96 ± 0.04	47.45 ± 0.10	1.636 ± 0.003	<0.001	0.54
10	10	5.00 ± 0.04	46.29 ± 0.09	1.985 ± 0.005	<0.001	0.74
12	10	5.44 ± 0.03	50.85 ± 0.13	2.189 ± 0.005		0.36

For each shear stress level applied (combination of bucket weights and water depths), the respective wave height and velocity, as well as the calculated shear stress value (mean ± SE) with its coefficient of variation (CV, $n = 10$) is given. The level of significance (P) refers to the test of differences between two consecutive shear stress levels (ANOVA, Scheffé *post hoc* test, $n = 10$).

tray comprised 21 vertical, living reed stems, randomly distributed over the tray bottom with their intact roots underneath. In each tray, the stems density of 175 stems m^{-2} corresponded to the mean reed density observed in 30 north-east German lakes (M. Brauns, unpubl. data). The root habitat tray contained a bunch of willow roots of about 120 cm^3, fixed in the tray by a stick. The sand habitat tray simply consisted of the 2 cm layer of sand. The stone habitat tray contained six angular basaltic stones of about 60 cm^3 each, and spaced at 5 cm distances.

The habitat trays each had a comparable surface area of 0.115 m^2. The structural complexity of the five habitats was quantified by their fractal dimension (FD). FD represents habitat complexity across all spatial scales, from surface roughness of single habitat elements to distance between these elements, of the five habitats arranged in the habitat tray. In this sense, structural complexity of the habitat at high resolution levels, like for example roughness of the stones or CWD surfaces could not be captured separately. However, although structural complexity at such high resolution level also influences the ability of invertebrates to withstand wave action (i.e. by providing anchorage points), none of the invertebrate species used in the experiments exhibited a body size matching the size of habitat surface crevices, so that they could have used them to fully escape from waves. FD was calculated following Frontier's grid method (Frontier, 1987) on size-comparable top-view digital pictures of the habitat trays. The frame of the habitat tray was taken as the first square of the grid, which was progressively split into finer grids until reaching a level of 4096 squares. The structural complexity of the five habitats increased in the sequence sand (FD = 1), CWD (FD = 1.29), stones (FD = 1.34), reeds (FD = 1.39) and tree roots (FD = 1.80).

The reduction of wave kinetic energy when the wave was passing through the habitats was quantified as the difference in shear stress in front of and behind the habitat tray. Ten replicated waves were produced for four different levels of shear stress, i.e. 0.43, 1.37, 1.64 and 2.19 N m^{-2}. Differences in shear stress values calculated in front and behind the habitat tray were tested using paired *t*-tests, and between-habitat differences using ANOVA with associated *post hoc* test (Scheffé procedure).

Invertebrate species

Five epibenthic invertebrate species [*Bithynia tentaculata* (L.) (Gastropoda), *Calopteryx splendens* (Harris) (Odonata), *Dikerogammarus villosus* (Sowinsky) (Crustacea), *Gammarus roeseli* Gervais (Crustacea) and *Laccophilus hyalinus* (DeGeer) (Coleoptera)], which are all common in the littoral habitats of German lowland lakes, were used for the experiments. All these species occur in the tested habitats, although *B. tentaculata* and *D. villosus* are eurytopic, *C. splendens* is more abundant in CWD, reeds and tree roots, *G. roeseli* generally occurs in tree roots and CWD, and *L. hyalinus* is mainly found in tree roots as well as between stones.

Moreover, these species were selected because they differ considerably in body shape, locomotion behaviour and attachment strategies, all of which should influence their sensitivity to wave impact. Thus, conically shaped *B. tentaculata* attaches by its foot. *Calopteryx splendens* has an elongated body and long legs bearing strong claws, which allow it to firmly grip a wide range of habitat types. *Dikerogammarus villosus* and *G. roeseli* are laterally compressed organisms and actively swim lying on their side, reducing their exposure to flow. *Dikerogammarus villosus* is also known to fix itself strongly in crevices with its two anterior large claws. *Laccophilus hyalinus* exhibits an oval outline and is a highly mobile organism.

Bithynia tentaculata, *C. splendens, G. roeseli* and *L. hyalinus* were collected in the River Spree upstream of Berlin, and *D. villosus* in Lake Müggelsee (Berlin, Germany). New individuals were taken for each experimental series using one of the habitats, in order to avoid individual adaptation to disturbance, or decreasing fitness of individuals. For better visibility on the videos, only large specimens were used (mean body length ± SE, $n = 100$ for each species: *B. tentaculata* 9.4 ± 0.07 mm, *C. splendens* 15.8 ± 0.3 mm, *D. villosus* 15.3 ± 0.2 mm, *G. roeseli* 13.9 ± 0.1 mm, *L. hyalinus* 4.8 ± 0.04 mm). Individuals were kept in oxygen-saturated water in separate aquaria and fed with appropriate food when not used for experiments.

Experimental design

Experiments followed a crossed design with the five habitats and the five invertebrate species. After 12 h adaptation to habitat conditions in the wave tank, 20 individuals were exposed to single waves of increasing shear stress for each habitat-species combination. The corresponding invertebrate density of 71 ind. m^{-2} represents the lower end of the density range observed in north-east German lakes (M. Brauns and M. Leszinski, unpubl. data), so that no artefacts in the responses of the species to hydraulic disturbance could be generated because of strong competition for living space. During the adaptation period, water was oxygenated and the habitat trays were caged to prevent dispersal of the individuals. Cages were removed shortly before each single wave was produced and replaced immediately after. Three replicated single waves per shear stress level were produced, with a time interval of 15 min, which allowed the individuals that had been detached by the previous wave to fix or hide themselves again. Since each of the three replicated waves corresponded to a distinct experiment and no consistent trend towards increasing or decreasing detachments comparing the three replicates was detected, the numbers of detached individuals resulting from each single wave were used as replicates.

For each wave produced, wave velocity and wave amplitude were recorded to calculate the bottom shear stress. After each wave, the top and side video records were analysed to count the number of individuals detached from the habitat. The shear stress was increased until 100% of the individuals were detached or the maximum applicable shear stress was reached. Mean number of detached individuals for each habitat-species combination, in the following referred to as detachment, was calculated as the overall number of detached individuals divided by the total number of generated waves.

Statistical analysis

Relationships between the proportion of detached individuals and shear stress were explained using sigmoid regression analysis ($\ln y = b_0 + b_1/t$). The sigmoid curve best fitted the observed response of the individuals to hydraulic disturbance since there is a critical shear stress threshold at the lower end of the curve at which individuals started to become detached. Detachments averaged for the five species studied were compared among habitats using an ANOVA with associated *post hoc* test (Scheffé procedure). In order to determine the extent to which the selection of species for the study influenced the detachment observed in specific habitats, the proportions of variance explained by species and habitats were calculated separately using multiple classification analysis (MCA, Andrews *et al.*, 1973). MCA is a parametric statistical technique for examining the interrelationship between several predictor variables and one dependent variable in the context of an additive model. It provides the part of explained variance by each predictor, both before and after taking the effects of all other predictors into account. The predictor with the higher explained variance has the greater influence on the dependent variable.

Relationships between the structural complexity of the habitats (expressed by their FD) and the detachment were explored using Spearman rank correlations. Similarly, Spearman rank correlations were also used to explore relationships between structural complexity of the habitats with habitat-specific reduction of shear stress. Deviation of the data from normality and homogeneity of variances were tested using Shapiro-Wilk and Levene tests before statistical analyses. All statistical tests and regressions were performed using SPSS (version 9.0; SPSS Inc., Chicago, IL, U.S.A.).

Results

Impact of wave-induced disturbance on benthic invertebrates

The five species exposed to waves showed a similar response to increasing shear stress in four (sand, CWD, stones and reeds) of the five habitats studied. In these four habitats, the number of detached individuals generally increased with increasing shear stress (Fig. 2). These disturbance-response relationships could be well described by sigmoid regression models (Table 2), except for *B. tentaculata* on stones, where the relationship was not significant ($P > 0.05$). Conversely, such a pattern was not observed in tree root habitat where only a few individuals of each species were detached even by the strongest waves (Fig. 2). Here, a significant regression ($R^2 = 0.52$, $P = 0.01$) could only be found for *B. tentaculata*.

Role of habitat structural complexity

Detachments averaged for the five species (mean ± SE) varied among habitats. More individuals were

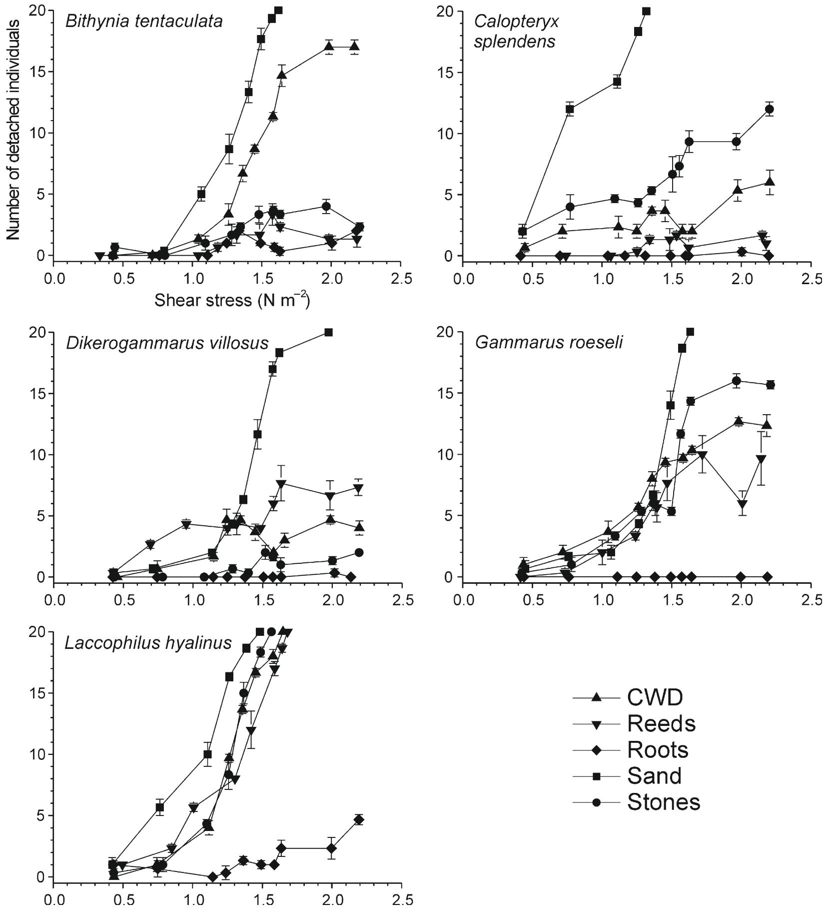

Fig. 2 Number of detached individuals from a maximum possible 20 in each habitat for the five species studied as a function of the shear stress caused by experimental waves. Plotted values represent the mean number of detached individuals (± SE) for three replicated waves. Results for each habitat are connected by lines. CWD, coarse woody debris.

Table 2 Sigmoid regression analysis ($\ln y = b_0 + b_1/t$) between number of detached individuals and shear stress

	CWD	Reeds	Roots	Sand	Stones
Bithynia tentaculata	0.81*** (7.9/−94.0)	0.48* (2.4/−56.3)	0.52* (3.3/−75.3)	0.96*** (8.0/−80.1)	0.02 n.s. (1.8/−26.0)
Calopteryx splendens	0.66* (1.8/−9.7)	0.64* (9.2/−157.8)	0.05 n.s. (−9.1/−14.3)	0.94*** (3.8/−12.5)	0.79*** (2.5/−8.5)
Dikerogammarus villosus	0.84*** (6.1/−71.3)	0.92*** (2.8/−15.3)	0.06 n.s. (−9.2/−14.4)	0.81*** (3.8/−24.0)	0.56** (3.7/−80.2)
Gammarus roeseli	0.92*** (3.1/−14.8)	0.94*** (6.6/−70.0)	0	0.77** (3.7/−21.0)	0.88*** (3.5/−21.3)
Laccophilus hyalinus	0.92*** (8.0/−78.6)	0.91*** (4.0/−21.5)	0.12 n.s. (−0.5/−5.0)	0.98*** (4.0/−16.7)	0.88*** (4.2/−25.0)

CWD, coarse woody debris; n.s., not significant.
For each test, the R^2 value (adjusted for degrees of freedom), the corresponding significance levels (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$) and the curve coefficients (b_0/b_1) are given.

detached on sand (20 ± 0) than on CWD (11.9 ± 1.7), stones (10.4 ± 1.9), reeds (7.9 ± 1.9) and tree roots (1.3 ± 0.5). The detachments were significantly higher (ANOVA, Scheffé *post hoc* test, $n = 75$) on sand than on all other habitats ($P < 0.001$, $n = 75$), and significantly lower on tree roots than on all other habitats ($P = 0.022$ at the lowest, $n = 75$). Conversely, no significant differences in detachments were observed between CWD, stones and reeds ($P > 0.05$, $n = 75$).

Comparison of the detachments of each species showed species-specific responses to wave-induced hydraulic disturbance according to habitats (Table 3). On CWD, more individuals of *B. tentaculata*, *G. roeseli* and *L. hyalinus* were detached than individuals of *C. splendens* and *D. villosus*. On reeds, more individuals of *D. villosus*, *G. roeseli* and especially *L. hyalinus* were detached than individuals of *B. tentaculata* and *C. splendens*. On stones,

Table 3 Mean number of detached individuals (average across replicates ± SE, $n = 3$) for the cross combinations of species and habitats studied

	CWD	Reeds	Roots	Sand	Stones
Bithynia tentaculata	8 ± 0.2	1.23 ± 0.0	1.47 ± 0.1	10.54 ± 0.4	2.23 ± 0.1
Calopteryx splendens	2.97 ± 0.1	0.8 ± 2.1	0.03 ± 0.0	13.27 ± 0.3	6.5 ± 0.3
Dikerogammarus villosus	2.9 ± 0.1	4.73 ± 0.1	0.03 ± 0.0	8.96 ± 0.2	0.9 ± 0.1
Gammarus roeseli	7.47 ± 0.1	5.07 ± 0.5	0.0 ± 0.0	8.5 ± 0.3	7.9 ± 0.2
Laccophilus hyalinus	10.54 ± 0.2	10.58 ± 0.3	1.47 ± 0.1	11.94 ± 0.3	9.62 ± 0.3

CWD, coarse woody debris.

more individuals of *C. splendens*, *G. roeseli* and *L. hyalinus* were detached than individuals of *B. tentaculata* and *D. villosus*. Even on sand and tree root habitats, differences in detachments among species were recorded (Table 3).

To determine the extent to which these species-specific responses might influence observed differences in the detachments among habitats, we conducted a MCA. Results showed that 77% of the variance in detachments was explained by habitat type (value corrected from the influence of the species factor) versus 47% by species (value corrected from the influence of the habitat factor – full model: $r^2 = 0.81$, $P < 0.001$, $n = 75$). Hence, the choice of the five species did not compromise the conclusion that the habitat had the strongest influence on detachment in wave experiments.

The impact of the wave-induced hydraulic disturbance on invertebrates was found to decrease along the gradient of habitat structural complexity parameterized by the FD (Fig. 3a). Detachments averaged for the five species were significantly negatively correlated to the FD of the habitats (Spearman's $\rho = -0.99$, $P < 0.001$, $n = 5$). Considering each species separately, significant negative correlations were found for *B. tentaculata* (Spearman's $\rho = -0.99$, $P < 0.001$), *C. splendens* ($\rho = -0.90$, $P < 0.05$) and *G. roeseli* ($\rho = -0.90$, $P < 0.05$).

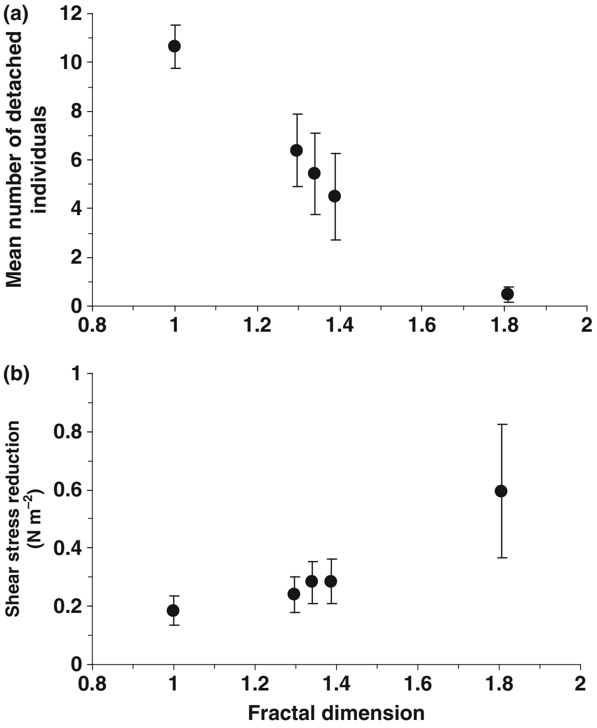

Fig. 3 Relationships to the fractal dimension of the habitats of (a) the mean number (average for the five species ± SE, $n = 15$) of detached individuals, and (b) the shear stress reduction (mean ± SE for four initial shear stress levels: 0.43, 1.37, 1.64 and 2.19 N m^{-2}, $n = 10$ each) caused by the habitats.

Shear stress in front of and behind the habitat

Shear stress measured in front of and behind the habitat trays differed significantly for all habitats ($P < 0.001$ for all tests, $n = 10$ per test). Shear stress reduction tended to increase in the sequence: sand, CWD, stones, reeds and tree roots (Fig. 4). Only waves of low initial shear stress (0.43 N m^{-2}) showed no significant differences in reduction of shear stress among habitats ($P > 0.05$, $n = 50$). For stronger waves (1.37, 1.64 and 2.19 N m^{-2}), shear stress reduction was significantly different between sand and stones ($P = 0.014$ at the lowest, $n = 50$), sand and reeds ($P = 0.001$ at the lowest, $n = 50$) except for waves of 1.37 N m^{-2}, as well as between roots and the other habitats ($P = 0.012$ at the lowest, $n = 50$). No significant differences were recorded between CWD, stone and reed habitats, except for waves of 2.19 N m^{-2}, where shear stress reduction in stones was significantly higher ($P < 0.001$, $n = 50$) than in CWD (Fig. 4). The reduction of shear stress caused by the habitat

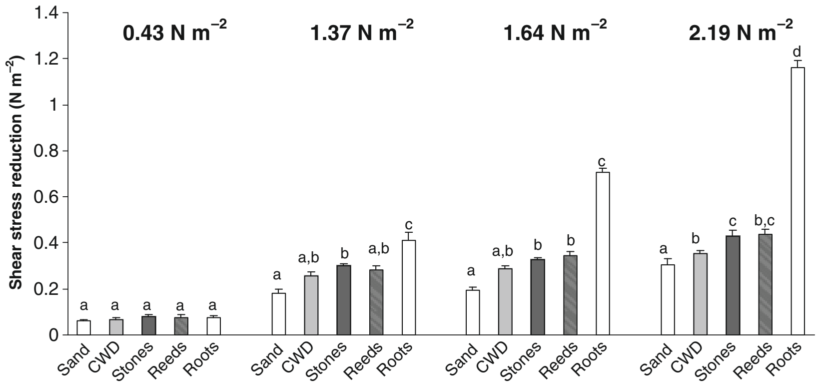

Fig. 4 Reduction of shear stress (mean ± SE, $n = 10$ each) caused by the five habitats studied under the four different shear stress levels indicated. Shear stress reduction was calculated as the difference between shear stress values measured in front of and behind the habitat tray. Bars with different letters indicate significant differences among habitats for a given shear stress level (ANOVA, Scheffé *post hoc* test, $n = 50$). CWD, coarse woody debris.

was correlated with the structural complexity of the habitat (Fig. 3b), as shown by the significant positive correlations found between habitat-specific shear stress reductions and habitat FD for three of the four shear stress levels tested (1.37 N m^{-2}: Spearman's $\rho = 0.90$, $P < 0.05$; 1.64 and 2.19 N m^{-2}: both $\rho = 0.99$, $P < 0.001$).

Discussion

Impact of wave-induced hydraulic disturbance on benthic invertebrates

In our experiments, clear relationships were found between wave-induced shear stress and invertebrate detachment for all habitats except tree roots, and for each species studied. Our observations were best described by a sigmoid regression model, which revealed a threshold of shear stress corresponding to the beginning of mass detachment of invertebrates. This threshold varied according to the habitat-species combination considered, but was mainly observed to be at 1.0–1.2 N m^{-2}. Furthermore, 50% of individuals were already detached at shear stress values from 1.5 N m^{-2}. Such shear stress values were produced in the wave tank by waves with an orbital velocity of 19–42 cm s^{-1}, and bottom shear stresses produced under natural conditions by boats are generally higher. For example, maximum orbital velocities measured in the littoral zones of Lake Langer See and the River Spree ranged from 21 to 44 cm s^{-1} for small private boats, up to 54 cm s^{-1} for freight barges and up to 65 cm s^{-1} for passenger ships (D. Franke, unpubl. data), which indicates that hydraulic disturbance created in the wave tank corresponded to the lowest disturbance experienced by benthic invertebrates in natural conditions. Moreover, due to their large dimensions, passenger ships or commercial barges create waves that tend to break before they reach the shoreline. Such breaking waves produce even more severe hydraulic conditions and the detachment of invertebrates is probably higher under those conditions than in the wave tank. Hence, detachment of invertebrates by waves should also occur under field conditions and is probably a widespread phenomenon in the littoral zones of navigable waterways.

Complex habitats provide refuge for invertebrates

The detachment of invertebrates by wave-induced hydraulic disturbance was found to be significantly reduced in complex habitats that provide numerous refuges and anchorage points enabling individuals to resist drag forces imposed by peaks in flow velocity. Sand did not offer suitable hiding or fixing options for any of the five species and as a result, mass detachment of individuals started here at low shear stress values (0.4–0.8 N m^{-2}). In contrast, root habitats offered maximal sheltering conditions for all the studied species, and the dense network of tiny, flexible branches of the root network allowed every species, irrespective of its size or gripping abilities, to enter the network and fix itself. Even *B. tentaculata*, for which the tiny root branches do not offer optimal surfaces for efficient foot adhesion, showed a low detachment here.

Slightly fewer individuals were detached in reed than in stone or CWD habitats. However, since no significant differences were recorded between these three habitats in the detachments of all five species combined, these habitats evidently offered a similar level of protection against detachment despite their differing FD. Nevertheless, the five species showed differences in detachments among these three habitats, and species-specific differences in detachments were also observed for a given habitat. Furthermore, significant negative correlations between detachment and habitat FD were found for only three of the five species studied. Thus, detachment did not only depend on habitat complexity, but also partially on the extent to which species-specific fixing or hiding capabilities matched the physical habitat characteristics. For example, the rough ridges of CWD provided good anchorage points for species fixing themselves with big claws, such as *C. splendens* and *D. villosus*, but not for either *B. tentaculata*, which needs smoother surfaces for efficient attachment, or for *G. roeseli* and *L. hyalinus*, which possess smaller claws. Similarly, reeds provided better sheltering conditions against waves for *B. tentaculata* and *C. splendens* than for *L. hyalinus* and the two crustaceans. Reed stems provided an ideal smooth surface for *B. tentaculata*, while *C. splendens* was able to fix itself by gripping the reed stems between its long legs. In contrast, the claws and legs of *L. hyalinus, D. villosus* and *G. roeseli* were far too small to grip reed stems firmly. Species such as *L. hyalinus* and *G. roeseli*, which do not exhibit morphological or behavioural characteristics matching the structural characteristics of the CWD, stone or reed habitats used in the experimental wave tank, were strongly detached.

Despite specific habitat-species relationships, the structural complexity of the habitat has proved to influence the degree of protection of benthic invertebrates against wave-induced hydraulic disturbance. The higher proportion of variance in detachments explained by habitat features alone, in comparison to the influence of the species used, supports the conclusion that there is a strong causal relationship between detachment and the structural complexity of the habitat. Comparable influences of habitat complexity in sheltering benthic invertebrates against hydraulic disturbance have been demonstrated for *Seratella ignita* (Poda) and *Gammarus pulex* (L.) exposed to high currents (Borchardt, 1993). In that study, the proportion of drifting individuals decreased as more and more woody debris was added to the sandy bottom of a circular flume. *Seratella ignita* started to drift at lower shear stress values (1.1 N m^{-2}) than *G. pulex* (3.1 N m^{-2}), a fact attributed to behavioural differences between the swiftly swimming *G. pulex* and the slowly crawling *S. ignita*.

Habitat complexity dissipates wave kinetic energy

Besides providing refuges for the organisms, the spatial structure of benthic habitats also influences the hydrodynamics in their surroundings (Grass, 1971). From the perspective of flow mechanics, the structure of the habitat provides obstructions to the unidirectional flow, transforming some portion of the mean flow into turbulent components. In turbulent flows, the kinetic energy is extracted by larger vortices from the mean flow, transferred by the cascade of turbulences towards smaller scales, where it finally dissipates into heat because of molecular viscosity (Tennekes & Lumley, 1972; Townsend, 1976). Correspondingly, higher structural complexity provides more obstacles to flow and dissipates a larger portion of kinetic energy. Notably, with almost 1.2 N m^{-2} of shear stress reduction, which corresponds to 54% of the shear stress caused by the strongest wave produced in the wave tank, roots were three to four times more efficient in dissipating kinetic energy than any other habitat studied. A direct implication for invertebrates is that in more complex habitats, hydraulic disturbance is attenuated after a short distance inside the habitat patch, so that even small patches of complex habitats may serve as effective refuges.

On the other hand, generated turbulences may potentially increase detachment of individuals since the erratic flow pattern creates drag forces constantly varying in direction. Shear-stress distribution depends on the spatial arrangement of the habitat elements providing obstacles to flow and is even more complex in presence of turbulences, so that the relative influences of refuges, dissipation of wave kinetic energy or turbulences on invertebrate detachment are difficult to assess separately. As a general pattern, habitat efficiency to dissipate wave energy was found to increase following the habitat sequence CWD, stones and reeds. In parallel, for species whose specific fixing capabilities do not strongly match fixing options of a specific habitat (i.e. *C. splendens* and reeds), intensity of detachment was found to follow a reverse habitat sequence. For example, *C. splendens* and *G. roeseli* were more detached in stone habitat than in CWD habitat. Similarly, *D. villosus* was more detached in reed habitat than in CWD or stone habitats. Hence, it is probably that refuges provided by complex habitats as well as how habitat structure matches species fixing capabilities, act as the main factor in sheltering invertebrates. Concomitantly, in more complex habitats, waves are attenuated after a shorter distance, improving sheltering conditions for invertebrates.

Implication for shoreline management

We could show that the effect of wave disturbance resulted in significant detachment of invertebrates even at moderate shear stress levels. Since ship-induced waves occur stochastically and create harsh hydraulic conditions, they constitute a major hydraulic disturbance for invertebrate inhabiting shoreline habitats. The threshold values at which invertebrates started to be detached were lowest in the sand habitat (0.4–0.8 N m^{-2}), intermediate in the other habitats (1.4–1.6 N m^{-2}) and not reached for tree roots even at the maximum shear stress levels produced in the wave tank (2.19 N m^{-2}). It can be concluded that network habitats such as tree roots, and to a certain extent also dense reed belts, provide efficient protection of invertebrates against wave-induced disturbance. Mechanistic explanations are that complex three-dimensional habitats provide both the best options for all species to hide or to fix themselves, and also the strongest dissipation of kinetic wave energy.

Consequently, complex habitats such as tree roots and dense reed belts should be protected to preserve a diverse and natural fauna in the littoral zone of inland waterways, as required by water policies. These habitats are often removed during shoreline stabilisation, which in urban areas results in two additive constraints on the littoral fauna, i.e. simplification of habitat structure and increase of hydraulic stress. Also, tree root habitats and reed stands may be heavily damaged if ship-induced waves occur repeatedly over the long-term (Ostendorp, 1989, 1999), amplifying the short-term ecological effects of ships passing by. These factors lead to a reduction in species richness and decreased abundances of the benthic communities (Bishop, 2003, 2004, 2005) in wash-zones. Thus, water managers should be able to reduce ship-induced disturbance in the littoral zone to a level lower than the detachment threshold for typical species, so that invertebrate assemblages in wash-zones maintain similar structure and abundance patterns as in non-wash zones.

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WATER-LEVEL FLUCTUATIONS

Potential effects of water-level fluctuations on littoral invertebrates in lowland lakes

Mario Brauns · Xavier-François Garcia · Martin T. Pusch

Abstract East-German lowland lakes are highly susceptible to climatic changes, as most lakes are groundwater fed and strongly dependent on the balance of precipitation and evapotranspiration in their catchments. As a significant decrease of precipitation at least during summer is forecasted, a substantial and permanent reduction of lake water levels can be expected. Water-level fluctuations will predominantly affect the eulittoral zone where submerged tree roots form an important habitat type in lowland lakes that will become unavailable for eulittoral invertebrates. Hence, we compared the invertebrate community from eulittoral root habitats with those of infralittoral habitats to test which components of the invertebrate community would be potentially affected by the loss of root habitats, and whether infralittoral habitat types could mitigate these effects. Species richness did not significantly differ between eulittoral roots and the infralittoral habitat types. Community composition of roots significantly differed from that of coarse woody debris, sand and stones but not from reed habitats. Abundances of Coleoptera, Trichoptera and abundances of piercer, predator, shredder and xylophagous species were significantly lower on sand than on roots. Conversely, there were no significant differences in community measures between reed and root habitats except abundances of Coleoptera. Our results suggest that the loss of eulittoral root habitats will cause a significant alteration of the littoral invertebrate community. This could be mitigated if unimpaired reed habitats are available in the infralittoral zone which may serve as a refuge for most species typical for root habitats. Our results need to be verified by direct observations, especially as the extent of future water-level fluctuations is currently not assessable and might be more severe than assumed.

Keywords Climate change · Habitat–species relationships · Reed · Roots

Introduction

According to current knowledge, the average air temperature in central Europe will increase by 3–5°C within the next century, depending on the future emissions of greenhouse gases (Intergovernmental Panel on Climate Change, 2001). Air temperature has

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Ecological Effects of Water-Level Fluctuations in Lakes

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already increased by up to 1°C in the time period 1891–1990 in East Germany (ATV-DVWK, 2003). Concomitantly, annual precipitation has slightly decreased by 50 mm/year in major parts of East Germany within the time period from 1961 to 1990 (ATV-DVWK, 2003). For the Federal state of Brandenburg, a rise in air temperature of 1.4°C by the year 2055 and a reduction of annual precipitation of up to 200 mm are predicted, which will mainly occur during summer (PIC, 2003). Thus, the subcontinental features of the climate will get more prominent. This will cause dramatic changes in regional hydrological budgets, with associated consequences for agriculture, forestry and water management (PIC, 2003). The expected alteration of the hydrological regime may severely affect lowland lakes in the eastern part of Central Europe, as their water level is strongly dependent on the groundwater level that in turn shows sensitive response to the precipitation regime. Hence, the forecasted reduction of annual precipitation and increasing of air temperatures may lead to a substantial reduction of mean water levels in groundwater supplied lakes. Moreover, the increased evapotranspiration in the catchments and a relative shift in precipitation towards winter may lead to higher amplitudes of seasonal water-level fluctuations. Hence, water-level fluctuations are expected to become a strong anthropogenic component in the function of lowland lakes in the eastern part of Central Europe. Most of the existing knowledge on the effects of human-altered hydrological regimes is derived from studies on reservoirs or regulated lakes, where water-level fluctuations up to 20 m can occur (e.g. Smith et al., 1987). There, water-level fluctuations were demonstrated to affect the shore zone of reservoirs directly by desiccation and bottom freezing (Hynes, 1961; Palomaki & Koskenniemi, 1993) but also to affect the littoral food web by the loss of food resources such as macrophytes (Wilcox & Meeker, 1991; Wilcox & Meeker, 1992; Hill et al., 1998). Benthic invertebrates are the biotic component of lake shores that are most severely affected by these alterations since their low mobility restricts their ability to follow the receding water. Consequently, in reservoirs and regulated lakes, invertebrate richness and abundance were lowest in the eulittoral zone and highest within the sublittoral zone below the drawdown limit (Smith et al., 1987; Koskenniemi, 1994; Palomaki, 1994). In lakes characterised by natural water-level fluctuations, the amplitude of the fluctuation is smaller and follows a more regular seasonal pattern. There, the highest invertebrate diversity and biomass are found in eulittoral and infralittoral zones of lakes (Czachorowski, 1989, 1993). Thus, increasing water-level fluctuations would cause a loss of eulittoral habitats with associated impacts on eulittoral invertebrates as a crucial biotic component of lake ecosystems. In this study, we examined the potential effects of water-level fluctuation on the eulittoral invertebrate community of six East-German lowland lakes. We compared invertebrate communities from eulittoral root habitats with those from four infralittoral habitats to test which components of the invertebrate community would be affected by the loss of the root habitats, and whether the infralittoral habitat types could mitigate these effects.

Methods

Invertebrate sampling

The six studied lakes are located in East Germany and cover different lake types, i.e. hypertrophic riverine lakes and groundwater supplied mesotrophic lakes (Table 1). Invertebrates samples were taken from the five major habitat types in East-German lowland lakes, i.e. roots within the eulittoral zone (0–0.2 m water depth) and coarse woody debris (CWD), reed, sand and stones within the infralittoral zone (0.2–1.2 m water depth). Sampling was conducted in October 2003 and in April 2004 on a total of 40 sampling stations (eight per habitat type). Each habitat type was sampled separately using the sampling technique best adapted to the degree of structural complexity of the habitat. This should ensure a maximum of sampling efficiency and allows for a comparison of samples from different habitat types. We took five subsamples from submerged roots of riparian alder trees (*Alnus glutinosa*) with a hand net (250-µm mesh, 24 cm width) and estimated the sampled area by multiplying hand net width with the respective sampling depth. Invertebrates from CWD habitats were brushed from three pieces of CWD with comparable states of decay, and subsamples were sieved through a mesh (250 µm). Subsequently, length and diameter of each piece of

Table 1 Geographical location, area, trophic status and hydraulic residence time (RT) of the studied lakes

	Geographical location		Area (km^2)	Trophic state	RT (year)
	Latitude	Longitude			
Grienericksee	53°06′22″	12°53′12″	2.69	Eutrophic	0.40
Langer See	52°24′32″	13°36′50″	2.51	Hypertrophic	0.10
Müggelsee	52°26′16″	13°38′55″	7.70	Eutrophic	0.16
Plauer See	52°23′33″	12°26′33″	6.70	Hypertrophic	0.01
Unteruckersee	53°16′41″	13°51′51″	10.40	Mesotrophic	2.00
Werbellinsee	52°55′16″	13°42′43″	1.80	Mesotrophic	54.79

CWD were measured, and surface area was calculated assuming a cylindrical shape. We took five 1 m sweeps from reed habitats using a hand net (250-µm mesh, 24 cm width). We estimated the sampled area of reed habitats by multiplying hand net width with length of the sampled area. Sand habitats were sampled with 10 subsamples using a modified Surber sampler for lentic conditions (area 0.05 m^2, 250 µm mesh). For stone habitats, we randomly chose 10 stones from each sampling station and brushed off attached invertebrates. From each stone, surface area was calculated based on its length, height and width assuming an ellipsoid shape. Subsequently, subsamples from each habitat type were pooled to create a composite sample per habitat type. Samples were preserved in the field, and invertebrates were identified in the laboratory to species level. Chironomidae and Oligochaeta could only be determined to family or order level, respectively, and were omitted from further analyses because information on their ecological traits, e.g. functional feeding groups, is imprecise on these taxonomic levels (Lenat & Resh, 2001). Similarly, non-indigenous species *Dreissena polymorpha* (Pallas, 1771) Bivalvia, *Atyaephyra desmaresti* (Millet, 1831), *Chelicorophium curvispinum* (Sars, 1895), *Dikerogammarus haemobaphes* (Eichwald, 1841), *Dikerogammarus villosus* (Sowinsky, 1894), *Echinogammarus ischnus* (Stebbing, 1906), *Gammarus tigrinus* (Sexton, 1939), *Pontogammarus robustoides* (Sars, 1894) (Crustacea) and *Potamopyrgus antipodarum* (Gray, 1843) (Gastropoda) were excluded from further analyses, as their occurrence is mainly independent from habitat type (e.g. Van den Brink et al., 1993; Devin et al., 2003) and their dominance could supersede compositional differences among habitats that are related to native species. Information on invertebrate functional feeding groups was taken from Schmedtje & Colling (1996).

Statistical analysis

Since sampling techniques for the different habitat types were not fully comparable, we converted species densities into relative abundances. Prior to analyses, we tested whether there are differences in the invertebrate community measures from autumn and spring using non-parametric Mann–Whitney test (SPSS, Version 9.0, SPPS Inc., Chicago). Since from 19 community measures only percentages of Gastropoda, Heteroptera, Scrapers, and Parasites were significantly different between seasons, we pooled the data from autumn and spring. We used non-metric multidimensional scaling (NMS) and analysis of similarity (ANOSIM, PRIMER, Version 5, Primer-E Ltd., Plymouth) to test for differences in community composition between eulittoral root and the four infralittoral habitat types using Bray–Curtis similarity as the distance measure. ANOSIM is based on the assumption that if the community composition of two habitat types significantly differ, the similarities between habitats should be lower than the similarities within a habitat. This is expressed by the R-statistic, which ranges from 0 to 1, where $R = 1$ if all replicates of a habitat type are more similar to each other than to any replicate from the other habitat type. Indicator species for each habitat type were defined using the indicator species analysis (Dufrene & Legendre, 1997) (PcOrd, Version 4.25, MjM Software, Gleneden Beach) where indicator values close to zero mean no indication and indicator values close to 100 mean perfect indication of a habitat type by a species (Dufrene & Legendre, 1997). Differences in species richness, relative abundance of major taxonomic and functional feeding groups between roots and the four infralittoral habitat types were tested with non-parametric Mann–Whitney tests (SPSS, Version 9.0, SPPS Inc., Chicago) using Bonferroni correction to adjust the level of significance of the pairwise comparisons.

Results

Non-metric multidimensional scaling ordination of the invertebrate community of root and the four infralittoral habitats revealed strong compositional differences (Fig. 1). NMS ordination of root and CWD samples showed that both habitat types were colonised by distinct communities (Fig. 1A) that significantly differ from each other (ANOSIM: R-statistic $= 0.37$, $P = 0.001$). Similarly, invertebrate communities significantly differed between root and sand (ANOSIM: R-statistic $= 0.65$, $P = 0.001$, Fig. 1C) and between root and stones (ANOSIM: R-statistic $= 0.49$, $P = 0.001$, Fig. 1D). NMS ordination of the invertebrate communities of root and reed revealed that samples from both habitat types strongly overlap (Fig. 1B). Consequently, ANOSIM did not detect significant differences between communities of both habitat types (R-statistic $= 0.05$, $P = 0.241$). Median invertebrate richness (range) ranged from 22 (9–37) on sand habitats to 15 (13–28) on stone habitats but did not significantly differ between roots (21, 14–52) and any of the infralittoral habitat types (Mann–Whitney test, $P > 0.05$). Conversely, differences between eulittoral root and the four infralittoral habitats were apparent in the abundances of the major taxonomic groups. Here, the strongest differences were found for Coleoptera as well as for Odonata, Ephemeroptera and Trichoptera (Table 2). For example, the abundance of Coleoptera was highest in the root habitat and significantly lower in reed, sand and stone habitats. Abundances of Odonata were highest in root habitats, but they were absent within the infralittoral zone from all but the reed habitats (Table 2). The abundance of Ephemeroptera was significantly lower on CWD than on roots, and abundance of Trichoptera was significantly lower on sand than on root habitats. Distinct indicator species were found in roots, CWD, sand and stones (Table 3). For example, the dragonfly *Ischnura elegans* (Vander Linden, 1820) and the water beetle *Haliplus flavicollis* (Sturm, 1834) were highly indicative for root habitats, while sand habitats were particularly characterised by species of the genus *Pisidium* (Bivalvia) (Table 3). No indicator species were found for reed habitats.

Major differences in the functional feeding group composition between eulittoral roots and the four infralittoral habitat types were found for sand habitats (Table 4). Here, relative abundances of piercer,

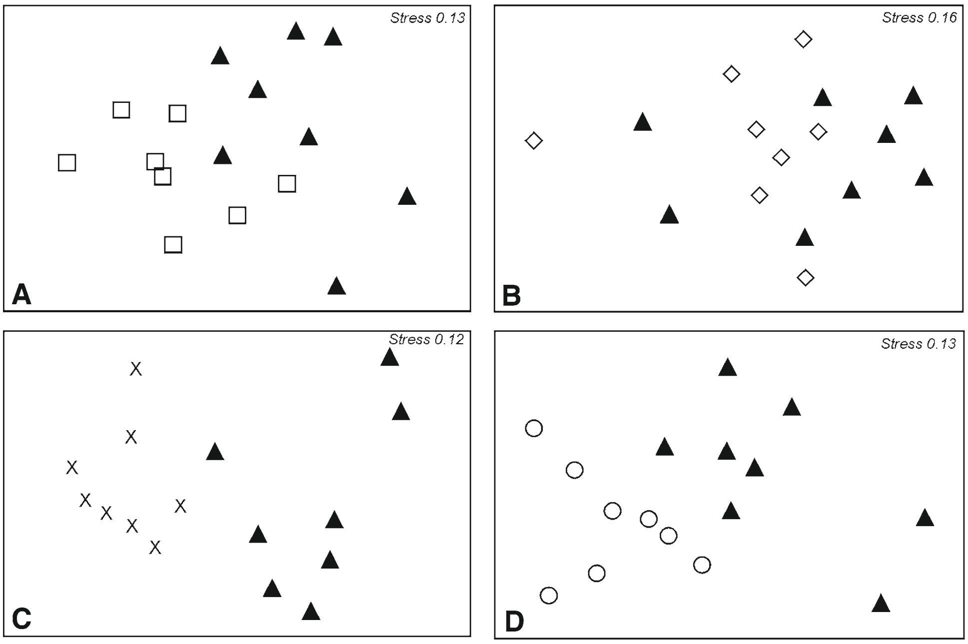

Fig. 1 Non-metric multidimensional scaling (NMS) ordination of the invertebrate community of roots (triangles) together with the invertebrate community of (**A**) coarse woody debris (squares), (**B**) reed (diamonds), (**C**) sand (crosses) and (**D**) stone habitats (circles)

Table 2 Median (range) relative abundances of the major invertebrate taxonomic groups at the five studied habitat types present in the eulittoral and infralittoral zone

	Eulittoral	Infralittoral			
	Roots	CWD	Reed	Sand	Stones
Bivalvia	0.0	0.0	0.0	48.1	0.0
	0.0–0.2	0.0–0.0	0.0–2.2	8.4–67.3	0.0–0.3
Coleoptera	9.6	4.5	1.4**	0.2**	0.4*
	1.4–37.0	0.0–56.1	0.0–5.0	0.0–3.1	0.0–21.3
Crustacea	0.0	0.0	0.0	0.0	0.0
	0.0–3.8	0.0–0.6	0.0–10.6	0.0–0.1	0.0–0.2
Ephemeroptera	16.3	0.7*	2.6	26.3	5.1
	7.7–48.5	0.0–27.8	0.0–35.6	0.2–57.3	0.2–54.0
Gastropoda	23.1	6.1	51.7	20.9	11.2
	3.8–73.3	1.5–71.7	23.6–92.7	0.0–76.9	0.1–65.9
Heteroptera	0.3	0.0	0.6	2.4	0.3
	0.0–3.8	0.0–0.9	0.0–20.7	0.5–6.9	0.0–1.0
Hirudinea	0.7	0.4	0.9	0.2	0.3
	0.0–4.8	0.0–3.3	0.0–2.8	0.0–2.1	0.0–1.5
Odonata	4.0	0.0	0.4	0.0	0.0**
	0.0–9.4	0.0–0.5	0.0–1.4	0.0–0.1	0.0–0.2
Trichoptera	27.4	75.7	23.1	3.7**	60.7
	11.3–42.3	19.8–98.1	4.3–67.3	1.5–19.0	18.0–97.3
Turbellaria	0.3	0.0	0.0	0.0	0.3
	0.0–35.8	0.0–11.8	0.0–1.8	0.0–0.1	0.0–13.3

Significantly lower abundances (Mann–Whitney test, Bonferroni adjusted P) between root and infralittoral habitats are indicated by asterisks (** $P < 0.01$, * $P < 0.05$)

predator, shredder and xylophagous species were significantly lower than on the roots habitats. Furthermore, abundances of shredder were significantly lower on all but the reed habitats (Table 4).

Discussion

Species richness did not differ between the five studied habitat types, indicating that all habitat types similarly contributed to the local biodiversity. However, invertebrate community composition differed significantly between roots and all but the reed habitat. Particularly, Coleoptera and Odonata were found in high abundances in roots, while their abundances were lower in the infralittoral habitats. This suggests that Coleoptera and Odonata are the components of the invertebrate community that will be most severely affected by increasing water-level fluctuations and that a loss of root habitats may lead to the disappearance of species in both taxonomic groups.

The strongest differences in the examined community parameters were found between root and sand habitats. Despite a similar level of species richness, both communities differed significantly and were characterised by indicator species that primarily reflect the physical properties of the habitat types. For example, roots constitute a three-dimensional structured habitat that provides niches for large-bodied species of Coleoptera and Odonata, while structurally uniform sand habitats were dominated by small Bivalvia such as *Pisidium*. Furthermore, root habitats provided various food resources such as periphyton or CPOM as indicated by the dominance of scrapers and collector/gatherers, while functional feeding group composition on sand was dominated by filter feeders that rely on seston. In the littoral zone of several US lakes, periphyton production accounted for 98% of the whole lake primary production (Vadeboncoeur et al., 2003), and carbon derived from this food resource was used by species of subsequent trophic levels. Hence, an extreme drawdown of the water level that would be paralleled by

Table 3 Indicator species analysis of the five studied habitat types present in the eulittoral and infralittoral zone

	Eulittoral	Infralittoral			
	Roots	CWD	Sand	Stones	Reed
Gastropoda					
Gyraulus crista			46*		
Valvata piscinalis			48*		
Bivalvia					
Pisidium casertanum			88***		
P. henslowanum			75***		
P. moitessierianum			38*		
P. nitidum			100***		
P. subtruncatum			50**		
P. supinum			50**		
Unio tumidus			63***		
Ephemeroptera					
Caenis horaria			61*		
Odonata					
Ischnura elegans	69***				
Heteroptera					
Micronecta sp.			79***		
Coleoptera					
Cercyon sp.	32*				
Dryops sp. larvae	33*				
Haliplus flavicollis	46*				
Orectochilus villosus larvae		43*			
Trichoptera					
Goera pilosa				46*	
Lype phaeopa		67**			
Molanna angustata			43**		
Tinodes waeneri				64**	

For each indicator species, its indicator value and level of significance (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$) are given

the loss of all, but the sand habitats would disrupt a major pathway of carbon in the littoral zone of lakes. This conjecture is supported by studies on an US reservoir, where strong water-level fluctuations caused a shift of food resources of invertebrates from benthic-derived carbon to pelagic-derived carbon (Black et al., 2003). Hence, sand habitats may not substitute root habitats if an alteration of the hydrological regimes would cause a receding water level within the studied lakes. In contrast to sand habitats, community composition of reed did not significantly differ from that of root habitats. Despite differences in the abundance of Coleoptera, none of the major taxonomic groups found in the root habitats were completely absent in the reed habitat, most likely as the result of a comparable degree of habitat complexity compared. Hence, dense reed habitats may substitute the loss of the root habitats. However, reed stands are subjected to various kinds of human impairments such as wave disturbance or eutrophication that reduces their stem density (Ostendorp et al., 1995). Consequently, the ability of reed habitats to substitute the loss of root habitats could be limited in lakes with significant human impacts on the lake shore.

In summary, we demonstrated that submerged roots of riparian trees constitute an important habitat in the littoral zone colonised by a distinct invertebrate community. However, eulittoral root habitat may fall dry for extended time periods if water-level fluctuations increase as predicted for East and Central Europe. The loss of root habitats could partially be

Table 4 Median (range) relative abundances of the invertebrate functional feeding groups at the five studied habitat types present in the eulittoral and infralittoral zones

	Eulittoral	Infralittoral			
	Root	CWD	Reed	Sand	Stone
Collector/gatherer	33.9	17.6	30.1	45.3	22.9
	16.9–44.6	2.1–37.9	9.6–50.2	14.7–64.5	5.3–62.5
Filterer	1.7	5.6	4.1	48.3	5.1
	0.0–6.8	1.4–9.3	1.3–7.2	9.6–69.2	1.8–8.7
Piercer	6.4	6.3	7.3	0.7**	5.1
	1.1–15.4	2.7–25.1	1.1–22.9	0.0–3.6	0.8–32.9
Predator	18.9	15.9	8.0	1.5**	14.8
	2.9–47.7	2.8–74.0	1.0–10.9	0.2–6.4	4.4–48.2
Scraper	24.2	37.0	43.8	12.0	28.6
	9.2–37.3	5.6–61.9	27.3–55.0	0.1–31.0	11.6–58.6
Shredder	7.0	2.3**	8.2	3.0**	1.8***
	5.0–20.4	0.1–6.3	2.0–14.1	0.3–5.8	0.0–4.9
Xylophagous	0.7	1.5	0.0	0.0**	0.0
	0.0–4.2	0.0–44.4	0.0–7.1	0.0–0.0	0.0–3.0

Significantly lower abundances (Mann–Whitney test, Bonferroni adjusted *P*) between root and the infralittoral habitat types are indicated by asterisks (*** $P < 0.001$, ** $P < 0.01$)

substituted by a dense infralittoral reed stand, which seems to offer similar habitat conditions. However, total habitat area available for the species found in root and reed habitats will be clearly reduced at lowered water levels. Conversely, CWD, stone and especially sand habitats may not provide an appropriate substitute habitat due to their limited habitat complexity. Our results on the potential effects of water-level fluctuations on littoral invertebrates have to be verified by further studies, especially as the amplitude of future water-level fluctuations is currently not assessable and might more be severe than assumed.

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Effects of human shoreline development on littoral macroinvertebrates in lowland lakes

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Summary

1. The shores of many lakes have been substantially altered by human developments such as erosion control structures or recreational beaches. Such alterations are likely to increase in the future, yet almost nothing is known about their impacts on the littoral macroinvertebrate community.

2. Macroinvertebrates were studied in seven German lowland lakes exhibiting natural shorelines (reference), retaining walls, ripraps and recreational beaches to examine impacts on the eulittoral (0–0·2 m water depth) and infralittoral (0·2–1·2 m water depth) communities associated with the three types of shoreline development.

3. Among sites, eulittoral species richness and abundance of Coleoptera, Gastropoda, Trichoptera, shredders and xylophagous species were lowest on beaches and retaining walls but ripraps did not differ significantly from natural shorelines. Retaining walls and ripraps had no significant impact on the infralittoral macroinvertebrate community. Conversely, beaches had significantly lower infralittoral species richness and abundance of Ephemeroptera, Trichoptera and shredders than natural shorelines. Furthermore, species richness was correlated positively with habitat heterogeneity expressed as number of habitat types.

4. Among lakes, whole-lake littoral macroinvertebrate density increased with increasing proportion of developed shorelines due to increasing abundances of Chironomidae. The remaining macroinvertebrate major groups decreased with increasing proportion of shoreline development.

5. *Synthesis and applications*. The biological impacts of shoreline development in lowland lakes depend upon the extent to which structural complexity and heterogeneity of littoral habitats are reduced. Hence, we recommend that management programmes focus upon the conservation of littoral habitat complexity and habitat heterogeneity. The biological effects of shoreline development may be assessed efficiently by combining an assessment of the morphological status of lakeshores and information on macroinvertebrate indicator species with a defined response to the loss of their preferred habitats.

Key-words: biodiversity, coarse woody debris, habitat complexity, lake management, macrophytes, recreational beaches, retaining walls, riparian clearcutting, ripraps

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Introduction

Lakeshores have always been a preferential place for human settlement and various other human activities (Liddle & Scorgie 1980; Ostendorp, Schmieder & Jöhnk 2004), leading to shoreline development and the discharge of waste water on lakeshores. While the discharge of waste water has been widely reduced, shoreline development represents a current threat to the ecological integrity of lakes world-wide (Stadelmann 1990; Bryan & Scarnecchia 1992; Engel & Pederson 1998; Elias & Meyer 2003; Toft *et al.* 2003; Teiber 2003). Moreover, the intensity of shoreline development is expected to increase in the future (Walz, Brüggemann & Ostendorp 2002; Schmieder 2004).

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Table 1. Area, trophic status, hydraulic residence time (RT), shoreline length (L_{shore}) and the percentages of natural shorelines (Natural), retaining walls and ripraps (Erosion control), and beaches on total shoreline length at the seven studied lakes

					Shoreline type (%)		
Lakes	Area (km^2)	Trophic status	RT (year)	L_{shore} (km)	Natural	Erosion control	Beach
Grienericksee	2·69	Eutrophic	0·40	6·4	76	21	3
Langer See	2·51	Hypertrophic	0·10	18·3	35	61	4
Müggelsee	7·70	Eutrophic	0·16	11·1	63	29	8
Plauer See	6·70	Hypertrophic	0·01	15·7	86	14	–
Ruppiner See	6·33	Eutrophic	11·00	36·8	87	13	–
Unteruckersee	10·40	Mesotrophic	2·00	16·7	91	8	1
Werbellinsee	1·80	Mesotrophic	54·79	24·4	83	11	6

In general, shoreline development is considered to impact the littoral zone through alteration or loss of littoral habitats such as a reduction of macrophyte stands, most prominently the littoral reed belts (Sukopp 1971; Radomski & Goeman 2001; Elias & Meyer 2003) and an alteration of sediment particle size composition (Jennings *et al.* 2003). Also, the amount of coarse woody debris (CWD) in the littoral zone can be reduced substantially in lakes with a high proportion of shoreline development (Christensen *et al.* 1996; Marburg, Turner & Kratz 2006).

The biological impacts of human shoreline development have been quantified mainly for littoral fish communities, particularly on spatial aggregation (Scheuerell & Schindler 2004), species richness (Jennings *et al.* 1999) and production (Schindler, Geib & Williams 2000; Radomski & Goeman 2001). Impacts on littoral macroinvertebrates are likely, as macroinvertebrates exhibit a stronger dependence on littoral habitats and are less mobile than fish. However, we are aware of only one study that examined the impacts of shoreline development on littoral macroinvertebrates. Bänziger (1995) compared macroinvertebrate communities of shorelines subjected to three different types of developments with those of five types of natural shorelines in Lake Geneva, a large prealpine Swiss lake. She found species diversity and abundance to be lowest at developed shorelines. However, the validity of these results in other lake types is unknown, and the impact of recreational use on littoral macroinvertebrates has, to our knowledge, never been examined. An understanding of the ecological impacts of shoreline development in various lake types forms a prerequisite for a scientifically based ecological management of lakeshores. In particular, this applies to the assessment of their ecological status as well as the identification and implementation of effective restoration measures to improve heavily degraded shores.

In this study, we aimed to quantify the impact of three types of shoreline development on macroinvertebrate communities of seven German lowland lakes differing in trophic status and hydrological regime. We compared two types of erosion control structures (retaining walls, ripraps) and one type of recreational use (beaches) with natural shorelines to test (1) for alterations of the macroinvertebrate communities associated with the three types of shoreline development and (2) whether alterations of the macroinvertebrate communities are also detectable among the studied lakes.

Methods

STUDY SITES

Seven study lakes were chosen to allow for a sampling design stratified by shoreline type. The lakes are located in North-east Germany (52°24′10″–53°18′40″ N, 12°52′40″–13°52′40″ E) and differ in trophic status and hydrological regime (Table 1). Within the lakes, four different shoreline types, i.e. natural shorelines (reference), beaches (recreational use), retaining walls and ripraps (erosion control structure) were chosen. Local ripraps consisted of layered, rectangular stones and covered the shore from above the water line down to a water depth of about 0·5 m.

As beaches and ripraps were not present in all studied lakes, a total of 20 stations were sampled.

MACROINVERTEBRATE SAMPLING

Macroinvertebrates were sampled in autumn (October 2003) and spring (April 2004) at each of the 20 stations both in 0–0·2 m water depth (referred to hereafter as eulittoral) and in 0·2–1·2 m water depth (referred to hereafter as infralittoral). Not all infralittoral habitat types were present at all shoreline types, which prevented a balanced sample design for reed and stone habitats (Table 2). Moreover, the presence of CWD habitats was restricted to natural shorelines because all developed shorelines were situated in urban areas where riparian trees were absent.

We sampled each habitat type separately using sampling techniques that were best adapted to the different degree of spatial complexity of the habitats. This ensured a maximum sampling efficiency and comparability of the samples. Macroinvertebrates from CWD habitats were brushed from three pieces of CWD with comparable states of decay, and subsamples were sieved trough a mesh (250 µm). Subsequently, length and diameter of

Table 2. Habitat types within the eulittoral and infralittoral zones sampled for macroinvertebrates. The number of replicates per habitat type is given in brackets

	Reference	Recreational use	Erosion control structure	
	Natural shoreline	Beach	Riprap	Retaining wall
Eulittoral	Roots (5)	Sand (5)	Stones (5)	Concrete (5)
Infralittoral	Coarse woody debris (5)	–	–	–
	Reed (5)	–	Reed (2)	Reed (2)
	Sand (5)	Sand (5)	Sand (5)	Sand (5)
	Stones (5)	–	Stones (2)	Stones (5)

each piece of CWD was measured, and surface area was calculated assuming a cylindrical shape. Similarly, 10 stones were chosen randomly from each sample point and attached macroinvertebrates were brushed off. From each stone, surface area was calculated based on its length, height and width. We took five 1-m sweeps from reed habitats using a hand net (250-µm mesh, width 24 cm). We estimated the sampled area of reed habitats by multiplying hand net width with length of the sampled area. We took five subsamples from submerged roots of riparian trees with a hand net (250-µm mesh, width 24 cm), and estimated the sampled area by multiplying hand net width with the respective sampling depth. Sand habitats were sampled with 10 subsamples using a modified Surber sampler for lentic conditions (area 0·05 m^2, 250 µm mesh). Retaining walls were sampled with 10 subsamples using a scratch net (250 µm mesh, Hydrobios, Germany). Here, the sampled area was calculated by multiplying net frame width (13 cm) with the respective sampling depth. Subsequently, subsamples from each habitat type were pooled to create a composite sample per habitat type. Samples were preserved in the field and macroinvertebrates were identified in the laboratory to the lowest taxonomic level possible. Information on the functional feeding groups was taken from Schmedtje & Colling (1996).

STATISTICAL ANALYSIS

Initially, we eliminated species from the data set that were recorded in only one lake. As there were no significant differences in community composition among seasons using analysis of similarity (ANOSIM, PRIMER, version 5; Primer-E Ltd, Plymouth, UK) for any of the four shoreline types, we pooled the data from both sampling dates for further analyses.

We constructed species–area curves (PCORD, version 4·25; MjM Software, Gleneden Beach) to verify whether species richness was affected by differences in the number of samples of each shoreline type. This analysis revealed that the curve for each shoreline type reached its asymptote, indicating that sampling effort was sufficient at all shoreline types (Fig. 1). We converted species densities into relative abundances and calculated relative abundances of the macroinvertebrate major groups, relative abundances of the functional feeding groups and species richness to test for differences between natural and developed shorelines by means of nonparametric Mann–Whitney *U*-tests (SPSS, version 9·0; SPPS Inc., Chicago, IL, USA).

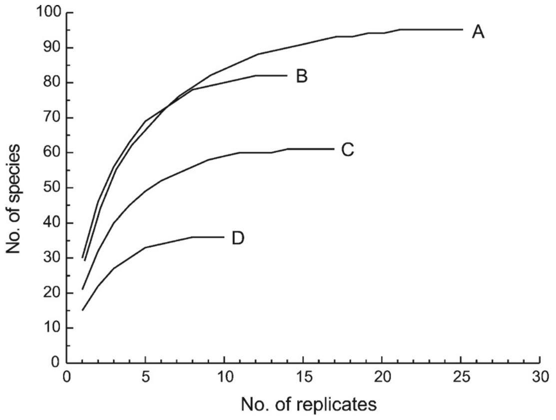

Fig. 1. Species–area curves for (a) natural shoreline, (b) riprap, (c) retaining wall and (d) recreational beach.

Indicator species analysis (IndVal, Dufrene & Legendre 1997) was used to detect macroinvertebrate species that are characteristic for a habitat or shoreline type, respectively (PCORD, version 4·25; MjM Software). We also tested whether species richness depended on habitat heterogeneity expressed as the number of habitat types using Spearman's correlation analysis (SPSS, version 9·0; SPPS Inc.).

For statistical analyses of the effects of shoreline development among lakes, we estimated whole-lake littoral macroinvertebrate density by calculating the weighted average density based on the proportion of shorelines represented by natural shorelines, shorelines with retaining walls and shorelines with recreational beaches (Table 1). Similarly, we calculated whole-lake relative abundances of the macroinvertebrate major groups. We restricted this analysis to the five lakes (Grienericksee, Langer See, Müggelsee, Unteruckersee, Werbellinsee) which had natural shorelines, shorelines with retaining walls and shorelines with recreational beaches.

Results

EFFECTS OF SHORELINE DEVELOPMENT – AMONG SITES

Among sites, eulittoral species richness was significantly lower on beaches and on retaining walls than on natural shorelines, but did not differ significantly between ripraps and natural shorelines (Fig. 2a). Relative abundances of Coleoptera, Crustacea, Gastropoda and Trichoptera were significantly lower on beaches than on natural shorelines and relative abundances of Gastropoda and Hirudinea were significantly lower on retaining walls than on natural shorelines (Table 3). IndVal analysis revealed *Bithynia tentaculata* (L.) (Gastropoda) (IV = 71·4, *P* = 0·016), *Ischnura elegans*

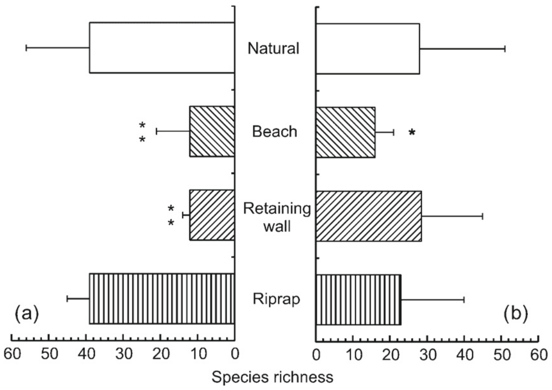

Fig. 2. Median species richness (+ max) of natural and developed shorelines (beach, retaining wall, riprap) within the (a) eulittoral and (b) infralittoral zones. Significant differences (Mann–Whitney *U*-test) between natural and each type of developed shorelines are indicated by asterisks (**$P < 0{\cdot}01$, *$P < 0{\cdot}05$).

Vander Linden (Odonata) (IV = 55·9, $P = 0{\cdot}046$), *Lype phaeopa* McLachlan (Trichoptera) (IV = 75·2, $P = 0{\cdot}004$) and *Platambus maculatus* (L.) (Coleoptera) (IV = 60·0, $P = 0{\cdot}038$) as highly characteristic species for natural shorelines. Moreover, the occurrence of *I. elegans*, *L. phaeopa* and *P. maculatus* was restricted to natural shorelines and relative abundance of *B. tentaculata* was significantly higher at natural shorelines than at beaches or retaining walls (Mann–Whitney *U*-test, $P = 0{\cdot}008$). None of the recorded species was characteristic for beaches or retaining walls, whereas *Dugesia lugubris/polychroa* (Turbellaria) (IV = 80·0, $P = 0{\cdot}003$), *Cyrnus trimaculatus* (Curtis) (Trichoptera) (IV = 79·4, $P = 0{\cdot}002$) and *Erpobdella octoculata* (L.,) (Hirudinea) (IV = 72·3, $P = 0{\cdot}020$) were highly characteristic species for ripraps. Differences between shoreline types were also discernible in the functional feeding group composition. The abundances of piercer, shredder and xylophagous species were significantly lower at beaches than on natural shorelines (Table 4). Similarly, the abundances of predator, shredder and xylophagous species were significantly lower on retaining walls than on natural shorelines. In contrast, we found no significant differences in the abundances of the functional feeding groups between ripraps and natural shorelines.

In contrast to the eulittoral zone, no significant differences were found in species richness (Fig. 2b) nor major macroinvertebrate or functional feeding groups (Tables 3 and 4) between retaining walls, ripraps and natural shorelines were found in the infralittoral zone. Conversely, infralittoral species richness, relative abundances of Crustacea, Ephemeroptera and Trichoptera (Table 3) and in relative abundance of shredders (Table 4) were significantly lower on beaches than on natural shorelines. None of the recorded infralittoral species was indicative for natural or developed shorelines.

Spearman's correlation analysis revealed that species richness was significantly positively correlated with the number of habitat types (Spearman's $\rho = 0{\cdot}77$, $P = 0{\cdot}000$, $n = 20$) and median species richness decreased from 63 species at natural shorelines with all five habitat types present to 17 species at recreational beaches with only one habitat type present.

EFFECTS OF SHORELINE DEVELOPMENT – AMONG LAKES

Among lakes, whole-lake littoral macroinvertebrate density increased with increasing proportion of developed shorelines and was almost three times higher in

Table 3. Median relative abundance (min–max) of macroinvertebrate major groups on the four shoreline types, given separately for eulittoral and infralittoral zones. Significant differences (Mann–Whitney *U*-test) between natural and each type of developed shorelines are indicated by asterisks (***$P < 0{\cdot}001$, **$P < 0{\cdot}01$, *$P < 0{\cdot}05$)

	Eulittoral zone				Infralittoral zone			
	Natural	Beach	Retaining wall	Riprap	Natural	Beach	Retaining wall	Riprap
Bivalvia	3·8 (0·0–9·1)	0·0 (0·0–0·2)	0·1 (0·0–1·8)	0·2 (0·0–27·1)	0·5 (0·0–5·3)	0·0* (0·0–0·1)	0·2 (0·0–5·6)	0·5 (0·0–20·3)
Chironomidae	74·4 (11·9–91·5)	91·7 (32·4–98·7)	87·1 (66·7–96·2)	85·7 (40·9–95·5)	87·6 (27·8–98·7)	96·0* (91·2–98·8)	82·3 (44·8–99·3)	86·0 (34·1–96·4)
Coleoptera	0·2 (0·0–2·2)	0·0* (0·0–0·0)	0·0 (0·0–0·1)	0·0 (0·0–0·2)	0·0 (0·0–2·1)	0·0 (0·0–0·0)	0·2 (0·0–0·2)	0·0 (0·0–0·1)
Crustacea	12·4 (0·4–69·7)	0·0* (0·0–6·1)	0·4 (0·1–7·0)	0·8 (0·1–30·7)	1·1 (0·0–38·4)	0·0* (0·0–0·4)	0·5 (0·0–46·3)	0·6 (0·0–28·9)
Ephemeroptera	1·3 (0·0–3·5)	0·0 (0·0–0·2)	0·0 (0·0–1·7)	1·3 (0·0–2·7)	0·2 (0·0–5·8)	0·0* (0·0–0·1)	0·1 (0·0–15·6)	0·4 (0·0–2·3)
Gastropoda	0·7 (0·2–6·7)	0·1* (0·0–0·4)	0·0** (0·0–0·0)	0·2 (0·1–0·5)	1·2 (0·0–12·5)	0·1 (0·0–0·5)	0·4 (0·0–1·3)	0·6 (0·1–6·5)
Hirudinea	0·0 (0·0–0·1)	0·0 (0·0–0·0)	0·0* (0·0–0·0)	0·0 (0·0–0·3)	0·0 (0·0–0·3)	0·0 (0·0–0·0)	0·0 (0·0–0·4)	0·0 (0·0–0·1)
Oligochaeta	1·2 (0·5–7·1)	6·6 (1·0–60·7)	10·9 (1·0–30·0)	1·6 (0·4–12·3)	2·6 (0·0–63·8)	3·1 (1·0–8·5)	9·8 (0·0–29·5)	4·0 (0·0–54·0)
Trichoptera	0·5 (0·4–0·8)	0·0** (0·0–0·1)	0·6 (0·1–2·7)	1·1 (0·1–5·4)	0·3 (0·0–1·2)	0·0*** (0·0–0·0)	0·6 (0·0–3·8)	0·1 (0·0–1·4)

Table 4. Median relative abundance (min–max) of the macroinvertebrate functional feeding groups on the four shoreline types, given separately for eulittoral and infralittoral zones. Significant differences (Mann–Whitney *U*-test) between natural and each type of developed shoreline are indicated by asterisks (***$P < 0·001$, **$P < 0·01$, *$P < 0·05$)

	Eulittoral zone				Infralittoral zone			
	Natural	Beach	Retaining wall	Riprap	Natural	Beach	Retaining wall	Riprap
Collector/gatherer	10 (7–17)	13 (11–16)	9 (7–11)	9 (11–16)	17 (4–38)	13 (13–16)	14 (5–41)	16 (7–29)
Filterer	15 (12–37)	17 (16–17)	20 (15–35)	16 (16–17)	16 (7–37)	17 (16–17)	16 (11–67)	17 (16–75)
Parasite	21 (6–35)	28 (26–35)	30 (25–36)	21 (6–28)	14 (2–23)	27*** (22–28)	15 (3–23)	17 (2–23)
Piercer	33 (5–45)	28* (5–45)	26 (20–38)	33 (5–45)	21 (5–42)	30 (29–30)	28 (6–45)	25 (3–33)
Predator	4 (3–13)	4 (3–4)	3* (3–4)	3 (2–5)	5 (1–8)	4 (4–5)	5 (3–23)	4 (3–9)
Scraper	6 (4–8)	8* (6–8)	6 (5–14)	8 (2–12)	11 (4–17)	8 (8–10)	10 (6–19)	10 (3–14)
Shredder	2 (1–16)	0** (0–1)	0* (0–1)	1 (0–2)	2 (0–11)	0* (0–1)	1 (0–3)	1 (0–8)
Xylophagous	4 (0–18)	0* (0–0)	0* (0–0)	0 (0–1)	0 (0–67)	0 (0–0)	0 (0–0)	0 (0–0)

Table 5. Whole-lake littoral macroinvertebrate density and whole-lake littoral relative abundances of the macroinvertebrate major groups

	Grienericksee	Langer See	Müggelsee	Unteruckersee	Werbellinsee
Whole-lake density	2250	8562	9148	3300	2184
Bivalvia	0·1	0·7	0·6	1·2	0·9
Chironomidae	86·5	96·4	84·6	72·5	76·9
Coleoptera	0·1	0·0	0·0	0·1	1·6
Crustacea	0·1	0·6	4·4	3·4	5·1
Ephemeroptera	1·7	0·1	0·7	0·2	3·5
Gastropoda	0·9	0·1	1·1	2·1	1·3
Hirudinea	0·1	0·0	0·0	0·0	0·0
Oligochaeta	9·0	0·6	6·8	18·5	8·0
Trichoptera	0·3	0·3	0·2	0·3	0·5

lakes with high proportions of shoreline development than in lakes with low proportions of shoreline development (Table 5). Similarly, the relative abundance of Chironomidae increased from 72·5% in Lake Unteruckersee with lowest proportions of shoreline development to 96·4% in Lake Langer See with the highest proportion of shoreline development. The remaining macroinvertebrate major groups, particularly Coleoptera, Gastropoda and Oligochaeta, decreased in abundance with increasing proportions of retaining walls or recreational beaches (Tables 1 and 5).

Discussion

Earlier studies on the impacts of human shoreline development on lakes focused mainly on littoral habitats and littoral fish communities (Christensen *et al.* 1996; Jennings *et al.* 1999; Radomski & Goeman 2001; Elias & Meyer 2003; Jennings *et al.* 2003; Scheuerell & Schindler 2004). Our study demonstrates that, independently of the lake type, shoreline development through erosion control structures and creation of recreational beaches had significant impacts on both eulittoral and infralittoral macroinvertebrate communities. However, the degree and spatial extent of the impacts differed between the types of shoreline development.

Within the eulittoral zone, the impacts of development on macroinvertebrate species richness and the abundance of several major taxonomic and functional feeding groups (Tables 3 and 4) can be attributed to the reduction of habitat complexity, as roots with their complex three-dimensional structure at natural shorelines were replaced by habitats with lower complexity at developed shorelines (concrete, sand, cf. Table 2). Habitat complexity is one of the key environmental factors influencing macroinvertebrate communities because complex habitats provide more ecological niches (O'Connor 1991), decrease the predation risk by limiting the foraging success of predators (Thompson 1987; Warfe & Barmuta 2004) and may also provide refuge against wind-induced wave disturbance. Consequently, natural shorelines harboured characteristic species such as *B. tentaculata*, *I. elegans* and *P. maculatus* with a strong preference for root habitats. This dependence upon the presence of a certain habitat type makes these species highly vulnerable to the loss of their preferred habitat. Consequently, habitat specialists are those components of the community that are affected most severely by human shoreline development.

In addition to structural properties, complex habitats exhibit a higher available surface for the growth of periphyton (Bowen, Kaushik & Gordon 1998) and the sedimentation of particulate organic matter (Taniguchi & Tokeshi 2004). Hence, functional feeding groups such as piercer, shredder and xylophagous species may have benefited from these food resources at natural shorelines.

Due to their low structural complexity, retaining walls and beaches did not have characteristic species in the eulittoral zone, indicating that there is no distinct community associated with these types of shorelines. Interestingly, ripraps had no significant impact on eulittoral macroinvertebrates in the studied lakes, even if ripraps had a distinct community that comprised mainly lithobiontic species. Presumably, the arrangement of stones at ripraps created a structural complexity of large and small crevices that resembled that created by root habitats at natural shorelines. This view is supported by experiments showing that colonization baskets filled with cement balls to mimic ripraps exhibited higher species richness and macroinvertebrate abundance than baskets with cement blocks that mimic retaining walls (Schmude *et al.* 1998).

Within the infralittoral zone, erosion control structures had no significant impact on the macroinvertebrate community. Similarly, infralittoral fish species richness and abundance did not differ significantly between natural and developed shorelines in US lakes (Bryan & Scarnecchia 1992). Our findings may be attributable to the limited spatial extent of retaining walls and ripraps, where impacts hardly extend to the infralittoral zone. However, reed habitats were present at only two of the five sampling stations for ripraps and retaining walls (Table 2). Hence, we cannot exclude completely the possibility that erosion control structures may impact infralittoral macroinvertebrate communities due to habitat loss even if we did not find significant impacts in the course of this study.

In contrast, recreational beaches affected the macroinvertebrate community of the infralittoral zone, which is likely to be attributed to the loss of all but the sand habitats. Similarly, intensive recreational use was demonstrated to cause a loss of reed stands at German lakeshores by more than 1 km of shoreline per year (Sukopp 1971).

As a common effect of all types of shoreline development, CWD was absent due to either removal from the littoral zone or to the lack of riparian trees that prevented CWD supply. Consequently, xylophagous species, particularly *L. phaeopa*, were nearly absent from developed shorelines. However, non-xylophagous species such as *Dreissena polymorpha* (Pallas) (Bivalvia), *Radix balthica* (L.) (Gastropoda) and *Tinodes waeneri* (L.) (Trichoptera) occurred on stone habitats at shorelines with erosion control structures in similar abundances to CWD habitats at natural shorelines. Hence, for these species CWD may be substituted by other habitat types exhibiting similar physical characteristics, such as stones. Similarly, France (1997) concluded that most species found on CWD habitats in boreal lakes used CWD as a habitat supplying biofilm or refuge against predation rather than as a direct food resource.

Species richness decreased with decreasing number of littoral habitats present at each shoreline type. The reduction of littoral habitat heterogeneity was especially apparent at beaches where all but the sand habitats were absent. Consequently, macroinvertebrate species richness was lowest here and we conclude that the impact of shoreline development on macroinvertebrates depends on the extent to which the heterogeneity of littoral habitats is reduced.

Among lakes, whole-lake littoral macroinvertebrate density increased with increasing proportion of shoreline development, most probably a result of the increasing abundances of Chironomidae in line with increases in their preferred sand habitats at recreational beaches and concrete habitats at retaining walls (Table 3). The remaining macroinvertebrate major groups decreased with increasing proportion of shoreline development, indicating that shoreline development may cause a homogenization of the macroinvertebrate community. This substantial reduction of whole-lake littoral biodiversity is most probably occurring in those lakes where shorelines have been modified to a large extent.

IMPLICATIONS FOR SHORELINE MANAGEMENT

In the littoral zone of lakes, the mosaic of habitat types creates a high spatial heterogeneity which is associated with a high diversity in food resources. Therefore, littoral macroinvertebrates species richness, abundance and biomass are higher than in the sublittoral or profundal zones (Särkkä 1983; Czachorowski 1993). Hence, human disturbances to the littoral zone affect a crucial biotic component of lake ecosystems whose diversity or biomass may not be substituted by communities from other lake zones. Thus, the strength of the impacts of shoreline development depended upon the extent to which habitat complexity and habitat heterogeneity are altered. Our results across lakes of different trophic state or hydrological regime indicate that the impact of shoreline development may also be applicable to other lake types. We recommend that management efforts to protect the integrity of lake ecosystems should place more emphasis on the morphological status of the littoral zone and that conservation of habitat complexity and habitat heterogeneity within the littoral zone should be a primary aim. In cases where shoreline development is inevitable, our results can be applied to weigh different types of shoreline modification or erosion protection against their biological impacts. Furthermore, our results may serve as the basis for a prediction system using indicator species with a defined response to the loss of their preferred habitat. By linking this approach with methods that focus on the assessment of the morphological status of lakeshores (e.g. Rowan *et al.* 2006), lake managers would be enabled to assess rapidly the biological effects of shoreline development. The dependence of macroinvertebrate communities on the presence of certain habitat types may also be used to develop and implement site-adapted simple and cost-effective restoration measures. Specifically, artificial enhancement of habitat complexity may offer a promising strategy in urban lakes that are subjected to several types of human shoreline development.

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Eulittoral macroinvertebrate communities of lowland lakes: discrimination among trophic states

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SUMMARY

1. Nutrient inputs from urban and agricultural land use often result in shifts in species composition of pelagic and profundal invertebrate communities. Here, we test if nutrient enrichment affects the composition of eulittoral macroinvertebrate communities, and, if so, if macroinvertebrate communities of five different habitat types reflect differences in trophic state.
2. Macroinvertebrate community composition of 36 lakes was significantly correlated with total phosphorus (TP) concentration, the proportion of coarse woody debris (CWD) and root habitats and the proportion of grassland.
3. However, macroinvertebrate communities of five major habitat types from eight lakes were more dissimilar among habitats than among trophic states. Community composition of reed and stone habitats was significantly correlated with wind exposure but not TP concentration, while macroinvertebrate composition of sand habitats was related to TP concentration and coarse sediments. In CWD and root habitats, both TP concentration and a predominance of invasive species covaried, which made it difficult to relate the observed compositional differences to either trophic state or to the effects of competition between native and invasive species.
4. Trophic state influenced the composition of eulittoral macroinvertebrate communities but to a lesser extent than has been previously reported for profundal habitats. Moreover, the effects of trophic state were nested within habitat type and were partially superseded by biotic interactions and small-scaled habitat complexity. Although eulittoral macroinvertebrate communities were not strong indicators of the trophic state of lowland lakes, they may be used to assess other anthropogenic impacts on lakeshores.

Keywords: eutrophication, habitat, invasive species, lakeshore, land use

Introduction

Anthropogenic eutrophication continues to be a major threat to lake ecosystems, despite efforts to reduce nutrient inputs into lakes. The construction of wastewater treatment plants greatly reduced the direct discharge of industrial and/or domestic wastewater, but many lakes still receive substantial inputs of phosphorus (P) and nitrogen from urban and agricultural land use (Behrendt, 1996; Carpenter *et al*., 1998; Sanyanga & Hlanga, 2004) and atmospheric deposition (Vitousek *et al*., 1997). Regardless of the source, inputs of nutrients can substantially alter the ecological function of lake ecosystems. For example, increased nutrients, especially P, often result in increased pelagic primary production (Vollenweider, 1968) and algal blooms, which may inhibit the growth of submerged macrophytes (Egertson, Kopaska & Downing, 2004) and benthic primary production (Vadeboncoeur *et al*., 2003; Chandra *et al*., 2005). Moreover, decomposition of algal biomasses may result in anoxic conditions in profundal habitats, adversely affecting community composition. For example, pioneering work by Thienemann (1918,

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1928) showed that the composition of profundal macroinvertebrate communities was strongly related to dissolved oxygen (DO) concentrations. This early work inspired the use of profundal macroinvertebrate communities to classify the trophic status of lakes (Thienemann, 1921; Saether, 1979; Brodersen & Lindegaard, 1999; Langdon *et al.*, 2006).

In contrast to a number of studies showing the efficacy of using profundal communities in monitoring the effects of eutrophication on lakes, only a few studies have focused on the use of macroinvertebrate communities of nearshore, stony habitats and fewer still have taken a multihabitat approach. For instance, Macan & Maudsley (1969) studied English lakes along a gradient from oligotrophic to eutrophic conditions and found that macroinvertebrate communities were only partially related to trophic state because wind exposure superseded the compositional differences among trophic states. In Danish lakes, only a few macroinvertebrate species colonising stony shores were significantly related to trophic state, while morphometric variables influenced the majority of species (Brodersen, Dall & Lindegaard, 1998). Similarly, Johnson & Goedkoop (2002) found that environmental factors other than nutrient concentration explained most of the variance of macroinvertebrate communities from wind exposed stony shores of Swedish lakes. However, the applicability of these results to other eulittoral habitats is unknown, and to our knowledge only one study has previously determined if littoral macroinvertebrate communities reflect lake trophic state across multiple habitat types (Tolonen *et al.*, 2001). In a study of a large Finish lake system, Tolonen *et al.* (2001) showed that macroinvertebrate communities of macrophyte, sand and stone habitats primarily differed among habitat types, while within each habitat type community composition differed among trophic states. However, total phosphorus (TP) concentrations (range 3–26 $\mu g\ L^{-1}$) did not exceed mesotrophic conditions (Vollenweider & Kerekes, 1982), and habitat types, such as coarse woody debris (CWD) and submerged tree roots were not studied.

In the present study, we use macroinvertebrate data from 36 lakes to test the hypothesis that eulittoral macroinvertebrate communities of North-German lowland lakes are related to differences in trophic state. Further, based on habitat-specific macroinvertebrate data from eight lakes, we test if macroinvertebrate communities of CWD, reed, root, sand and stone habitats comparably reflect among-lake differences in trophic state.

Methods

Sampling

Lake-specific analysis. Macroinvertebrates were collected in autumn 2001 (September–December) and spring 2002 (April–July) from six equidistant sampling sites situated along the shoreline of 36 North-German lowland lakes (Table 1, Fig. 1). A composite macroinvertebrate sample was taken from each sampling site (water depth <1.2 m) using standardised kick-sampling (10 min. sampling effort, hand net: 250-μm mesh, width 24 cm). In the laboratory, samples were sorted and counted using a stereo-dissecting microscope, and individuals were identified to the lowest taxonomic level possible.

Electric conductivity, DO concentration, pH and water temperature were recorded at each sampling site using a multiparameter probe (HydroLab H20; HydroLab Corporation, Austin, TX, U.S.A.). Habitat availability at the sampling sites was expressed as the proportion of CWD, pebbles, reed (*Phragmites australis*, Cav. Trin. ex Steud.), sand, stones, submerged macrophytes and roots (e.g. if roots were present at three of the six sampling sites they accounted for 50% availability). Root habitats consisted of submerged roots of riparian alder trees (*Alnus glutinosa*, L.) and constitute an important habitat type in the eulittoral zone of North-German lowland lakes.

Land use within a buffer zone around each lake (from the shoreline to 500-m inland) was estimated by GIS (ArcView, version 3.2, Esri, Redlands, CA, U.S.A.). Data on the lake surface area, TP concentration (annual mean concentrations in 2001), water residence time and trophic state were provided by the Regional Environmental Agency (Landesumweltamt Brandenburg). The 36 lakes were assigned to trophic state classes by the Regional Environmental Agency in 2001 (Länderarbeitsgemeinschaft Wasser [LAWA], 1998) using TP concentration, chlorophyll *a*, and water transparency and the classification system of Vollenweider & Kerekes (1982).

Habitat-specific analysis. Eulittoral macroinvertebrate samples were collected from 33 sampling sites in eight lakes in October 2003 and April 2004 (Table 1).

Table 1 Lake area (Area), residence time (RT), trophic state and total phosphorus concentration (TP, mean annual concentration of 2001) of 38 lakes

Code	Lake	Area (km^2)	RT (year)	Trophic state	TP ($\mu g\ L^{-1}$)
Ba	Blankensee	2.9	1.2	Hypertrophic	366
Be1	Beetzsee, southern basin	4.0	1.5	Hypertrophic	97
Be2	Beetzsee, middle basin	1.9	1.5	Hypertrophic	97
Be3	Beetzsee, northern basin	2.6	1.5	Hypertrophic	97
Br	Breitlingsee	5.1	2.8	Hypertrophic	121
Fa	Fährsee	2.1	4.0	Mesotrophic	43
Gi	Grienericksee	0.7	4.2	Eutrophic	37
Gl	Glienicker See	0.7	6.8	Eutrophic	29
Gr	Grimnitzsee	7.8	4.6	Eutrophic	50
Gu	Gülper See	4.4	0.6	Hypertrophic	278
Ho	Hohennauener See	3.6	3.4	Hypertrophic	104
Ku	Küstrinsee	2.2	6.0	Mesotrophic	27
La	Langer See	2.5	0.1	Hypertrophic	168
Lu1	Lübbesee, southern basin	2.1	5.0	Mesotrophic	22
Lu2	Lübbesee, northern basin	0.9	5.0	Mesotrophic	22
Me	Mellensee	2.2	3.3	Hypertrophic	96
Mu	Müggelsee	7.3	4.8	Eutrophic	108
Ne	Neuendorfer See	3.0	2.4	Hypertrophic	86
Pa	Parsteiner See	8.9	7.7	Mesotrophic	31
Pl	Plauer See	6.7	2.8	Hypertrophic	121
Ra	Rangsdorfer See	2.4	1.5	Hypertrophic	113
Ro	Röddelinsee	1.8	9.0	Eutrophic	52
Ru1	Ruppiner See, northern basin	1.7	8.2	Eutrophic	108
Ru2	Ruppiner See, southern basin	6.3	8.2	Eutrophic	108
Sa	Sacrower See	1.1	19.3	Eutrophic	122
Sc	Schwielochsee	11.5	2.0	Hypertrophic	159
Sm1	Scharmützelsee, southern basin	10.7	9.9	Eutrophic	64
Sm2	Scharmützelsee, northern basin	1.2	9.9	Eutrophic	64
Sn	Schauener See	1.5	3.1	Hypertrophic	222
So	Stolpsee	3.8	6.4	Eutrophic	27
St	Stechlinsee	4.2	22.8	Oligotrophic	13
Sw	Schwielowsee	7.9	2.8	Hypertrophic	157
Un	Unteruckersee	10.4	9.2	Mesotrophic	25
We	Werbellinsee	7.8	22.1	Mesotrophic	26
Wi	Wittwesee	1.6	5.5	Mesotrophic	14
Wo	Wolziger See	5.6	5.7	Eutrophic	102
Wu	Wummsee	1.5	11.8	Oligotrophic	18
Ze	Zechliner See	1.8	11.3	Mesotrophic	26

Underlined codes represent lakes sampled for habitat-specific analysis.

At each sampling site (water depth <1.2 m), the main habitat types (CWD, reed, roots, sand and stones) were sampled. Sampling effort differed among the different habitat types. Macroinvertebrates were brushed from three pieces of CWD (with bark) and sieved through a 250-μm mesh. The length and diameter of the CWD was measured to estimate surface area. For reed habitats, sampling consisted of five 1-m sweeps using a hand net (250-μm mesh, width 24 cm). The area of reed habitats sampled was estimated by multiplying hand net width by the length of the sampled area. In addition, reed stem density was determined by counting stems within a 0.25 m^2 area in each reed habitat. Five sub-samples from root habitats were collected with a hand net (250-μm mesh, width 24 cm), and the area sampled was estimated by multiplying hand net width by the water depth. Although the sampling techniques used for reed and root habitats did not permit the sampled area to be precisely quantified, they assured an efficient sampling of highly mobile species such as Dytiscidae (Coleoptera) that frequently colonise these structurally complex habitats. Sand habitats were sampled by taking 10 modified Surber samples (area 0.05 m^2, 250-μm mesh). At each site, sediment particle size (three size fractions: fine <0.03 mm; middle

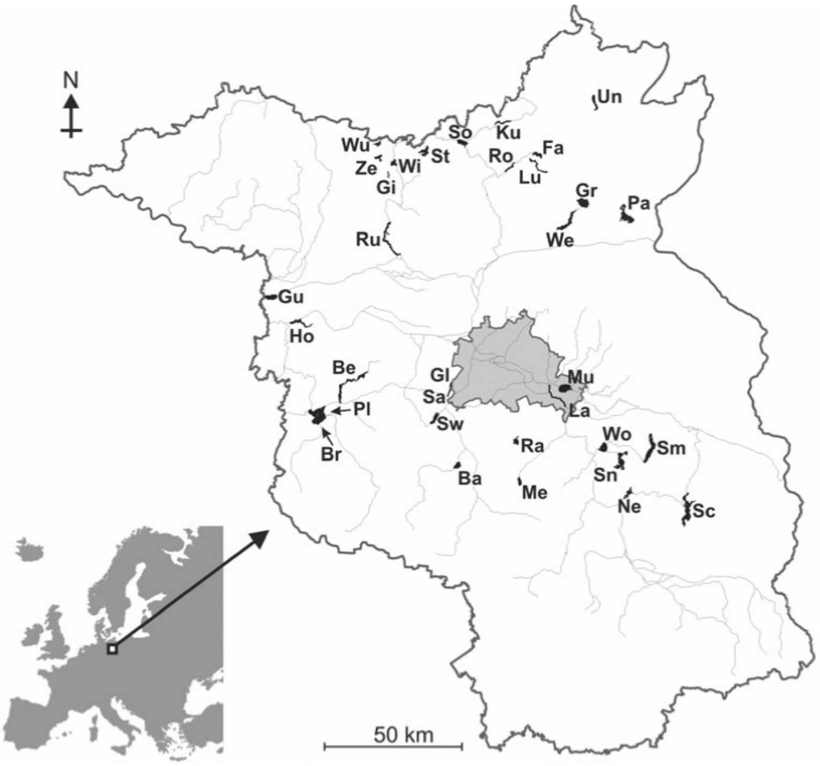

Fig. 1 Map of Europe (lower left), the federal states of Berlin (grey) and Brandenburg showing the location of the 38 study lakes. For lake codes see Table 1.

0.063–1.12 mm and coarse >2 mm, Analysette 3 Pro, Fritsch, Germany) was determined on the surficial sediment (top 5 cm) collected with a gravity corer (inner diameter 5 cm, UWITEC, Mondsee, Austria). Stone habitats were sampled by brushing macroinvertebrates from 10 arbitrarily selected stones. The length, height and width of the individual stones were used to calculate surface areas, assuming an ellipsoid shape. Surface areas estimated by ellipsoid surface calculation did not differ from estimations based on the more precise foil wrapping method (paired *t*-test, $P = 0.760$, $n = 20$). The multiple sub-samples for each habitat type were pooled in the field and processed as described above.

Wind exposure of each sampling station was calculated using the formula of Brodersen (1995) that combines data on frequency and velocity of the wind, fetch area and water depth at the sampling site. Wind data from nearby meteorological stations was provided by the German Weather Service.

Statistical analyses

Prior to statistical analyses, species that were recorded from only a single lake were removed from the lake- and habitat-specific datasets. Furthermore, we tested if macroinvertebrate community composition differed between sampling dates using analysis of similarity (ANOSIM, PRIMER, version 5, Primer-E Ltd., Plymouth, U.K.). No differences were noted between seasons for the lake-specific community (*R*-statistic = 0.036, $P = 0.057$) or for the CWD (*R*-statistic = 0.047, $P = 0.146$), root (*R*-statistic = 0.017, $P = 0.325$) and stone (*R*-statistic = 0.017, $P = 0.579$) habitats. By contrast, communities of reed (*R*-statistic = 0.205, $P = 0.001$) and sand (*R*-statistic = 0.071, $P = 0.032$) habitats differed, but, albeit significant, the differences (as shown by the *R*-statistics) were small between sampling dates. Consequently, data from both sampling dates were pooled for further analyses.

Non-metric multidimensional scaling ordination (NMS) was used to examine relationships between macroinvertebrate community composition, TP concentration and other selected environmental variables. Non-metric multidimensional scaling was performed on square root-transformed relative abundances for lake-specific data and on square root-transformed densities (individuals m^{-2}) for habitat-specific data using the PC-ORD software (version 4.25, MjM Software, Gleneden Beach, OR, U.S.A.). Square root-transformation was used as it results in a medium down-weighting of common species and allows for a good discrimination of sampling sites (Clarke & Warwick, 2001).

Bray–Curtis distance was used in NMS ordination with the stability criterion set at 0.0001, 100 iterations to evaluate stability and initial step length set at 0.2. The appropriate dimensionality was chosen based on results of a Monte Carlo test (100 runs, $P = 0.01$). The final run was carried out with the optimum dimensionality as the starting configuration and by applying varimax rotation (McCune & Grace, 2002). Pearson's correlation (SPSS version 9.0, SPSS, Chicago, IL, U.S.A.) between lake scores from the NMS axes and environmental variables was performed to determine the best predictors of the variability in community composition. For correlation analyses, environmental data were tested for deviation from normality and transformed when necessary using arcsine square root-transformation on proportional and Box–Cox transformation (Box & Cox, 1964) on continuous data.

In addition to the habitat-specific analyses, we tested if trophic state or habitat type was the more important driver of macroinvertebrate community composition in lowland lakes. Using pooled macroinvertebrate data for each lake and habitat type, we calculated Bray–Curtis dissimilarities for all combinations with habitat type nested within trophic state ($n = 30$) and with trophic state nested within habitat type ($n = 15$). Between-group differences were tested using a Mann–Whitney test (SPSS version 9.0, SPSS), assuming that if trophic state was the more important driver of macroinvertebrate community composition then compositional dissimilarities among trophic states within a habitat type would be higher than dissimilarities among habitat types within a given trophic state.

Results

Lake-specific analysis

Total phosphorus concentration was significantly correlated with NMS axis 1 and lakes were arranged by trophic state, with oligo- to mesotrophic lakes being grouped in the upper left and eu- to hypertrophic lakes in the lower right part of the NMS plot (Table 2, Fig. 2). However, oligotrophic Lake Wummsee as well as several eutrophic and hypertrophic lakes such as Mellensee and Neuendorfer See were positioned closer to the mesotrophic lakes, indicating similarities in community composition (Fig. 2). Only 23% of all species recorded were significantly correlated with NMS axis 1, among them *Dreissena polymorpha* (Pallas) (Bivalvia) and *Lype phaeopa* (McLachlan) (Trichoptera) that decreased in abundance along NMS axis 1 (Table 3). On NMS axis 2, lakes were arranged along a gradient of decreasing proportion of CWD and roots and increasing conductivity (Fig. 2, Table 2). Lakes with high proportions of CWD, roots and a low conductivity were characterised by high abundances of *Palpomyia* sp. (Diptera), *Oulimnius* sp. (Coleoptera) and *Gammarus pulex* (L.) (Crustacea), whereas the invasive crustaceans *Dikerogammarus* sp. and *Pontogammarus robustoides* (Sars) were characteristic for the lakes with high conductivity and low proportions of allochthonous habitats (Table 3). Hence, these findings indicate that TP and habitat characteristics were the main factors influencing the composition of the eulittoral macroinvertebrate communities.

Table 2 Environmental variables included in the lake-specific analysis and Pearson's correlation coefficients with non-metric multidimensional scaling (NMS) axes (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$)

		NMS	
Number of axes		3	
Stress		0.13	
Cumulative variance (%)		86.0	
Variable (unit)	**Mean (min–max)**	**Axis 1**	**Axis 2**
Land use (%)			
Agriculture	17 (0–55)		
Forest	41 (0–93)	−0.46**	0.54***
Grassland	7 (0–24)	0.66***	−0.43**
Impervious surface	12 (0–60)		−0.54***
Water	8 (0–20)	−0.41**	
Habitat type (%)			
Coarse woody debris	39 (0–100)		0.56***
Pebbles	6 (0–83)	−0.44**	0.41*
Reed	60 (17–100)		
Roots	28 (0–100)	−0.51***	0.62***
Sand	50 (17–100)	−0.51**	
Stones	12 (0–67)	−0.53***	
Submerged macrophytes	18 (0–50)		0.48**
Lake water			
Conductivity (μS cm^{-1})	510 (216–1001)	0.45**	−0.61***
Dissolved oxygen (mg L^{-1})	10.7 (8.6–12.7)		
pH	8.5 (7.7–8.9)		
Temperature (°C)	13.0 (7.3–21.4)		
Total phosphorus (μg L^{-1})	89 (13–366)	0.76***	−0.70***
Hydrology			
Water residence time (year)	8.6 (0.0–57.8)	−0.35*	0.55***

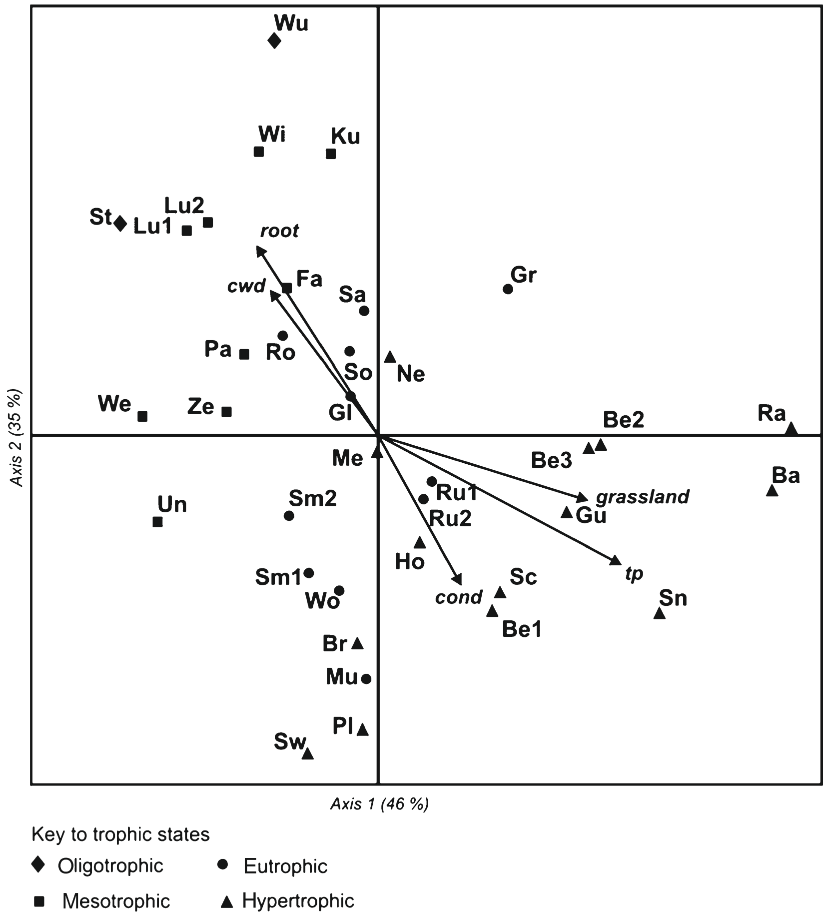

Fig. 2 Non-metric multidimensional scaling (NMS) ordination of 36 lakes of the lake-specific analysis. Only the first two NMS axes are shown as axis 3 explained only 5% of the variance. The trophic state of each lake is superimposed. The most important environmental variables (italic) (Pearson's r to NMS axes >0.55) are displayed as vectors (*cond*, conductivity; *cwd*, proportion of coarse woody debris habitats; *grassland*, proportion of grassland; *root*, proportion of root habitats; *tp*, total phosphorus). For lake codes see Table 1, for stress, number of axes and cumulative explained variance see Table 2.

Habitat-specific analysis

The relative importance of TP and habitat type was further studied on the habitat-specific level with an initial comparison of dissimilarities. Dissimilarity among trophic states within a given habitat type (median = 77.6, range 68.8–89.6) was lower than dissimilarity among habitat types within a given trophic state (median = 84.8, range 51.8–93.0) (Mann–Whitney test, $P = 0.001$). Based on this result, we performed NMS analyses on habitat-specific macroinvertebrate communities to test whether discrimination of trophic state by macroinvertebrate communities differed between habitat types.

Coarse woody debris

Non-metric multidimensional scaling and correlation analyses showed that TP concentration was significantly correlated with community composition along NMS axis 1 (Table 4). Furthermore, this axis was correlated with densities of the invasive crustaceans *Dikerogammarus villosus* (Sowinsky) ($r = -0.90$, $P = 0.000$) and *Chelicorophium curvispinum* (Sars) ($r = -0.83$, $P = 0.000$). For example, mean density (± SE) of *C. curvispinum* increased markedly from 5 ± 3 individuals m^{-2} in mesotrophic to 919 ± 667 individuals m^{-2} in hypertrophic lakes.

Reed

Community composition of reed habitats was significantly correlated with conductivity, wind exposure and water residence time but not TP concentration (Table 4). Furthermore, wind exposure was significantly correlated with stem density ($r = -0.73$, $P = 0.001$). Densities of Ephemeroptera *Cloeon dipterum* (L.) and *Caenis luctuosa* (Burmeister) were highly correlated with NMS axis 1 (both $r = -0.69$, $P = 0.002$).

Table 3. Pearson's correlation coefficients of macroinvertebrate species with non-metric multidimensional scaling axes of the lake-specific analysis

Species	Axis 1	Axis 2
Alboglossiphonia heteroclita	0.60	
Brachytron pratense		0.67
Centroptilum luteolum		0.67
Chironomidae	0.68	
Cyrnus flavidus		0.60
Dikerogammarus sp.		−0.60
Dreissena polymorpha	−0.80	
Gammarus pulex		0.78
Halesus radiatus		0.58
Haliplus fulvus		0.57
Hydroglyphus hamulatus		0.60
Kageronia fuscogrisea		0.59
Leptophlebia marginata		0.65
Lype phaeopa	−0.63	
Nemoura cinerea		0.61
Oulimnius sp.		0.79
Oxyethira sp.		0.67
Palpomyia sp.		0.80
Pontogammarus robustoides		−0.65
Potamopyrgus antipodarum	−0.77	
Stagnicola sp.		0.62

Only species with correlation coefficients >0.55 are shown ($P < 0.001$).

Roots

Community composition of root habitats was correlated with TP concentration, conductivity, pH, water residence time and DO (Table 4). Similarly, the density of the native *G. pulex* was negatively ($r = -0.74$, $P = 0.002$) and the density of the invasive *P. robustoides* was positively ($r = 0.76$, $P = 0.002$) correlated with NMS axis 1.

Sand

Community composition of sand habitats was correlated with TP concentration and sediment particle size (Table 4). In particular, sediment particle size was a strong predictor of macroinvertebrate composition. Densities of almost 45% of all species recorded from sand habitats were significantly negatively correlated with NMS axis 1, which was explained by an increase in the middle particle fraction (0.063–1.12 mm) and a decrease in the coarse particle fraction (>2 mm). Ordination of sampling sites along NMS axis 2 followed a gradient of increasing TP concentration and decreasing proportion of the fine particle fraction (<0.03 mm) (Table 4). However, only 9% of all species recorded were significantly correlated with this axis.

Stones

Community composition of stone habitats was significantly correlated with wind exposure and water residence time but not TP concentration (Table 4);

Table 4 Environmental variables included in the habitat-specific analysis and Pearson's correlation coefficients with the non-metric multidimensional scaling axes (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$)

		Coarse woody debris	Reed		Roots	Sand		Stones	
Number of axes		2	3		2	2		2	
Stress		0.14	0.11		0.09	0.12		0.09	
Cumulative variance (%)		70.3	75.6		89.7	78.5		79.0	
	Mean (min–max)	Axis 1	Axis 1	Axis 2	Axis 1	Axis 1	Axis 2	Axis 1	Axis 2
Habitat attributes									
Sediment particle size (%)									
<0.03 mm	0.7 (0.0–3.7)						−0.49*		
0.063–1.12 mm	88 (13.6–100)					0.47*			
>2 mm	12 (0.1–85)					−0.45*			
Stem density (no. m^{-2})	129 (40–240)								
Wind exposure	0.8 (0.0–2.6)		0.63**					0.69***	
Lake water									
Conductivity (µS cm^{-1})	552 (371–791)	0.59*	−0.53*		−0.72**		−0.49*	−0.88***	
Dissolved oxygen (mg L^{-1})	11 (8.6–12.6)				0.67**				
pH	8.0 (6.3–8.6)	0.62*			−0.80***	0.44*		−0.73***	
Temperature (°C)	9.4 (6.4–11.6)						−0.66***		
Total phosphorus (µg L^{-1})	77 (25–168)	0.53*			−0.83***		0.52**		
Hydrology									
Water residence time (year)	12.3 (0.0–54.8)			−0.48*	0.73**			0.62**	−0.54*

hence, community composition responded in a complex pattern to these environmental factors. The density of invasive species was negatively correlated with NMS axis 1. For example, the strongest correlation was shown by *D. polymorpha* ($r = -0.97$, $P = 0.000$); this species increased more than 10-fold from lakes with high water residence times (groundwater supplied lakes) to lakes with low water residence times (riverine lakes). Conversely, densities of lotic species, such as *Oulimnius tuberculatus* (Müller) (Coleoptera) ($r = 0.56$, $P = 0.017$) and *Theodoxus fluviatilis* (L.) (Gastropoda) ($r = 0.64$, $P = 0.005$) increased along NMS axis 1.

Discussion

Lake-specific analysis

Distinct differences in composition of eulittoral macroinvertebrate communities were found between oligotrophic and hypertrophic lakes. However, similarities between oligotrophic and mesotrophic and between mesotrophic and eutrophic lakes indicated that community composition between these trophic states was less distinct. Even the compositional differences between oligotrophic and hypertrophic lakes were not unequivocally related to differences in TP concentration, as the proportion of grassland was also related to community composition. Grasslands are predominantly used as pasture, and hence it seems unlikely that they constitute a potential source of nutrient inputs. This conjecture was also supported by the lack of a significant relationship between grassland and TP concentration (Pearson's $r = 0.23$, $P = 0.174$). However, lakes with a high proportion of grassland in their buffer zones often lacked of riparian trees, as this type of land use usually extended to the lakeshore. Hence, we assume here that grassland may reflect the effects of human-generated shoreline modification and a decrease in the amount of CWD in the littoral zone (Christensen *et al*., 1996). This is supported by the distribution of the wood-associated *L. phaeopa* (Hoffmann & Hering, 2000) which decreased in abundance as the proportion of grassland increased. Similarly, the low abundances of *D. polymorpha* in hypertrophic lakes may not be directly related to trophic state (Ludyanskiy, McDonald & MacNeil, 1993), but may rather indicate a lack of suitable habitat such as CWD. Indeed, macroinvertebrate community composition was strongly related to the presence of CWD and root habitats, both of which contribute to habitat heterogeneity and are known to be good predictors of macroinvertebrate community composition (Nilsson, Elmberg & Sjöberg, 1994; Heino, 2000; Harrison & Hildrew, 2001).

Habitat-specific analysis

Macroinvertebrate communities were more dissimilar among habitat types than among trophic states, indicating the importance of intrinsic habitat properties in determining community composition. Trophic state was shown to be a good predictor of the community composition of CWD, root and sand habitats, while community composition of sand habitats was also determined by small-scale differences in the structural complexity of sediments. As more species were related to particle size than to TP concentration, we conclude that trophic state may not be the primary factor determining the shift in community composition observed in sand habitats. For CWD and root habitats, considerably higher densities of invasive crustaceans were related to high trophic state. However, the predominance of invasive species in hypertrophic lakes may not necessarily be related directly to increased TP concentration, but may rather be a result of the low water residence times in these hypertrophic lakes. In the lowland lakes studied here, low water residence times reflect a connection to a larger river system that also serves as a commercial navigation route. Furthermore, as commercial navigation is known to accelerate the dispersal of invasive species (de Vaate *et al*., 2002; Grigorovich *et al*., 2003; Duggan *et al*., 2005), there is a higher probability for these lakes to be colonised by invasive species. As hypertrophic state and the predominance of invasive species coincided, the observed compositional differences among trophic states cannot be unambiguously related to differences in TP concentration, as mass occurrences of invasive species might similarly affect community composition (Hall & Mills, 2000; Rahel, 2002). Hence, two alternative explanations are possible for the observed differences in community composition of CWD and root habitats. Eutrophication might have caused an extinction of native species and a subsequent colonisation of the vacant ecological niches by invasive species. Alternatively, invasive species might have outcompeted native species, implying that biotic interactions and not trophic state resulted in the observed differences. At least *D. villosus* might actively displace native species regardless of trophic state, because it exerts a strong predatory impact on native species (Dick, Platvoet & Kelly, 2002; Krisp & Maier, 2005; MacNeil & Platvoet, 2005). Thus, it remains unclear whether the predominance of invasive species in the hypertrophic lakes studied here was the cause or the consequence of the alteration of the macroinvertebrate communities of the CWD and root habitats and whether these communities discriminate among trophic states.

Wind exposure but not TP concentration was significantly correlated to macroinvertebrate community composition of the reed and stone habitats. Moreover, this result was unaffected by the smaller range of TP concentration in the habitat-specific dataset (no oligotrophic lakes), as the correlation coefficient between TP and lake-specific NMS axis 1 decreased only slightly (from $r = 0.76$, $P = 0.000$ to $r = 0.66$, $P = 0.000$) after omitting oligotrophic lakes (TP < 27 μg L^{-1}) from the lake-specific correlation analysis. Assuming that the effect of TP range on statistical results was similar in the habitat-specific dataset, we conclude that the lack of a significant relationship between trophic state and macroinvertebrate community composition of reed and stone habitats was not an artefact of the study design. This finding is also supported by earlier studies that have shown how eulittoral macroinvertebrate communities on stony shores reflect environmental variables other than trophic state (Barton & Carter, 1982; Dall *et al.*, 1984; Johnson & Goedkoop, 2002).

While community composition in stone habitats was directly related to wind exposure, community composition in reed habitats reflected more the effect of wind exposure on stem density. Increasing the density of macrophyte stands has been shown to influence community composition by providing refuges against predation (Diehl, 1992; Tolonen *et al.*, 2003; Warfe & Barmuta, 2004; Rennie & Jackson, 2005). In our study, a high density of reed stands also seemed to favour the sedimentation of organic detritus, which was reflected in higher densities of the detritus collecting mayflies' *C. luctuosa* and *C. dipterum* (Schmedtje & Colling, 1996).

Macroinvertebrate community composition was related to conductivity, pH and DO in the habitat types. However, as these environmental variables exhibited little variability and did not reach extreme values that would directly affect community composition, we conclude that there is no mechanistic relation between conductivity, pH, DO and macroinvertebrate community composition.

In conclusion, trophic state influenced the composition of the macroinvertebrate community of the eulittoral zone, but not as much as has been previously reported for profundal communities (Thienemann, 1921; Saether, 1979; Brodersen & Lindegaard, 1999; Langdon *et al.*, 2006). Furthermore, our study showed that the effects of trophic state were nested within habitat type, and were partially superseded by biotic interactions and small-scaled habitat complexity (Fig. 3). For example, the influence of trophic state on macroinvertebrate communities of stone habitats was seemingly counteracted by wind exposure (Fig. 3), lending support to a number of other studies (Macan & Maudsley, 1969; Brodersen *et al.*, 1998; Johnson & Goedkoop, 2002). Moreover, our results indicate that eulittoral macroinvertebrate communities of the lowland lakes are not a reliable indicator of trophic state, as they were influenced by a number of factors, such

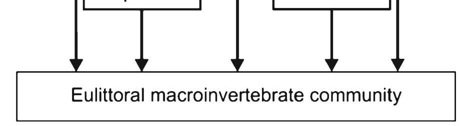

Fig. 3 Conceptual diagram representing the major environmental factors influencing the eulittoral macroinvertebrate communities of lowland lakes. Environmental variables act at different spatial scales, and connectivity of the lake to a larger river system influences macroinvertebrates either directly by accelerating the immigration of invasive species, or indirectly by increasing nutrient loads resulting in eutrophication. Land use influences macroinvertebrates directly through the alteration of littoral habitat structure, and indirectly via nutrient loading. Nutrient load determines the trophic state that in turn influences conditions in habitats in the lake ecosystem. Wind exposure and habitat type influence macroinvertebrates directly and substantially modify the effect of trophic state on the composition of the macroinvertebrate community.

as lake connectivity, habitat type, land use and wind exposure (Fig. 3). However, our results suggest that eulittoral macroinvertebrates may be useful for assessing other anthropogenic impacts such as human-generated effects on littoral habitats.

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Regulation of nutrient uptake in eutrophic lowland streams

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Abstract

We studied nutrient uptake in relation to water chemistry, stream hydrodynamics, and ecosystem metabolism in two eutrophic lowland streams located near Berlin, Germany. Ambient nutrient uptake rates ranged from 0.180 to 12.880 g NO_3-N m^{-2} d^{-1}, from 0.035 to 0.517 g NH_4-N m^{-2} d^{-1}, and from 0.017 to 0.750 g PO_4-P m^{-2} d^{-1}. Temporal and spatial variability in nutrient uptake rates within single streams were mainly controlled by concentrations of metabolic substrates (i.e., nutrients, dissolved organic carbon, and dissolved oxygen) and rates of ecosystem metabolism, highlighting the importance of assimilative nutrient uptake. According to stoichiometric accounts, dissimilative uptake of dissolved inorganic nitrogen was an important uptake mechanism. Thus, nutrient uptake was subject to controls similar to those reported from pristine study sites, indicating that basic patterns of nutrient retention are comparable in pristine and eutrophic streams. In contrast to pristine streams, eutrophic streams exhibited long nutrient uptake lengths (in the range of several kilometers), as elevated uptake rates could only partially compensate for high nutrient loads. Our results indicate that ecosystem nutrient uptake is unable to efficiently reduce nutrient exports from the investigated eutrophic lowland streams.

The intrinsic ability of stream ecosystems to store or even eliminate inorganic nutrients is termed nutrient retention. Nutrient retention is generally analyzed by applying the nutrient spiraling concept, which combines the evaluation of the antagonistic processes of nutrient cycling and transport in running waters (Webster and Patten 1979; Newbold et al. 1981; Stream Solute Workshop 1990). In pristine headwater streams, nutrient retention has been demonstrated to effectively reduce nutrient loads (e.g., Peterson et al. 2001). These results give rise to the assumption that nutrient retention could potentially counteract water quality problems originating from point and diffuse anthropogenic sources. However, excessive nutrient loads due to wastewater discharge can cause low load-specific nutrient retention efficiencies (Haggard et al. 2001; Martí et al. 2004).

Under pristine conditions, channel morphology, hydrologic interaction between surface and hyporheic water, and the geologic origin and grain size of streambed sediments (Munn and Meyer 1990; Valett et al. 1996; Gücker and Boëchat 2004), as well as biological productivity and ambient nutrient concentration (Martí and Sabater 1996; Dodds et al. 2002; Hall and Tank 2003), appear to be important determinants of nutrient retention. However, the functioning of nutrient retention is especially interesting in eutrophic streams, whose nutrient exports affect downstream rivers, lakes, and estuaries. Nevertheless, little is known about the rates, mechanisms, and controls of nutrient uptake in eutrophic streams.

In this study, we examined nutrient uptake in two eutrophic lowland streams. To assess ammonium, nitrate, and phosphate uptake rates and lengths in relation to a variety of potential controls, such as water chemistry, stream hydrodynamics, and ecosystem metabolism, we conducted seasonal short-term nutrient addition experiments in four eutrophic stream reaches. We aimed to test the following four hypotheses:

1) Nutrient uptake rates in eutrophic lowland streams are high.
2) The temporal and spatial variability in nutrient uptake depends on the variability in ecosystem metabolism and nutrient concentrations.
3) Nutrient uptake capacities in eutrophic lowland streams are overwhelmed by high nutrient loads.
4) Ecosystem inorganic nitrogen : phosphorus uptake ratios differ from Redfield ratios because of the importance of dissimilative nitrogen uptake (i.e., nitrification and denitrification).

Methods

Site descriptions—Both investigated lowland streams, the Erpe and the Demnitzer Mill Brook (DMB), are tributaries to the River Spree in and upstream of Berlin, Germany. To account for different stream sizes, we studied

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a third-order section of the Erpe at 52°29′14″N and 13°38′42″E and a first-order section of the DMB at 52°25′14″N and 14°14′7″E. Agriculture is the dominant land use in the catchments of both investigated streams. Hence, the streams receive considerable nutrients through diffuse source inputs. Additionally, point sources of nutrients, such as tile drainages, septic tank spillways, and private and municipal sewage plants, contribute substantially to the high nutrient concentrations in these drainage systems (Köhler et al. 2002).

All studied stream reaches are eutrophic. In 2002, nutrient concentrations ranged from 0.03 to 0.3 mg L^{-1} NH_4-N, 0.8 to 16.4 mg L^{-1} NO_3-N, and 0.01 to 0.27 mg L^{-1} soluble reactive phosphorus (SRP) and followed typical seasonal patterns (Köhler et al. 2002). Highest SRP concentrations occur in summer, and highest concentrations of dissolved inorganic nitrogen (DIN) occur in winter. Organic carbon concentrations in the stream water do not exhibit discernible seasonal patterns and ranged from 4.8 to 11.2 mg L^{-1} dissolved organic carbon (DOC) and from 0.4 to 4.9 mg L^{-1} particulate organic carbon (POC) in 2002.

Large sections of both streams were incised and straightened in the 1970s. Primary production in the Erpe is dominated by submerged macrophytes (*Potamogeton pectinatus* L. and *Sparganium emersum* Rehmann) growing from May to September. In the smaller stream, the DMB, benthic diatom blooms occur in the unshaded channel in spring, while dense stands of emergent macrophytes (mainly *Phalaris arundinacea* L., *Glyceria maxima* [Hartman] Holmberg, and *G. fluitans* [L.] Brown) shade the stream channel from early summer to fall. In both streams, submerged and emergent macrophytes are removed annually in the fall by local water management authorities. The streambeds consist of clogged and anaerobic fine-sandy sediments with high contents of organic carbon (5.9% ± 2.2% dry weight; mean ± standard deviation).

Sampling—The temporal variability in nutrient uptake and in its controls was investigated in five seasonal campaigns in 2002. To account for spatial variability in these structurally homogeneous, incised and straightened streams, we chose two stream reaches in each stream, one of which was only affected by diffuse agricultural nutrient inputs (hereafter referred to as Erpe-D and DMB-D) and the other of which was affected by additional point-source inputs of nutrients by wastewater treatment plants (Erpe-P and DMB-P). In each sampling campaign, nutrient uptake as well as stream hydrodynamics were studied using short-term nutrient and conservative tracer release experiments (Stream Solute Workshop 1990). Ecosystem metabolism was measured with the dissolved oxygen (DO) change technique (Odum 1956; Marzolf et al. 1994). Simultaneously, water samples were taken and analyzed for background nutrient, DOC, and POC concentrations. Additionally, stream water was sampled weekly for physicochemical analyses.

Chemical analyses—Nitrate concentrations were determined by ion chromatography (CDD-6A, Shimadzu Deutschland) with electrochemical ion suppression (ERIS, Alltech Deutschland). We determined ammonium and SRP spectrophotometrically (Hach DR/2000) according to the German standard methods (Wasserchemische Gesellschaft 1992). DOC was quantified using a liquid chromatography–organic carbon detection system (DOC-Labor Huber), and total organic carbon (TOC) contents of seston were quantified with a thermal conductivity analyzer (Vario EL, Elementar).

Hydrodynamics—To investigate stream hydrodynamics as potential controls of nutrient uptake, short-term constant-rate conservative tracer addition experiments were conducted in each reach in each sampling campaign. To evenly distribute the injected tracer solution over the entire width of the advective channel, we used a branching hose system connected to a peristaltic pump. Known concentrations of NaCl (used as a conservative tracer in our experiments) were injected upstream of the studied stream reaches until a plateau concentration was observed at the end of the investigated reaches (Stream Solute Workshop 1990). Plateau concentrations resulted in increases in conductivity between 113 and 262 μS cm^{-1}, corresponding to the 0.11- to 0.32-fold measure of the background conductivity. Breakthrough curves of NaCl were recorded at intervals of 15 s at the start, in the middle, and also at the end of the investigated stream reaches using conductivity meters with data loggers (600XLM and 6920, Yellow Springs Instruments). Conductivity meters were calibrated with standard solutions and cross-calibrated with stream water directly before the experiments. Hydraulic parameters were estimated from the conservative tracer data by least-squares using OTIS-P, a one-dimensional advection–dispersion model that includes transient storage and lateral inflow (Runkel 1998). Transient solute storage, characterized by the transient storage zone size (A_S; i.e., the cross-sectional area of the storage zones), by the relative transient storage zone size (A_S/A; i.e., transient storage zone size divided by main channel cross-sectional area), and by the storage zone exchange coefficient (α; i.e., the fraction of water entering the storage zones per unit of time), describes the temporary detainment of solutes in zones of stagnant or slowly moving water (Harvey and Wagner 2000). Turnover times of water ($T_W = [1/\alpha]$; i.e., the residence time due to advection and longitudinal dispersion) and of storage ($T_H = [A_S/(\alpha A)]$; i.e., the residence time due to transient storage) were calculated from the model parameters. Hydraulic uptake lengths (S_H) were calculated as the product of T_W and average water velocities.

Ecosystem metabolism—To estimate whole-stream metabolism, which is another potential control of nutrient uptake, an open-system two-station diel oxygen mass balance technique was used (Marzolf et al. 1994). We measured DO concentrations at the start and end of each stream reach for 36 h using cross-calibrated DO meters with data loggers (600XLM and 6920, Yellow Springs Instruments).

To account for oxygen exchange between the stream water and the atmosphere, we estimated reaeration coefficients based on DO change rates and DO deficits at night. Here we used an adaptation of the single-station approach of Young and Huryn (1996), developed by E. Martí (pers. comm.). Briefly, we adopted the regression approach between DO change rates and DO deficit at night from Young and Huryn (1996), but we determined DO change rates as the difference between upstream and downstream DO concentrations corrected for average travel times. Normalized reaeration coefficients (K^{20}_{oxy}) obtained with the above-described method ranged from 18.1 to 73.8 d^{-1} and were in the range of data reported from other lowland streams (Thyssen and Erlandsen 1987) and other stream types (Melching and Flores 1999; Mulholland et al. 2001). To evaluate the reliability of our reaeration estimates, we conducted a short-term propane tracer experiment according to Marzolf et al. (1994), in parallel to a K^{20}_{oxy} estimation described above in the Erpe-D reach in May 2002. Reaeration measured by the "snapshot" propane tracer method (K^{20}_{oxy}: 36.3) corresponded well with our estimate based on upstream/downstream DO differences (K^{20}_{oxy}: 34.6).

Community respiration (CR_{24}) and gross primary production (GPP) were calculated according to Marzolf et al. (1994), with the modification for air–water exchange of oxygen suggested by Young and Huryn (1998), and to obtain areal rates, we divided by the wetted bed surface area of the reach.

Nutrient uptake—To estimate nutrient uptake, we performed additions of combined ammonium and phosphate and combined nitrate and phosphate in parallel to conservative tracer injections (Stream Solute Workshop 1990). Single-nutrient addition experiments may cause methodological artifacts because they alter the DIN : SRP ratio. To avoid such artifacts, we conducted combined DIN and SRP injections and adjusted the DIN : SRP ratio of the injection solution to that of the stream water. Prior to each experiment and during the plateau phase, water samples were taken at eight equidistant stations along the stream reaches. In our experiments, experimental increases in ammonium, nitrate, and phosphate concentrations (I_C; i.e. experimental concentrations [C_{EXP}] divided by ambient concentrations [C_{AMB}]) ranged from 1.9 to 3.0. Using the conservative tracer results, we corrected concentrations of injected nutrients for dilution (Stream Solute Workshop 1990). However, dilution was small (i.e., <3.4%) and was detectable only in 7 out of the 20 samplings. Nutrient uptake length (S_W) was calculated as the negative inverse of the slope (k) of the regression between the natural logarithm of the dilution-corrected concentration of injected nutrients and the distance downstream, thus:

$$S_W = -\frac{1}{k} \tag{1}$$

Subsequently, areal nutrient uptake rates at ambient concentrations (U_{AMB}) were calculated as the product of discharge (Q) and C_{AMB} divided by the product of S_W and the width of the wet perimeter (w) of the stream reach (Stream Solute Workshop 1990):

$$U_{AMB} = \frac{Q \cdot C_{AMB}}{w \cdot S_W} \tag{2}$$

Uptake velocities (V_f) were calculated as the quotient of U_{AMB} and C_{AMB}:

$$V_f = \frac{U_{AMB}}{C_{AMB}} \tag{3}$$

Nutrient uptake length is a measure of a stream's load-specific nutrient uptake efficiency. According to the nutrient spiraling concept, uptake length is determined by the variability in specific nutrient load ([L/w]; i.e., nutrient load divided by stream width) and in areal nutrient uptake rate (U) (Stream Solute Workshop 1990). To evaluate nutrient dynamics in eutrophic streams, we visualized the $S_W - [L/w] - U$ continuum for our data set as well as for the data of Webster et al. (2003), from relatively pristine study sites, as a three-dimensional graph.

Molar ratios of ambient dissolved inorganic nitrogen (DIN; i.e., nitrate and ammonium) uptake rate (U_{DIN}) and phosphate uptake rate (U_{SRP}) were used to evaluate the importance of assimilative versus dissimilative DIN uptake processes. Molar $U_{DIN} : U_{SRP}$ ratios that are much higher than molar N : P ratios of aquatic organisms should indicate that biotic assimilation is not the dominant uptake process. Further, ratios between ambient nitrate uptake rate (U_{NO_3}) and DOC concentration (C_{DOC}) were calculated as a rough estimate of the availability of DOC to support denitrification.

To estimate the contribution of nitrification to ammonium uptake, we fitted a two-compartment model for ammonium and nitrate fluxes to the longitudinal nitrate concentration profile obtained during the ammonium addition experiments (Mulholland et al. 2000; Bernhardt et al. 2002). Ambient nitrification rates ($U^{NIT}_{NH_4}$) were expressed as fractions of ecosystem ammonium uptake (%) and as absolute rates (g NH_4-N m^{-2} d^{-1}). Further, ratios between $U^{NIT}_{NH_4}$ and DO concentration (C_{DO}) were calculated to compare the availability of DO to support nitrification in both streams.

Evaluation of the nutrient addition approach—The nutrient addition technique has been demonstrated to overestimate ambient uptake rates (Dodds et al. 2002) and uptake lengths (Mulholland et al. 2002), depending on the increase in concentration. Therefore, we tried to keep experimental increases in nutrient concentration (I_C) low. To evaluate the degree of overestimation in our study, we conducted a series of several separate short-term ammonium and nitrate addition experiments with increasingly higher nutrient concentrations from 14 to 16 August and 19 to 23 August in the DMB-D reach. Subsequently, uptake lengths (S_W) and uptake rates at experimental concentrations (U_{EXP}), as well as uptake rates at ambient concentrations (U_{AMB}), were calculated for each short-term addition, as described previously. For each series of experiments, we

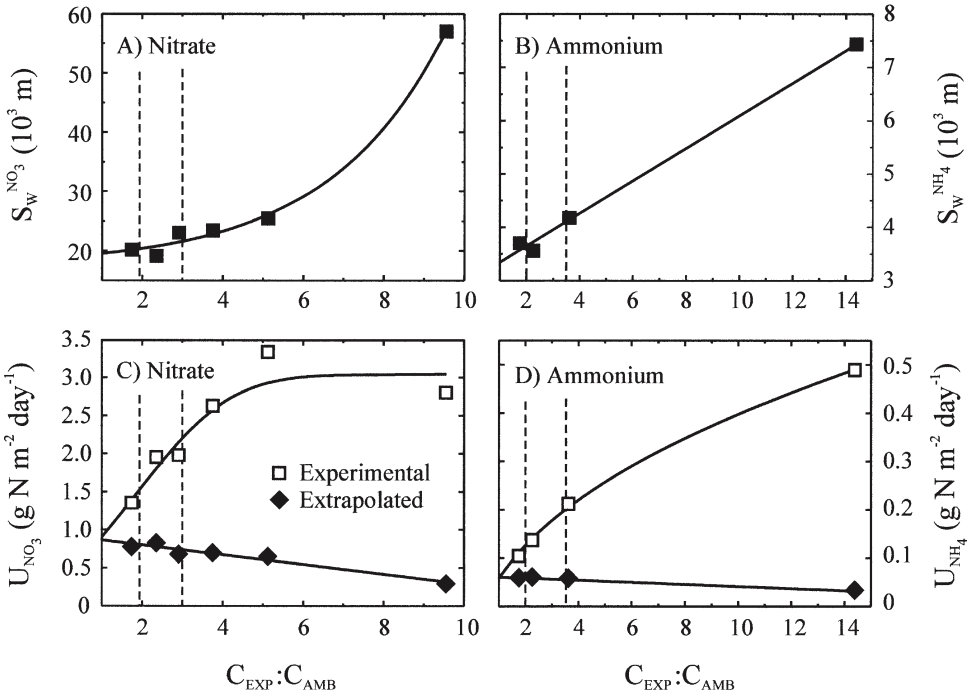

Fig. 1. (A, C) Short-term nitrate and (B, D) ammonium addition experiments with increasingly higher concentrations were performed to evaluate the reliability of the nutrient addition approach. Nutrient uptake lengths (filled squares), uptake rates at experimental concentration (open squares), and extrapolated ambient uptake rates (filled diamonds) are depicted as a function of concentration increase. C_{EXP} = experimental nutrient concentration; C_{AMB} = ambient nutrient concentration. Y-axis intercept points represent values of ambient uptake parameters corrected for methodological artifacts of the nutrient addition technique (P_{EXTRA}). Dotted lines indicate minimum and maximum increases in concentration (I_C) applied in the seasonal sampling campaigns. Y-axis values of intercept points between dotted lines and concentration kinetics of nutrient spiraling parameters (P_{SIM}) were used to estimate degrees of over- and underestimation of ambient parameters due to the nutrient addition technique.

extrapolated the relationship between S_W and I_C and between U and I_C back to the ambient nutrient concentration (ordinate intercept points in Fig. 1). Extrapolated values of S_W and U at ambient concentrations (P_{EXTRA}) should be a reliable measure of ambient nutrient uptake parameters (Dodds et al. 2002; Mulholland et al. 2002).

Subsequently, we introduced the minimum and maximum I_C values from all nutrient additions performed during the five seasonal sampling campaigns in all stream reaches (dotted lines in Fig. 1) into the regression equations between uptake parameters and I_C obtained from the above-described evaluation experiments. We thus simulated uptake parameters (P_{SIM}) that mimic the variability of over- or underestimation of ambient uptake in our data from the seasonal sampling campaigns. The percentage difference between the extrapolated uptake parameters at ambient concentrations (P_{EXTRA}) and the simulated uptake parameters accounting for I_C (P_{SIM}) was taken as an accuracy measure for our nutrient uptake results.

According to this calculation, the nitrate and ammonium uptake lengths measured with the experimental concentration increases (I_C) applied in our study overestimate ambient uptake lengths by 3.7% to 10.6% and 8.9% to 22.4%, respectively (Fig. 1A,B). The nitrate and ammonium uptake rates at ambient concentrations (U_{AMB}) reported here should underestimate ambient rates by 6.5% to 14.9% and 3.3% to 8.3%, respectively (Fig. 1C,D). Thus, the nutrient addition approach applied in our study caused moderate overestimation of ambient uptake lengths and moderate underestimation of ambient uptake rates for ammonium and nitrate. Interestingly, uptake rates were not saturated by the high experimental concentrations applied in our study (uptake rates at experimental concentration in Fig. 1C,D). Consequently, the high ambient nutrient concentrations did not saturate uptake rates as well. Hence, a basic assumption for the application of the nutrient addition method was fulfilled (Stream Solute Workshop 1990).

Statistical analyses—Data were first tested for normality and homogeneity of variances using Shapiro–Wilk, Bartlett, and Cochran tests. Spearman rank correlations were calculated to reveal relationships between metabolic variables and temperature and between ratios of DIN and SRP uptake rate and ratios of DIN and SRP concentration in the respective stream reaches.

Relationships between nutrient uptake and its potential determinants (i.e., the hydrochemical, morphometric, hydrodynamic, and metabolic variables measured) were explored by applying uni- and bivariate nonlinear regression analyses. Distributions of residuals and Durbin–Watson coefficients indicated that simple linear and multiple linear regression models did not adequately fit the data, even after logarithmic, square-root, or inverse transformation of variables. Bivariate nonlinear regression

Table 1. Hydrologic and hydrodynamic characteristics of the lowland stream reaches. Data are median values (ranges) from five sampling campaigns in 2002.

	Stream water depth, d (m)	Discharge, Q ($m^3\ s^{-1}$)	Velocity, v ($m\ s^{-1}$)	Dispersion, D ($m^2\ s^{-1}$)	Cross-section area, A (m^2)	Cross-section area of storage zone, A_S (m^2)	$A_S : A$	Storage exchange coefficient, α ($10^{-4}\ s^{-1}$)	Turnover time of water, T_W (min)	Turnover time of storage, T_H (min)	Hydraulic uptake length, S_H (m)
DMB-D	0.27 (0.22–0.30)	0.023 (0.013–0.040)	0.091 (0.080–0.133)	0.178 (0.144–0.202)	0.26 (0.16–0.30)	0.009 (0.005–0.012)	0.037 (0.016–0.076)	1.30 (1.23–1.32)	128 (126–135)	4.8 (2.0–9.7)	699 (613–1,013)
DMB-P	0.25 (0.20–0.31)	0.022 (0.012–0.042)	0.089 (0.081–0.132)	0.183 (0.130–0.197)	0.25 (0.15–0.32)	0.008 (0.005–0.011)	0.036 (0.016–0.074)	1.29 (1.28–1.39)	129 (120–131)	4.7 (1.9–9.6)	680 (624–973)
Erpe-D	0.46 (0.44–0.48)	0.164 (0.130–0.195)	0.150 (0.130–0.164)	0.198 (0.085–0.253)	1.30 (1.02–1.40)	0.095 (0.073–0.123)	0.072 (0.054–0.120)	5.40 (4.10–6.80)	31 (25–41)	2.3 (1.8–2.9)	283 (192–366)
Erpe-P	0.77 (0.72–0.79)	0.511 (0.468–0.607)	0.177 (0.161 – 0.200)	0.718 (0.527–1.142)	2.97 (2.88–3.04)	0.704 (0.649–0.848)	0.244 (0.214–0.286)	8.00 (7.47–8.90)	21 (19–22)	5.3 (4.4–5.7)	230 (193–254)

analyses were checked for multicollinearity and variance inflation.

To evaluate controls of seasonal nutrient uptake dynamics on different spatial scales, regression analyses were conducted using data on three different levels of aggregation using (1) seasonal data from single stream reaches, (2) pooled data from reaches of the same stream, and (3) pooled data from all stream reaches. Similar results derived from regression analyses performed at different levels of aggregation would indicate that the same independent variables that explain seasonal nutrient uptake dynamics can also explain spatial variability of nutrient uptake rates (i.e., variability in uptake rates between different reaches of the same stream or between different lowland streams)

Results

Hydrodynamics—Discharge, current velocity, and stream water depth remained quite stable during the sampling period, but differences were observed between the studied streams. Discharge and water depth in the third-order Erpe study reaches were greater than in the first-order DMB reaches, with median values measuring 7 to 22 and 1.7 to 3.1 times greater. Median discharge, current velocity, and stream depth in DMB reaches were very similar. Also, variation in discharge, current velocity, and stream depth was comparable in both DMB reaches. In contrast, median discharge and water depth in the Erpe-P reach were 3.1 and 1.7 times greater, respectively, than in the Erpe-D reach. Flow and water depth variation were higher in the Erpe-D reach as well (ranges: 0.139 vs. 0.065 $m^3\ s^{-1}$ and 7 vs. 4 cm, respectively). However, current velocities were only slightly higher in the Erpe-D reach (Table 1). Interestingly, absolute and normalized transient storage zone sizes were relatively high in the Erpe-P reach compared to the DMB reaches and the Erpe-D reach (Table 1). Concomitantly, the Erpe-P reach was the only stream reach under study exhibiting small side-pools.

Ecosystem metabolism—Community respiration dominated the ecosystem metabolism of the investigated stream reaches, so that GPP : CR_{24} ratios were generally less than one and values of net ecosystem production (NEP) less than zero (Table 2). In only 1 out of 20 measurements did GPP : CR_{24} ratios and NEP slightly exceed values of one and zero, respectively. Rates of GPP and CR_{24} exhibited a pronounced seasonal variability and ranged from <0.1 and 3.9 g O_2 m^{-2} d^{-1}, respectively, in winter to 58.9 and 69.5 g O_2 m^{-2} d^{-1} in spring.

In both studied reaches of the Erpe, rates of GPP and CR_{24} were positively correlated with temperature (Spearman rank correlations, $r > 0.90$, $p < 0.05$, $n = 5$). In the DMB, no positive relationships between ecosystem metabolism and temperature were observed because of the presence of emergent macrophytes, which did not contribute to instream DO production but shaded the stream channel in summer, when temperatures were high. Accordingly, rates of instream GPP tended to be inversely related to the biomass of emergent macrophytes (Gücker, et al.

Table 2. Ecosystem metabolism of the lowland stream reaches. Data are median values (ranges) from five sampling campaigns in 2002.

	Gross primary production, GPP (g DO m^{-2} d^{-1})	Community respiration, CR_{24} (g DO m^{-2} d^{-1})	GPP : CR_{24}	Net ecosystem production, NEP (g DO m^{-2} d^{-1})
DMB-D	3.74 (0.05–18.01)	24.3 (3.9–33.8)	0.11 (0.01–0.74)	−13.1 (−30.1 to −3.8)
DMB-P	2.60 (0.02–58.92)	35.1 (4.4–52.4)	0.07 (<0.01–1.12)	−16.6 (−35.5 to 6.5)
Erpe-D	8.47 (0.07–32.13)	12.4 (6.1–33.1)	0.50 (0.01–1.00)	−6.0 (−16.7 to −0.1)
Erpe-P	27.53 (0.05–46.55)	59.2 (17.6–69.5)	0.40 (<0.01–0.79)	−21.5 (−42.0 to −12.7)

2006) in the DMB-D and the DMB-P reach when data from the December sampling campaign (with low metabolic rates due to low temperature) were excluded from the analyses (Spearman rank correlations, $r < -0.89$, $p = 0.051$ and 0.106, $n = 4$). In the DMB, the highest rates of GPP occurred during the diatom bloom in the unshaded channel in spring.

Nutrient uptake—Ambient nutrient uptake rates exhibited a high temporal variability and ranged from 0.035 to 0.517 g NH_4-N m^{-2} d^{-1}, from 0.180 to 12.880 g NO_3-N m^{-2} d^{-1}, and from 0.017 to 0.750 g SRP m^{-2} d^{-1} (Table 3; Fig. 2, for ammonium and nitrate). In winter (i.e., the December sampling campaign), uptake rates were lower than in other seasons. However, uptake rates did not show a systematic seasonal pattern from early spring to fall. In the Erpe-P reach, nitrate and phosphate uptake rates were higher than in the other stream reaches (Table 3). Vertical uptake velocities (V_f) ranged from 3.9×10^{-3} to 6.0×10^{-2} mm s^{-1} for ammonium, from 2.1×10^{-4} to 2.8×10^{-2} mm s^{-1} for nitrate, and from 4.2×10^{-3} to 6.9×10^{-2} mm s^{-1} for phosphate. As was the case with uptake rates, uptake lengths showed a high temporal variability and ranged from 1,310 to 30,657 m for ammonium, from 4,601 to 167,763 m for nitrate, and from 960 to 9,358 m for phosphate (Table 3; Fig. 2, for ammonium and nitrate). Moreover, uptake lengths were higher in winter than in other seasons. The Erpe-P reach exhibited higher uptake lengths of ammonium and phosphate, but lower uptake lengths of nitrate than the other stream reaches (Table 3).

Estimated ambient nitrification rates ($U_{NH_4}^{NIT}$) ranged from 0.008 to 0.238 g NH_4-N m^{-2} d^{-1} (Table 3). In the Erpe, 63% (36 to 89; median and range) of the ammonium uptake during the addition experiments was due to nitrification. In the DMB, significantly less of the ammonium taken up was nitrified (paired t-test, $p < 0.01$, $n = 10$). Here only 29% (7 to 61) of the ecosystem ammonium uptake was due to nitrification. According to

Table 3. Ecosystem nutrient uptake of the investigated lowland stream reaches. Data from five sampling campaigns in 2002.

	Sampling campaign	Ammonium uptake rate, U_{NH_4} (g N m^{-2} d^{-1})	Nitrification rate, $U_{NH_4}^{NIT}$ (% U_{NH_4})	Ammonium uptake length, $S_W^{NH_4}$ (m)	Nitrate uptake rate, U_{NO_3} (g N m^{-2} d^{-1})	Nitrate uptake length, $S_W^{NO_3}$ (m)	Phosphate uptake rate, U_{PO_4} (g P m^{-2} d^{-1})	Phosphate uptake length, $S_W^{PO_4}$ (m)
DMB-D	Spring	0.109	7	1,777	2.11	17,977	0.081	960
	Early summer	0.061	16	3,404	0.69	23,081	0.070	2,142
	Late summer	0.188	34	1,310	0.38	10,304	0.071	2,074
	Fall	0.160	23	1,928	0.36	28,860	0.030	7,087
	Winter	0.035	62	8,421	0.29	167,763	0.017	8,932
DMB-P	Spring	0.085	9	2,486	1.98	20,946	0.077	1,551
	Early summer	0.066	22	3,641	0.83	19,082	0.072	2,107
	Late summer	0.097	41	2,885	0.18	27,534	0.041	4,180
	Fall	0.117	36	3,077	0.24	47,834	0.046	4,783
	Winter	0.050	57	6,643	0.47	121,902	0.024	8,100
Erpe-D	Spring	0.214	55	4,720	1.83	25,552	0.037	2,322
	Early summer	0.282	54	1,367	1.31	8,444	0.152	974
	Late summer	0.174	36	1,586	0.39	11,529	0.185	1,436
	Fall	0.059	79	2,094	0.19	18,569	0.086	1,637
	Winter	0.112	73	4,914	0.41	38,184	0.017	4,670
Erpe-P	Spring	0.307	64	7,665	11.38	8,595	0.262	4,821
	Early summer	0.383	62	2,162	12.88	4,601	0.750	3,645
	Late summer	0.517	44	2,028	7.96	6,977	0.578	4,502
	Fall	0.240	76	5,609	5.00	13,534	0.398	5,369
	Winter	0.076	89	30,657	5.01	25,695	0.178	9,359

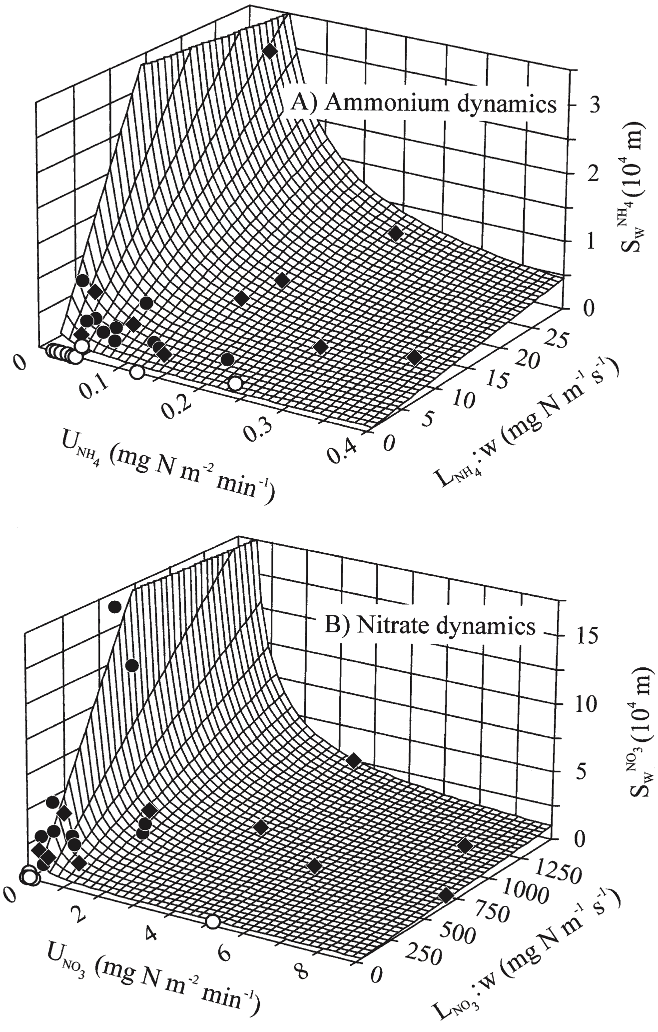

Fig. 2. Patterns of (A) ammonium and (B) nitrate uptake and transport in the eutrophic lowland streams (DMB: filled circles; Erpe: diamonds) compared to the data reported by Webster et al. (2003) from more pristine streams (open circles). Note that we report data from two streams, each studied in two stream reaches on five dates, whereas Webster et al. (2003) reported data from 11 streams without replication.

paired Wilcoxon tests ($p < 0.05$, $n = 10$), $U_{\mathrm{NH_4}}^{\mathrm{NIT}} : C_{\mathrm{DO}}$ as well as $U_{\mathrm{NO_3}} : C_{\mathrm{DOC}}$ ratios in the Erpe were significantly higher than the respective ratios in the DMB.

Relationships between nutrient uptake and its potential determinants—Significant relationships between molar $U_{\mathrm{DIN}} : U_{\mathrm{SRP}}$ ratios and molar $C_{\mathrm{DIN}} : C_{\mathrm{SRP}}$ ratios (Fig. 3) were revealed in the DMB ($r = 0.93, p < 0.01, n = 10$) and in the Erpe ($r = 0.78$, $p < 0.01$, $n = 10$), as well as for pooled data from both streams ($r = 0.68, p < 0.01, n = 20$). Molar ratios between DIN and SRP concentrations ($C_{\mathrm{DIN}} : C_{\mathrm{SRP}}$) and between DIN and SRP uptake rates ($U_{\mathrm{DIN}} : U_{\mathrm{SRP}}$) were 173 (41 to 1,220; median and range) and 37 (5 to 125), respectively (Fig. 3).

We found several significant ($p < 0.05$) and marginally significant ($p < 0.1$) nonlinear relationships between environmental variables and ambient phosphate, nitrate, and ammonium uptake rates (U_{AMB}) when conducting regression analyses for the seasonal data of single stream reaches. Similar (i.e., the same independent variables and similar regression models) but more significant relationships emerged when data from both reaches of the respective stream were pooled (Table 4), indicating that the same independent variables can also explain spatial variability of nutrient uptake rates within the same stream. No significant relationships were detected after pooling data from both streams, indicating that the controls of nutrient uptake differ between the studied streams.

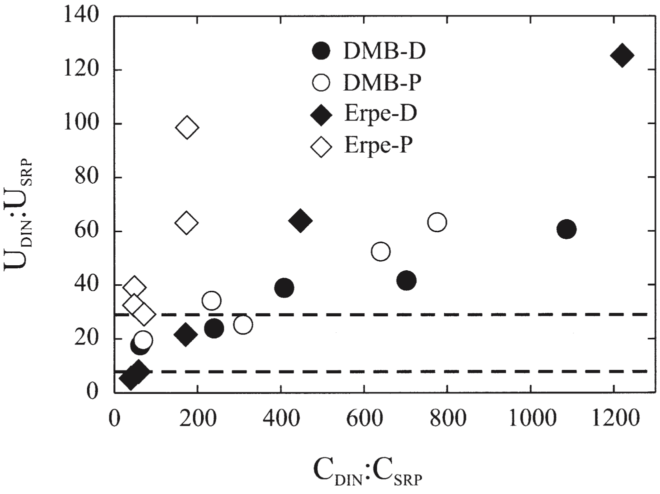

Fig. 3. Stoichiometric evaluation of DIN uptake in the eutrophic lowland streams. $U_{\mathrm{DIN}} : U_{\mathrm{SRP}}$ ratios higher than the range of N : P ratios reported for freshwater organisms indicate that dissimilative nitrogen uptake occurs. Dashed lines indicate the N : P range reported for freshwater organisms.

In the DMB, ambient nutrient uptake rates were positively related to ambient nutrient concentrations and metabolic rates (Table 4, Eqs. 1–5). Also, phosphate uptake rates in the Erpe were positively related to ambient phosphate concentrations and metabolic rates (Table 4, Eqs. 6, 7). However, variability in nitrate and ammonium uptake rates in the Erpe was explained by different independent variables (Table 4, Eqs. 9, 10). Here, rates of nitrate uptake were best explained by concentrations of DOC. Ammonium uptake rates were most closely related to ambient ammonium and DO concentrations. Interestingly, no significant relationships between uptake rates and stream hydrodynamics were found in either stream ($p > 0.1$), although there was considerable temporal and spatial variability in stream hydrodynamics.

Discussion

Nutrient uptake—Areal nutrient uptake rates measured in our study were generally high compared with values presented in previous studies (e.g., Doyle et al. 2003; Webster et al. 2003). In contrast, mass transfer coefficients (i.e., uptake rates normalized for concentration) were generally low, indicating that from the intersite perspective, nutrient uptake rate in the studied eutrophic streams was

Table 4. Significant nonlinear relationships between nutrient uptake and its potential determinants.†

	Regression model	df adj. r^2	df	F
DMB	$U_{\mathrm{PO_4}}=0.052\ C_{PO_4}^{0.18}\ GPP^{0.18}$ (1)	0.81***	8	38.3
	$U_{\mathrm{PO_4}}=-3.55+3.6\ GPP^{0.0014}$ (2)	0.61*	9	8.7
	$U_{\mathrm{NO_3}}=0.14+0.0013\ C_{NO_3}^{2.5}-20.6\ CR_{24}^{-2.0}$ (3)	0.97***	8	175.3
	$\ln(U_{\mathrm{NO_3}})=-2.2+0.16\ C_{NO_3}-1.6\ e^{-GPP}$ (4)	0.96***	8	160.1
	$U_{\mathrm{NH_4}}=0.034+0.41\ C_{NH_4}^{3.0}+0.022\ GPP^{0.50}$ (5)	0.74*	8	16.8
Erpe	$U_{\mathrm{PO_4}}=0.059+3.6\ C_{PO_4}^{2.0}+0.0027\ e^{CR_{24}(17CR_{24})^{-1.0}}$ (6)	0.90***	8	49.7
	$U_{\mathrm{PO_4}}=0.073-1.8\ C_{PO_4}\ \ln(C_{PO_4})^{-1.0}-0.083\ e^{-GPP}$ (7)	0.89***	8	42.8
	$U_{\mathrm{PO_4}}=0.013^{\,C_{PO_4}\ 0.063^{-1.0}}$ (8)	0.66**	9	22.4
	$U_{\mathrm{NO_3}}^{0.50}=0.080\ DOC^{2.5}$ (9)	0.97***	9	322.6
	$U_{\mathrm{NH_4}}=-1.4+0.0063\ CR_{24}+0.62\ \ln(DO)$ (10)	0.46*	8	6.5

† C, nutrient concentration (mg L^{-1}); CR_{24}, community respiration (g DO m^{-2} d^{-1}); DO, dissolved oxygen (mg L^{-1}); DOC, dissolved organic carbon (mg L^{-1}); GPP, gross primary production (g DO m^{-2} d^{-1}); NH_4, ammonium (NH_4-N); NO_3, nitrate (NO_3-N); PO_4, phosphate (SRP); U, uptake rate (mg m^{-2} min^{-1}).

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

low in relation to nutrient supply. Concomitantly, uptake lengths in the studied streams were in the range of kilometers. According to nutrient spiraling theory (Stream Solute Workshop 1990), long uptake lengths indicate that uptake processes cannot efficiently compensate for nutrient loads. In this sense, uptake lengths in the kilometer range (e.g., after wastewater discharge) indicate an overload of the system (Haggard et al. 2001; Martí et al. 2004). In our study, ammonium uptake lengths were much shorter than nitrate uptake lengths. For energetic reasons, ammonium is the preferentially assimilated nitrogen compound (Ward and Wetzel 1980). Moreover, intense nitrification due to well-oxygenated stream water contributed significantly to ecosystem ammonium uptake and consequently also to the relatively short ammonium uptake lengths.

Uptake processes—The molar $U_{\mathrm{DIN}} : U_{\mathrm{SRP}}$ ratio of 37 (5 to 125; median and range) indicates that DIN uptake was at least partially decoupled from biotic assimilation (Fig. 3), as molar N : P ratios of aquatic organisms should vary between 7 and 30 (Sommer 1994; Chrzanowski and Kyle 1996). Further, molar $U_{\mathrm{DIN}} : U_{\mathrm{SRP}}$ ratios correlated with molar $C_{\mathrm{DIN}} : C_{\mathrm{SRP}}$ ratios, despite the fact that phosphorus was the stoichiometrically least-abundant inorganic nutrient in the studied streams (Fig. 3). Hence, dissimilative nitrogen uptake processes likely contributed heavily to DIN uptake and made the community's relative nitrogen demand (i.e., $U_{\mathrm{DIN}} : U_{\mathrm{SRP}}$ ratios) fairly different from Redfield ratios, even at low $C_{\mathrm{DIN}} : C_{\mathrm{SRP}}$ ratios (Fig. 3, lower left part). As nitrate uptake dominated total DIN uptake (Table 3), denitrification should account for much of the dissimilative DIN uptake in the investigated streams.

It is worth noting that $U_{\mathrm{DIN}} : U_{\mathrm{SRP}}$ ratios in the investigated eutrophic streams were much lower than $C_{\mathrm{DIN}} : C_{\mathrm{SRP}}$ ratios but were still much higher than Redfield ratios (Fig. 3). Hence, nutrient concentration ratios may neither be indicative of the relative rates of nutrient cycling nor be of nutrient limitation in these eutrophic streams. Consequently, nutrient concentration ratios should be interpreted with caution not only for pristine but also for eutrophic streams (Dodds 2003).

Our nutrient addition experiments could not separate biotic uptake processes from abiotic adsorption to the stream sediments, which might be another important uptake mechanism. However, a clear separation between abiotic and biotic processes might generally be problematic, as both processes may interact (i.e., that biological uptake can occur after initial abiotic adsorption to the sediments; Peterson et al. 2001). Adsorption has been demonstrated to be an important uptake mechanism for phosphate and ammonium in oligotrophic streams (Mulholland et al. 1990; Triska et al. 1994). In the nearby mesotrophic River Spree, whose sediments exhibit a geochemical composition similar to the ones observed in our streams, phosphate sorption processes of sediments were found to be negligible (Schulz and Herzog 2004), indicating that adsorption sites for nutrients may already be occupied in streams with constantly high nutrient concentrations. For ammonium, nitrification rates of up to 89% of ecosystem ammonium uptake illustrate that abiotic sorption may not be the dominating process.

Relationships between nutrient uptake and its potential determinants—In these lowland streams, nutrient uptake rates were related to concentrations of metabolic substrates (i.e., nutrients, DOC, and DO) and to rates of ecosystem metabolism. No relationships between nutrient uptake rates and hydrodynamic variables were observed. Hydrodynamic variables were in the range of data reported in the literature (e.g., Runkel 2002; Webster et al. 2003) but exhibited typical traits of deep, soft-bottom lowland streams, such as high values of longitudinal dispersion and relatively small values of Manning's roughness coefficients (Sukhodolov et al. 1997; Wilcock et al. 1999). Also, the low values of normalized transient storage sizes ($A_{\mathrm{S}} : A$) compared to reported values (Runkel 2002) are not surprising, as the fine-sandy organic sediments present in the studied streams should not exhibit extended hyporheic zones (Morrice et al. 1997). We hypothesize that variability in hydrodynamics was too small in these incised and straightened streams, so that hydrodynamics did not exert control on uptake rates. Such relationships were also absent in an interbiome comparison of ammonium uptake in 11 hydrodynamically relatively similar streams, in which the assimilative nitrogen demand of the stream biota was assumed to control DIN uptake (Webster et al. 2003). Thus, relationships between nutrient uptake and stream hydrodynamics are more likely to be found in regional comparisons of morphologically contrasting stream reaches (Gücker and Boëchat 2004).

In contrast, most of the seasonal and spatial variability in nutrient uptake rates within single lowland streams was explained by both concentrations of metabolic substrates and rates of ecosystem metabolism (Table 3). Rates of GPP and CR_{24} were generally high compared with the range of data that has been reported for pristine streams (Lamberti and Steinmann 1997; Mulholland et al. 2001; Webster et al. 2003). Maximum rates of GPP and CR_{24} in the Erpe-P reach were among the highest in the literature. In fact, eutrophic lowland streams have previously been demonstrated to exhibit extremely high rates of GPP and CR_{24} (Körner 1997), indicating a high assimilative demand for inorganic nutrients.

In the DMB, temporal and spatial variability in the uptake rates of all inorganic nutrients was best predicted by both nutrient concentrations and metabolic rates. Relationships between nutrient uptake rate and nutrient concentration can generally be expected in pristine streams, in which uptake rates are not saturated and variation in nutrient concentrations occurs (Dodds et al. 2002; Mulholland et al. 2002). Also, relationships between nutrient uptake rate and ecosystem metabolism have previously been found in pristine streams (Mulholland et al. 2000; Hall and Tank 2003). Here we provide evidence that these relationships are also valid for incised and straightened, eutrophic streams.

In the Erpe, additional metabolic substrates (i.e., DO and DOC) were important for ammonium and nitrate uptake, respectively. A potential explanation for these differences is the supply of metabolic substrates for nitrification and denitrification, as indicated by ratios of ammonium uptake rate due to nitrification and DO concentration ($U_{NH_4}^{NIT} : C_{DO}$) and ratios of nitrate uptake and DOC concentration ($U_{NO_3} : C_{DOC}$), respectively. In the Erpe, $U_{NH_4}^{NIT} : C_{DO}$ and $U_{NO_3} : C_{DOC}$ ratios were significantly higher than the respective ratios in the DMB, indicating a poorer supply of these metabolic substrates for nitrification and denitrification in the Erpe. This indicates that a poorer supply of DO and DOC to nitrification and denitrification in the Erpe caused a significant dependency of DIN uptake rates on these metabolic substrates.

Nutrient uptake efficiency of eutrophic streams—In contrast to areal nutrient uptake rate (U), uptake length (S_W) is a measure of the load-specific nutrient uptake efficiency of streams. Variability in U and specific nutrient load (L/w) determines S_W (Stream Solute Workshop 1990). In our data set, considerable independent variability in both L/w and U occurred, so that variation in S_W could not be attributed to a single parameter (Fig. 2). However, compared with more pristine streams, the relative importance of variability in L/w in determining S_W was greater (Fig. 2).

Specific nutrient load (L/w) is nutrient concentration (C) multiplied by specific discharge (Q/w). In our data set, C varies by factors of 27 for SRP, 21 for NO_3-N, and 10 for NH_4-N, whereas Q/w varies by a factor of 13. Therefore, variability in C seems to be more important in determining S_W of SRP and NO_3-N than variability in Q/w.

Moreover, a comparison between our data set from human-altered, eutrophic streams and the data reported by Webster et al. (2003) for more pristine study sites reveals that, from the intersite perspective, high ammonium (Fig. 2A) and nitrate (Fig. 2B) uptake lengths in our study were caused by high DIN loads. Resulting increases in uptake rates could only to a minor degree compensate for these high DIN loads.

Research on lotic ecosystem functioning has concentrated on relatively pristine streams. In studies of human-altered streams, ecosystem processes such as nutrient spiraling and productivity have been widely ignored (Paul and Meyer 2001). Recently, Royer et al. (2004) and Inwood et al. (2005) examined sedimentary denitrification, which is one of the key processes affecting ecosystem nitrogen uptake in pristine streams, in eutrophic streams. Interestingly, the authors concluded that this process was unable to significantly reduce nitrate export from the investigated eutrophic headwater streams. Here we presented a comprehensive analysis of nutrient uptake in two incised and straightened, eutrophic lowland streams and evaluated the regulation of nutrient uptake efficiency in such streams.

Nutrient uptake rates were related to both concentrations of metabolic substrates and rates of ecosystem metabolism, highlighting the importance of assimilative nutrient uptake. Furthermore, dissimilative DIN uptake was an important uptake mechanism. Hence, nutrient uptake in these eutrophic streams was subjected to similar controls as in more pristine streams, indicating that the qualitative nature of nutrient retention is comparable in pristine and eutrophic stream ecosystems. From the intersite perspective, absolute uptake rates were high, whereas concentration-specific uptake rates (i.e., V_f) were low. Thus, uptake rates could only to a very limited degree compensate for high nutrient loads, resulting in long nutrient uptake lengths.

Our findings are in contrast to results from relatively pristine streams, in which efficient nutrient retention has been evidenced (Peterson et al. 2001), and thus our findings call into question whether this functional property of stream ecosystems is similarly effective in human-altered, eutrophic streams. Nutrient uptake is clearly incapable of efficiently retaining nutrients in the eutrophic lowland streams under study. Consequently, water quality problems cannot be efficiently mitigated by merely relying on natural nutrient retention. Nutrient retention in streams may only be effective when excessive nutrient loading is reduced by efficient wastewater treatment at point sources or by measures to diminish diffuse sources.

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Differential retention and utilization of dissolved organic carbon by bacteria in river sediments

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Abstract

The differential ability of natural sediment biofilms to store and metabolize specific dissolved organic carbon (DOC) fractions was studied with a set of perfusion experiments that combined a chromatographic method for the analysis of several DOC fractions with the measurement of bacterial abundance and activity. High proportions of low-molecular-weight substances and polysaccharides and low but significant proportions of humic substances were retained in sediment cores after perfusion. Bacterial abundance and production in these cores were high (1.7–3.0 $\times$ 10^9 cells cm^{-3} and 0.7–12.0 μg C cm^{-3} h^{-1}, respectively). Bacterial abundance, production, and turnover times were correlated with the retention of various DOC fractions, especially polysaccharides, indicating a differential microbial utilization of DOC. Temperature as well as the quantity and quality of retained organic matter were the major factors that influenced bacterial production. However, particulate organic carbon represented the main energy source for sediment bacteria. It is concluded that certain fractions of DOC may be readily utilized for bacterial growth, irrespective of molecular size. Instead, the presence and abundance of specific chemical groups might be decisive. Hence, the processing of organic substrates by the microbial biofilm may largely influence the biogeochemistry of DOC in river waters.

Dissolved organic carbon (DOC), whatever its form or origin, either directly or indirectly represents the ultimate source of organic carbon for sustaining the metabolism of heterotrophic bacteria. Processes such as extracellular decomposition of organic macromolecules and selective consumption of specific DOC fractions enable bacteria to exert a considerable influence on quantity and quality of DOC in natural waters (e.g., Fiebig and Marxsen 1992; Findlay et al. 1993; Volk et al. 1997). On the other hand, the metabolic activity of bacteria can be affected by the ambient concentration and composition of DOC (e.g., Kaplan and Bott 1989; Amon and Benner 1996; Baker et al. 1999). Thus, in a number of ways, bacteria may exert an influence on the carbon biogeochemistry of aquatic ecosystems.

In running waters, sediments are the major site of bacterial metabolism (Fischer and Pusch 2001). Their large internal surface area promotes colonization of these sediments by bacterial biofilms (Lock 1993; Brunke and Fischer 1999; Fischer 2002). These biofilms are supplied with nutrients and oxygen by flowing interstitial water, which originates either from the overlying water column being forced into the sediment interstices by physical processes or from groundwater exfiltration (Brunke and Gonser 1997; Pusch et al. 1998). The hyporheic biofilms retain inorganic and organic solutes (e.g., Fischer 2002), and thus they can buffer the supply of organic substrates so that short-term changes in the quality and quantity of DOC need not have an immediate effect on biofilm metabolism (Freeman and Lock 1995; Fiebig 1997).

Unraveling the functioning of the DOC metabolism in the biofilm is difficult because of the methodological problems encountered in measuring microbial activity and in the chemical fractionation of DOC. One particular problem is the difficulty in relating microbial activity to concomitant bacterial DOC utilization. Some recent studies stressed that there are differences in the availability of DOC originating from various sources for bacterial growth or respiration (Battin et al. 1999; Wiegner and Seitzinger 2001). However, it has so far been problematic to make an instantaneous distinction between DOC fractions that may support significant growth of heterotrophic bacteria and the more refractory DOC fractions that do not. Amon and Benner (1996) hypothesized that DOC availability was largely indicated by molecule size, with the larger molecules being more rapidly turned over.

Bacterial production in hyporheic sediments has so far been measured in only very few studies (Findlay and Sobczak 2000). Bacterial productivity in sediments is assumed to be at least a partial function of the amount of sediment organic matter. Whereas a correlation between particulate organic matter and bacterial production has been revealed for river sediments (Brunke and Fischer 1999; Findlay and Sobczak 2000; Fischer et al. 2002), a causal relationship between DOC retention and bacterial production in situ still remains an open question.

In order to reveal relationships between the occurrence and retention of various fractions of DOC in sediments of a lowland river, and concomitant bacterial growth, we characterized DOC in interstitial water and at the same time estimated bacterial abundance and production in the sediments through which this water flowed. We performed these measurements using the natural bacterial community on their indigenous substrate. Thus, we could address the following questions. (1) Does the passage of interstitial water through sediments and the concomitant bacterial activity within these sediments substantially change the quality of DOC? If so,

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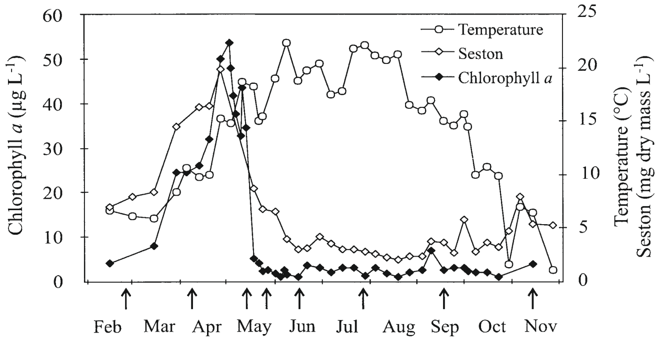

Fig. 1. Temperature, seston concentration, and Chl *a* concentration in the Spree water column in 1998. Arrows indicate the dates when sediment bacterial and DOC variables were measured.

which fractions are preferentially retained within the sediments and utilized by the bacteria? (2) Does quality and quantity of DOC in interstitial water have an immediate effect on bacterial metabolic activity in the sediments? If so, which fractions of the DOC have a specific influence on this activity?

Materials and methods

Study site—Sandy sediments were taken from the Spree, a sixth-order river ~40 km upstream of Berlin, Germany (52°22′N, 13°49′E). In this section, the Spree is a lowland river with sandy sediments in the main channel. Unconfined, shifting sands covered ~20% of the river bottom area (Fischer and Pusch 2001). In 1998, a distinctive vernal phytoplankton bloom developed, followed by an extended clear-water stage. Between February and November 1998, seston concentrations ranged from 2 to 20 mg L^{-1} (Fig. 1). At a mean discharge of 11.5 m^3 s^{-1}, the mean water depth was 1.3 m, mean width was 25 m, and maximum flow velocities in the main channel were 50–60 cm s^{-1}. The sediments had an organic matter content of ~1% ash-free dry mass (loss on ignition), a homogenous particle size distribution with a median particle size of 0.5 mm, high hydraulic conductivity (k = 0.001–0.004 m s^{-1}), and dark manganese and iron oxide coatings on the individual quartz sand particles. To obtain field replicate samples, we sampled three sites located within a 2-km reach. We took four sediment cores (6 cm in diameter) from each of the three sites on each of eight occasions in 1998 (Fig. 1). From each core, we subsampled smaller cores using 20-ml polyethylene syringes with their tips cut off. These smaller cores had a volume of 24 ml (7.6 cm in length and 2.0 cm in diameter), and they were stored at 2–4°C for 6–9 h until the start of experimentation.

Experimental setup—The sediment cores were perfused with prefiltered river water (8- and 0.45-μm pore size cellulose nitrate filters) freshly taken at each sampling date from the same section of the River Spree. Mean (±SD) perfusion rate was 6.0 ± 0.3 ml cm^{-2} h^{-1}, resulting in a mean residence time of 0.5 h. This flow rate was based on estimates of in situ interstitial flow obtained from model calculations (Thibodeaux and Boyle 1987) and dye experiments conducted in laboratory flumes (authors' unpubl. data). The filtered river water was perfused through the sediment cores with a 16-channel peristaltic pump (Ismatec IPC-16 S) in an upward flow and once-through mode, entering the cores from their originally uppermost sediment layer (Fig. 2). Thus, the infiltration of river water into the sediments was simulated. We used Tygon tubing (Norton) and precombusted glassware for pumping and storage of water, respectively. The tubing was rinsed for 2 h with warm (50°C) micropure water and for 2 h with cold micropure water before usage. Vials for collecting DOC samples were washed with NaOH, HCl, and micropure water before use.

The general experimental setup was as follows. During a settling time of 8–10 h, the 12 cores of each sampling date were perfused with prefiltered river water. Nine cores (three from each site) were used for DOC and production measurements, and three (one from each site) served as controls in the production measurements. The perfused water was discarded, and perfusion was continued for 10 h to measure DOC retention in the sediments. Duplicate controls for DOC measurements were run within the same system by use of empty syringes. There were no significant differences between DOC concentrations before and after the passage of

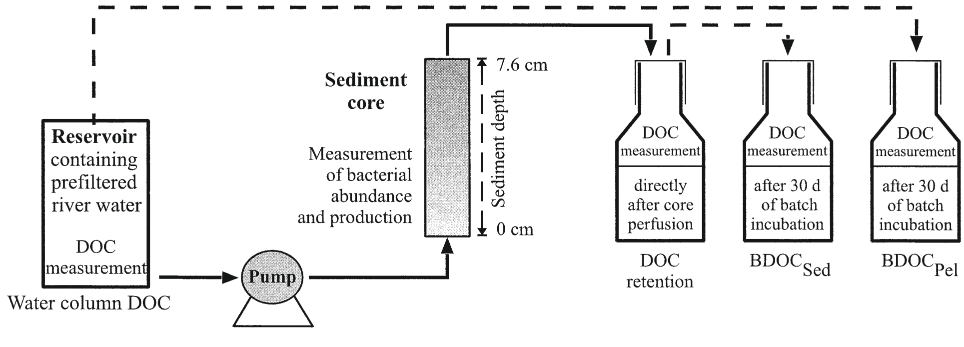

Fig. 2. Schematic view of the experimental setup used for measuring bacterial production and DOC retention in sediment cores and for BDOC. The solid lines indicate the transport of water in core-perfusion experiments. The dashed lines indicate that water before and after perfusion through the sediment cores was subjected to 30-d batch incubation for measurement of $BDOC_{Pel}$ and $BDOC_{Sed}$, respectively (*see also Materials and methods section*).

river water through the tubing and the empty syringes (paired *t*-test, $p = 0.55$, $n = 11$). Subsequently, bacterial production was measured for 12 h as described below. All incubations were made at in situ temperatures ranging 7–22°C (±1°C), except on 26 May 1998. On that date, the incubation temperature was 18°C, which was 3°C higher than the in situ temperature but was the same temperature as in the previous and following measurements. Thus, bacterial activities during the algal bloom and the clear-water stage could be compared under the same thermal conditions.

DOC analysis—DOC in the river water before and after perfusion through the sediment cores was quantified and characterized by liquid chromatography followed by organic carbon detection (LC-OCD; Huber and Frimmel 1994; Hesse and Frimmel 1999; Sachse et al. 2001). This method combines size-exclusion chromatography via stainless steel columns (250 × 20 mm) packed with TSK HW-50S resin (Toyopearl), ultraviolet (UV) detection of the spectral absorption coefficient at a wavelength of 254 nm, and infrared (IR) detection of the eluting carbon fractions after UV oxidation of DOC at wavelength of 185 nm in a cylindrical UV thin-film reactor (Gränzel; Huber and Frimmel 1991). Phosphate buffer (0.029 mol L^{-1}, pH 6.5) was used as the mobile phase. The flow rate was 1 ml min^{-1}, and the sample injection volume was 2 ml.

Polysaccharides (PS), humic substances (HS), low-molecular-weight acids (LMWA), and two groups of low-molecular-weight substances (LWS, representing amino acids, mono- and disaccharides) were fractionated, oxidized, and subsequently quantified by IR detection. The fraction of PS shows no absorption in the UV range. HS include humic and fulvic polyelectrolytic acids that are UV active because of aromatic groups. LMWA are defined as low-molecular-weight carboxylic acids such as several metabolites in biological and chemical processes. Fractions were identified by use of standards (humic and fulvic acid standards from the IHSS) and simple compounds of different origin, and by characterizing the biological availability of each fraction (Sachse et al. 2001). For molecular-weight calibration, saccharides (raffinose, maltose, glucose, glycerin, and methanol from Merck) and polydextranes (M_p = 830, 4,400, 9,900, 21,400, and 43,500 g mol^{-1} from Polymer Standards Service) were used. The calibration curve was obtained by plotting the retention times of the standards against the logarithm of their molecular weights by use of the program "Geltreat" (I. Perminova unpubl. data). Molecular weights of HS in the water samples were calculated by comparing their retention times with the calibration curve. Total DOC was quantified by IR detection after UV oxidation, bypassing the chromatographic unit.

DOC retention and biodegradable DOC (BDOC)—We defined DOC retention in sediments and BDOC as indicators of bacterial DOC utilization in sediments and the water column. These variables were calculated from differences in DOC between the river water and the perfused and/or incubated water (Fig. 2). (1) DOC retention in sediment cores was calculated from changes in DOC concentrations before and after perfusion through sediment cores. This fraction corresponds to BDOC sensu Kaplan and Newbold (1995). (2) $BDOC_{Sed}$ was defined as the amount of DOC consumed during core perfusion and subsequent 30 d of batch incubation of the perfused water. (3) $BDOC_{Pel}$ was defined as the amount of DOC consumed after 30 d of batch incubation of river water (BDOC sensu Servais et al. 1989). Batch incubations for the measurements of $BDOC_{Pel}$ and $BDOC_{Sed}$ were made with 150-ml samples in precombusted glass flasks. Samples were inoculated with 1.5 ml of prefiltered (2-μm pore size) river water and incubated for 30 d at 20°C in the dark. After the incubation, concentration and composition of DOC were measured (Servais et al. 1989) (*see Fig. 2*).

Bacterial abundance and production—Bacterial production in the perfused sediment cores was estimated from leucine incorporation rates into bacterial protein (Kirchman 1993). After sampling for DOC measurements, we added L-[U-^{14}C]leucine (Amersham; specific activity 11.3 GBq $mmol^{-1}$) and unlabeled L-leucine to the perfusion water in order to achieve a final concentration of 50 μM and a final specific activity of 7 Bq $nmol^{-1}$. The cores were perfused with leucine for 12 h and then fixed by a 4-h perfusion of 5% formaldehyde in prefiltered river water. Leucine uptake in the perfusion water can be neglected in this setup. Only a small amount of pore water was later sampled with the sediments, and biomass and production of bacteria in the sediments exceed those in the river water by factors of 500–1,000 per volume, respectively (Fischer and Pusch 2001). Three control cores—one from each site—were perfused with a mixture of L-[U-^{14}C]leucine, unlabeled L-leucine, and 5% formaldehyde. The number of controls was later reduced, because activity in controls was low (always <8% of the activity in living sediments). The leucine-incorporation method had previously been tested in a similar experimental setup for linearity of uptake over long time intervals (36 h), for isotope dilution, and for substrate saturation (Marxsen 1996; Fischer and Pusch 1999).

On the next day, the sediment was carefully removed from the cores and divided into depth layers of 0–1.9, 1.9–3.8, 3.9–5.7, and 5.7–7.6 cm. These layers are referred to in the results as 1-, 3-, 5-, and 7-cm depths. The sediment from each layer was mixed, and a 0.5-cm^3 aliquot was used to determine bacterial abundance and production, as described elsewhere (Fischer and Pusch 1999, 2001). In brief, subsamples used for bacterial cell counts were taken after a 10-min sonication step and diluted with a sterile filtered aqueous solution of 3.5% formaldehyde, 0.85% NaCl, and 1 mM pyrophosphate. Bacteria were stained with the use of 4′,6-diamidino-2-phenylindol at a final concentration of 10 mg L^{-1}. After 40 min of dark incubation, bacteria were filtered onto black polycarbonate filters (Nuclepore, pore size 0.2 μm). At least 200 bacteria within at least 10 microscopic fields were directly counted by epifluorescence microscopy.

Protein was extracted from the remaining samples with the use of hot trichloroacetic acid at 5% final concentration. The precipitate was filtered onto 0.2-μm pore size polyester filters (Oxyphen). Filters were thoroughly rinsed with deionized water and then put into 4-ml scintillation pico-vials, completely dissolved in 0.5-ml solvent (Soluene; Packard Instruments) and mixed with 2.5 ml of scintillation fluid

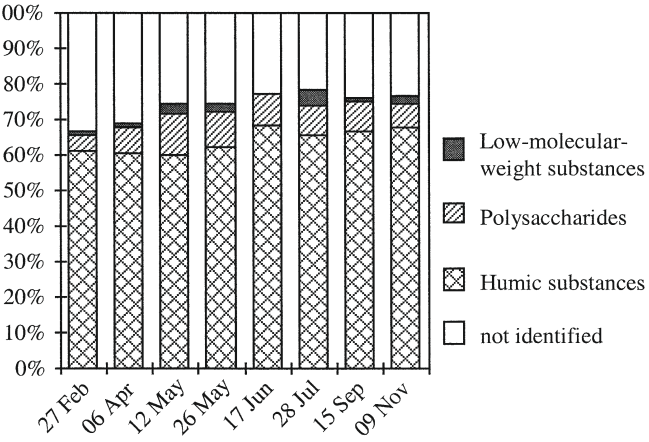

Fig. 3. Composition of DOC in the Spree water column in 1998.

(Hionic Fluor; Packard). Radioactive decays were measured in a Canberra Packard 1900 scintillation counter. Bacterial carbon production was calculated from leucine incorporation rates under the assumption of 7.3 mol % leucine in total protein and a carbon : protein ratio of 0.86 (Simon and Azam 1989). Isotope dilution was low (1.1–1.3; Fischer and Pusch 1999) and was therefore disregarded in the production estimates. Turnover times of bacterial carbon were estimated by dividing bacterial biomass by carbon production assuming a biomass of 22 fg C for a single bacterium (Fischer and Pusch 2001).

Q_{10} *values*—The metabolic rates of bacteria generally increase with temperature, within certain physiological limits. The magnitude of this increase can be characterized by the ratio of rates measured across a temperature increase of 10°C (Q_{10}; Lampert 1984). To evaluate the effect of temperature on bacterial production, we calculated (1) the "ecosystem effective Q_{10}" of bacterial production per unit of sediment volume, which includes the effect of seasonally changing bacterial abundances, and (2) a "community-specific Q_{10}" that characterizes temperature dependence as the bacterial production divided by bacterial cell number.

Data analysis—In total, 69 sediment cores were used for the experiments. These divide into eight sampling dates with three sites each and three replicate cores per site. In February 1998, only two sites were sampled, and bacterial abundance was not determined. We performed calculations and statistics on three levels of data aggregation. (1) Bacterial production, abundance, and turnover times were first estimated for single samples (four depth layers from each core, $n = 276$ for production, $n = 252$ for abundance and turnover) to examine their vertical distribution within the sediment cores. (2) Bacterial variables were then aggregated by adding the results of the different depth layers of each core. This was done to compare bacterial variables with DOC retention and $BDOC_{Sed}$, which were also determined for the entire cores ($n = 69$). (3) Temperature, DOC before incubation, and $BDOC_{Pel}$ differed only by sampling date. Therefore, these comparisons were made between sampling dates ($n = 8$), which include measurements from the river water on the respective sampling date as well as data from nine sediment cores each and bacterial data from four depth layers of each core. Data were analyzed with the software SPSS (release 6.0; SPSS) by use of nonparametric tests. Spearman rank correlations were used to reveal the relationships of bacterial data with DOC amount and composition. Kruskal-Wallis tests were performed to test the effects of sediment depth on bacterial abundance and production.

Results

DOC—Total DOC in the studied time period ranged from 5,920 to 7,400 μg L^{-1}. DOC composition showed a similar pattern throughout the year with HS > PS > LWS (Fig. 3). Despite the low variability in total DOC concentrations, there were marked seasonal changes in the PS and LWS fractions. Among the fractions detectable by chromatography (Fig. 4A), PS peaked first (mean elution time, 25.6 min)

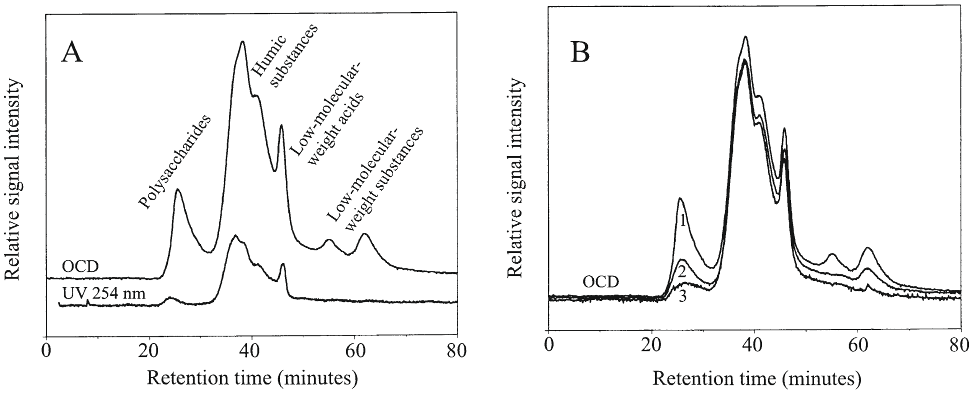

Fig. 4. (A) LC-OCD elution diagram of the DOC composition in the Spree water column, 12 May 1998. Upper line, OCD; lower line, UV detection at 254 nm. (B) LC-OCD elution diagrams of the DOC composition in Spree water, 12 May 1998, before perfusion through river sediments (upper line, 1), after perfusion (central line, 2), and after core perfusion and subsequent 30 d of batch incubation ($BDOC_{Sed}$, lower line, 3).

and made up 4.5%–11.5% of the total DOC. PS concentrations were highest in May, during the peak algal bloom (854 μg L^{-1}), and lowest in February (269 μg L^{-1}). HS were the major DOC fraction, accounting for 59%–68% of the total DOC (mean elution time, 38.2 min). LMWA only occurred at low concentrations (up to 160 μg C L^{-1} in February; mean elution time, 45.5 min) and were not detected during spring or summer. Typically, one or two additional peaks occurred in the river water after mean elution times of 55.1 and 61.9 min, respectively (Fig. 4A). This fraction was not UV active. It is referred to as LWS, is made up of sugars and amino acids (A.S. and I. Perminova unpubl. data), and made up $\leq$4.6% of the total DOC (Fig. 3). The concentration of these substances ranged 22–289 μg L^{-1} and was quantified only when distinct peaks occurred. Other DOC eluting after >50 min and not showing any distinct peaks consisted of other low-molecular-weight aliphatic substances, which could not be assigned to a specific DOC fraction. This mixture contributed 11.7%–16.7% to total DOC. A proportion of 3.8%–17.7% of the total DOC was hydrophobic and was therefore not chromatographable. The mean (±SD) spectral absorption coefficient measured at 254 nm was 8.5 ± 1.0 m^{-1} for the humic fraction and close to zero for the other fractions identified, indicating a substantial proportion of aromatic structures in the humic fraction of the DOC only.

Vertical distribution of bacterial abundance and activity—Bacteria were relatively homogenously distributed in space and time within the sandy habitats (Fig. 5A). However, we observed a slight decrease of bacterial abundance with increasing sediment depth (Kruskal-Wallis test, $\chi^2 = 14.5$, $p < 0.01$, $n = 252$). Mean (±SD) abundance was 2.66 ± 0.26 × 10^9 bacteria cm^{-3} in 1-cm sediment depth and 2.17 ± 0.38 × 10^9 bacteria cm^{-3} in 7-cm sediment depth.

Bacterial production varied more strongly in space and time than bacterial abundance (Fig. 5B). Mean (±SD) production ranged from 0.70 ± 0.28 μg C cm^{-3} h^{-1} in February at 7-cm depth to 12.0 ± 2.3 μg C cm^{-3} h^{-1} in July at 1-cm depth. The production was highest in the upper sediment layer and decreased significantly with increasing sediment depth (Kruskal-Wallis test, $\chi^2 = 137$, $p < 0.001$, $n = 270$), so that production at 7-cm sediment depth was always less than one-third of the production measured at 1-cm sediment depth. Production did not differ significantly between the sampling sites (Kruskal-Wallis test, $\chi^2 = 0.91$, $p = 0.63$, $n = 270$).

Turnover times of bacterial carbon were in a range of 3.5–220 h, which is equivalent to specific growth rates of 6.9–0.11 d^{-1}. The variation in turnover times of bacterial carbon was primarily driven by bacterial production; therefore, similar statistical relationships with sediment depth applied. We thus found the shortest turnover times of 4.8 ± 0.9 h in the uppermost sediment layer in July at 22°C and the longest turnover times of 76 ± 47 h in the lowermost layer in November at 7°C (Fig. 5C). Mean cell-specific bacterial production was in a range of 0.4–4.4 fg C h^{-1}.

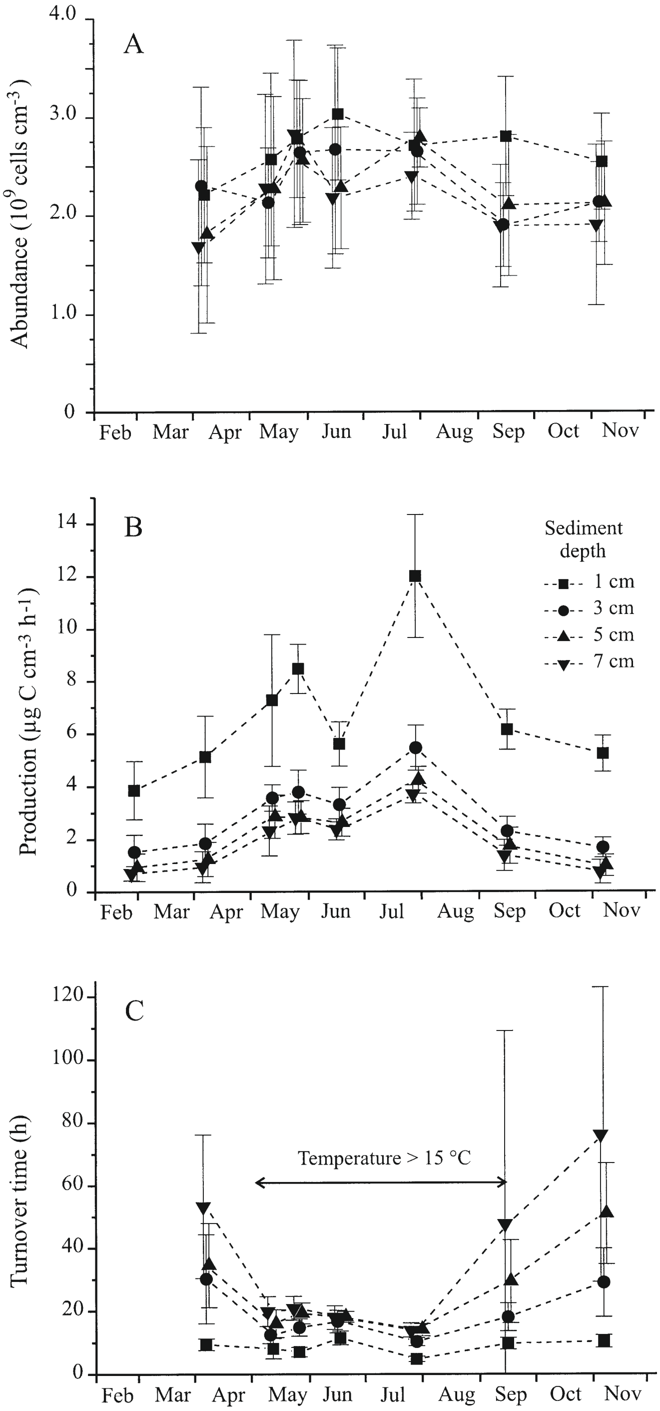

Fig. 5. (A) Bacterial abundance, (B) production, and (C) turnover times of bacterial carbon (C) in four depth layers of sediments of the River Spree, 1998. Means ± SD, $n = 9$, ($n = 6$ in February). Symbols from each sampling date have been spread to improve clarity.

Retention efficiencies for DOC fractions—Retention characteristics differed markedly for the various DOC fractions (Figs. 4B, 6). A total mean (± SD) of 898 ± 429 μg DOC L^{-1} (14% of the input DOC) was retained in the cores. Retention was most effective in May during the peak algal bloom, with 1,500 μg DOC retained per liter of perfused water (20% of the total DOC), when total DOC in the river

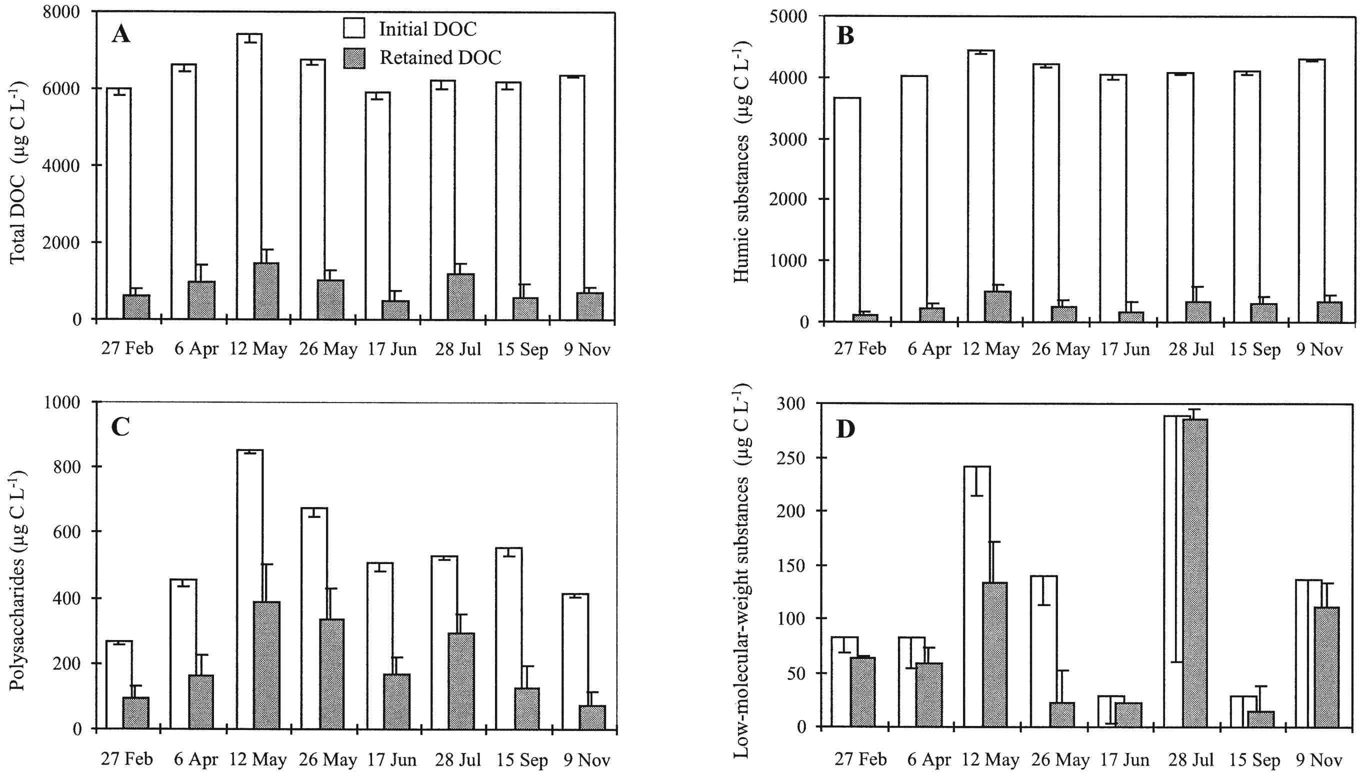

Fig. 6. Initial concentrations of dissolved organic compounds in Spree water and the proportions retained in sediment cores. (A) Total DOC, (B) HS, (C) PS, and (D) LWS. Means ± SD; $n = 4$ analytical replicates for initial concentrations, $n = 9$ ($n = 6$ in February) experimental replicates for retained organic compounds.

water was highest. PS were retained very effectively by up to 56% on 28 July (mean, 39%). HS were retained less effectively than total DOC (3.2%–11.4% of the input DOC; mean, 7%). The LWS were retained in the sediment cores by up to 98% (mean, 66%) (Fig. 6).

$BDOC_{Pel}$ and $BDOC_{Sed}$ amounted to 10.7%–21.6% and 17.1%–27.7% of the total DOC, respectively (Fig. 7). Both peaked during the vernal algal bloom in May and were lowest in November. The concentration of $BDOC_{Pel}$ comprised 80% of $BDOC_{Sed}$ and was significantly lower (paired *t*-test, $p < 0.001$, $n = 8$). However, the composition of the retained DOC was very similar to that of $BDOC_{Pel}$. Retained DOC and $BDOC_{Pel}$ were mainly made up of PS and LWS. HS were also retained to a certain extent within the sediment cores (Fig. 4B) but remained nearly the same in batch incubations.

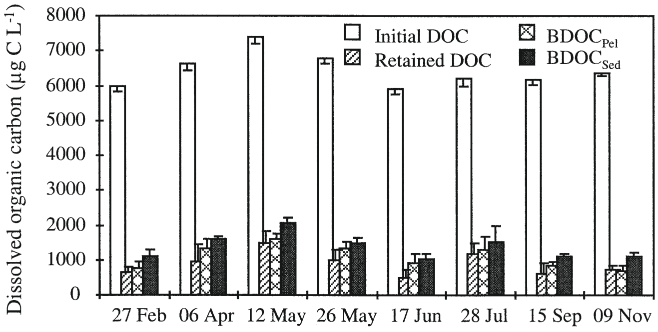

Fig. 7. Initial DOC in Spree water, DOC retained in sediment cores, biodegradable organic carbon after 30 d of batch incubation ($BDOC_{Pel}$), and biodegradable organic carbon after core perfusion and 30 d of batch incubation ($BDOC_{Sed}$). Means ± SD; $n = 4$ analytical replicates for initial concentrations, $n = 4$ experimental replicates for $BDOC_{Pel}$, and $n = 9$ ($n = 6$ in February) experimental replicates for retained DOC and for $BDOC_{Sed}$.

Bacterial production within whole sediment cores was most strongly correlated with the incubation temperature ($r_S = 0.9$, $p < 0.001$, $n = 69$). Of interest, total DOC in the river water did not correlate significantly with bacterial variables, whereas $BDOC_{Pel}$ and $BDOC_{Sed}$ both correlated significantly with bacterial production and turnover times (Table 1). We also found significant correlations between bacterial production and DOC retention ($r_S = 0.59$, $p < 0.001$) and with the retention of several fractions of DOC, in particular with the PS fraction ($r_S = 0.84$, $p < 0.001$) in those cores. Correlation coefficients of DOC variables with production or turnover times were higher than with abundance (Table 1), which might reflect the causal relationship between bacterial activity and DOC retention.

Temperature effects—Because there were no significant differences in abundance, production, and turnover times between the sampling sites, we aggregated results from all sites in order to calculate seasonal means for the bacterial vari-

Table 1. Spearman rank-correlation coefficients between bacterial variables in sediment cores and temperature, DOC, and DOC retention in sediment cores. Levels of significance are $*p < 0.05$, $**p < 0.01$, and $***p < 0.001$.

Environmental variable, DOC retention	Bacterial production ($n = 69$)	Bacterial abundance ($n = 63$)	Turnover time of bacterial carbon ($n = 62$)
Temperature ($n = 6$)	0.90***	0.40**	−0.89***
Total DOC ($n = 8$)	0.00	0.17	−0.10
$BDOC_{Pel}$ ($n = 8$)	0.45***	0.08	−0.37**
$BDOC_{Sed}$ ($n = 69$)	0.37**	0.19	−0.34**
Retention of			
DOC ($n = 69$)	0.59***	0.52***	−0.41**
PS ($n = 69$)	0.84***	0.60***	−0.66***
HS ($n = 69$)	0.34**	0.32*	−0.16
LWS ($n = 69$)	0.17	0.14	−0.24

ables. Bacterial variables calculated per sampling date (means for nine cores from April to November and six cores in February) were significantly correlated with temperature: (abundance, $r = 0.80$, $P < 0.05$, $n = 7$; production, $r = 0.91$, $p < 0.01$, $n = 8$; turnover time, $r = -0.96$, $p < 0.01$, $n = 7$). The ecosystem effective Q_{10} value, which was calculated from production per standard volume of sediment in a temperature range 10–20°C, was 2.2 (Fig. 8). The cell-specific Q_{10} value, calculated as production divided by abundance, was 1.8.

Discussion

DOC retention in sediments is the result of abiotic and biotic processes. Extracellular polymers in biofilms provide the primary sorption sites for DOC, which then diffuses into the biofilm. Here, it is stored and subsequently utilized by bacteria (Freeman and Lock 1995; Fiebig 1997). Thus, abiotic and biotic processes are closely connected within the biofilm, where extracellular polymers and bacteria act as a functional entity (Fischer 2002). The correlation between bacterial production and DOC retention in our study supports the hypothesis of a microbially mediated DOC retention. It has long been known that bacterial growth at low substrate concentrations is enhanced by the proximity of solid surfaces (Heukelekian and Heller 1940). ZoBell (1943) argued that solid surfaces may retard the diffusion of extracellular enzymes and hydrolyzates away from attached bacterial cells and thus promote bacterial activity, a hypothesis that was recently corroborated by modeling (Vetter et al. 1998). However, in studies elsewhere it was difficult to find relationships between the activity of sediment bacteria and bulk DOC concentrations (Vervier et al. 1993; Sobczak et al. 1998). Stronger relationships could be shown when particle surfaces were included into models of DOC concentrations and bacterial activity (Brunke and Fischer 1999).

In our study, we were able to directly compare DOC composition with bacterial activity. The composition of DOC in the Spree is typical of many freshwater ecosystems (Thurman 1985; Pusch et al. 1998). However, the chemical composition of DOC does not necessarily reflect the availability of DOC fractions for the microbial community because of varying microbial turnover times of these DOC fractions. Their selective retention and the correlations between bacterial activity and retained DOC give a better insight into the significance of DOC for sediment bacteria.

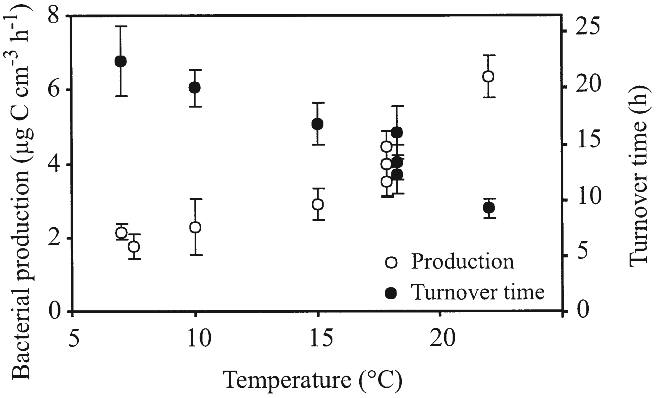

Fig. 8. Effects of temperature on bacterial production and on turnover times of bacterial carbon calculated for the upper 7.6 cm of sediments of the Spree River. Means ± SD, $n = 9$ ($n = 6$ at 7.5 °C).

High-molecular-weight PS, possibly originating from algal exudates, were retained and probably decomposed effectively within the sediment cores. Evidence exists from planktonic systems that bacteria utilize high-molecular-weight substances (Tulonen et al. 1992; Amon and Benner 1996), particularly PS (Weiss and Simon 1999), to meet their substrate requirements. In a study that used plug-flow biofilm reactors with stream water, PS were among the substrates that were preferentially utilized by biofilm bacteria (Volk et al. 1997).

The fractions containing mono- and disaccharides and amino acids were only found in low concentrations in the Spree water column, and these fractions were retained very effectively in the sediment cores. In contrast, when leucine was perfused through the sediment cores in 50-μM concentrations for bacterial production measurements, >80% of this load was recovered at the outflow from the cores. However, the 20% retained from the 50-μM concentration still are a large increase in retention as compared with the low concentrations of naturally occurring LWS, which are retained by up to 100%. The sediments were thus able to retain larger amounts of amino acids when a pulse with high concentrations became available, as described by Fiebig (1992). Initially, these amino acids are mainly retained abiotically in sediments, and they are then subsequently microbially utilized (Fiebig and Marxsen 1992; Fiebig 1997). Rapid bacterial utilization of amino acids, with gross turnover times of several days for the bulk amino acid pool, has also been reported in pelagic freshwater environments (e.g., Münster 1993; Weiss and Simon 1999).

HS are generally considered to be refractory (e.g., Thurman 1985). They can even have inhibitory effects on metabolic processes in biofilms (Meyer et al. 1987; Freeman et al. 1990), which are possibly caused by the complexation and inactivation of bacterial enzymes (Boavida and Wetzel

1998). In other studies, HS were at least partly bioavailable to the bacterial community (e.g., Tranvik 1990; Volk et al. 1997), but they supported fourfold less bacterial production per unit of carbon than nonhumic substances from the same environment (Moran and Hodson 1990). In the present study, approximately equal amounts (but a much lower percentage) of HS and PS were retained in the sediment cores (Fig. 6B,C), which could potentially be utilized by bacteria. Probably, the varying degree of utilization of HS by bacteria is related not only to the enzymatic properties of bacteria but also to differences in the chemical structures of their substrates. Carbohydrates and amino acids can be bound chemically to HS in significant amounts and thereby enhance the apparent availability of HS. These labile components made up 30% of the utilized ''humic substances'' in a biofilm reactor study (Volk et al. 1997). Because of their coupling to HS, these labile substances would have been included in the analysis of the HS pool in our study and thus increase the apparent retention of this DOC fraction.

The average amount of biodegradable organic carbon ($BDOC_{Pel}$ and $BDOC_{Sed}$) in the Spree water column was lower than in Belgian rivers studied by Servais et al. (1989). In particular, BDOC as a proportion of total DOC was lower than in most other studies on BDOC in rivers (Servais et al. 1989), a calcareous stream (Volk et al. 1997), riverine hyporheic interstices (e.g., Claret et al. 1998), and a riverine wetland (Mann and Wetzel 1995). This is probably due to efficient utilization of DOC in the Spree, so that the river water was already depleted in labile DOC at the time of sampling because of intense microbial metabolism in situ. Our results from May and June 1998 support this assumption: during spring, algae from the water column may be an important source of labile DOC, especially PS. Correspondingly, BDOC was highest on the sampling date 12 May. In the middle of May, the chlorophyll *a* content, as an indicator of algal biomass, decreased dramatically (Fig. 1). Concomitantly, the amount (Fig. 6C,D) and proportion (Fig. 3) of labile substances decreased strongly in the river water. It is therefore concluded that this change in riverine DOC composition was caused mainly by bacteria, analogous to the bacterial decomposition of DOC in the laboratory incubations.

Despite the good correlation between DOC retention and bacterial production, DOC retained in the sediment cores accounted for only 11% (June) to 33% (February) of the carbon required for bacterial production. This paradox can be explained as follows. Particulate organic matter (POM) was the primary carbon source for sediment bacteria, as was also suggested for interstitial bacteria in the riparian zone of the alpine Enns River (Brugger et al. 2001). The Spree is rich in seston and nutrients, which could fuel a level of high bacterial production when transported into the sediments via infiltrating river water. Including the hyporheic biofilm, POM built up a standing stock within the sediments of ~8.2 mg C cm^{-3} sediment volume. If this POM was the sole carbon source for bacteria and if the growth efficiency of bacteria was 30% (Meyer et al. 1987), this carbon would be turned over by bacteria in only 8.6 d in July (at 1-cm sediment depth), but in 147 d in February (at 7-cm sediment depth). Thus, the sedimentary bacterial community was highly dependent on the continuous input of fresh organic matter, both as POC and DOC. In part, DOC may be leached from POM because of cell lysis and bacterial extracellular enzymes, and bacteria may release DOC during anabolic processes. Thus, certain DOC fractions may be cycled rapidly within the sediments, and their contribution to bacterial metabolism could be higher than calculated via the apparent DOC retention (Fiebig 1992).

Bacterial abundance and production in the Spree sediments were high compared with other running waters, probably because of the high surface area of the shifting sand substratum and a good supply with oxygen and nutrients in the uppermost sediment layer (Fischer et al. 2002). The sediments here act as a fixed-film reactor, providing a ''hot spot'' of bacterial activity within the river ecosystem. Production in the upper sediment layer was significantly higher than in the lower layers, probably because of the enhanced availability of labile organic matter. Furthermore, the biochemical composition of POM also strongly influences bacterial activity in river sediments (Brunke and Fischer 1999; Fischer et al. 2002). Thus, besides temperature, the supply of high-quality POM and DOC seem to determine bacterial production in river sediments.

Our results show that bacterial activity can be controlled by naturally occurring changes in DOC quality. Although DOC of various size classes was immobilized in sediments, high-molecular-weight PS and, if present, LWS were retained most efficiently. Both PS and LWS were also quickly degraded in batch incubations. This contrasts with the ''size-reactivity continuum model'' (Amon and Benner 1996), according to which most high-molecular-weight DOC would be more reactive than most low-molecular-weight DOC. In our study, high-molecular-weight DOC was utilized to a greater extent than the LWS on account of the higher concentration of the high-molecular-weight DOC. However, because LWS were present in much lower concentrations, their utilization by bacteria may have resulted in a more rapid turnover. The obvious contradiction of our results with the ''size-reactivity continuum model'' can thus be explained with the presence of diagenetically young, highly reactive LWS in the River Spree, whereas LWS in oceans are supposed to be the oxidized products of humification processes and are diagenetically extremely old (Amon and Benner 1996). As can be seen by the spectral adsorption coefficient (Fig. 4A), the HS from the River Spree prevailed in the fraction with retention times <40 min, which represents molecular weights >1 kDa. This medium-molecular-weight organic matter clearly was least retained by hyporheic sediments and was most refactory in batch incubations, whereas DOC low and high in molecular weight was retained in the river sediments during a short residence time of 0.5 h. After subsequent 30 d of batch incubation, the quality of the DOC was further changed from a relatively wide molecular-weight spectrum to a narrower spectrum mainly composed of HS. This means that certain compounds of DOC may be readily utilized for bacterial growth irrespective of the molecular weight. We hypothesize that the availability of DOC for bacteria is rather controlled by the presence, abundance, and steric accessibility of specific chemical functional groups than by molecular size.

These findings also have implications for our knowledge of the microbial metabolism of organic matter on the ecosystem level. Most water enters rivers via exfiltrating groundwater, which passes the river sediments. Also, flowing river water temporarily infiltrates into sediments at ripple and dune structures. When the river water passes the sediments, the compounds mentioned above will be stripped off by a combination of physical retention and microbial degradation. About two thirds of the Spree sediments are open-framed, permeable sediments in which bacteria can exhibit high metabolic rates (Fischer and Pusch 2001). This permeable share of the river bottom thus makes up 16,650 m^2 within 1 river km, with half of it to be assumed to be infiltration and exfiltration areas, respectively. On the basis of the infiltration rate used here, this results in an infiltration rate of 140 L s^{-1}. Hence, the average river discharge of 11.5 m^3 s^{-1} would be infiltrated each 82 km, which means roughly every 2 d at an average flow velocity of 0.4 m s^{-1}. Because we found 900 μg C L^{-1} to be retained in the sediments, this would result in the retention of 1.3 g DOC m^{-2} d^{-1} in infiltration zones or 10.8 kg DOC km^{-1} d^{-1}. These values are in a realistic scale compared with DOC sources from primary production and groundwater exfiltration (Fischer and Pusch 2001).

Thus, the riverbed sediments serve as a highly effective sink for organic matter, and the activity of the sedimentary biofilm largely influences the organic carbon biogeochemistry in the river water. The importance of that "liver" function of the river sediments will be greatest in rivers with a diverse channel morphology, including dynamic sediment structures that favor the exchange of river water with the bottom sediments.

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Use of fluorescently labeled *Lycopodium* spores as a tracer for suspended particles in a lowland river

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Abstract. Fluorescently labeled spores of the clubmoss *Lycopodium clavatum* L. (mean diameter = 42 μm, ρ = 1175 kg/m^3) were used as a tracer to estimate transport distances and vertical deposition velocities of fine particulate organic matter (FPOM), dominated by phytoplankton and detritus flocs, in a 6th-order lowland river (River Spree, Germany). Three experiments were conducted at discharge levels of 7.9, 8.8, and 14.8 m^3/s, which were in the middle of the range of discharge levels in the River Spree. The number of spores in suspension declined exponentially with distance from the site of tracer release. Mean transport distances of the tracer particles ranged from 3000 m to 10,660 m and increased with higher flow velocities. Correspondingly, vertical deposition velocities decreased from 8.4 m/d to 4.7 m/d with higher flow velocities. Also the ratio between measured vertical deposition velocities and calculated quiescent-water fall velocities fell from 0.63 to 0.38. Although the *Lycopodium* spores cannot represent a wide range of natural suspended particles because of their uniform size and density, they can be used to determine which factors influence the flux of POM from the pelagic to the benthic zone. When comparing a broad range of stream sizes with regard to their retention efficiency, discharge seems to be a key factor regulating particle retention.

Key words: tracer, *Lycopodium* spores, FPOM, retention, transport, sedimentation, lowland river.

The organic matter budget of medium-sized lowland rivers (orders 4–6) is mainly determined by primary production of fine particulate organic matter (FPOM) in the pelagic zone and by intensity of interactions between the pelagic and benthic zones, the so-called pelagic–benthic coupling. Transfer of suspended matter from the pelagic to the benthic zone is most effective in running waters where the hydraulic radius is low. Such conditions are found when discharge is low, or when complex substrate structures are present (Prochazka et al. 1991, Snaddon et al. 1992, Maridet et al. 1995). The latter serve as very effective retention structures, and include debris dams (Speaker et al. 1984, Ehrman and Lamberti 1992, Chergui et al. 1993), submerged macrophytes (Petticrew and Kalff 1992), riparian vegetation (Ehrman and Lamberti 1992, Maridet et al. 1995), filter-feeding macroinvertebrates (Welker and Walz 1998, Wotton et al. 1998, Strayer et al. 1999), cobbles (Prochazka et al. 1991, Chergui et al. 1993), and riffles (Speaker et al. 1984, Prochazka et al. 1991).

The retention efficiency of a river section is usually investigated by tracer experiments. Most of these experiments have been conducted in headwater streams where allochthonous coarse particulate organic matter (CPOM) dominates organic input (Vannote et al. 1980). Therefore, marked leaf litter or wood pieces were used as particulate tracers (Young et al. 1978, Jones and Smock 1991, Prochazka et al. 1991, Ehrman and Lamberti 1992, Snaddon et al. 1992, Chergui et al. 1993). In higher-order streams, FPOM dominates the suspended load (Vannote et al. 1980). For the estimation of transport distances of FPOM, natural seston has been labeled with ^{14}C and reinjected into small rivers up to the 3rd-order (Jones and Smock 1991, Newbold et al. 1991, Cushing et al. 1993). However, the use of radiolabeled seston is often restricted by licensing requirements, especially in larger rivers where high amounts of tracer are needed. As an alternative seston analog, corn pollen (Miller and Georgian 1992, Webster et al. 1999), glass beads (Webster et al. 1999), and fluorescently labeled bacteria (Hall et al. 1996) were used successfully at discharges <200 L/s. However, there are only a few studies on the retention efficiency for FPOM in medium-sized and large rivers. Minshall et al. (1983) found that headwaters generally were the most retentive and downstream reaches the least. Lower reaches behaved more like a conduit with carbon atoms passing through at a rate comparable to water velocity (Minshall et al. 1992). Most larger European rivers are straightened and disconnected from their floodplain, which may fur-

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ther reduce their retention efficiency (Petersen and Petersen 1991). The River Spree is a typical medium-sized stream affected by river regulation, and we were interested in studying whether the statements of Minshall et al. (1983, 1992) were applicable. Was FPOM just transported in this type of river, or did benthic retention, at least at lower discharge levels, influence the seston load significantly?

Suspended matter in large rivers is often dominated by light cohesive material like detritus flocs and phytoplankton. For the seston of the River Spree, median still water settling velocities of only 0.9 to 5.2 m/d were determined (Prochnow et al. 1996). Therefore, we assumed that previously used tracer particles like corn pollen and glass beads (Miller and Georgian 1992, Webster et al. 1999) had settling velocities too high to be representative for the suspended load in the River Spree. Reynolds et al. (1990) had already used the considerably lighter spores of the clubmoss *Lycopodium clavatum* L. (Lycopodiophyta) to study suspension and settlement of particles in circulating channels. We chose these spores as tracer particles to investigate how much FPOM is lost from the flowing water in the River Spree, labeling them fluorescently before use. We also took sediment samples and installed cylindrical sediment traps in the river reach to compare the number of retained tracer particles with the loss of tracer particles calculated from the water samples.

Methods

Study site

The River Spree is a typical lowland river in northern Germany with a catchment area of ~10,000 km^2 and a mean slope of only 0.01%. It originates in the Lusatian mountains (Saxonia, Germany) at an elevation of 580 m, and flows for 400 km to Berlin through several shallow lakes. A detailed description of the Spree, its tributaries, and lakes is given by Köhler (1994).

We investigated the *Krumme Spree* (lat 52°07′N, long 14°00′E), a 21.1-km-long 6th-order section of the River Spree, which connects 2 lakes (Lake Neuendorfersee and Lake Schwielochsee). The Krumme Spree is dammed by 2 weirs, once immediately at the outflow of Lake Neuendorfersee and again between the 2 lakes. As a result of straightening measures between 1906 and 1912, the Krumme Spree now has a trapezoid channel profile with a mean width of ~25 m and is accompanied by numerous cut-off meanders. The central part of the river bed is covered with shifting sand, and the lateral parts are densely colonized by unionid mussels.

Tracer experiments were conducted on 31 August 1998, 20 April 1999, and 27 April 1999. In April 1999, river discharge was artificially regulated, enabling us to repeat our experiments at 2 different discharge levels within 1 wk.

Staining of the Lycopodium *spores*

The spores of *L. clavatum* are covered with a hydrophobic wax layer that must be removed before labeling (Käss 1992). Therefore, 250 g of spores (Carl Roth GmbH & Co., Karlsruhe) were soaked overnight at room temperature in 750 mL of a 5% solution of detergent. The next day the suspension was heated to 70°C for 15 min while being stirred continuously. Subsequently the spores were put on filter paper in a Büchner-funnel, the liquid was removed with a vacuum pump, and the remaining detergent was rinsed out with several litres of warm water. The spores were then dried by vacuum for 15 min. The following staining procedure with 5–(4,6–dichlorotriazin–2–yl) aminofluorescein (DTAF) (Sigma–Aldrich Co., Deisenhofen) was carried out as described by Sherr et al. (1987) for the preparation of fluorescently labeled bacteria. The spores were resuspended in 800 mL 0.05 M Na_2HPO_4–0.85% NaCl solution (adjusted to pH 9), mixed with 200 mg DTAF, and incubated in a water bath at 60°C for 2 h. The spores were then repeatedly rinsed with Na_2HPO_4–0.85% NaCl solution and dried at 60°C for several days.

The mean diameter of the stained *Lycopodium* spores was 42 μm (SE = 0.4 μm, n = 100). The density of 1.15 to 1.20 g/cm^3 was determined with a gas pycnometer (Micromeritics ACCUPYC 1330). Thus, the settling velocity of the spores calculated from the Stokes equation would be 0.154 mm/s (= 13.30 m/d) at 16.4°C (river temperature on 31 August 1998), 0.127 mm/s (= 10.98 m/d) at 9.5°C (20 April 1999), and 0.144 mm/s (= 12.42 m/d) at 13.8°C (27 April 1999).

Experimental design

For each experiment, *Lycopodium* spores that were soaked for ~12 h were suspended in ~20 L of river water. Fluorescein sodium salt was added for the determination of the mean flow velocity. This suspension was evenly distributed among 5 buckets and poured into the river simultaneously at transect station T0, covering a channel width of 8 m around the thalweg of the river. Water samples were taken at 5 transect stations with increasing distance from each other, located 830 m (= T1), 1630 m (= T2), 2580 m (= T3), 5130 m (= T4), and 8630 m (= T5) downstream of T0. At each of the 5 transect stations, water samples were taken 50 cm below the water surface at 5 locations distributed over the channel width to determine seston and tracer concentrations. Samples were taken at 2 to 30 min intervals. We chose short sampling intervals while the spore-fluorescein peak passed by, and longer sampling intervals subsequently, especially at the transects further downstream, where we expected the spore concentration–time curve to be longer. In April 1999, additional water samples were taken 20 cm above the river bottom at T2 and T5, to check the vertical distribution of the tracer particles in the water column.

Before each experiment, flow velocity was measured at each transect station at 1-m intervals across the river width at 10 cm below the water surface and at 62% of the water depth, respectively. Based on those velocity measurements, we divided the river cross-sections at each transect station into 5 segments, which were characterized by similar flow velocity (Fig. 1). These segments were considered to be representative of a certain part of the river cross-section and, therefore, for a certain part of the discharge. One sample per segment was taken and multiplied by the share of this segment of the discharge or, in case of the sediment samples described below, of the river bottom. Results obtained for each of the individual segments per transect were added to determine values for the whole transect.

During the experiment in August 1998, we installed cylindrical sediment traps (inside diameter: 4.6 cm, length: 36 cm) at the same locations where water samples were taken. We also took samples of the sediment surface at those locations with a tube corer, after the spores had passed by, to determine the sedimentation rate of spores and natural seston.

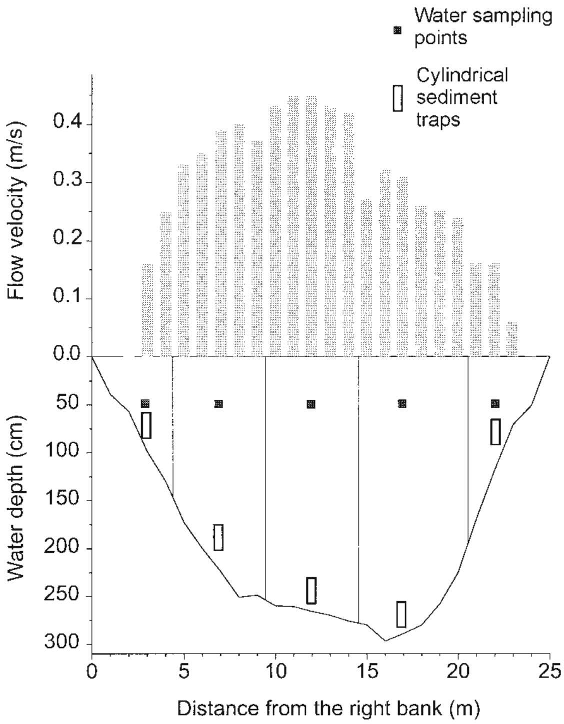

FIG. 1. River cross-section at transect station T2, showing water sampling points and cylindrical sediment trap locations. Gray columns indicate the flow velocity 10 cm below the water surface.

Three days after the 1st experiment in April 1999, the weirs were opened to increase the discharge artificially from 7.9 m^3/s to 14.8 m^3/s. We took water samples at T2 for 9 h immediately after the opening of the weirs, to measure the number of particles resuspended by the increase in flow velocity. Water samples were taken at 5 locations distributed over the channel width at a height of 20 cm above the bottom and in the middle of the channel 50 cm below the water surface.

Sample processing

The concentration of fluorescein sodium in the water samples was determined with a spectrofluorophotometer (Shimadzu RF-5001 PC and RF-5301 PC). Subsequently, the water samples were filtered on black 8-μm cellulose nitrate filters (Sartorius) and the spores were counted on the whole filter under 100× magnification with an epifluorescence microscope (Nikon Microphot-FXA). The Nikon filter set consisted of an EX 420–490 excitation filter, DM 510 beam splitter and BA 520 barrier filter. The samples from the sediment traps were treated the same. The sediment samples were rinsed with a strong jet of water over a 112-μm sieve to separate the spores from the coarse sediment particles. We then resuspended the rinse water, took 3 subsamples, filtered them, and counted the spores in the same way as described above.

Calculations

The mean flow velocity in the river reach was determined by dividing the 8630 m distance from the site of tracer release to the last transect station by the time that was needed until 1/2 of the co-injected fluorescein sodium salt had passed that point. To estimate the mean depth of the river channel during the experiments, we calculated a relationship between the water level at the beginning of the Krumme Spree and the mean water depth over 90 measured cross-sections within the studied river reach.

To calculate *Lycopodium* losses, we integrated the concentration–time curves of the particulate tracer at each transect. We had to extrapolate the tail of the curves using an exponential decay function because logistic limitations required us to stop sampling at each transect station before all the spores had passed. However, the extrapolated part was usually <10% of the total number of spores at transects T1 to T4, and 13–18.5% at T5.

Using nonlinear regression, the loss of spores from the flowing water with distance was fitted with the exponential decay function (Reynolds et al. 1990):

$$N(x) = N_0 * e^{-kx} \qquad [1]$$

where N(x) is the number of spores at distance x from the release, N_0 is the number of originally released spores, and k is the longitudinal deposition rate. To estimate N_0, small amounts of *Lycopodium* spores were suspended in water and counted after filtering. One gram of *Lycopodium* powder contained $4.89*10^7$ spores (SE = $0.29*10^7$ spores, $n = 7$). Therefore, it was estimated that ~$1.22*10^{11}$ spores had been released in the experiment in August 1998, and $1.28*10^{11}$ and $2.03*10^{11}$ spores were released in the 2 experiments in April 1999, respectively. However, our results indicated that extraordinary high tracer losses occurred between the input at T0 and the 1st sampling transect T1, which may have been caused by particle aggregations in the highly concentrated *Lycopodium* suspension that was poured into the river at T0. Therefore, the amount of released tracer particles was not integrated in our calculations but it was used to check the results. Based on that examination, the values from 2 sampling sites, T1 on 31 August 1998 and T4 on 27 April 1999, were evaluated and found to be outliers. If the number of tracer particles in suspension at T1 on 31 August 1998 was included in our nonlinear regression, the curve would indicate $1.63*10^{11}$ released spores, which is significantly more than the N_0 estimated from our spore counts. At T4 on 27 April 1999, we calculated from our water samples about twice as many *Lycopodium* spores in suspension as had been released at T0.

According to Cushing et al. (1993) the mean transport distance S of a single spore before deposition was calculated using the equation:

$$S = 1/k \qquad [2]$$

where k is the longitudinal deposition rate taken from equation 1. The mean time T in suspension can then be estimated with the equation:

$$T = S/v \qquad [3]$$

where v is the mean flow velocity obtained from the transport of the co-injected fluorescein dye. The vertical deposition velocity:

$$v_{DEP} = d * v * k \qquad [4]$$

at which the *Lycopodium* spores were transferred from the water column with mean depth d (assumed to be fully mixed) to the stream bottom can be derived from equations 1 to 3.

Results

Hydrological conditions during experiments

Discharge, water temperature, mean flow velocity, and mean water depth at the dates of the 3 tracer experiments are listed in Table 1. Mean flow velocity was lower on 31 August 1998 than on 20 April 99, even though the discharge was higher. This phenomenon could have been caused by the presence of macrophytes in summer and, more probably, by adjustments of the weirs prior to our investigations in August 1998.

TABLE 1. Hydrological conditions and transport data for *Lycopodium* spores. ± values indicate the error of parameters derived from the longitudinal deposition rate, caused by its standard error (SE). – = no data.

	31 August 1998	20 April 1999	27 April 1999
Hydrological conditions			
Discharge (m^3/s)	8.8	7.9	14.8
Water temperature (°C)	16.4	9.5	13.8
Mean flow velocity (cm/s)	18.3	19.5	32.4
Mean water depth (cm)	159	155	179
Transport data			
Longitudinal deposition rate (m^{-1})	0.000333 (SE = 0.000022)	0.000218 (SE = 0.000004)	0.000094 (SE = 0.000022)
Mean transport distance (m)	$3.00*10^3$ ($\pm 0.20*10^3$)	$4.58*10^3$ ($\pm 0.08*10^3$)	$10.66*10^3$ ($\pm 2.04*10^3$)
Mean time in suspension (min)	273 (±18)	391 (±7)	549 (±103)
Vertical deposition velocity (m/d)	8.4 (±0.6)	5.7 (±0.1)	4.7 (±1.1)
Settling velocity calculated from the Stokes equation (m/d)	13.3	11.0	12.4
Settling velocity calculated from the cylindrical sediment traps (m/d)	7.9	–	–

Transport distances of the Lycopodium *spores*

Comparison of spore concentrations in the water samples taken 50 cm below the water surface and 20 cm above the river bottom at T2 and T5 showed differences in the number of passed particles of ≤10% for the 2 experiments in April 1999. Therefore, the near-bottom samples were not used because it was presumed that particle concentrations within the water column were similar.

The values for N_0 calculated by nonlinear regression (Fig. 2) were markedly lower for all 3 experiments than the estimates of the number of released *Lycopodium* spores obtained from counting. The value on 31 August 1998 ($N_0 = 7.89*10^{10}$, SE = $0.42*10^{10}$) was 35% lower than the estimate, on 20 April 1999 ($N_0 = 8.12*10^{10}$, SE = $0.07*10^{10}$) it was 37% lower, and on 27 April 1999 ($N_0 = 16.18*10^{10}$, SE = $0.87*10^{10}$) it was 20% lower. The longitudinal deposition rates of the *Lycopodium* spores and derived parameters like mean transport distances, mean times in suspension, and vertical deposition velocities are reported in Table 1. The vertical deposition velocity of the *Lycopodium* spores was 63% of the still water settling velocity calculated by the Stokes equation on 31 August 1998, 52% on 20 April 1999, and 38% on 27 April 1999. The relationships of vertical deposition velocity to mean flow velocity, discharge, and water depth are shown in Fig. 3.

Sedimentation and resuspension of the Lycopodium *spores*

The trapping rate of sediment traps depends highly on the particle concentration in the river water (Rathke et al. 1981). Consequently, the trapping rate declined exponentially with distance from T0. We compared the areal deposition of tracer particles calculated from the water samples with the number of particles found in the cylindrical sediment traps and in the sediment samples (Fig. 4). The values obtained from the cylindrical sediment traps and from the sediment samples were quite similar, except for T2 (at 1630 m). Both values were at T1 (at 830 m) considerably higher than the loss of spores calculated from the water samples. There was good accordance between the 3 estimates at the other transect stations.

The mean deposition velocities of seston and *Lycopodium* spores could be calculated not only from the longitudinal decrease in the flowing water, but also from the cylindrical trap samples. Therefore, the trapping rate, expressed as grams dry mass of suspended matter or number of tracer particles per area and unit of time of exposure of each trap, was divided by the mean particle concentration in the river water over the trap (Kozerski 1994). The mean deposition velocity calculated by that method was 20.1 m/d (SE = 2.6 m/d, n = 22) for seston and 7.9 m/d (SE = 0.8 m/d, n = 22) for the *Lycopodium*

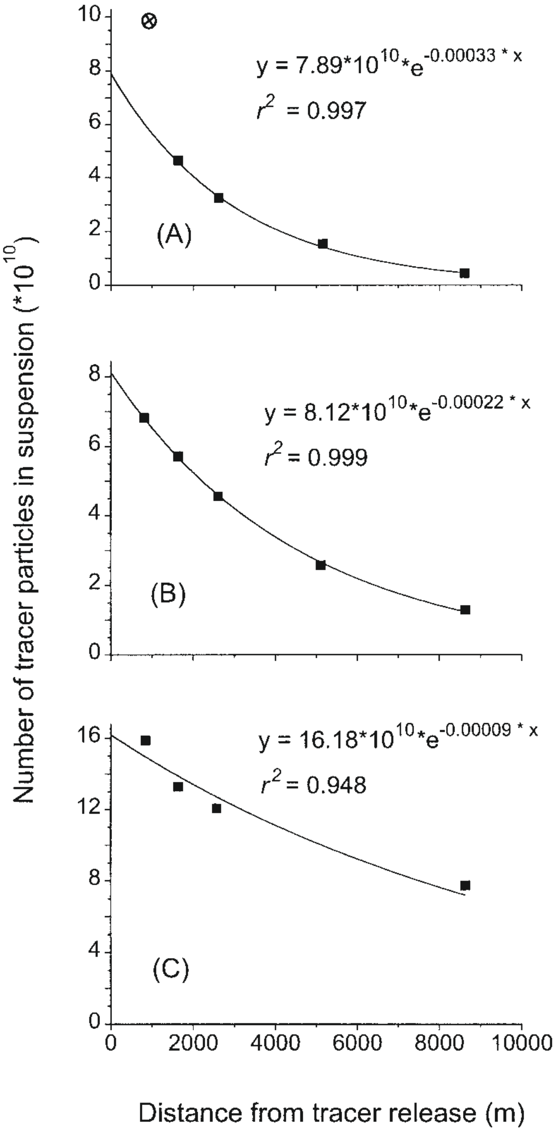

FIG. 2. Loss of spores from flowing water with distance during experiments on 31 August 1998 (A), 20 April 1999 (B), and 27 April 1999 (C). The ⊗ in panel A indicates a value that was considered an outlier. Another outlier, the value from T4 on 27 April 1999 ($N_{5130\text{ m}}$ = 38.9*10^10), is not shown.

spores (Table 1), which was ~25% less than the v_{DEP} that was determined for the spores from the water samples.

Our measurements of particle resuspension at transect station T2 between the 2 experiments in April 1999 showed that ~8*10^9 *Lycopodium* spores were resuspended within the first 9 h after the increase in discharge from 7.9 m^3/s to 14.8 m^3/s caused by the opening of the weirs. This result corresponded to ~11% of the number of tracer particles settled between T0 and T2 on 20 April 1999.

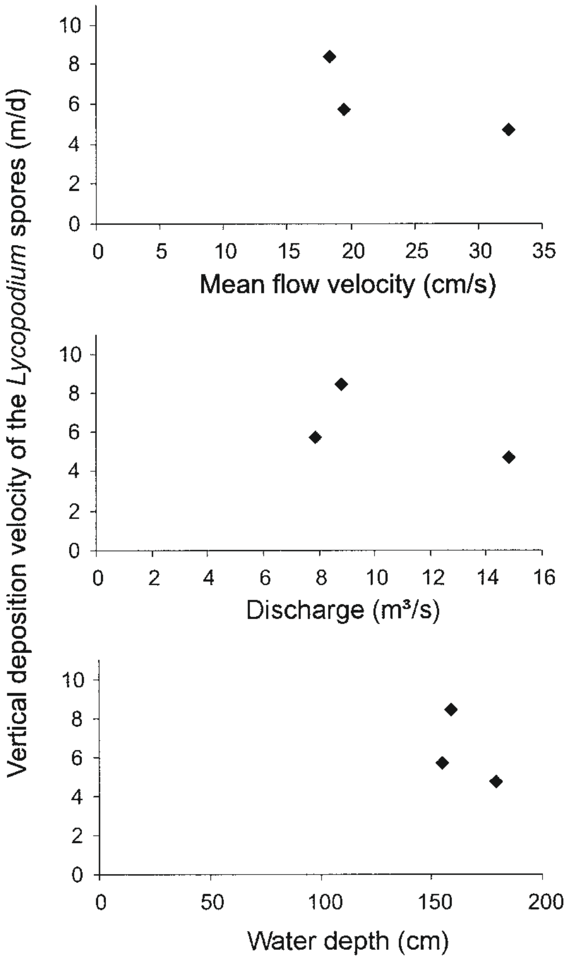

FIG. 3. Mean vertical deposition velocity of the *Lycopodium* spores in relation to mean flow velocity, discharge, and water depth.

Discussion

Use of Lycopodium *spores as tracer particles for FPOM*

Experiments with *Lycopodium* spores in circulating channels showed that the loss of particles from suspension in flowing water follows an exponential decay function (Reynolds et al. 1990). Exponential decay functions have also been repeatedly used to calculate loss rates and transport distances of particulate tracers and FPOM in field experiments (Jones and Smock 1991, Miller and Georgian 1992, Cushing et al. 1993). However, these field studies, which revealed transport distances between 1.8 and 800

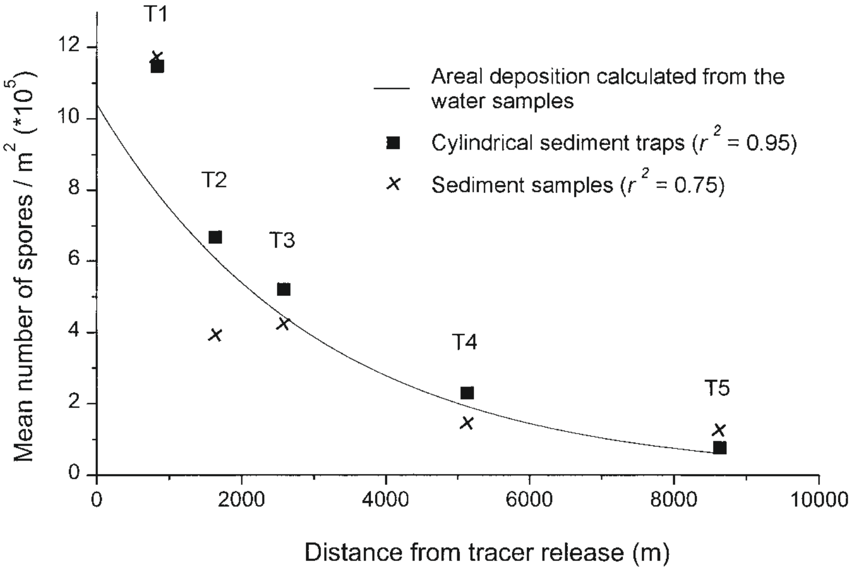

FIG. 4. Weighted mean number of tracer particles/m^2 found in the cylindrical sediment traps and in the sediment samples at the 5 transect stations (T1–T5) for the 31 August experiment. r^2 values were calculated by comparing the areal deposition calculated from the water samples and the number of spores/m^2 found in the sediment traps and the sediment samples, respectively.

m, were conducted in streams with a discharge of <0.8 m^3/s, a maximum depth of 0.34 m, and a seston composition that was considerably different from that in the River Spree. Suspended matter in the River Spree has a much lower density than the 1690 kg/m^3 reported for natural seston by Kazmierczak et al. (1987) or the 2020 kg/m^3 described by Cushing et al. (1993). It consists of light cohesive material with a high water content and densities between 1000 kg/m^3 and 1200 kg/m^3 (Prochnow et al. 1996). Phytoplankton and detritus flocs are the dominant fraction of the FPOM (Kozerski et al. 1991), which has an organic content of ~45%. Particles with still water settling velocities <2.4 m/d contribute at least 40 to 50% to the total suspended matter load. Median still water settling velocities of 0.9 to 5.2 m/d were determined (Prochnow et al. 1996). Therefore, previously used tracer particles like corn pollen or glass beads (Miller and Georgian 1992, Webster et al. 1999) had settling velocities that were too high to be representative for suspended matter in the River Spree. We chose to use the significantly lighter *Lycopodium* spores as a seston analog, with still water settling velocities of 11 to 13.3 m/d, calculated by the Stokes equation. These values are still considerably higher than the median still water settling velocities of the seston of the River Spree, but under natural hydraulic conditions the fraction in the seston with higher settling velocities makes up the mass of particles being lost from the flowing water through sedimentation. *Lycopodium* spores thus can be considered as an analog for that fraction of the suspended matter that mainly contributes to the settling flux in lowland rivers. This assumption is supported by the finding that the mean deposition velocity of the seston, calculated by the cylindrical sediment trap measurements, was 20.1 m/d and thus even higher than the mean deposition velocity of 7.9 m/d calculated for the *Lycopodium* spores.

Sedimentation of the Lycopodium *spores*

The comparison of the areal deposition of tracer particles calculated from water samples, sediment samples, and cylindrical sediment traps that was conducted during the experiment in August 1998 revealed very similar estimates for the loss of particles along the study reach. We suppose that the water samples should provide the best estimate as several hundred water samples were taken compared to only 20 sediment samples and 22 sediment trap samples. The estimates obtained from the cylindrical sediment traps were closer to the values calculated

TABLE 2. Comparison between particle characteristics, hydrological conditions, and transport data of different kinds of tracers for fine particulate organic matter (FPOM).

	Corn pollen (Miller and Georgian 1992)	^{14}C-labeled natural FPOM (Cushing et al. 1993)	Fluorescently labeled *Lycopodium* spores (this study)
Particle characteristics			
Diameter (μm)	87	53–102	42
Density (kg/m^3)	1092	2020	1175
Hydrological conditions			
Stream order	2	2 and 3	6
Water depth (cm)	13/15	14–34	155–179
Mean flow velocity (m/s)	0.24–0.38	0.27–0.29	0.18–0.32
Discharge (m^3/s)	0.15–0.22	0.25–0.67	7.88–14.79
Transport data			
Mean FPOM transport distance (m)	122–190	580–800	3000–10,660
Vertical deposition velocity (m/s) (v_{DEP})	$2.1*10^{-4}/2.6*10^{-4}$	$0.7–1.6*10^{-4}$	$0.5–1.0*10^{-4}$
Quiescent-water fall velocity (m/s) (v_{FALL})	$2.6*10^{-4}–3.1*10^{-4}$	$1.0–1.3*10^{-3}$	$1.3–1.5*10^{-4}$
$v_{DEP}/v_{FALL}*100$ (%)	78–110	7–12	38–63

from the water samples than the estimates obtained from the sediment samples. This result may be explained by the high spatial heterogeneity found in the sediment samples, presumably caused by substrate heterogeneity. The highest difference between the areal deposition calculated from the water samples and the direct measurement of settled particles by sediment samples and sediment traps was recorded at T1. This transect station was considered to be an outlier with regard to the water samples because the number of tracer particles in suspension was extraordinarily high. However, very high numbers of tracer particles were also found in the sediment samples and in the cylindrical sediment traps. Therefore, we suppose that the true number of suspended tracer particles at T1 was lower than the measured value, but presumably higher than the value calculated by nonlinear regression.

Breakdown of spores during transport

Newbold et al. (1982) defined carbon turnover length as the average or expected downstream distance traveled by a carbon atom during its residence in the stream in a fixed or reduced form. It is calculated by the division of the mean downstream velocity by the rate coefficient of carbon respiration. Carbon respiration can also take place during transport but the maximum mean time in suspension of the tracer particles during our experiments was ~9 h. Therefore, the breakdown of spores during transport should have been of minor importance in our experiments.

Comparison with previous investigations

Table 2 summarizes results obtained from the use of different types of model particles as tracers for FPOM in running waters, ranging from 42 μm to 102 μm in size. Corresponding to the 10 times higher discharge and the 5 times higher water depth of the River Spree, the mean transport distances of 3000 m to 10,660 m were 1 order of magnitude higher than in the streams investigated before. Our results compared to previous investigations indicate that the spatial extent of the organic carbon spirals increases with discharge (Fig. 5). It is remarkable that nearly all values are close to the regression line, even though a broad variety of tracer particles was used, which differed several orders of magnitude in their quiescent-water fall velocity. The transport distances of fluorescently labeled bacteria (FLB) determined by Hall et al. (1996) at discharges <6 L/s show the greatest deviation from the regression line. However, the v_{DEP} of the FLB ($9.3*10^{-5}$ m/s) was in the range of values determined for *Lycopodium* spores, even though the settling velocity of the FLB was >3

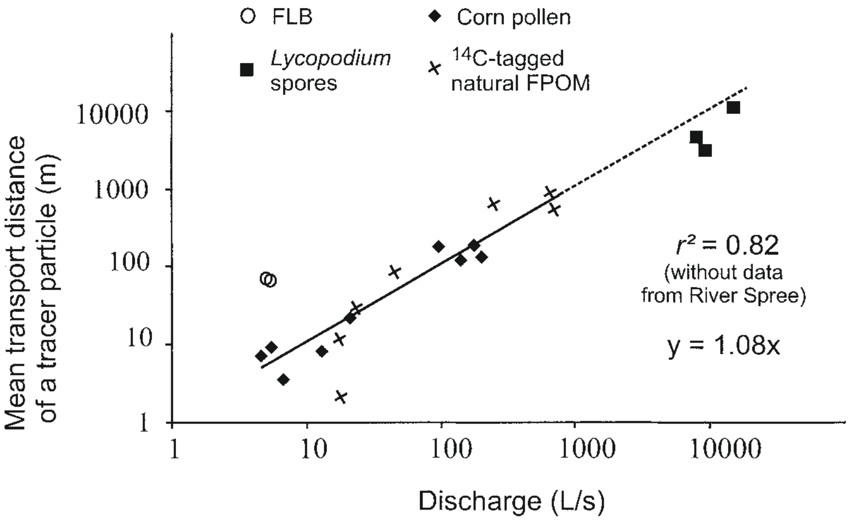

FIG. 5. Transport distances of tracer particles in relation to discharge. Data for ^{14}C-tagged natural fine particulate organic matter (FPOM) were taken from Jones and Smock (1991) and from Cushing et al. (1993). Data for corn pollen are from Miller and Georgian (1992) and from Webster et al. (1999). Data for fluorescently labeled bacteria (FLB) were reported by Hall et al. (1996). The dotted line represents the extension of the regression line calculated from data from previous investigations to the discharge level of the River Spree.

orders of magnitude lower than that of the *Lycopodium* spores. Settling velocity for FLB was 1690 times less than v_{DEP} (Hall et al. 1996). We determined v_{DEP} values for *Lycopodium* spores that were between 38 and 63% of the temperature-corrected quiescent-water fall velocities (v_{FALL}), and this % was higher with lower flow velocities. This result was very similar to those obtained from experiments with *Lycopodium* spores in circulating channels over a range of water depths and flow velocities, in which v_{DEP} values were ~50 to 60% of those that might have been anticipated from the Stokes equation (Reynolds et al. 1990). The v_{DEP} values of *Lycopodium* spores were only slightly lower than v_{DEP} values of radiolabeled FPOM in Smiley Creek and in the upper Salmon River, even though v_{FALL} of the *Lycopodium* spores was ~1 order of magnitude lower than that of radiolabeled FPOM (Cushing et al. 1993). V_{DEP} values of radiolabeled FPOM ranged from 7 to 12% of the v_{FALL} values (Cushing et al. 1993), whereas Miller and Georgian (1992) found that v_{FALL} approximately equaled v_{DEP} of corn pollen. Our results support the statement of Hall et al. (1996) that v_{FALL} bears little relation to v_{DEP}. The v_{DEP}: v_{FALL} ratio seems to increase with decreasing particle size and density, corresponding with an increasing importance of mechanisms other than settling for the removal of suspended particles within a river reach. Consequently, in contrast to v_{FALL}, v_{DEP} does not vary much among particles of different size and density.

Previous experiments with *Lycopodium* spores in circulating channels suggested that water depth was the main variable determining the rate of sinking loss (Reynolds et al. 1990). Nevertheless, flow velocity influences the horizontal distance traveled by the residual spore suspension through the time period required for complete settlement. In our study, we could not determine which hydraulic parameter determined the loss of particles from suspension in the River Spree because of the low number of data points (Fig. 3). However, v_{DEP} values and v_{DEP}: v_{FALL} ratios decreased with increasing mean flow velocity, probably because of increasing shear stress with higher mean flow velocity (Reynolds et al. 1990, Cushing et al. 1993).

In conclusion, fluorescently labeled *Lycopodium* spores are suitable model particles for investigation of the retention of FPOM in plankton-rich running waters. Although the spores cannot represent the wide range of natural suspended particles because of their uniform size and density, their settling characteristics approach those of the particles that dominate the flux of POM from the pelagic to the benthic zone. Therefore, they can be used to detect variables that influence this pelagic–benthic coupling. Further investigations are necessary to detect the importance of morphological structures such as shifting sand or macrophyte beds for particle retention in large rivers.

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The role of micro-organisms in the ecological connectivity of running waters

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SUMMARY

1. Riparian zones hold a central place in the hydrological cycle, owing to the prevalence of surface and groundwater interactions. In riparian transition zones, the quality of exfiltrating water is heavily influenced by microbial activities within the bed sediments. This paper reviews the role of micro-organisms in biogeochemical cycling in the riparian-hyporheic ecotone.

2. The production of organic substances, such as cellulose and lignin, by riparian vegetation is an important factor influencing the pathways of microbial processing in the riparian zone. For example, anaerobic sediment patches, created by entrainment of allochthonous organic matter, are focal sites of microbial denitrification.

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3. The biophysical structure of the riparian zone largely influences in-stream microbial transformations through the retention of organic matter. Particulate and dissolved organic matter (POM and DOM) is retained effectively in the hyporheic zone, which drives biofilm development and associated microbial activity.
4. The structure of the riparian zone, the mechanisms of POM retention, the hydrological linkages to the stream and the intensity of key biogeochemical processes vary greatly along the river continuum and in relation to the geomorphic setting. However, the present state of knowledge of organic matter metabolism in the hyporheic zone suggests that lateral ecological connectivity is a basic attribute of lotic ecosystems.
5. Due to their efficiency in transforming POM into heterotrophic microbial biomass, attached biofilms form an abundant food resource for an array of predators and grazers in the interstitial environments of rivers and streams. The interstitial microbial loop, and the intensity of microbial production within the bed sediments, may be a primary driver of the celebrated high productivity and biodiversity of the riparian zone.
6. New molecular methods based on the analysis of the low molecular weight RNA (LMW RNA) allow unprecedented insights into the community structure of natural bacterial assemblages and also allow identification and study of specific strains hitherto largely unknown.
7. Research is needed on the development and evaluation of sampling methods for interstitial micro-organisms, on the characterization of biofilm structure, on the analysis of the biodegradable matter in the riparian-hyporheic ecotone, on the regulation mechanisms exerted on microbiota by interstitial predators and grazers, and on measures of microbial respiration and other key activities that influence biogeochemical cycles in running waters.
8. Past experiences from large-scale alterations of riparian zones by humans, such as the River Rhine in central Europe, undeniably demonstrate the detrimental consequences of disconnecting rivers from their riparian zones. A river management approach that uses the natural services of micro-organisms within intact riparian zones could substantially reduce the costs of clean, sustainable water supplies for humans.

Keywords: ecosystems, microbial ecology, organic matter, riparian rivers

Introduction

In the hydrological cycle, running waters play the role of veins in the landscape, concentrating runoff from the catchment and transporting it to the erosion base. Riparian zones accompanying stream courses are places where groundwater trickling through soils, fractured bedrock and alluvial deposits mixes with river water in shallow, saturated bed sediments. Thus, riparian zones form the interface between subsurface and surface waters. This transition does not only change the hydrological conditions of water flow, but also changes profoundly the flux and composition of organic and inorganic materials. These changes are largely due to the biochemical activity of the interstitial micro-organisms. The extent of microbial activities is largely influenced by the area of contact and degree of chemical and biological interactions between terrestrial and aquatic habitats, which is summarized as ecological connectivity (Stanford & Ward, 1993; Ward & Stanford, 1995).

In order to maintain a water balance, the flow of rivers and streams is replaced by discharge of groundwater from a given catchment within a relatively short time period of hours to days, and within only a few weeks for a larger catchment. Hence, a large amount of the water flux from the catchment passes continually through the riparian ecotone, where about 50% of the output of nitrogen and phosphorus from the catchment (Behrendt, 1996), and a high proportion of the dissolved organic carbon (DOC) (Fiebig, 1995), are retained. Because it occurs underground, however, interstitial microbial processing and transformation of materials and their influence on biogeochemical flux and water quality was, until recently, widely ignored both by the public and by science (Naiman & Décamps, 1990).

The biogeochemical flux of matter through the riparian zone is closely coupled to hydrological flow paths (see Huggenberger *et al.*, 1998). Falling through the canopy of upland and riparian vegetation, rain water leaches considerable amounts of low-molecular weight organic matter from plant surfaces. In the pedosphere (soil environment) rainwater is enriched by soluble components of the plant litter stored there, which has already been processed by invertebrates. Roots in the rhizosphere (the environment near roots) exude organic compounds of low molecular weight that micro-organisms can assimilate very effectively. After the various chemical and biochemical reactions occurring in the unsaturated soil layers, groundwater trickling through the saturated zone towards a stream is enriched in refractory fractions of dissolved organic matter (DOM). In addition, a variety of inorganic cations and anions and gases such as carbon dioxide may dissolve into the groundwater, and microbial activity may reduce the concentration of dissolved oxygen. The detailed composition of this mixture depends upon the nature of the geologic hydrological, biological and anthropogenic processes prevalent in the area.

This catchment-specific mixture of surface and groundwater enters the riparian ecotone where redox and other biophysical gradients may be very steep, which implies important biogeochemical consequences for the fate of the transported matter. Several reasons for steep gradients in riparian zones may be offered. First, alluvial deposits often deepen in the riparian zone due to overbank deposition (Huggenberger *et al.*, 1998). This results in a prolonged residence time and increased opportunity for microbial processing of materials. Second adsorption, precipitation or changing availability of electron acceptors is effectively mediated within many alluvial deposits with corresponding influences upon biochemical transformations of matter (Dahm *et al.*, 1998). Third, mixing of groundwater with river water in the unstable sediments in the alluvial bed sediments of the channel and floodplain produces the so-called hyporheic zone (Orghidan, 1959; Schwoerbel, 1961; Stanford & Gaufin, 1974). This mixing zone mediates rapid changes in the biophysical environment, producing many possibilities for material transformations, such as microbial oxidation of inorganic compounds (Harvey & Fuller, 1998) or the precipitation of certain DOM fractions (cf. Thurman, 1985). Fourth, dissolved and particulate matter is stored in alluvial sediments owing to the filtering effect of the porous medium and its biological assemblages (Newbold *et al.*, 1982).

All these features are in some way or another influenced or controlled by the dynamics of water flow (cf. Findlay, 1995; Jones, 1996). Sediment and debris movements during floods create heterogeneous and temporally dynamic riparian zones, which are ecologically connected to the neighbouring landscape elements (Wissmar & Swanson, 1990). Interactions can occur above and below the surface enhancing hydrological linkages and opportunities for microbial transformations (Brunke & Gonser, 1997). Floods rework riparian areas and produce open-framed sediment structures with high porosity. During rising water, stream water penetrates alluvial sediments, causing a temporary reversal of lateral flow. This may restart biochemical transformations that had ceased because of the depletion of a specific substrate or terminal electron acceptor during drier phases when water is flowing toward the stream. In large gravel bed rivers, this connectivity can extend several or many kilometres from the stream channel, as in the case of the Flathead River, Montana (Stanford & Ward, 1988; Stanford, Ward & Ellis, 1994). During floods, the magnitude of this connectivity between the riparian zone and the stream can change dramatically. Flooding results in the stream extending its influence throughout the riparian zone (Junk, Bayley & Sparks, 1989), converting parts of the floodplain into channels and recharging the alluvial aquifer.

Clearly, ecological connectivity between the riparian zone and running waters is highly variable in time and space and substantially influences the quantity and quality of matter present and modes of transformations in a river ecosystem. Because a major part of the microbial biomass present in benthic, hyporheic and aquifer sediments appears to be located in epilithic biofilms (Wuhrmann, 1972; Kasimir, 1990; Hirsch & Rades-Rohkohl, 1983; Ellis, Stanford & Ward, in press), the microbes themselves are affected by changes in these shifting environments to a much lesser extent than their substratum. In that context, 'live' sediments show the same functional properties as artificial fixed-phase-reactors, where attached bacteria predominate (Siegrist & McCarthy, 1987; Gantzer, Rittmann & Herricks, 1988).

Heterotrophic micro-organisms, especially bacteria, are quantitatively the most important initial consumers of the organic carbon entrained in running waters. Most of the production by algae and higher plants consists of macromolecules, which are hydrolyzed by extracellular enzymes before they are taken up by micro-organisms. This consumption is a crucial step in delaying the export of organic carbon and, hence, enhancing its subsequent availability within the running water ecosystem as a whole. While bacterial activity is well known for its ability to degrade certain categories of organic matter, the importance of bacterial productivity in the trophic base of lotic food webs is now widely recognized (Marxsen, 1988; Meyer, 1990a; Hall, 1995).

Most bacterial production in running waters occurs in biofilms, while relatively little production occurs in the water column. Biofilms cover most substratum surfaces in the streambed and are mixed assemblages of bacteria, fungi and algae, even in the hyporheic zone. Indeed, twenty-four genera of algae were collected from the large alluvial aquifers of the Flathead River, Montana. Some algae, apparently entrained by the aquifer, were collected up to 4 km from the river channel (Ellis, Stanford & Ward, in press). All these organisms are embedded in or associated with a polysaccharide matrix secreted be the organisms themselves (Lock, 1993). This matrix enhances the immobilization of dissolved organic carbon (DOC), and even particulate organic carbon (POC) of a certain size, and allows the exchange of matter within syntrophic associations of micro-organisms. Thus, the availability of organic carbon to the heterotrophic micro-organisms associated with the biofilms is increased, which is especially important in a generally nutrient-poor environment with episodic peaks of nutrient concentration. This mechanism seems to be part of a life strategy that allows a high level of bioproduction in an environment often characterized by a general paucity of organic carbon.

Moreover, biofilms can be consumed either by microbial consumers, such as certain ciliates and nematodes, or by larger organisms adapted for scraping and collecting the biofilms or simply ingesting the sediment with biofilms attached. The essential conclusion is that microbial biofilms above and below ground are key organizers and controllers of channel and riparian food webs and the flux of materials through the channel and interstitial hydrosystem of rivers.

In this paper we examine the role of micro-organisms in the ecological connectivity of lotic ecosystems. We evaluate the mechanisms of microbial incorporation of DOC and POC into lotic and riparian food webs and associated influences on transformation and flux of organic matter as it moves from terrestrial to aquatic components of the river ecosystem. We discuss new methods available for examining the role of micro-organisms in running waters and research needs. The paper concludes with some practical aspects of managing running waters in a manner that reduces detrimental human influences on the microbial functioning of these vital ecosystems.

Overview of organic carbon in streams: sources, chemical heterogeneity and characterization

The ultimate source of nearly all natural organic matter in stream ecosystems is photosynthesis, generally with only minor contributions from chemotrophic (mostly nitrifying) bacteria. Reduced carbon compounds present in particulate or dissolved forms can be separated into materials produced in the terrestrial environment and transported to the stream (allochthonous sources) and those produced within the stream itself (autochthonous sources). From a budgetary or mass balance perspective, the relative contribution of these sources depends upon the geographic setting (biome), geomorphic setting (stream reach), hydrological conditions (baseflow or stormflow) and degree of anthropogenic disturbance upstream (deforestation, land use) (Webster & Meyer, 1997). In some desert, grassland, glacial and other streams with little or no riparian vegetation, primary production is associated mostly with the stream bed (Minshall, 1978), and is derived from algae, cyanobacteria, bryophytes and macrophytes (Lamberti & Steinman, 1997). A significant portion of the organic matter budgets of these streams originates from autochthonous production. But, in most other small streams and rivers, particularly in forested regions, organic compounds of terrestrial origin dominate

(Fisher & Likens, 1973). This picture changes in larger rivers, which are wide enough to prevent shading by riparian vegetation and deep enough to prevent abundant production of benthic algae (Vannote *et al.*, 1980). These algal biofilms are scoured during floods (Biggs & Close, 1998; Uehlinger, 1991), providing an inoculate for phytoplankton growth in downstream reaches. In turn, primary production in slack waters, such as eddies, backwaters, oxbows and lakes intercalated into the river continuum, produces huge amounts of biomass that drive microbial metabolism in higher-order reaches (Koehler, 1994; Thorp & Delong, 1994).

The importance of seasonal inputs of organic carbon from meteorological and biological sources, such as rainfall through a forest canopy, leaf litter deposition and autochthonous primary production is well known from the classic study of Fisher & Likens (1973) and many others since then. In contrast, knowledge of geologic inputs, especially the degree to which soil water from the vadose zone contributes organic carbon to streams and the dynamics of the chemical and biological changes occurring within the riparian phreatic zone, is extremely limited (Hemond, 1990). Additionally, an appreciation of importance of the hyporheic zone as a regulator of biophysical fluxes is recent (Triska *et al.*, 1989; Dahm *et al.*, in press).

The chemical nature of organic matter in streams, both particulate and dissolved, is complex. Even the distinction between these two forms, operationally defined by filtration (Wotton, 1994), is not a simple matter, because dissolved organic matter can rapidly adsorb and desorb from particulate surfaces. Filtration through the best glass fibres or membranes allows some particles and colloids to pass into the filtrate. The most common measurement of organic matter is as carbon, because C content is relatively constant, between 40 and 50% by weight of most organic particulates (Gjessing, 1976). Dissolved organic carbon (DOC) is easily measured by oxidation to CO_2, but this analysis provides limited biological information since the various carbon fractions are not identified or quantified. Additionally, the analysis of POC using commercial carbon analysers without a preconcentration step is subject to questions about the oxidation efficiency.

The characterization of carbon fractions is a laborious procedure and at the molecular level a relatively small portion of the total pool, generally less than 25% of the carbon, has been identified (Larson, 1978). Elemental analysis that includes estimates of the H, N, O and S content provides constraints on the relative contributions of aliphatic and aromatic carbon to the total (Sun *et al.*, 1997). Groups of molecules such as carbohydrates (Johnson, Burney & Sieburth, 1981), amino acids (Undefriend *et al.*, 1972), lipids or proteins have been measured with colorimetric methods; and, the determination of individual molecules within the pool of carbohydrates (Sweet & Perdue, 1982; Gremm & Kaplan, 1997), amino acids (Lytle & Perdue, 1981), or volatile fatty acids (Peldszus, Huck & Andrews, 1996) by gas or liquid chromatography is very sensitive. Molecular size determinations by gel permeation chromatography and ultrafiltration are of questionable accuracy (Aiken, 1984), but still of use in a relative sense, and other techniques, such as viscometry and colligative property measurements, have been proposed (Aiken & Malcolm, 1987). The aromatic or aliphatic nature of organic matter and the contributions of various functional groups such as aldehydes, ketones and alcohols can be determined with nuclear magnetic resonance spectroscopy (McKnight *et al.*, 1985).

Humic substances and biodegradable organic matter often cannot be precisely or fully categorized as having a particular molecular structure. Humic substances in aquatic environments are most often characterized by their acid/base behaviour with macroreticular XAD resins (Aiken, 1988), and biodegradable organic matter (Servais, Anzil & Ventresque, 1989) is characterized with bioassays. Humic substances are of particular importance in stream water and groundwater because they tend to be the dominant form of DOC, comprising from 50 to 80% of the organic carbon. Most of the humic substances in these waters are the more hydrophilic fulvic acids that are soluble at pH 1 rather than the more hydrophobic humic acids that precipitate at pH 1. There are humic substances that form from algal-derived molecules (McKnight, Aiken & Smith, 1991), but humics that derive from leaf litter, and are altered during transport through soil horizons by biotic and abiotic processes, are quantitatively more important in stream ecosystems. These complex molecules historically have been considered both chemically and biologically refractory (Cummins *et al.*, 1972), but recent studies have shown that both photolytic (Geller, 1985;

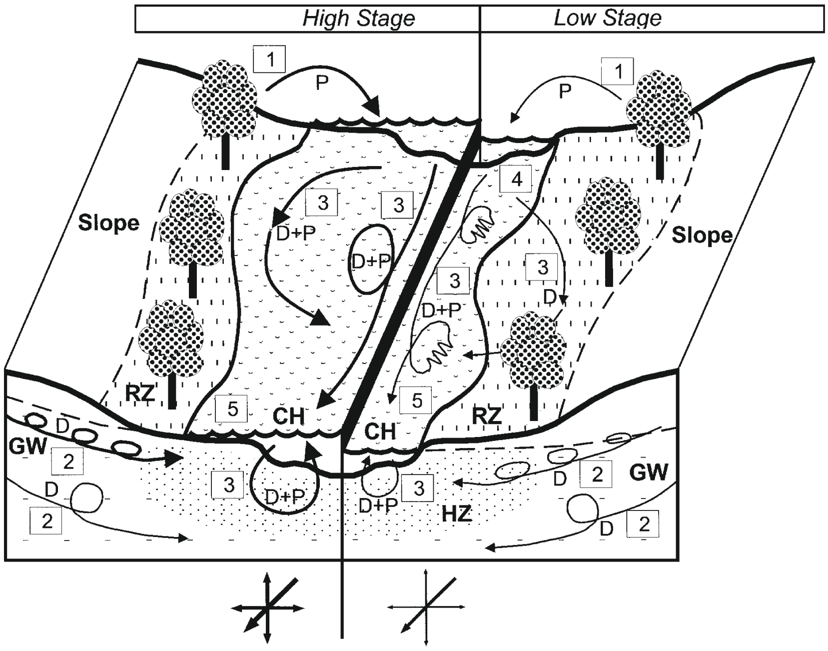

Fig. 1 Cross-section through an idealized riparian zone (RZ, vertical hatching, with tree symbols) of a stream at low stage (right) and high stage conditions (left) and showing major transport vectors of organic matter. Abbreviations are P = particulate organic matter, D = dissolved organic matter, CH = stream channel (tight horizontal hatching), GW = groundwater (wide horizontal hatching) and HZ = hyporheic zone (dotted area). Numbers in boxes refer to transport vectors and are explained in the text. The width of vector arrows indicates relative importance. Transport is considered cumulatively in a three-dimensional context (longitudinal, vertical and lateral), and is summarized by the two clusters of arrows at the bottom of the figure.

Wetzel, Hatcher & Bianchi, 1995) and microbiological (Volk, Volk & Kaplan, 1997) alteration of humic molecules may play an important role in the structure and function of stream ecosystems.

Biodegradable organic matter (BOM) in streams is comprised of both low molecular weight (Kaplan & Bott, 1983) and high molecular weight (Meyer, Edwards & Risley, 1987; Amon & Benner, 1996) components. However, measuring the composition of BOM is difficult because of the presence of poorly characterized humic substances and the large number of monomeric or smaller polymeric molecules present in low concentrations. Detection of concentration changes in batch cultures with either composite measurements, like DOC or more specific characterizations, typically requires extended incubation periods, the concentration of substrate, or both. Alternatively, the metabolism of DOC or fractionated DOC in batch culture can be inferred from measurements of bacterial growth or respiration. Unfortunately, the conversion of bacterial densities to units of organic carbon requires knowledge of carbon content per cell (Theil-Neilsen & Sondergaard, 1998) and growth yield (Meyer et al., 1987), two parameters that are difficult to estimate accurately.

As an alternative to batch cultures, plug-flow biofilm reactors colonized by micro-organisms in stream water have been used to measure the concentration (Kaplan & Newbold, 1995) and composition (Volk et al., 1997) of BOM. The large biomass to DOC ratio within the bioreactor permits direct measurements of concentration changes within the DOC pool over a period of a few hours. BOM characterized from a single stream averaged 25% of the DOC, and was composed of 75% humic substances, 30% carbohydrates, 4% amino acids and 39% DOC > 100 kDa (Volk et al., 1997). The carbohydrate component of the BOM was primarily polysaccharide and 57% humic bound, and the amino acids were almost exclusively present in the combined form and 77% humic bound. The large contribution of humic substances and polysaccharides to the BOM pool raises questions about the fundamental properties that make a molecule susceptible or resistant to microbial decomposition, and the roles of exoenzymes (Hoppe, 1983) in ecosystem metabolism.

Organic input vectors

General pathways

The distribution and nature of heterotrophic microbial activity in running waters depends on the availability of organic substrates which, qualitatively and quantitatively, in turn depends on how a stream is embedded within, and interacts with, its surrounding terrestrial environment. From the microbial perspective, we discern four major categories of organic input vectors within a river corridor (Fig. 1):

1 allochthonous surface and

2 subsurface transfers of organic carbon derived from terrestrial primary production;

3 redistribution within the channel and the riparian zone by stream flow, especially during floods;

4 autochthonous primary production within the stream itself; and

5 processing during the storage time of organic matter within a stream or floodplain reach.

In each case, particulate, as well as dissolved, organic matter is made available as a substrate for microbial activity, although the proportions vary according to the vectors involved. For example, in the second-order, forested Bear Brook 'meteorological' surface inputs comprised 98% particulate, matter whereas 'geological' inputs (surface and subsurface waters) comprised 83% dissolved matter (Fisher & Likens, 1973).

The relative importance of these pathways of organic matter input is influenced dramatically by stream discharge (Fig. 1). The same is true for the retention and decomposition processes (see below). If a high load of organic carbon exists and retention in the bed sediments is low, the efficiency of carbon retention clearly is lower during high discharge periods than at base flow. Microbial processing of organic matter takes place continuously in the active channel but decomposition of organic matter deposited in the varial or parafluvial portions of the channel decreases during dry periods. Hence, storage-dominated periods and processing-dominated phases exist in relation to the hydrograph and the associated extent of bed sediment saturation. Floods mediate long distance transport and exchange of POM between the channel, the hyporheic zone and the riparian zone (Gurtz *et al.*, 1987; Gregory *et al.*, 1991; Jones & Smock, 1991; Naegeli *et al.*, 1995) but the frequency and importance of these events vary among stream types.

Allochthonous surface inputs

Particulate organic matter (POM) derived from catchment vegetation (wood, leaves, flowers, fruit, pollen, etc.) can be transferred from the riparian zone into the stream either as direct fall (i.e. from vegetation projecting over the stream) or as lateral input (e.g. due to the action of wind or flooding). Most of this material is classified as coarse POM (> 1 mm), e.g. 86% of total carbon inputs to eastern deciduous forests (Wallace *et al.*, 1995). Both modes of input are influenced by site-specific factors such as aspect, bank slope, weather, proximity of vegetation to the stream and vegetation type and density (Cushing, 1988; Wallace *et al.*, 1995; Weigelhofer & Waringer, 1994). Direct inputs are generally higher than lateral inputs [e.g. 431–824 g and 40–163 g DW $m^{-2} yr^{-1}$, respectively, in small streams in the Coweeta catchments (Webster *et al.*, 1990)], although the latter can dominate in streams in arid, open areas (Cushing, 1988). In the extreme streams may receive little or no direct input of terrestrial plant material, as in desert or arctic streams (Naiman & Sibert, 1978; Peterson, Hobbie & Corliss, 1986). Clearly, great variability may be expected in the quality and quantity of surficial POM transferred into running waters.

The input frequency of surficial POM varies according to the source, but in the temperate latitudes input of autumn-shed leaves is very predictable. For example, in deciduous forest streams of the eastern U.S.A. 58% of total annual litter inputs occur in autumn (Webster, Wallace & Benfield, 1995). Frequently, autumn input is followed by a second distinguishable peak caused by the input of bud involucres and inflorescences in spring (e.g. Short & Ward, 1981; Moser, 1991). A substantial proportion of the carbon in leaves can be leached rapidly, directly after entering the stream (e.g. 3–19% within 3 days depending on species, McDowell & Fisher, 1976), although this appears to depend on whether the leaves enter the stream as fresh or dried material (Gessner & Schwoerbel, 1989). Inputs of leaf litter can thus also lead to a seasonally significant, surficial input of DOC (e.g. 42% of the annual input of DOC to Bear Brook; McDowell & Likens, 1976). However, leaching alone does not account for the observed DOC concentration because of the uptake and metabolism by microbial biomass associated with decomposing particulate matter (Meyer, 1990b). Experimental enrichments with leaf leachate are immobilized rapidly by streambed sediments (Kaplan & Bott, 1983; McDowell, 1985), suggesting that this source of DOC is readily accessible to heterotrophic micro-organisms. In tropical forests, leaf inputs tend be rather continuous year around (Stout, 1980). Some coniferous forests also sustain leaf fall (Bray & Gorham, 1964).

Long-term degradation rates of leaves retained in the stream depend on the extent of conditioning before entering the stream, and also vary according to species (Petersen & Cummins, 1974; Moran & Hodson, 1989). During degradation, physical stressors, invertebrate shredding and microbial decomposition cause fragmentation of the leaves. This finer material can be trapped within bed sediments, intercepted by particle feeders, or exported and intercepted later downstream. Insect fragmentation increases the release of high molecular weight DOC from leaves by leaching of DOC from faecal pellets and mechanical breakdown of the leaves (Meyer & O'Hop, 1983). This might be a significant in-stream source of DOC in small streams at base flow. As leaf mass declines, the proportions of cellulose and hemicellulose decline proportionately, but the proportions of lignin and nitrogen (especially protein) increase (Suberkropp, Godshalk & Klug, 1976; Webster & Benfield, 1986). Lignin enrichment suggests microbial recalcitrance, whereas protein enrichment is a result of microbial colonization of the leaf material (Kaushik & Hynes, 1971).

A less predictable, but often abundant, source of allochthonous POC is woody debris, especially in forested streams (Harmon *et al.*, 1986; Hedin, 1990; Webster & Meyer, 1997). On average, streams in deciduous forests receive much higher direct inputs of wood than lateral inputs (Jones & Smock, 1991; Moser, 1991; Bretschko & Moser, 1993; Weigelhofer & Waringer, 1994; Webster *et al.*, 1995). Although the rate of input (≈ 100–$400\,\mathrm{g\,m^{-2}\,yr^{-1}}$) is similar to that of leaf litter, the consequences of wood inputs for the organic carbon budget and microbial activity in streams are very different, due to the infrequency of wood inputs. Moreover, wood is mostly recalcitrant with a high lignin content and a low surface area to volume ratio. Hence, microbial degradation takes several years or decades depending on species (Melillo *et al.*, 1983). Wood carried into running waters also can produce focal sites of metabolism (Hedin, 1990) by the creation of deposition zones behind debris dams. These enhance the retention of smaller particles, such as leaves (Bilby, 1981; Smock, 1990) and hasten release of DOC into the water column (Meyer, 1990b).

Depending on stream morphology, increasing discharge and flooding can have a significant impact on the surficial exchange of organic carbon between the riparian zone and the stream. Most importantly, flooding moves POM such as wood, leaves and fine POM, including bacteria, into the stream channel in some reaches and deposit it on floodplains in others (cf. Cuffney, 1988; Jones & Smock, 1991; Wainwright, Couch & Meyer, 1992).

Allochthonous subsurface inputs

While allochthonous, surficial inputs of organic carbon to streams originate largely from riparian and floodplain vegetation, subsurface inputs of DOC can, in theory, be derived from a large proportion of the catchment. This will depend on the geohydrological conditions influencing the transfer of water containing DOC from the catchment to the stream.

Precipitation contains little DOC (e.g. 0.2–$0.8\,\mathrm{mg\,L^{-1}}$ in Mid Wales, Neal *et al.*, 1986), but rainfall is enriched when intercepted by vegetation, especially in the autumn (e.g. up to $16\,\mathrm{mg\,L^{-1}}$ in a deciduous forest (Meyer & Tate, 1983). Precipitation reaching the soil surface then becomes further enriched due to DOC from fresh and decaying plant litter. Enrichment varies with soil type (Thurman, 1985). Then the DOC load undergoes a series of transformations as it is translocated down through the soil profile, as illustrated by the well-understood process of podsolization (Cronan & Aiken, 1985; Thurman, 1985). During soil passage and further transmission through the catchment, physical adsorption and microbial degradation reduce concentrations considerably. Indeed, most groundwaters generally contain low DOC concentrations (Chapelle, 1993), especially reduced proportion of labile components (McDowell & Likens, 1988).

Ellis *et al.* (in press) suggested that, in shallow alluvial aquifers, vertical immigration of organisms and DOC through infiltration and percolation of water from floodplain surface soils (i.e. via spring snowmelt on the floodplain) may be an important process for the ecology of alluvial aquifers. River stage variations from flow changes due to hydropower operations may also result in the flushing of unsaturated sediments and the subsequent movement of dissolved organic carbon into the hyporheic zone.

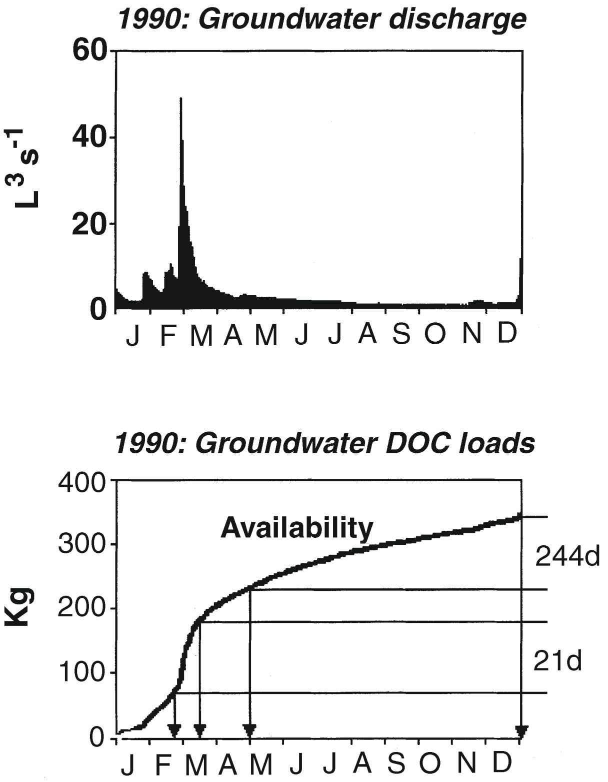

Fig. 2 Hydrograph (top) and seasonal availability (bottom) of dissolved organic matter (DOM) in the Breitenbach, a first order stream in central Germany predominately driven by groundwater flux (see text).

Spatial and temporal variation in the sources of subsurface discharge delivered to the stream channel will influence the quantity and quality of DOC available for microbial processing in the riparian and hyporheic zones, as well as in the stream itself. For example, a headwater stream in central Germany received in 21 days as much DOC via subsurface discharge as in the rest of the 244 days of the same year (Fiebig, 1995; Fig. 2). According to the variable source area model (Anderson & Burt, 1978; Anderson & Kneale, 1982), in a given catchment only water from certain areas with rapid infiltration contributes to stream flow, and these areas expand as the amount of infiltration increases. Hydrological connectivity between the riparian zone and the stream, often mediated by zones of preferential flow through the hyporheic zone, influences not only the quantitative transfer of DOC, but also attenuation of DOC by the microbiota before it reaches the stream channel.

During baseflow, subsurface discharge in streams may be dominated by deep or phreatic groundwater (Freeze & Cherry, 1979), with generally low DOC concentrations ($<2\,\mathrm{mg\,L^{-1}}$, Thurman, 1985). This has been proposed as the reason why streams at baseflow have often very low DOC concentrations (Kaplan & Newbold, 1993). While this appears logical, several issues remain. First, even at baseflow, shallow groundwater (soil water) with high DOC concentrations may be found adjacent to stream channels (e.g. Fiebig, 1995). Even though the hydrostatic force exerted on this water at baseflow is probably low, it seems improbable that none or very little of this water and its DOC load reaches the stream. However, experiments have shown that stream sediments can immobilize DOC across a broad range of concentrations (Fiebig & Lock, 1991; Kaplan & Newbold, 1995), so that subsurface discharge, whatever its source, can probably deliver significant quantities of DOC to the stream ecosystem even at base flow. If indeed water flux in a stream reach is dominated by groundwater, immobilization and microbial utilization of only a small amount of DOC from this source could have significant impact on the organic carbon budget (Hynes, 1983). Second, Oliver *et al.* (1983) reported that 90% of the DOC in a blackwater river was less than 30 years old, whereas the carbon in deeper groundwater was hundreds to thousands of years old (Thurman, 1985). While some of this 'young' DOC may be derived from direct surface inputs of organic carbon, it is plausible that much of it could be derived from shallow subsurface discharge. Perhaps DOC discharged into streams at baseflow is much less recalcitrant than often assumed because it is derived from near surface rather than phreatic sources. Clearly, well-planned sampling strategies are needed to demonstrate directly the sources and quality of DOC carried by groundwater discharge into streams at baseflow.

As infiltration of precipitation into the soil increases, dramatic changes may occur in the hydrological connectivity across the catchment and between the riparian zone and the stream. The variable source area concept suggests that stormflow in a stream may be generated from the displacement of water stored within the catchment from previous precipitation events (Sklash & Farvolden, 1979, 1982; Hornberger, Bencala & Knight, 1994). These previously isolated reservoirs of ground and soil water (comprising the variable source areas), probably contain variable concentrations of DOC, thereby sending variable loads as groundwater transmission to the stream increases with increasing precipitation in the catchment (Cronan, 1990). In a wide range of running waters in different biomes, DOC concentration increases with discharge (Thurman, 1985), although there are exceptions (e.g. McDowell & Wood, 1984). However, the relationship between DOC concentration and discharge during a storm event can vary between the rising and falling limbs of the hydrograph and over time, depending on the preceding conditions. The most common situation is a clockwise hysteresis, whereby DOC concentrations at a given discharge are higher on the rising than the falling limb (Hope, Billett & Cresser, 1994).

Sometimes the routing of subsurface water during high flow events is enhanced by natural macropores or zones of preferential flow within the catchment (Beven & Germann, 1982). In a Welsh catchment, high concentrations of DOC were observed in riparian pore water. Interstitial microbial processing was minimized by high flow rates in macroporous flow paths and surface drainage ditches and high quality DOC in the form of amino acids was concentrated in riparian soil water and the adjacent stream water (Fiebig, Lock & Neal, 1990).

Irrespective of the pathways involved, DOC available for sessile micro-organisms in the riparian and hyporheic zones may increase by several orders of magnitude during storm events (Fiebig *et al.*, 1990; Fiebig, 1995). Sessile microorganism within the hyporheic zone are probably adapted to dynamic DOC flux and experimental evidence suggests that ephemeral increases in the DOC load from the floodplain or from upland allochthonous sources are efficiently retained in the hyporheic zone (Fiebig, 1992). Although DOC concentrations in stream water may increase during storm events, the stream system as a whole tends to be highly retentive of organic carbon.

Autochthonous inputs

Rooted plants growing in stream channels may provide substantial input of organic carbon (Hill & Webster, 1983; Marxsen, Schmidt & Fiebig, 1997). Net primary production of selected macrophytes from streams in the eastern U.S.A. ranged from 18 to 1310 g m^{-2} yr^{-1} (Webster *et al.*, 1995). Not all macrophyte production is surficial, since some species have extensive root systems sometimes accounting for over 80% of the standing crop (Hill & Webster, 1983). Rooted macrophytes contribute organic carbon directly to the hyporheic zone and they can be a major source of autochthonous detritus for microbial decomposition. However, macrophyte production is a minor portion of total primary production in many streams (e.g. 9%, Fisher & Carpenter, 1976; 15%, King & Ball, 1967). Algal biofilms on the bed sediments predominate.

Epilithic algal production is commonly observed in streams, but benthic algae also often grow in fine sediment (epipsammon), or on the surface of soft sediments (epipelon). Ellis *et al.* (in press) showed that algae can penetrate deeply into the bed sediments. They observed measurable chlorophyll in floodplain deposits hundreds of metres lateral to the Flathead River (Montana, U.S.A.) channel. Mean net primary production of attached algae ('periphyton') in a range of streams in the eastern U.S.A. varied between 0.7 and 1460 g m^{-2} yr^{-1} (Webster *et al.*, 1995), which is similar in magnitude to the NPP of macrophytes quoted above. In addition to their significance as POM, algal exudates can also be an important source of DOM in running waters. Much of this material is thought to be low molecular weight and utilized directly by heterotrophic bacteria directly within the epiphytic biofilm community (Haack & McFeters, 1982; Rounick & Winterbourn, 1983). Algal exudates accounted for up to one third of DOC concentrations in a Piedmont stream for brief periods during times of peak primary production (Kaplan, Larson & Bott, 1980), and can also induce daily fluctuations in stream DOC concentrations (Kaplan & Bott, 1982).

Longitudinal changes

The conditions described above are characteristically modulated along the river corridor in relation to orography (Fig. 3). The general view is that high gradient headwater streams, often with a limited riparian and hyporheic area (Fig. 3a), carry water, wood debris and sediments (Bilby, 1981) into the middle reaches, where cut and fill alluviation takes over and dynamic, expansive floodplains and braided channels are created. Riparian vegetation and soil development are patchily distributed and many successional patterns are evident in the midreaches (Tabacchi *et al.*, 1998). Hydrological connectivity is high in both the vertical and lateral directions

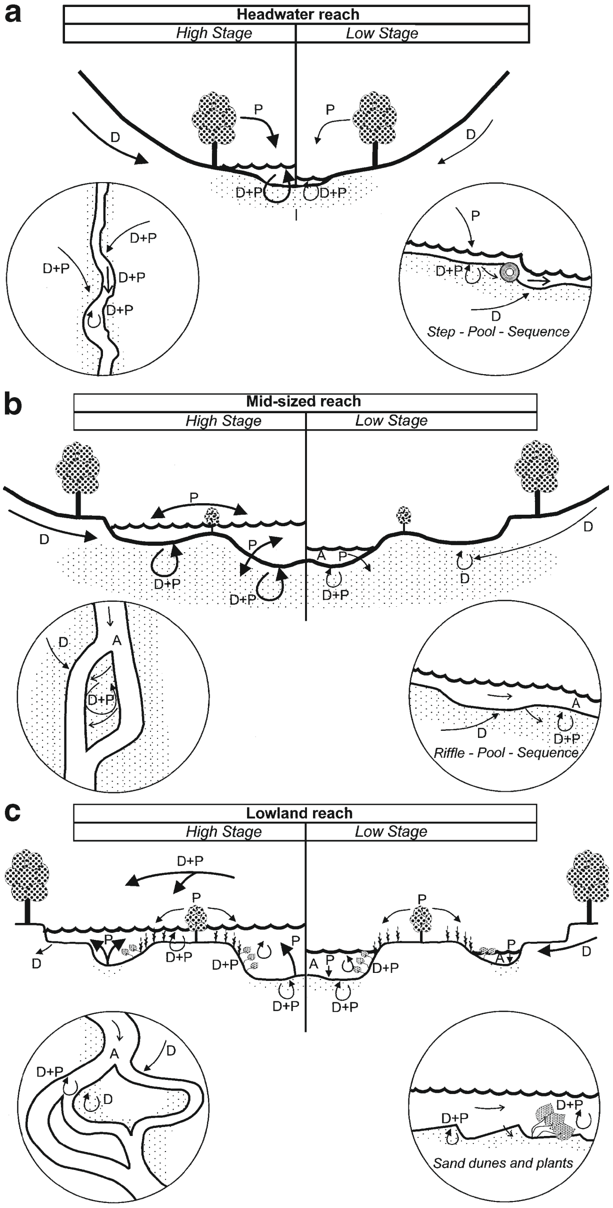

Fig. 3 Schematic views of metabolic pathways (arrows) for organic matter in headwaters (a), mid-sized rivers (b) and lowland rivers (c). Circled inserts in a-c illustrate the dominant processes and fluxes that probably enhance retention of organic matter at flood (left) and base (right) flows. Symbols as in Fig. 1, except A = assimilation by algae and macrophytes. The dotted lines are the boundaries of the hyporheic zone.

between the surficial waters of the river and the hyporheic zone (e.g. Farnleitner & Kasimir, 1996) (Fig. 3b). The sediment transport energy of the system dissipates in the midreaches permitting only sand and silt to reach the lowland river landscape. However, discharge increases in a downstream direction. Hence, lowland rivers characteristically have landscapes with little relief and expansive riparian forests that and are either flood pulsed or wetland dominated.

In flood pulse systems (Junk *et al.*, 1989; Petts, 1990), minerals eroded from the upper part of the catchment are transported via floods deep into heavily forested floodplains via braided or meandering channels. Therefore, these lowland floodplains generally are well supplied by nutrients and are very productive (Spink *et al.*, 1998) but subject to stochastic redistribution (Cuffney, 1988) (Fig. 3c). Mosaics of mineralized and organic deposits occur in relation to dynamic redox gradients in surface and subsurface flow paths (Gregory *et al.*, 1991; Bajkiewicz-Grabowska, 1993; Higler, 1993; Succow & Jeschke, 1990).

Discharge in 'true' lowland rivers is derived from catchments having little relief and porous substrata. Flood flows are highly attenuated by retention in complex channel systems and marshes or swamps. Suspended matter settles in the riparian zone which is therefore enriched in nutrients compared to the more remote floodplain areas (Mulholland, 1981; Higler, 1993). Limited oxygen availability in permanently water-saturated sediments retards the mineralization of organic matter produced or retained in these wetlands (Westermann, 1993). Slow anaerobic pathways of microbial decomposition eventually lead to the production of methane (Holland, Whigham & Gopal, 1990; Westermann, 1993; Boon & Sorell, 1995). Also, a considerable part of that organic matter is stored within growing layers of peat (Benke & Meyer, 1988; Succow & Jeschke, 1990). The presence of huge amounts of particulate and dissolved organic matter produced in the slow moving river water or on the continually saturated floodplains fuels intense microbial denitrification, both in the groundwater and in the river (Fustec *et al.*, 1991; Bruesch & Nilsson, 1993; Westermann, 1993).

Stanford & Ward (1993) characterized the longitudinal corridor of alluvial rivers as being structured like beads on a string. From headwaters to river mouth aggraded floodplains alternate between constrained reaches, where bedrock outcrops limit riparian development. Lateral and vertical interactions between surface and groundwater also exist continuously from headwaters to mouth, but the extent of the interaction fluctuates in relation to the extent of alluviation. Even in lowland reaches, the

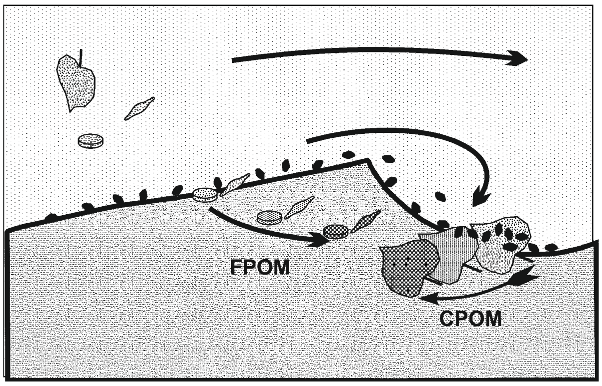

Fig. 4 Entrainment of fine (FPOM) and coarse particulate organic (CPOM) matter in bed sediments by downwelling of stream water and by burial in shifting sediments.

exchange of water between the river and its bed sediments can be induced by inorganic and organic roughness elements (Savant, Reible & Thibodeaux, 1987; Huettel, Ziebis & Foerster, 1996). Water and materials are 'pumped' into the sediments to depths several times the height of the ripple, bar, dune or other sedimentary structures imposing roughness on the channel (Rutherford, 1994). Interstitial flow velocity will be four to seven orders of magnitude lower than the free stream velocity, depending upon the structure of the deposits (Savant *et al.*, 1987; Rutherford, Latimer & Smith, 1993; Rutherford, 1994; Huggenberger *et al.*, in press). Except in very fine sediments (silts and clays) vertical water flux seems to be sufficient to maintain aerobic conditions deep into the river bed and floodplain deposits (Edwards, Meyer & Findlay, 1990; Buddensiek *et al.*, 1990; Rutherford *et al.*, 1993; Stanford, Ellis & Ward, 1994). Therefore, significant amounts of POM can be entrained, stored and transformed by microbial activity in the bed sediments of alluvial streams. Even in the sandy sediments of lowland streams (Metzler & Smock, 1990) and rivers (cf. Rutherford *et al.*, 1993), the hyporheic zone is a major site of organic matter processing within the riverine ecosystem (Edwards *et al.*, 1990; Rutherford *et al.*, 1993).

Retention of organic carbon

Transport and retention of particulate organic matter

Particulate organic matter (POM) accumulates on the river bottom or inundated portions of the floodplains during periods of receding or low flow. However, these surficial deposits form a more temporary storage pool that may be washed away by the next flood. If POM is entrained into the bed sediments, it may be available for microbial communities for a long time. Coarse POM may be stored in pockets between inorganic substrata, while fine POM may fill interstitial spaces. Large woody debris may be stored in bed sediments for centuries (Harmon *et al.*, 1986). Owing to relative temporal stability, entrainment of POM in the sediments may directly influence microbial processes in riparian ecotones and even the resilience of the carbon cycle in the entire ecosystem. Humans have altered the retention of POM by many running waters worldwide. Indeed, over 50% of leaf input was flushed out of a channelized reach studied by Petersen & Petersen (1991).

Entrainment of POM in sediments

In contrast to DOM, POM may be physically retained in great amounts by the filtration effect of the bed sediments. The hyporheic zone is a dynamic ecotone with a 'transport phase' and a 'stationary phase' which enables the gradual formation of microsites with differing exchange capacities thereby creating an whole array of retentive structures with differing characteristics for transient storage. The hyporheic zone is a photic, mechanical and biochemical filter (Vervier *et al.*, 1992) that enables extensive microbial decomposition of POM particles through prolonged retention times. The mineralization of POM may be viewed as 'final retention', or as an irreversible carbon sink. However, some functions of the hyporheic filter are active only episodically and only in certain areas of a floodplain, while others may be more or less continuous.

Sedimentation

Detritus particles settle out of the water column in areas of reduced flow competence. Therefore pools, eddies, backwaters and inundated floodplains are major sites of POM accumulation. Structures like leaf packs in small streams, log jams in floodplains or debris dams in river channels increase sedimentation rates and help prevent resuspension of particles (Smock, Metzler & Gladden, 1989; Gregory *et al.*, 1991; Mulholland, 1981; Jones & Smock, 1991;

Bretschko & Moser, 1993; Cushing, Minshall & Newbold, 1993; Kozerski, 1994). In these 'hot spots' of POM accumulation and degradation (Smock *et al.*, 1989; Hedin, 1990), the velocity and biochemical pathways of microbial processing will vary with the POM supply, availability of inorganic nutrients and redox conditions (Dahm, Carr & Coleman, 1991).

Burial by shifting sediments

Downstream migration of ripples, dunes and entire gravel sheets usually entrains POM (Savant *et al.*, 1987; Meyer, 1988; Metzler & Smock, 1990; Rutherford, 1994; Findlay, 1995; Naegeli, Huggenberger & Uehlinger, 1996). These structures migrate by the erosion of individual sediment particles at the upstream side, followed by redeposition in the 'dead zone' on the downstream side of the structure (cf. Richards, 1982; Carling, 1990). Hence, POM particles deposited in the dead zone will be buried (Fig. 4).

This form of sediment transport and POM trapping is a widespread and nearly permanent phenomenon on the bottoms of lowland streams and rivers consisting of coarse sand (Metzler & Smock, 1990; Rutherford *et al.*, 1993). During autumnal storms, coarse POM abundant at that time is buried deeper, thus forming a storage pool that may be released gradually over the year (Herbst, 1980; Smock, 1990). In gravel-bed rivers, bars of various configurations migrate by the same process burying wood parallel to the direction of flow. (Bridge *et al.*, 1986; Carling & Glaister, 1987; Naegeli *et al.*, 1996).

Vertical hydraulic entrainment

Well-sorted and open frame sediments (Freeze & Cherry, 1979; Huggenberger *et al.*, 1998) are highly transmissive and produce vertical hydraulic gradients (VHG). The pattern of VHG is produced by local differences in water pressure caused by hydrostatic or hydrodynamic processes (Lee & Cherry, 1978; Boulton, 1993). These are mainly generated by longitudinal changes of the cross-sectional area of the channel, by changes in the gradient of the water surface, or by deviations of the direction of river flow from that of groundwater flow (cf. Williams, 1993). Following these pressure gradients, surface water and interstitial water is exchanged by means of downwelling and upwelling. By the former process, POM particles may be transported deep into the sediments (Huettel *et al.*, 1996; Valett, Fisher & Stanley, 1990, 1994) (Fig. 4).

Vertical interactions have been well studied in riffle–pool sequences of gravelly and sandy streams (Valett *et al.*, 1990; Hendricks, 1993, 1996; Hendricks & White, 1995; Jones, Fisher & Grimm, 1995). In the transition zone from pools to riffles, where the cross-sectional area of the stream narrows, downwelling of stream water into the streambed sediments has often been observed, with corresponding upwelling at the end of the riffle. Horizontal nominal transport velocity of interstitial water in the hyporheic zone is about 1/1000 of surface velocity in gravel-bed streams (Pusch & Schwoerbel, 1994). Similar 'pumping' phenomena due to uneven pressure distribution, have also been demonstrated near riffles and dunes that are regularly present on sandy river bottoms (Rutherford, 1994; Huettel *et al.*, 1996). Small particles suspended in the surface water may penetrate to depths several times the dune height.

In larger gravel-bed streams and rivers, vertical hydrological exchange operates at a variety of spatial scales. Single boulders may produce increased vertical hydrological linkage (Williams, 1993), which eventually leads to elevated POM concentrations in the hyporheic zone of a riffles (Pusch, 1996, 1997). At the floodplain scale, a substantial portion (30% or more) of the stream flow may infiltrate at the upstream end (Stanford, Ward & Ellis, 1994). Similar reach-scale vertical linkages frequently occur in rivers flowing over karstified bedrock (Vervier & Gibert, 1991; Deutscher Verband fuer Wasserwirtschaft und Kulturbau (DVWK); 1996). All of these processes may entrain POM in the bed sediments.

Lateral hydraulic entrainment

Depending on the ratio of water levels in the stream and the accompanying floodplain aquifer, exchange of stream and subsurface water does not occur solely in the vertical direction through the stream bed, but also in the lateral direction through the channel margins (Stanford & Ward, 1988; Stanford *et al.*, 1994). If stream water infiltrates into the aquifer, the riparian zone, and even the entire floodplain sediments, may also act as lateral retention sites for DOM and POM. Most stream reaches do not permanently gain or lose groundwater, but the direction of water flux is reversed with

Table 1 Conceptual model of orogaphic influences on lateral ecological connectivity in stream ecosystems

Orography	Upland	Lowland
Hydrological permeability of sediment	High	Low
Heterogeneity of sediments	High	Low
Temporal occurrence of lateral subsurface hydrological linkage	Continuously	Discontinuously
Spatial occurrence of lateral subsurface hydrological linkage	Discontinuously	Continuously
Organic matter fractions transferred (and retained)	DOM, FPOM, CPOM	DOM, scarcely FPOM
Biota transferred	Micro-, Meio- and Macrobiota	Microbiota
Pathways of microbial degradation of organic matter in the lateral hyporheic zone	Mostly aerobic or partially aerobic and anaerobic (including nitrate respiration)	Mostly anaerobic (including nitrate respiration)

fluctuating relative water levels (Whiting & Pomeranets, 1997). The temporal and spatial occurrence of these hydrological linkages largely depends on the hydrological permeability of floodplain sediments and the discharge regime (Wroblicky *et al.*, 1998). In upland streams and rivers, subsurface flow often follows specific subsurface channels, and downwelling and upwelling phenomena may occur within the same reach. In contrast, hydrological exchange of lowland rivers with phreatic aquifers accompanying them occurs in a more diffuse way, depending on the general pattern of relative water levels on a much larger scale. Thus, lateral subsurface ecological connectivity differs markedly between these stream types, which is summarized conceptually in Table 1.

Impact of floods on sedimentary POM

Floods often reduce POM in surficial sediments (Short & Ward, 1981; Snaddon, Stewart & Davies, 1992). However, POM is reported to be deposited during floods at the channel surface, in the sediments, on adjacent river banks and on the floodplain (Cummins *et al.*, 1983; Leichtfried, 1988; Smock, 1990; Jones *et al.*, 1995; Naegeli *et al.*, 1995). In a period of frequent flood disturbance in a low order reach of a perialpine gravel bed river (R. Necker, Switzerland), POM as AFDM in the uppermost 40 cm of the river sediment increased with the number of floods from 2 kg m^{-2} AFDM, when no flood occurred, up to 8 kg m^{-2} after four floods (Naegeli *et al.*, 1995). Fine POM is washed out of the sediments throughout the corridor during the highest phase of a spate and redeposited in higher concentrations during the receding phase (Pusch & Schwoerbel, 1994). Thus, spates are periods of extensive mass transfer and exchange in running waters. It may lead both to a net loss and a net accumulation of POM, depending on the amount previously stored, on the POM load during the spate, and on the specific retention efficiency of a given sediment patch with respect to the particle sizes supplied by the river.

Immobilization of DOM

In contrast to POM, DOM is more transient and exportable because it is in the soluble phase (Mulholland, 1997). However, high exports give a misleading picture of the role of DOC in running waters because the material exported may have been recycled a number of times within the food web before being exported. Perhaps the most significant evidence for the intense and often rapid turnover of DOC in running waters is the growing body of direct and indirect evidence for its efficient immobilization, which mostly occurs on sediment surfaces (Lock & Hynes, 1976).

Immobilization of DOM can occur as purely physical process involving physical sorption to mineral surfaces, such as iron, aluminium oxides (McKnight *et al.*, 1992) and clay (Dahm, 1981). On the other hand, most wetted surfaces in the sediment are colonized by microbial biofilms, which remove DOM from the water efficiently (Lock & Hynes, 1975; Kaplan & Bott, 1983; McDowell, 1985; Fiebig & Lock, 1991; Vervier & Naiman, 1992). Due to analytical difficulties, it is often unclear exactly which components of the DOM load are preferred by the micro-

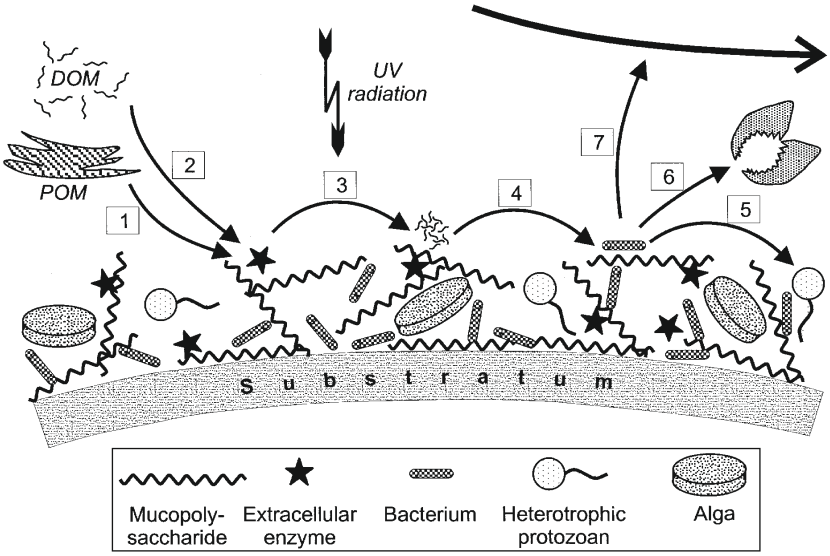

Fig. 5 Metabolic pathways (numbered arrows) for organic matter in streams mediated by microbial biofilms on and within the bed sediments. 1, DOM adsorption and storage. 2, POM entrainment and storage. 3, biochemical cracking of organic polymers by extracellular enzymes or UV radiation. 4, assimilation of monomers and biomass production by bacteria. 5, predation on bacteria by microfauna. 6, biofilm grazing by macrofauna. 7, hydrological losses (e.g. during floods).

organisms. While it is clear that low-molecular-weight DOM, such as carbohydrates and amino acids, are readily immobilized (e.g. McDowell, 1985; Fiebig, 1992), there is also evidence that biofilms must also be capable of immobilizing at least certain components of the higher-molecular weight fraction (McDowell, 1985; Fiebig & Lock, 1991).

Although aquatic biofilms are biological components of the benthic and hyporheic sediments, immobilization of DOM by the biofilms can occur by abiotic, as well as biotic means. Biotic immobilization occurs when heterotrophic micro-organisms, bacteria in particular, have direct access to the water above the substratum, and can use their cell wall transport systems to transfer DOM from the aqueous medium into their cells. This direct, biotic immobilization is a rate limited process restricted to low-molecular organic matter, which constitutes only a small proportion of the total DOM in natural waters (Thurman, 1985).

The efficiency of DOM immobilization is increased markedly by abiotic processes associated with the polysaccharide matrix (Fig. 5). The matrix has a charged surface, which means that biofilms can act as an ion exchange systems (Costerton *et al.*, 1987; Freeman *et al.*, 1995). DOM that has adsorbed at the surface, including high-molecular-weight material such as humic and fulvic acids, can then diffuse into the polysaccharide matrix, where it may be stored before at least some of this material is utilized by the microbes (Freeman & Lock, 1995; Fiebig, 1997). Extracellular enzymes released by the heterotrophic micro-organisms in the biofilm degrade at least certain fractions of the immobilized, higher-molecular-weight DOM (Meyer *et al.*, 1987), and the efficiency of this process is enhanced by the biofilm's ability to accumulate these enzymes within the polysaccharide matrix (Lock, 1993; Chappell & Goulder, 1994).

Abiotic immobilization by biofilms is important in the retention of the low molecular weight DOM most readily utilized by the heterotrophic micro-organisms, especially when DOM loads are high in the stream (Fiebig, 1992). This method of storage means that even highly labile organic matter can have relatively long (in the order of weeks) mean residence times in the sediment following its initial immobilization, if tight cycling between the organic matter and successive generations of bacteria is taken into account (Fiebig, 1997). It is now becoming clear that the combination of biotic and abiotic immobilization processes associated with aquatic biofilms provides a highly effective means by which dissolved organic matter can be retained within the running water ecosystems and incorporated into the food web.

Transformation of organic matter

Transformations of POM

General patterns of POM processing. The availability of POM to microbiota in the hyporheic zone depends both on the physical structure and on the biochemical composition of the organic matter. These features of a given POM particle change rapidly during its stay within the aquatic phase, and therefore microbial processing of a specific POM particle depends largely on its 'life history', i.e. its origin, age and the various steps of transformation it has undergone.

Shortly after POM has entered the stream, its nutritional value is reduced by the leaching of easily soluble components (≈5–25% loss for dead leaves from deciduous trees). Subsequently, the size of the POM particles is reduced by physical abrasion on the stream bottom. At the same time, the particles are subject to biological processing. The exterior and interior surfaces of leaves and twigs are mainly colonized by aquatic hyphomycetes (Gessner, Meyer & Schwoerbel, 1991), while bacteria rapidly colonize smaller particles and mineral surfaces, forming biofilms (Lock *et al.*, 1984). The microbial attack on dead plant tissue is a two-stage process (Overbeck & Chróst, 1990). First the easily degradable cell components are metabolized rapidly, like surficial layers of the cell walls, which are weakened and fragmented by the loss of pectin and hemicelluloses. The cell contents within the plant tissue (i.e. cell organelles and storage compounds, consisting mainly of carbohydrates, proteins, amino acids, nucleic acids and lipids) are broken down as well. These cell compounds are often rich in nutrients, like organically bound nitrogen and phosphorus. In the next step the main components of the cell walls are hydrolyzed enzymatically, as cellulose and lignin. For the assimilation of these compounds, which are poor in N and P, micro-organisms need inorganic nutrients from the ambient water. As a result, during 'conditioning' of POM, the content of protein rises in the biofilm and its C/N ratio drops (Kaushik & Hynes, 1971; Bärlocher & Kendrick, 1973; Suberkropp *et al.*, 1976; Odum, Kirk & Zieman, 1979; Rosset, Bärlocher & Oertli, 1982; Mann, 1988) and nutrient content in stream water drops (Mulholland, 1992).

This preconditioned organic matter, which is densely colonized by microbiota, forms a preferred food source for detritivorous invertebrates (Mann, 1988). Shredding invertebrates cut up macroscopic particles (coarse particulate organic matter=CPOM) into fragments they can ingest. Filter feeders and collectors ingest fine particulate organic matter (FPOM). During the intestinal passage, some enzymes produced by micro-organisms, such as xylases, cellulases and carbohydrases, remain active and similar enzymes of endosymbiontic bacteria are added (Sinsabaugh, Linkins & Benfield, 1985). At this point, the original cellular structures of the plant are mostly disintegrated. The compaction of mixed POM particles into faecal pellets, which are densely colonized by microbiota, seems to be a decisive step (Rounick & Winterbourn, 1983; Wotton, 1994; Wallace *et al.*, 1995) leading to the final stages of the decomposition of POM and characterized by a continuous rise in C/N ratio (Ward & Cummins, 1979).

Significance of the biofilm for POM processing. In streambed sediments, bacteria and hyphomycetes colonize most internal surfaces, forming in later stages of colonization a complex biofilm. Bacteria cover bare mineral surfaces with a polysaccharide glycocalyx, which may amount to several times their cell biomass (Bärlocher & Murdoch, 1989). This mucoid coating facilitates the adherence of other microbiota, and traps POM particles that are transported by interstitial water current (Fig. 5). The adherence of POM is probably decisive for the development of more complex biofilms, as they both act as additional elements that are structuring the biofilm spatially, and as substrates for bacterial growth. Hence, the sedimentary concentration of this 'loosely associated particulate organic matter' (LAPOM), especially its protein content, correlates well with community respiration rates in hyporheic sediments (Pusch & Schwoerbel, 1994). The LAPOM fraction thus exhibits a rapid turnover, which has been estimated at twice per year in a mountain stream (Pusch, 1996). That rate is much greater than the 0.1 per year given as a mean for the turnover of benthic POM by Hedin (1990).

As a food source, POM is only accessible to bacteria and hyphomycetes after cleavage of the organic macromolecules into soluble monomers that can be transferred through the cell wall for assimilation (Overbeck & Chrost, 1990). Therefore, micro-organisms produce extracellular hydrolytic enzymes that raise the ambient concentration of dissolved organic micromolecules within the biofilm (Marxsen & Witzel, 1991; Moran & Hodson, 1989). This spatial confinement of released DOM, together with the high POM concentrations in sediments, are probably the decisive reasons why an overwhelming majority of sediment bacteria is found to be attached to surfaces, instead of being suspended in the pore water (Kasimir, 1990).

Processing of large woody debris (LWD). The decomposition rate of large woody debris (LWD), i.e. logs and branches, is much slower than that of leaf litter, because of its unfavourable ratio of surface area to volume. Microbiota decompose wood aerobically only within a thin surficial layer because of low oxygen content deeper in the wood. The limitation to surficial breakdown is also caused by the fact that there are few xylophagous freshwater invertebrates capable of boring holes, which accelerates the decomposition of wood in terrestrial and marine environments (Anderson & Sedell, 1979; Cummins *et al.*, 1983). The anaerobic decomposition rate of coarse POM is even much lower (Cummins, 1974; Cummins *et al.*, 1984). Hence, tree trunks embedded into stream and river sediments may persist for many decades and even many centuries (Anderson *et al.*, 1978; Swanson, Lienkaemper & Sedell, 1976). However, if submerged wood is exposed both to microbial decomposition and to physical abrasion by strong current velocity or moving bed load, it may lose more than a centimetre in width per year (Ward & Aumen, 1986). The most active micro-organisms decomposing submerged wood are bacteria, such as *Bacillus* sp., *Enterobacter* sp., and actinomycetes.

Microbial processing of organic matter in riparian and hyporheic zones

The biological breakdown of interstitial organic matter depends largely on the contact time (Findlay, 1995). Consequently, as discussed above, the retention efficiency of a specific reach is the key factor controlling riverine organic matter loads. Microbial activity in the riparian and hyporheic zone of a specific stream is determined by the spatial extent of the exchange of matter between surface and interstitial waters and the level of heterotrophic activity.

If the hyporheic zone is viewed as an ecotone with the major input of energy coming from the surface, the level of heterotrophic activity should follow a spatial gradient, with generally decreasing activities in downward and lateral directions from the channel. However, there are only a few streams or rivers where such spatial profiles of interstitial microbial activity have been measured up to now (Hendricks, 1993; Ellis *et al.*, in press). Knowledge of microbial activities in the hyporheic zone remains fragmentary.

In the study by Ellis *et al.* (in press) bacterial densities decreased progressively in the interstitial waters of the hyporheic zone, as site distance from the river increased. Only 2–3% of the total microbial density measured in the river water column (3.1×10^5 cells mL^{-1}) occurred at hyporheic sites most distant (4 km) from the river (9.0×10^3 cells mL^{-1}). However, this pattern was not observed in the more permanent epilithic community of the hyporheic zone. Although it was hypothesized that hyporheic sites near the river channel would show increased levels of production due to higher quality DOC from riverine downwelling, ^{3}H-thymidine experiments showed no clear patterns. Craft (1998) measured microbial community respiration along the same spatial gradient across the Flathead River floodplain. Respiration ranged between 0.10 and 0.17 mg O_2 dm^{-3} h^{-1} and no relation to distance from the river was apparent. Concentrations of DOM did not vary with distance, either (Stanford, Ellis & Ward, 1994).

In contrast, a sharp vertical decline of community respiration was observed between 10 and 20 cm sediment depth in a third-order softwater mountain stream (Steina) in the German Black Forest (Pusch, 1996). The level of heterotrophic activity in that hyporheic zone was at 1.7 g O_2 m^{-2} day^{-1} (= 0.55 g C m^{-2} day^{-1}) as an annual mean for combined riffle and pool subsections from 5 to 45 cm sediment depth. This value is about twice that estimated by Craft (1998) on an aerial basis. However, in the Flathead River, channel water circulates hundreds to thousands of metres into the floodplain sediments, forming a massive hyporheic zone. The considerable spatial variability of hyporheic community respiration in both studies suggests strong influence by patches of differing sediment composition that form 'hot spots' of microbial activity. In contrast to the marked gradients in the riffle of the Steina, there was hardly any vertical pattern in the pool and activity was five times lower (Pusch, 1996).

Grimm & Fisher (1984) measured hyporheic community respiration at about 4 g O_2 m^{-2} day^{-1} in shallow (2–17 cm strata) bed sediments of Sycamore Creek, Arizona, located in the hot, arid south-western U.S.A. Lateral inputs of POM in that sparsely vegetated region are limited and 85% of the heterotrophic activity in the stream-bed sediments was fuelled by labile DOM and POM derived from benthic algae (Jones, Fisher & Grimm, 1995; Jones & Holmes, 1996).

Some 95% of the heterotrophic activity in the hyporheic zone can be attributed to micro-organisms $< 100\,\mu m$, mostly bacteria (Pusch & Schwoerbel, 1994). Although hyphomycetes are believed to be rare in most subsurface environments (Bärlocher & Murdoch, 1989), studies of a large gravel bed river in north-western Montana showed that fungal biovolume exceeded bacterial biovolume at some hyporheic sites and hyphae were common in many hyporheic samples (Ellis *et al.*, in press). In the Steina hyporheic zone, $1\,cm^3$ of sediment was colonized by about 1×10^9 bacterial cells (Fischer, Pusch & Schwoerbel, 1996). Tests using the respiratory indicator dye CTC, however, showed that only 9% of hyporheic bacteria exhibit respiratory activity, which is roughly equal to the percentage in other aquatic habitats. Activity was more than twice as high in the LAPOM fraction than in the SAPOM fraction. Perhaps dormant cells are adapted to transient concentrations of other compounds and therefore 'turn on' only during limited periods. As a result of microbial processing of non-woody POM, interstitial waters may be substantially enriched with inorganic nitrogen and phosphorus, which enables elevated benthic primary production in upwelling sites (Valett *et al.*, 1990, 1994; Jones *et al.*, 1995b).

We conclude that hyporheic community respiration in small streams seems to reach roughly the same level as community respiration in the benthic zone (Pusch, 1996). But, in larger alluvial rivers with extensive hyporheic zones, hyporheic community respiration may be many times or even an order of magnitude higher than benthic respiration (Naegeli & Uehlinger, 1997; Craft, 1998). The contribution of the hyporheic zone to total ecosystem respiration varies from 40% to over 90% in relation to geomorphic, climatological and hydrographic characteristics of the respective streams (Grimm & Fisher, 1984; Pusch, 1996; Fuss & Smock, 1996; Naegeli & Uehlinger, 1997; Mulholland *et al.*, 1997). The interstitial microbial community may be adapted to frequent changes in the supply of organic matter through the storage capacity of the mucopolysaccharide layer for organic molecules and by the substantial biological reserve of inactive cells. However, additional studies in an array of rivers are needed to understand fully the processing of organic matter in the riparian and hyporheic zones. It is clear, however, that microbial production and respiration in the bed sediments is a major, if not dominant, component of total ecosystem carbon flux.

Transformations of DOM. The bulk of organic matter entering the riparian zone is of a size incapable of being transported across the cell membrane (> 1000–10 000 Da). In order for this material to enter the food web it must be reduced to a size capable of transport either by the biotic process of microbial extracellular enzymes, or through the abiotic process of UV radiation.

Processing of organic matter by extracellular enzymes. Extracellular enzymes are the crucial first biological processing step for much of the organic matter generated within or transported into all ecosystems because of the fundamental limitation on the size of molecule which can be transported across biological membranes (cf. Fig. 5). Fungi and bacteria generate the bulk of extracellular enzymes capable of degrading macromolecules and polymers. The majority of animals (with the exception of molluscs) do not have such a capability.

The existence of extracellular enzyme activity is well established in lotic ecosystems (reviewed in Lock, 1993; Jones & Lock, 1993; Chappell & Goulder, 1994). However, there are several major aspects of environmental enzymology which require investigation, some of which are particularly pertinent to the riparian corridor:

1 How much enzymatic protein is present within the sediments and at surfaces within the riparian corridor?

2 What is the extent of protection from denaturation and how long do enzymes persist in an active state within the riparian corridor?

3 What is the rate of transfer of enzymatic material into and out of the riparian corridor?

4 UV reactivation of humus-enzyme complexes.

To our knowledge, the first two have not been investigated for any ecosystem, but clearly require study if we are to develop a robust model of material/energy transfer within the riparian foodwebs.

The transfer of enzymes into and out of the riparian corridor has not been investigated *per se*, however, Chappell & Goulder (1994) have shown that enzymes discharged from sewage works may be transported several km downstream and provided some evidence that enzyme activity may accumulate within biofilms below the discharge point. This supports the concept that enzymes produced in the catchment/riparian corridor (both terrestrial and aquatic in origin) may be trapped within the river itself. Thus, the catchment/riparian corridor may not only be providing organic matter to the river (Wetzel, 1990), but may also be providing some of the enzymes to process organic matter of whatever origin.

A final and unusual perspective on extracellular enzymes concerns the potential for 're-activation' of enzymes bound within so-called humus-enzyme complexes. The complexation of enzymes with humic materials has been shown to inactivate the enzyme. However, the exposure of these complexes to certain wavelengths of ultraviolet radiation results in varying degrees of restoration of enzymatic activity (Wetzel, 1992; see below). Thus, the shallow water areas of the riparian corridor could be important sites of enzyme reactivation for enzymes originating from the adjacent terrestrial landscape or from upstream. This could produce production 'hotspots.'

We can expect that extracellular enzyme activity will have a major role to play in setting the level of production within the riparian corridor via creation of small transportable organic molecules and release of inorganic nutrients from organic macromolecules and polymers for subsequent use by autotrophic and heterotrophic organisms.

Metabolism, storage and inhibition. The metabolism of river biofilms has been measured as dark respiration, heat output and electron transport system activity. Associated measurements have included uptake rates for specific radio labeled compounds and bacterial growth rate measurements using ^{3}H thymidine. These aspects of lotic metabolism have been extensively reviewed already and interested readers are referred to these (Meyer, 1990b; Lock, 1993, 1994) and will not be discussed further. However, the topics of storage and inhibitory phenomena have received much less attention and they raise some interesting questions.

Information on microbial storage products in rivers and streams is extremely limited. Blenkinsopp *et al.* (1991) specifically examined seasonal trends in biofilm storage products, finding that glycogen tended to be stored by autotrophically dominated biofilms, while poly hydroxy alkanoates (PHA) dominated under conditions high in allochthonous carbon supplies. As might be expected, seasonal shifts occur between these two storage products with PHA dominant in the autumn (high allochthonous OM inputs) and glycogen in the spring (high autochthonous OM inputs). These observations are of considerable relevance to insect larval nutrition and feeding studies. A simultaneous study that tracked storage product pools alongside traditional measures of algal and bacterial biomass could be very illuminating. Hitherto, inexplicable patch selection by insects might be due to microbial storage product 'hot-spots.' This might be an especially profitable line of study within the diverse autochthonous/allochthonous mosaic of the riparian corridor.

It has also recently been demonstrated that biofilms may be substantially buffered against changes in the organic substrate supply. Freeman & Lock (1995) showed that biofilms, which were experimentally deprived of exogenous OM, were able to exhibit unaffected metabolic activity for 3 weeks (at which point the study was terminated). Because endogenous storage reserves (PHA) were not utilized during that period, it would seem that the polysaccharide matrix and any previously adsorbed or entrained organic served as the OM supply. If this turns out to be a general feature of biofilms, this would serve as an agent to even out the availability of pulsed OM inputs. Such a mechanism could be of considerable energetic and material importance within those parts of riparian corridor characterized by intermittent/variable water flows.

Ford & Lock (1987) presented circumstantial evidence suggesting that organic matter > 1000 Da (either a component or components) had an inhibitory effect upon river biofilm metabolism. Considerable evidence in support of hypothesis was obtained in a subsequent experimental study (Freeman & Lock, 1992). We therefore have a situation where dissolved organic matter (> 1000 Da) may simultaneously serve as both a source of energy and materials for biofilms, while one or more components of this pool also may depress extracellular enzymatic activity (a mechanism for supply of microbially transportable/metabolizable moieties) and biofilm metabolic processes. Because of the intimate connection between the terrestrial environment (the major lotic DOM source) and the river, such phenomena may be extremely important at the point of entry of terrestrial (soil/groundwater) DOM within the riparian corridor. This potential dual role of DOM as (a) an energy/material supplier and (b) a metabolic regulator, could be a major feature of hyporheic processes.

UV radiation – abiotic organic matter processing? It is important to remember in any discussion of UV radiation that UVB has been part of the fabric of the biosphere since life began, when even the current 'ozone shield' was not present. Studies to date of UV radiation have focused upon the shorter wavelength UVB (280–320 nm) radiation and it is likely to have equivocal effects within the riparian corridor (see review by Karentz *et al.*, 1994).

UVB has been widely shown to disrupt metabolic processes and damage cellular structures and DNA (Karentz *et al.*, 1994). But many of these findings have been based upon short-term studies (of hours and days) and Bothwell, Sherbot & Pollock (1994) have elegantly shown as a consequence of long-term studies (3–4 weeks) that ecosystem responses to UVB cannot be predicted from short-term single trophic level assessments. In this study, it was shown that chironomid larvae were more sensitive to UV than epilithic algae, resulting in a substantial increase in algal biomass as a consequence of reduced grazing pressure. Such counter-intuitive findings serve as an important warning when considering 'impacts' of UV and of course other potential stressors within ecosystems.

UVB has a potential role in accelerating nutrient regeneration and the conversion of microbially recalcitrant organic matter (humics) into moieties that can be assimilated (Strome & Miller, 1978; Geller, 1986; Kieber, McDaniel & Mopper, 1989; Lindell, Graneli & Tranvik, 1996). In the latter study, they reported a sixfold increase in pelagic bacterial biomass in response to water irradiated with simulated sunlight. In a study conducted in the Arctic (M. A. Lock & T. E. Ford, personal communication), exposure of river water to 24–48 h of natural daylight resulted in changes in organic matter which, when supplied to river biofilms, approximately doubled their metabolic activity. A second positive role is the potential for UV re-activation of humus-enzyme complexes (Wetzel, 1992), which has been discussed above.

While UV radiation is attenuated through water, the areas of relatively shallow water (channel meanders, ox-bows, seeps, etc.) to be found within riparian corridors will mean that the impact of UV is likely to be high. It is predicted that dissolved organic matter in the riparian corridor will potentially undergo photylytic changes, the intensity of which may change on a seasonal basis in the higher latitudes. Thus, the biofilms on the upper surfaces of sediments, entrained debris (e.g. wood) and stones will be in the front-line of any stimulatory/inhibitory phenomena. The biofilms of the lower surfaces of stones attached to subsurface sediments will stand to gain from the positive aspects of UV radiation while being shaded/insulated to varying degrees from the negative aspects. Because of the frequently shallow nature of water within riparian corridors, they are predicted to be major sites of UV mediated organic matter modification.

Methods for the assessment of interstitial microbial activity

Biological sampling of subsurface sediments. That scientific progress concerning the ecology of the hyporheic zone has lagged behind studies of the benthic zone is related to the technical problems associated sampling interstitial environments (Table 2, cf. Williams, 1993; Fraser & Williams, 1997; Mauclaire, Marmonier & Gibert, 1998). For the measurement of microbial activity *in situ*, it is necessary to sample the sediments without substantially disturbing them and water flux rates should be close to natural (cf. James, 1974; Bott *et al.*, 1978; Jeppesen, 1979). However, alternatives to drilling or excavation for studying microbial processes remain elusive.

Measures of biological processing. Heterotrophic bacteria appear to dominate the microflora of most subsurface ecosystems (Madsen & Ghiorse, 1993). Thus, in well-oxygenated stream-bed sediments, community respiration rate has been repeatedly used as an overall measure for the level of degradation of organic matter, including DOM, in the benthic and hyporheic zones (Grimm & Fisher, 1984; Pusch & Schwoerbel, 1994; Pusch, 1996; Jones *et al.*, 1995a; Naegeli & Uehlinger, 1997) (Table 3). Similar results may be expected from methods measuring the evolution of CO_2, and metabolic heat

Table 2 Methods used for sampling biota in subsurface sediments

Method	Description	Quantitative sampling	Shortcomings of method	References
Karaman–Chappuis-dig	Digging a pit in exposed gravel bars, sampling of exfiltrating interstitial water	No	Disturbance of sediments by digging	Chappuis, 1942 Karaman, 1954
Bou–Rouch pump	Ramming a perforated tube into stream-bed sediments and pumping of interstitial water	Mostly no	Unknown sampling space Filtration effect by subsurface sediments alters particle composition pumped to the surface	Bou & Rouch, 1967 Husmann, 1971 Williams & Hynes, 1974 Stanford & Ward, 1988
Sediment coring	Extraction of cylindrical samples using a hollow cylinder driven into the sediment	Yes	Only feasible with sandy or muddy sediments	Williams & Hynes, 1974 Fiebig, 1992 Jones *et al.*, 1995
Standpipe coring	Retrieval of a sediment sample into an opening near the tip of the standpipe by twisting it	No	Feasible with sandy or gravelly sediments	Williams & Hynes, 1974 Williams, 1981
Freeze-coring	Extraction of a cylindrical sediment sample frozen to a central standpipe driven into the sediments	Mostly yes	Destroys fragile microfauna, needs electric stationing for macroinvertebrates	Stocker & Williams, 1972 Bretschko, 1981
Exposure of colonization chambers (single chambers or combined in vertical containers)	Incubation of sieved or artificially remixed sediments within perforated plastic chambers, vertical containers or pipes enabling easy retrieval of chambers	Mostly yes	Chambers contain artificially changed sediment composition Needs appropriate incubation time up to one year	Schwoerbel, 1967; Coleman & Hynes, 1970; Panek, 1991; Pusch, 1996; Eisenmann, Traunspurger & Meyer, 1997
Sediment exposure in wells	Exposure of sediments in drilled wells	Mostly yes	See above Difficulty in undisturbed retrieval over water level	Hirsch & Rades-Rohkohl, 1990; M. Pusch, unpublished

Table 3. Methods used for the measurement of biological processing of organic matter in stream sediments

Principle of measurement	Experimental setup	Application suitable for	Evidence of results	Shortcomings of method	References
Respiration rate of sediment biota (decline of O_2 concentration with time)	Respiration bell with internal stirring	Measurement of benthic community respiration (BCR) = Benthic oxygen demand (BOD)	Biochemical mineralization of POM, DOM, nitrification and methane oxidation	No unidirectional water current No renewal of water during measurement	Hansmann *et al.*, 1971 Bott *et al.*, 1978
see above	Respiration chamber with troughflow	see above	see above	— —	Bott *et al.*, 1978
see above	Stirred chamber with sediment core	Measurement of hyporheic community respiration (HCR)	see above	Probable formation of internal O_2- gradients during measurement	Grimm & Fisher, 1984
see above	Perfused chamber with sediment core	see above	see above	Difficult to get undisturbed sediment samples in gravel-bed streams	Pusch & Schwoerbel, 1994 Jones, 1995 Naegeli *et al.*, 1995
Rate of CO_2-evolution (increase of CO_2-concentration with time)	see above	Measurement of benthic community metabolism	Mineralization of POM, DOM, and methane	Measurement of CO_2 concentration in the field	Hedin, 1990
See above, but with use of ^{14}C- or fluorescent-labeled substrates	Stirred chamber, or perfused sediment column	Measurement of OM processing in the hyporheic zone	see above	Costly apparatus in the lab needed, columns only suitable for sandy sediments	Marxsen, 1981; Fiebig, 1992 Marxsen & Fiebig, 1993
Rate of production of metabolic heat	Perfused column filled with biofilm-coated glass beads	see above	Level of (bio)chemical (oxidative) metabolism	see above	Lock & Ford, 1985
Percentage of respiring bacterial cells	Small, stirred sediment samples (few g) with added INT-formazan or CTC, followed by sonication	Activity of electron transport system (ETS) in any kind of sediment	Qualitative measure of bacterial activity	Sonication procedure may be ineffective	Rodriguez *et al.*, 1992 Schaule *et al.*, 1993 Fischer *et al.*, 1996
Activity of extracellular enzymes	Small, stirred sediment samples (few g), with added fluorescent-labelled substrate (e.g. MUF-substrate)	Bacterial activity in any kind of sediments	Potential degradation rate for specific components	Potential rates are of limited relevance for ecosystem studies	Sinsabaugh & Linkins, 1988 Jones & Lock, 1989 Marxsen & Witzel, 1991 Marxsen & Fiebig, 1993

(Hedin, 1990; Lock & Ford, 1985). With the measurement of CO_2 evolution, possible errors in the estimation of OM degradation are circumvented. However, because anaerobic and aerobic conditions may occur in closed framework substrata within otherwise well oxygenated bed sediments of the hyporheic and riparian zone, oxygen-consuming processes other than the oxidation of organic carbon, such as nitrification and methane oxidation, may be quantitatively important (Dahm *et al.*, 1991; Hendricks, 1993; Triska, Duff & Avanzino, 1993; Jones *et al.*, 1995; Claret *et al.*, 1997; Dahm *et al.*, 1998).

In retentive stream reaches, massive input of POM may lead to oxygen depletion in stream-bed sediments, and thus generate sediment patches, or microzones in the biofilms, that are anaerobic (Dahm *et al.*, 1991; Vervier, Dobson & Pinay, 1993; Hendricks, 1993), where POM is processed by fermentation. These anaerobic pathways become prevalent in deeper strata of the hyporheic zone and in lowland streams with fine sediments. The final process is methanogenesis (Zaiss, 1988; Dahm *et al.*, 1991; Triska *et al.*, 1993). Methane often is emitted within gas bubbles rising from the sediments (Boon & Sorrell, 1995), which also may contain oxygenated compounds such as CO_2 and N_2O (Triska *et al.*, 1993). Hence, as noted above some, if not most, hyporheic zones may have aerobic/anaerobic intercalaries, with the prevailing microbial processes highly dependant on the local redox level (Jones *et al.*, 1995). A common feature of stream-bed sediments is intense microbial denitrification, if concentrations of organic matter and nitrate are high and oxygen saturation low (Duff & Triska, 1990; Triska *et al.*, 1993; Holmes *et al.*, 1994; Claret *et al.*, 1997). Facultative anaerobes that can switch to nitrate as terminal electron acceptor as dissolved oxygen is depleted probably dominate in such systems (Triska *et al.*, 1993).

More detailed approaches for the measurement of the metabolism of specific trophic levels aim to quantify the relative contribution of specific taxonomic or functional groups of microbiota in total heterotrophic activity within stream-bed sediments (cf. Maltby, 1992; Kemp *et al.*, 1993). Productivity of aquatic hyphomycetes may be quantified, using ^{14}C-labelled acetate that is incorporated into the ergosterol component of the cell wall (Newell & Fallon, 1991; Suberkropp & Weyers, 1996). For the measurement of bacterial production, methods well known from plankton ecology, such as uptake of [^3H]-thymidine (Fuhrman & Azam, 1982), [^3H]- or [^{14}C]-leucine (Kirchman *et al.*, 1985; Simon & Azam, 1989), may be used for sediment bacteria (Marxsen, 1996). The percentage of respiring bacterial cells in sediments may be estimated by adding the redox dyes INT or CTC, which produce fluorescent formazan (Blenkinsopp *et al.*, 1991; Rodriguez *et al.*, 1992; Fischer *et al.*, 1996). However, the extraction of bacterial cells from the sediments, the presence of mineral particles in these samples, which also can show some fluorescence, and the small size of most bacteria sampled from nutrient-poor hyporheic zones (Ellis *et al.*, 1998) render microscopic counts difficult.

Identification of micro-organisms using molecular methods. Despite the relevance of bacteria for the biogeochemical cycling of matter, little is known about their taxonomic composition. Some studies have described aquatic bacterial communities based on physiological responses among strains or on morphological characteristics from micrographs (Yamakanamardi & Goulder, 1995; Koelbel-Boelke, Tienken & Nehrkorn, 1988a,b). These studies show the high metabolic versatility of bacterial strains derived from water or biofilm samples. Conventional methods for taxonomic classification of bacteria (e.g. biochemical tests, DNA–DNA homology determination) rely on the cultivation of the strain to be characterized. However, bacteria sampled in aquatic environments and recovered by cultivation sometimes are less than 1% viable in comparison to total cell counts.

The problem of the nonculturability can now be overcome to some extent by the advent of molecular techniques that allow direct identification of bacteria in samples. Techniques that can be applied directly to natural samples are:

1 low-molecular-weight RNA (LMW RNA) analysis (LMW RNA = 5*S* rRNA+tRNA);

2 application of specific antibodies (mono-or polyclonal); and

3 PCR-amplification of 16S-rDNA genes followed by 16S rDNA-sequence analysis and probing (Amann, Ludwig & Schleifer, 1995).

In the LMW, RNA-based techniques begin by filtering water or scratching biofilms from surfaces of rocks. The LMW RNA fraction is extracted and purified as described in detail by Hoefle (1990a,b) and

Hoefle & Brettar (1996). The RNA is 3′end-labelled with 32P and analyzed by high-resolution acrylamide gel electrophoresis. Gels are incubated with X-ray film and the RNA banding pattern on the film is analyzed by computerized scanning. The film displays three distinct groups of bands caused by the different number of nucleotides of the 5S rRNA, class 1 tRNA and class 2 tRNA. These three classes of LMW RNA molecules form a pattern that is unique for every species and allows the identification of pure cultures to species level (Hoefle & Brettar, 1996).

In samples from natural communities, the whole LMW RNA pattern is usually too diverse, due to the overlay of several single patterns, so that it cannot be analyzed as a whole, as can be done for pure cultures. In such heterogeneous bacterial assemblages, the 5S rRNA pattern can be used as a first indicator of the diversity of the community. Assuming that every 5S rRNA band represents one species of the community, the number of the 5S rRNA band can indicate the number of species present and the intensity of the respective band the species' abundance. The ratio of 5S bands vs. the number of species can be checked by partial or total sequencing of the single 5S rRNA band. The 5S rRNA fraction of the LMW RNA profiles can be further used to identify single members of a natural community by sequencing their 5S rRNA and comparing with a known 5S rRNA database (Hoefle & Brettar, 1995).

Using the techniques described above, the overall community structure of bacteria can be analysed, which allows assessment of the dynamics of a specific community over space and time. In lotic environments, which are frequently disturbed, the study of microbial successions, e.g. after floods or downstream of a sewage outfall, might be of interest. Another field of research would be the assessment of the exchange of bacteria between various habitats. This would be of interest for safety reasons, e.g. for the exchange between a river and the adjacent groundwater aquifer that is used for the abstraction of drinking water. The transfer of pathogenic, or genetically engineered bacteria, could be shown using the new techniques. The same would be useful to prove the presence of bacteria with beneficial features, as the ability for nitrification and denitrification, or degradation of xenobiotics in groundwater.

In order to relate the taxonomic identification to the biogeochemical potential of the bacterial community, studies on the bacterial physiology are needed. However, this can only be achieved with culturable bacteria. As shown in a marine environment (Brettar & Hoefle, 1993), a specific species may have constant physiological features, which provide information on its biogeochemical potential in its habitat.

Many ecological questions focus on special 'ecofunctional groups', i.e. bacteria able to catalyze specific biogeochemical processes. As nitrogen is a matter of special concern for surface and groundwater, nitrifiers and denitrifiers can be regarded as 'ecofunctional' groups of prime interest. Their presence and proportion in the bacterial biocoenosis can be followed using the LMW RNA technique. If the ecofuntional group consists of only a few species, as assumed (e.g. for nitrifying bacteria), species-targeted single-cell detection techniques (e.g. fluorescent antibodies or oligonucleotide probing) can be applied (Gresikowski, Greiser & Harms, 1996). For ecofunctional groups such as denitrifiers whose species composition in an unstudied environment is hard to predict, antibodies or probes can be used that are specific for an enzyme that is crucial for the physiological pathway under consideration, e.g. nitrite reductase for denitrifying bacteria (Ward, Cockroft & Kilpatrick, 1993).

Single-cell detection techniques, such as fluorescent antibodies, allow detection of the cell directly in its environment. By using that technique, Gresikowski *et al.* (1996) and Schaefer & Harms (1996) could follow the distribution of nitrifying bacteria between water and suspended particulate organic matter in the River Elbe and River Ems in Germany. In this way, the ecological niche of a bacterial species in its environment can be studied (Brettar *et al.*, 1994).

In summary, a comprehensive study on the microbial community of a stream needs at least three levels:

1 the overall analysis of the community giving an overview on the diversity and identification of dominant species;

2 the strain level with the identification of strains and physiological work on relevant species and

3 the single-cell approach (e.g. fluorescent antibodies or molecular probes) to study the ecological niche of a specific species or ecofunctional group directly in the habitat.

The ultimate goal of this approach will be to identify the major bacterial catalysts of the biogeo-

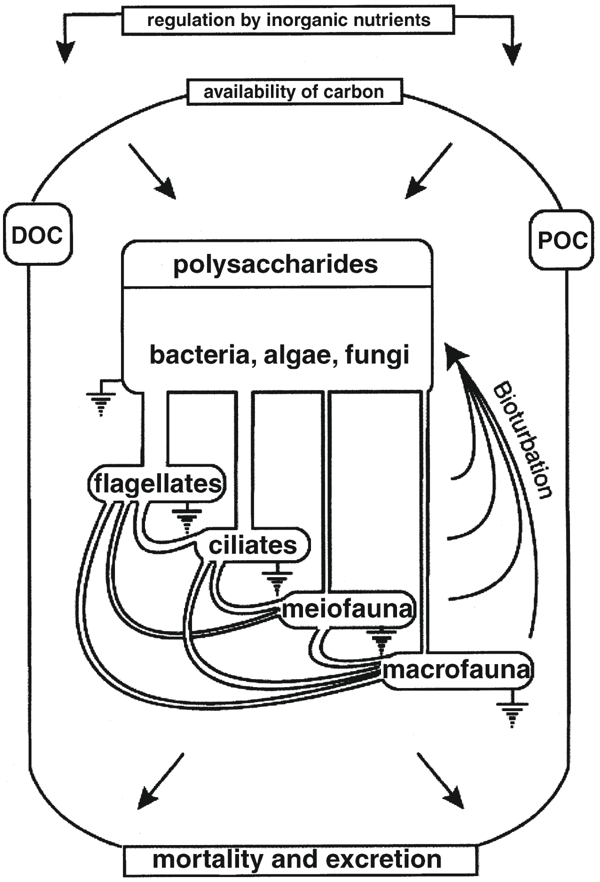

Fig. 6 Energy flow among trophic guilds and organic carbon resources within hyporheic food webs (the 'earth' symbol denotes respiratory energy loss) (redrawn from Eisenmann, 1998).

chemical cycle of matter (Hoefle & Brettar, 1995; Tiedje, 1995).

Transfer of organic carbon through the food web

The production of microbial biomass on the basis of the 'organic wastes' produced in food webs has been called the 'microbial loop' in the pathway of energy transfer through any ecosystem. Thus, organic carbon is not only transported through the food web via a cascade, but is continually resupplied to lower trophic levels. Their efficiency in the production of live, organic matter makes organoheterotrophic bacteria a valuable nutritional resource for higher organisms (cf. Farnleitner & Kasimir, 1996). This created a second mainstem in the foodweb, the 'detritus foodweb', which branches off the direct use of photosynthetic products. Bacterial cells are the potential objects of individual predation by other bacteria, by many groups of protozoa, and by specialized nematodes and rotifers (Fig. 5). Moreover, the bacterial biofilms on sediment surfaces are grazed by small crustaceans or insect larvae, suspended bacteria are actively filtered by rotifers and small mussels, and sediments are ingested as a whole by sediment collectors, like oligochaete worms (Fenchel, 1978, 1980; Montagna, 1995). Thus, the detritus pathway of energy transfer to higher trophic levels increases the productivity of the invertebrate and vertebrate fauna considerably. Predator–prey interactions involving macro-and meiofauna, protozoa and bacteria lead to complex regulatory cycles, and diverse patterns of carbon flow (Fig. 6). At present, we have only a poor understanding of these processes and their ecological implications (Meyer, 1990a), although there is some indication that groundwater bacteria might be heavily preyed upon by metazoan consumers (Kinner *et al.*, 1998; Ward *et al.*, 1998). Certainly the microbial loop must play some substantial role in the idea that riparian zones are hot spots of biodiversity and bioproduction.

Protozoa and other predators increase bacterial activity by the release of nutrients and growth factors, so that bacterial populations are kept in a more productive state (Clarholm, 1984; Elliott *et al.*, 1984; Giere, 1993; Ratsak, Maarsen & Kooijman, 1996). Moreover, metazoan faeces trigger a feedback pathway of energy flow, as these nutrient-rich particles are utilized by bacteria and other consumers (Shepard & Minshall, 1981; Wagner, 1991). Bioturbation can further enhance organic carbon transfer indirectly by redistribution of nutrients within the biofilm (Aller & Aller, 1992; Bak, van Duyl & Nieuwland, 1995). Excretion and mortality create further important loops in the flow of matter, especially at the microbial levels (Azam *et al.*, 1983; Capriulo, 1990; Meyer, 1990a). However, the analysis of the impact of grazing and excretion on bacterial productivity is complicated by the fact that only a minor fraction of about 10% of total interstitial bacteria seems to be metabolically active (Harvey & Young, 1980; Bott & Kaplan, 1985; Marxsen, 1988; Fischer *et al.*, 1996).

Prey availability is one of the main structuring factors in microbial food webs (Kemp, 1990). Bacteria develop defensive strategies against grazing, such as attachment, morphological adaptation (e.g. filamentous growth) or encystment. Interstitial habitats offer moreover a high variety of refugia in micropores or within the polysaccharide matrix of biofilms. Obviously, important interactions between prey and predators in porous systems are based on the high complexity of spatial structures (Eisenmann *et al.*, 1998). Highly diverse protozoan assemblages found on interstitial substrata incubated in rivers (Pratt, Horwitz & Cairns, 1987; Foissner, Unterweger & Henschel, 1992; Packroff, 1994) probably reflect numerous ecological niches generated by the great variety of microhabitats and differential prey availability.

Studies of the dynamics of micro-organisms and meiofauna in stream sediments are limited (cf. Schmid-Araya, 1994; Stanford *et al.*, 1994; Eisenmann *et al.*, 1997). Recent studies on the Flathead River (Montana, U.S.A.) (Ellis, Stanford & Ward, in press) and the Necker River (Switzerland) verified that the vast majority of micro-organisms are associated with sediment surfaces; suspended or free living bacteria were minor components of the interstitial microbial assemblage. Hence, exposing standardized substrata for colonization seems to be an appropriate way to obtain comparable data on interstitial communities in coarse sediments that cannot be sampled by simple coring. A colonization time of 4 weeks at minimum seems to be necessary in order to approximate equilibrium in microbial communities (Bott & Kaplan, 1985; Lamberti & Resh, 1985; Foissner *et al.*, 1992), which is clearly influenced by seasonal aspects and substratum characteristics. After retrieval of the substrata, the detachment of the mixed epilithic communities from the sediments for microscopic examination is a critical methodical step. Simple shaking of the sediments only will result in the detachment of the upper layer of the biofilm, while the more efficient technique of sonication destroys at least protozoan cells. After counting, the results can either be related to the surface area of the sediment particles that were examined, or to the sediment volume. On the basis of such investigations, not only the population dynamics of bacteria, protozoa and micrometazoa can be assessed. In addition, the grazing pressure of bacterivorous organisms can be estimated using specific grazing rates that are known from laboratory measurements (e.g. Bott & Kaplan, 1990; Epstein & Sharis, 1992; Borchardt & Bott, 1995; Eisenmann, 1998). These estimates may give some insight into the carbon flow through the foodweb of these interstitial habitats, which improves our understanding of riverine microbial ecology considerably.

Research needs and future directions

At least four general areas of research needs concerning the role of micro-organisms in modifying the connection of stream ecosystems to their catchments may be listed:

1 patterns of geological inputs of organic matter and energy;

2 the nature of biodegradable organic matter and its impact on ecosystem metabolism;

3 processes that occur at the particle surfaces or the liquid/solid interface; and,

4 the role of ecosystem level processes, such as organic matter decomposition on community and population level phenomena.

Our knowledge of how water moves through the riparian zones and the hyporheic zone is extremely limited. Even the sources and quality of DOC discharged through the riparian zone into running waters at baseflow are hardly known. Actual measurement of hydraulic conductivity and vertical hydraulic gradients are few, and these need to be connected with information on water quality changes within zones of active upwelling and downwelling. Therefore, the coupling of hydrological and biological investigations at the same study site is needed in more studies. The dynamics of water movement within the near stream environment will influence what microbial processes occur within that zone. Especially for biological research, present sampling methods of interstitial waters and sediments (e.g. standpipes, freeze-coring and exposed sieved sediments) have to be better developed, compared and evaluated (cf. Fraser & Williams, 1997; Mauclaire *et al.*, 1998). Biases related to substratum size and surface structure and artificial substratum (sterilized gravel, glass beads) require careful assessment. A special challenge will be the appropriate measurement of microbial activity in very dynamic areas of the riparian zones, like temporally saturated or unsaturated sediments and those with seasonal redox cycles.

Some data are available on the concentrations and composition of biodegradable organic matter (BOM) in streams, but the kinetic information needed appropriately to scale these measurements to the stream environment is missing. What, for example, is the distribution and residence time of BOM within a stream reach, and how does that impact the contributions of BOM constituents to stream ecosystem metabolism? What are the characteristics of DOM that make it susceptible or resistant to degradation, and do abiotic factors such as UV exposure play an important role in the conversion of refractory to labile organics? Such questions concerning the differential retention mechanisms for DOM and POM could partially be answered by conducting controlled experiments in large-scale flumes.

Catchments apparently have an organic matter signature that provides homing cues for migrating fishes (cf. Hasler & Wasby, 1951). To what extent does organic matter from a catchment provide a clue to the structure of the community of heterotrophic bacteria that use this energy source? Do changes in the quantity and quality of DOM from seasonal or hydrological influences bring about genotypic and phenotypic changes in microbial communities?

Particle surfaces, both in the seston and the benthos, are especially important sites of microbial activity and material transformation in streams. Despite of their biogeochemical importance, relatively little is known about the basic ecology of these bacteria (Leff, 1994). Other questions emerge in this regard. How does the magnitude of carbon cycling on particles compare with the activity supported by organic matter present in the water column (carbon spiraling)? What is the role of exoenzymatic transformation of POM to DOM to the flow of energy and carbon in stream ecosystems? Further attempts are also needed to separate different fractions of the hyporheic biofilm by visual (e.g. confocal laser scanning microscopy or photometry, Becker *et al*., 1997), physical (sonication), chemical or immunological (specific staining) methods. The use of specific dyes to stain the mucopolysaccharide matrix (Underwood, Paterson & Parkes, 1995) is a good example of methodological progress in the investigation of biofilm structure. Further progress is to be expected by the use of molecular-biological and molecular-genetic methods. The applicability and efficiency of methods for interstitial investigations that are possibly already being used in marine, lake or soil ecology should be tested for lotic interstitial studies. For example, the use of immunological or genetic markers to identify different taxonomic or physiological groups may provide needed insight on population dynamics, transport efficiencies and specific activity. The implications of microbial dynamics for higher trophic levels in the interstitial environment of riparian and hyporheic zones is a nearly virgin field of research.

Clearly, a more distant aim will be to derive and examine a general unifying theory on the microbial characteristics of hyporheic zones in different types of running waters. The hyporheic corridor concept (Stanford & Ward, 1993) appears like a robust approach to linking longitudinal changes to catchment characteristics. Does this idea apply across latitudes and biomes in a microbial ecology context? Is it testable? Surface–subsurface interactions in lowland streams, big rivers and in tropical streams are hardly known at present.

Finally, and perhaps most importantly, the cumulative effects of the growing human population on riparian interactions have urgently to be quantified. Unwise use of floodplains and channelization, which often results in river incision due to a lack of bedload/sediment, and dam building, clearly have severe implications for the sustainability of channel and floodplain functions and interactions, particularly the self-purification capacity (Vervier *et al*., 1993; Pusch, 1996; Claret, Marmonier & Braverd, 1998) mediated by interstitial micro-organisms.

Management implications and restoration

Functions of riparian zones in water management

Shallow aquifers in the alluvial sediment of river floodplains constitute the most important source of drinking water worldwide. This has certainly been one of the historical reasons for the common tendency of human populations to concentrate along river valleys. This source of drinking water seems almost unlimited, as it is not only refilled by precipitation and by lateral input from the hillslopes, but is additionally recharged by infiltration of river water through the riparian zone. In many cases, the river constitutes the steadiest and amplest recharge source, so that much of the drinking water that is produced as 'groundwater' in water works is really river water that has been underground for only a short time (e.g. in the

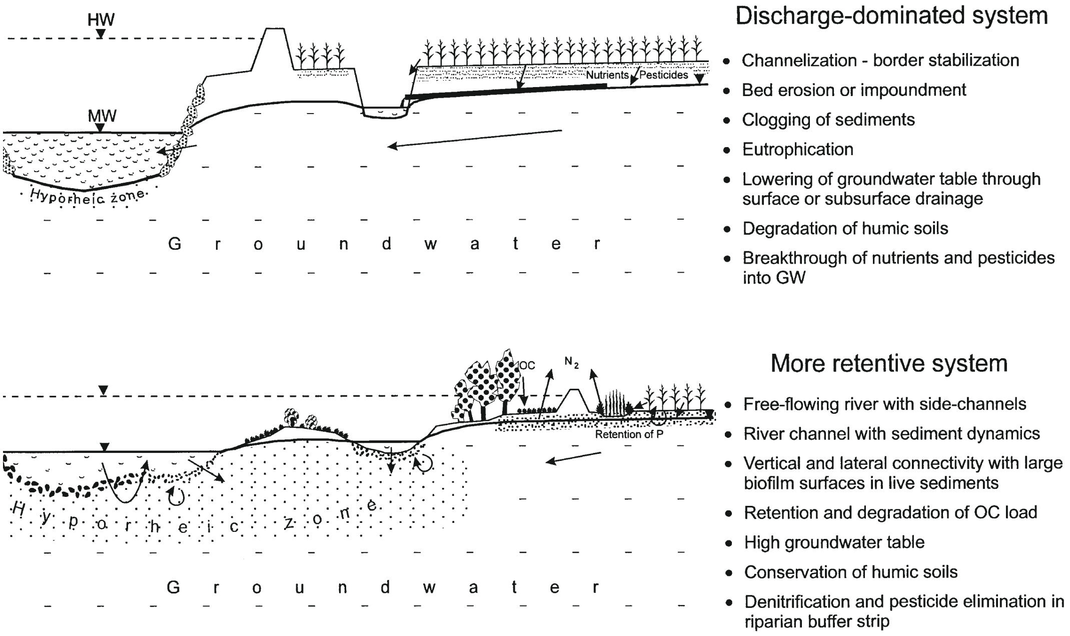

Fig. 7 Contrasting structure and function in two idealized river ecosystems with different water resource management regime (boxes).

German cities of Berlin, Frankfurt, Munich and in the Ruhr District).

Most rivers in densely populated regions now serve as a dilution medium and conveyor belt for untreated or treated liquid wastes. Hence, the re-use of river water for human consumption is only possible if it is naturally or mechanically purified. Riparian zones are focal sites for natural purification owing to the circulation of water through the vast internal surface area of alluvial sediments, either by infiltration into the hyporheic zone or by inundation of the floodplain (Sontheimer, 1991; McMahon & Boehlke, 1996). Suspended particles may be retained physically by the filtration effect of the subsurface sediments or by sedimentation on the floodplain. Dissolved substances may be efficiently adsorbed to interstitial biofilms, flocculate at sediment surfaces or be retained through complexation by humic substances (Sontheimer, 1991). Similar processes retain substances that reach the riparian zone as diffuse inputs from cropland as water moves from the uplands to the stream channel. As we have discussed in detail above, riparian zones sequester and transform organic matter and inorganic nutrients, largely due the activities of interstitial micro-organisms.

This biological self-purification effect in the riparian ecotone relates to the fact that most organic substances that are released by humans form energetic resources for bacteria, fungi or invertebrate animals. The biological decomposition of these substances is usually very effective, since the organisms are mostly attached to the solid surfaces of the sediment particles, forming a biofilm which efficiently interacts with the flowing water. Because bacteria can survive for extended periods in a dormant state, biofilms can react to immobilize even pulses of contaminants. Degradation efficiency is enhanced by the presence of anaerobic zones or pockets forming steep redox gradients. This enables the decomposition of compounds that are not accessible to microbial attack in aerobic conditions, such as nitrate transformation by denitrification in the presence of halogenated hydrocarbons and other organic matter supplied with the river water (Triska *et al.*, 1993; Freedman *et al.*, 1997; Claret *et al.*, 1998).

Similar mechanisms apply to the purification of water that drains diffusely from lateral hillslopes or terraces from densely populated areas or intenively farmed catchments. This runoff usually enters the alluvial sediments, where the riparian vegetation generally is very productive. The river may supply additional organic matter during the inundation phase, so that floodplain sediments and soils are highly enriched in organic matter. Oxygen supply in the saturated soils is limited. Hence, soil organic matter is decomposed by micro-organisms often using nitrate as terminal electron acceptor, resulting in the denitrification of water moving through the riparian zone toward the river (Peterjohn & Correll, 1984; Pinay & Décamps, 1988; Pinay *et al.*, 1990; Fustec *et al.*, 1991; Johnston, 1991; Bruesch & Nilsson, 1993; Faafeng & Roseth, 1993; Jones & Holmes, 1996; McMahon & Boehlke, 1996; Schroeder *et al.*, 1996; Claret *et al.*, 1998). Rates of nitrogen loss due to denitrification in natural wetlands average at about 0.1–0.2 $\text{mg m}^{-2}\,\text{yr}^{-1}$, removing 40–100% of subsurface inputs. However, in riparian forests adjacent to agricultural areas, denitrification rate may rise to more than 3 $\text{mg m}^{-2}\,\text{yr}^{-1}$, retaining 61% of inputs (Lowrance *et al.*, 1984). In contrast, phosphates predominantly enter running waters adsorbed to soil particles. Hence, aerobic soils vegetated by dense grasses are most efficient in phosphorus retention (61–83%; Osborne & Kovacic, 1993). In riparian wetlands, phosphorus net retention has been determined at about 0.2 $\text{g m}^{-2}\,\text{yr}^{-1}$, or 30–80% of inputs (Johnston, 1991). However, due to the episodic occurrence of soil erosion these numbers are subjected to considerable temporal variation.

In summary, riparian zones and floodplains contain a mosaic of soil and vegetation types above and below ground, including saturated soils with aerobic and anaerobic pore waters mediated by microbial activity. They are retentive systems ('landscape filters') that release water that is poor in suspended or dissolved constituents. However, these systems may be functionally overwhelmed by increased inputs of nutrients and by structural changes incurred during human use of the landscape (Lowrance *et al.*, 1984; Naiman & Décamps, 1990; Johnston, 1991; Henry & Amoros, 1995; Correll, Jordan & Weller, 1997).

Management problems in degraded floodplains – the case of the Upper River Rhine Valley (Germany). The alluvial sediments of the Upper Rhine Valley River in southern Germany, i.e. the 300 km of the river downstream of the Swiss border, form the largest aquifer in western Europe, which is now used heavily for drinking water supply. Until the first decades of the nineteenth century, the river channel was distinctively braided (in the upstream section) or meandering (in the downstream section). From 1815 to *c.* 1880, the river was subjected to the 'Rhine correction' engineered by Johann G. Tulla, which aimed to accelerate river discharge to facilitate the draining of the floodplain, to prevent floods and to gain arable land. The river channel was straightened artificially by the construction of groins in the bifurcation zone of the river and by cutting off the bends in the meandering zone. Additionally, the riverbanks were stabilized and levees built, so that the power of the river itself could be used to accelerate drainage (Kern, 1992; KHR-Arbeitsgruppe, 'Anthropogene Einfluesse auf das Abflussregime', 1993).

Some years after the completion of the 'Rhine correction,' substantial bed erosion of the river (river incision) in the upstream section of the valley and a concomitant large-scale lowering of the groundwater table of more than 10 m were observed. Thus, the original floodplain forest died and was replaced by a vegetation typical of semiarid landscapes. The new cropland in the floodplain was affected accordingly (cf. Bravard *et al.*, 1997). In 1932, the first impoundment for hydroelectric power generation and navigation purposes was built at the upstream end of the valley at Kembs, a prelude to a whole series of similar plants. It soon became apparent that the impoundments aggravated river management problems by retention of bed load, which accelerated erosion downstream. For example, after the construction of the seventh dam at Gerstheim, the riverbed 2.5 km downstream eroded up to 2.5 m in the first 15 months after the dam was closed, equivalent to a volume of 370 000 m^3 of sediment (KHR, 1993). Thus, environmental problems with the first dam produced hydrological arguments to build the next one downstream in order to stabilize the riverbed. This fundamental problem of river engineering has remained basically unresolved. The upstream section of the Upper Rhine Valley is now transformed into a chain of ten impoundments, with hydroelectric plants, navigation locks and huge levees.

Some of the water management problems that emerged there may be briefly summarized.

1 Downstream of the regulated river section (at the lower end of the Upper Rhine Valley), flood peaks have increased by 25% since 1882, due to the loss of floodplains, which formerly retarded the discharge and due to the fact that the flood peak of the River

Rhine and those of its main tributaries now arrive simultaneously (Kern, 1992; KHR, 1993).

2 Drinking water resources have diminished, because clogging of the bed sediments with fines deposited in the impoundments impedes recharge of the floodplain aquifer by river water (Trémolières *et al*., 1993).

3 Groundwater quality is now affected by heavy inputs of nitrate and pesticides released from highly fertilized cornfields and vineyards in the floodplain. This effect is aggravated by a loss of peaty soil through dewatering of the floodplain, thus allowing the rapid transit of anthropogenic substances to the groundwaters (e.g. Driescher & Gelbrecht, 1993).

4 Gravel bars that once mediated the microbial self-purification process have been removed from the river (Carbiener & Trémolières, 1990; Vervier *et al*., 1993). In the upper reaches of the Rhine in Switzerland, these effects are intensified by hydropower peaking, which heavily affects the biofilms on surficial sediments by causing rapidly fluctuating shear stress and by intermittent drying.

5 The original riverine fish assemblage has vanished, so that now omnitopic fish species as cyprinids dominate. The typical vegetation and fauna of the floodplain have retreated to small relict areas.

These and other human impacts have largely inactivated the natural ecological functions of the river floodplains. Pollution is transmitted downstream rather than being immobilized retained and transformed in the alluvium.

Modes of remediation. The free 'ecological services' provided by live river sediments and intact riparian zones in water management can only be restored if river dynamics are revived and the hydrologicaland ecological linkages between the river and its floodplain are restored (Kern, 1992; Osborne *et al*., 1993; Statzner & Sperling, 1993; Klein *et al*., 1994; Henry & Amoros, 1995) (Fig. 7).

The first task will be to stop bed erosion (incision) of the river, and to raise the water level of the river and in the floodplain aquifers (cf. Gore, 1985; Petersen, Petersen & Lacoursière, 1992; Dieplinger, Leberl & Zauner, 1996; Wissmar & Bestcha, 1998). Shallow step-weirs, constructed without impounding the river, and the addition of supplementary coarse bed-load may be required. Indeed, bed incision of the River Rhine below the most downstream dam at Iffezheim is now artificially offset by annual addition of 180 000 m^3 of coarse gravel as supplementary bed load (KHR, 1993). In a similar case on the River Danube near Vienna, bed erosion is being stabilized by the input of oversized boulders that are thought to 'armour' the river bottom (Dieplinger *et al*., 1996). However, these 'engineer's solutions' will not replace the natural ecological functions of intact riparian zones.

The second step is to re-establish the exchange of water, sediment, organic matter and other compounds between the river and the riparian zones of the floodplains (Stanford *et al*., 1996). Riparian buffer strips can be used to restore natural filtration (Petersen *et al*., 1992; Osborne & Kovacic, 1993). Levees should be removed and withdrawn to the edge of the lower terrace, as currently planned in a section of River Elbe (Germany) (Jaehrling, 1995). As a key measure to raise groundwater levels in the floodplain, the flow of river water into backwaters in the floodplain has to be re-established. These may serve as infiltration sites, flood retention areas and as valuable habitats for riverine species. This has already been accomplished to some degree on reaches of the lower Rhine (Germany) and Danube (Austria) rivers (Dieplinger *et al*., 1996).

In the case of the upper Rhine, parts of the floodplain have been re-opened by constructing retaining reservoirs, which are flooded at high stage of the river (Klaiber, 1996). However, in areas where the floodplain has already been transformed to farmland, human attitudes and cultures will have to embrace flood-tolerant agricultural uses. Hence, changes in navigation, hydroelectric power generation and farming of the riverine landscape will be inevitable, if restoration of an intact riparian corridor is the goal.

Restoration of hydrological linkages between the river and the riparian zone will bear dividends in the form of increased retention, storage and detoxification of pollutants, as mediated by the self-purification activity of biofilms within the natural mosaic of aerobic and anaerobic microzones of naturally functioning alluvial bed sediments. This revival of the biogeochemical functions of riparian zones does not necessarily mean a complete restoration of the historic riparian structures that once had existed. Neither does it necessarily require the expenditure of great financial resources, because the river can do most of the work (Stanford *et al*., 1996). The trick is teaching management how to use natural processes based on contemporary river ecosystem science (Statzner & Sperling, 1993; Statzner *et al.*, 1997).

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Regulation and Seasonal Dynamics of Extracellular Enzyme Activities in the Sediments of a Large Lowland River

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Abstract

We tested whether seasonal changes in the sources of organic substances for microbial metabolism were reflected changes in the activities of five extracellular enzymes in the eighth order lowland River Elbe, Germany. Leucine aminopeptidase showed the highest activities in the water column and the sediments, followed by phosphatase > β-glucosidase > α-glucosidase > exo-1,4-β-glucanase. Individual enzymes exhibited characteristic seasonal dynamics, as indicated by their relative contribution to cumulative enzyme activity. Leucine aminopeptidase was significantly more active in spring and summer. In contrast, the carbohydrate-degrading enzymes peaked in autumn, and β-glucosidase activity peaked once again in winter. Thus, in sediments, the ratio of leucine aminopeptidase/β-glucosidase reached significant higher medians in spring and summer (5-cm depth: ratio 7.7; 20-cm depth: ratio 10.1) than in autumn and winter (5-cm depth: ratio 3.7, 20-cm depth: ratio 6.3). The relative activity of phosphatase in the sediments was seasonally related to both the biomass of planktonic algae as well as to the high content of total particulate phosphorus in autumn and winter. Due to temporal shifts in organic matter supply and changes in the storage capacity of sediments, the seasonal peaks of enzyme activities in sediments exhibited a time lag of 2–3 months compared to that in the water column, along with a significant extension of peak width. Hence, our data show that the seasonal pattern of extracellular enzyme activities provides a sensitive approach to infer seasonal or temporary availability of organic matter in rivers from autochthonous and allochthonous sources. From the dynamics of individual enzyme activities, a consistent synoptic pattern of heterotrophic functioning in the studied river ecosystem could be derived. Our data support the revised riverine productivity model predicting that the metabolism of organic matter in high-order rivers is mainly fuelled by autochthonous production occurring in these reaches and riparian inputs.

Introduction

Bacteria in biofilms play a key role in the degradation and transformation of organic matter (OM) in rivers [18, 19, 43]. This OM originates from two main autochthonous sources, i.e. algal exudates and detritus [52], as well as from allochthonous sources, e.g. decaying, dissolved, and particulate material from terrestrial vascular plants [24, 55]. Only the dissolved fraction with low molecular weight can be directly utilized by bacteria [12]. The concentration of this low-molecular-weight dissolved organic matter (DOM) within the entire pool of OM is low; however, this fraction is mainly labile and turned over rapidly [21, 31]. Bacteria and other microorganisms gain access to this pool of OM by producing extracellular enzymes degrading high-molecular-weight OM [12]. Hence, the action of extracellular enzymes usually marks the first step in the microbial degradation of organic compounds. Additionally, the rate of enzymatic activity can limit the rate of substrate uptake by microorganisms and consequently their growth [11]. Extracellular enzymes are substrate specific, and hence the measurements of extracellular enzyme activities (EEA) provide insights into the specific functional profile of microbial communities [49].

Therefore, EEA have been widely studied in marine and limnetic waters [13, 28], and their role in OM cycling is well established [53]. Moreover, investigations have been conducted on EEA in river water [27, 50] as well as sediments of small streams [32, 44]. However, data on EEA in sediments of high-order rivers are rare

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[48]. In running waters, benthic (surface) and hyporheic (subsurface) sediments represent ecosystems with a large inner surface area and high storage capacity for OM [42]. Biomass and metabolic activities, including EEA, of the biofilm assemblages in these sediments greatly exceed those of the water column [46], even in higher order reaches [20]. Furthermore, there is some evidence that environmental factors controlling EEA are linked to quantity and quality of OM, which is in turn influenced by hydrological dynamics and sediment permeability in rivers [3, 44, 57]. In general, vertical water exchange between the surface (benthic) and the subsurface (hyporheic) sediments increases the intensity of aerobic microbial metabolism in stream sediments [17, 42]. In addition, temperature and pH directly influence EEA [10, 44].

The OM composition as well as temperature and pH vary seasonally under temperate climates. Algal exudates and detritus, which are found at relatively high levels in many temperate inland waters during spring and summer, seem to be easily degradable substrates and immediately available for bacteria in both the water column and sediments [1, 2, 44]. During autumnal leaf fall as well as floods, the input of allochthonous OM is high. Hence, during the year, material from various origins replenishes the sedimentary pool of OM.

Seasonal changes in specific OM are thought to be reflected by shifts in the relative contributions of individual enzymes to total EEA. Because allochthonous OM has higher C/N ratios than autochthonous OM [26], it is likely to provide better substrate conditions for carbohydrate than for protein-degrading enzymes. In addition, some evidence suggests that elevated activities of α- and β-glucosidase are closely related to bulk OM [6, 46]. In laboratory studies, leucine aminopeptidase (LAP) activity was seen to be closely related to the content of labile OM released by algae, and this indicates close algal–bacterial coupling [22]. A study on aggregate degradation showed a close link between protein content and peptidase activity; an inverse relation of phosphatase to individually organic phosphorus and labile organic phosphorus was found in lake sediments [38].

EEA have been studied in various scenarios including in interstitial waters of a temperate river [6], in epipsammic and epilithic biofilms of small streams under maritime and Mediterranean climate conditions [10, 44, 45], and on biofilms grown on artificial substrata [30]. However, information on the seasonal dynamics of specific extracellular enzymes in river sediments is both fragmentary and scarce. Here, we present the seasonal activity dynamics of an array of extracellular enzymes along with some of their potential substrates in a large lowland river in a temperate climate. EEA were measured both in near-shore sediments and in the water column to evaluate the connectivity of both ecosystem compartments. Overall, we tested whether:

1. the specific EEA show typical seasonal dynamics in the water column and in the sediments due to seasonal differences in environmental factors;
2. these dynamics can be explained based on the seasonally shifting availability of certain substrate compounds, which may be traced by standard particulate organic carbon (POC) quality parameters;
3. the seasonal patterns of EEA in the sediments exhibit a time lag with respect to those in the water columns because of temporal delay in OM supply.

Materials and Methods

Study Sites. The study sites were located in the River Elbe, an eighth order lowland river in Germany, at km 598 from its source near the town of Coswig, Germany (51°51′N, 12°28′E) [57]. The average longitudinal gradient in this river section is about 0.021%. The water quality is mainly influenced by mass developments of planktonic algae due to high nutrient loads (annual mean total nitrogen 4.36 mg L^{-1}, total phosphorus 0.25 mg L^{-1}). As the Elbe is a navigable river, the banks are protected by numerous stone groynes, which were built perpendicular to the flow direction at a distance of about 100 m from each other [57], to maintain a minimum water level for navigation during low water periods. The areas with reduced flow between the groynes, the so-called groyne fields, form a spacious habitat near the shore [9]. They represent artificial structures in the river that can be characterized by mostly plane sediment surfaces, reduced flow velocities of overlying water, and reduced transport of sediments compared to the mid-channel. Because of this, groyne fields are dominated by sedimentation processes, except for flood events. In general, the water in a typical groyne field is completely replaced by water from the river channel within 30–60 min at intermediate water level (mean discharge 337 m^3 s^{-1}; R. Schwartz, pers. comm.). Three neighboring groyne fields at km 598 were investigated in parallel [57]. In each of these, one central position at 12-m distance from the shore was sampled.

Sampling Procedure. Field samples were taken at monthly intervals from May 2001 to April 2002, except for January and February 2002, when major floods with a discharge of more than 760 m^3 s^{-1} and ice hindered access to the sampling sites. At each site, piezometers (steel pipes, internal diameter 5 cm) with perforations (5 mm) were inserted into the sediment down to two depth layers (0–5 and 15–20 cm). In this article, these depth levels are described as either 5 cm or surface sediments and 20 cm or subsurface sediments. For the collection of sediment, 10 L of interstitial water was extracted with a hand pump after discarding the first 2 L [5, 7]. The fine particle fraction of sediment passing through a 90-μm mesh net was filtered onto Whatman GF/F filters. This particle fraction of ~0.7–90 μm (d50 ranges between 3 and 8 μm in the Elbe) is moved by interstitial flow within the framework sediment [8] (M. Brunke, unpublished data) and is therefore referred to here as mobile fine interstitial particles (MFIP). Dry mass, POC, and particulate nitrogen (PN) contents were determined separately in the MFIP to examine their roles as substrate and/or colonization site. The coarse particle fraction of sediment >90 μm–5 mm, which contributed about 70% to mass of total sediment, is referred to here as sediment. Subsamples of sediment were taken to determine the contents of total POM, POC, and PN as well as bacterial abundance and activities of five extracellular enzymes. To detect total particle size distribution and the sorting coefficient $(d10/d60)^{0.5}$, complete sediment samples from each sampling site were taken with a sediment corer, dried at 105°C, and sieved through a standard set of sieves with mesh sizes decreasing from 20 mm to 63 μm. Interstitial water was collected by inserting a submersible electric pump with 90-μm mesh net immediately after the sediment samples were taken. In these samples, physicochemical variables (temperature, pH, dissolved oxygen), total phosphorus (TP), soluble reactive phosphorus (SRP), chlorophyll *a* (chl *a*), and phaeopigments were analyzed. Additionally, two samples of surface water were collected on each sampling date, and physicochemical variables, POC and PN contents, chl *a*, phaeopigments, bacterial abundance, and the activities of five extracellular enzymes were determined. All samples were immediately stored on ice until being processed in the laboratory within 20 h. From the results of POC and PN, the C/N ratio was calculated. The C/N ratio, the chl *a* content, and the chl *a*/phaeopigment ratio were taken as indicators of potential food quality of POC for destruents and consumers. The POC/chl *a* ratio was interpreted as an indicator of the origin of the POC, as high ratio indicates a high percentage of matter derived from allochthonous production. Additionally, low POC/chl *a* ratios indicated high-quality OM.

Chemical Analyses. Total phosphorus (TP) in surface and interstitial water was determined without filtration. Filtered (0.45-μm filters) water samples were taken to analyze SRP with the molybdenum blue method [37]. During the sampling period, SRP and TP concentrations were determined in March, April, June, October, November, and December. To assess chl *a* and phaeopigment contents in surface and interstitial water, samples were filtered onto glass fiber filters (Whatman GF/F) and subsequently frozen. Hot alcohol (90%, 78°C) was used for the extraction of phytopigments. After homogenization (Polytron PT 3000), extraction was continued for 12 h at room temperature in the dark. The samples were then centrifuged for 10 min at 2700 × *g*, and the clear extract was used for spectrophotometry (Shimadzu UV-2401 PC) according to standard methods [16].

OM in Seston, MFIP, and Sediment. Samples for POC and PN in surface and interstitial water and samples for chl *a* and phaeopigments in surface and interstitial water were filtered onto glass fiber filters (Whatman GF/F). Samples on filters as well as sediment samples were dried to constant weight at 105°C. Total POM was determined in sediment samples as ash-free dry mass. For that purpose, subsamples of 15–25 g wet weight were subsequently combusted for 6 h at 550°C. POC and PN content of dried samples were determined using a CNS analyzer (Vario EL, Elementar Analysensysteme GmbH). Dried sediment samples were ground prior to the analysis with an analytical ball mill (Pulverisette 6, Fritsch) for 15 min, and inorganic carbon was removed from seston, MFIP, and sediment samples with 1 M HCl. Triplicate subsamples of sediments were filled into cylindrical silver foil capsules (9-mm height, 5-mm diameter; Lüdi AG, Flawil, Switzerland), whereas duplicate subsamples of seston and MFIP filters were wrapped in aluminum foil for analysis. The calibration curve was established using acetanilide (limit of detection C < 0.004 mg; N < 0.004 mg). C/N ratios were calculated as molar ratios.

Bacterial Abundance. Bacterial abundance was determined in surface water and sediments. The subsamples for bacterial abundance were fixed in a sterile-filtered aqueous solution containing 3.5% formaldehyde, 0.85% NaCl, and 1 mM pyrophosphate (final concentration). After a 10-min sonication step and rigorous vortexing, supernatants of sediment subsamples were diluted again (dilution factor = 25). Samples for bacterial cell counts in sediments were taken from the supernatant; samples of surface water were used directly. Bacteria were stained using 4′,6-diamidino-2-phenylindiol (DAPI) [41] at a final concentration of 10 mg L^{-1}. After 40 min of incubation in the dark, bacteria were filtered onto black polycarbonate filters (Nuclepore, pore size 0.2 μm) and mounted on slides using antifading solution (AF1, Citifluor, London). At least 200 bacteria within 10 or more microscopic fields were enumerated by epifluorescence microscopy (Nikon FXA Microscope, HBO 100 W, Ex 330–380, DM 400, BA 400, immersion objective CF N DIC Plan Achromate 100×).

EEA. In this study, the term "extracellular enzymes" is used for all enzymes that act extracellularly including enzymes joined to bacterial cells and particles and also free enzyme particles dissolved in liquid phase.

Activities of LAP, phosphatase, β-D-glucosidase, α-D-glucosidase, and exo-1,4-β-glucanase were determined. LAP was selected to assess organic nitrogen decomposition, as it is involved in the final step of protein degradation, catalyzing a large number of peptides with an L-configuration [11]. Phosphatase cleaves polyphosphates and also orthophosphoric monoesters, both resulting in orthophosphate release [11]. The pH in the water column and sediments of the Elbe River is neutral (pH 7–9); therefore, probably a mixture of alkaline and acid phosphatase was determined. Exo-1,4-β-glucanase, β-glucosidase, and α-glucosidase are characterized as carbohydrate-degrading enzymes (CHDE). Exo-1,4-β-glucanase and β-glucosidase are involved in the degradation of cellulose [15], whereas α-glucosidase is active in the final step of amylose degradation.

The fluorogenic substrate analogs methylcoumarinyl (MCA) and methylumbelliferyl (MUF) substrates (Sigma) were used to measure the potential EEA (V_{sat}) in surface water and sediment [29, 33]. Three replicates and two controls were prepared from each sample. To measure EEA in surface water, 8 mL of surface water was used, and in sediment, 3 g of wet sediment (volumes were determined) was diluted with 8 mL of sterile filtered (0.2-μm pore size) interstitial water. After boiling the controls for 30 min, 1 mL of the substrate analog was added and given in saturation concentrations. Each enzymatic activity was then determined in saturation kinetics (sediment samples: LAP 400 μM, phosphatase 350 μM, β-glucosidase 320 μM, α-glucosidase 250 μM, exo-1,4-β-glucanase 250 μM; surface water samples: LAP 150 μM, phosphatase 150 μM, β-glucosidase 120 μM, α-glucosidase 120 μM, exo-1,4-β-glucanase 120 μM). All samples (replicates and controls) were incubated for 1–4 h at ambient surface water temperature under continuous shaking in the dark and then boiled for 3 min. Then 1 mL of 0.1 M alkaline glycine buffer (pH 10.0) was added to cooled samples. Finally, hydrolysis of the substrate analog was measured by determining the fluorescence of the supernatant (Shimadzu RF-5001 PC spectrofluorometer, 1.5 nm slit, 360-nm MCA/365-nm MUF excitation, 440-nm MCA/450-nm MUF emission). Standard MCA (7-amino-4-methyl-coumarin) and MUF (4-methyl-umbelliferone) solutions were used for calibration. The maximal reaction velocity activities (V_{sat}) were related to the volume of sediment or surface water (volume-specific EEA) and to bacterial cells (cell-specific EEA).

Short-Term Temperature Dependence of EEA. To obtain data on the short-term temperature dependence of each enzyme, three replicate sediment samples (mixed samples from the surface) and two controls were incubated with substrate analogs at saturation concentration for 1–4 h at six different temperatures (2.4, 7.1, 12.0, 17.0, 24.0, and 29.0°C) under continuous shaking in the dark. They were further processed as described above.

Statistical Analyses and Mathematical Calculations or Analyses of Data. Resulting data were transformed by the natural logarithm to achieve normal distribution. Paired *t*-tests were used to analyze differences between 5- and 20-cm sediment depth for microbial and environmental data. Seasonal variations were assessed using one-way analysis of variance (ANOVA) followed by Tukey's test. Percentages of EEA in cumulative EEA were transformed by the arcsin before using ANOVA [58]. Spearman rank correlation coefficients (r_s) were used to examine the relationship between EEA and environmental data. In addition, we calculated normalized cell-specific EEA for 20°C using the regression equations from experiments on the short-term temperature dependence of EEA. Statistical analyses were performed with software package SPSS 9 (SPSS Inc., Chicago, IL, USA).

Results

Physicochemical Conditions. During sampling, river discharge peaked in July and September 2001 as well as in March 2002 (Table 1). The particle composition of the nearshore sediments was characterized by d10 = 0.59 ± 0.07 mm, d50 = 3.4 ± 0.9 mm, and d60 = 4.4 ± 1.0 mm and a sorting coefficient of 0.37 ± 0.04 (mean ± SD, n = 3). About 70% of the sediment was smaller than 5 mm, the upper limit of the sampled fraction. Dissolved oxygen (DO) concentrations were significantly higher, and pH values and conductivity were slightly higher in the water column than in interstitial waters (Tables 1, 2). DO showed a significant vertical gradient in the sediments between 5- and 20-cm sediment depth during some warmer months (May, June, August). The conductivity ranged from 381 to 498 $\mu S\ cm^{-1}$ in the water column and from 369 to 491 $\mu S\ cm^{-1}$ in the sediments. The content of TP was significantly higher in interstitial waters than in the water column in November, December, March, and April. In interstitial water, TP concentrations peaked in November and December and reached their lowest in June and October, when the discharge was also lowest (Tables 1, 2).

OM in Seston, MFIP, and Sediment. The POC and PN concentrations in the water column were highest from April until August and lowest from September until March, with the C/N ratios being vice versa (Table 1). The concentration and quality of MFIP, as reflected by their dry mass, contents, and percentages of POC and PN, were significantly higher in surface than in subsurface sediments ($p < 0.05$; paired *t*-test). In surface sediments, the seasonal dynamics of MFIP showed some similarity to that of seston, with high values of dry mass

Table 1. **Discharge, physicochemical, and biological variables in the water column in the Elbe River at Coswig during the sampling period May 2001–April 2002 (mean, *n* = 2)**

	May 01	*Jun 01*	*Jul 01*	*Aug 01*	*Sep 01*	*Oct 01*	*Nov 01*	*Dec 01*	*Mar 02*	*Apr 02*	*Annual median*
Discharge ($m^3 s^{-1}$)	300	225	523	274	527	258	410	355	587	417	341
Temperature (°C)	18.8	22.0	22.0	20.9	14.8	15.6	5.8	2.0	8.0	13.0	11.4
pH	9.47	8.83	7.82	8.30	7.70	7.70	7.55	7.63	7.91	8.7	7.8
Dissolved oxygen concentration (mg L^{-1})	9.3	9.9	10.6	9.1	8.1	9.0	11.5	11.4	11.9	12.9	11.0
Orthophosphate (mg L^{-1})	45	75	140	140	125	129	98	75	51	19	76
Total phosphorus (mg L^{-1})	240	300	290	260	290	208	199	184	147	200	203
Dissolved organic carbon (mg L^{-1})	7.0	6.0	6.5	6.6	6.7	5.6	5.8	6.3	5.4	5.4	6.3
Seston dry mass (mg L^{-1})	41.0	33.8	38.0	21.6	50.0	32.7	21.2	15.3	26.6	31.4	29.0
POC seston (mg L^{-1})	9.1	7.5	8.3	5.2	4.4	4.0	4.0	1.6	4.7	6.9	4.5
PN seston (mg L^{-1})	1.30	1.06	1.19	0.70	0.52	0.47	0.43	0.29	0.44	0.93	0.54
C/N ratio seston	7.0	7.1	7.0	7.4	8.6	8.5	9.5	10.3	10.7	7.5	8.5
Chl *a* (μg L^{-1})	237.2	56.8	64.9	66.8	13.1	29.4	7.2	4.38	46.2	172	37.8
Phaeopigment (μg L^{-1})	29.0	26.4	44.9	23.6	8.5	8.5	6.8	4.6	6.5	12.8	8.5
Chl *a*/phaeo ratio	8.2	2.2	1.4	2.8	1.5	3.5	1.1	1.0	7.1	13.5	1.8
POC/Chl *a* ratio	38.5	63.0	128	77.9	236	191	554.0	365	102	40.0	160
Bacterial abundance (10^6 cells mL^{-1})	8.7	7.1	8.3	6.1	5.4	5.2	4.1	5.0	5.1	7.0	5.3

and content of POC and PN in August, but which persisted also through September and October (Table 2). The C/N ratio in MFIP of subsurface sediments was consistently higher than that of surface sediments, with the exception of the time after the flood in July 2001, when probably allochthonous POM with a high C/N ratio was entrained into the river and its surficial sediments. The percentages of PN and POC in dry mass of MFIP exhibited highest values in May and June, indicating a highly labile nature of MFIP at that time. The percentage of POC was 9.5–37 times higher in MFIP than in the sediments, and the percentage of PN 40–94 times higher.

Sediments (particle size 90 μm–5 mm) generally exhibited low organic contents. Significantly higher contents of total POM, POC, and PN in sediment dry mass were found in 5-cm compared to 20-cm sediment depth. The vertical gradient in POM content was steepest from August through October. In spring and summer, the C/N ratios were lower in the water column than in the sediments.

Chl a and Phaeopigment Concentration, POC/Chl a Ratio. Chl *a* and phaeopigments were enriched in interstitial waters compared to the water column (Tables 1, 2). In interstitial water, the chl *a*/phaeopigment ratio was significantly lower, indicating chl *a* degradation. Contents were generally higher in 5-cm sediment depth than in 20-cm depth. In the water column, chl *a* was significantly higher in spring and summer (March to August) than in autumn and winter (September to December, Table 1). Algal spring blooms occurred in May 2001 and April 2002. In interstitial waters, the duration of the peaks in chl *a* and phaeopigment concentrations were extended compared to the water column. These variables were significantly higher in May, August, and September than in November and December (Table 2). In general, the POC/chl *a* ratios were higher in the sediments than in the water column, with similar seasonal dynamics in both compartments. POC/chl *a* ratios were significantly lower from March to August than from September to December (Tables 1, 2), with the exception of July, suggesting a higher proportion of allochthonous sources in total POM from September to December, and during the flood event in July.

Bacterial Abundance. The abundance of bacteria in sediments was 150–215 times higher than in the water column (Table 1). In the water column, bacterial abundance was significantly higher in summer than in autumn and winter (Table 1). In surface sediments, bacterial abundance peaked from August to October, and in subsurface sediments, it peaked in August. In both sediment layers, bacterial abundance was lowest during the July flood and in November and December (Table 2).

Table 2. Physicochemical and biological variables of the interstitial water and sediment in the Elbe River during the sampling period May 2001–April 2002 (median, $n = 3$)

	May 01		*Jun 01*		*Jul 01*		*Aug 01*		*Sep 01*		*Oct 01*		*Nov 01*		*Dec 01*		*Mar 02*		*Apr 02*		*Annual median*	
Sediment depth (cm)	*5*	*20*	*5*	*20*	*5*	*20*	*5*	*20*	*5*	*20*	*5*	*20*	*5*	*20*	*5*	*20*	*5*	*20*	*5*	*20*	*5*	*20*
Temperature (°C)	18.0	17.6	20.7	19.3	22.8	22.8	21.2	20.9	14.5	14.8	15.4	15.3	5.6	5.7	3.5	3.4	8.1	7.8	14.2	13.4	14.4	14.4
pH	8.1	7.3		7.2	6.8	6.7	7.5	7.2	7.4	7.3	7.2	7.2	7.3	7.2	7.0	7.0	7.6	7.6	7.5	7.3	7.4	7.2
Oxygen concentration (mg L^{-1})	5.3	2.4		1.2	6.7	6.1	4.8	2.0			4.5	4.0	10.1	9.7	3.8	4.7	5.2	4.4	4.3	3.2	5.0	4.1
Orthophosphate (mg L^{-1})				120							107	96	99	73	86	95	98	102	62	73		
Total phosphorus (mg L^{-1})				270							1239	185	7773	9881	8711	4175	466	1221	2714	2300		
MFIP dry mass (mg L^{-1})	565	986	444	246	954	721	1452	635	1357	566	1638	470	793	360	881	784	305	192	504	231	697	493
POC MFIP (mg L^{-1})	46	84	33	20	61	48	88	48	78	42	82	33	53	25	55	48	20	17	35	17	50	40
PN MFIP (mg L^{-1})	5.4	0.9	3.8	1.9	6.5	4.7	7.6	4.8	9.0	4.2	8.0	3.2	5.1	2.2	5.9	4.0	2.0	1.4	3.6	1.5	5.2	3.8
C/N ratio MFIP	8.6	9.2	8.5	9.4	9.4	9.2	9.7	9.4	8.9	10.0	9.6	10.6	10.3	10.6	9.4	10.4	9.8	10.0	9.6	9.9	9.4	10.0
Chl *a* (µg L^{-1})	157	163	120	29	78	90	151	120	186	111	66	28	51	21	42	16	99	87	225	107	82.4	36.8
Phaeopigment (µg L^{-1})	211	195	118	18	42	88	377	231	409	404	176	62	79	31	116	68	28	18	102	31	115.7	65.1
Chl *a*/Phaeo ratio	0.85	0.88	1.00	1.92	2.20	1.03	0.64	0.58	0.50	0.46	0.54	0.47	0.80	0.63	0.42	0.43	2.80	3.41	2.20	1.51	0.68	0.61
POC/Chl *a* ratio	260	290	400	600	780	920	620	170	1110	310	740	880	730	1210	1990	5180	220	280	180	360	580	670
Total POM (% dry mass)	0.65	0.56	0.54	0.46	0.51	0.45	1.21	0.66	1.03	0.48	2.43	0.79	0.60	0.50	0.80	0.52	0.77	0.57	0.81	0.46	0.79	0.52
POC sediment (% dry mass)	0.29	0.27	0.30	0.20	0.21	0.16	0.69	0.33	0.57	0.20	1.53	0.44	0.26	0.21	0.36	0.22	0.38	0.26	0.40	0.16	0.39	0.22
PN sediment (% dry mass)	0.016	0.011	0.010	0.008	0.012	0.010	0.017	0.017	0.029	0.011	0.042	0.013	0.012	0.011	0.014	0.010	0.013	0.010	0.017	0.011	0.017	0.010
C/N sediment	25.9	24.9	31.9	23.8	19.1	16.6	27.1	26.9	17.9	18.1	28.7	35.1	17.9	19.6	24.3	29.9	29.3	27.2	23.4	15.4	24.3	24.3
Bacterial abundance (10^9 cells cm^{-3})	1.30	1.03	1.34	0.81	0.67	0.64	1.70	1.31	1.60	0.85	1.87	1.08	0.65	0.69	0.98	0.77	1.28	1.00	1.05	1.02	1.24	0.92

Bacterial abundance was significantly higher in 5-cm than in 20-cm sediment depth ($p < 0.05$, paired t-test). Particularly steep vertical gradients in bacterial abundance were found from August through October, when also the POM content of these two sediment layers differed largely.

EEA

Spatial Pattern of EEA. EEA per volume were 80–550 times higher in sediments than in the water column (Figs. 1, 2). Also, the cell-specific EEA were 1.5–3.5 times higher compared to the water column, except for cell-specific LAP activity, which was only one half of that in the water column. The relative activity levels of the various enzymes were similar in the water column and in the sediments. LAP showed the highest absolute potential of activities (V_{sat}), followed by phosphatase > β-glucosidase > α-glucosidase > exo-1,4-β-glucanase.

In general, EEA were mostly significantly higher in surface than in subsurface sediments (by about 21–46%, $p < 0.05$, paired t-test), which can be attributed to higher values between May and October. CHDE showed activity peaks in August and September in surface sediments, but not in subsurface sediments (Figs. 2b–d). In surface sediments, the activity ratios of LAP/CHDE (β-glucosidase, α-glucosidase, exo-1,4-β-glucanase) were significantly lower than in subsurface sediments (paired t-test, $p < 0.05$, Figs. 2a–d), indicating a significantly steeper vertical gradient in the sediments for CHDE compared to LAP (paired t-test, $n = 30$; $p < 0.05$).

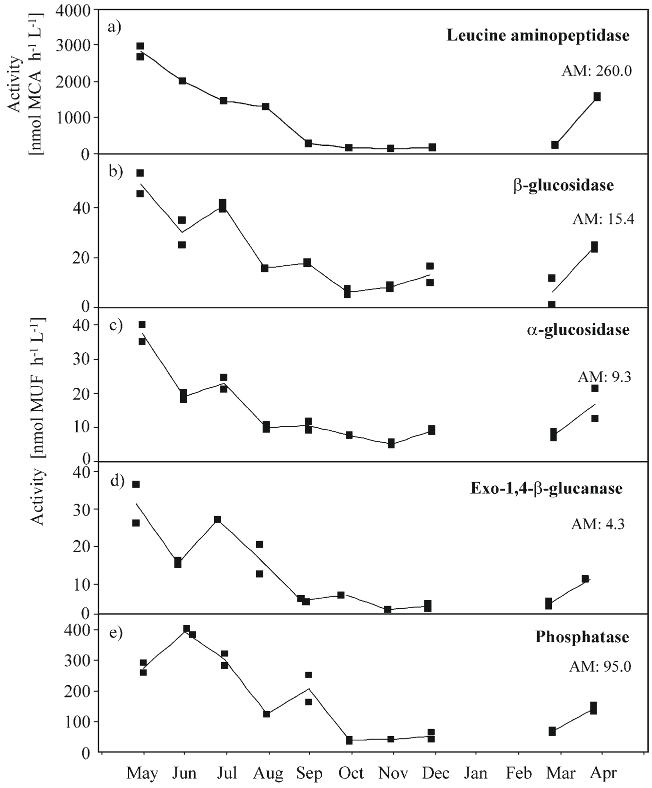

Figure 1. Extracellular enzyme activities in the water column. Monthly means (line, $n = 2$) and the annual median (AM) are given.

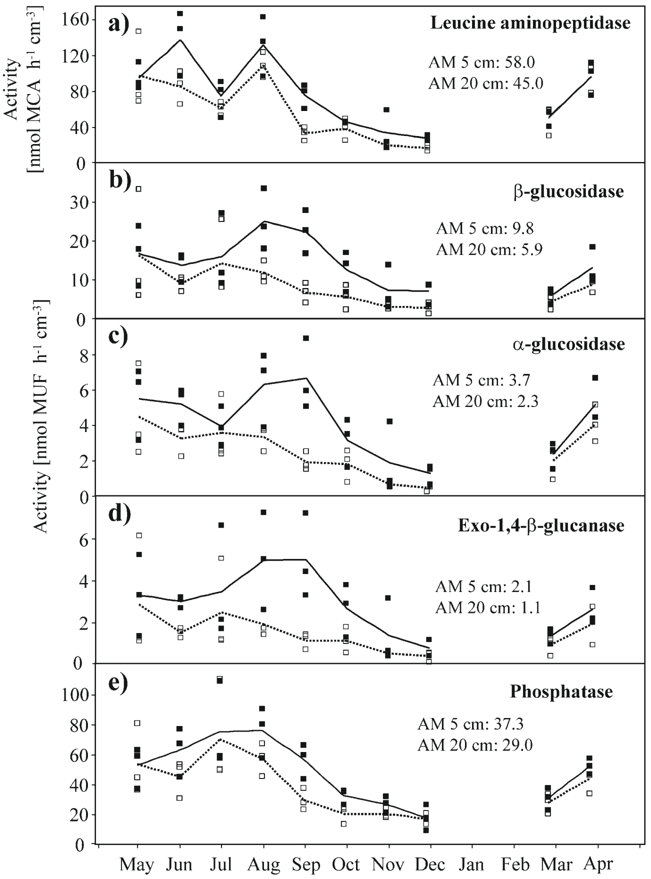

Figure 2. Extracellular enzyme activities in the sediments at 5-cm sediment depth (■) and 20-cm sediment depth (□). Monthly means at 5-cm sediment depth (*drawn through line*, $n = 3$) and at 20-cm sediment depth (*dashed line*, $n = 3$) and annual medians (AM) are given.

Seasonal Dynamics of EEA. Both volume- and cell-specific EEA showed significant seasonal dynamics in the water column (Fig. 1) as well as in surface (5-cm depth) and subsurface sediments (20-cm depth; Table 3, Fig. 2). The medians of EEA were 63–91% (water column) and 57–82% (sediments) higher during the warmest months (May–August) than during the coldest months (November–March). EEA peaked from May until July in the water column (Figs. 1a–e), whereas in surface sediments, elevated activities persisted through September (Figs. 2a–e), and for CHDE even through October (Figs. 2b–d). Highest total CHDE activity in surface sediments was found in August and September (Figs. 2b–d), whereas LAP peaked in earlier months (Fig. 2a). Significantly, lowest EEA were found from October until March in the water column and from November until March in the

Table 3. One-way analysis of variance (ANOVA) testing the seasonal differences (*df* = 3) of extracellular enzyme activity in sediments (5- and 20-cm depth combined; *n* = 60)

Extracellular enzyme activity	*F-value*	*p-Value*	*Significant differences in absolute EEA between the seasons*
Leucine aminopeptidase	27.9	<0.0001	Spring and summer > autumn and winter
Phosphatase	26.7	<0.0001	Spring and summer > autumn and winter
β-Glucosidase	9.8	<0.0001	Summer > autumn and winter; spring > winter
α-Glucosidase	12.7	<0.0001	Spring and summer > autumn and winter
Exo-1,4-β-glucanase	7.5	<0.0001	Spring, summer, autumn > winter

sediments. The seasonal dynamics of cell-specific EEA showed many similarities to that of volume-specific EEA. Cell-specific EEA in both habitats peaked in July, when bacterial abundance was lowest, then decreased sharply in October. After which, cell-specific EEA generally exhibited its lowest values from October until December.

Percentages in Cumulative EEA. We found significant seasonal differences in the percentages of EEA in cumulative EEA in the sediments and in the water column (Table 4, Figs. 3, 4,). Because of the distinct seasonal dynamics of LAP and β-glucosidase, the LAP/β-glucosidase ratios in the water column were significantly higher in spring and summer (median 6, range 36–280) than in autumn and winter (median 16, range 14–29). In the sediments, this ratio was also significantly higher in spring and summer (surface: median 7.7, range 5.4–10.1; subsurface: median 10.1, range 8.0–11.7) than in autumn and winter (surface: median 3.7, range 3.4–5.0; subsurface: median 6.3, range 5.1–8.1). The percentages of LAP in sediments were positively correlated with the chl *a*/phaeopigment ratio ($r_s = 0.48$, $n = 60$, $p < 0.0001$) and negatively with the C/N ratio of MFIP ($r_s = 0.30$, $n = 60$, $p < 0.05$) and the POC/chl *a* ratio ($r_s = 0.54$, $n = 60$, $p < 0.01$). Thus, elevated LAP activity was related to the presence of fresh autochthonous OM rich in nitrogen. The percentages of β-glucosidase activity in sediments were significantly related to the content of sedimentary POC ($r_s = 0.75$, $n = 60$, $p < 0.0001$) and also to the dry mass of MFIP ($r_s = 0.58$, $n = 60$, $p < 0.0001$). The percentages of phosphatase were positively correlated to TP content ($r_s = 0.42$, $n = 33$, $p < 0.05$) and to discharge ($r_s = 0.38$, $n = 60$, $p < 0.01$).

Table 4. One-way analysis of variance (ANOVA) testing the seasonal differences (*df* = 3) of percentage of extracellular enzyme activity in cumulative activity in sediments (5- and 20-cm depth; without EEA of July; *n* = 54)

Extracellular enzyme activity	*F-value*	*p-Value*	*Significant differences in the percentage of EEA between the seasons*
Leucine aminopeptidase	6.8	<0.0001	Spring and summer > autumn and winter
Phosphatase	3.3	<0.01	Autumn and winter > spring and summer
β-Glucosidase	3.5	<0.01	Autumn and winter > spring and summer
α-Glucosidase	3.2	<0.05	Spring > winter
Exo-1,4-β-glucanase	3.0	<0.05	No significant differences

Short-Term and Seasonal Temperature Dependence of EEA. We found a linear temperature dependence of all V_{sat} over a range from 2.0 through 29.0°C instead of an exponential relationship both in the short-term experiments and in seasonal field measurements (Table 5). The regression between temperature and EEA obtained in the short-term experiments reached higher coefficients of determination ($r^2 = 0.84$ for exo-1,4-β-glucanase and $r^2 > 0.90$ for all other enzymes) than that in the seasonal field measurements ($r^2 = 0.30$–0.60). The activation energies of all measured enzymes calculated from the Arrhenius regression of the temperature/activity relationship were linear from 2.0 through 29.0°C, but lower for the seasonal relationship than of short-term relationship (Table 5).

Relationship between EEA and Environmental Variables. Spearman rank correlations showed that environmental variables influenced the EEA significantly,

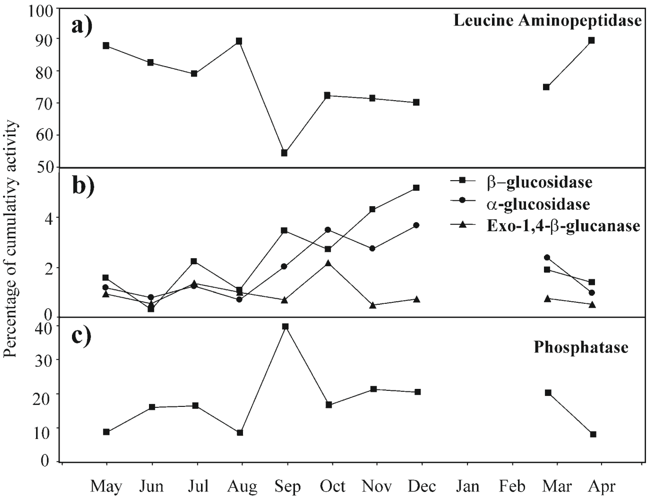

Figure 3. Percentages of extracellular enzyme activities in cumulative activity in the water column (means, *n* = 2).

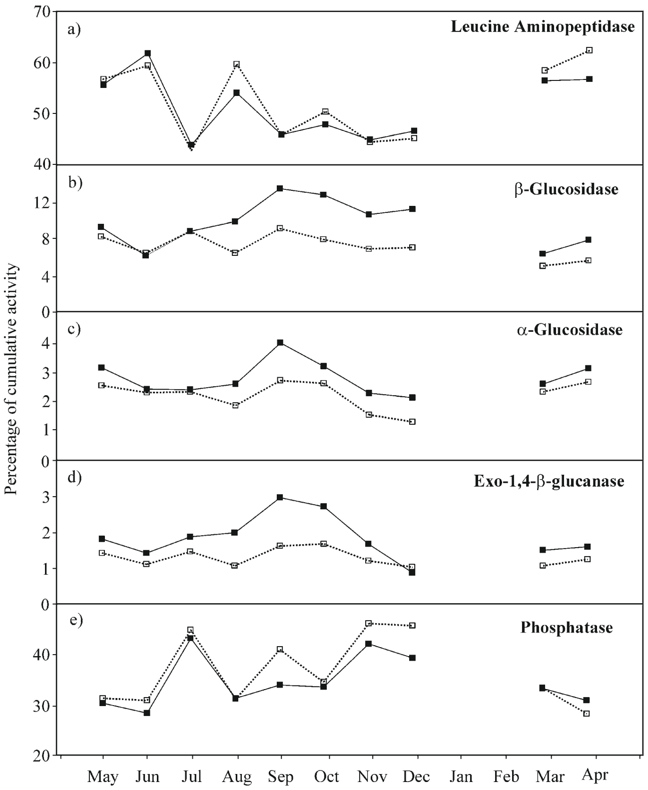

Figure 4. Percentages of extracellular enzyme activities in cumulative activity in the sediments at 5-cm sediment depth (■) and 20-cm sediment depth (□) (medians, $n = 3$).

but there were characteristic differences between individual EEA and also between habitats (Tables 6, 7). All specific EEA correlated highly significantly, besides with temperature, also with bacterial abundance both in the water column and in the sediments. In the water column, EEA, particularly LAP, correlated significantly with pH, but not in the sediments.

In the water column EEA correlated also closely with variables of substrate quantity and quality such as POC and PN in seston, phaeopigments, and chl *a* along with the C/N ratio. These variables of substrate quantity and quality also correlated closely with each other ($r_s \geq 0.77$, $n = 20$, $p < 0.01$). In sediments, the correlations of EEA with substrate parameters were generally weaker, although significant, which was probably because of higher amounts of refractory OM in sediments. In sediments, activities of CHDE correlated significantly with the POM (POC, PN) content in MFIP and in sediments, and with phaeopigments, which again showed a close relationship of CHDE to total POM. Also, POC and PN in MFIP correlated closely with each other ($r_s = 0.96$, $n = 60$, $p < 0.001$) as well as total POM, POC, and PN in the sediment ($r_s = 0.83$, $n = 20$, $p < 0.001$). LAP correlated strongest with the C/N ratio in MFIP, POC/chl *a* ratio ($r_s = -0.54$, $n = 60$, $p < 0.01$), and the chl *a*/phaeopigment ratio ($r_s = 0.38$, $n = 60$, $p < 0.01$), which demonstrated the close relation of this enzyme to high-quality OM. In the data set of cell-specific EEA normalized for 20°C using the laboratory results on temperature dependence, the influence of other environmental variables, in particular, of OM variables on EEA, can be seen more clearly, as the influence of seasonal temperature dynamics and bacterial abundance is eliminated (Table 8). Exo-1,4-β-glucanase and β-glucosidase correlated significant with total POM and PN content of sediment, whereas LAP correlated significant with chl *a*/phaeopigment ratio and POC/chl *a* ratio. Phosphatase correlated significantly with total phosphorus content, chl *a*/phaeopigment ratio, and C/N ratio.

Discussion

Control of EEA by Temperature and pH Dynamics. Temperature exerts a direct physiological control on EEA [36, 47], which was also shown by our short-term temperature/activity relationship. In seasonal field studies, this physiological relationship may be partially masked by community succession and numerical response [2] but was also significant. In the temperature range 2–29°C, we found a linear temperature/activity relationship

Table 5. Regression statistics for the temperature dependence of enzyme activities in the short-term experiments and in the seasonal field study

	Short-term temperature/activity relationship					*Seasonal temperature/activity relationship*				
	Linear regression of V_{sat}					*Linear regression of V_{sat}*				
Enzyme	*Slope*	*Intercept*	*r^2*	*AE (kJ mol^{-1})*	*r^2*	*Slope*	*Intercept*	*r^2*	*AE (kJ mol^{-1})*	*r^2*
Leucine aminopeptidase	2.7	8.9	0.97	48	0.98	4.4	14.5	0.50	44	0.62
β-Glucosidase	0.58	0.36	0.91	53	0.95	0.66	4.5	0.32	38	0.40
α-Glucosidase	0.2	0.45	0.93	58	0.97	0.2	1.1	0.50	50	0.53
Exo-1,4-β-glucanase	0.18	(−)0.4	0.84	76	0.95	0.15	0.66	0.30	54	0.47
Phosphatase	1.9	6.45	0.96	47	0.98	2.6	11	0.60	42	0.69

Linear regressions of V_{sat} on incubation temperature in °C and activation energy (AE), which were calculated from an Arrhenius regression, i.e. plotting log EEA *versus* incubation temperature as 1 per unit Kelvin.

Table 6. Spearman rank correlation coefficients (r_s) between microbial and environmental variables in the water column ($n = 20$)

Environmental/microbial variables	*Bacterial abundance*	*LAP*	*Phosphatase*	*β-Glucosidase*	*α-Glucosidase*	*Exoglucanase*
Temperature	0.65**	0.75**	0.76**	0.60*	0.72*	0.76**
pH Value	0.75**	0.91**	0.68**	0.64*	0.71**	0.78**
POC in seston	0.90**	0.91**	0.76**	0.67*	0.71**	0.86**
C/N ratio of seston	−0.86**	−0.69**	−0.52*	−0.64**	−0.74**	−0.91**
Chl *a*	0.84**	0.87**	0.60*	0.65**	0.70**	0.87**
Bacterial abundance	0.93**	0.84**	0.88**	0.95**	0.95**	

* $p < 0.05$.
** $p < 0.01$.

both for seasonal and short-term data set and no change in the interactive structure of investigated enzymes according to the Arrhenius regression. Activation energies of all investigated enzymes were lower in the seasonal relationship compared to the short-term relationship, which was probably because of seasonal stimulation of EEA by changes in OM supply and bacterial community composition. In some studies, temperature was considered to be a primary factor governing biofilm activities mainly in nutrient-poor streams [25, 39], which is thought to be due to temperature stimulation of algal growth, and to a lesser extent in mesotrophic and eutrophic streams and rivers [30, 49]. This implies that substrate availability—and not temperature—was the primary factor controlling EEA. Our results did not support this view, as temperature directly influenced all investigated EEA in our short-term experiments conducted under conditions of substrate saturation in the sediments. Surprisingly, we found linear temperature dependencies for all EEA between 2 and 29°C instead of an exponential curve with a uniform Q 10 value. This suggests a higher Q 10 value at lower temperatures (2–12°C) than at higher temperatures (12–22°C).

The activity of the studied enzymes is positively pH dependent (Bittl, 1999, thesis). Hence, the significantly higher pH during high autotrophic production in the water column may have increased EEA during spring to some extent. In lake water, activities of LAP and β-glucosidase exhibited an optimum at pH 8 [11] (Bittl, 1999, thesis), which is consistent with our findings. The positive correlation between phosphatase activity in the water column and pH values indicated that this activity was dominated by alkaline phosphatase rather than acid phosphatase.

Spatial Distribution and Temporal Dynamics of EEA. Because of the higher OM content and the higher bacterial abundance, the volume-specific and cell-specific EEA in the sediments greatly exceeded that of the water column in the Elbe River, with the exception of cell-specific LAP activity, which is probably more dependent on readily usable OM. Within the sediments, the EEA were significantly higher in surface (5-cm depth) than in subsurface sediments (20-cm depth) because of higher POM quantity and quality (indicated by higher chl *a* content and lower POC/chl *a* ratios) and higher DO content in surface sediments. As OM in sediments is subjected to diagenetic alteration, EEA was there even more directly controlled by the quality of OM than in the water column. The activities of CHDE (β-glucosidase, α-glucosidase, exo-1,4-β-glucanase) decreased vertically more steeply with depth than that of LAP (utilizing organic nitrogen from macromolecules). A similar vertical shift of the activity ratio of protein/CHDE corresponding with the changing composition of degradable OM was found in marine sediments [14, 40].

Absolute EEA were generally higher during the warmest months (May–August) than during the coldest months (November–March). Because of the gradual accumulation and storage of phytoplankton biomass in the sediments during summer and early autumn, seasonal activity peaks in the water column appeared in

Table 7. Spearman rank correlation coefficients (r_s) between microbial and environmental variables in sediments ($n = 60$)

Environmental/microbial variables	*Bacterial abundance*	*LAP*	*Phosphatase*	*β-Glucosidase*	*α-Glucosidase*	*Exoglucanase*
Temperature	0.29*	0.65**	0.74**	0.61**	0.55**	0.55**
PN in MFIP	0.36**	0.06	0.24	0.41**	0.26*	0.37*
C/N ratio in MFIP	−0.28*	−0.49**	−0.44**	−0.44**	−0.49**	−0.41**
Chl *a* in MFIP	0.46**	0.55**	0.46**	0.49**	0.59**	0.49**
Total POM sediment	0.63**	0.21	0.22	0.46**	0.39**	0.49**
Bacterial abundance		0.57**	0.50**	0.70**	0.70**	0.76**

* $p < 0.05$.
** $p < 0.01$.

Table 8. Spearman rank correlation coefficients (r_s) between cell-specific extracellular enzyme activities (normalized for 20°C) and environmental variables in sediments (n = 60)

Environmental variables	*LAP*	*Phosphatase*	*β-Glucosidase*	*α-Glucosidase*	*Exoglucanase*
Discharge	0.18	0.46**	0.34**	0.39**	0.43**
Chl *a* /Phaeo ratio	0.59**	0.31*	−0.03	0.51**	0.04
POC/chl *a* ratio	−0.39**	0.12	0.21	−0.39**	0.19
Total POM sediment.	0.15	−0.24	0.31*	0.11	0.36**
PN sediment	−0.23	−0.17	0.42**	0.16	0.42**

* $p < 0.05$.
** $p < 0.01$.

the sediments with a time lag of 2–3 months and with a significant extension of peak width (Figs. 5a, b). We detected no monthly time lag between seasonal patterns of EEA in surface and subsurface sediments, which indicates more intense vertical connectivity in these river sediments than it was found in a Mediterranean stream [44], where no seasonality of EEA was detected at 7- to 10-cm sediment depth.

Controls on EEA by Bacterial Abundance and Substrate Availability. EEA in the sediments were significantly correlated with bacterial abundance, which is not surprising, as bacteria are the main producers of extracellular enzymes. Additionally, specific EEA were controlled by substrate availability. With the exception of the summer flood in July, POC/chl *a* and C/N ratios were lower in spring and summer than in autumn and winter, suggesting a higher proportion of autochthonous high-quality POM in spring and summer. Carbon from autochthonous primary production is commonly easier to assimilate, contains more biochemical energy per unit mass [52], and is immediately available for bacteria in the water column and also in sediments [1, 2, 44]. Hence, absolute rates of all measured EEA were favored by algal abundance.

After normalizing the EEA for 20°C, and by the calculation of cell-specific EEA, the influence of the seasonal courses of temperature and bacterial abundance could be mathematically eliminated. Like that, it could be demonstrated that bulk POM availability in stream bed was a significant driver of β-glucosidase and exo-1,4-β-glucanase activity dynamics (see also [6, 46]), which especially peaked with the autumnal input of allochthonous organic matter-enriched carbohydrates relative to proteins [26, 34]. It seems that the CHDE, which generally exhibit lower activity compared to peptide degrading enzymes, are produced by microbiota for the processing of qualitatively poor and time-persistent particulate substrates [35, 54]. The higher absolute activity of β-glucosidase compared to α-glucosidase found in our study supports the view that cellulose is the predominant carbon source for sediment bacteria, rather than starch or glycogen. Cell-specific phosphatase activity was influenced by algal biomass and TP content. Thus, high percentages of phosphatase activity were correlated with TP peaks in late autumn and winter, possibly originating from allochthonous inputs from the river catchment. During the flood event in summer, the proportion of allochthonous OM increased, and the bacterial assemblage immediately increased the proportional activities of phosphatase and CHDE to utilize the improved supply of allochthonous OM. LAP activity was significantly correlated with the percentage of fresh autochthonous, easily degradable high-quality OM. This suggests that LAP activity was controlled by algal–bacterial coupling [22, 23], which led to higher activity ratios of LAP/CHDE in spring and summer, when autochthonous production peaks. Hence, seasonal dynamics of specific EEA was not only caused by variations in temperature and bacterial abundance, but also by varying supply of major substrates. Thus, our data show that the seasonal pattern of EEA provides a sensitive approach to infer seasonal or temporary inputs of OM in rivers, as has similarly been found for lakes [4].

A Generalized Seasonal Pattern of Heterotrophic Metabolism in the River Ecosystem. The seasonal sequence of characteristic patterns of EEA activity enables us to derive a generalized seasonal pattern of EEA in the river we investigated, which is illustrated in Fig. 5. As the patterns for 20-cm sediment depths were, in many aspects, similar to those of 5-cm sediment depth, only the 5-cm sediment depth pattern is shown.

During the *spring bloom of phytoplankton in May*, which is reflected by peaks of chl *a* concentration, POM quantity and quality (low POC/chl *a* ratio, low C/N ratio) in the water column, bacterial abundance, and also the activity of most enzymes reach their highest values there during the annual cycle. Chl *a* concentration also peaks in interstitial water as well as POC content and POM quality of MFIP. Thus, sediments are already densely colonized by bacteria, causing significant EEA, even if total POC content of sediments still remains low at that time. Because of high percentages of autochthonous OM, the percentages of LAP in cumulative EEA in the water column and in surface sediments reach an espe-

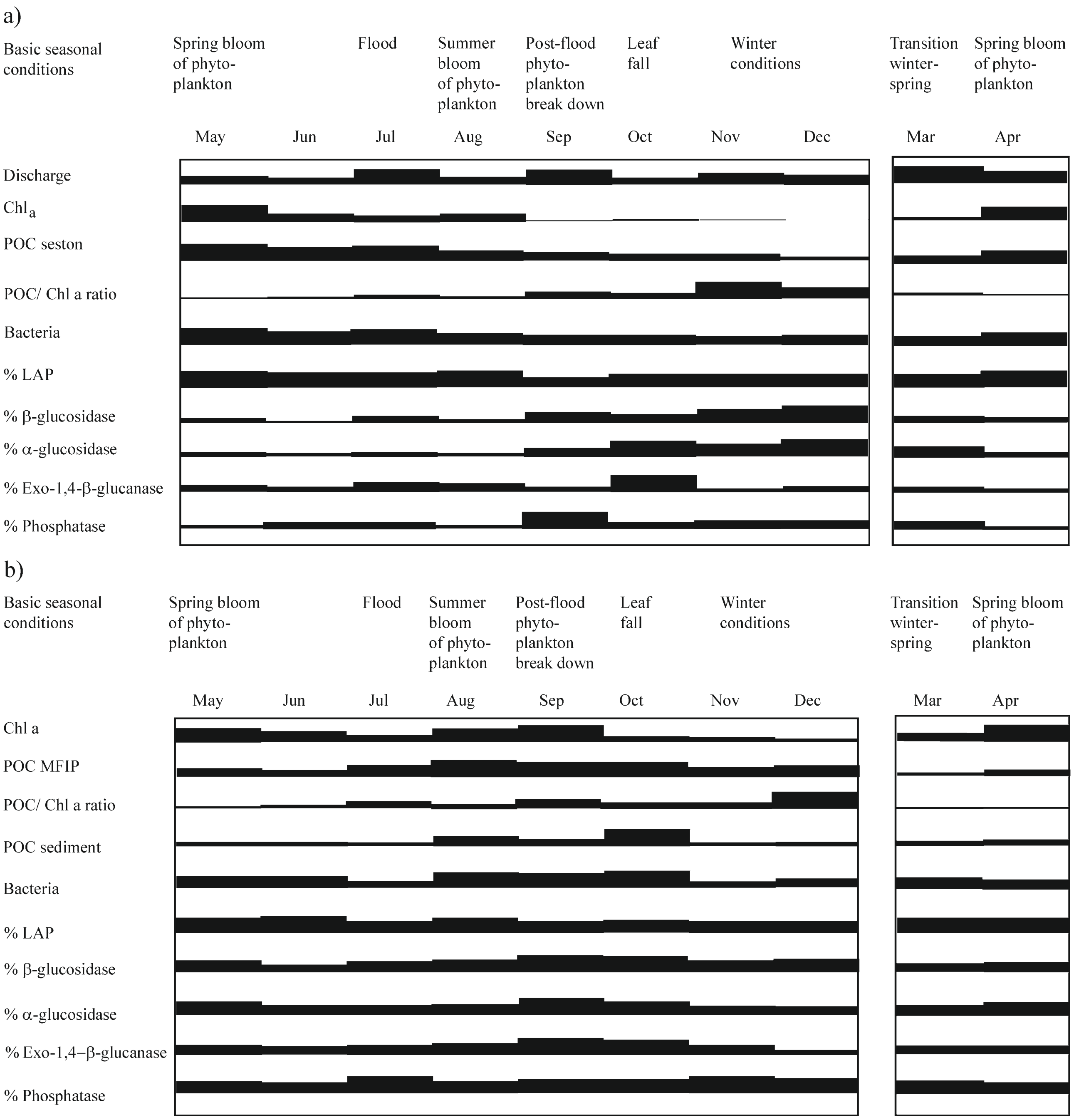

Figure 5. Scheme illustrating the seasonal dynamics of environmental variables, bacterial abundance, and percentages of EEA in cumulative EEA (a) in the water column and (b) at 5-cm sediment depth in the River Elbe. Line width indicates the relative seasonal level of the variable.

cially high level. High input of MFIP POM also causes increased percentages of CHDE activity in sediments. In the water column and in sediments in *June*, chl *a* concentration and POC content decrease, which leads to decreasing absolute EEA compared to May. Moreover, chl *a*, POC contents in MFIP, and percentages of CHDE also decrease in the sediments because of lower connectivity between the sediment layers [3] due to decreasing discharge at this time. As mainly autochthonous OM is present in the river, the percentage of LAP in total EEA remains high.

In *July*, the absolute EEA remain at a high level because of high temperature. By the *summer flood* in July, more allochthonous OM is entrained into the river and trapped by the sediments. In consequence, LAP activity is decreased in the sediments, whereas those of phosphatase and CHDE are increased compared to other summer months. In mesocosm experiments with lake water, LAP activity is even inhibited by terrestrial carbon [56].

In *August*, with low water discharge prevailing again, the chl *a* concentration in the water column slightly increases, whereas POC content and bacterial abundance decrease. This causes lower activities of CHDE than in other summer months, whereas LAP still remains high. At the sediment, a high benthic chl *a* concentration, a high POC content of MFIP, as well as an increase in sedimentary POC content (occurring for the first time in the seasonal cycle now) cause a high bacterial abundance there. Taken together, this causes the annual peaking of EEA.

In *September*, the differences in chl *a* concentration and OM content between water column and sediment are most pronounced. In the water column, the breakdown of phytoplankton with receding solar insulation causes a rapid decrease of chl *a* concentration and the quantity and quality of OM, which lead to a low level of absolute EEA, to lowest percentage of LAP activity in the water column, and to an increased concentration of particulate organic phosphorus, which causes an increasing percentage of phosphatase activity in total EEA. Like in lake water [11], an increase in β-glucosidase activity was observed during that time in the water column. Algal detritus and allochthonous matter are retained quickly in the sediments, as reflected by the high POC content in MFIP. Benthic chl *a* concentrations remain high. Thus, high numbers of bacteria still persist in the sediments, producing a high absolute EEA.

In *October*, because of low chl *a* concentration and low POM content, only low absolute EEA are present in the water column. The high input of allochthonous OM from the riparian zone due to autumnal leaf fall causes a peak of exo-1,4-β-glucanase activity hydrolyzing cellulose mainly derived from vascular plants. Like during the flood in summer, a high proportion of allochthonous OM is retained in the sediments (high POC/chl *a* ratio) together with the collapsed benthic algal biomass. Thus, the highest sedimentary POM content is found in October, paralleled by still high absolute activities of CHDE in surface sediments, but lowest cell-specific EEA because of decreasing POM quality.

During the *winter time* (starting in November), low temperature, chl *a* concentration, along with substrate quantity and quality lead to minimal absolute EEA. The higher percentages of glucosidase activities and decreasing percentages of LAP activity indicate increasing degradation of refractory organic compounds. This is parallel to marine waters, where a higher proteolysis/glycolysis ratio is also found during production (particularly autotrophic) and a lower ratio when degradation predominates [35]. TP supplied from the riparian zones causes a significantly higher percentage of phosphatase activity in total EEA. In the *March transition* from winter to spring, absolute EEA are still low because of low temperature and OM content. The initiation of algal growth is first reflected by an increase in chl *a* concentration in the sediments, which is paralleled by a concomitant increase of LAP in the sediment, but not in the water column. In contrast, the percentage of β-glucosidase decreases. During the *spring bloom of phytoplankton in April 2002*, chl *a* concentration, POM quantity and quality, along with percentages of EEA reached similar values as during the phytoplankton bloom in May 2001 in the water column and the sediments, which suggests a regular occurrence of the described seasonal pattern.

Conclusion

The bacterial assemblage in the Elbe River responded to seasonal shifts in substrate availability by changing the composition of the extracellular enzymes released. LAP increased in percentage, when autochthonous production of labile easily degradable OM was high. In contrast, the proportion of CHDE peaked when total POM content was highest. The percentage of phosphatase activity was directly correlated with TP content and algal biomass. In the sediments, seasonal dynamics of EEA were mitigated because of their storage capacity for OM. EEA peaks in the sediments exhibited a time lag of 2–3 months compared to the water column and a considerable temporal extension of EEA peaks. As rivers are ecosystems that are most frequently dominated by heterotrophic processes, their system-level functioning can be regarded as complementary to the mostly autotrophic functioning of lakes. Hence, the significance of the seasonal dynamics of EEA is principally comparable to that of phytoplankton succession found in lakes (e.g. [51]). As for these phytoplankton dynamics, the EEA dynamics can potentially also be used to identify characteristic types of heterotrophy in rivers shaped by geomorphology, biome, or anthropogenic alterations. Finally, our results show that even in a high-order river, there is a high sedimentary activity of extracellular enzymes degrading labile organic substances (LAP and β-glucosidase), most probably produced by planktonic and benthic algae. Thus, our data corroborate the hypothesis of the revised Riverine Productivity Model [52] that the metabolism of OM in high-order rivers is mainly fuelled by autochthonous production occurring in these reaches and by riparian inputs.

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A river's liver – microbial processes within the hyporheic zone of a large lowland river

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Abstract. Little is known on microbial activities in the sediments of large lowland rivers despite of their potentially high influence on biogeochemical budgets. Based on field measurements in a variety of sedimentary habitats typical for a large lowland river (Elbe, Germany), we present results on the abundance and production of sedimentary bacteria, the potential activity of a set of extracellular enzymes, and potential nitrification and denitrification rates. A diving bell was used to access the sediments in the central river channel, enabling us to sample down to 1 m sediment depth. Depth gradients of all measures of microbial activity were controlled by sediment structure, hydraulic conditions, as well as by the supply with organic carbon and nitrogen. Microbial heterotrophic activity was tightly coupled with the availability of carbon and nitrogen, whereas chemolithotrophic activity (nitrification rate) was related to the available surface area of particles. In the central bed of the river, bacterial production and extracellular enzyme activity remained high down to the deepest sediment layers investigated. Due to the large inner surface area and their connectivity with the surface water, the shifting sediments in the central channel of the river were microbially highly active There, vertically integrated bacterial production amounted to 0.95 g C m^{-3} h^{-1}, which was 2.9 to 5.5 times higher than in the nearshore habitats. We conclude that carbon and nitrogen cycling in the river is controlled by the live sediments of the central river channel, which thus represent a "liver function" in the river's metabolism.

Introduction

Large rivers with a relatively diverse morphological structure have the potential of high microbial activity and thus of an intense turnover of organic matter and inorganic solutes. It can be deducted from the analysis of biogeochemical budgets that river networks remove 37–76% of the total N-input mainly via denitrification, with a high proportion being removed in the high order sections of the rivers (Seitzinger et al. 2002). Large rivers are therefore important for the biogeochemical budgets of catchments (Behrendt and Opitz 1999; Seitzinger et al. 2002), even if the water depth-related retention decreases along a river continuum (Allan 1995; Alexander et al. 2000). Large rivers also process high amounts of organic carbon (Fischer et al. 2002) and thus play a pivotal role in the carbon biogeochemistry of estuarine and coastal regions of the sea (Moran et al. 1999; Raymond and Bauer 2001). However, it is largely unknown how this metabolism is related to specific morphological structures present in rivers less impacted by human alterations.

In streams, these microbial processes occur to a large extent in the hyporheic zone (Pusch et al. 1998; Storey et al. 1999; Fischer and Pusch 2001). Microbially mediated chemical dynamics in the hyporheic zone exert control on materials cycles in the active channel and associated riparian vegetation (Stanford and Ward 1993). Availability of substrates and of terminal electron acceptors is the major determinant of microbial activity (e.g. Hedin et al. 1998). Therefore, gradients of physico-chemical conditions should lead to a spatial separation of the energy-yielding microbial processes. These gradients occur in different spatial scales – e.g. in a decimeter scale in a sediment profile, and in a micrometer-scale within the biofilm. By this, the intrinsic heterogeneity of sediments and the heterogeneity of the sedimentary biofilm allow the parallel existence of seemingly antagonistic processes, for example denitrification (anaerobic) and nitrification (aerobic) (Hedin et al. 1998; Storey et al. 1999; Gieseke et al. 2001). This functional diversity on a spatial scale can be enhanced in rivers by the temporal variability of hyporheic flow paths (Brunke and Gonser 1997; Hinkle et al. 2001), and by circadian variation in oxygen and nutrient concentration of the surface water that is transported into the hyporheic zone (Kaplan and Bott 1989). Large rivers are often characterized by frequent turnover of sediment structures by bedload transport (e.g. Elliott and Brookes 1997; Carling et al. 2000; Sauer and Schmidt 2001). Consequently, geomorphological and hydrodynamic features also influence the spatial characteristics of biogeochemical gradients in the sediments (Vervier et al. 1993; Fischer et al. 2003; Wilczek et al. 2004).

Despite the obvious importance for biogeochemical budgets, there still exists great uncertainty about the functioning of the turnover of matter in large rivers, and the role of the hyporheic zone, because of the relatively small ratio of sediment surface to the discharge of the river. General concepts of river ecology emphasize the importance of the hyporheic zone for ecosystem functioning (e.g. Ward 1989; Townsend 1996), but microbial activities in the sediments of large lowland rivers are widely unknown. This gap between theoretical significance and lack of sound data is due to a variety of technical problems researchers face in large rivers. Few data exist on the general level of microbial activity there, and even less on potential differences in various sediment types (habitats) on the river bottom, which would enable ecologists to define hot spots of microbial activity. This information is needed to broaden our view on ecosystem functioning of large rivers, and to evaluate the impact of river engineering or river restoration measures on in situ microbial metabolism (Dahm et al. 1998; Ward et al. 2001).

Hence, our study aimed at the following questions: (i) What are the levels of microbial activity to be found in various types of sediments in a lowland river? (ii) What is the vertical extension of the microbially active hyporheic zone in a large lowland river? (iii) Which factors control microbial activity in the hyporheic zone, and how do available electron donors and terminal electron acceptors influence microbial activity in different types of river sediments? (iv) What are the implications for the functioning of large-river ecosystems?

Material and methods

Study sites and sampling procedure

Samples were taken in October 2001 at two sites of the 8th order lowland river Elbe in Germany: (i) downstream of Dresden around river km 426.5 (51°03′ N, 13°40′ E, = German Elbe km 61.5) and (ii) upstream of the city of Coswig around river km 598 (51°51′ N, 12°28′ E, = German Elbe km 232.5) (Figure 1, Table 1). Two habitats were sampled at each site, the center of the riverbed within the main river channel, and the nearshore area of the river. At each habitat, three replicate locations were sampled (distance between locations 100 m each) with the exception of the nearshore zone at Dresden, where only one location could be sampled. Samples from the river channel were taken using a diving bell (base area 6 m^2) run by the Office of Water and Navigation Magdeburg. The diving bell was operated with the internal air pressure being increased according to the water depth where the sediments were investigated. Samples from the nearshore zone in Dresden were collected on the right bank that was artificially reinforced by large stone embankment. Further downstream, the banks of the Elbe are in long sections protected by stone groynes (wing-dams, 20–30 m long) perpendicular to the flow direction in a distance of about 100 m from each other (Figure 1). The nearshore sediments in the flow-reduced areas between groynes (Brunke et al. 2002) were sampled at Coswig. The central riverbed in Dresden consisted of a framework of coarse sediments (gravel and stones) filled by sand, whereas at Coswig it consisted of homogenous coarse sands. It was more heterogenous between the groynes, where it consisted of a matrix of coarse gravel and also contained sand and fine organic components (Table 2).

Table 1. Discharge characteristics (daily means, observation time 1991–2000) of the Elbe River at the sampling sites Dresden and Coswig.

	Dresden[a] (m^3/s)	Coswig[b] (m^3/s)
Minimum discharge	89.1	87.5
Mean annual minimum discharge	109	126
Mean discharge	307	331
Mean annual maximum discharge	1320	1250
Maximum discharge	1740	1940
Discharge in October 2001	210	250

[a] Gauging station Dresden, German Elbe km 59.

[b] gauging station Lutherstadt-Wittenberg, German Elbe km 214.

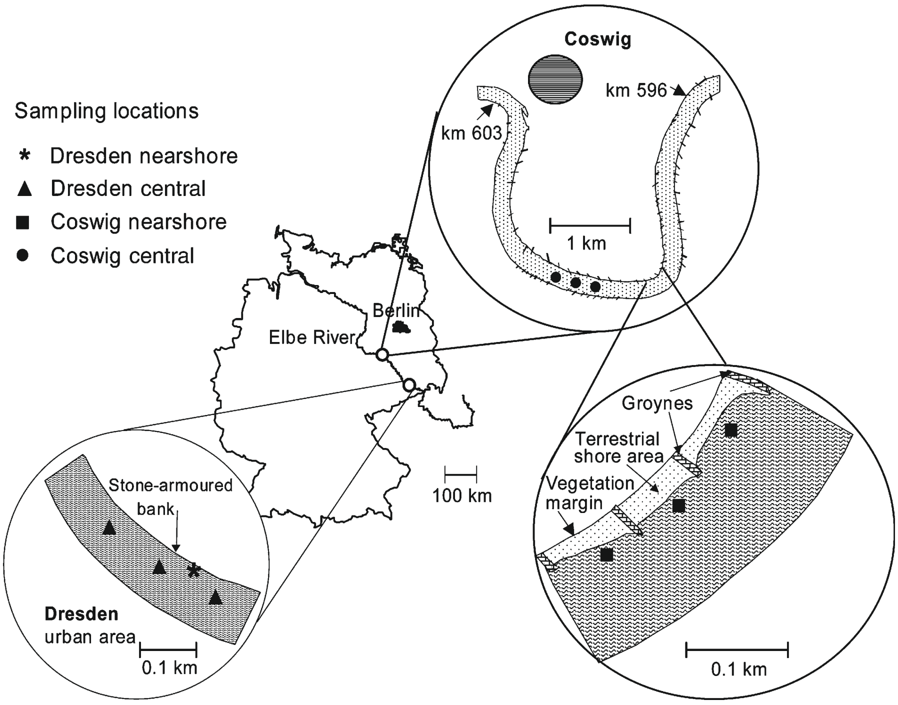

Figure 1. Location of the study sites: Map of Germany showing the river Elbe, and details of the investigated river reaches and sampling locations.

Table 2. Sediment characteristics and channel morphometry of the sampling sites Dresden and Coswig (mean ± sd, $n = 3$).

	Dresden		Coswig	
	Central riverbed	Nearshore riverbed[a]	Central riverbed	Nearshore riverbed
d10 (mm)	1.1 ± 0.4	0.6	0.82 ± 0.34	0.59 ± 0.07
d50 (mm)	13.6 ± 3.2	44.0	2.4 ± 0.9	3.4 ± 0.9
d60 (mm)	19.0 ± 3.2	47.6	2.9 ± 1.0	4.4 ± 1.0
S_o	0.24 ± 0.04	0.11	0.53 ± 0.06	0.37 ± 0.04
Fraction < 5 mm (%)	35	17	88	68
Water depth (m)	2–3	0.5	2–3	0.5–1.2
Total channel width (m) (width of nearshore area)	120 (30)		120 (60)	

[a] Dresden nearshore, $n = 1$.

S_o = sorting coefficient $(d10/d60)^{0.5}$. Nearshore areas consisted of stone embankments in Dresden and of flow-reduced areas between groynes in Coswig.

At each location, piezometers (steel pipes, internal diameter 5 cm) with perforations (diameter 5 mm) were inserted into the sediment down to four depth layers (0–5, 20–25, 50–55, 100–105 cm). In the following, these depth levels are described as 5, 25, 55 and 105 cm depth. For the collection of sediment, 10 l of interstital water were extracted with a hand pump after discarding the first two liters (Bou and Rouch 1967; Brunke and Fischer 1999). The particulate fraction passing a 90 μm mesh net is referred to in the following as mobile fine interstitial particles (MFIP) and was analyzed separately in order to examine its role as substrate and colonization site. The fraction > 90 μm was collected as sediment samples. Subsamples were taken from each layer in order to determine bacterial abundance, production, potential denitrification and nitrification rates, and the activity of four extracellular enzymes (β-glucosidase, phosphatase, leucine-aminopeptidase, exo-1,4-β-glucanase). Samples were immediately stored on ice until being processed in the laboratory within 48 h. Additionally, loss on ignition, carbon, and nitrogen content were determined from the sediment samples. The latter variables were also determined for the MFIP. Thus, results on sediment characteristics refer to the < 5 mm fraction at all sampling sites independent of their overall sediment characteristics, which facilitates comparisons. Additionally, some of the results were extrapolated on a river bottom area unit considering the differing particle compositions, as described in the calculations section.

Hyporheic water was collected immediately after the sediment samples were taken, by inserting a submersible electric pump into the piezometer. In these samples, chlorophyll a and physicochemical variables were analyzed. Water chemistry was not measured in 5 cm sediment depth, because in this depth uncontrolled mixing with pelagic water can occur during the sampling procedure. Samples from river water were collected from the center of the river flow.

Chemical analyses

Nitrate, nitrite, sulfate, and chloride were analyzed using a ion chromatograph (Shimadzu) equipped with suppressor technique to reduce background conductivity. Ammonium concentrations were determined spectrophotometrically (Hach DR/2000, Loveland, Colorado, USA) modified for small sample volumes according to the German standard methods (DEW 1985). Phosphate was measured spectrophotometrically according to the German standard methods (DEW 1985). The results are given for NO_3-N, NO_2-N, NH_4-N, PO_4-P, or SO_4-S. At Coswig, oxygen content of the interstitial water was measured *in situ* using an aluminum-coated oxygen microsensor (Microx TX Microoptode, PreSens, Germany) with a spatial resolution of 1 cm. In each sediment depth, six replicated measurements were performed in steps of 5 cm in the mid-river habitat and of 1 cm in the nearshore habitat.

Sediment composition

Sediments (10 l) were taken from each location, dried, and sieved through a standard set of sieves comprising mesh sizes from 63 μm through 63 mm in order to examine the particle size distribution and the sorting coefficient (S_o = d10/d60)$^{0.5}$ of the sediments.

Total particulate organic matter (POM) was determined as loss on ignition. Subsamples of 15–25 g wet weight were dried to constant weight at 105 °C, and subsequently combusted for 6 h at 550 °C in order to determine POM as ash-free dry mass. Particulate organic carbon (POC) and nitrogen (PON) content were determined using a CNS Analyser (Vario EL, Elementar Analysensysteme GmbH). About 50 g of the dried sediment samples were ground with an analytical ball mill (Pulverisette 6, Fritsch) for 15 min. Triplicate subsamples were filled into cylindrical silver foil capsules (9 mm height, 5 mm diameter; Lüdi AG, Flawil, Switzerland) for analysis. Inorganic carbon was removed with 1 M HCl. The calibration curve was established using acetanilide. Hot ethanol (90%, 78 °C) was used for the extraction of phytopigments. Extraction was applied for 12 h at room temperature in the dark. The clear ethanol-pigment-mixture was used to determine chlorophyll *a* and phaeopigments with a spectrophotometer (UV-2401 PC, Shimadzu) according to the German standard methods (DEW 1985).

Bacterial production

Subsamples of 1 cm^3 sediment were taken from each depth and weighed into precombusted 10 ml centrifuge vials containing 4 ml of fresh, filtered (0.2 μm pore size) river water. The vials were then kept at 4 °C until the experiment, which was started within 36 h after sampling. Bacterial production was measured using the leucine-incorporation method (Kirchman 1993) modified for use in river sediments (Fischer and Pusch 1999). We used L-[U$-^{14}$C]-leucine (Amersham Ltd., specific activity 11.4 GBq/mmol) diluted with cold L-leucine to a specific activity of 148 Bq/nmol leucine, and incubated the samples in vials at 20 °C with gentle shaking. For each habitat, six controls (two for each depth layer) were fixed with 3.2% formaldehyde (final concentration) immediately at the start of the incubation. Bacterial carbon production was calculated from leucine incorporation assuming 7.3 mol% leucine in total protein, and a carbon/protein ratio of 0.86 (Simon and Azam 1989). Measurements at the various sediment depths were integrated in order to calculate total bacterial production in the uppermost 1 m sediment layer.

Bacterial abundance

Subsamples for bacterial cell counts were taken from the supernatant of the incubated samples, after a 10 min sonication step and rigorous vortexing. They were diluted with a sterile-filtered aqueous solution of 3.5% formaldehyde, 0.85% NaCl, and 1 mM pyrophosphate. Bacteria were stained using 4′,6-di-amidino-2-phenylindol (DAPI) (Porter and Feig 1980) at a final concentration of 10 mg/l. After 40 min. of dark incubation, bacteria were filtered onto black polycarbonate filters (Nuclepore, pore size 0.2 μm) and mounted on slides using anti fading solution (AF1, Citifluor, London). At least 200 bacteria within at least 10 microscopic fields were counted by epifluorescence microscopy (Nikon FXA Microscope, HBO 100 W, Ex 330–380, DM 400, BA 400, immersion objective CF N DIC Plan Achromate 100×). Bacterial biomass was estimated using the abundance data from the Elbe sediments, and cell volumes determined in a comparable lowland river (Spree, Germany; Fischer et al. 2002). Turnover times of bacterial carbon were then calculated as biomass/production.

Denitrification potential

The acetylene (C_2H_2) block method (Sørensen 1978; Seitzinger et al. 1993) was used to determine the potential denitrification rate. The C_2H_2 block method is based on the linear accumulation of N_2O during incubation of sediments with C_2H_2 added in order to inhibit the bacterial reduction of N_2O to N_2. Assays were initiated within 36 h after sampling. About 10 to 20 g wet sediment samples were filled into 250 ml bottles sealed by rubber plugs. Headspace was replaced by N_2 for 20 min; 50 ml of N_2-saturated, sterile filtered river water with KNO_3 (1 mM) and glucose (1 mM) as carbon source was then added with a syringe in order to provide optimal conditions for denitrification. After 30 min of preincubation on a shaker (150 rpm, 25 °C), 10 ml N_2- and C_2H_2-saturated site water was injected to each sample. The first N_2O analysis was carried out 30 min after C_2H_2 injection. Samples were incubated for 5 h on a shaker at 23 °C and N_2O was analyzed using a gas chromatograph (Shimadzu GC-17A) equipped with a ^{63}Ni electron capture detector (oven temperature 50 °C, detector temperature 300 °C, nitrogen carrier gas flow 30 ml min^{-1}). N_2O concentrations in the samples were calculated from the measured head-space concentration (Dahlke and Remde 1998). All values for denitrification rates are given in N_2O-N. Because the production of N_2O was found to be linear, denitrification rates were estimated by the amount of N_2O after preincubation and after 5 h incubation.

Nitrification potential

Potential nitrification rates were obtained by the measurement of the accumulation of nitrite in subsamples containing $KClO_3$ inhibiting the oxidation of nitrite (Belser and Mays 1980; Wolff and Remde 1998). Assays were initiated within 36 h after sampling. About 30 to 40 g wet weighed sediment samples were filled into 50 ml tubes and covered with 20 ml buffer (0.33 mM $MgSO_4$, 0.18 mM $CaCl_2 \cdot 3H_2O$, 8.5 mM NaCl, 0.01 M phosphate buffer, pH 7.6) and 1 ml $KClO_3$ (3 mM). After 30 min of preincubation on a shaker (200 rotations min^{-1}, 25 °C), 1 ml NH_4Cl (3.7 mM) was added and the first subsample for nitrite measurement was taken. The second subsample was taken after 4 h, and nitrite was detected as described above. Preinvestigations showed that the incubation period of 4 h was within the linear phase of nitrite accumulation.

Extracellular enzyme activities

The action of extracellular enzymes usually marks the first step in the microbial degradation of organic compounds. It can limit the rate of substrate uptake by microorganisms, and consequently their growth (Chrost 1991). Because extracellular enzymes are substrate-specific, the measurement of EEA provides insight into the specific functional profile of microbial communities (Sinsabaugh and Linkins 1988). Fluorogenic substrate analogues (methylcumarinylamid (MCA)-substrates and methylumbelliferyl (MUF)-substrates, Sigma) were used to measure the potential extracellular enzyme activities (V_{max}) of leucine aminopeptidase, β-glucosidase, exo-1,4-β-glucanase and phosphatase (Hoppe 1993; Marxsen et al. 1998). These enzymes were chosen because they hydrolyse the major organic constituents (proteins, carbohydrates and organophosphoric esters) of allochthonous and autochthonous origin. Three replicates and two controls of each sediment sample were prepared using 3 g of wet sediment and 8 ml of filtered (0.2 μm) river water. After boiling the controls for 30 min, 1 ml of the substrate analogue (saturation concentration) was added to replicates and controls. The samples were incubated for 1–2 h at 22 °C in the dark under continuous shaking, and killed by boiling for 5 min. When cooled down to room temperature, 1 ml of 0.1 M alkaline glycine buffer (pH 10.5) was added. To samples used for measuring phosphatase activity, the glycine buffer was added before boiling. After centrifugation (5 min at 4000 × *g*), hydrolysis of the substrate analogue was measured by determining the fluorescence of the supernatant (Shimadzu RF-5001 PC spectrofluorometer, 1.5 nm slit, 360 nm (MCA) or 365 nm (MUF) excitation, 440 nm (MCA) or 450 nm (MUF) emission). Standard MCA (7-amino-4-methyl-coumarin) solutions and standard MUF (4-methyl-umbelliferone) solutions were used for calibration.

Calculations and statistical analyses

Spearman rank correlations were used to reveal relationships between bacterial variables and environmental factors. Data were then $\log_{10}$ transformed, and two-factor analysis of variance was used to test for possible effects of habitat and sediment depth on hyporheic water chemistry, particulate organic matter, and bacterial activity. Multiple comparisons were made with Tukey's HSD test. Analyses were performed with the software SPSS (release 9.0, SPSS Inc.). Curve fittings and regression calculations were made using Origin 6.1 (Microcal Software Inc.).

In order to relate the measured bacterial activity to in-situ conditions, the particle size distribution of *in-situ* sediments was considered. Because significant proportions of the total sediment had particles sizes >5 mm that could not be sampled with the piezometers (Table 2), we first calculated the surface area of all particle sizes, assuming spherical shapes and using the radius of the arithmetic mean in each size class. We set this area as 1, and subtracted the proportion of surface area that was provided by particles >5 mm. Thus, the maximal factor 1 would indicate that all sediments were smaller than 0.5 mm. The resulting factors were 0.88 for Coswig central riverbed, 0.72 for Coswig nearshore riverbed, 0.43 for Dresden central riverbed and 0.18 for Dresden nearshore sediments.

Results

Sediment characteristics

Clear vertical gradients of the measured variables existed in the sediments at most locations, showing marked differences between the various habitats (Tables 3 and 4). In deep sediment layers, nitrate concentration generally decreased with sediment depth. No consistent trend was found for ammonium concentrations. Nitrate concentrations in the sediment pore water were significantly higher at Dresden than at Coswig, whereas ammonium concentrations were particularly high (up to 630 μg l^{-1}) in the interstitial zone at Coswig (Tables 3 and 4). Here, ammonium concentrations exceeded those of the water column by far. In Dresden, ammonium concentrations in the pore water were lower than in the water column. In contrast, nitrate concentration was lower in the pore water than in the water column at most locations (Table 3). At the Coswig midriver habitat, molecular oxygen decreased linearly down to 40 cm sediment depth. No molecular oxygen was found below this depth. In the nearshore habitats however, molecular oxygen was depleted already at depths between 5 and 10 cm (Figure 2).

POM contents were higher in nearshore than in mid-river areas, and decreased significantly with sediment depth (Table 3). The amount of mobile fine interstitial particles (MFIP) showed no consistent trend with sediment depth. However, MFIP concentrations were significantly higher at the Dresden site than at Coswig (Table 4). There were also significant interactions between sediment depth and habitat, as MFIP concentrations decreased with sediment depth nearshore at Coswig, and increased at the other locations. The proportion of carbon as well as of nitrogen in these particles decreased significantly with increasing sediment depth. C:N ratios increased slightly with sediment depth, and C:N ratios were higher between the groynes nearshore at

Table 3. Characteristics of particulate organic matter and water chemistry at the sites Dresden and Coswig (mean ± sd, $n = 3$), itemized for sediment depths and habitats.

Site	Depth (cm)	POM (% dry mass)	MFIP (mg l^{-1})	MFIP-C(%)	MFIP-N(%)	MFIP-C:N	Chl *a* (µg l^{-1})	NH_4-N (µg l^{-1})	NO_3-N (mg l^{-1})
Coswig surface water	–						12.6	15	4.09
Coswig central riverbed	5	0.46 ± 0.09	69 ± 23	6.4 ± 1.0	0.74 ± 0.14	10.1 ± 0.3			
	25	0.45 ± 0.04	89 ± 23	6.3 ± 0.3	0.85 ± 0.10	8.7 ± 0.8	45.3 ± 12.8	158 ± 185	2.28 ± 1.67
	55	0.36 ± 0.12	273 ± 225	4.1 ± 1.7	0.43 ± 0.18	11.1 ± 0.5	18.4 ± 7.3	290 ± 297	0.31 ± 0.31
	105	0.28 ± 0.08	3485 ± 5418	2.5 ± 0.8	0.25 ± 0.08	11.9 ± 2.5	3.5 ± 2.5	379 ± 298	0.06 ± 0.07
Coswig nearshore area	5	0.91 ± 0.09	1129 ± 295	5.6 ± 0.1	0.57 ± 0.04	11.5 ± 0.9			
	25	0.54 ± 0.21	692 ± 293	6.7 ± 2.7	0.56 ± 0.16	13.6 ± 1.4	6.8 ± 7.2	14 ± 16	0.65 ± 1.03
	55	0.44 ± 0.26	321 ± 215	5.9 ± 3.2	0.46 ± 0.18	14.4 ± 2.3	0.4 ± 0.4	43 ± 34	0.63 ± 1.10
	105	0.68 ± 0.39	302 ± 65	7.1 ± 2.7	0.46 ± 0.21	18.9 ± 4.5	−0.2 ± 0.5	151 ± 67	0.10 ± 0.17
Dresden surface water	–						18.2	64	3.92
Dresden central riverbed	5	0.67 ± 0.10	918 ± 456	6.9 ± 1.4	0.83 ± 0.20	9.8 ± 0.4			
	25	0.66 ± 0.27	1727 ± 2004	7.2 ± 2.4	0.78 ± 0.37	11.5 ± 2.6	10.8 ± 8.6	23 ± 11	3.38 ± 0.29
	55	0.72 ± 0.16	1955 ± 1039	5.8 ± 1.1	0.58 ± 0.12	11.8 ± 1.0	5.1 ± 9.6	22 ± 14	2.83 ± 0.13
	105	0.56 ± 0.08	4098 ± 3421	2.7 ± 0.8	0.26 ± 0.10	12.5 ± 1.1	−0.3 ± 1.7	17 ± 4	1.98 ± 0.61
Dresden nearshore area	5	3.43	849	5.7	0.59	11.2			
	25	1.19	3086	5.4	0.59	10.7	25.6	57	4.05
	55	0.63	3732	2.9	0.31	10.7	10.8	24	7.18
	90	0.48	2472	1.5	0.18	10.2	−0.7	23	n.d.

POM = particulate organic matter; MFIP = mobile fine interstitial particles; chl *a* = chlorophyll *a*; n.d. = not determined.

Table 4. Results of two-factor analysis of variance for particulate organic matter and water chemistry testing the effect of habitat and sediment depth.

Factors	POM (df; *F*; *p*)	MFIP (df; *F*; *p*)	MFIP-C (df; *F*; *p*)	MFIP-N (df; *F*; *p*)	MFIP-C:N (df; *F*; *p*)	Chl *a* (df; *F*; *p*)	NH_4-N (df; *F*; *p*)	NO_3-N (df; *F*; *p*)
Habitat	3; 16; <0.001	3; 15; <0.001	3; 3.4; <0.05	3; 1.3; 0.30	3; 12; <0.001	3; 8.0; <0.01	3; 5.2; <0.01	3; 15; <0.001
Depth	3; 15; <0.001	3; 1.7; 0.19	3; 9.2; <0.001	3; 12; <0.001	3; 3.3; <0.05	2; 13; <0.001	2; 0.56; 0.58	2; 12; 0.001
Depth × habitat	9; 4.9; <0.01	9; 2.6; <0.05	9; 2.0; 0.09	9; 1.2; 0.36	9; 1.4; 0.25	6; 1.3; 0.32	6; 0.39; 0.88	6; 2.7; <0.05

POM = particulate organic matter, MFIP = mobile fine interstitial particles, chl *a* = chlorophyll *a*.

Coswig than in the other habitats (Tables 3 and 4; all comparisons specified here were confirmed by Tukey's post-hoc tests, $p < 0.01$). The trends for the biochemical composition of POM were similar to those described for MFIP, i. e. carbon and nitrogen content significantly decreased with sediment depth (data not shown, $p < 0.01$).

Microbial activity rates

Mean bacterial abundance in the uppermost mid-river sediment layer was up to 1.4×10^9 cm^{-3} at Dresden, but only 4.7×10^8 cm^{-3} at Coswig. Bacterial abundance decreased significantly with sediment depth, but still reached 1.4×10^8 cm^{-3} at 105 cm sediment depth as a mean of all locations. Bacterial

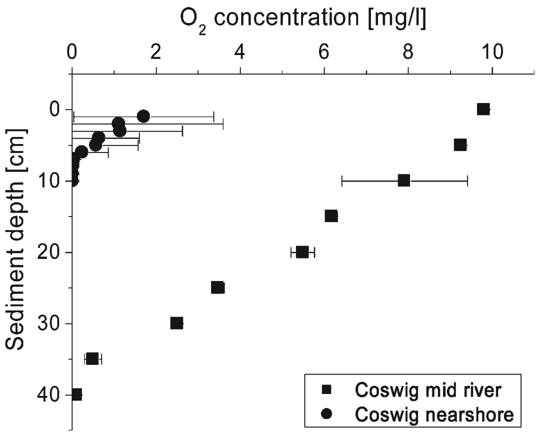

Figure 2. Dissolved oxygen concentrations in nearshore and mid-river sediments. Arithmetic means and standard deviations of 3 (mid-river) and 15 (nearshore) depth profiles.

production showed the same pattern as abundance, with rates of up to 2.5 μg C cm^{-3} h^{-1} in the uppermost sediment layer at Dresden (Tables 5 and 6). Turnover times of bacterial carbon resulting from these data were 7.9 ± 1.9 h in the 5 cm sediment layer. Turnover times increased towards deeper sediment layers (df = 3, $F = 9.7$, $p < 0.001$), where they were highly variable.

Leucine aminopeptidase, a peptide degrading enzyme, and alkaline phosphatase, a phosphomonoester-degrading enzyme, showed the highest activities at all sampling locations (mean values: 134 nmol MCA cm^{-3} sediment h^{-1} and 71 nmol MUF cm^{-3}, respectively). Activity of β-glucosidase (mean: 16 nmol MUF cm^{-3} sediment h^{-1}), which degrades disaccharides, was higher than that of the polysaccharide-degrading exo-1,4-β-glucanase (mean: 4.9 nmol MUF cm^{-3} sediment h^{-1}; determined in Coswig only). As for the other variables of bacterial activity, the activity of extracellular enzymes decreased significantly with increasing sediment depth (Tukey's post-hoc tests, $p < 0.01$) (Tables 5 and 6).

Potential nitrification rates reached 97 ng NO_2-N cm^{-3} h^{-1} at Dresden and 3.0 ng NO_2-N cm^{-3} h^{-1} at Coswig. Nitrification thus was significantly higher at Dresden than at Coswig, and strongly decreased with increasing sediment depth at all habitats (Tukey's post-hoc tests, $p < 0.01$). Potential denitrification rate also decreased significantly with sediment depth. Highest rates were measured in the nearshore habitats (Dresden, 16.8 μg N_2O-N cm^{-3} h^{-1} and Coswig, 5.7 μg N_2O-N cm^{-3} h^{-1}). Rates at the midstream locations were 2–3 μg N_2O-N cm^{-3} h^{-1} in the uppermost sediment layer (Tables 5 and 6).

Patterns and controls of microbial activity

Spatial patterns were similar for many microbiological variables. Bacterial abundance, production, activity of four extracellular enzymes, and denitrification rate significantly correlated with each other. Generally, these measures of bacterial activity correlated significantly with amount and quality of organic matter and with nitrate concentration, but not with MFIP concentrations (Table 7), indicating the tight coupling of heterotrophic processes with organic matter supply. Potential nitrification rate showed a different pattern than the other microbial variables, as it correlated with MFIP concentration, but not with organic matter. Potential nitrification rate had a negative correlation with ammonium concentration and a positive correlation with nitrate concentration (Table 7).

For most biotic variables, the variation between sediment depths was of higher statistical significance than that between habitats (Table 6). This decrease of microbial activity with sediment depth approached an exponential fit in the Coswig nearshore riverbed, whereas it was close to a linear fit in the Coswig central riverbed (Figure 3). In particular, the habitats differed in the slope of the decrease in microbial activity over the upper 25 cm of sediment. Bacterial activity (relative means of bacterial abundance,

Table 5. Bacterial abundance and activity at the sampling sites Dresden and Coswig (means ± sd, $n = 3$), itemized for sampling stations and sediment depths.

	Depth	Abundance (10^8 cells $\sqrt{\text{cm}^{-3}\,\text{h}^{-1}}$)	Production (µg C $\sqrt{\text{cm}^{-3}\,\text{h}^{-1}}$)	Phosphatase (nmol MUF $\sqrt{\text{cm}^{-3}\,\text{h}^{-1}}$)	β-Glucosidase (nmol MUF $\sqrt{\text{cm}^{-3}\,\text{h}^{-1}}$)	Leucine aminopeptidase (nmol MCA $\sqrt{\text{cm}^{-3}\,\text{h}^{-1}}$)	$\sqrt{\text{Exo}-1,4-\beta}$-glucanase (nmol MUF $\sqrt{\text{cm}^{-3}\,\text{h}^{-1}}$)	Nitrification rate (ng NO_2-N $\text{cm}^{-3}\ \text{h}^{-1}$)	Denitrification rate (µg N_2O-N $\text{cm}^{-3}\ \text{h}^{-1}$)
Coswig central riverbed	5	4.69 ± 0.38	1.74 ± 0.15	59.91 ± 3.01	8.81 ± 1.42	123.77 ± 12.40	2.39 ± 0.38	3.00 ± 1.35	2.69 ± 2.79
	25	4.76 ± 0.43	1.59 ± 0.28	58.32 ± 2.92	7.66 ± 0.94	123.57 ± 13.09	2.07 ± 0.23	1.26 ± 0.38	1.33 ± 0.78
	55	3.19 ± 0.66	1.11 ± 0.29	36.41 ± 6.15	4.56 ± 0.53	70.80 ± 3.78	1.26 ± 0.09	1.05 ± 0.63	0.65 ± 0.18
	105	1.27 ± 0.90	0.32 ± 0.28	5.18 ± 5.07	1.30 ± 1.22	17.21 ± 15.78	0.21 ± 0.30	0.27 ± 0.70	0.24 ± 0.04
Coswig nearshore area	5	8.11 ± 2.48	2.19 ± 0.77	91.70 ± 24.89	22.61 ± 10.17	157.27 ± 19.19	4.93 ± 1.83	2.87 ± 0.35	5.70 ± 1.71
	25	3.15 ± 0.78	0.62 ± 0.19	37.40 ± 11.68	6.01 ± 1.87	63.53 ± 9.73	1.37 ± 0.33	2.00 ± 0.66	0.64 ± 0.16
	55	1.91 ± 1.13	0.24 ± 0.25	29.50 ± 22.96	3.99 ± 3.40	43.79 ± 28.16	0.52 ± 0.88	0.31 ± 0.43	0.24 ± 0.29
	105	1.62 ± 1.20	0.20 ± 0.27	23.56 ± 15.70	3.21 ± 2.82	32.87 ± 23.14	0.68 ± 0.66	0.92 ± 0.45	0.37 ± 0.48
Dresden central riverbed	5	9.59 ± 1.95	2.41 ± 0.45	59.86 ± 7.76	12.72 ± 4.05	136.25 ± 6.96		58.90 ± 13.96	2.33 ± 1.04
	25	6.73 ± 1.30	1.33 ± 0.16	40.02 ± 10.82	6.01 ± 0.73	90.54 ± 28.16		38.54 ± 14.74	0.60 ± 0.34
	55	4.23 ± 0.86	0.49 ± 0.14	30.90 ± 3.48	2.47 ± 0.83	106.58 ± 25.80		15.54 ± 6.17	0.068 ± 0.031
	105	1.43 ± 0.84	0.07 ± 0.34	4.09 ± 3.72	0.87 ± 0.47	49.08 ± 23.05		4.10 ± 0.25	0.018 ± 0.005
Dresden nearshore area	5	13.8	2.52	75.88	30.20	84.37		97.34	16.84
	25	6.09	1.81	45.07	9.00	86.62		49.34	2.61
	55	2.88	0.67	29.65	5.35	64.22		20.59	1.43
	90	0.78	0.11	13.36	0.83	43.87		5.26	0.084

Table 6. Results of two-factor analysis of variance for bacterial activity testing the effect of habitat and sediment depth.

Factors	Abundance (df; *F*; *p*)	Production (df; *F*; *p*)	β-Glucosidase activity (df; *F*; *p*)	Leucine-amino-peptidase activity (df; *F*; *p*)	Nitrification (df; *F*; *p*)	Denitrification potential (df; *F*; *p*)
Habitat	3; 2.0; 0.14	3;3.2; <0.05	3; 1.9; 0.16	3; 1.9; 0.17	3; 170; <0.001	3; 6.2; <0.01
Depth	3; 23; <0.001	3; 55; <0.001	3; 33; <0.001	3; 13; <0.001	3; 75; <0.001	3; 29; <0.001
Depth× habitat	9; 0.9; 0.57	9; 2.8 <0.05	9; 1.3; 0.28	9; 1.9; 0.10	9; 20; <0.001	9; 1.8; 0.13

production, and enzyme activity) was only 5% lower in 25 cm sediment depth than in 5 cm sediment depth. In contrast, bacterial activity in 25 cm depth was 65% lower than in 5 cm depth at Coswig nearshore riverbed. An intermediate decrease of 39% was found in Dresden (mean for both habitats). A similar pattern, but a stronger decrease with sediment depth was determined for denitrification.

Correction for particle size distribution was used to integrate bacterial production over 1 m sediment depth. The integrated bacterial production was highest in the central streambed at Coswig. It ranged from 0.17 g C m^{-3} h^{-1} in the nearshore sediments in Dresden to 0.95 g C m^{-3} h^{-1} in the Coswig central streambed. Intermediate values of 0.33 and 0.32 g C m^{-3} h^{-1} were calculated for the nearshore sediments at Coswig and in the central streambed at Dresden, respectively.

Table 7. Spearman rank correlation coefficients between bacterial variables and environmental factors.

Environmental factor	*n*	Bacterial production	β-glucosidase activity	Leucine amino-peptidase activity	Denitrification rate	Nitrification rate
MFIP	40	n.s.	n.s.	n.s.	n.s.	0.47**
MFIP-C percentage	40	0.42**	0.53***	0.46**	0.32*	n.s.
MFIP-N percentage	40	0.62***	0.66***	0.66***	0.49**	n.s.
MFIP C:N ratio	40	−0.56***	−0.42**	−0.58***	−0.43**	n.s.
Chlorophyll *a*	28	0.72***	0.60**	0.47*	0.63***	n.s.
POC >90 µm	40	0.48**	0.62***	0.34*	0.54***	n.s.
PON >90 µm	40	0.62***	0.69***	0.49**	0.69***	n.s.
NO_3-N	30	0.49**	0.46**	0.64***	0.39*	0.69***
NH_4-N	30	n.s.	n.s.	n.s.	n.s.	−0.61***

Levels of significance are *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, n.s = not significant at a 0.05% level.

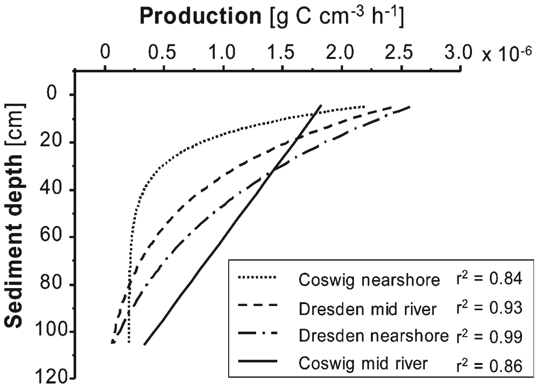

Figure 3. Bacterial production in samples of particles sizes <5 mm, vertically interpolated over 1 m sediment depth. $n = 12$ at each of the four sampling stations, besides Dresden river bank, were $n = 4$. Data shown in Table 5.

Discussion

Our findings demonstrate that an extended, microbially active hyporheic zone exists in the Elbe River. We found high rates of microbial activity stretching down to 1 m sediment depth at the mid-river habitat in Coswig. Results of bacterial production measurements revealed that bacterial activity in the uppermost sediment layer can reach the same order of magnitude as in a 6th order lowland river (Fischer et al. 2002), and was considerably higher than in most studies of small streams (e.g. Marxsen 2001). The relative activity of the four extracellular enzymes – leucine aminopeptidase > alkaline phosphatase > β-glucosidase > exo-1,4-β-glucanase – suggested that a high proportion of organic matter were proteins mainly derived from algae, and was typical for benthic epilithic biofilms in running waters (Chappell and Goulder 1994; Romaní and Marxsen 2002). Despite their potentially high activities, studies on extracellular enzymes in benthic and hyporheic sediments of running waters are particularly rare (Marxsen and Fiebig 1993; Sinsabaugh and Findlay 1995). The absolute rates of β-glucosidase activity were in the range of those found in a small, unpolluted stream (Marxsen and Fiebig 1993), for the other enzymes comparable data do not exist. Comparisons with potential nitrification and denitrification rates with those reported from other running waters are problematic because of a variety of methods used. Potential denitrification rates in Elbe sediments exceeded those measured in other running waters (e.g. García-Ruiz et al. 1998; Sheibley et al. 2003), probably because of high nitrate concentrations in the Elbe River and in the adjacent ground water, and because of the fact that we measured denitrification under optimized conditions here (Richardson et al. 2004). Published rates of nitrification cover a similar order of magnitude as in the Elbe River (e.g. Sheibley et al. 2003).

At each location, all bacterial variables measured showed a depth gradient in their activity. These gradients generally corresponded with gradients in organic matter and oxygen concentration. Although deficiency of oxygen is generally assumed to limit many microbiological processes in sediments, it has recently been found that the availability of labile organic matter limits bacterial heterotrophic activity in various aquatic ecosystems irrespective of oxygen concentration (Kristensen et al. 1995; Bastviken et al. 2001), and that a close interplay between both electron acceptors and donors exist in hyporheic environments (Hedin et al. 1998). At the Coswig mid-river and nearshore habitats, we measured high potential microbial activity in deeper sediment layers lacking molecular oxygen (Figures 2 and 3). This indicates that substrate rather than oxygen availability regulates microbial activity in the hyporheic zone of the Elbe River.

The potential for various microbial processes covaried tightly in the Elbe sediments, even if these processes seem to functionally exclude each other. For example, nitrification and denitrification both peaked in the upper sediment layer, and were highly correlated to each other when Dresden and Coswig samples were analyzed separately. This correlation can be attributed to the heterogeneity of the sediments that offers micro-niches for a high diversity of microbial processes occurring in close proximity to each other. Most bacteria capable of respiratory denitrification are facultative anaerobes that use molecular oxygen as electron acceptor under aerobic conditions (Tiedje 1988). Many bacteria can even perform aerobic denitrification within their natural habitat (Patureau et al. 2000). This metabolic flexibility would help these bacteria to cope with the varying availability of molecular oxygen in river sediments. Also, the spatial micro-heterogeneity and the metabolic flexibility contribute largely to the high rate of microbial metabolism found in these sediments.

However, the dynamics of nitrification rates differed from the other variables in the correlation matrix (Table 7). This can be traced back to significant differences in the hyporheic nitrification rates between Dresden and Coswig. Although there was a highly significant decrease in nitrification rates with increasing sediment depth, this decrease was not correlated with variables describing organic matter, because of the chemolithotrophic nature of the nitrification process. In contrast, organic carbon can even inhibit nitrification, in particular at high C:N ratios. It is argued that under these conditions heterotrophic bacteria would compete for $NH_4{}^+$, thus reducing the availability of $NH_4{}^+$ for nitrifying bacteria (Strauss and Lamberti 2000). However, availability of oxygen was probably most important for nitrification. This would explain the sharp decrease of potential nitrification rates with depth particularly in the Coswig mid-river sediments, where concentrations of NH_4-N were relatively high and organic carbon content was low. Surface area of fine interstitial particles (MFIP) seemed to influence nitrification rate, which was not the case for the other bacterial variables (Table 6). Thus, nitrifying bacteria may be imported into the hyporheic zone via MFIP. Additionally, the (mostly negatively loaded) surfaces of MFIP are probably important because they provide binding places for reduced nitrogen ions, as for $NH4^+$. In Dresden, the concentration of these MFIP was higher than in Coswig, especially in the microbially active upper sediment layers. Consequently, nitrification rates were higher in Dresden, which lead to depletion in dissolved ammonium and accumulation of nitrate in the pore water.

Bacterial activity in the deeper sediments was particularly high at sites with significant sediment turnover. In the central river bed, a uniform grain size distribution of coarse sand and fine gravel provides vast surface areas for the colonization by bacteria, and large interstitial spaces enable import of matter from the overlying water via turbulent dispersion (Rutherford et al. 1993). Intense perfusion by pumping mechanisms and frequent turnover of sediment structures by bedload transport occurs in these regions (e.g. Carling et al. 2000; Sauer and Schmidt 2001; Fischer et al. 2003). These mechanisms will eventually expose bacteria from deeper layers to changing environmental conditions. Our study shows that the bacterial community can cope with these changing conditions. It therefore seems that the activity in this spatially extended zone is closely related to hydrodynamics and sediment movement, as shown before for a smaller (6th order) lowland river (Fischer et al. 2003).

The spatial extension of microbial processes in river sediments often depends on hyporheic water flow that carries nutrients and terminal electron acceptors to the biofilms (Brunke and Gonser 1997; Brunke and Fischer 1999; Battin 2000). As an example, nitrification rates depend on the flux of oxygen from the water column into the sediment interstices. Denitrification and other heterotrophic processes depend on the supply with organic matter along similar flow paths (Baker et al. 1999; Sobczak et al. 2003; Lefebvre et al. 2004). Low activity rates in deep sediment layers thus are either caused by reduced connectivity with the water column or by long hyporheic flow paths during which the substances that fuel microbial metabolism are stripped off the interstitial water. The result of both is reduced substrate supply in these deep sediment layers. Our results corroborate these hypotheses. In nearshore habitats dominated by sedimentation processes, activity was high in the uppermost sediment layer, and sharply decreased towards deeper sediments. Vertical exchange between sediment pore water and the water column is restricted in these sedimentation zones, leading to reduced microbial activity in deeper sediments. In the central river bed, with its more pronounced vertical connectivity, activity was not as high in the uppermost layer as in the sedimentation zones. The depth-integrated activity, however, was 2.9 fold higher than in the adjacent nearshore habitats. The shifting sediments of a free-flowing river, the ecosystem's compartment where several biochemical reactions run at high rates, thus represent a "liver function" in the river's metabolism (Figure 4). These sediments are well connected to the flowing water column via rapid vertical hydrological exchange. In natural lowland rivers, vast areas of the riverbed are covered with these unstable shifting sediment structures (Church 2002), which should exhibit intense hyporheic metabolism.

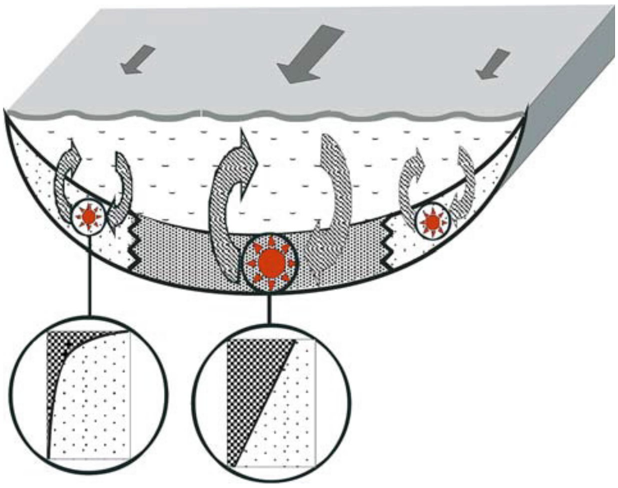

Figure 4. Schematic representation of the ecological functioning of central river sediments as a 'river's liver'. The shifting sediments on the central river bottom of a free-flowing lowland river are well connected to the flowing water column via rapid vertical hydrological exchange. Hence, particulate and dissolved organic matter is constantly transfered into the sediments, where it is partially retained. Thus, the sediments are oxygenated down to a larger depth, and well supplied by organic matter. This enables microorganisms to run their biochemical reactions at high rates down to a considerable sediment depth. In contrast, the nearshore sediments are only badly connected with the water column, and exhibit a much lower microbial activity in deeper sediments. The vertical integration of the activities within the central sediments results in a significant total effect on ecosystem metabolism. This intense hyporheic metabolism thus represents a "liver function" in the river's metabolism.

We used our production data in order to estimate theoretical carbon turnover lengths (Webster and Meyer 1997) by comparison of carbon transport with respiration, including bacterial growth with 30% efficiency (Benner et al. 1988). Such calculations only provide rough estimates due to uncertainties concerning bacterial production measurements and growth efficiency (Bastviken et al. 2003), but are scarce for large rivers. Based on the concentration of total organic carbon in the flowing water of 10 g C m^{-3} during sampling time (Wilczek et al. in press), the mean discharge of the Elbe (Table 1), and the vertical profiles of bacterial production (Table 2), total amounts of 113 and 256 g C h^{-1} were turned over per meter river profile length at Dresden and Coswig, respectively. From that, theoretical carbon turnover lengths can be estimated of about 100 km at Dresden, but only 50 km at the Coswig site with its highly active river bed (Figure 3). The short spiralling length at Coswig underlines the important role that unconsolidated, hydrologically well connected sediments can play in carbon turnover even in large rivers. A comparison with data compiled by Webster and Meyer (1997) shows that the carbon turnover length estimated for the Elbe is an order of magnitude shorter than would be expected by a regression of discharge versus turnover length for a set of 26 streams and rivers from various biomes. This is probably caused by a high proportion of autochthonous, easily degradable organic material (Wilczek et al. in press) as well as by the high interstitial surface area and high retention efficiency in the sediments of the Elbe. Calculations on the turnover of organic nitrogen result in uptake lengths in the same order of magnitude than turnover lengths for organic carbon. However, uptake lengths for nitrogen are probably highly underestimated by such calculations, because the laboratory methods used included nitrate and carbon amendments and aimed to compare habitats rather than provide actual ambient rates (Richardson et al. 2004).

Hence, our findings indicate that it is probably this metabolic activity in the sediments of the central river channel that caused the marked dynamics of carbon and nitrogen compounds in lowland river sections, reported by balancing studies (Alexander et al. 2000; Raymond and Bauer 2001; Seitzinger et al. 2002). In recent concepts of river ecology, the importance of the hyporheic zone as an influential factor on surface water conditions is restricted to lower stream orders (reviewed by Ward et al. 2001). The riverine productivity model (RPP; Thorp and Delong 2002) deals specifically with sources of organic carbon in constrained reaches of larger rivers and is well applicable to the Elbe, but it does not localize the degradation of organic matter. Our findings may not only complement the RPP, but also shed new light on the predictions of the River Continuum Concept (Vannote et al. 1980) concerning the longitudinal mass balance in river networks. For that purpose, it would be valuable to know under which conditions this ‘river’s liver’ would be able to counterbalance net exports of carbon, nitrogen and phosphorus from low order streams via uptake, transformation, and release of transported matter (Fisher et al. 1998; Kaplan and Newbold 2003). The metabolic functionality of streambed sediments is impacted by human alterations in river flow or morphology reducing lateral and vertical connectivity (Dahm et al. 1998). In the case of the Elbe and of other large rivers, the role of groynes and other engineering measures on riverine microbial processes is just beginning to be recognized.

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Microbial respiration within a floodplain aquifer of a large gravel-bed river

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SUMMARY

1. Aerobic respiration, productivity and the carbon turnover rate of microbial biofilms were determined at hyporheic and phreatic sites in the Kalispell Valley alluvial aquifer along a transect extending 3.9 km laterally from the main channel of the Flathead River, a sixth order river in Montana (U.S.A.). The effect of experimentally increasing bioavailable organic carbon (acetate) on the respiration rate of biofilms in this carbon-poor [dissolved organic carbon (DOC) < 2 mg L^{-1}] aquifer was also measured.
2. Chambers containing natural substratum were placed *in-situ* and allowed to colonise for 20 weeks. After 4, 12 and 20 weeks, they were taken to the laboratory where oxygen flux was measured in a computer-controlled, flow-through respirometry system.
3. Respiration ranged from 0.01 to 0.33 mg O_2 dm^{-3} h^{-1} across sites, with means ranging from 0.10 to 0.17 mg O_2 dm^{-3} h^{-1}. Productivity estimates ranged from 0.18 to 0.32 mg C dm^{-3} day^{-1} (mean 0.25, SE 0.03). The total organic carbon (TOC) of the microbial biofilms ranged from 18.2 to 29.7 mg C dm^{-3}. Turnover rate ranged from 3.2 to 5.6 $year^{-1}$ with a mean of 4.2 $year^{-1}$.
4. At the hyporheic site very close to the river, respiration did not significantly increase when samples were supplemented with labile carbon. Respiration increased with increasing DOC addition at hyporheic sites more distant from the river, suggesting a carbon-limitation gradient within the hyporheic zone. Microbes at the phreatic site did not respond to increasing DOC addition, suggesting that the phreatic biofilm is adapted to low carbon availability.
5. Comparing the volume of the alluvial aquifer (about 0.7 km^3) to that of the river benthic sediments (to 0.25 m depth, which amounts to about 1.6×10^{-4} km^3) within the Flathead Valley, leads to the conclusion that interstitial microbial productivity is orders of magnitude greater than benthic productivity. Alluvial aquifers are often voluminous and microbial production is an enormous component of ecosystem production in rivers such as the Flathead.

Keywords: alluvial floodplain, hyporheic, microbial, respiration, river ecology

Introduction

An extensive food web composed of an abundant and diverse assemblage of over 70 taxa of interstitial invertebrates, exists within the alluvial aquifer of the Kalispell Valley floodplain in Montana (Stanford, Ward & Ellis, 1994; Ward, Stanford & Voelz, 1994) and hundreds of organisms have been collected from vertically integrated well samples up to 3 km from the Flathead River. The abundant interstitial biota existing in the alluvial aquifers of the Flathead River is paradoxical, because dissolved organic carbon (DOC) is uniformly low (<2 mg L^{-1}), which should

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substantially limit the microbial food base (Ellis, Stanford & Ward, 1998).

This problem underscores the generally recognised need to understand the ecology of the interstitial biofilms that mineralise organic matter entrained in alluvial aquifers from the river and its floodplain (Pusch *et al.*, 1998). Researchers have observed declining dissolved oxygen (DO) and DOC with increased interstitial residence time of infiltrating surface river waters (Jeppesen, 1982; Whitman & Clark, 1982; Bott, Kaplan & Kuserk, 1984; Grimm & Fisher, 1984; Baker, 1986; Rutherford & Hynes, 1987; Williams, 1989; Hedin, 1990; Vervier & Naiman, 1992; Findlay *et al.*, 1993; Pusch & Schwoerbel, 1994). However, DO and DOC fluxes vary greatly among and within the various hyporheic zones studied, reflecting the complex mosaic of interstitial riverine habitats (Malard & Hervant, 1999). Interstitial microbial production, which is driven by the concentration and supply of DOC, forms the energy base for an invertebrate foodweb within alluvial aquifers and can influence many biophysical processes that control the distribution and abundance of riverine organisms (Bott *et al.*, 1984; Bott & Kaplan, 1985; Barlocher & Murdoch, 1989; Williams, 1989; Hendricks, 1993; Gibert *et al.*, 1994; Stanford *et al.*, 1994; Findlay & Sobczak, 1996; Ellis *et al.*, 1998; Pusch *et al.*, 1998). Hence, the rate and spatial variability of microbial respiration and productivity in relation to DOC supply is key to understanding the contribution of interstitial processes to riverine productivity in large, gravel-bedded rivers with expansive alluvial aquifers.

Studies conducted in the oligotrophic Flathead River demonstrated a complex hydrologic labyrinth of phreatic, hyporheic and surface river water interactions in the extensive alluvial floodplain aquifers (about 10 km long through gravel and cobble alluvium) (Stanford *et al.*, 1994; Poole *et al.*, 1997). Alluvial aquifers associated with large gravel-bed rivers may be characterised by spatially and temporally varying contributions of hyporheic and phreatic waters. We define the hyporheic zone of gravel-bed rivers as that portion of the alluvial floodplain aquifer where river and ground water (and associated materials) exchange rapidly. Phreatic ground water has a long residence time in the aquifer or its source is hypogean and has a very different chemical signature (Stanford & Ward, 1988).

Ellis *et al.* (1998) showed that, in close proximity to the Flathead River, interstitial microbial productivity (0.4–6.9 μg C m^{-2} h^{-1}) was based mainly on biofilms on rocks (epilithic), as opposed to micro-organisms free living in the ground water, and the variance in bacterial density was significantly explained by distance from the river channel. To elaborate these findings and examine the trophic paradox of enormously abundant interstitial invertebrates throughout the aquifer, we examined the spatial characteristics of aerobic respiration and productivity of microbial biofilms in relation to their proximity to the active channel of the mainstem Flathead River. We expected that microbial respiration rate would decrease along the hyporheic to phreatic gradient, because bacterial density and bioavailable riverine dissolved organic matter and associated DOC would progressively decline. We also conducted experiments on potential limitation of biofilm metabolism by bioavailable DOC. The specific objectives of this study were to:

1. determine the respiration rate of microbial biofilms at various points extending kilometres laterally from hyporheic to phreatic areas of the alluvial aquifer;
2. determine the carbon turnover rate of the microbial biofilm at the various sites; and
3. determine the effect of experimentally increasing bioavailable organic carbon on biofilm respiration rate.

Methods

Study site

The alluvial aquifer located in the Kalispell Valley in north-western Montana, U.S.A., is about 5–6 km wide, 13 km long and 10 m deep (Fig. 1). Porous montane alluvium (hydraulic conductivity of 0.1–10 cm s^{-1}), deposited by postglacial outwash, is underlain by an impermeable layer of tertiary clay. Surface water from the Flathead and Whitefish River systems and laterally influent ground waters from the Salish, Swan and Whitefish Mountain Ranges saturate the alluvium within the Kalispell Valley. The aquifer is hydraulically connected with the Flathead River (mean Q, 340 m^3 s^{-1}) and is fed, to a lesser extent, by the Whitefish River (mean Q, 20 m^3 s^{-1}) and other small tributaries (Stanford *et al.*, 1994). Extremely porous ancient subterranean river channels (palaeochannels)

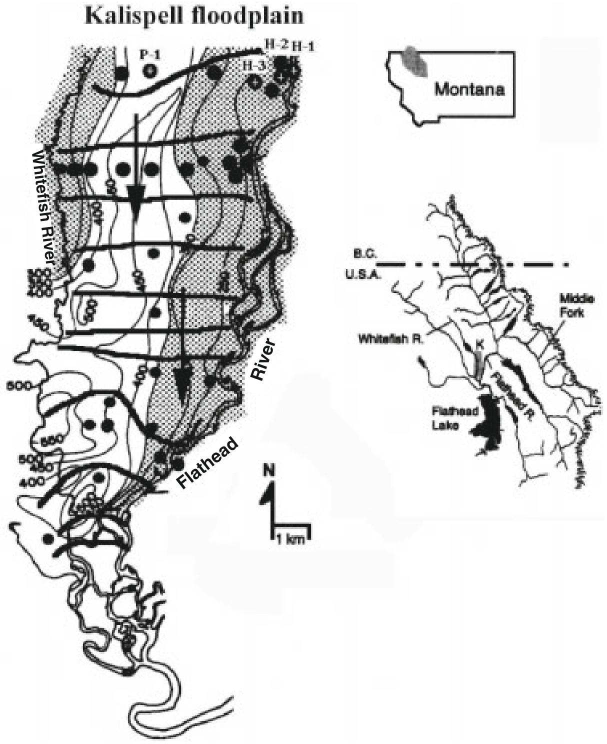

Fig. 1 The alluvial floodplain aquifer in the Kalispell Valley, Montana (stippled area indicates hyporheic). Bold contours depict height of the water table (1.5 m isopleths). Thin contours are isopleths of specific conductance (μS cm^{-1}) of the groundwater. Arrows indicate the direction of groundwater flow (declining height of water table). Solid circles are wells including the study sites H-1, H-2, H-3 and P-1 (modified from Stanford & Ward, 1988).

braiding throughout the valley appear to have a very strong connection to the Flathead River, as indicated by fast recharge rates and a high concentration of DO (>50% saturation) (Stanford *et al.*, 1994). These palaeochannels extend kilometres laterally from the main river and metres vertically. Interlaced between the palaeochannels are deposition areas of gravel, sand and silt, where the flow is reduced and oxygen concentration declines.

The Flathead River is oligotrophic, reflecting its relatively pristine catchment (Stanford *et al.*, 1992). The Flathead Lake Biological Station has monitored river chemistry about monthly since 1977. Nitrite plus nitrate nitrogen and soluble reactive phosphorus (SRP) concentrations were routinely at or below detection limits (2.0 and 0.4 μg L^{-1}, respectively). However, nitrate and SRP concentrations of water samples collected from wells in the centre of the aquifer were an order of magnitude higher (Stanford *et al.*, 1994). Mean DOC concentration for the Flathead River was 1.64 mg L^{-1}, whereas DOC in water samples taken from the monitoring wells throughout the floodplain averaged around 1.17 mg L^{-1} (Ellis *et al.*, 1998). This suggests possible carbon limitation of microbial metabolism within the aquifer (Stanford & Ward, 1988).

Well selection

The Kalispell Valley alluvial aquifer has been studied extensively since the mid-1980s (Stanford & Ward, 1988, 1993; Stanford, 1993; Stanford *et al.*, 1994; Ward *et al.*, 1994; Ellis *et al.*, 1998) using an extensive grid of monitoring wells. The wells were installed to a depth of approximately 6 m, using a hollow auger drill, and perforated by 5 cm × 5 mm slots below the water table. Four of these established monitoring wells, three located in palaeochannels and one below the Flathead River channel, extend 3.9 km along a transect perpendicular to the river (Table 1). The relative affinity of each site to the river channel was clearly indicated by increasing phreatic conditions as distance from the river increased.

Construction of incubation chambers

Field incubation chambers were constructed of rigid tubular polypropylene mesh 40 cm long by 8 cm diameter (4 cm diameter in the P-1 well) with 36–50% open area and a square weave pattern (Conwed Plastics, Minneapolis, MN, U.S.A.) (Fig. 2a). Upper and lower openings were covered by 1 mm nylon mesh. Each chamber was filled with stones 8–12 mm diameter (with a porosity of 38% and a volume of 0.994 dm^3 in large chambers and 0.222 dm^3 in small chambers) collected from an exposed gravel bar (natural substrata were used, because comparisons of bacterial density and productivity on natural rock surfaces and ceramic clay tiles by Ellis *et al.* (1998) showed markedly higher values of both on the rock surfaces). Gravels of this size were common in the alluvium of the floodplain and allowed a large surface area to volume ratio without compromising interstitial flow rates. Rocks were cleaned with hot tap water, rinsed once with 5% HCl for 10 s, rinsed several times with filtered distilled water and autoclaved to remove all residual bacteria and nutrients from the surface. Chambers

Table 1 Physical, chemical and biological characteristics of the four study wells. Sites H-1, H-2 and H-3 were hyporheic and P-1 was more phreatic in character. Distance is measured from the Flathead River. The biological data are presented as a ratio of invertebrates that are obligate groundwater forms (stygobites) to invertebrates that utilise surface waters for at least a portion of their life cycle (amphibites) (i.e. Plecoptera) (see Stanford *et al*., 1994). Benthic invertebrates dominated in H-1, which was in the river channel. Abbreviations: Alkalinity (ALK), specific conductance (COND), dissolved organic carbon (DIC), nitrite plus nitrate nitrogen ($NO_2/3$-N)

	Analysis								
Site	Distance (km)	ALK (mg L^{-1})	COND (μS cm^{-1})	DIC (mg L^{-1})	DOC (mg L^{-1})	DO (mg L^{-1})	$NO_2/3$-N (μg L^{-1})	Biota Stygobites/ amphibites	River affinity
H-1	0.00	90	126	21	1.8	10.8	44	NA	High
H-2	0.02	100	133	22	1.1	7.2	83	1.41	High
H-3	0.65	149	213	34	1.0	6.8	518	1.67	Intermediate
P-1	3.90	199	291	38	0.9	3.8	938	43.8	Low

NA: Not applicable.

were cleaned with hot tap water, rinsed once with 5% HCl for 10 s and rinsed several times with filtered distilled water. Four filled chambers and an empty chamber (blank) were held together using 1.25 cm wide vinyl strapping and 7.6 cm diameter PVC spacers (10 cm high). Rings of foam (1.25 cm wide) around each spacer, and an extra spacer placed at the bottom of the chamber set fitted with a plastic plug, retained interstitial water within each chamber during insertion and removal from the wells. Chamber sets were removed by first inserting a solid, thin-walled PVC sleeve (8.5 cm diameter) down the well, which sealed against the foam rings attached to the spacers, and securing the sleeve to the nylon cord supporting the chamber set. Sealing the chambers before removal protected the fragile biofilm from possible disruption, drying and exposure to air. Then, by pulling up the rope and attached chamber sleeve, the chambers and interstitial water were removed together and submerged in a large trough filled with well water. At this point, the sleeve was removed and the chamber set disassembled underwater.

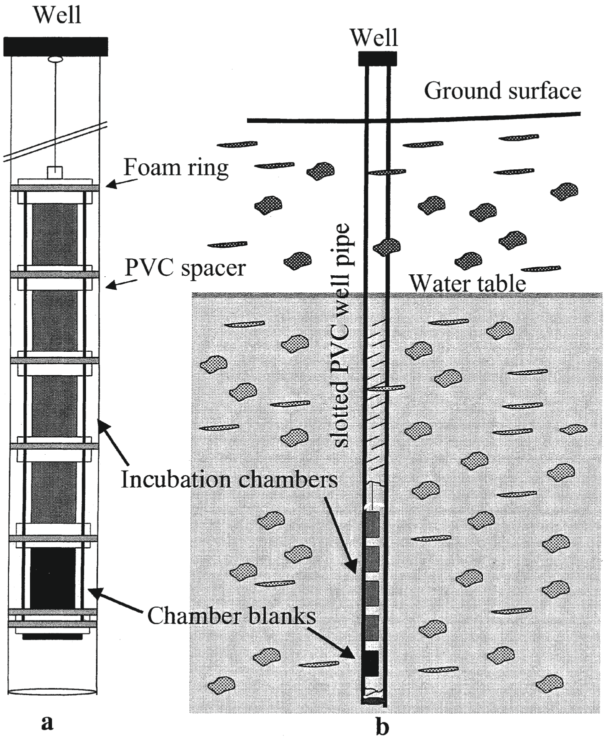

Fig. 2 (a) *In-situ* incubation chamber diagram shown inside of well. (b) Cross-sectional view of alluvial aquifer representing *in-situ* incubation chamber below water table in slotted PVC well.

Incubation in wells

Chamber sets were suspended 0.5 m above the bottom of each well, using nylon cord secured to the well cap, before spring run-off 1995 (Fig. 2b). Chambers were removed from the wells after 4, 12 and >20 weeks incubation time, corresponding to the rising limb, falling limb and base flow of the hydrograph (H-1 chambers were not removed at the 12-week incubation period because of inaccessibility of chambers during high flow). After removal from the well, each chamber was sealed in individual watertight containers and transported to the Flathead Lake Biological Station (30 min travel time). After laboratory measurements were concluded (about 24 h), the chambers were returned to the well site.

Determination of in-situ conditions

After the chambers were removed, the wells were pumped for 10 min to clean the gas powered diaphragm pump and tubing, then 60 L of water pumped from the well was placed within a sterile polypropylene carboy. This water was transported back to the lab and used to fill the *in-vitro* respiration measurement systems. Dissolved oxygen and temperature measurements were taken within the well before and after pumping using a YSI model 58 DO meter with a YSI model 5739 DO probe and a YSI model 3000 temperature-level-conductivity meter (YSI Incorporated, Yellow Springs, OH, USA). These measurements were used to set initial temperature and DO concentration in the respiration measurement chamber system.

Determination of respiration rates

Chambers were removed from one well at a time and transported to the laboratory. Then, one at a time, each incubation chamber was placed within a respiration measurement system consisting of a PVC sediment chamber holder and Plexiglas O_2/temperature probe chamber connected by TYGON SE-200 FEP lined tubing; modified after Pusch & Schwoerbel (1994) (Fig. 3). The measurement system was filled with 800 mL of well water (300 mL for P-1 incubation chambers) previously calibrated to *in-situ* DO (using bubbled nitrogen gas to lower DO and bubbled air to raise DO) and temperature, carefully purged to remove any air bubbles, sealed and immersed in a temperature controlled circulating water bath set to *in-situ* temperature measurements (Intermatic Model 2325, Thermo Forms, Mulietta, OH, USA). An internal circulation rate of 45 mL min^{-1} was maintained by attaching the chamber system to a peristaltic pump (Masterflex Model 77000-30, Cole-Parmer Instrument Co., Vernon Hills, IL, USA).

Microbial respiration was determined by measuring oxygen flux within the sealed chamber system. Dissolved oxygen and temperature were measured with a Strathkelvin model 1302 oxygen electrode with a model 781b DO meter and a TC-101 type T thermocouple temperature sensor. Using DATACAN V-BUS data acquisition software (Sable Systems, Inc., Salt Lake City, UT, U.S.A.), 3000 readings were integrated and recorded each minute over a 4-h period on an IBM compatible computer. Respiration analysis was performed using DATACAN V-BUS data analysis software (Sable Systems, Inc.). First, oxygen measurement runs were corrected for linear baseline drift using pre and post run zero O_2 baseline measurements. Then, noise spikes were replaced with linear interpolations of data points before and after the spike. Next, temperature data were examined to ensure stable temperatures throughout the run (runs with drifting temperature were not analysed). Finally, a linear regression was calculated for the run and the slope recorded. For each set of four sediment filled incubation well chambers analysed, a fifth incubated chamber blank (no sediments) was run. The resulting oxygen consumption by the microbial biofilm growing on the chamber blank was subtracted from the sediment chamber runs.

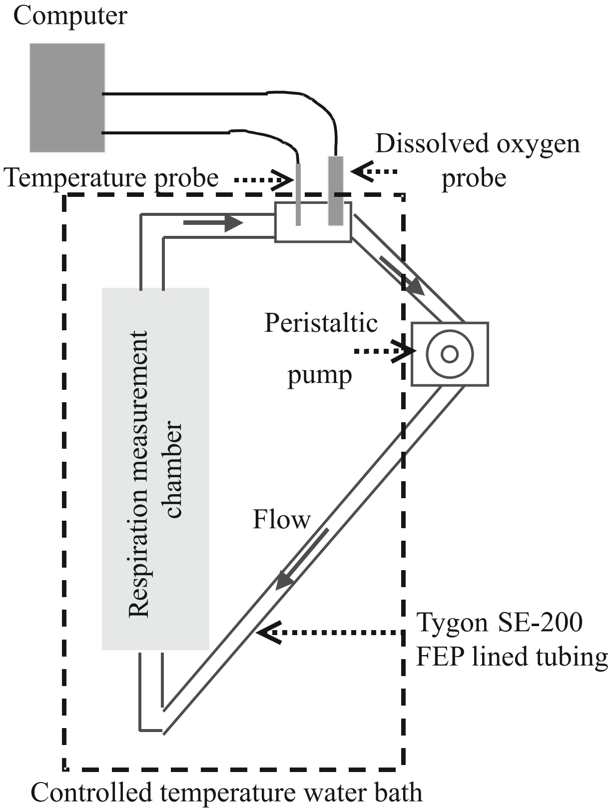

Fig. 3 *In-vitro* closed flow-through respiration chamber measurement system.

Response to DOC supplementation

Following the last time-series oxygen flux measurements (>20 weeks incubation), subsamples of about

20 stones from each field chamber were removed and placed into a smaller respiration chamber system. Midway through a 4-h respiration analysis, the natural DOC in the well water was supplemented with four treatment levels of acetate; an additional 0.1, 0.25, 0.5, 1 and 1.5 mg C L^{-1} ($n = 4$ for each treatment at each site). Response was measured as change in oxygen flux after addition compared with the preaddition background.

Determining organic carbon content of microbial community

Following the last time series of oxygen flux measurements, four subsamples of 10 stones each from the field chambers were removed ($n = 16$ for each well). These were placed in 125 mL Erlenmeyer flasks (fired at 500 °C for 12 h) with 30 mL carbon free water and sonicated for 20 min to remove the epilithic microbial biofilm. The resulting slurry was analysed for total organic carbon (TOC) using an Oceanography International Corporation trapping-desorption module and infrared CO_2 gas analyser (persulphate digestion; infrared CO_2 detection method; Menzel & Vaccaro, 1964).

Determination of spatial relations

Statistical tests (ANOVA/MANOVA) were performed using SYSTAT V.5.02 (SYSTAT, Inc, SPSS Science, Chicago, IL, USA). Comparisons of microbial respiration were made between: (1) the four incubation chambers at each site and the four sampling sites on the last sampling date (mature biofilms); (2) the four incubation chambers at each site and the three sampling dates; and (3) the four incubation chambers at each site and the four experimental DOC addition concentrations and the four sampling sites.

Results

Temperature ranged from 0.7 to 13.1 °C and DO concentration ranged from 45 to 101% saturation for the three hyporheic sites throughout the study. The phreatic site had a temperature range of 5.7–8.8 °C and DO concentration ranged from 15 to 60% saturation. Respiration measurements of the microbial community attached to the chamber blanks ranged from 0.00 to 0.03 mg O_2 dm^{-3} h^{-1} and never accounted for more than 10% of the total incubation chamber respiration measurements.

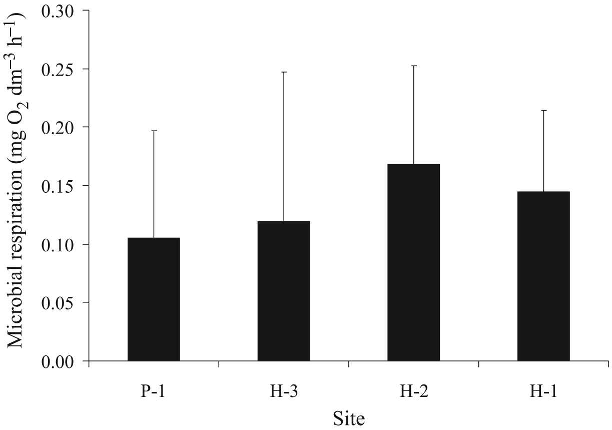

Fig. 4 Microbial respiration (mg O_2 dm^{-3} h^{-1}) of mature aquifer biofilms. Sites are arranged with increasing river affinity from left to right. Error bars represent 1 SD.

Respiration activity of mature microbial communities (incubated for over 20 weeks) ranged from 0.01 to 0.33 mg O_2 dm^{-3} h^{-1} for the four sites with the means ranging from 0.10 to 0.17 mg O_2 dm^{-3} h^{-1} (Fig. 4). There were no significant differences between the sites ($P > 0.05$, ANOVA).

To transform the respiration data from mg O_2 to mg C, the equation $R(C) = R(O_2) \times 0.375 \times 0.85$ was used; where $R(C)$ = respiration (mg C dm^{-3} h^{-1}), $R(O_2)$ = measured respiration (mg O_2 dm^{-3} h^{-1}), 0.375 = the weight ratio of carbon to oxygen in CO_2, and 0.85 is the respiratory quotient (Bott & Kaplan, 1985). Daily productivity of the mature biofilms was then calculated using the equation P (mg C dm^{-3} day^{-1}) = $R(C) \times 0.24 \times 24$ h; where 0.24 is a biosynthesis to respiration factor (Bott & Kaplan, 1985). Microbial productivity rates were estimated as 0.18, 0.22, 0.31 and 0.26 mg C dm^{-3} day^{-1} for the sites P-1, H-3, H-2 and H-1, respectively (mean 0.24, SE 0.03). Using the respiration (mg O_2) to microbial productivity (mg C) factor 0.08 (Sorokin & Kadota, 1972) yielded similar estimates of 0.19, 0.23, 0.33 and 0.27 mg C dm^{-3} day^{-1} for the sites P-1, H-3, H-2 and H-1, respectively (mean 0.26, SE 0.03).

Time series analysis (Fig. 5) showed no significant differences in microbial respiration relative to incubation time ($P > 0.05$, ANOVA). Excluding sampling runs (measurements of the chamber sets from a well) where $n = 1$, minimum respiration rate ranged from 0.01 to 0.07 mg O_2 dm^{-3} h^{-1} and maximum rate

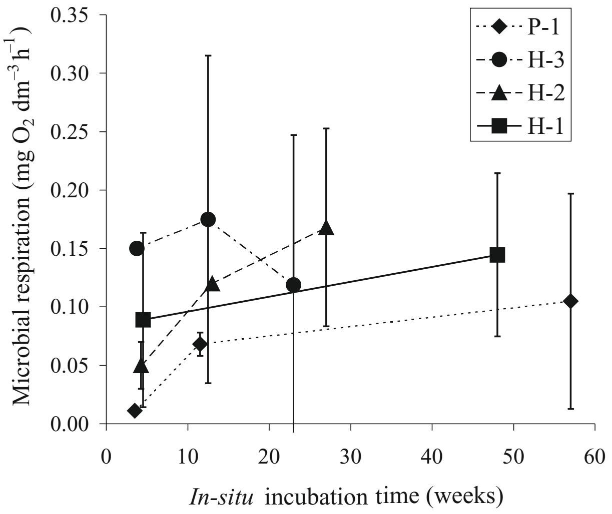

Fig. 5 Microbial respiration (mg O_2 dm^{-3} h^{-1}) of aquifer biofilms at 4, 12 and >20 weeks of *in-situ* incubation. Error bars represent 1 SD.

ranged from 0.07 to 0.35 mg O_2 dm^{-3} h^{-1}. Higher rates tended to be observed as the microbial assemblage matured (respiration increased with incubation time).

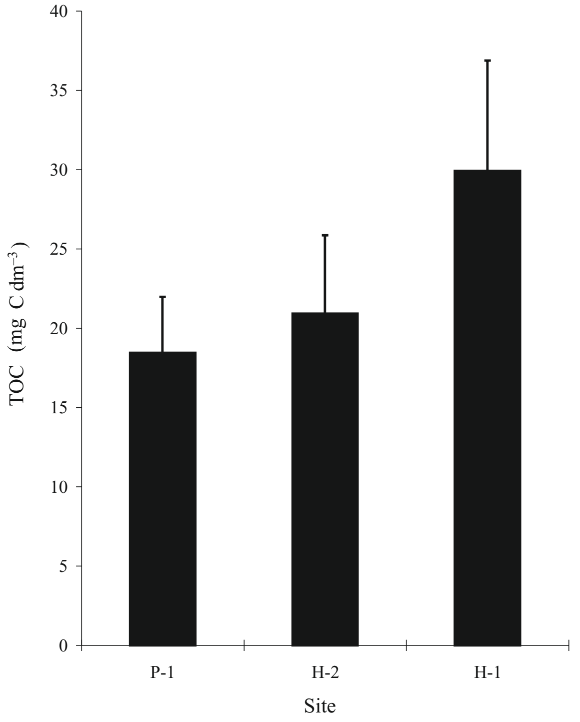

Fig. 6 Total organic carbon (TOC, mg C dm^{-3}) of mature biofilms. Sites are arranged along the phreatic–hyporheic gradient from left to right. Error bars represent 1 SD.

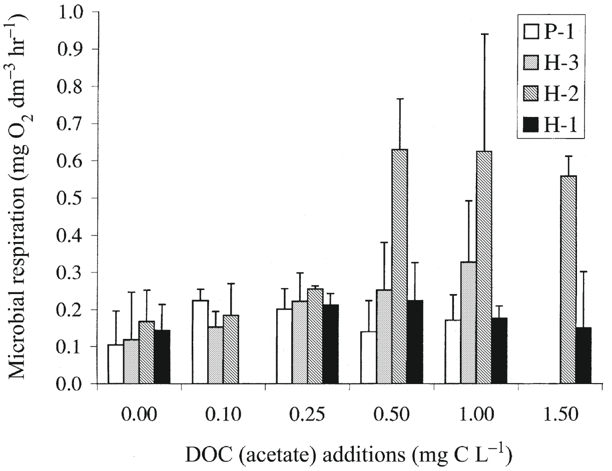

Fig. 7 Microbial community metabolic response to an experimental labile dissolved organic carbon (DOC) supplement (acetate) measured as oxygen consumption. Error bars represent 1 SD.

The TOC of the microbial biofilm from P-1, H-2 and H-1 sites (the H-3 site was not included because of chemical contamination during laboratory preparation of the samples) indicated a trend of increasing organic carbon associated with increasing river affinity (Fig. 6). Both the P-1 and H-2 sites were significantly lower than the H-1 site located directly below the river channel ($P < 0.001$ and 0.05, respectively, ANOVA). However, there was no significant difference between the P-1 and H-2 sites. Turnover rates (productivity/biomass carbon) ranged from 3.2 to 5.6 $year^{-1}$ with a mean of 4.2 $year^{-1}$.

Experimental additions of a labile carbon source (acetate) to the microbial biofilm significantly increased respiration in over 95% of the runs ($P < 0.05$, MANOVA) (Fig. 7). Of the 17 experimental boxes (site × treatment), 10 of the means were significantly higher than preaddition background ($P < 0.05$, ANOVA). Treatments for the P-1 site were 0.1, 0.25, 0.5 and 1.0 mg C L^{-1} [mean DOC for the four sampling sites is 1.2 mg L^{-1} (Table 1), and averaged 1.2 mg L^{-1} for all floodplain monitoring wells (Ellis *et al.*, 1998)]. Mean response of the biofilm ranged from an increase in oxygen depletion of 0.04–0.12 mg O_2 dm^{-3} h^{-1}. Although the respiration increase was significant over background ($P < 0.01$, ANOVA), altering the treatment had no discernible effect. The treatments also ranged from 0.1 to 1.0 mg C L^{-1} for the H-3 site, with a mean response ranging from 0.03 to 0.21 mg O_2 dm^{-3} h^{-1} increase in microbial respiration. However, at the H-3 site, there was a trend of increasing respiration associated with an increasing DOC treatment. At the H-2 site, this increase became significant ($P < 0.01$, MANOVA) and a fifth treatment of 1.5 mg C L^{-1} was added to the series. At this site very near the river, respiration increases were 0.02, 0.12, 0.46, 0.46 and 0.39 mg O_2 dm^{-3} h^{-1} for the DOC additions of 0.1, 0.25, 0.5, 1.0 and 1.5 mg C L^{-1}, respectively. An increase of 0.46 mg O_2 dm^{-3} h^{-1} represents a respiration rate of 0.63 mg O_2 dm^{-3} h^{-1}, a productivity of 1.2 mg C m^{-3} day^{-1} and a turnover rate of 21 $year^{-1}$. Treatments for the H-1 site were 0.25, 0.5, 1.0 and 1.5 mg C L^{-1}. Response to acetate supplementation ranged from a mean of 0.01–0.08 mg C dm^{-3} h^{-1}. This site showed the least response to acetate with only one of the four means significantly different from preaddition background values ($P < 0.05$, ANOVA).

Discussion

Respiration activity of mature microbial communities for the four sites (range 0.01–0.33 mg O_2 dm^{-3} h^{-1}, means 0.10–0.17 mg O_2 dm^{-3} h^{-1}; Fig. 4) were very similar to those obtained during the same time period in the hyporheic zone of the Nyack floodplain (fifth order reach of the Middle Fork Flathead River), approximately 50 km upstream (mean hyporheic community respiration was 0.18 mg O_2 dm^{-3} h^{-1} and ranged from 0.06 to 0.36). Pusch & Schwoerbel (1994) found similar respiration activity (mean respiration of 0.326 mg O_2 dm^{-3} h^{-1}; ranging from 0.064 to 0.96) in the shallow hyporheic sediments of a third order mountain stream in southern Germany (Steina, Black Forest). The values in this study were higher than those reported by Naegeli *et al.* (1995) (0.05–0.07 mg O_2 dm^{-3} h^{-1}) for the hyporheic community of a pristine cold water prealpine gravel-bed river in Switzerland (Necker) and lower than Jones (1995) reported (0.4–1.8 mg O_2 dm^{-3} h^{-1}) for a warm water sonoran desert stream in Arizona, U.S.A. (Sycamore Creek).

The uniform means of the respiration measurements at the four sites indicated relatively equivalent aerobic microbial activity on a macro scale (metres to kilometres) throughout the alluvial aquifer with relative length of flow path having only a minor influence on community respiration. This may, in part, be influenced by the lower river stage during our autumn/winter measurements. River-aquifer exchange may be reduced at low flow and higher river stages during spring freshet may induce seasonal variability (Baker, Dahm & Valett, 2000). Also, nutrient and carbon loading from the river is certainly augmented by water percolation through surface sediments, which would also influence the aquifer processes seasonally and spatially. Thus, the interactions of the river seasonal hydrograph and seasonal variation in water exchange through percolation may affect carbon loading to the aquifer, such that a straightforward correlation between the hyporheic–phreatic gradient and microbial productivity was masked. Based on the order of magnitude range in individual chamber measurements and variability at each site on a micro scale (metres or less), the microbial community may be very patchy. Barlocher & Murdoch (1989) also found great variability in bacterial and fungal communities on individual hyporheic substratum. This only adds to the difficulty in observing potential patterns on a floodplain scale.

Rates of microbial production (estimated as 0.18–0.19, 0.22–0.23, 0.31–0.33 and 0.26–0.27 mg C dm^{-3} day^{-1} for the sites P-1, H-3, H-2 and H-1, respectively; mean 0.24–0.26, SE 0.03) seemed very low in relation to the seemingly abundant metazoa in the aquifer observed by Stanford *et al.* (1994). Turnover rates (productivity/biomass carbon) ranged from 3.2 to 5.6 $year^{-1}$ with a mean of 4.2 $year^{-1}$ were uniformly low but TOC of the microbial biofilm increased with increasing river affinity (means of 18.2, 20.8 and 29.7 mg C dm^{-3} for sites P-1, H-2 and H-1, respectively) (Fig. 6). This same trend was documented by Ellis *et al.* (1998) for bacterial density in the Kalispell Valley floodplain. For a greater perspective, we compared respiration and productivity estimates from the Kalispell Valley aquifer to various measures of stream benthic productivity in other studies, which were also calculated from community respiration measures. Hedin (1990) investigated benthic community respiration in a woodland stream (New Hampshire, U.S.A.) and measured a range of 26–340 mg C m^{-2} day^{-1} using *in-situ* sediment incubation chambers filled 5 cm deep. This extrapolates to a productivity estimate of 0.12–1.6 mg C dm^{-3} day^{-1}. Bott *et al.* (1985) measured respiration in four temperate streams and reported seasonal means ranging from 0.19 to 5.79 g O_2 m^{-2} day^{-1}. This reflects stream productivity ranging from 0.31 to 9.3 mg C dm^{-3} day^{-1} assuming

5 cm depth. Productivity was estimated at about 0.83 (SD 0.12) mg C dm^{-3} day^{-1} for the Flathead River benthos (5 cm depth) in the study area during September using O_2 flux data from *in-situ* incubation chambers in a previous study (Perry, Perry & Stanford, 1987). Thus, our estimates of 0.25 mg C dm^{-3} day^{-1} for the aquifer was within the lower range of stream benthic productivity values and presumably influenced by the oligotrophic status of this pristine catchment.

Microbial productivity within the Kalispell Valley aquifer per unit area was approximately 30% that of the Flathead River benthic community. Comparing the volume of the alluvial aquifer (about 0.7 km^3 to the stream benthic sediments 0.25 m depth; about 1.6×10^{-4} km^3) in the Flathead Valley leads to the conclusion that total aquifer productivity is much greater than benthic productivity, possibly by orders of magnitude. Microbial production within the alluvial aquifer apparently is a large component of riverine ecosystem production in large glacially scoured river systems, such as the Flathead. Moreover, the microbial assemblage is significantly more responsive to DOC addition (Fig. 7), suggesting the hyporheic zone of the river is most important in terms of microbial metabolism and probably total bioproductivity of the interstitial food web as a whole.

The pattern of increasing microbial respiration in response to increasing DOC along the phreatic–hyporheic groundwater gradient (Fig. 7) suggested possible community or metabolic adaptations of the microbial biofilms. The dramatic response of the biofilm to DOC addition at the H-3 and H-2 sites indicated that DOC is limiting and very tightly cycled in these areas. Saturation, however, occurred at a relatively low level (1.5 times background). Hyporheic sediments probably receive the higher quality algal exudates associated with channel scouring during peak flow events (Findlay *et al.*, 1993). The microbial community close to the river channel may have adapted to utilising high quality DOC (labile short chain carbon molecules) associated with river scouring events. In sediments below the river channel (site H-1), DOC limitation may be replaced by phosphorus or nitrogen limitation. In phreatic areas far from the river, it is unlikely that pulses of higher quality DOC reach the microbial community. In these areas, there may be a steady supply of low quality DOC (non-labile long chain carbon molecules) (Findlay *et al.*, 1993; Hendricks, 1993). The microbial community may be adapted to utilizing lower quality DOC inputs from the river, soil percolation after rain events or deep groundwater sources.

We focused this research on aerobic microbial respiration to quantify the food resources available to the aquifer biota. We assumed that in the very porous alluvium of the Flathead River aquifer, with abundant oxygen (typically >50% saturation), microbial productivity would be dominated by heterotrophic decomposition of organic compounds using aerobic respiration to maximise energy liberation (Gounot, 1994). However, we recognise the extremely complex and dynamic nature of the Flathead River interstitial environment, including the heterogeneous porewater chemistry and the likelihood of anaerobic microzones within the gravel lattice of the aquifer. Anaerobic microbial respiration (using nitrate, ferric ions or sulphate as alternative electron acceptors) may prove to be an important component of the hyporheic food web (Findlay, 1995; Findlay & Sobczak, 2000). Anaerobic respiration is only slightly less efficient than aerobic processes and may account for a significant proportion of the total hyporheic productivity (Storey, Fulthorpe & Williams, 1999). Indeed, Baker, Dahm & Valett (1999) found that most of the experimentally injected acetate retained in the oxygen depleted sandy hyporheic zone of a first order stream in New Mexico occurred through anaerobic pathways.

Identification of a physiological or community composition change in the microbial community in relation to the hyporheic–phreatic gradient may be key to understanding the varied metabolic response to the labile DOC (acetate) addition experiments (Storey *et al.*, 1999). Coupling a spatial, temporal and quality assessment of organic carbon loading to the aquifer from riverine versus floodplain sources (litter layer, seasonally flooded soils and the vados zone) would aid in identifying the patch dynamics of interstitial aquatic microbial assemblages and metabolic processes (Findlay & Sobczak, 2000). Indeed, the results of our study infer (see also Baker *et al.*, 2000) that the primary source of labile organic compounds driving interstitial microbial production is the floodplain, not the river.

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Comparison of bacterial production in sediments, epiphyton and the pelagic zone of a lowland river

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SUMMARY

1. The microbial metabolism of organic matter in rivers has received little study compared with that of small streams. Therefore, we investigated the rate and location of bacterial production in a sixth-order lowland river (Spree, Germany). To estimate the contribution of various habitats (sediments, epiphyton, and the pelagic zone) to total bacterial production, we quantified the contribution of these habitats to areal production by bacteria.

2. Large areas of the river bottom were characterized by loose and shifting sands of relatively homogenous particle size distribution. Aquatic macrophytes grew on 40% of the river bottom. Leaf areas of 2.8 m^2 m^{-2} river bottom were found in a 6.6 km river stretch.

3. The epiphyton supported a bacterial production of 5–58 ng C cm^{-2} h^{-1}. Bacterial production in the pelagic zone was 0.9–3.9 μg C L^{-1} h^{-1}, and abundance was 4.0–7.8 × 10^9 cells L^{-1}. Bacterial production in the uppermost 2 cm of sediments ranged from 1 to 8 μg C cm^{-3} h^{-1}, and abundance from 0.84 to 6.7 × 10^9 cells cm^{-3}. Bacteria were larger and more active in sediments than in the pelagic zone.

4. In spite of relatively low macrophyte abundance, areal production by bacteria in the pelagic zone was only slightly higher than in the epiphyton. Bacterial biomass in the uppermost 2 cm of sediments exceeded pelagic biomass by factors of 6–22, and sedimentary bacterial production was 17–35 times higher than in the overlying water column.

5. On a square meter basis, total bacterial production in the Spree was clearly higher than primary productivity. Thus, the lowland river Spree is a heterotrophic system with benthic processes dominating. Therefore, sedimentary and epiphytic bacterial productivity form important components of ecosystem carbon metabolism in rivers and shallow lakes.

6. The sediments are focal sites of microbial degradation of organic carbon in a sand-bottomed lowland river. The presence of a lowland river section within a river continuum probably greatly changes the geochemical fluxes within the river network. This implies that current concepts of longitudinal biogeochemical relationships within river systems have to be revised.

Keywords: bacterial production, lowland rivers, macrophytes, pelagic zone, sediments

Introduction

Stream sediments are generally covered by biofilms, which are densely colonized by bacteria and exhibit intense microbial metabolism (e.g. Lock, 1993; Fischer, Pusch & Schwoerbel, 1996; Marxsen, 1999). The contact area between stream water and these biofilms

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is extended in the hyporheic and the riparian zones. Because of their large inner surface areas and great storage capacities for organic matter (Brunke & Gonser, 1997; Pusch *et al.*, 1998), these ecotones are assumed to dominate the heterotrophic metabolism of streams (Hendricks, 1993; Pusch & Schwoerbel, 1994; Sobczak, Hedin & Klug, 1998). Less than 1 of the community respiration in these streams occurs in the water column (Fuss & Smock, 1996; Naegeli & Uehlinger, 1997).

In higher order streams and rivers, the proportion of the hyporheic and riparian zones in the cross-sectional area of the stream channel generally decreases substantially in comparison with smaller streams, and so does the retentiveness for organic matter (Minshall *et al.*, 1983). In running water ecology it is therefore assumed that the contribution of the benthic, hyporheic, and riparian zones to total ecosystem metabolism decreases with higher stream order (Vannote *et al.*, 1980). High pelagic primary production can particularly be found in mid-regions of rivers where water is not too deep or too turbid to prevent autochthonous production (Reynolds & Descy, 1996), and in large rivers with constricted channels where allochthonous inputs are reduced (Thorp & Delong, 1994). This general longitudinal pattern can be altered by artificial impoundments (Ward & Stanford, 1983) or natural lakes along the river course which serve as additional plankton sources. In general, surface-associated heterotrophic processes should reduce in importance in relation to pelagic metabolism along the longitudinal course of a river (i.e. with increasing stream order) (Schwoerbel, 1994a; Allan, 1995). However, the microbial metabolism of organic matter in rivers has received little study compared with that of small streams, so that little empirical evidence exists to support this assumption. In contrast, in the blackwater Ogeechee River benthic bacteria were found to be a major driver of system respiration. Bacterial respiration was estimated to contribute almost 100% to system respiration (modal value of 97%), and benthic bacterial respiration was ≥ 97% of total bacterial respiration (Edwards, Meyer & Findlay, 1990).

In the present study, we compared bacterial production, as a measure of heterotrophic bacterial activity, in three habitats of a sixth-order lowland river (Spree, Germany): the pelagic zone, the epiphyton and the sediments. We also mapped the spatial distribution of these habitats in a 6.6-km long river stretch. In this section, we estimated the density of macrophyte vegetation and the leaf area susceptible to epiphyton colonization. To estimate the contribution of the various habitats to total bacterial production in the Spree, we calculated production rates on an areal basis of sedimentary, pelagic and epiphytic bacteria. We hypothesized that even in the phytoplankton-rich River Spree, benthic heterotrophic activity by bacteria would dominate the heterotrophic metabolism of the whole running water ecosystem.

Methods

Study site

The Spree rises at 397 m above sea level in the Lusatian Mountains at the Czech/German border and flows, after a course of 400 km, into the River Havel, a tributary of the River Elbe (Fig. 1). In most of its course, the river flows through lowlands consisting of porous glacifluvial sands partially covered with peat. There, it passes several glacigenic lakes and reservoirs, where the river water is heavily loaded by phytoplankton (Köhler, 1994). These flow-through lakes together with the orography and geology of the catchment considerably mitigate the flow regime of the river, so that floods hardly occur during summer. The site we investigated was located approximately 40 km east of Berlin in the lower Spree section of the so called Müggelspree'. This sixth-order section of River Spree flows in a wide glacigenic valley which is characterized by a low longitudinal gradient of 0.015%, a mean water depth of 1.25 m, and a mean channel width of 25 m.

The phytoplankton supplied by lakes and reservoirs keeps growing within the free-flowing river sections, especially during spring (Köhler, 1994; Köhler & Bosse, 1998). Primary production of 0.9 g C m^2 day^{-1} (seasonal mean 1993–95; J. Köhler unpubl. data) is well within the range of large rivers (0.6–1.7 g C m^2 day^{-1}; Descy, Everbecq & Smitz, 1988). Thus, in its middle and lower sections, the Spree is a typical lowland river rich in seston and phytoplankton, with sandy sediments in the main channel. Losses of phytoplankton in this river stretch are high (Köhler & Bosse, 1998) because of turbulence (Sukhodolov, Thiele & Bungartz, 1998), sedimentation

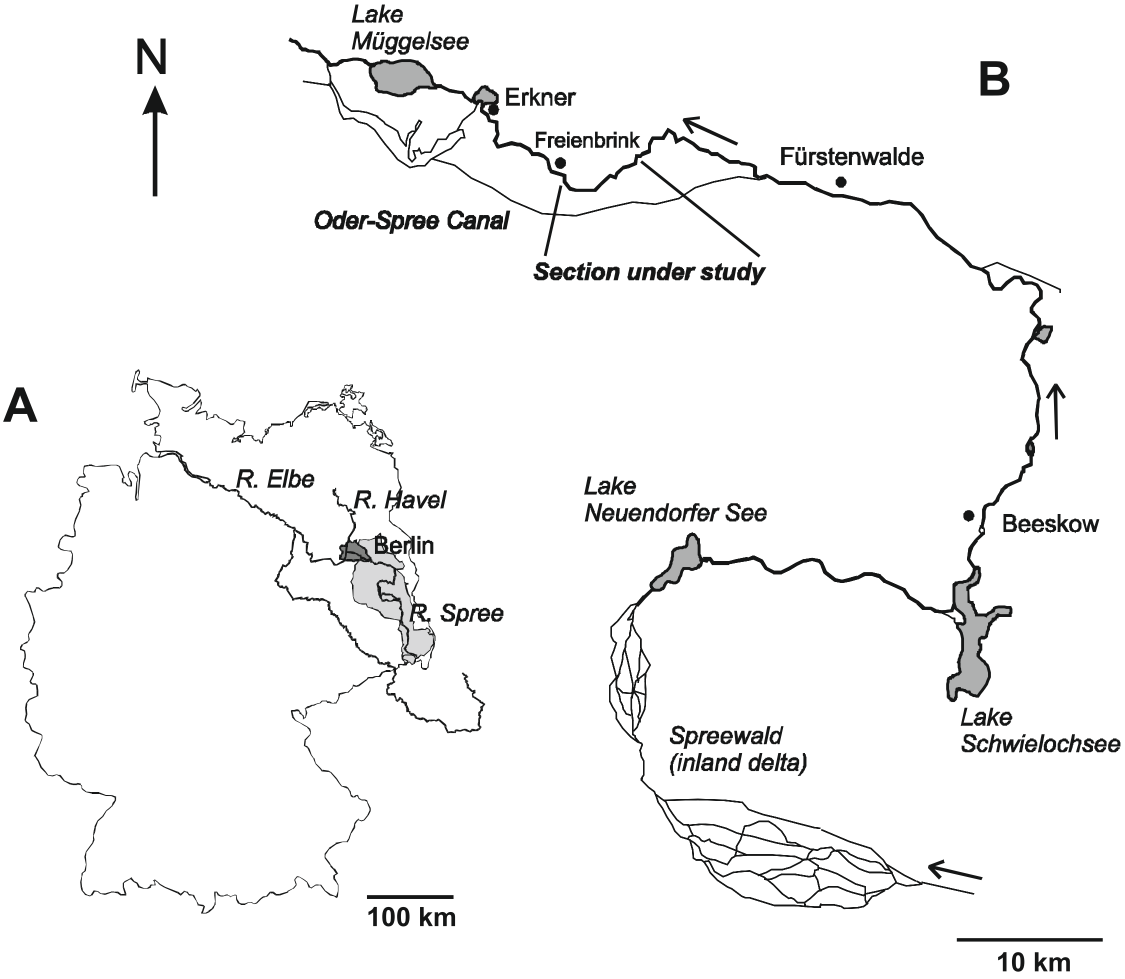

Fig. 1 (a) Map of Germany with the Rivers Spree, Havel, and Elbe, the catchment of the R. Spree (shaded light grey) and the city of Berlin (shaded dark grey), (b) Map of the R. Spree, and location of the investigated river section. Arrows indicate flow direction.

(Wanner & Pusch, 2000) and mussel filtration (Pusch, Siefert & Walz, 2001).

Macrophytes have increased in density during the last 5 years, paralleled by a decrease in the concentration of total seston and planktonic algae during the summer months (M. Pusch *et al.*, unpubl. data). Flow velocities at mean discharge ranged from 0–20 cm s^{-1} in macrophyte stands close to the river banks to 50–60 cm s^{-1} above the shifting sands and the stands of *Potamogeton pectinatus* L. in the mid-channel.

We took samples from the sediments, the epiphyton and the pelagic zone on four dates (August 1997, October 1997, March 1998 and June 1998). On each sampling date, we sampled all the habitats within a time span of 5 days to minimize variability caused by environmental changes.

Bacterial abundance and production: sediments

For each sampling campaign, we took five sediment cores from each of two different sediment types in the River Spree: (1) shifting sands that were low in organic matter and had a relatively homogenous particle size distribution and coatings of iron and manganese oxides; (2) stratified sandy sediments that were higher in organic matter content, had a more heterogenous particle size distribution and a smaller median particle size (Fischer, 2000). The uppermost 2 cm of the cores were examined in this study. Subsamples of 1 cm^3 sediment were taken with a 2-mL polyethylene syringe with the tip cut off and filled into precombusted 10 mL centrifuge vials containing 4 mL of fresh, sterile-filtered (0.2 μm pore size) river water. The vials were then kept at 4 °C until the experiment, which was started within 5 h after sampling. Particulate organic matter (POM) was determined as loss on ignition. Subsamples of 15–25 g wet weight were dried to constant weight at 105 °C, and subsequently burnt for 6 h at 550 °C in order to determine POM as ash free dry mass. The remainders of the samples were pooled for each sediment type, dried, and sieved through a standard set of sieves comprising of mesh sizes from 63 μm to 6.3 mm in order to examine particle size distribution and the coefficient of particle size heterogeneity [sorting coefficient, $\mathrm{So} = (\mathrm{d25}/\mathrm{d75})^{0.5}$] of the sediments (Schwoerbel, 1994b).

Bacterial production was measured using the leucine incorporation method (Kirchman, 1993) as modified by Fischer & Pusch (1999). We used L-[U-^{14}C]leucine (Amersham International, Amersham, U.K., specific activity 11.6 GBq mmol^{-1}) diluted with cold L-leucine to a specific acitivity of 148 Bq nmol^{-1} leucine, and incubated the samples in vials at *in situ* temperatures, with gentle shaking. Two controls for each set of five samples were fixed with 3.2% formaldehyde (final concentration) immediately at the start of the incubation. Bacterial carbon production was calculated from leucine incorporation assuming 7.3 mol percentage leucine in total protein, and a carbon/protein ratio of 0.86 (Simon & Azam, 1989).

The subsamples used for bacterial cell counts were taken after a 10-min sonication step (Brunke & Fischer, 1999; Fischer & Pusch, 1999) and diluted with a sterile filtered aqueous solution of 3.5% formaldehyde, 0.85% NaCl and 1 mM pyrophosphate. Bacteria were stained using 4′,6-diamidino-2-phenylindol (DAPI) (Porter & Feig, 1980) at a final concentration of 10 mg L^{-1}. After 40 min of dark incubation, bacteria were filtered onto black polycarbonate filters (Nuclepore, pore size 0.2 μm). At least 200 bacteria within at least 10 microscopic fields were directly counted by epifluorescence microscopy (Nikon FXA Microscope, HBO 100 W, Ex 330–380, DM 400, BA 400, immersion objective CF N DIC Plan Achromate 100×).

Bacterial abundance and production: epiphyton and pelagic zone

Leaves of three of the most abundant macrophyte species in the Spree – *Sagittaria sagittifolia* L. (Alismataceae VENT.), *Sparganium emersum* REHMANN (Sparganiacea RUDOLPHI), *P. pectinatus* L. (Potamogetonaceae DUM.) – were randomly cut from 10 to 40 cm below the water surface. For *S. sagittifolia* and *S. emersum*, discs of 11.6 and 9.2 mm in diameter, respectively, were cut out with a corkborer. Five leaf discs of *S. sagittifolia* were added to 20 mL scintillation vials containing 5 mL of prefiltered river water; for *S. emersum*, six leaf discs were used (replication: five lots of five or six discs and two lots with killed controls for each species). For *P. pectinatus*, which has filamentary leaves, five pieces of 0.17–0.25 g total fresh weight were weighed into each of the five replicate and two control vials. Samples were incubated for 90 min at a leucine concentration of 1500 nM with 1480 Bq nmol^{-1} specific activity. Further processing of the samples was performed according to Fischer & Pusch (1999).

Pelagic samples of 4.8 mL river water were mixed with 0.2 mL leucine immediately after sampling to achieve a final concentration of 100 nM leucine. Incubation time was 50 min and specific activity was 11 562 Bq nmol^{-1} leucine. Incubation was terminated by adding formaldehyde to a final concentration of 3.2 . Bacteria from the pelagic zone were counted as described above for sediment bacteria.

Bacterial biomass estimates

Photographs of DAPI stained bacteria were taken and analysed using a Nikon SMZ-U stereo microscope with a drawing tube attached to a digital graphics tablet. Length and width of 100 bacteria per sample, taken from at least two photographs, were recorded and their biovolumes were calculated according to Fry (1988). Bacterial volume (V in μm^3) was converted into carbon (C in fg) using the allometric model $C = 104.5 \times V^{0.59} \times 0.86$, where 104.5 is the protein (in fg)/biovolume (in μm^3) conversion factor and 0.86 the carbon/protein conversion factor (Simon, Alldredge & Azam, 1990; a discussion of volume/biomass conversion factors is found in Fischer, 2000).

Sediment and macrophyte mapping

In July 1995, the distribution of sediments and macrophytes were mapped by scuba diving in 130 transects of 1 m width at 50 m intervals, on a 6.6-km stretch of the River Spree. During the field mapping, mean water depth was 1 m. Therefore, this depth was used for further calculations. The percentage of river bed covered by macrophytes was estimated, as well as the percentages of the dominating sediment types. Macrophyte cover was scaled in four classes: 0, no macrophytes; 1, single shoots; 2, cover < 50%; 3, cover 50–100%. Sediment types were defined on the basis of the dominating particle size classes and the degree of consolidation.

Determination of area-specific leaf surfaces

Single leaves and above-ground shoots of the three species of submerged macrophytes were photocopied and optoelectronically scanned. Subsequently, their fresh and dry masses were determined. The surface areas of the scanned leaves and shoots were then determined by image analysis (ImageP, 2H + K Meßsysteme, Berlin) to calculate regression models of biomass and surface areas for each of the plant species. The resulting areas were doubled to account for both sides of the leaves. Power functions were used to calculate surface areas from dry mass of whole plants of *S. sagittifolia* and *S. emersum* to account for the lower surface/biomass ratio of larger plants. The surface of the more fragile *P. pectinatus* was calculated by linear regression.

In August 1998, the above-ground biomass of the three species was harvested in the model section from five replicate areas, each of 0.25 m^2, for each species and each class of macrophyte cover (single shoots, < 50% cover, > 50% cover). The number of above-ground shoots was also counted in these 45 areas, and considered in the calculations. The fresh mass was measured after drop off, the dry mass after drying the complete harvest at 60 °C to constant mass. Fresh and dry masses of plants were extrapolated to obtain estimates of total macrophyte biomass.

Results

Sediments

In the 6.6 km river reach, 20% of the river bottom was covered with shifting sandy sediments. This sediment type was mainly found in the thalweg of the river (Fig. 2a). The median particle size class of these shifting sediments ranged from 0.5 to 0.9 mm, and the coefficient of particle size heterogeneity ranged from 0.48 to 0.71. The remaining areas in the middle of the river were covered with mixed substrates consisting of sand and gravel and were partly consolidated by ochre and microphytobenthos. Stratified sand of several subtypes was found closer to the banks, covering 43% of the river bottom. Their, mean particle size was smaller than in shifting sands (paired samples *t*-test, $P = 0.02$, $n = 4$) and ranged from 0.28 to 0.32 mm. Stratified sediments were also more heterogenous than shifting sediments (paired samples *t*-test, $P < 0.01$, $n = 4$), with sorting coefficients of 0.20–0.43. Near the banks, 14% of the bottom area was covered with mud. Stones, partly from bank stabilization works, covered 11% of the river bottom, and woody debris was found on about 5% of the river bottom.

Macrophytes

Macrophytes were found on 40% of the river bottom area in the 6.6 km river stretch (Fig. 2b). *Sparganium emersum* and *Sagittaria sagittifolia* were the dominant species covering 21 and 16%, respectively, in the covering classes 2 and 3. *Potamogeton pectinatus* (2%) and *Ranunculus* sp. L. (5%) were frequently found in the middle of the river, whereas *Nuphar lutea* L. (3%) predominantly grew close to the margins and in more stagnant zones. At the land–water interface, *Phalaris arundinacea* L. (5%) was abundant.

Macrophyte mass was strongly correlated with leaf surface area for three dominant species. Conversion of dry mass (DM) in grams to leaf area (LA) in square centimeters was done by the following regression models: $\mathrm{LA} = 495.4\ \mathrm{DM}^{0.818}$ (linearized $r^2 = 0.78$, $P < 0.001$) for *S. sagittifolia*, $\mathrm{LA} = 443.3\ \mathrm{DM}^{0.577}$ (linearized $r^2 = 0.80$, $P < 0.001$) for *S. emersum* and $\mathrm{LA} = 1068\ \mathrm{DM}$ ($r^2 = 0.86$, $P < 0.001$) for *P. pectinatus*. The LA : DM ratio was highest for *P. pectinatus* (1068 cm^2 : 1 g). This ratio was also used for the calculation of *Ranunculus* sp. LA, because *Ranunculus* also had filamentous, densely growing leaves. The regressions of macrophyte DM versus LA were used to estimate the LA per area of river bottom. By these estimates, the four dominant species provided a total leaf surface area of 2.8 $m^2\ m^{-2}$ in the 6.6 km stretch, with *S. sagittifolia* contributing approximately 45%, *S. emersum* 24% and *P. pectinatus* and *Ranunculus* sp. together contributing 31% to the total LA. The total DM of these taxa was 48 $g\ m^{-2}$.

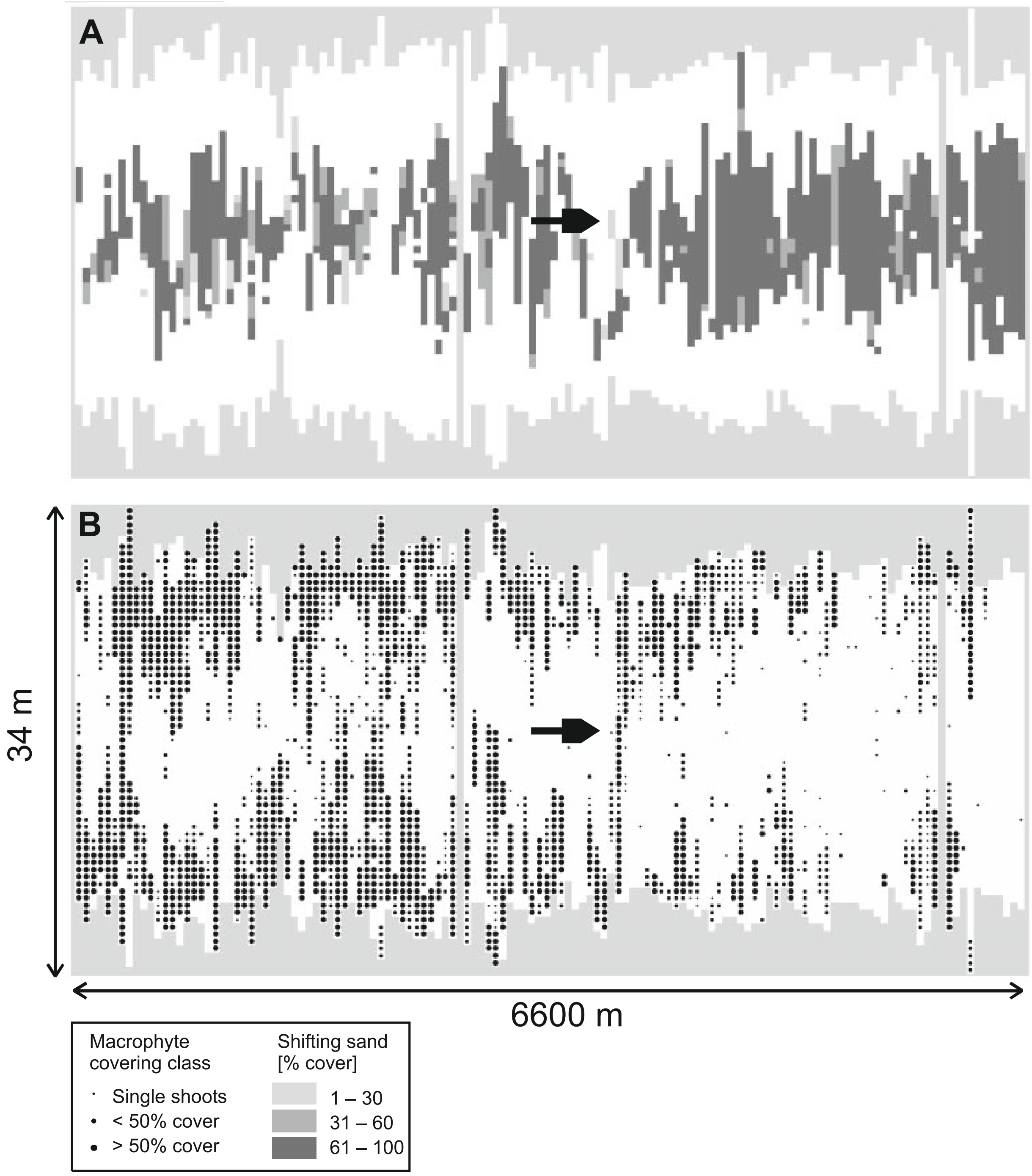

Fig. 2 Distribution of (a) shifting sand, (b) aquatic macrophytes in the Spree, mapped in 130 1 m wide transects at 50 m intervals in August 1995. River margins are depicted in light grey, the two interruptions of the river channel are because of bridges crossing the river. Arrows indicate flow direction.

Bacterial abundance and production

In the pelagic zone, bacterial production amounted to 0.86–3.9 μg C L^{-1} h^{-1} and abundance was 4.0×10^6–7.8×10^6 L^{-1} (Tables 1 and 2). In the sediments, bacterial production per unit volume was about three orders of magnitude higher than in the pelagic zone. It ranged from 1.1 to 4.5 μg C cm^{-3} in shifting sands and was higher (paired samples *t*-test, $P = 0.07$, $n = 4$) in stratified sands, where it ranged from 1.9 to 8.1 µg C cm^{-3}. Bacterial abundance was 0.84×10^9–3.8×10^9 cm^{-3} in shifting sands, and 1.6×10^9–6.7×10^9 cm^{-3} in stratified sands, respectively. Epiphytic bacterial production, measured per area of leaf surface, ranged from 5 to 58 ng C cm^{-2} h^{-1}. Epiphytic bacterial production varied strongly with season and between different macrophyte species (Table 1). Bacterial production in epiphyton on *S. emersum* and *S. sagittifolia* was lowest in June, whereas on *P. pectinatus* it was lowest in October. On most occasions, production per plant surface area was higher on *S. emersum* and *S. sagittifolia* than on *P. pectinatus*.

Throughout the year, pelagic bacteria were significantly smaller than sediment bacteria ($P < 0.0001$, $n = 1200$, Mann–Whitney *U*-test). Mean bacterial volume was 0.032 0.024 µm^3 in the pelagic zone and 0.061 0.056 µm^3 in sediments, resulting in a mean biomass of 14.1 6.6 fg for the pelagic zone and 22.0 12.1 fg in sediments. Bacterial biomass per cell did not differ significantly in the different sediment types ($P = 0.94$, $n = 800$, Mann–Whitney *U*-test). However, there were significant differences between seasons (Kruskal–Wallis Test, $\chi^2 = 18.1$, d.f. = 3, $P < 0.001$, $n = 800$). The lowest value was calculated for March (19.3 9.0 fg C cell^{-1}) and the highest for October (24.0 13.1 fg C cell^{-1}). Although bacteria were smaller in the pelagic zone, the turnover time for bacterial carbon (production/biomass) was longer in this habitat (29–61 h) than in sediments (11–30 h) (paired samples *t*-test, $P = 0.06$, $n = 4$).

On a square meter basis, bacterial biomass in the uppermost 2 cm of the shifting sand sediments surpassed that in the pelagic zone by factors of 6–22. Bacterial production in the sediments was 17–35 times higher than in the pelagic zone. Bacterial production in the epiphyton was lower than in the pelagic zone. The highest contribution of epiphytic production, accounting for 67% of pelagic production, was measured in October 1997 (Fig. 3).

Discussion

Bacterial production in the pelagic zone of the River Spree was comparable with that in the two European lowland rivers Meuse and Seine (Servais, 1989; Servais & Garnier, 1993) and slightly higher than in

Table 1 Bacterial production in various habitats of the Spree measured at *in situ* temperatures (means SD; $n = 3$ for the pelagic zone, $n = 5$ for epiphyton and $n = 5$ for sediment)

		Bacterial production						
			Epiphyton (ng C cm^{-2} h^{-1})				Sediment (0–2 cm depth) (µg C cm^{-3} h^{-1})	
Sampling date	Temperature (°C)	Pelagic zone (µg C l^{-1} h^{-1})	*Sagittaria sagittifolia*	*Sparganium emersum*	*S. emersum detritus*	*Potamogeton pectinatus*	Stratified sand	Shifting sand
August 1997	21.3	2.27 0.06	58 6	58 3	–	11 11	2.56 0.07	2.03 0.26
October 1997	13.5	1.35 0.07	40 7	31 12	53 10	5.3 1.8	5.41 2.36	2.40 0.12
March 1998	6.8	1.05 0.16	–	–	–	–	2.51 0.98	1.30 0.46
June 1998	21.2	3.84 0.04	25 2	8.4 1.9	–	24 7	4.41 0.62	3.24 0.84

Table 2 Bacterial abundance and biomass turnover in the pelagic zone and in sediments of the Spree (means ± SD; $n = 3$ for the pelagic zone, $n = 5$ for sediments)

			Sediment			
	Pelagic zone		Stratified sand		Shifting sand	
Sampling date	Abundance (10^6 cells cm^{-3})	Turnover time (h)	Abundance (10^9 cells cm^{-3})	Turnover time (h)	Abundance (10^9 cells cm^{-3})	Turnover time (h)
August 1997	5.33 ± 0.34	38.1	4.54 ± 0.72	44.3 ± 6.8	3.45 ± 0.93	23.9 ± 3.8
October 1997	4.00 ± 0.41	48.5	1.91 ± 0.13	22.9 ± 8.4	1.17 ± 0.31	29.8 ± 4.8
March 1998	4.59 ± 0.17	71.5	4.42 ± 1.44	40.6 ± 21.3	2.23 ± 0.48	25.0 ± 10.4
June 1998	7.79 ± 0.70	33.2	2.86 ± 0.56	12.9 ± 3.2	1.50 ± 0.19	12.1 ± 3.2

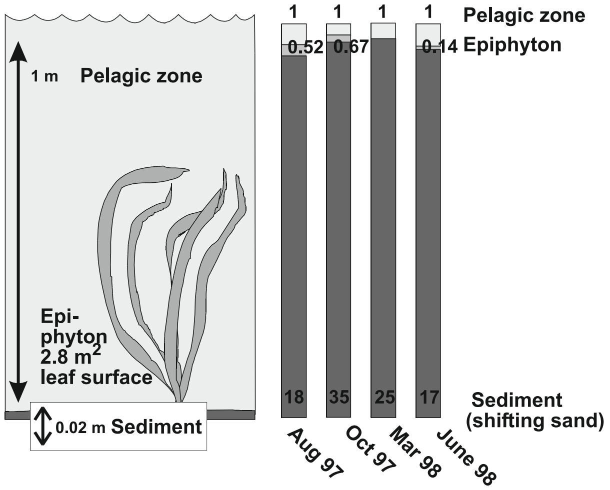

Fig. 3 Comparison of total production on an areal basis by bacteria in sediments, epiphyton, and the pelagic zone of the Spree. Production in the pelagic zone is always set as 1.

the blackwater Ogeechee River (0.028–2.12 µg C L^{-1} h^{-1}; Edwards & Meyer, 1986). It was markedly higher than in most lakes (Cole *et al.*, 1988) but lower in the strongly heterotrophic Hudson River estuary (Findlay *et al.*, 1991).

Epiphytic bacterial production per leaf surface area varied from 5.3 to 58 ng C cm^{-2} h^{-1} in our study, which was the same order of magnitude as found in two studies on wetland macrophytes (Moran & Hodson, 1989; Thomaz & Wetzel, 1995) and slightly lower than on *Zostera marina* from the Baltic Sea (Törnblom & Søndergaard, 1999).

Aquatic macrophytes in the Spree, as in many other aquatic ecosystems, provided extensive leaf areas which were susceptible to bacterial colonization. Therefore, it is surprising that only recently epiphytic bacterial productivity has been compared with that in the pelagic zone at the ecosystem level. In a study on shallow, eutrophic lakes, Theil-Nielsen & Søndergaard (1999) demonstrated that epiphytic bacterial production can be comparable with pelagic bacterial production. In a lake densely populated with macrophytes, it even exceeded pelagic bacterial production by up to seven times. In the Spree, epiphytic bacterial production was lower than pelagic bacterial production. However, macrophyte cover may vary annually (Sand-Jensen *et al.*, 1989), and streams and rivers may be much more densely populated with aquatic macrophytes than the Spree. A dry mass of 300–400 g m^{-2} dominated by *Ranunculus* sp. was found in British calcareous streams (Owens & Edwards, 1962), and even higher dry masses of 500 g m^{-2} or more dominated by *P. pectinatus* have been reported from several polluted running waters of the northern temperate zone (e.g. Krausch, 1976; Jorga & Weise, 1977; Madsen & Adams, 1988). Using our regression model, these biomasses would result in a leaf area of 30–50 m^2 m^{-2} as compared with 2.8 m^2 m^{-2} found in the Spree. It may be predicted that in these streams epiphytic heterotrophic activity will far exceed its pelagic counterpart. It is therefore necessary to include epiphytic metabolism in ecosystem studies of macrophyte-dominated waters.

However, both pelagic and epiphytic bacterial production in the River Spree were minor in comparison to sedimentary production. This was the result of higher abundance, larger cell size and higher production per cell in the sediments.

Bacterial abundance and production was higher in the Spree sediments than in those of most other riverine ecosystems studied. However, bacterial production has so far mostly been measured in small streams where allochthonous organic matter prevailed (Marxsen, 1999). Bacterial production as high as in Spree sediments was also found in Ontario streams (Hudson, Roff & Burnison, 1992) whereas in the upper sediment layer of the tidally influenced Hudson River production was found to be 10 times lower than in the Spree (Austin & Findlay, 1989). The only larger river examined, the Ogeechee River in Georgia, U.S.A., is a typical blackwater river characterized by high concentrations of humic substances. There, abundance of bacteria was about 5–10 times, production 10–20 times lower than in the Spree (Findlay, Meyer & Risley, 1986; Meyer, 1988). One reason for this apparent discrepancy might have been the relatively high autochthonous primary production occuring in the Spree which complements the supply with allochthonous organic matter.

Most of the studies mentioned above were conducted using the thymidine incorporation method, which may bear serious methodological problems if applied to sediments (Kaplan, Bott & Bielicki, 1992). Because various conversion factors are involved in the calculation of bacterial production from thymidine as well as from leucine incorporation, the comparison of the results may be ambiguous. Although the leucine incorporation technique is thought to be superior to the thymidine method (Simon & Azam, 1989; Marxsen, 1996), the results can also be biased by several sources of error which are discussed in detail by Marxsen (1996) and Fischer & Pusch (1999). However, it seems clear that bacterial production in sediments is controlled by temperature, oxygen supply and amount and quality of organic matter (Sander & Kalff, 1993; Findlay & Sobczak, 2000; Fischer, 2000).

In spite of high bacterial production in the Spree, our data concur with respiration data from the same river section. Böhme (1994) estimated community respiration rates in the Spree using a single station oxygen time curve analysis. He found total community respiration rates of 8.1–21.3 g O_2 m^{-2} day^{-1} (3.0–8.0 g C m^{-2} day^{-1} calculated with a respiratory quotient of 1), of which 80% (2.4–6.4 g C m^{-2} day^{-1}) was attributed to the benthic zone from May to July. If we assume a bacterial growth efficiency of 30% (Benner *et al.*, 1988), total bacterial respiration calculated from means of our measurements at four dates would amount to 2.1 (March 1998)–4.4 (October 1997) g C m^{-2} day^{-1} and thus would be in the same range. These are relatively high values compared with benthic respiration measured in other rivers, which ranged between 0.03 and 3.3 g C m^{-2} day^{-1} (Sinsabaugh, 1997; recalculated from annual means). As our data are calculated assuming that only bacterial respiration down to 2 cm sediment depth contributes to ecosystem metabolism, these still seem somewhat underestimated. As we have shown earlier, there is also potential for high bacterial production in deeper sediment layers if these are hydrologically connected to the water column (Fischer, 2000).

In interpreting our production data, bacterial production within the sediments and the extent to which these sediments are hydrologically connected to the water column must be differentiated. The comparison of our production estimates with Böhme's (1994) respiration measurements suggests a mean sediment depth of about 2–3 cm contributing to total ecosystem metabolism if it is assumed that the respiration rate of other major benthic biota was negligible (Pusch & Schwoerbel, 1994). In the field, the calculated value will be subject to substantial variation; highly permeable sediments with a structured surface strongly enhance vertical hydraulic connectivity (Huettel, Ziebis & Forster, 1996). Therefore, in the shifting sands relatively high bacterial activities were still found at sediment depths of 20 cm (Fischer, 2000). On the other hand, sediments that are strongly stratified or with an armour of ochre in the uppermost layer, are barely permeable and would contribute little to ecosystem metabolism.

Which carbon sources fuel bacterial production and respiration? Macrophytes, in addition to providing colonization areas for epiphytic biofilms, exert many direct and indirect effects on river ecosystems. They reduce flow velocity and promote particle sedimentation (Sand-Jensen, 1998), thus enhancing pelagic-benthic coupling. By consolidating hummocks on the river bottom, they also increase river-groundwater exchange rates (Hendricks & White, 1988). Macrophytes may thus improve the supply of carbon and nutrients to benthic and hyporheic bacteria. Measurements of sestonic particulate organic carbon (POC) at two stations along the Spree provided retention estimates of 1.2 g POC m^{-2} day^{-1} retained in the investigated reach (M. Pusch, unpubl. data).

Within the investigated section of the River Spree, there are additional carbon sources which must be added to net retention to achieve a more complete carbon budget (Table 3). First, pelagic and benthic primary production occur. Pelagic primary production has been calculated to be 0.9 g C m^{-2} day^{-1}

Table 3 Sources and respiration of sedimentary organic carbon in the investigated section of the Spree. Seasonal means estimated on a square meter basis

Carbon source	Carbon ($g\ m^{-2}\ day^{-1}$)
Retention in the river reach, import–export (M. Pusch *et al.*, unpubl.) Seasonal mean 1997/98	1.2
Pelagic primary production (J. Köhler unpubl.) Seasonal mean 1993–95	0.9
Benthic primary production (microphytes) (M. Böhme & J. Köhler, unpubl.) Seasonal mean 1993–95	≈ 0.1
Benthic primary production (macrophytes) (this study) 1995	0.08–0.17
DOC via groundwater exfiltration (Driescher & Gelbrecht, 1999)	0.23–1.4
DOC via surface runoff and interflow	x_1
POC via surface runoff	x_2
POC (leaf litter) (estimate after Benfield, 1997)	≈ 0.27
Sum of carbon sources	$3.4 + x_1 + x_2$
Respiration estimate (Böhme, 1994)	2.4–6.4
Respiration estimate (this study)	2.1–4.4

(seasonal mean 1993–95; J. Köhler, unpubl. data), but may have been lower in 1997/98 because of denser growth of macrophytes. The retention of *in situ* pelagic primary production amounted to 0.77 g C m^{-2} day^{-1} in spring and 0.47 g C m^{-2} day^{-1} in summer 1995 (Köhler & Bosse, 1998).

Aquatic macrophytes may also be an important source of carbon. These plants had an above-ground biomass of approximately 24 g C m^{-2} in our study. The production/biomass ratio of annual aquatic macrophytes is relatively low (1.2–2.6 on an annual basis; Westlake, 1982) so that the carbon production of these plants does not exceed the peak biomass by much. The carbon supply of the four investigated taxa was therefore estimated to range from 0.08 to 0.17 g C m^{-2} day^{-1}, not including below-ground biomass. The actual carbon supply by macrophytes may be substantially higher than this 1995 estimate, because macrophyte density has increased since that time. Small amounts of carbon may also be added by benthic microphytes (0.1 g C m^{-2} day^{-1}; J. Köhler & M. Böhme, unpubl. data) and by the riparian macrophyte taxa not included in our measurements.

In addition to the autochthonous carbon sources, allochthonous carbon is entrained into the investigated river section (Table 3). Within the observed river stretch, about 1 m^3 s^{-1} of water was added by groundwater exfiltration, which equals a mean groundwater exfiltration rate of 130 L m^{-2} day^{-1}. With a dissolved organic carbon (DOC) concentration of 1.8–10.8 mg L^{-1} (Driescher & Gelbrecht, 1999), groundwater would thus contribute 0.23–1.4 g C m^{-2} day^{-1}. This carbon may be effectively retained by the sedimentary biofilm and subsequently utilized by bacteria (Fiebig & Lock, 1991; Fischer, 2000). Percolation of precipitation through floodplain soils (interflow) probably entrains additional DOC into the river.

Particulate organic carbon (POC) from the floodplain enters the river through erosional processes. These POC inputs may be high (Wainwright, Couch & Meyer, 1992; Veyssy *et al.*, 1999), but were not quantified for the Spree. Coarse particulate organic matter (CPOM) enters the river as litter from the riparian vegetation. As a rough estimate, an input of 200 g dm m^{-2} $year^{-1}$ can be assumed for the Spree (estimated from Benfield, 1997), which equals an additional carbon input of 0.27 g m^{-2} day^{-1}.

All the organic carbon fluxes mentioned above exhibit pulses during specific seasons or hydrological events. Algal production and losses of algal biomass are highest during spring (Köhler & Bosse, 1998), whereas autochthonous CPOM from macrophytes and allochthonous CPOM from leaves are more available in autumn. The availability of allochthonous DOC for the bacterial community might change as a result of alterations in discharge and precipitation. Changes in substrate availability, however, are buffered by the retention capacity of the sediments (Metzler & Smock, 1990) and of the microbial biofilms (Freeman & Lock, 1995). We observed no net accumulation of organic matter, although effective retention of organic carbon has been documented for the Spree (Wanner & Pusch, in press). The cumulative carbon sources for the investigated segment of the Spree are in the same order of magnitude as measured (Böhme, 1994) or calculated (this study) bacterial respiration. It therefore appears that the organic matter is efficiently utilized and that the annual supply of organic matter in this river reach is in a steady state with the carbon utilization.

Finally, factors exist that theoretically allow the maintenance of a higher bacterial production than might appear possible. First, bacterial and other living biomass can be recycled within the food web. Thus in retentive systems, the amount of carbon available for assimilation by consumers may be significantly higher than the organic inputs (Strayer, 1988). Additionally, chemolithoautotrophic bacteria build up biomass using carbon dioxide without the need for organic substrates, e.g. in upwelling sites of anoxic groundwater. The additional biomass provided by these chemolithoautotrophic bacteria is probably insignificant for the total pool of POC, but products of their metabolism (e.g. acetate) are easily degradable substrates for heterotrophic bacteria (e.g. Baker, Dahm & Valett, 1999).

Intense system respiration in high order streams has been shown in some longitudinal studies (Webster, Wallace & Benfield, 1995). Naiman *et al.* (1987) found that medium-sized rivers were focal sites of degradation of organic matter. However, the boreal rivers they studied showed only a small overall efficiency in the degradation of the inputs of organic matter into the river system. For the high-gradient 8th-order Salmon River, Minshall *et al.* (1992) even found that the lower reaches behaved more like a conduit for carbon. Thus, the efficient use of organic carbon resources found by us has rarely been reported from higher order streams. That feature of a river therefore might be correlated with a temperate climate and a low channel gradient, including a very mitigated temporal flow regime. It can be hypothesized that river networks that end in an extended lowland section may show a longitudinal pattern in the geochemical transport of matter that greatly differs from others lacking a lowland section. The export of matter from river systems including lowland sections to the sea would be much lower, at least as long as these rivers are not altered too severely by man. In many cases, this pattern would decisively alter the basic picture of longitudinal changes within river systems drawn in the River Continuum Concept (RCC) (Vannote *et al.*, 1980; Minshall *et al.*, 1985).

In conclusion, our study supports the view of the lowland river Spree as a heterotrophic system. On a square meter basis, total bacterial production was clearly higher than primary productivity. In the vegetation period with high macrophyte development, epiphytic bacterial production could be as high as pelagic bacterial production. However, benthic bacterial production surpassed combined epiphytic and pelagic bacterial production by factors of 12–25 (Fig. 3). Thus, even in the phytoplankton-dominated Spree, the heterotrophic system metabolism was dominated by the activity of benthic heterotrophic bacteria. Intense pelagic–benthic coupling probably supplied the sediment microbiota with carbon and nutrients. The carbon-utilizing processes appeared to be in a steady state with the carbon supply from autochthonous and allochthonous sources. The water column thus serves as the medium that transports carbon and nutrients to the foci of heterotrophic metabolism. These foci are located in the biofilm of the sediments and, to a lesser extent, of the epiphyton. This focus of microbial metabolism in the sediments of a lowland river renders that type of ecosystem very efficient in the retention of organic carbon, and also concerning nutrients (Behrendt & Opitz, 1999). Thus, the presence of such an important sink of organic matter has major implication for biogeochemical fluxes within river networks, and for coastal marine ecosystems.

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Use of the [^{14}C]Leucine Incorporation Technique To Measure Bacterial Production in River Sediments and the Epiphyton

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Bacterial production is a key parameter for the understanding of carbon cycling in aquatic ecosystems, yet it remains difficult to measure in many aquatic habitats. We therefore tested the applicability of the [^{14}C]leucine incorporation technique for the measurement of bulk bacterial production in various habitats of a lowland river ecosystem. To evaluate the method, we determined (i) extraction efficiencies of bacterial protein from the sediments, (ii) substrate saturation of leucine in sediments, the biofilms on aquatic plants (epiphyton), and the pelagic zone, (iii) bacterial activities at different leucine concentrations, (iv) specificity of leucine uptake by bacteria, and (v) the effect of the incubation technique (perfused-core incubation versus slurry incubation) on leucine incorporation into protein. Bacterial protein was best extracted from sediments and precipitated by hot trichloroacetic acid treatment following ultrasonication. For epiphyton, an alkaline-extraction procedure was most efficient. Leucine incorporation saturation occurred at 1 μM in epiphyton and 100 nM in the pelagic zone. Saturation curves in sediments were difficult to model but showed the first level of leucine saturation at 50 μM. Increased uptake at higher leucine concentrations could be partly attributed to eukaryotes. Addition of micromolar concentrations of leucine did not enhance bacterial electron transport activity or DNA replication activity. Similar rates of leucine incorporation into protein calculated for whole sediment cores were observed after slurry and perfused-core incubations, but the rates exhibited strong vertical gradients after the core incubation. We conclude that the leucine incorporation method can measure bacterial production in a wide range of aquatic habitats, including fluvial sediments, if substrate saturation and isotope dilution are determined.

Most organic carbon metabolism in running waters occurs on or in sediments (38, 42). Bacteria play a key role in organic carbon processing (10, 64) and influence many aspects of the chemistry and biology of river ecosystems (43). The quantification of bacterial production in sediments is therefore important for holistic studies of these ecosystems. However, methodological problems make it difficult to measure production rates of intact bacterial communities in many aquatic habitats.

Several methods have been suggested for the measurement of bacterial production in natural aquatic systems (e.g., see references 19, 20, 46, and 62). One of the most promising approaches consists in the measurement of leucine incorporation into bacterial protein (24, 50). This technique provides more-direct results for bacterial carbon production than the more widely used thymidine method (18, 22), because it measures an increase of a major biomass fraction. It is also one order of magnitude more sensitive, because over time bacterial cells incorporate about 10 times more leucine than thymidine (50). In addition, the method has potential to measure production of anaerobic bacteria (8, 32). Leucine incorporation into bacteria has been tested extensively in pelagic systems (e.g., see references 21, 24, 44, 50, and 60) and is now commonly used for the measurement of bacterial production in these environments (23). Recently, adaptations for other habitats (soil [4], epiphyton [54], leaf litter [51], and sediments [30, 58]) have been tested.

However, the leucine incorporation technique is still far from being a routine assay and relies on assumptions that have not been thoroughly tested in many aquatic habitats. In this study we examined several of these critical questions about the application of the [^{14}C]leucine method in a variety of aquatic habitats. (i) Can free and incorporated leucine be completely recovered from sediments? (ii) Can leucine incorporation into protein be saturated, and can internal and external isotope dilution be excluded? (iii) Do high leucine concentrations stimulate bacterial activity? (iv) Is leucine taken up solely by bacteria, even if high concentrations are used? (v) Does the incubation technique—vial incubation versus perfused-core incubation—affect bacterial production estimates?

Our aim was to develop methodologies for routine measurements of bacterial production in aquatic habitats that have received little attention, most notably sediments. We also compared our bacterial production estimates with those determined in other riverine habitats, such as the water column (pelagic zone) and the biofilm on aquatic plants (epiphyton).

MATERIALS AND METHODS

General methods. Sediment was sampled by using a sediment corer from shifting sands in the 6th order River Spree, approximately 40 km upstream of the city of Berlin in Germany. These sediments were characterized by low organic matter content (loss on ignition, <1% ash-free dry mass), a homogeneous particle-size distribution with a median particle size of 0.5 mm, high hydraulic conductivity ($k = 0.001$ to 0.004 m/s), and the presence of manganese and iron oxide coatings. Further information on the River Spree and the study site is found in references 26 and 52. The upper 4-cm-thick strata of five sediment cores were pooled, using fresh samples taken on the day of each experiment. Sediments were mixed gently with a spatula, and subsamples with wet weight of 0.5 g were weighed into sterile 10-ml centrifuge vials containing 4 ml (2 ml in the respiratory-activity experiment) of fresh, sterile-filtered (pore size, 0.2 μm) river water. The vials were stored at 4°C for up to 5 h prior to experiments.

L-[U-^{14}C]leucine (Amersham Ltd.) at a specific activity of 11.6 GBq/mmol was diluted with cold L-leucine to achieve the specific activities given for the various experiments. In order to simulate in-stream conditions, samples were incubated at in situ temperatures with gentle shaking. The incubation was terminated by the addition of formaldehyde (final concentration, 3.2%).

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If not stated otherwise, the following procedure was used for the further processing of the samples. The fixed samples were vortexed, sonicated (10 min, 60% power) in a sonication bath (Elma T 710 DH) and vortexed again. After this step, a subsample could be taken in order to determine bacterial abundance. To the remaining samples, including the sediments, trichloroacetic acid (TCA) was added to a final concentration of 5%. In order to dissolve the nonprotein fraction of the cells, the samples were then incubated at 95°C for 30 min. After cooling on ice, the remaining precipitate was filtered onto 0.2-μm-pore-size membrane filters (polycarbonate filters [Nuclepore] or RoTrac polyester filters [Oxyphen GmbH, Grosserkmannsdorf, Germany]). Filters were thoroughly rinsed with deionized water to eliminate unincorporated leucine. The amount of radioactivity in the filtrate was recorded. Filters were then put into 4-ml scintillation picovials, completely dissolved in 0.5 ml of solvent (Soluene; Packard), and mixed with 2.5 ml of scintillation fluid (Hionic Fluor; Packard). Radioactive decays were measured in a Canberra Packard 1900 scintillation counter. Controls were fixed with formaldehyde (final concentration, 3.2%) immediately at the start of the incubation and generally contributed less than 10% of the total leucine incorporation.

Additionally, an alkaline extraction procedure (14, 30) was tested. Briefly, protein was extracted from sediments at 25°C for 20 h (experiment one) and 40 h (experiment two and epiphyton experiments) with a solution of 0.3 M NaOH, 25 mM EDTA, and 0.1% sodium dodecyl sulfate (SDS). Protein was precipitated with TCA, washed with TCA, and redissolved in NaOH as described by Marxsen (30). An aliquot of 0.8-ml volume was mixed with 4.2 ml of scintillation cocktail (Ultima Gold; Packard) in a 6-ml scintillation minivial and measured as described above.

The results are given as rates of leucine incorporation into protein. Bacterial carbon production can be calculated from these values by using conversion factors given by Simon and Azam (50). Statistical analyses were performed using the software SPSS (Release 6.0; SPSS Inc.).

Substrate saturation. A wide range of leucine concentrations was tested in three saturation experiments conducted under the following different incubation conditions. (i) For the experiment conducted in March 1997, leucine concentrations ranged from 0.05 to 200 μM, incubation temperature was 13°C, incubation time was 3 h, and the specific activity of leucine was 296 Bq/nmol of leucine. (ii) For the experiment conducted in May 1997, these conditions were 0.5 to 200 μM, 17°C, 1.5 h, and 148 Bq/nmol of leucine, respectively. For that conducted in February 1998, they were 3 to 300 μM, 5°C, 2 h, and 92.5 Bq/nmol of leucine, respectively. The resulting incorporation velocities were iteratively fitted to the hyperbola function of the Michaelis-Menten enzyme kinetics by using nonlinear regression (Origin 4.0; Microcal Software Inc.) (28, 44, 60). The plot was used for calculations of the theoretical maximum uptake velocity ($V_{\max}$) and of the sum of the half saturation constant and the natural leucine concentration [$(K_t + S_n)$] as measures of substrate affinity.

Stimulation of bacterial metabolism by added leucine. The electron transport system of metabolically active bacteria reduces the vital stain 5-cyano-2,3-ditolyl tetrazolium chloride (CTC), thus building up the red fluorescent compound CTC-formazan. This compound accumulates in active bacteria and can be microscopically viewed (45). In order to test whether added leucine has an effect on bacterial respiratory activity, sediments were incubated with 4 nM (final concentration) CTC and cold leucine at final concentrations of 0, 2, 50, and 200 μM. After 2 h of incubation at 17°C, samples were fixed and processed within 2 days. Bacteria were counterstained with DAPI (4′,6-diamidino-2-phenylindole) and enumerated immediately after filtration onto black polycarbonate filters (pore size, 0.2 μm) (Nuclepore), using a Nikon FXA photomicroscope and the filter sets EX 330-380, DM 400, and BA 400 for cells stained with DAPI and EX 420-490, DM 510, and BA 580 for CTC-stained bacteria (16, 41).

Bacterial DNA replication activity was tested by adding [^{3}H]thymidine (final concentration, 100 nM; specific activity, 925 kBq/nmol; incubation temperature, 17°C; incubation time, 30 min) to samples containing cold leucine at concentrations of 0, 2, 50, and 200 μM. We extracted labeled DNA as described by Moran and Hodson (36) for measuring bacterial production on plant detritus, with the following modifications: fixed samples were cooled on ice immediately, and ice-cold TCA was added to a final concentration of 5%. Samples were then sonicated for 10 min in a cooled sonication bath and vortexed, and half of the volume of each sample was filtered onto polycarbonate filters (pore size, 0.2 μm) (Nuclepore). Filters were rinsed four times with ice cold TCA (concentration, 5%) to remove unincorporated label. The filtration apparatus was kept cool during this procedure. In order to hydrolyze DNA, filters were then incubated for 30 min at 100°C in capped vials containing 2 ml of TCA (concentration, 5%). The components that were insoluble in hot TCA (mainly proteins) were then filtered onto a second polycarbonate filter. An 0.8-ml subsample of the filtrate containing the dissolved DNA was mixed with 4 ml of scintillation cocktail (Ultima Gold; Packard) in a 6-ml scintillation minivial for counting.

Eukaryotic organism leucine uptake. The proportion of eukaryotic organism leucine uptake was assessed at leucine concentrations of 2, 50, and 200 μM. A mixture of colchicine and cycloheximide (final concentrations, 0.01 and 0.02%, respectively) was added to five vials for each treatment. In combination, these antibiotics effectively inhibit eukaryotic organism reproduction and feeding and have no direct effect on bacterial growth (49). After 1 h, leucine was added (specific activity, 148 Bq/nmol of leucine; temperature, 15°C; *n*, 5). Short incubation times (50 min) were applied to reduce indirect effects of dead eukaryotic cells on bacterial growth. A second experiment was conducted in winter by using leucine at only the 200-μM concentration (specific activity, 92.5 Bq/nmol of leucine; temperature, 5°C; *n*, 7).

Effects of incubation technique. We compared bacterial protein production measured in sediment slurries in incubation vials with results obtained with a perfused-sediment-core technique (30, 31). Sediment cores of 7.6-cm length and 2-cm inner diameter were taken from the river bed and perfused with prefiltered river water in a once-through mode at a rate of 18.2 ml h^{-1} (residence time, 30 min) for 24 h at 20°C. We obtained this rate as a rough estimate of in situ interstitial flow by model calculations (53) and by dye experiments conducted in laboratory flumes. Four cores were perfused with the flow directed from the top sediment layer toward the deeper sediment layer ("top-down perfusion"), and four additional cores were perfused in the opposite direction ("bottom-up perfusion"). Subsequently, leucine was added to the stock of perfusion water to a final concentration of 50 μM and a specific activity of 7 Bq/nmol of leucine. A ninth core was sterilized with 5% formaldehyde and served as a control. Leucine perfusion lasted for another 12 h and was terminated by perfusing a solution of 5% formaldehyde for 4 h. Sediment cores were then cut into four sections corresponding to depths of 0 to 1.9, 1.9 to 3.8, 3.8 to 5.7, and 5.8 to 7.6 cm. Protein was extracted from 0.5-cm^3 aliquots of the sediments, and its activity was measured as described above. The sediment cores for the slurry incubation were cut in the same way before incubation, and aliquots of 0.5 cm^3 from each depth were incubated in vials and processed as described above.

Measurements of production by bacteria in epiphyton and the pelagic zone. We tested two protein extraction methods for epiphyton and assessed the substrate saturation concentration of leucine in this habitat. In July 1997, we randomly cut leaves located at 10 to 40 cm below the water surface of one of the most common species (*Sagittaria sagittifolia* L., *Alismataceae* Vent.) and dissected discs of 1 cm^2 with a corkborer. Five leaf discs each were then pooled and allotted to 20-ml scintillation vials containing 5 ml of prefiltered river water. Before we determined leucine saturation for epiphytic bacteria, the two protein extraction methods were tested (leucine concentration, 1,500 nM; specific activity, 2,960 Bq/nmol; incubation time, 90 min; incubation temperature, 21°C). The incubation was terminated by adding formaldehyde to final concentration of 3.2%, and leaf discs were then sonicated at 100% power for 10 min. By the alkaline-extraction method, protein was extracted at 25°C for 40 h in a solution of 0.3 M NaOH, 25 mM EDTA, and 0.1% SDS. Protein was precipitated with TCA, washed three times, and redissolved in NaOH as described by Marxsen (30) for sediment samples. A 0.8-ml aliquot of sample and 4.2 ml of scintillation cocktail (Ultima Gold; Packard) were mixed in a scintillation minivial and measured. For acidic extraction, TCA was added to the samples after sonication at final concentration of 5%. Samples were then incubated for 30 min at 95°C. Subsequently, aliquots were filtered and washed as described above for the sediment samples.

The saturation experiment was conducted by using the alkaline-extraction method and leucine concentrations of 30, 120, 400, 1,000, 2,000, and 4,000 nM. Incubation time was 90 min, at 21°C and at a specific activity of 2,960 Bq/nmol of leucine. For pelagic-zone samples, 0.2 ml of leucine was added to 4.8 ml of river water, resulting in final leucine concentrations of 10, 20, 40, 80, 140, and 200 nM. Incubation time was 50 min, temperature was 17°C, and specific activity was 11,562 Bq/nmol of leucine. Incubation was terminated by adding formaldehyde to final concentration of 3.2%. Samples were processed as described above for the sediment samples, but with the sonication step excluded.

RESULTS

Extraction of protein from sediment samples. TCA extraction in combination with sonication and filtration of the precipitate maximized extraction of bacterial protein from sediments. In addition, polycarbonate filters (0.2-μm pore size (Nuclepore) produced significantly lower control values than the more-commonly used cellulose nitrate filters over a wide range of leucine concentrations (paired *t*-test, $P = 0.03$, $n = 8$). However, we found that the stability of the polycarbonate filters was not sufficient in all cases. Damage occurred during filtration to approximately every tenth filter. RoTrac polyester filters (Oxyphen GmbH) needed longer solubilization times but produced both low leucine adsorption and high resistance to TCA.

A total of 102.6% ± 3.6% (mean ± standard deviation) (n = 6) of the added label was recovered after 2 h of incubation, subsequent sonication, and TCA extraction. On the filter remained 2.73% ± 0.43% of the recovered label, of which 93.0% was incorporated into bacterial protein and 7.0% was abiotically adsorbed to sediment particles and to the filter itself. Of the total added label 97.3% ± 4.5% was recovered in the filtrate. We were unable to routinely recover bacterial protein from sediments by the alkaline-extraction method. In the first experiment (20 h of alkaline extraction), the radioactive label recovered in protein amounted to only 1.5% of the protein determined with the TCA extraction method. In the second experiment (40 h of alkaline extraction), 10.8% of the protein determined with the TCA extraction method was found.

Substrate saturation. None of our substrate saturation experiments with sediments revealed typical Michaelis-Menten kinetics. In general, there seemed to be a depression or a plateau at the leucine concentration of 50 μM, followed by increased leucine uptake at higher concentrations (Fig. 1a, b, and c). In order to account for a possible multiphasic leucine uptake, we performed fitting for data obtained at leucine concentrations up to 50 μM as well as for the complete data set (concentrations up to 200 or 300 μM). The former was much closer to the measured data, thus exhibiting a significantly lower chi-square value. We therefore calculated the parametric values of ($K_t + S_n$) and V_{max} separately for concentration ranges of up to 50 μM and up to 200 (or 300) μM. At up to 50 μM ($K_t + S_n$) for leucine ranged from 6.0 to 12.6 μM, with V_{max} of 652 pmol of leucine cm^{-3} h^{-1} in the February experiment and 1,105 and 1,525 pmol of leucine cm^{-3} h^{-1} in the May and March experiments, respectively. At up to 200 μM V_{max} values were 2,088 and 2,261 pmol of leucine cm^{-3} h^{-1} for the March and May experiments, respectively (Table 1).

Isotope dilution. The ratio of V_{max} to the incorporation rates measured by using a specific leucine concentration represents the isotope dilution at that leucine concentration (44, 60). Isotope dilution for the leucine concentration of 50 μM varied from 1.1 to 1.3 for saturation curves calculated for leucine concentrations up to the 50 μM. However, isotope dilution would be higher if all available data (acquired at concentrations up to 200 or 300 μM) were incorporated into the calculation of V_{max} (Table 1).

Stimulation of bacterial metabolism by added leucine. The sediments were colonized by $1.9 \times 10^9 \pm 0.19 \times 10^9$ bacteria cm^{-3}, with a mean proportion of respiratorily active cells of 26.8% ± 2.9%. The mean rate of [^{3}H]thymidine incorporation into DNA was 3.65 ± 0.91 pmol cm^{-3} h^{-1}. The CTC and thymidine experiments revealed no significant effects of added leucine on bacterial electron transport activity (i.e., respiratory activity) (analysis of variance [ANOVA], $P = 0.42$, $n = 20$) and DNA synthesis (ANOVA, $P = 0.89$, $n = 20$). Using the data of the experiment, the minimum difference in the percentage of active bacteria calculated with 90% confidence of detection (see equation 10.36 in reference 66) was 3.5%. The minimum detectable difference in the rate of thymidine incorporation was 0.98 pmol cm^{-3} h^{-1}.

Eukaryotic organism leucine uptake. We found clear effects of leucine concentration on leucine incorporation rate (two-way ANOVA, $F = 225$, $P < 0.001$, $n = 30$). However, we also detected significant effects of the antibiotics on leucine incorporation ($F = 5.02$, $P = 0.035$) and two-way interactions between the use of antibiotics and leucine concentration ($F = 4.12$, $P = 0.029$). Differences between treatments with and without antibiotics were significant only at the leucine concentration of 200 μM (t-test, $P = 0.05$, $n = 5$). At that leucine concentration, leucine incorporation in samples with antibiotics was 20% lower than that in samples without antibiotics, with a 95% confidence interval of 0 to 40%. A second experiment supported these results; samples containing antibiotics had 35% lower leucine incorporation than those without antibiotics (t-test, $P = 0.013$, $n = 7$), with a 95% confidence interval of 9 to 61%.

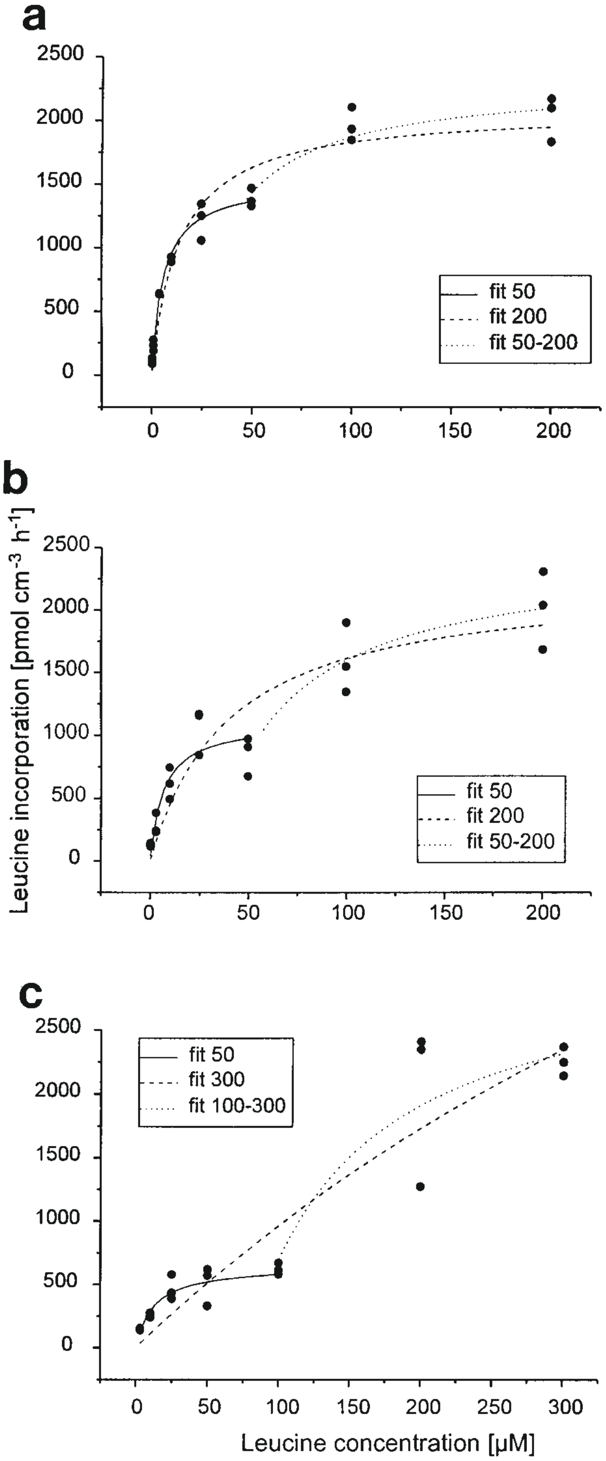

FIG. 1. Kinetics of uptake of leucine for sediment bacteria with fitting by using the Michaelis-Menten equation. Fittings are shown for leucine concentrations up to 50 μM (solid lines), up to 200 or 300 μM (dashed lines), and 50 to 200 μM or 100 to 300 μM (dotted lines). Experiments were conducted in March 1997, at incubation temperature of 13°C (a), in May 1997, at incubation temperature of 17°C (b), and in February 1998, at incubation temperature of 5°C (c).

Effects of incubation technique. Incorporation of leucine into protein measured in sediment cores significantly differed from that measured in incubation vials. In vials, incorporation rates were equal at all sediment depths (ANOVA, $F = 0.53$, $P = 0.68$, $n = 16$). In contrast, leucine incorporation in per-

TABLE 1. Parametric values for leucine incorporation into protein by bacteria in sediments[a]

Date	Leucine concn (μM)	V_{meas}[b] (pmol cm^{-3} h^{-1}) ± SD	$K_t + S_n$ (μM) ± SE	V_{max} (pmol cm^{-3} h^{-1}) ± SE	V_{meas}/V_{max} ratio	Chi-squares, r^2, P (n)[c]
March 1997	Up to 50	1,387 ± 74	6.0 ± 0.7	1,525 ± 50	1.10	4,797, 0.99,*** (18)
	Up to 200		14.1 ± 2.3	2,088 ± 88	1.51	26,730, 0.98,*** (24)
	50–200		19.2 ± 4.7	2,313 ± 124	1.67	21,031, 0.96,*** (9)
May 1997	Up to 50	850 ± 156	6.7 ± 2.8	1,105 ± 130	1.30	27,062, 0.91,*** (15)
	Up to 200		40.6 ± 13.0	2,261 ± 253	2.66	70,496, 0.86,*** (21)
	50–200		37.8 ± 13.5	2,460 ± 281	2.89	57,533, 0.70,** (9)
February 1998	Up to 50	507 ± 154	12.6 ± 5.8	652 ± 104	1.29	7,738, 0.78,*** (12)
	Up to 300		776 ± 697	8,444 ± 5834	16.7	92,618, 0.40,** (21)
	100–300		78.2 ± 44.3	3,155 ± 633	6.22	129,389, 0.14 N.S. (9)

[a] Calculations were performed by non-linear regression of saturation curves using the Michaelis-Menten equation. Results are given for all data of each experiment (up to 200 and 300 μM), for data at leucine concentration up to 50 μM, and for data at leucine concentration exceeding 25 or 50 μM.

[b] Rate of incorporation of leucine into protein by bacteria in sediments at added leucine concentration of 50 μM.

[c] Chi-square values are given for nonlinear regression, and r^2 and P values are for modified Lineweaver-Burk plots (65). ***, $P \leq 0.0001$; **, $P \leq 0.01$; N.S., $P >$ 0.05.

fused sediment cores significantly declined from the inflow layer to the outflow layers (ANOVA, $F = 101, P < 0.0001, n = 32$). Leucine incorporation was highest in the 0-to-1.9-cm-deep layer of the top-down-perfused cores and in the 5.7-to-7.6-cm-deep layer of the bottom-up-perfused cores. Incorporation rates measured in cores clearly exceeded those measured in vials in the inflow layers, and incorporation rates were lower in the outflow layers (Fig. 2). Leucine incorporation calculated per whole sediment core did not differ significantly among the methods: it amounted to 3.23 ± 0.32 nmol cm^{-3} h^{-1} for the vial incubation, 3.19 ± 0.10 nmol cm^{-3} h^{-1} for the top-down-perfused core incubation, and 3.36 ± 0.16 nmol cm^{-3} h^{-1} for the bottom-up-perfused core incubation. Thus, we found no significant effect of the applied method alone on leucine incorporation (two-way ANOVA, $F = 0.74$, $P = 0.49$, $n = 48$), but we found a highly significant effect of the sediment depth ($F = 14.5, P < 0.001, n = 48$). This effect was strongly modified by the method, as two-way interactions between the sediment depth and method were strong ($F = 40$, $P < 0.001$, $n = 48$).

Bacterial production in epiphyton and the pelagic zone. The alkaline- and TCA extraction methods recovered similar amounts of leucine incorporated into protein from epiphytic biofilms (*t*-test, $P = 0.8$, $n = 10$). Although Levene's test showed no significant differences between the variances for the treatments ($P = 0.18$), we noticed that the samples that were treated with the TCA extraction method contained large undisrupted leaf particles which made subsampling more difficult and probably increased the variability between measurements. Apparently, the label was not completely extracted from the leaves, so that subsamples containing larger leaf particles exhibited higher activities. We therefore used the alkaline-extraction method for further investigations. However, adding a homogenization step to the TCA extraction procedure should probably make both methods equivalent.

Leucine incorporation into bacterial protein of the epiphytic biofilm was close to saturation at concentrations above 1,000 nM (Fig. 3). We calculated an isotope dilution of 1.3 for a leucine concentration of 2,000 nM. ($K_t + S_n$) for leucine was 621 nM in the epiphyton, with a V_{max} of 70 pmol cm^{-2} h^{-1} (Table 2). In the pelagic zone, leucine incorporation was close to saturation at concentrations above 80 nM (Fig. 4). The calculated isotope dilution was 1.2 at that concentration (it was 1.1 at 140 nM). ($K_t + S_n$) of pelagic bacteria was 20 nM and thus much lower than those for bacteria in sediments and epiphyton. The V_{max} was 1,718 pmol liter^{-1} h^{-1} (Table 2).

DISCUSSION

Extraction methods. The alkaline-extraction method, which was successfully applied by Bååth (4) and by Marxsen (30), was not suitable for protein extraction from River Spree sediments. Possibly, the iron and manganese coating on the sediment particles interfered with the complex-forming EDTA used in this technique. The combustion method of Tuominen (58) measures the total leucine uptake into bacteria. However, the intracellular pool of leucine not incorporated into proteins may be high (50), and bacterial production thus might be overestimated with the combustion method. In our study, hot TCA extraction combined with filtration of the precipitate yielded good results, was less time-consuming than the alkaline extraction, and does not require an oxidizer like the combustion method does. However, it is more expensive in terms of filters and solubilizer needed.

Substrate saturation of leucine. Saturation of nutrient uptake rates occurs if enzyme-dependent or transporter-dependent steps limit nutrient influx into the cells (7). In pure cultures, leucine is taken up via active transport systems that produce a biphasic saturation curve (1). However, it seems

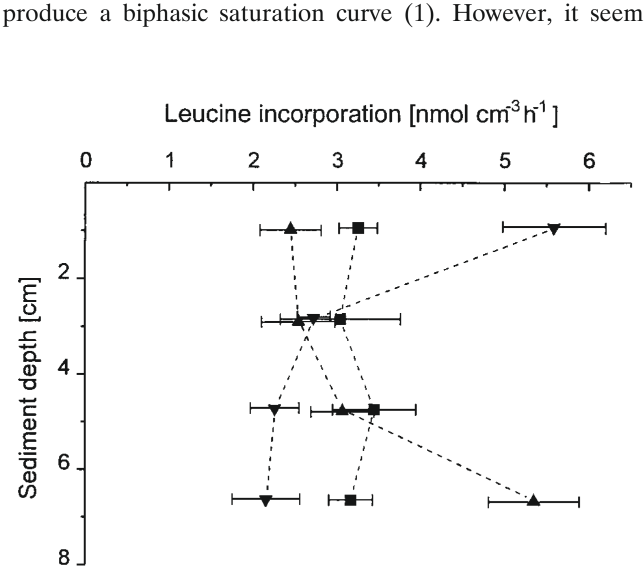

FIG. 2. Leucine incorporation of sediment bacteria incubated in vials (■), top-down-perfused cores (▼), and bottom-up-perfused cores (▲). Experiments were performed in August 1998, at incubation temperature of 20°C. Data are expressed as mean ± 1 standard deviation (n = 4).

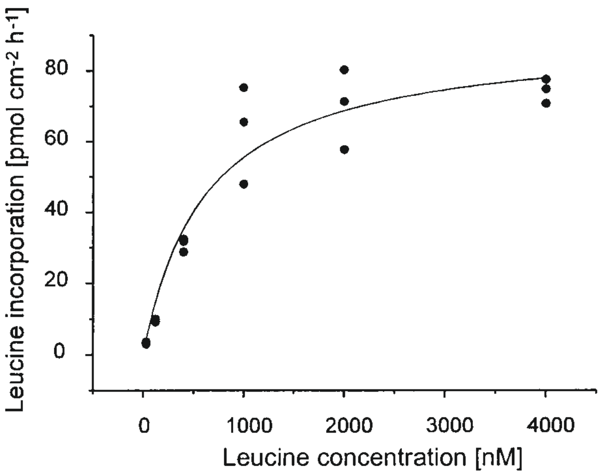

FIG. 3. Kinetics of uptake of leucine for epiphytic bacteria with fitting by using the Michaelis-Menten equation. The experiment was performed in July 1997, at incubation temperature of 21°C.

obvious that kinetic diversity of a natural bacterial population will not yield simple one-enzyme–one-substrate saturation curves of the Michaelis-Menten type. Kinetic variability can be caused by several factors, e.g., diffusion gradients of enzymes and substrates in the biofilm matrix (29, 40), the physiological heterogeneity of natural bacterial populations (27, 63), and the influence of additional limiting factors (1, 7). A bi- or multiphasic mode of substrate uptake has therefore been postulated for marine pelagic environments (3, 59, 63).

Leucine incorporation of bacterial communities in sediments of the River Spree also seems to be at least biphasic with a close fit to the Michaelis-Menten saturation curve for leucine concentrations up to 50 μM. We therefore intend to conduct saturation experiments prior to measuring bacterial production in sediments, with 50 μM as a leucine concentration for guidance. This concentration has been shown to saturate leucine incorporation in streambed sediments (30), and incorporation was close to saturation in lake sediments (58) and in the hyporheic zone of a prealpine stream (6). Values for bacterial production calculated from uptake of leucine at 50 μM concentration therefore represent conservative estimates of bacterial activity. For epiphytic bacteria on leaves of *S. sagittifolia* from the River Spree, leucine incorporation was saturated at leucine concentrations above 1,000 nM. This is slightly higher than the saturation concentration range (400 to 800 nM) found for epiphytic bacteria present on detritus of *Juncus effusus* from the Talladega Wetland (54) and on eelgrass (*Zostera marina*) leaves (56). The saturation leucine concentration of 100 nM we found for pelagic-zone bacterial communities of the River Spree is within the range of those found for eutrophic lakes (21, 44).

Why are substrate affinities so different for pelagic, epiphytic, and sediment bacteria? Differences in the assimilation of leucine by bacterial communities among these habitats can be explained by specific nutritional conditions in their environments: as leucine uptake is enhanced by the presence of glucose (1), bacteria living in biofilms that effectively trap dissolved organic carbon (12, 17, 33) might be physiologically adapted to these conditions. However, Bright and Fletcher (5) and van Loosdrecht et al. (61) argued that the observed variability of K_t values is an indirect effect due to the differences in the environments of the cells, unaccompanied by change of the bacterial assimilation behavior. Mass transfer by diffusion through the biofilm should then be the limiting step, and the observed (K_t + S_n) and V_{max} values of biofilm bacteria should not reflect physiological differences among the bacterial communities.

Isotope dilution. The calculation of V_{max} yields a potential maximum leucine incorporation rate at which the value for external isotope dilution is one (no isotope dilution) and internal isotope dilution is minimized due to feedback inhibition of de novo synthesis of leucine (25, 44). Considering that V_{max} is reached only at an infinite substrate concentration, the values calculated for isotope dilution at the leucine concentration of 50 μM are low (range, 1.1 to 1.3) and imply external leucine concentrations of 5 to 15 μM.

These calculated external leucine concentrations do not always accord well with the calculated data for (K_t + S_n). For the fitting at 50 μM, data seem to be realistic: for the March experiment, with a theoretical isotope dilution of 1.1 and (K_t + S_n) value of 6.0 μM (Table 1), the natural substrate (leucine) concentration, S_n, should be 5 μM, whereas K_t should be approximately 1 μM. For the May and February experiments, with a theoretical isotope dilution of 1.3, K_t should approach negative values if S_n is calculated via isotope dilution. However, values for (K_t + S_n) as well as for V_{max} show larger variations in these experiments, and a K_t of approximately 1 μM would well fit into the range of the standard errors of these data. In contrast, the theoretical isotope dilutions for the complete data set as well as for the data acquired in the 50 to 200 μM range are in a realistic range only for the March experiment and far too high for the May and February experiments. For the latter, other processes, which cannot be described by the Michaelis-Menten equation, seem to have been important.

The calculated isotope dilution can also be verified by comparing it to the amino acid content of the interstitial water: dissolved amino acids are immobilized rapidly in sediment biofilms by a combination of microbial and abiotic mechanisms (11, 12). The existence of a large pool of dissolved amino acids within the sediments is therefore improbable. In various interstitial waters, median concentrations ranging from 5 to 100 μM were found (55); this range is of the same order of magnitude as the natural leucine concentrations that can be calculated with our isotope dilution data (5 to 15 μM for concentrations up to 50 μM, and 25 and 75 μM for those up to 200 or 300 μM). These dissolved amino acids are most often combined rather than free (55), but after they are hydrolyzed with extracellular enzymes, their uptake might compete with that of

TABLE 2. Parametric values for leucine incorporation into protein by bacteria in epiphyton and in the pelagic zone[a]

Habitat	V_{meas}[b,c] ± SD	(K_t + S_n) (nM) ± SE	V_{max}[c] ± SE	V_{max}/V_{meas} ratio	Chi-square, r^2, P (n)[d]
Epiphyton	69.8 ± 11.4	621 ± 155	90.1 ± 6.8	1.29	65.7, 0.97,*** (18)
Pelagic zone	1,417 ± 91	20.4 ± 2.8	1,718 ± 61	1.21	11,236, 0.99,*** (18)

[a] Calculations were performed by nonlinear regression of the saturation curves by using the Michaelis-Menten equation.

[b] Rate of incorporation of leucine into protein by bacteria in epiphyton at an added leucine concentration of 2,000 nM and by bacteria in the pelagic zone at 80 nM.

[c] The values are reported as picomoles of leucine cm^{-2} h^{-1} for bacteria in epiphyton and picomoles of leucine $liter^{-1}$ h^{-1} for bacteria in the pelagic zone.

[d] See Table 1, footnote *c*, for an explanation of the statistical values.

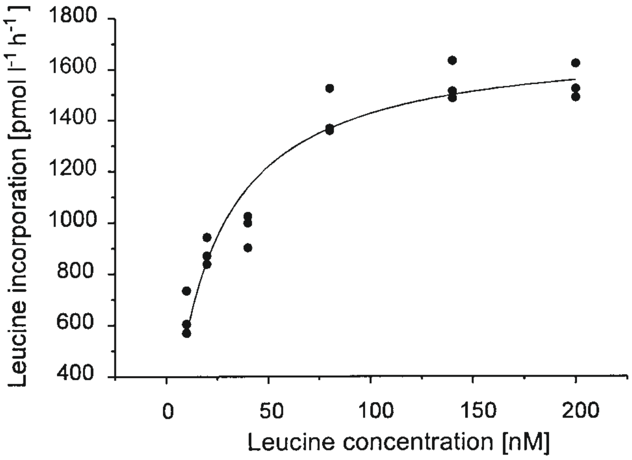

FIG. 4. Kinetics of uptake of leucine for pelagic-zone bacteria with fitting by using the Michaelis-Menten equation. Experiments were performed in May 1997, at incubation temperature of 17°C.

dissolved free amino acids (47) like the added [^{14}C]leucine. The concentration of dissolved free amino acids in aquatic environments is generally in the lower nanomolar range (55) and should therefore not contribute significantly to isotope dilution.

However, on a small (microliter) scale, microzones containing much higher ambient leucine concentrations are likely to occur in the sediments. Pelagic algae and other organic matter might be trapped here and release exudates in close proximity to the bacteria. Therefore, in these "hot spots" of heterotrophic metabolism, local isotope dilution might be higher. Multiphasic uptake kinetics with K_t values in the higher micromolar range and high V_{max} values might here be of evolutionary use for sediment bacteria.

Changes in bacterial activity. In marine, pelagic environments, the addition of nanomolar concentrations of leucine repressed biosynthesis of leucine and did not alter the rate of protein synthesis (24, 25). In the eutrophic environment of the River Spree even micromolar additions of leucine did not significantly alter the activity of sediment bacteria. However, this might not be true for oligotrophic systems. Leucine might here be respired by bacteria to a greater extent, and additionally protein turnover might occur (25), leading to an overestimation of bacterial production.

Eukaryotic organism leucine uptake. A variety of eukaryotic organisms are capable of osmotrophic uptake of organic compounds. Whereas heterotrophic protozoa can only feed osmotrophically in highly organically enriched environments (48), heterotrophy is well known for a multitude of marine and freshwater algal species (reviewed in reference 57). Facultative heterotrophy can be seen as a selective advantage of benthic algae in rivers, which are often transported into deeper, dark sediment layers (personal observation). Compared to bacteria, however, protozoa and most benthic algae probably are poor competitors for dissolved organic carbon, due to their lower surface-to-volume ratio and lower substrate affinity. This concept is in accordance with our finding of substantial leucine uptake by eukaryotes (20 to 35%) only at concentrations of 200 μM.

Effects of incubation technique. Sampling and laboratory incubation of sediments from natural habitats always imply a disturbance of the in situ gradients of reduced carbon and electron acceptors. This procedure might therefore enhance bacterial activity (13, 35, 39), although in other studies (9, 30, 37) little effect of sediment disruption on bacterial production has been revealed. Disturbance effects can be minimized by incubating the sediments as whole cores that are perfused with river water or groundwater at natural rates (30, 31). In our study, differences of bacterial activity due to sediment disturbance are unlikely, because in the River Spree these sands are prone to steady movement caused by the current and thus form a very dynamic habitat. We attribute the higher bacterial production in the surface layer of the sediment core, and the sharp decrease with depth, to an enhanced oxygen and nutrient supply of the uppermost layer caused by the steady water flow. The flow in perfused sediment cores reduces diffusion limitation and therefore enhances leucine incorporation.

Loss of the added leucine by bacterial incorporation in upper sediment layers and abiotic adsorption is unlikely to account for the lower activity in deeper layers of the perfused cores, because 80.6% ± 1.3% ($n = 8$) of the added tracer was recovered at the outflow and a gradual rather than a sudden decrease should have occurred in consecutive layers if it were due to adsorption. Rather than leucine, oxygen is probably the key factor responsible for the observed pattern: estimated bacterial production was as high as 8.7 ± 0.9 μg of C cm^{-3} h^{-1} in the upper layer (to 1.9 cm depth) of the perfused cores. If a bacterial growth efficiency of 30% (34) is assumed, bacteria in this layer should consume 3.9 mg of O_2 within a 12-h incubation time. By perfusion of oxygen-saturated water at a rate of 18.2 ml h^{-1}, 2 mg of oxygen was supplied to the core during the 12-h incubation. This means that at approximately 1-cm sediment depth oxygen depletion occurs and anaerobic metabolism should prevail. The same calculations can be performed by using data from the bottom-up-perfused cores, where leucine incorporation rates exhibited a striking symmetry with those for the top-down-perfused cores (Fig. 2). Oxygen should be consumed in the 7.6-to-5.7-cm-deep layer of the bottom-up-perfused cores, and anaerobic metabolism should prevail in the upper sediment layers. Bacterial abundance as well as organic matter was roughly equally distributed within the upper 10 cm of the shifting Spree River sands (15). Therefore, oxygen, and to a lesser extent leucine and nutrients, from the flowing water limit bacterial protein production in deeper sediment layers.

By maintaining a steady water flow, the perfused-core method reflects the natural conditions occurring in a river bed, where water frequently infiltrates and convectively flows within the sediments (53). If experiments aim at the estimation of bacterial production in the natural environment, the dissolved organic carbon and oxygen contents of the water that is used for perfusion should approach natural conditions. The perfused-core method makes possible long incubation times (30), which allow for the use of a low-specific-activity tracer, resulting in extremely low control values. However, as the perfused water does not circulate, a greater volume of radioactive waste (with low specific activity) is produced than by vial incubation methods. For a study of the basic principles of bacterial production measurements, the incubation in vials seems appropriate, because comparable nutrient and oxygen conditions can here be maintained in parallel.

Conclusions. Bacterial production can be measured by the leucine incorporation method in a wide range of aquatic habitats, including fluvial sediments. In the sediments, substrate saturation was achieved only at high leucine concentrations, which have rarely been applied in previous studies. Therefore, bacterial production measurements can be interpreted correctly only if substrate saturation experiments involving large concentration ranges are performed concomitantly and if isotope dilution is estimated. The perfused-core incubation technique simulates in situ conditions more closely than vial incubations, as vertical concentration gradients, which influence bacterial metabolism substantially, develop.

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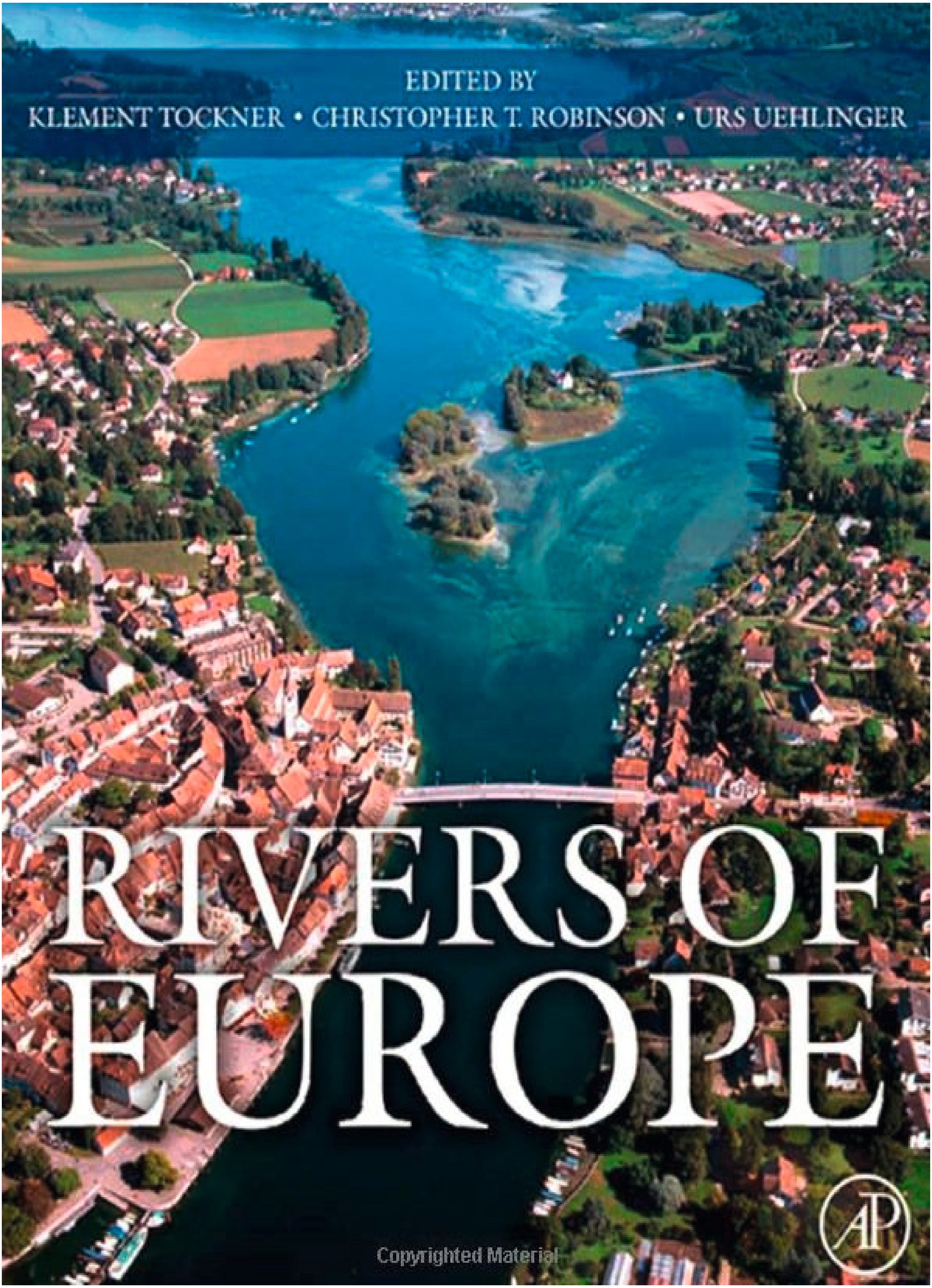

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RIVERS OF EUROPE

Chapter 14

Rivers of the Central European Highlands and Plains

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14.1. INTRODUCTION

The ecoregion of the central European highlands and plains is drained by some of the main rivers that flow into the Baltic and North Seas, including the Weser, Elbe and Oder Rivers. In addition to these rivers, this chapter describes some smaller but peculiar rivers such as the Em (Sweden), Skjern (Denmark), Spree (Germany) and Drawa (Poland) Rivers (Figure 14.1a,b, Table 14.1).

The landscape of the north-eastern Central European Plains was mostly shaped by the huge ice cap of the latest glacial period (Weichsel Glacial) that ended 10–12 000 years ago. Although only the northern part of the ecoregion was covered by ice, the remaining area was reshaped by periglacial processes as well. The glacial advance partly followed the pattern of the earlier Saale glacial period some 230–130 000 years ago, which completely covered the Central European Plains. Much of the landscape is therefore dominated by glacial and periglacial geomorphic elements such as moraines, outwash plains adjacent to terminal moraines, different types of lakes (ice-scour lakes, moraine-dammed ribbon lakes, kettle lakes, and glacial drift-plain lakes formed under the ice sheet), large glacial valleys, and large lowland plains consisting of glaciofluvial deposits. The different retreat stages of the glacial sheet produced a sequence of glacial valleys forcing meltwaters towards the North Sea. These valleys are still partially used by some rivers today, including the Elbe, Spree, Warta and Skjern. As river sediments mainly consist of sand, sediment transport occurs nearly continuously, creating ripples or subaqueous sand dunes often reaching a crest height of up to 1.5 m. Regional ecological characteristics of the streams and rivers in the ecoregion have been summarized by Petersen and Gislason (1995) and Statzner and Kohmann (1995).

As the landscape is relatively young and the sediment load of lowland rivers rather small, there also are numerous lakes interconnected by small to medium-sized rivers. Because the river basins are rarely underlain by solid bedrock, there is a high infiltration capacity following precipitation and typically little seasonal variation in river discharge. Only the larger rivers originating in the highlands bordering the region have major floods, as exemplified by the great Oder flood in 1997 and the great Elbe flood in 2002. With their relatively constant flow, larger rivers (Weser, Elbe, Oder) have been used for navigation for many centuries and their channels have been modified for navigation via the construction of, for example groynes that narrow the river.

Climate ranges from subatlantic in the western Central European Plains to subcontinental in the eastern areas. In parts of the Elbe and Oder catchments, potential evapotranspiration exceeds precipitation, so that vegetation suffers from significant water stress in summer. There, drought regularly produces extensive periods of low flow that stops navigation for weeks to months during summer. With climate change, an increase in annual precipitation and a shift timing from summer to winter is predicted for the western, subatlantic part of the ecoregion, while in the eastern part no increase in annual precipitation is expected.

14.2. WESER

The Weser River exhibits a balanced longitudinal sequence of geomorphologically distinctive river sections typical of the Central European Highlands and Plains. Both headwater rivers (Werra and Fulda) originate in the central German highlands in Thuringia and Hessia, respectively, and are nearly the same size. The river is called the Weser after their confluence, and crosses the highlands (called Oberweser) until it enters Lower Saxony in the north German lowlands (Mittelweser). At the mouth at the North Sea north of Bremen, an estuary is formed called the Unterweser, which is finally followed by a 46 km section that crosses the wadden-sea

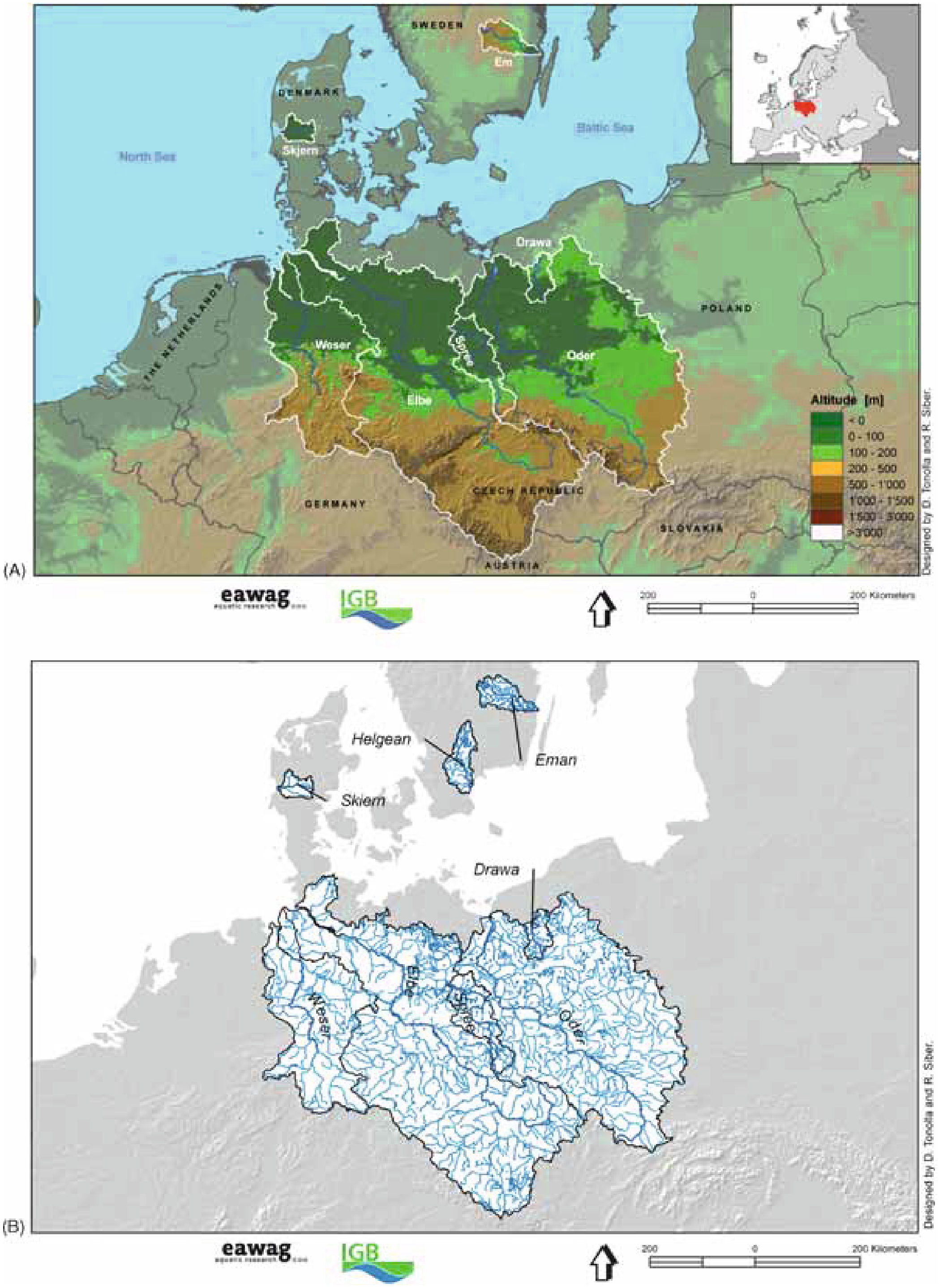

FIGURE 14.1 Digital elevation model (upper panel) and drainage network (lower panel) of Rivers of the Central European Highlands and Plains.

named Außenweser. The Weser has undergone severe anthropogenic alterations due to the high population density in the catchment, extensive agriculture, channelization and use for navigation, as well as significant effluent loads from wastewater treatment plants and salt mines. Salinization transformed the former freshwater river into a brackish water river for several decades. In 1992 and 2000, salt–water pollution of the Werra and Weser was reduced and freshwater assemblages have gradually recovered.

14.2.1. Biogeographic and Geological Setting

The headwaters Werra and Fulda as well as the upstream part of the Weser (Oberweser) belong to the continental biogeographic region, while the middle and lower Weser (Mittel-, Unter- und Außenweser) belong to the Atlantic region. The Weser was not glaciated during the Weichsel glaciation period.

Highlands in the central and northern part of Germany geologically consist of a variety of Palaeozoic and Mesozoic formations. In contrast, the plains of northern Germany are dominated by Neozoic formations that were partially reshaped by Pleistocene glaciations. Following the late Carbon era, the mid-European mainland was bordered by seas in the north and south. A transgression of the Zechstein Sea produced thick salt deposits that are now found in Lower Saxony, Hessia and Thuringia (Feldmann et al., 2002). At the end of the Mesozoic, the Variszic rock mass was covered by three characteristic levels of sandstone, shell limestone and keuper, the so-called 'Germanic trias'. These deposits now form the spines of several steep mountain chains and escarpments in southern Lower Saxony, Weserbergland and the northern Harz. At the end of the Jura, pressure from the Mesozoic sediments caused deformations of the Zechstein salt-scales underneath, resulting in salt domes and salt anticlines. Tectonic movements at the end of the Cretaceous period caused the development of vulcanos in the Vogelsberg and Rhön.

In the Quarternary, ice masses of the Elster glacial period extended from Scandinavia to the northern highlands in Lower-Saxony, reaching a thickness of 700–4000 m. The ablating glaciers pushed against the general orographic gradient rising towards the south, producing large icewater reservoirs. These reservoirs remodeled the landscape via glacial erosion and forced several rivers to change their beds. Afterwards, the Weser flowed north through the mountain gate of Porta Westfalica. During the Holstein interglacial warm period and the Saale-Fuhne glacial period, the mid-terrace-gravel was deposited and is a resource in demand today.

Glaciers did not reach the Weser catchment during the subsequent Weichsel glacial period. Tundra vegetation that covered northern Germany during a warming climate since 13 000 years B.C. was first replaced by coniferous forest and then by deciduous forest around 7000 B.C. This landscape was then altered by humans who populated the catchment some 2500 years later (Feldmann et al. 2002; Hantke 1993). Beech, which now dominates forests in most of the catchment, migrated to Central Europe in the Bronze age (2000–1000 B.C.). Discontinuities in the longitudinal gradient of the Weser produced during earlier glacial periods were modified later by fluvial erosion, so that nowadays the river shows a balanced longitudinal profile.

14.2.2. Physiography, Climate, and Land Use

The Fulda, the left-side headwater of the Weser, originates from the basalt formation of the Rhön at 850 m asl. The upper river follows a deeply eroded valley, mainly through sandstone formations. In the middle reach, the valley widens near Kassel to a width of 3 km, followed again by a narrow passage through sandstone formations until the Fulda joins the Werra at the city of Hann. Münden at 117 m asl. The sources of the Werra originate at the border of the Thuringian forest and the Thuringian slate mountains at ~800 m asl. From the city of Meiningen, the Werra flows north and follows a line between the Rhön in the west and the Thuringian forest in the east. Subsequently, the Werra flows through the Zechstein salt deposits until it reaches Hann. Münden. From there, the upper Weser section called Oberweser flows through a geological and morphological diverse section of the highlands of Lower-Saxony. North of the city of Hameln, resistant sandstones of the Rhät formation are crossed in a relatively narrow valley between the Weserbergland and the Wesergebirge. Breaching the Jurassic Malm layers of the Wiehengebirge at Porta Westfalica, the Weser enters the north German lowlands. Here, the river course changed frequently during the Pleistocene, and today crosses quaternary gravels and wetland clays (Lüttig 1974).

The northern area of the Weser has a marine climate with average temperatures of ~17 °C in July and near 0 °C in January. Precipitation ranges from 600 to 800 mm/year. In the highlands of the southeast catchment, the climate is more continental with temperatures averaging 17 °C in July and −3 °C in January. Here annual precipitation averages 800 mm, reaching local maxima of 1600 mm in the mountains.

The influence of man on the rivers of the Werra and Weser began with neolithic settlements. In the medieval age, most of the catchment was deforested. Distinctive mammals like aurochs, wisent, brown bear, beaver and otter nearly vanished before the end of the 13th century. Regular forestry started in the 18th century to ensure a sufficient supply of wood. Log driving started in the 12th century, and towpaths were built to move ships and boats upstream. Later, coordinated river training was untertaken with artificial deepenings, bank reinforcements and the construction of barrages. Today, the morphology of the natural river channel and its floodplain is heavily transformed by river training and agricultural use.

Industries have been developed in a few cities along the Werra, Fulda and Weser. In the lower Weser, the Mittelland Canal crosses the river near the city of Minden, which connects Berlin with the Ruhr industrial area, thus providing a waterway between the Rhine, Weser and Elbe rivers. At the transition point to the tidal reach, the town of Bremen was founded with its port, which in the 19th century built another port called Bremerhaven 70 km downstream, to enable the access by larger ships. Industrial exploitation of the salt domes (Zechsteinsalzlager) in Hessia and Thuringia by mining and the potash industry since the early 20th century have heavily polluted the Werra and Weser by their salt effluents.

The fertile soils of the Mittelweser floodplains have been completely modified for intensive farming. Agriculture and cattle ranching extend down to the waterline, resulting in the destruction of riverbanks, water pollution by faeces, inputs of fertilisers and pesticides, and elimination of riparian vegetation by browsing. The Oberweser is less affected in that respect. Gravel is extracted in many places along the entire river, resulting in numerous gravel pits in the floodplain that are filled by groundwater and open to potential pollution.

14.2.3. Geomorphology, Hydrology, and Biochemistry

The Fulda drains a catchment area of 6941 km^2 and has a mean slope of ~0.7 for 218 km until the city of Hann. Münden, where it has a mean discharge of 58 m^3/s. The Werra drains a catchment area of 5496 km^{2}and flows with a mean slope of 0.6 for 292 km until it reaches its confluence with the Fulda, where it has mean discharge of 51 m^3/s. The Weser, below the confluence of Werra and Fulda at 117 m asl, flows 432 km towards the estuary in the North Sea at Bremerhaven. The river is sectioned into the Oberweser (Rkm 0–204) from Hann. Muenden to Minden, the Mittelweser (Rkm 204–366) from Minden to Bremen, the Unterweser (Rkm 0–74, new counting) from Bremen to Bremerhaven, and the Außenweser (Rkm 74–120) from Bremerhaven to the lighthouse 'Roter Sand' within the North Sea. The main tributaries are the Diemel (left-side), Leine (right-side), Aller (right-side), and Hunte (left-side). The largest tributaries, Aller and Leine, bring waters from the western Harz Mountains, which receive up to 1600 mm of precipitation per year.

The total drainage area of the Weser is 46 306 km^2, ranging from 50°N to 53°N and from 8°E to 9°E. Meanean channel slope is 0.48 for the Oberweser and 0.16 for the Mittelweser. Today, tides run up the river until the barrage of Bremen-Hemelingen with a recent tidal range of 4.3 m (originally 0.7 m).

14.2.3.1 Hydrology

The discharge regime follows a pluvio–nival type characterized by high flows in winter and a low water period from June to October. Floods usually occur from December to January and March to April. A distinctive low water period that mainly occurs in the Werra and Oberweser is attenuated by a large reservoir on the Eder River, a left tributary to the Fulda River, to facilitate navigation on the Oberweser. Upstream of the inflow of the Aller River, the Weser has a mean discharge of 208 m^3/s, to which the Aller adds 108 m^3/s on average. Thus the discharge of the Mittelweser at Intschede/Bremen averages 326 m^3/s (mean low water 117 m^3/s, mean high water 1210 m^3/s). In the Außenweser and Unterweser, tidal amplitudes, and the risk of storm tides, have considerably increased through channel deepening for navigation of even larger ships.

Annual precipitation has historically shown an increasing tendency (5% increase from the period 1931–1960 to the period 1961–1990), with a decreasing share in summer and autumn (Engel 1995). Along the river, the Grohnde nuclear powerplant at Rkm 125, Veltheim coal powerplant at Rkm 177, Minden-Petershagen coal powerplant at Rkm 214, and the Landesbergen oil power station at Rkm 252 increase water temperatures by about 5–9 °C. Due to these heat inputs, the annual mean temperature of the river increases by 3–4 °C in the first 150 Rkm (Bäthe 1992; FGG Weser 2003). Annual temperature of the Weser averages 11–16 °C, with a maximum temperature of 30 °C found in the impoundments of the Mittelweser during hot summer periods. Winter minima are 1–8 °C, and since 1996 the freezing of the Weser has again been observed. Formerly, salt wastewaters discharged from the potash industry had essentially prevented the river from freezing.

14.2.3.2 Biogeochemistry

The Weser is officially classified as 'critically polluted' (beta- to alpha-mesosaprobic), and in some sections even as 'heavily polluted' (alpha-mesosaprobic). Better water quality can only be found in the Aller upstream of the inflow of the Leine, and in the lower Fulda (Niedersächsisches Landesamt für Ökologie 2001). Most reaches of the Werra are classified as 'polluted' (beta-mesosaprobic). Additionally, the Werra has a high nutrient load, as only half of the wastewater produced in the Thuringian Werra catchment area is treated (Thüringer Landesanstalt für Umwelt und Geologie 2007).

In last decades, the pollution load of the Weser from municipal and industrial point sources has been reduced by the construction of modern sewage treatment works. Since the early 1990s, autotrophic biomass production has increasingly affected water quality through so-called secondary pollution (Bäthe & Coring 2002; Herbst 1995). Nitrogen and phosphorus enter the Weser from numerous point and diffuse sources, so that river concentrations allow unlimited and occasionally excessive growth of algae. Algal growth is additionally favoured by inputs of potassium from the potash industry (Coring 2008), and high solar radiation because the riverbanks are mostly without riparian trees. From April until October, the dissolved oxygen (DO) budget of the Werra and Weser is influenced by the biomass and activity of phytoplankton. Impounded sections of the Werra and Weser show significant DO deficits with minima near 1 mg/L at low flow in hot summer (Bäthe & Coring 2002; Herbst 1995). Although concentrations have declined since the late 1980s due to improved wastewater treatment, phosphorus concentrations still average 130–150 μg/L in the

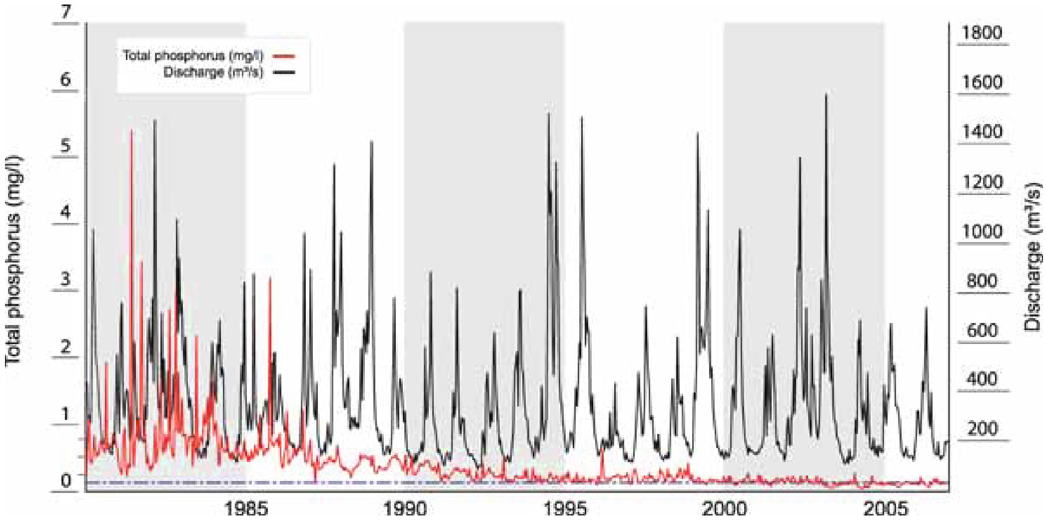

FIGURE 14.2 Long-term dynamics of phosphorous concentrations and discharge at the Bremen/Hemelingen measuring station (data: FGG Weser).

lower Mittelweser (Figure 14.2), and 200–600 μg/L in the Oberweser. Ammonium concentrations have decreased and now usually do not exceed 0.2 mg/L NH_4–N at the Bremen/Hemelingen monitoring station, whereas nitrate concentrations, which currently range between 2 and 5 mg/L, have only slightly decreased.

The Werra and Weser have been heavily polluted by salt effluents from the potash industry in Hessia and Thuringia. Chloride concentrations peaked at 27 mg/L. in 1992 and at 9 g/L in 1997 in the Werra downstream of the mining region at Gerstungen (Figure 14.3). Chloride pollution has largely changed the flora and fauna of both rivers (Bäthe 1992, 1995, 1996, 1997, 2008; Coring 2008; Deutscher Verband für Wasserwirtschaft und Kulturbau 1998). The osmotic effects were further aggravated by the fact that chloride discharge was discontinuous and much lower on weekends, thus chloride concentrations varied weekly by several g/L. The ionic composition that resulted in the river differed from that found in natural marine or brackish waters. The high content of potash and magnesia affected most aquatic organisms at sublethal or even toxic levels. For instance, potassium causes toxic effects in aquatic organisms at concentrations $>$80 mg/L (Halsband 1976). For a long period, maximum salinity values in the lower Werra were higher than those of the Baltic Sea. From 1990 to 1992, a reduction in chloride concentration by $\sim$63% was recorded for the lower Werra, and since 2000 the concentration has not exceeded 2.5 g/L Cl$^-$ at Gerstungen due to improved techniques of salt production and better effluent regulation. The chloride concentration also is diluted to a concentration of 400 mg/L by the city of Bremen some 505 km downstream. Colonization of the river by aquatic biota improved with the decrease in potassium concentrations below 100 mg/L (Deutscher Verband für Wasserwirtschaft und Kulturbau 1998).

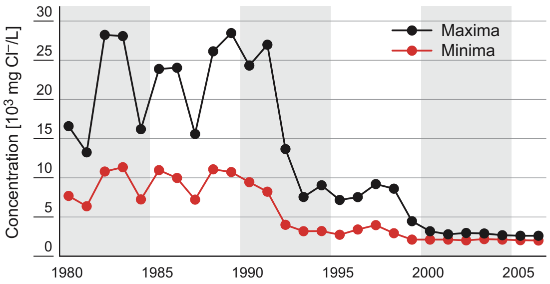

FIGURE 14.3 Chloride concentrations in the Werra at the Gerstungen monitoring station.

14.2.4. Aquatic and Riparian Biodiversity

The first studies on the biodiversity of the Weser were induced by impacts to the fishery caused by river training that included several impoundments and gravel abstraction (Keller 1901). Additional impairments in fish populations were caused by wastewater inputs, increasing potassium concentrations, and extensive algal blooms (Buhse 1963, 1974; Halsband 1973). During the 1950s, the extinction of some amphipods was recorded, followed by taxa of Plecoptera, Ephemeroptera, Mollusca, and Bivalvia. To provide food for the remaining fish, the invasive *Gammarus tigrinus* was introduced to the Werra (Schmitz 1960). At the same time, *G. tigrinus* migrated from the Weser estuary into the Mittelweser and began spreading upstream (Bulnheim and Scholl 1980; Bulnheim 1984). The aquatic invertebrate assemblages of Weser and Werra changed to groups that could tolerate the brackish water conditions.

14.2.4.1 Phytoplankton, Zooplankton, and Zoobenthos

Phytoplankton of Fulda, Werra and Weser is limited by the availability of dissolved nutrients, the presence of numerous impoundments, and water salinity. Phytoplankton assemblages of the Werra consist of ~30 species and are dominated by the diatoms *Thalassiosira pseudonana, Thalassiosira weisflogii, Cyclotella meneghiniana,* and *Stephanodiscus hantzschii*. Chlorophyll concentrations can increase to >150 μg/L in the lower Werra during the summer, and peak concentrations of 625 μg/L were measured in 1995 (Deutscher Verband für Wasserwirtschaft und Kulturbau 1998). Since 2002, aquatic macrophytes have become abundant in the saline Werra, and is paralleled by a decrease in phytoplankton (Coring 2008).

Except for short periods, phytoplankton in the Weser predominantly originates from the Werra. Fast growing diatoms display high biomass within the free-flowing Oberweser (Photo 14.1). Since zooplankton are found only sporadically, the algal biomass is consumed mostly by macrozoobenthos. In the impoundments of the Mittelweser, much of the phytoplankton settles and is microbially decomposed, creating significant DO deficits. During the growing period from April to October, centric diatoms dominate the phytoplankton along the entire Weser. Besides centric diatoms, volvocales and chlorococcales are also abundant. Benthic pennate diatoms enter the water column only during high flows. During low flows, coccale nanoplankton develop after sedimentation of the diatoms. With lower salt concentrations, green and blue–green algae have appeared in the lower Werra since 2004.

From 1986 to 1992, a total of 87 taxa of macrozoobenthos have been recorded in the Weser. As a consequence of lower salt concentrations, the number of taxa has now risen to 168. During the high salinity period, native species such as *Anodonta* spp., *Unio* spp., *Theodoxus fluviatilis, Asellus aquaticus, Gammarus fossarum, Gammarus pulex, Gammarus roeseli, Potamanthus luteus, Ephoron virgo*, and several trichopterans were replaced by species from other aquatic ecosystems and only 25% of the earlier freshwater taxa remained (Bäthe 1992). Ecological functions of the benthic community were done by *G. tigrinus,* Oligochaeta, *Cheli-Apocorophium lacustre, Potamopyrgus antipodarum, Cordylophora caspia,* Chironomidae, and *Dendrocoelum lacteum*. Besides *G. tigrinus,* the amphipods *Chelicorophium curvispinum, Ch. lacustre,* and *Chelicorophiummultisetosumwere* common in the Weser. *C. A. lacustre*, a genuine brackish-water species that expanded from the Weser estuary, colonised the Weser up to the city of Hann. Münden by 1990. Depending on the degree of salinity and phytoplankton biomass, Corophiidae can show high population densities (e.g. *C. A. lacustre* at 437000 ind./m^2 and *A. multisetosum* at ~4000 ind./m^2).

According to their halotolerance, *C. A. lacustre* today colonises the Unterweser, the Oberweser, and most of the navigable Werra, while *C. multisetosum* is confined to the Mittelweser in reaches with low current velocities at lower densities. Originating from the Aller, the freshwater *C. curvispinum* migrated into the Weser at chloride concentrations of 410 mg/L. Today, this species is common throughout the

PHOTO 14.1 Weser at Rkm 96 upstream of the city of Höxter. The river channel is protected here against lateral erosion by perpendicular rip–rap groynes overgrown by grass. The river corridor is bordered by dikes, and the floodplain is mostly used as grassland and crop fields (Photo: J. Bäthe).

Weser and the navigable section of the Fulda. The halotolerant bivalvia of the Weser can attain high biomasses of 8–47 g/m^2 (*Dreissena polymorpha*), and 0.7–8.1 g/m^2 (*Corbicula fluminalis*). Since 1998, the invasive amphipod *Dikerogammarus* is found in the Weser and the navigable Fulda.

Low abundances of Trichoptera that appeared since 1993, including *Hydropsyche bulgaromanorum*, *H. pellucidula*, *Ceraclea dissimilis*, *Cyrnus trimaculatus*, *Ecnomus tenellus*, *Hydroptila* spp., *Lasiocephala basalis*, *Polycentropus flavomaculatus*, *Psychomyia pusilla*, *Rhycophila dorsalis* Gr., and *Tinodes waeneri*, indicate an improvement in water quality in the Weser. Recolonisation of the Mittelweser by *T. fluviatilis*, which had disappeared in the early 1960s, also began in 1993. The mussels Anodonta spp. and Unio spp. have spread into the Oberweser since 1995, tolerating salinities of 1.3–2.2 (chloride concentrations of 620–1150 mg/L). Sensitive insects like *Caenis luctuosa*, *Heptagenia sulphurea*, *Serratella ignita*, and *Leuctra fusca* have returned to the river at a maximum salinity of 2.8. Another typical mayfly of the Weser is *Ephoron virgo*, which returned in 1996 after 40 years of absence.

14.2.4.2 Fish, Amphibians and Mammals

The lower Werra and Fulda as well as the upper Oberweser belong to the barbel fish region. Downstream, the barbel-bream fish region extends from Rkm 44 to Rkm 204 (Buhse 1990). Due to river training, the Mittelweser cannot be assigned to any particular fish-region, and today the characteristic fish is the common bream. The first channelisation of the Weser caused a decrease in the numbers of migrating Atlantic salmon, sea trout, Atlantic sturgeon, houting, smelt, allis shad, twaite shad, herring, river lamprey, and sea lamprey (Keller 1901). In the Mittel- and Unterweser, river training still continues to further improve conditions for navigation. After the Second World War, toxic potassium concentrations caused fish kills (Buhse 1963, 1974; Halsband 1973, 1976), and up to 1990 the fishery was dominated by roach, European eel, and perch (Niedersächsisches Landesamt für Wasser und Abfall 1991). After salinity levels decreased, the ichthyofauna diversity of the Oberweser again increased. Today, 26 species have been recorded in surveys with chub, common dace, roach, European eel, perch, and European bullhead as well as barbel being most common (Figure 14.4).

14.2.5. Management and Conservation

The Weser and its tributaries provide important ecological services to society, including drinking water (e.g. for Bremen), sewage removal, water for irrigation, cooling water for powerplants and industrial facilities, hydropower, habitat for organisms, and recreation and tourism. Several of these services compete for water quantity and quality. Today, the fishery provides little economic benefit. Presently, navigable river sections represent 89 km of the Werra, 109 km of the Fulda, 117 km of the Aller, 97 km of the Leine, and all 487 km of the Weser. The first shipping traffic was recorded in the 12th century and today navigation is concentrated on the river section between Minden and Bremen, connecting the Mittelland Canal to the seaport of Bremen.

From 1906 to 1910, the dam in Bremen/Hemelingen was built to stop the erosion caused by the deepening of the Unterweser. The dam at Doerverden (1907–1913) was built to counteract groundwater lowering caused by increasing drainage of the landscape for farming. Five more dams were constructed (Petershagen 1953, Schlüsselburg 1956, Landesbergen 1960, Drakenburg 1956, Langwedel 1958) to provide sufficient water depth for navigation by large barges. In addition, levees were built, backwaters and streams were straightened, and a reallocation and consolidation of agricultural lands changed former floodplains for modern agriculture. Since 1982, the Mittelweser has been deepened and now provides a water depth of 3 m during low flows to maintain navigation of 1350 tons ships between Minden and Bremen. The Werra is impounded by 58 weirs and the Fulda by 60 weirs.

The Flussgebietsgemeinschaft Weser (FGG Weser), as the administrative unit responsible for the river, began studies in the Werra, Fulda, Weser and Aller in 1965. Since 1975, a measuring program was established and then amended by a general ecological planning group in 1996 (Arbeitsgemeinschaft zur Reinhaltung der Weser 1996). This program planned the reintroduction of migrating fish (1996), guidelines for pollution accidents in 2002, and a monitoring plan for rivers of the Weser catchment in 2007 (FGG Weser 2007). A comprehensive evaluation of the environmental condition of the Weser catchment is available to assist in future management plans (FGG Weser 2005). A further decrease in nutrient and sewage loads is a priority in the future management of the Weser. The Weser, Werra, Fulda and Aller have been severely affected by anthropogenic pressures created by multi-purpose uses. The main factors impairing the ecology and ecological services of the Weser system are well known among ecologists and river managers,

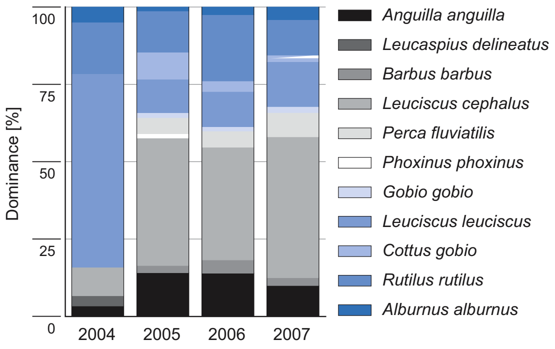

FIGURE 14.4 Fish species in the Oberweser and their dominance structure in the years 2004–2007.

but still must be appreciated in a socio-economic context. The decrease in sewage and salt loads, as well as the re-establishment of the native fauna and flora, including the investments towards this success, have been widely accepted by society. Future management plans should include flood protection and the restoration of natural river functions and services.

14.3. ELBE

With a length of 1094 km, the 8th order River Elbe (Czech: *Labe*) is the third longest river in central Europe (after the Danube and Rhine). It drains more than half the area of the Czech Republic and more than 25% of Germany. Smaller parts of its catchment also lie in Austria and Poland. Starting from its source in the Czech Giant's Mountains (Krkonoše), several reaches of the river have special touristic interests such as the scenic river canyon in Elbsandsteingebirge that forms the Czech–German border, the riverbanks that add to the scenery of the historic city of Dresden, and the floodplain forests along its middle course. The Elbe is often seen as a river still possessing a natural river bed with active floodplains; for example on one 622 km stretch from Ustí nad Labem to Geesthacht there are no impoundments. Indeed, its banks are still subject to fluvial dynamics and the largest contiguous floodplain forest of central Europe has been preserved along its course. In this river section, intensive biological activity occurs, reflected in significant changes in the composition of riverine dissolved and particular matter, making it an interesting site for limnological research. Most of the river from Pardubice to Hamburg is used for navigation, and the river has 24 impoundments within its first 350 km. The phytoplankton biomass coming from these impoundments, further supported by significant nutrient loads downstream, affects the water quality along most of the river, especially near Hamburg. In the tidal section downstream of Hamburg, the water increasingly mixes with seawater before flowing through the Elbe estuary to the North Sea.

14.3.1. Biogeographic Setting

During the Weichsel Glacial period, the northeast Elbe catchment and neighbouring regions were covered by an ice sheet. As the orography in northern Europe is generally inclined northward, meltwaters from the glacier, as well as river discharge, accumulated near the southern front of the glacier and formed large lakes, that is a precursor of the Baltic Sea. Glacial impoundments that formed in northern Eurasia were probably temporarily connected by periglacial rivers. Parts of such periglacial river valleys are still used by the Elbe and tributaries like the Havel and Spree. These periglacial rivers were east-west migration corridors, connecting formerly isolated rivers from western Europe to Lake Baikal (Schäfer 1997).

14.3.2. Physiography, Climate, and Land Use

Below the source pool at 1386 m asl in the Giant's Mountains, the headwaters of the river form a mountain stream with a scenic waterfall of 35 m. After leaving the mountains, the river enters the Bohemian Cretaceous basin and flows through entrenched valleys, an optimal situation for constructing reservoirs. In the Bohemian basin, the river forms a large bend successively redirecting the Elbe from the southeast to the northwest. Downstream, the Elbe merges near Mělník with the Vlatava (Moldau) River, which exceeds the Elbe in length (430 km versus 367 km), in catchment size (twofold larger) and discharge. Downstream of the confluences of the Vlatava and Ohře (Eger) rivers, the Elbe enters the Bohemian uplands where. There, the river valley cuts into volcanic bedrock at the Střekov castle near Ustí nad Labem, where the river is impounded by the last weir in its the Czech segment (Photo 14.2). This section is followed by a scenic river canyon that breachs the Elbsandsteingebirge. After flowing 365 km, and with about 30% of its final discharge, the river crosses the Czech–German border near the village of Schmilka. The river then flows for another 95 km through uplands and loess-covered lowlands, forming a number of islands. The romantic silhouette of Dresden mirrored in the Elbe has prompted UNESCO to include this valley section in its world cultural heritage list. Downstream of the historic city of Meißen, the river enters the North German lowlands, thus forming the border between the upper and middle Elbe. In the lowlands, the river partially follows ancient glacial valleys formed during the Elster, Saale and Weichsel Glacial periods. The river flows over bedrock only at the cities of Torgau and Magedeburg, which causes significant problems for navigation due to changes in gradient and depth.

The discharge of the Elbe increases considerably from inputs by the large right tributaries Schwarze Elster and Havel as well as by the left tributaries Mulde and Saale. Near Magdeburg, the river splits into several branches that were mostly closed in historical times but are partially used at high flows. Downstream of Magdeburg, the Elbe valley widens to ~20 km and crosses glacial deposits, and then enters a glacial valley partially used by the Havel tributary today. At the village of Geesthacht upstream of Hamburg (German Rkm 586), the middle Elbe ends and the river is now influenced by tides of the North Sea. Today the tidal influence is limited upstream by the large weir impounding the Elbe at Geesthacht, which is the only weir within the German river section. The tidal range in the lower Elbe has been largely increased by man through substantial deepening of the channel, which was done to allow passage of large ocean ships to reach the port of Hamburg. This port was mostly built along a 15-km long anastomosing reach of the Elbe bordered by two larger river branches, the Norderelbe and Süderelbe. Downstream, the Elbe forms a funnel-shaped river mouth that originally included many islands. Today, some rare freshwater tidal areas are preserved in some places. Salt waters from

PHOTO 14.2 Elbe near Ustí n.L. (Aussig) with the ruins of the medieval Střekov (Schreckenstein) castle built in the 14th century on a phonolith rock to protect navigation on the river. In the 19th century the castle towering the free flowing river had been a favourite subject of romantic painters, musicians and poets Upper: Painting by Ferdinand Lepié 1856 (Museum Ustí nad Labem), with the railway line Dresden – Prague which had been completed five years before. Lower: Today's view with the structures of the weir 10 m in height in front of the silhouette of the industrial town of Ustí. The weir was completed in 1936 to impound the river section in order to improve navigation at low water levels. (Photo: D. Fiker, Ustí).

the North Sea increase salinity downstream of Glückstadt. At Cuxhaven, salinity reaches a level of 18–30 per mil, and the sandy river shores gradually change into the vast tidal flats bordering the North Sea.

Climate in the Elbe catchment ranges from maritime in the northwest to subcontinental in southeast. Mean air temperature ranges from 8–9 °C in the lowlands to 1–3 °C on upland ridges. Temperature extremes range between −29 °C and +39 °C in the German part of the catchment, and between −42 °C and +40 °C in the Czech part (IKSE 2005). The mean number of ice days (daily maximum <0 °C) per year is 15–30 in the lowlands but reaches 100 on mountain peaks. The mean number of summer days (daily maximum >25 °C) per year is 15–50 in the lowlands and 5–20 in the uplands. Precipitation in the catchment averages 612 mm but differs greatly between sub-basins. One third of the catchment receives <550 mm, especially in the sub-basins of the Vlatava, Ohře, Saale and Havel. Precipitation minima are found in the Ohře and Saale catchments with many places receiving only 430–450 mm rainfall per year. Mountain ridges in the catchment receive between 1000 and 1800 mm of precipitation. Highest daily rainfall recorded was 345 mm in Nová Louka in the Iser Mountains in July 1897, and 312 mm in the same region at Zinnwald in the East Erzgebirge Mountains in August 2002 (IKSE 2005). Precipitation mostly occurs in summer (May–October), especially in the upper catchment, while precipitation is highest in winter in high mountain areas where snow cover may reach 150 cm in the Giant's Mountains (IKSE 2005).

There are ~25 million people living within the 148 242 km^2 Elbe catchment, 75% of which live in Germany and 25% in the Czech Republic. All major urban centers present in the catchment are on the Elbe or a large tributary, including Prague, Leipzig, Berlin and Hamburg. The sewage water produced in the catchment is treated in over 1600 wastewater treatment plants (Behrendt et al. 2004a). Land use in the catchment is dominated by crop fields (51%), forests (29%), other agricultural uses (12%), and settlements and roads (7%). Surface waters make up only 1.3%, but peak in the catchment of the Elde tributary (10%). This catchment includes, besides others, the largest lake within the borders of Germany, Lake Müritz. Some 25% of the lower catchment downstream of Hamburg is used as pastureland (Becker & Lahmer 2004).

14.3.3. Geomorphology, Hydrology, and Biogeochemistry

14.3.3.1 Geomorphology

The Elbe and its upper tributaries originate in the geologically old, upland region of Bohemia and thus exhibit a relatively regular longitudinal profile in channel slope. This profile historically stimulated long-distance navigation on the river. In the German section, the channel gradient decreases to 13–17 cm/km, so that the middle Elbe forms large meanders that have been cut through at various locations since the 16th century. Here, the floodplains are often covered by a layer of clay mostly formed in the time period between medieval forest clearings and the development of a contiguous dyke system along the Elbe. In this section, sedimentation of suspended matter during floods in the floodplain near the river channel has increased the ground level in the valley centre. More distant floodplain areas partially lost drainage capacity and developed into marshes and alder swamps. Some smaller tributaries do not enter the Elbe directly, but flow parallel to the Elbe before entering some distance downriver (Schwartz 2006). At some places, sandy sediments have been developed into dunes by the wind.

14.3.3.2 Hydrology

The runoff rate in the Elbe catchment averages 5.5 L/km^2/s, and varies from 4 L/km^2/s in the north tributaries of the Elde and Schwarze Elster to nearly 12 L/km^2/s in the Stör catchment in the northwest. With a runoff rate of 5.9 L/km^2/s, the Czech part of the catchment contributes a nearly average amount (Behrendt et al. 2004a). The length of the river between its source upstream of Spindlerův Mlýn (Spindlermühle) to the Czech–German border is 367 km, and from there to its mouth at Cuxhaven is 727 km, a total 1094 km. However, the largest tributary of the Elbe, the Vlatava (Moldau) River, has a length of 430 km, thus the total river length equals 1247 km from a hydrological point of view.

The flow regime of the Elbe is a rain-snow type. Hence, floods mainly occur in winter, but may also can occur in summer such as the extreme flood in August 2002. Discharge of the Elbe averages 101 m^3/s at the gauge station Brandýs n. L. just upstream of the confluence with the Vlatava River, and is 336 m^3/s in Dresden, 715 m^3/s at the gauge station inWittenberge, and 859 m^3/s at the gauge station Zollenspieker just upstream of Hamburg. Total discharge into the North Sea near Cuxhaven is estimated at 870 m^3/s (IKSE 2005). The largest tributaries of the river are the Vlatava (mean discharge = 154 m^3/s), Ohře (38 m^3/s), Mulde (73 m^3/s), Saale (115 m^3/s) and Havel (115 m^3/s) rivers. The travel time of river water at mean discharge is 5 days for the 137-km long impounded section from the Elbe's confluence with the Vlatava river to the Czech–German border. The travel time from the border to Magdeburg is 4 days, from there to Geesthacht (upstream of Hamburg) 4 days, and from there within the deep tidal section of the river to Cuxhaven 26 days (IKSE 2005).

14.3.3.3 Biogeochemistry

Along its course, the Elbe changes gradually from a mountain stream rushing over rocks to a gravel-bed river in most of the Czech section and in the upper German part, until finally meandering as a sand-bed river through the lowlands. In the middle Elbe, water depth of the river channel is about 1.5–2.5 m during mean low water and 3–4 m at mean discharge (Büchele 2006). Due to impoundments in the Czech section, the river downstream lacks a sediment load and the river is incised in several sections. Depth erosion was quantified being up to 1.6 m within 130 years. In the section downstream of Torgau, erosion actually continues at a rate of 2 cm/year. Depth erosion and subsequent lowering of the water table threatens construction near the river and hampers navigation over the bedrock outcrop in the channel at the city of Torgau. It also threatens the ecological integrity of the middle Elbe biosphere reserve which aims to protect water-dependent floodplain fauna and flora, and especially the persistence and natural regeneration of characteristic softwood and hardwood floodplain forests. In the lowlands of the Elbe downstream of Lutherstadt Wittenberg, bottom sediments mainly consist of sand and sediment transport continuously occurs at all discharge levels. Here, subaqueous dunes occur at heights of >1.5 m and lengths of several hundred metres (Nestmann & Büchele 2002). These dunes constantly move and pose difficulties to navigation.

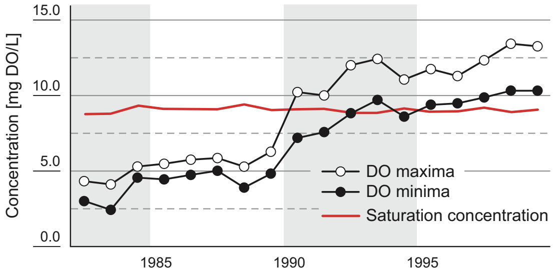

FIGURE 14.5 Long-term dynamics of the DO concentrations at the measuring station Schnackenburg (Elbe-km 475, 140 km upstream of Hamburg), reflecting the sudden improvement of water quality with the breakdown of east German industry in 1990 (data by Niedersächsischer Landesbetrieb für Wasserwirtschaft und Küstenschutz Lüneburg).

The dominance of agricultural land-use in the catchment is directly reflected in the nutrient inputs, estimated at 12 354 tons/year P, and 259 950 tons/year N on average for the freshwater section of the Elbe from 1993 to 1997. Nitrogen mainly comes from diffuse sources (73% of total N inputs), as nitrogen inputs from point sources, especially wastewater treatment plants, have been greatly reduced since the late 1980s. Diffuse nitrogen sources are mainly groundwater inputs to small tributaries (114 960 tons/year). The proportion of diffuse phosphorus inputs was 42% during 1993–1997 (Behrendt et al. 2004a, 2004b). Diffuse inputs of phosphorous and nitrogen peaked in the 1970s and 1980s when the massive use of fertilizers created a significant surplus in agricultural areas. In the German part of the catchment, this was drastically changed in 1990 when the use of fertilizer nearly stopped. Since then the use of fertilizers has increased again moderately. Focal areas of diffuse inputs of phosphorous are upland regions with significant soil erosion and former wetlands that have been drained for crop fields (Behrendt et al. 2004a). Natural values for nutrient concentrations in the Elbe system, based on background nutrient immissions, are estimated at <50 μg/L of total phosphorous and <1 mg/L of total nitrogen (Behrendt & Opitz 1999).

Up to 1990, the water quality of the Elbe was dominated by massive inputs of poorly treated wastewater from adjacent cities and factories. The section in and downstream of Dresden was so polluted that no existing degradation level could be assigned using the biological assessment saprobic system. With the breakdown of East German industries and subsequent improvement of wastewater treatment plants, the loading by organic as well as inorganic contaminants has been greatly reduced (Figure 14.5).

Transparency of the water now allows extensive growths of planktonic algae (Figure 14.6), and the river has changed from a heterotrophic ecosystem to a highly eutrophic one. It now suffers from substantial 'secondary pollution' by autotrophically produced biomass. Planktonic algae are thriving on the high nutrient levels in the river, except for the lowermost section. The phosphorus and silica load of the river in summer mostly appears as algae and detritus. Besides the availability of nutrients, algal growth is further supported by the relatively shallow river channel of the sand-bed middle Elbe in Germany that provides sufficient light for algal growth. Additionally, algal growth is favoured by the constant inoculation of plankton from impoundments in the Czech section of the Elbe. A similar situation is found in nearly all of the tributaries with a catchment size >1000 km^2; all exhibit chlorophyll concentrations that exceed the limits set for good ecological status (Behrendt et al. 2004a).

Phytoplankton, mostly diatoms, enter the free-flowing section of the Elbe in Germany in high concentrations with a seasonal mean (April–October, 1994–2006) of 45 μg chl-*a*/L at Schmilka (Rkm 4), and increasing at Schnackenburg (Rkm 475) to 128 μg chla/L. Maximum concentrations can reach >300 μg chla/L (data by ARGE-Elbe), and concentrations exhibit high intra- and inter-annual dynamics (Pusch & Fischer 2006). Typically, a spring phytoplankton peak occurs

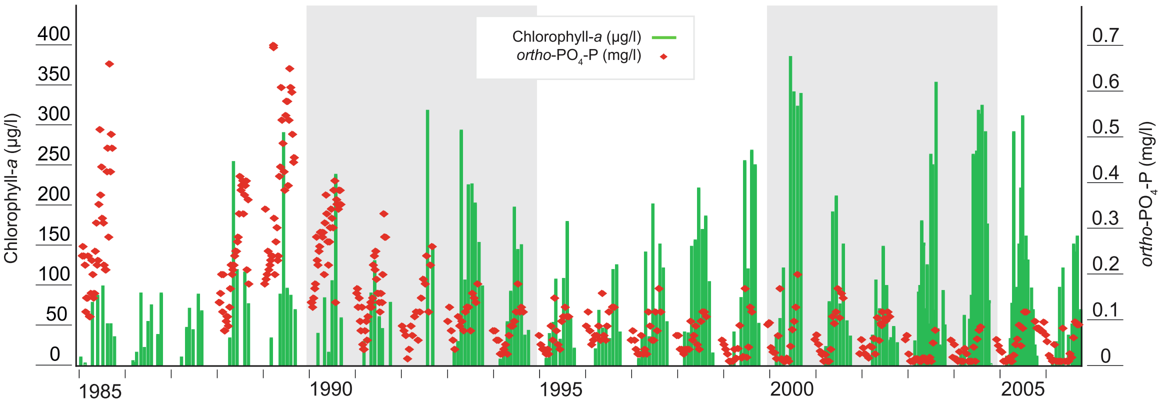

FIGURE 14.6 Long-term development of the concentrations of chlorophyll-*a* and ortho-phosphate at the measuring station Schnackenburg (Rkm 475, 140 km upstream of Hamburg; data by ARGE Elbe).

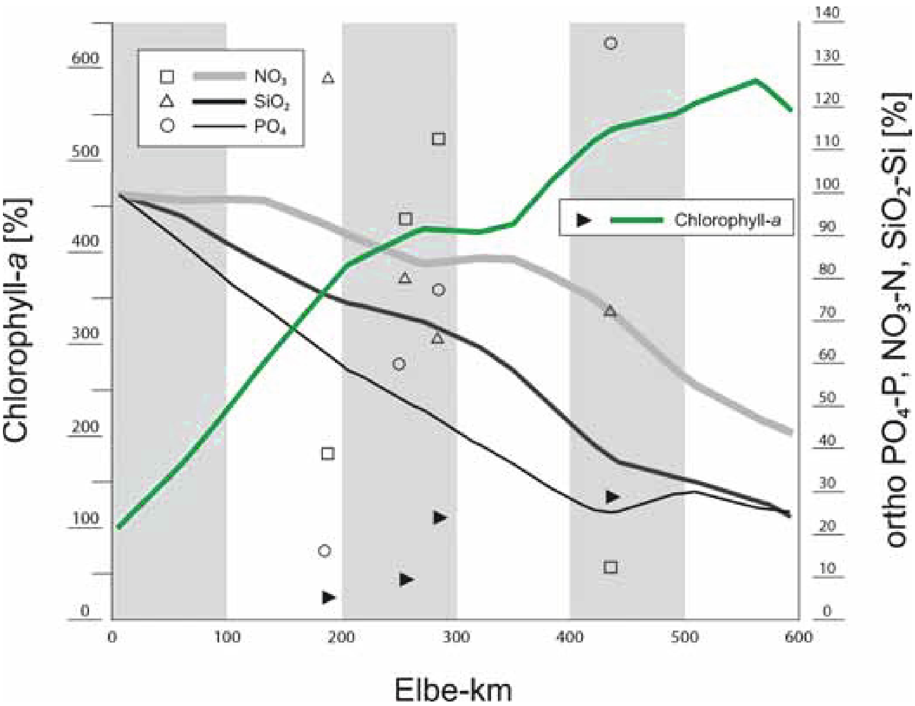

FIGURE 14.7 Longitudinal changes of chlorophyll-*a* and nutrient concentrations in the German section of the Elbe during a travel time of the river water of 6–9 days. Starting values at Rkm 3.9 (Schmilka) are set as 100%. Means are from four Lagrangian sampling campaigns. Samplings were conducted on 26.6.–5.7.2000 at low discharge, on 24.7.–1.8.2005 at medium discharge, on 8.5.–15.5.2006 at high discharge and on 6.8.–15.8.2007 at medium discharge. Extra symbols represent concentrations in the tributaries Schwarze Elster (Rkm 198), Mulde (Rkm 259), Saale (Rkm 291), and Havel (Rkm 438). Data and graph by Federal Institute of Hydrology.

in the upper middle Elbe, while in the lower section chlorophyll concentrations are high, although dynamic, during the growing period (Figure 14.7). Higher chlorophyll concentrations occur due to longer water residence times in dry years, although this pattern can be dampened due to nutrient and light limitation as well as by zooplankton grazting in the most downstream reach. The high primary productivity leads to conspicuous longitudinal patterns in dissolved inorganic nutrient concentrations. Along the course of the river, nitrate, ortho-phosphate and silicate concentrations decrease significantly during summer low-flow situations. Ortho-phosphate–P and silicate–Si concentrations in downstream reaches may drop below 0.01 and 0.15 mg/L, respectively, and limit additional phytoplankton growth, while nitrate–N rarely falls below 1 mg/L (Figure 14.7) (data by ARGE-Elbe). Hence, the high primary productivity in the free-flowing section of the Elbe shows characteristic seasonal dynamics similar to lakes with a spring bloom, a clear water phase, and summer blooms (Figure 14.8). Due to intensive photosynthesis, DO concentrations are often supersaturated in this section, and pH values can exceed 9.

The large biomass of planktonic algae fuels intensive recycling by microbiota, which mostly takes place in the river sediments. Sedimentary microbial activity is not limited to the sediment surface but can reach up to ~1 m into the sediment. Microbial activity within the sediments is sustained by a continuous supply of nutrients and substrates provided by the fluvial transport of sediments and

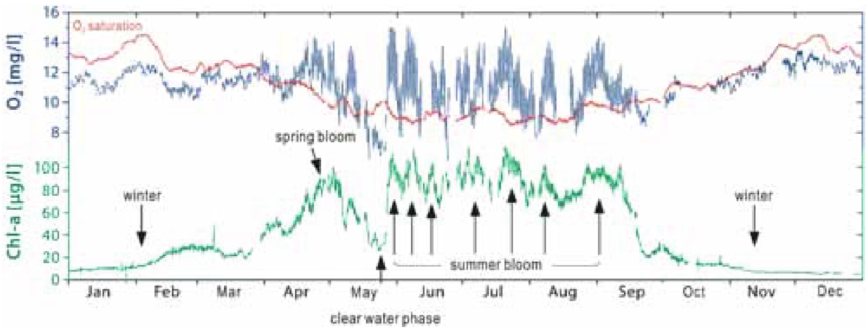

FIGURE 14.8 Seasonal course of chlorophyll-*a* and DO concentrations at Cumlosen (Rkm 470, 145 km upstream of Hamburg) in 1998, with DO saturation concentration added in red, reflecting the river's marked plankton dynamics (data by Landesumweltamt Brandenburg).

hydrologic connectivity between sediments and river water (Fischer et al. 2005). Through the intense hydraulic coupling of river water with sediments, a measurable fraction of the river's load of organic matter is retained, for example 2.5 tons of particulate organic matter per river km in winter (Schwartz & Kozerski 2006). Based on measurements of microbial metabolism in the river sediments using a diving bell, it was estimated that 1.4% of transported organic carbon is degraded per river km. Highest metabolic rates were measured in the oxic uppermost 40 cm of the shifting sandy sediments present in the central river bed. Degradation of organic matter was also high in muddy sediments near the shore in the so-called groyne fields, but the high rates were limited to a shallow superficial layer (Fischer et al. 2005). Retention of nitrogen was estimated at 10–20 tons of NO_3–N per river km and year. Besides the mid-stream sediments, high nitrogen retention also occurred at places on the shore where groundwater exfiltrates from the floodplain aquifer (Pusch & Fischer 2006).

In spite of the significant retention of organic matter, the production/respiration ratio in the Elbe is often >1 during summer, and large masses of living algae are transported along the river to the estuary. There, the die-off and subsequent decomposition of living biomass can cause severe oxygen deficiency with saturation values of 30% and less (data by ARGE Elbe). In contrast to other rivers, this estuarine zone of DO depletion is in the freshwater tidal section of the Elbe (Bergemann et al. 1996). DO depletion is caused by multiple factors that are related to the high input of algal biomass, long water residence times and river morphology. Due to long residence times, grazing by zooplankton can regulate algal biomass in the lower Elbe. Zooplankton regularly reaches concentrations of >1000 rotifers per litre in the lower middle Elbe (Holst 2006), and >1000 copepods per litre are regularly found in the freshwater part of the Elbe estuary. River morphology also contributes to the algal die-off because artificially deepened sections (16-m shipping depth) reduce light availability for algae and increase water residence times, particularly within and downstream of the port of Hamburg. Finally, depletion of nutrients (namely silica) can impede the sustainability of a high biomass of living and growing algae in the estuary (BfG 2006). The nutrients which are set free by algal die-off significantly contribute to the eutrophication of the North Sea.

Today the ecological status of the Elbe in most of its sections is estimated as moderate based on benthic invertebrates. The status of the fish fauna has been estimated to be even good according to the assement tool applied, while phytoplankton density and communities indicate a poor status (data from ARGE Elbe). The river is still significantly contaminated with heavy metals, and the Mulde tributary and deeper Elbe sediments still show even high concentrations. The Czech section of the Elbe as well as the Mulde and Saale tributaries are still significantly loaded with chlorinated carbohydrates (data from ARGE Elbe).

14.3.4. Aquatic and Riparian Biodiversity

14.3.4.1 Riparian Flora and Fauna

Water-dependent fauna and flora along the Elbe are protected within a series of reserves of differing status. In the Giant's Mountains, the Czech-Polish Krkonoše National Park and biosphere reserve holds elements of subarctic fauna and flora seen as glacial relicts, and boasts 40 ha of peat bogs designated as a Ramsar international wetland site. While most of the central Bohemian river section has been largely transformed, a relict floodplain forest at the confluence of the Vlatava and Elbe rivers still harbours snails and fairy shrimps (Anostraca) typical for floodplains, while the diversity of riverine species is significantly reduced there due to water pollution (IKSE 2005).

Along the German river section, 32 natura 2000 areas, 10 important bird areas and a large UNESCO biosphere reserve border the river. Along the German lowland section of the Elbe, the biosphere reserve 'Flusslandschaft Elbe' extends over 400-km covering 1257 km^2 within the Länder of Sachsen-Anhalt, Brandenburg and Mecklenburg-Vorpommern. In Sachsen-Anhalt, the largest contiguous floodplain forest in Central Europe has been preserved with a large diversity of water-dependent woodland and grassland habitats, including softwood and hardwood floodplain forests (Scholz et al. 2005). It also harbours the only population of beaver that persisted in Central Europe during the 19th and 20th centuries. The beaver population that was reduced to 90 individuals in 1950, has largely expanded and recolonized large parts of north-east Germany (IKSE 2005). In the floodplains, large populations of fairy shrimps (Anostraca) colonize temporary pools formed behind dikes during high water levels. The downstream park section in Brandenburg, Niedersachsen and Mecklenburg-Vorpommern features a 0.5–3 km wide relict floodplain before the dikes, wet pasturelands behind the dikes, as well as dunes with dryland fauna and flora. It boasts a high density of stork with ~500 used nests being regularly counted. The tidal section of the Elbe downstream of Hamburg has along its shores and islands the largest freshwater tidal mudflat in Europe.

14.3.4.2 Fish Communities

The current fish and lamprey fauna of the Elbe consists of 94 species of which 34 occur solely in the marine and brackish area (ARGE-Elbe 2000). The river sections with the highest diversity of fish are the brackish water habitat with 59 species, and the middle Elbe harbouring 52 species. Fish assemblages in the estuary are dominated by anadromous species in terms of numbers, mostly by smelt and alvine, although contributing only 7% to species richness (Thiel & Potter 2001). Most species inhabiting the Elbe estuary represent peculiarities compared to other European estuaries. For instance, the alvine is a species listed in the European Habitats Directive and special conservation measures must be considered.

In total, 17 diadromous fishes occur in the Elbe, of which 10 use the middle Elbe for spawning habitat or migration (Pezenburg et al. 2002). Formerly, large populations of these fish migrated upstream, including the Atlantic salmon, Atlantic sturgeon, European eel and smelt, all of high importance for the fishery (IfB 2004; Von dem Borne 1882). The original populations of the Elbe salmon and Elbe sturgeon, and also the migrating form of the houting, have become extinct since the middle of the 20th century (ARGE Elbe 2001, Pezenburg et al. 2002). Recent measures aimed to reintroduce salmon have succeeded in the first natural reproduction of returning adult salmon in Saxony (SLL 2003) and Brandenburg (Zahn 2003). Hence, there is hope that this migrating fish will be re-established in the Elbe in time. Additionally, there are attempts to reintroduce the Atlantic sturgeon (Kirschbaum & Gessner 2002) and migrating populations of houting.

Eel populations of the Elbe have also been considerably diminished as part of a European-wide trend (IfB 2004). The upstream migration of glass eel has especially decreased during the last 20 years in the Elbe, as well as in all other estuaries of Central and Western European rivers (Dekker 2003). In order to stabilize and protect the eel populations of the Elbe, a basin wide management plan is needed. Lampreys, especially the river lamprey, were also formerly caught in large numbers in the Elbe and processed as fodder up to the middle of the last century (Thiel & Salevski 2003). The decrease in populations was caused partly by poor water quality, but also by the construction of the weir in Geesthacht upstream of Hamburg that prevented access to spawning habitats upstream (Dierking & Wehrmann 1991; Gaumert & Kämmereit 1993). During the 1990s, river lamprey reappeared in significant numbers in the lower Elbe (Thiel & Salevski 2003), and new spawning habitats were discovered in the Stepenitz tributary (Lill & Winkler 2002). The number of animals migrating upstream also increased after the construction of a by-pass channel that circumvented the Geesthacht weir. In contrast, sea lamprey, which probably also depend on habitats in tributaries of the lower Elbe, remain rare.

Of the 43 native freshwater fishes in the Elbe, 40 occur only in the middle Elbe. The rheophilic common dace, ide and asp (Fladung 2002; Scholten 2002) occur regularly and are abundant, while the blue bream shows significant interannual variation in abundance. Barbel have increased their populations in the middle Elbe (ARGE Elbe 2005). Other fish such as burbot and vimba, that formerly had large populations (Bauch 1958), have significantly decreased in numbers since. The migrating form of the burbot suffers especially due to the disconnection of its feeding habitats in the lower Elbe from the spawning habitats in the middle Elbe and its tributaries by the construction of Geesthacht weir (Koops 1959, 1960). The spirlin is classified as missing species (Pezenburg et al. 2002).

Silver carp, bighead carp, grass carp, brown bullhead, white sturgeon und rainbow trout have been classified as invasive fishes, as these were introduced into the basin of the middle Elbe after 1900 (ARGE-Elbe 2000). The status of the whitefin gudgeon is unclear (Scholten 2000; Freyhof et al. 2000). Overall, 13 of 94 fish species of the Elbe have been classified as potentially endangered, rare or endemic. These include euryhaline species such as river lamprey and sea lamprey, allis shad, and twaite shad, Atlantic salmon and houting, but also seven limnic species such as brook lamprey, asp, barbel, whitefin gudgeon, bitterling, weatherfish and spined loach. According to the Habitats Directive (European Union 1992), the member states of the European Union have a special responsibility for their preservation. A network of designated habitats must be developed and engineering measures adapted to meet species conservation goals (FGG Elbe 2004).

14.3.4.3 Macroinvertebrates

In the Elbe, ~600 species of benthic macroinvertebrates have been recorded. (Schöll & Fuksa 2000). The most predominant ones are flatworms (Tricladida), snails and mussels (Mollusca), oligochaet worms (Oligochaeta), leeches (Hirudinea), crustaceans (Crustacea), insects (e.g. Ephemeroptera, Trichoptera, Plecoptera, Chironomidae), freshwater sponges (Spongillidae) and bryozoans (Bryozoa). The local composition of invertebrate assemblages is determined by the physical, chemical and biological conditions that gradually change along the river course, as well as by anthropogenic alterations like wasterwater discharge and hydraulic engineering measures.

The Elbe headwaters in the Giant's Mountains are inhabited by the triclad *Crenobia alpina* as a characteristic coolwater species, and is considered to be a glacial relict. The numerous rivulets that flow together to create the mountain river Elbe exhibit torrential flow, a rocky-stony streambed, high oxygen saturation and low water temperatures, and thus are colonized by a rich stonefly fauna (e.g. *Perla* spp.). Due to releases of air-borne contaminants (SO_2, NO_x) from fossil fuel combustion, acid-sensitive species, such as some mayflies (Ephemeroptera) and amphipods (Gammaridae), are rare in these headwaters. Downstream of the mountain area, organic pollution and impoundments affect invertebrate assemblages. In the impoundments, the original rheophilic fauna of the Elbe is mostly replaced by lentic species or generalists.

The river section cutting through the Elbsandsteingebirge has a high species richness. In particular, snails (*Radix peregra*), European fingernail clam (*Sphaerium corneum*), and caddisflies (*Hydropsyche contubernalis*) are found. At a few locations upstream of Dresden, unionid mussels (*Anodonta anatina*, occasionally *Unio pictorum*) can be found. Between Dresden and Magdeburg, six species of pollution-tolerant leeches (including *Glossiphonia complanata*) can be found. Near Riesa, some individuals of the Chinese mitten crab (*Eriocheir sinensis*) have been found, which migrated

600 km from their reproduction sites in the tidal Elbe downstream of Hamburg. Between Magdeburg and Geesthacht, the density and richness of triclads, leeches, as well as some insect species strongly decreases by a still unknown reason. This section is dominated by sow bugs (*A. aquaticus*, Isopoda) as well as scuds (*G. tigrinus*). The stones used in groynes protecting the shores from erosion are predominately covered by sessile species such as Hydrozoa (*C. caspia*) and Bryozoa (*Paludicella articulata, Plumatella fungosa, Plumatella emarginata and Plumatella repens*). Further, the Asian dragonfly (*Gomphus flavipes*), a typical inhabitant of large, sandy rivers, has been recorded again (after its last record in 1929). The constantly moving sand-bed sediments in the central channel of the Elbe are colonized by the specialized annelid *Propappus volki*. In the impounded reach upstream of the weir Geesthacht, the zebra mussel *D. polymorpha* reaches its highest density at 4000 ind./m^2. As the life cycle of this species involves a 14-day free-swimming larval stage, the populations at Geesthacht probably originate from the supply of larvae from the Bohemian segment of the Elbe.

The number of benthic invertebrate species decreases in the tidal section between Geesthacht and Hamburg. Fluctuating water levels prevent the colonisation of groyne heads by many lithophilic species. Here the shrimp *Palaemon longirostris* may be found, a brackish water species that often migrates far upstream in rivers. The zone of continuously shifting salinity between Hamburg and Cuxhaven limits the osmoregulation of many organisms, and consequently the area is colonised by a few extremely euryhaline species, such as the crustaceans *Jaera albifrons*, *Gammarus zaddachi* and *Bathyporeia* sp., as well as the hydrozoan *Laomedea* sp. The density of the barnacle *Balanus improvisus* increases along the gradient of rising salinity. Populations of three mud shrimps *C. curvispinum, C. lacustre* and *Chelicorophium volutator* are established in the estuaries of the North and Baltic Seas, whereby *C. curvispinum* tolerates the lowest salinity and *C. volutator* is found at the highest salinity. North of Cuxhaven, marine species dominate, including the blue mussel, the European green crab and small marine scuds (e.g. *Gammarus salinus*).

Historic records of the invertebrate assemblages in the Elbe reveal a close relationship to the pollution status of the river at a given date, involving a dramatic reduction in species richness with increasing pollution level and decreasing DO content. In particular, insects and large mussels suffered a considerable loss up to the 1980s. Since 1990, numerous species have reappeared that that had not been present for several decades of severe pollution in the Elbe (Figure 14.9). An impressive example is the return of the mayfly species *Oligoneuriella rhenana* in the Elbe section crossing the Elbsandsteingebirge Mountains at the Czech–German border in 1996. This mayfly is an ecologically sensitive species and characteristic for middle-sized, fast flowing rivers. Some tributaries of the Elbe in the Czech Republic probably served as refugia for this species. Presently, *O. rhenana* has expanded its range in the river, colonizing downstream to Magdeburg.

Current invertebrate assemblages of the Elbe significantly differ from that known from the 19th century due to changes in water quality, hydraulic engineering measures, and navigation. Passing ships can create waves of >30 cm in height at the shoreline, which resuspend fine sediments and dislodge invertebrates (Brunke & Guhr 2006). Additionally, the introduction of new species has altered invertebrate assemblages. In the 1990s, several invasive species appeared, such as the Black Sea isopod *Jaera istri* and the scud *Dikerogammarus villosus*. These are two typical Danubian species that migrated via the Main-Danube canal, finished in 1992, and then via the Rhine and Mittelland Canals into the Elbe. In particular, *D. villosus* populated long sections of the Elbe within a short period of time.

14.3.5. Management and Conservation

14.3.5.1 Economic Importance

In the Czech part of the catchment, the Elbe and its tributaries are retained in 19 reservoirs with a volume >0.3 million m^3, a sum of 167 million m^3. The reservoirs are mainly used to retain floods and to increase discharge at low water levels. The Elbe itself is impounded by 24 weirs that are mostly smaller, except the reservoirs Labská und Les Království that hold 11 million m^3. Impoundments allow navigation by ships with a draught of at least 2 m within a 170-km section of the river between the uppermost harbour near Pardubice and Ustí nad Labem (IKSE 2005). Thus, the Elbe has been transformed into a chain of impoundments with few free-flowing reaches remaining. Historically, hydropower was used in the upper Elbe to drive mills by the construction of numerous weirs built from wood or stones, which were also used for timber rafting. In 1841, a regular ship connection was established between Prague and Dresden (IKSE 2005). By 1874, a navigation chain line was established between Hamburg and Ustí nad Labem (formerly Aussig), that is an iron chain 668 km long with chain links each 18 cm long was laid on the river bed and used by specially designed steamboats to which barges were tied.

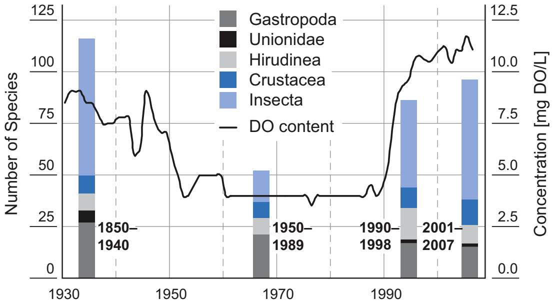

FIGURE 14.9 Historic development of dissolved oxygen content of the Elbe in Magdeburg, and of species richness within selected groups of benthic invertebrates in the river recorded within the whole freshwater section of the river in Germany.

Another peculiarity of navigation on the Elbe was the paddle-steamers that still cruise around Dresden as excursion boats. Today, inland cargo transport on the Elbe is limited technically and economically by the fact that planned minimum depth for navigation is only 1.6 m, and that depth is not met for more than three months each year (average for in the river section upstream of Magdeburg since 1990; data from the Federal Waterways and Shipping Administration). Barges, therefore, often may be only partially loaded and with lower transport fees, so that cargo transport by barges has greatly decreased since 1990.

Near Torgau, water from the Elbe is used via bank filtration to supply drinking water to the urban cities of Leipzig and Halle, both situated in a region receiving low precipitation. The risks produced by major floods on the Elbe have been increased by reducing the former floodplain area to 16% by the construction of levees for use as crop fields (Kausch 1996). After the great flood in 2002 it was widely discussed to leave more space for the river to decrease flood risks. Since then, Elbe dikes have been moved back at only two sites, and other floodplain areas will in the future be used as polders. In contrast, dikes have been raised further in most of the German river segment.

14.3.5.2 Conservation and Restoration

Even after considerable improvements in water quality since 1990, the Elbe significantly suffers from anthropogenic pressures such as nutrient inputs, hydro-morphological alterations and navigation. The shores, sediments in the groyne fields of the lower middle Elbe (Photo 14.3), and fine sediments in the lower Elbe are still heavily contaminated by heavy metals and organic contaminants, for example some 50 kg of deposited lead (Pb) has been estimated for a typical groyne field (Schwartz & Kozerski 2006). The Czech segment of the river is impounded for most of its length, while the shores of the upper middle Elbe in the German section are mostly fixed by stone rip–rap or by 6900 groynes extending into the river channel. There, vertical erosion is combatted by the addition of 20 000–80 000 tons/year of a sand–gravel mixture into various reaches. As the lower middle Elbe is paralleled by a canal (Elbe-Seitenkanal), which forms an alternative use for navigation between Magdeburg and Hamburg, barge navigation on the Elbe and options for river management have been discussed controversially for many years between authorities and initiatives to protect the Elbe (Pusch 2006). Additional controversial discussions relate to river training measures on the Elbe section bordering the UNESCO World Heritage of the Dessau-Wörlitz landscape park, and the construction of an additional Elbe bridge within the UNESCO World Heritage of the Dresden Elbe valley. In many places along the Elbe efforts have already been taken to preserve diverse shoreline structures, to enable fish migration to tributaries, to reconnect oxbow lakes, to replant floodplain forest, and to find alternative ways of shore protection than traditional ones. The lower Elbe has been deepened to 16-m depth to allow the passage of large container ships to the port of Hamburg. These deepening efforts counteract actions to attenuate dissolved oxygen deficiencies that regularly occur there.

14.3.5.3 Perspective

The improvement in water quality from the former bad to the present moderate status after 1990 constitutes one of the most impressive success stories in river management.

PHOTO 14.3 The Elbe near the village of Cumlosen (upper right) at Rkm 467–470. The lowland section of the river channel is nearly totally fixed by perpendicular groynes made of stones. On the left bank some broken groynes may be seen, which are less filled with sediment deposits than others. Ancient river channels are visible on the left and right banks; the left side has a hardwood floodplain forest (Photo: Federal Institute of Hydrology).

After alleviation of the formerly dominating saprobic pollution pressure, a set of other significant pressures appeared to be limiting ecosystem structure and function, such as eutrophication, morphological alterations, interruptions of sediment load and fish migration, and hydrodynamic impacts by inland navigation. For instance, even after the construction of a by-pass channel, the weir in Geesthacht upstream of Hamburg still forms a major obstacle for fish migration, especially for larger fish species. This hampers the successful re-introduction of migratory fishes such as salmon and strurgeon. Hence, management options for the river depend on its future use for inland navigation and hydropower generation, as well as on more effective retention of diffusive inputs of nutrients from agriculture. While diffuse inputs from agriculture may be reduced by changing agricultural practices, and the retention of effluents by riparian buffer strips, hydromorphological deficiencies could be considerably improved by redesigning groynes to create overflow shallow shore areas, by re-opening and creation of side channels, by the protection of shallow waters from ship-induced wave action, by the construction of effective fish ladders at weirs, and by moving dikes farther away from the river.

14.4. ODER

The Oder (Polish and Czech: *Odra*) is the sixth largest river flowing into to the Baltic Sea, with an annual discharge volume of 17.3 km^3.. Being 854-km long, the Oder is the second longest river in Poland (after the Vistula). Only 6% of the catchment area lies in the Czech Republic and 5% in Germany. The Oder catchment stretches from the Sudety Mountains to the Szczecin Lagoon on the southernmost margin of the Baltic Sea. It is asymmetrically shaped, with major left-side tributaries only found in the upper and middle segments of the river. The lowermost left tributary, the Lusatian Neisse (Nysa Łużycka), together with the lower Oder forms the German–Polish border. Most of the catchment consists of lowlands, especially the largest right-side tributary, the Warta River, which exceeds the Oder in length. Downstream of Szczecin (Stettin), the river flows into the Szczecin Lagoon (Zalew Szczeciński, Oderhaff). Here the river is divided into three branches between the islands of Usedom and Wolin that eventually reach the Baltic Sea in the Bay of Pomerania. From its mouth, the Oder is navigable for ocean ships up to Szczecin, and for inland navigation for a length of 717 km until the small city of Koźle 40 km upstream of Opole. The biogeography of the region is largely determined by the Weichsel glacial period and the post-glacial formation of melt-water lakes in the basin of the Baltic Sea. The post-glacial recolonization of the Oder system by aquatic biota therefore followed similar patterns as in the Elbe and Vistula rivers.

14.4.1. Physiography, Climate, and Land Use

The Oder rises in the Sudety Mountains, Czech Republic, at 634 m asl, only 20 km east of the city of Olomouc which borders another major river, the Morava. Headwater streams lie in the Oderské Vrchy Hills near the settlement of Město Libavá. The Oder first flows southeast, then follows a valley heading northeast, called Moravian Gate, that allows passage between the Sudety Mountains in the west and the Beskid Mountains in the east. The river then passes the city of Ostrava, the second largest urban area in the Czech Republic after Prague, an industrial centre based on coal mining and the steel industry.

After crossing the Czech–Polish border, the river reaches the upper Silesian lowlands south of the city of Racibórz at an altitude of ~200 m asl. The river then flows northwest where it receives several major left-hand tributaries that drain the Sudety Mountains, such as Nysa Kłodzka, Bystrzyca, Kaczawa, Bóbr and Nysa Łużycka (Lusatian Neisse). The Oder passes through the scenic historic city of Wrocław (Breslau), which was originally built on several islands of the Oder. Near the city of Głogów, the river receives its major right-side tributary in Silesia, the Barycz. The Barycz is a pure lowland river originating between the cities of Ostrów Wielkopolski and Ostrzeszów, and follows a glacial valley with low slope (20–30 cm/km). It drains extensive wetland areas. Near the city of Krosno Odranskie, the Oder receives the left-side tributary Bóbr. The Bóbr is 268 km long, has a catchment area of 5900 m^2, and a mean slope of 2.8 m/km. The upper headwaters of the Bóbr in the Giant's Mountains (Karkonosze) in the area of Jelenia Góra are adjacent to the Elbe River. The direction of the Oder abruptly changes north at the confluence with the Nysa Łużycka (Lusatian Neisse) south of the German city of Eisenhüttenstadt. The Lusatian Neisse originates in the Czech Jizera Mountains east of Liberec, soon after reaching the border triangle of the Czech Republic, Poland and Germany near the German city if Zittau. For 197 km (of a total length of 254 km) it forms the German–Polish border until its confluence with the Oder. Downstream of the confluence, at 32 m asl, the Oder passes the old Hansa city of Frankfurt (Photo 14.4).

At the former Prussian fortress of Kostrzyn, the Warta River joins with the Oder, contributing 40% to its discharge. At 808 km in length, of which 50% is navigable, the Warta exceeds the Oder in length at the confluence. The Warta, together with its right-side tributary, the Noteć, drains a pure lowland area of 54 529 km^2. The Warta originates near the famous city and pilgrimage place of Czestochowa, then heads north through agricultural landscapes. It flows into Lake Jeziorsko reservoir (42.3 km^2 area, 202 million m^2) near the city of Lódź, then turns west near the city of Konin, again flows north towards the city of Poznań, and finally flows again west for the rest of its course. It receives the Noteć tributary near the city of Gorzów Wielkopolski. The Drawa River (see below) is a tributary of the Noteć.

PHOTO 14.4 The Oder River downstream of the city of Frankfurt. The straightened river channel is fixed by perpendicular groynes and ancient river channels are visible. The river corridor, which is bordered by dikes, has only sparse tree cover because the trees suffer from ice drift that may occur during high water levels in winter (Photo: Oder-Luftbild, Lebus).

The lower Wartas valley, up to the confluence with the Oder, harbours a vast wetland protected by the Warta Mouth (Ujście Warty) National Park.

After the confluence with the Warta, the Oder enters the ~15 km wide Oderbruch valley, which forms part of the Eberswalde–Toruń glacial valley. The Oderbruch originally formed a vast floodplain with meanders and anabranches of the Oder until the river course was straightened and shortened by 25 km from 1746 to 1753 by order of the Prussian King Friedrich II. The downstream end of the Oderbruch, at 1.5 m asl, marks the place where the Oder breached the moraines of the Weichelian glacial period to flow to the Baltic Sea. Downstream of Schwedt, the river splits into the West Oder and East Oder branches, encompassing a vast polder wetland which today forms the heart of the German–Polish Lower Oder Valley International Park.

The slow flowing river then passes the historic Pomeranian capital and seaport of Szczecin (Stettin) and Lake Dąbie, which has a surface area of 56 km^2. Shortly downstream the river enters the Szczecin lagoon (Zalew Szczecziński, Oderhaff) with a surface area of 900 km^2 but a mean depth of only 4 m. This lagoon flows into Pomeranian Bay via three channels, first the Peenestrom (which also receives the Peene River) separating the German mainland from the island of Usedom, second the Swina (Swine) separating the islands of Usedom und Wolin (including Kanał Piastowski built 1875–1880), and third the Dwinow channel separating Wolin from the Polish mainland. Flow direction in these three channels may be reversed by northerly winds, and the Swina River has a delta at its southward end. The Swina enters Pomeranian Bay at the small seaside port city of Świnoujście (Swinemünde). The total length of the Oder is 912 km if the lagoon and Swina sections are included. Average channel slope is 0.7 (Köhler & Chojnacki 1996). The catchment area upstream of Szczecin equals 118 861 km^2, while the total catchment area contributing to Pomeranian Bay is 136 528 km^2 (Behrendt & Dannowski 2005). The Warta contributes an area of 54 529 km^2 to the Oder catchment.

A sub-continental climate dominates most of the Oder catchment and is reflected by cold winters that regularly results in the formation of significant ice cover on the Oder for about one month. Mean precipitation in the catchment is only 587 mm, of which 133 mm contributes to river runoff, which equals 5.0 L/km^2/s. While the southern slopes of the Sudety Mountains receive 700 to >1500 mm of precipitation, the Poznań region receives a low of <400 mm (Behrendt & Dannowski 2005). Average July temperature is 18.5 °C, average January temperature −1.5 °C. Snow cover lasts for 40–60 days, and the vegetation period is ~220 days. Land use in the catchment is urban area at 4.0%, arable land 54%, grassland 7.7%, forest 31%, and waterbodies at 1.3% (Behrendt & Dannowski 2005). The sub-basin with the highest forest percentage (54.4%) is the Drawa (see ch. 14.8).

14.4.2. Geomorphology, Hydrology, and Biogeochemistry

Based on the physiogeographic division of Poland, the Oder catchment covers six units, including the Sudety-Mountains, Saxonian–Lusatian Lowlands, Silesian–Cracow Highlands, Central Polish Lowlands, Southern Baltic Lake District, and the Southern Baltic Littoral (Behrendt & Dannowski 2005). The upper river flowing through the

PHOTO 14.5 The Oder River downstream of the city of Frankfurt during the great flood in 1997, with the regular river channel visible in the background. (Photo: M. Pusch).

Moravian Gate uses a tectonic fault that allows it to cross the geologically old mountain ridges bordering the Bohemian–Moravian basin to the north. The river is divided into three geomorphologically and hydrologically different areas: the upper Oder from the source to Wrocław, the middle Oder from Wrocław to the mouth of the Warta River, and the lower Oder from the Warta tributary to the mouth into the Szczecin Lagoon. Discharge in the high Sudety basin of the Oder has a nival regime, while streams in the rest of the catchment have a pluvial-nival regime with highest discharge in March and April. A particular hydrologic characteristic of the Oder is summer floods (Photo 14.5) that occur mainly in August. These are caused by Mediterannean cyclones heading north, which can produce heavy rainfalls in the Erzgebirge and Sudety Mountains (Landesumweltamt Brandenburg 1997).

The largest tributary, the Warta, enters the Oder at Rkm 618 and contributes on average 224 m^3/s (Gorzów gauging station, Landesumweltamt Brandenburg 1994). Average discharge of the Oder equals 522 m^3/s at the gauge Hohensaaten-Finow at Rkm 665. However, runoff there varies by a factor of 31 between the lowest (111 m^3/s, September 1921) and highest (3475 m^3/s, April 1888) discharge values recorded (Uhlemann & Eckoldt 1998). At the gauge station Hohensaaten-Finow, the lowest and highest reported water levels were 0.84 m and 7.78 m, respectively. Flow velocity in the lower Oder between Eisenhüttenstadt and Schwedt averages 0.36 m/s at mean water level (Landesumweltamt Brandenburg 1994). In the lower Oder, water temperatures range between −0.4 and 28.8 °C (Water and Navigation Authority Eberswalde). Summer water temperatures typically exceed 20 °C for at least one month, while winter temperatures may fall below 0 °C, a situation that leads to the formation of anchor ice. On average, the Oder is patially covered by ice 50 days per year (Schönknecht & Gewiese 1988).

The Oder catchment is populated by 16 million inhabitants, of which 1.5 million live in the Czech Republic, and 0.7 million in Germany. Mean population density is 135 inhabitants/km^2. The Oder receives inputs of 11 tons/year of cadmium, 175 tons/yr of copper, 113 tons/yr of lead and 1190 tons/year of zinc (data for the time period 1993–1997). These result in estimated loads near the mouth of 3 tons/year of cadmium, 67 tons/year of copper, 40 tons/year of lead and 331 tons/year of zinc. In comparison to the Rhine and Elbe, heavy metal loads, especially from sub-basins, of the upper river are high for cadmium and lead (Behrendt & Dannowski 2005). Nutriernt loads from point sources were estimated at 7970 tons/year for phosphorius and 45,300 tons/year for nitrogen between 1993 and 1997. In comparison to other large river catchments, loads in the Oder are high for phosphorous, indicating a good potential for further reduction, for example by improvement of wastewater treatment plants. The loads for nitrogen are relatively low, which may be explained by the relatively low percentage of inhabitants connected to wastewater treatment plants (Behrendt & Dannowski 2005). Diffuse nutrient inputs, especially from agricultural areas, were dramatically reduced with the political changes in 1990, with a moderate increase since. A significant proportion of the nutrient load in the river is retained. River loads near the mouth (gauge station Krajnik Dolny) were estimated at 4732 tons/year ammonium–N, 42 022 tons/year nitrate–N, and 5072 tons/year total phosphorous. Accordingly, the Oder has a high eutrophication potential with average nutrient loads of 3.45 mg/L total N and 0.17 mg/L total P. Median dissolved oxygen (DO) concentrations of the Oder are 9–10 mg/L. In periods of high temperatures and low discharge, DO concentrations decrease temporarily to 3–6 mg/L. Due to the general shallowness of the river, it is efficently reoxygenated by physical gas exchange through the water surface.

14.4.3. Aquatic and Riparian Biodiversity

14.4.3.1 Fish Communities

The fish inventory of the Oder comprises 53 native riverine fish and lamprey species, (Wolter & Freyhof 2005). Three native fishes, such as sturgeons and Atlantic salmon, must be considered extinct today. Restoration programs are running for two of these species, Atlantic salmon and Baltic sturgeon (*Acipenser oxyrinchus*); the latter program headed by the Institute of Freshwater Ecology and Inland Fisheries in Berlin. Salmon disappeared from the river in the middle of the 1840s (Gerhard 1893) and initial stocking programs began in 1869. From 1869 to 1879, 12 000 to 320 000 salmon hatchlings were stocked annually, in total 1 522 600 hatchlings (Gerhard 1893). The first salmons were recaptured in the Oder in 1872 and in the Warta in 1874. In the upper Oder, no salmon were recorded after 1876, while catches in the Warta continuously increased up to 1130 salmon with individual weights of 6–15 kg in 1887 (Gerhard 1893). Heavy pollution from industrial effluents in the upper Oder has been considered as the main reason for the later decline in the abundance of migratory fish (Pax 1917). Interestingly, Jobst (1571) had already emphasized a better taste of fish from the Warta. In Poland, a stocking program for salmon was restarted in 1995, and from 1996 to 1999 between 11 403 and 75 443 hatchlings were stocked annually (Bartel 2001). No returning adults have been reported so far. Eight fishes have been recorded to be much more abundant before river regulation, including river lamprey, sea trout, vimba, nose carp, barbel, burbot, crucian carp, and swamp minnow; the latter two due to the loss of floodplain waterbodies. Most probably, other riverine species with similar habitat requirements also declined, but this is not clearly shown using historical records.

The dramatic impacts of river regulation on fish assemblages are evident in the nearly total decline in the populations of barbel, nose carp, and vimba, which are seen as characteristic species for typical riverine habitat conditions. Barbel was one of the most abundant fish, accompanied by nose carp and vimba, and common until the end of the 19th century (von dem Borne 1882). Today, vimba is lacking in the middle and upper Oder, and nose carp as well as barbel are rare. In the middle Oder, there were important spawning sites for long distance migratory species. Today, these reaches are dominated by eurytopic fishes such as common bream, silver bream, and roach. This clearly indicates a human-induced shift in river status from a fast-flowing barbel region to a slow-flowing bream region due to regulation. Accordingly, limnophilic and eurytopic fish occur much more upstream in the river compared to pre-regulation times. Including non-native species, a total of 67 freshwater fish and lamprey species have been recorded in the Oder basin. Non-native species were introduced mainly at the end of the 19th and in the second half of the 20th century. Recently, 11 non-native species have been recorded in the basin, but none has established reproducing populations (Wolter 2007). The immigration of additional species via the Vistula-Oder waterway is expected.

14.4.3.2 Macroinvertebrates

Between 1998 and 2001 about 270 species or higher taxa were found in the Oder. Adding earlier surveys conducted since 1992 in the river bordering Germany increases this number to ~370 species. The zoobenthos is dominated by Tricladida, Mollusca, Oligochaeta, Hirudinea, Crustacea, Insecta (Ephemeroptera, Trichoptera, Plecoptera, Chironomidae), Spongillidae and Bryozoa. The density of individuals varied from 0 to 10 000 ind./m^2 between river reaches, position of a sample in the river, and season. The natural longitudinal gradients in physical and chemical characteristics have been changed by regulation in the Oder, thus most rhithral assemblages have been replaced by potamal taxa or by habitat generalists. This is especially evident in the middle Oder. Most benthic invertebrates in the Oder are categorized as filter feeders, predators, grazers or sediment feeder. The density of filter-feeders increases from the upper to the middle Oder. In the upper river, the zoobenthic community inhabits the riverbed relatively homogenously. In contrast, the zoobenthos is mainly concentrated downstream on large stable rip–rap stones along the banks, sessile and semi-sessile macroinvertebrates in particular. The center of the river where high bedload transport occurs is inhabited by only a few species. Areas without bedload transport that may be found upstream of impoundment weirs deviate from this distribution pattern.

In the headwaters of the Oder, the stoneflies *Perla burmeisteriana* and *Leuctra albida* were found in epirhithral to metarhithral reaches near the village of Jakubcovice. Typical species also included the caddyflies *Hydropsyche saxonica* and *Potamophylax* sp. At Svinov near Ostrava, the Ephemeroptera *B. buceratus, Baetis fuscatus, Heptagenia coerulans* and *Ecdyonurus starmachi* indicate that the river is epipotamal character. With the wastewater input from the urban area of Ostrava/Bohumin, the density of leeches increases (*Erpobdella octoculata, Glossiphonia heteroclita*) and the caddisfly and mayfly fauna are similar to that of large rivers (*Baetis rhodani, B. fuscatus*, *H. contubernalis, H. pellucidula*).

The town of Koźle marks the beginning of the impounded navigable reach of the Oder that extends 185 km upstream of the city of Wrocław (Breslau). The reduction in flow velocity causes the disappearance of most lotic species, and the impounded middle Oder is inhabited by the amphipod *G. tigrinus*. Immediately downstream of weirs do lotic species of the genus *Baetis*, *Hydropsyche* and *Cheumatopsyche* occur at low densities. Downstream of the last weir at Brzeg Dolny, the abundance of characteristic species show values typical of large rivers: tricladids (*D. lacteum*, *Dugesia lugubris*, *Dugesia tigrina*), snails (*Bithynia tentaculata,*

TABLE 14.1 General characterization of the Rivers of the Central European Highlands and Plains

	Weser	Elbe (with Spree)	Oder (with Drawa)	Em	Skjern	Spree	Drawa
Mean catchment elevation (m)	193	258	164	195	49	92	103
Catchment area (km^2)	46 306	148 242	118 861	4460	2490	10 105	3289
Mean annual discharge (km^3)	10.3	27.4	17.3	1.0	1.1	1.1	0.7
Mean annual precipitation (cm)	70.1	61.2	58.7	59.3	89.2	56.6	59.2
Mean air temperature (°C)	8.2	8.3	8.2	5.9	7.6	9.0	7.9
Number of ecological regions	3	4	5	1	2	3	2
Dominant ($\geq$25 %) ecological regions	6; 70	22; 70	22	59	6	22	10; 22
Land use (% of catchment)							
Urban	7.4	6.8	4.0	1.6	2.4	11.6	1.0
Grasland	12.8	9.2	7.7	1.1	0.7	5.6	5.1
Cropland	48.6	50.8	54.0	11.4	76.4	38.2	31.4
Shrub	0.9	2.0	1.6	6.1	6.7	2.0	1.3
Forest	28.9	29.0	30.8	74.1	11.0	37.0	55.8
Barren	0.3	0.8	0.4	0.0	0.1	3.0	1.4
Wetland	0.8	0.2	0.2	0.6	2.5	0.2	0.1
Open water	0.4	1.3	1.3	5.2	0.2	2.4	3.9
Protected area (% of catchment)	0.6	4.3	1.5	0.3	3.1	0.1	3.5
Water stress (1–3)							
1995	2.0	2.0	2.0	1.0	1.0	2.0	1.8
2070	2.1	2.9	3.0	1.0	1.0	3.0	2.7
Fragmentation (1–3)	3	3	2	3	2	3	2
Number of large dams (>15 m)	15	86	21	0	0	1	0
Native fish species	38	52	53	29	24	37	39
Nonnative fish species	5	8	11	2	2	7	2
Large cities (>100 000)	6	17	15	0	0	2	0
Human population density (people/km^2)	204	169	135	16	42	306	30
Annual gross domestic product ($ per person)	23 434	14 068	5583	26 394	34 592	17 237	4551

For data sources and detailed exlanation see Chapter 1.

P. antipodarum), and mussels (*D. polymorpha*, *Sphaerium corneum*, *S. rivicola*, and *S. solidum*) are abundant. Among the five large mussels found *Anodonta cygnea*, *A. anatine U. pictorum* and *U. tumidus* dominate; *Pseudanodonta complanata* occurs more rarely.

The rip–rap stones are covered with the dwelling tubes of *C. curvispinum* that locally occur at densities of >100 000 ind./m^2. Other sessile, colony-forming species living there are freshwater sponges (*Spongilla fragilis*), bryozoans (*P. articulata*), and freshwater polyps (*C. caspia*). The insect fauna consists mainly of caddisflies like *H. contubernalis* and *Hydropsyche bulgaromanorum*, mayflies (especially *Heptagenia sulphurea*) as well as midges (Chironomidae). Among chironomids, species of the genus *Chironomus*, *Robackia demeijerei* and *Glyptotendipes pallens* dominate. The dynamic river-sand deposits in the river provide suitable habitat for specialized species like *R. demeijerei* and *Lipinella araenicola*.

The invertebrate assemblage of the lower Oder differs little from that of the upper river. The constant presence of the snails *Viviparus viviparus* and *T. fluviatilis* is noteworthy, which often reach densities of >100 ind./m^2. Another frequent invertebrate is the waterbug *Aphelocheirus aestivalis* that preferentially inhabits the gravel-sandy river bottom in areas with average flow velocities. Among the beetles, *Limnius volckmari* is a typical element of the potamal fauna that inhabit the lower Oder. Between Ratzdorf and Widuchowa other red-listed species attain significant abundances, such as the riverine dragonflies *Gomphus flavipes*, *Gomphus vulgatissimus*, *Ophiogomphus cecilia*, and *Calopteryx splendens,* as well as the molluscs *P. complanata* and *Sphaerium solidum* (Table 14.1).

Our knowledge about the original benthic invertebrate fauna in the Oder before major anthropogenic impacts is poor. Detectable changes in the zoobenthic community of the river may be generally explained by changes in water quality, river-training, and immigration of new species. The present rating of the water quality of the Oder lies between a saprobic index of 1.8 (headwaters at Jakubčovice nad Odrou) and 2.2 (at Svinov/Ostrava), which corresponds to the quality classes (moderately polluted) and II–III (critically polluted). As the Oder historically never was as heavily polluted as the Rhine or Elbe, some molluscs like *T. fluviatilis*, *P. complanata*, and *Unio tumidus* occur in the Oder and never went extinct like in the Elbe. However, more sensitive species, especially some molluscs, stoneflies and mayflies, have become extinct in the Oder because of poor water quality. The spread of some of those species listed as typical for the Oder would be seen as a positive sign towards a typical invertebrate assemblage. Besides water quality, river training has also contributed to the changes in the invertebrate community of the river. The construction of groynes and embankments provided habitats for lithophilic species such as *Ancylus fluviatilis*, *B. tentaculata*, and *D. polymorpha*. On the contrary, shortening and fixation of the riverbed has increased flow velocity and erosion, which in turn deteriorated habitat conditions on the river bottom.

A total of 21 invasive invertebrates have been recorded (Table 14.2), which is low in comparison with the River Rhine with 30 invasive species. Most of these invasive species arrived in the river at the beginning of the 20th century, for example *C. curvispinum,* while others arrived later (e.g. *G. tigrinus* presumably around 1980). Since 2000, the amphipod *D. villosus* has been found in the Oder, which it had reached via the north German canal system after the completion of the Main-Danube canal in 1992. The cooling water filters of barges have been identified as major vectors, so that further invasions are likely. In contrast, the gender mussel *Corbicula* that had spread rapidly in the Rhine basin does not seem to spread further east into the sub-continental climate of the Oder system with its cold winter temperatures.

TABLE 14.2 Invasive benthic invertebrates in the Oder, with geographic origin

Species name	Original ecoregion
Cordylophora caspia	Pontocaspis
Dugsia tigrina	North America
Ferrissia wauteri	Southwest Europe
Lithoglypus naticoides	Pontocaspis
Physella acuta	Southwest Europe
Potamopyrgus antipodarum	New Zealand
Viviparus viviparus	East-Europe
Corbicula fulminea	Asia
Dreissena polymorpha	Pontocaspis
Branchiura sowerbyi	South Asia
Hemimysis anomala	Pontocaspsis
Limnomysis benedeni	Pontocaspis
Echinogammarus ishnus	Pontocaspis
Chelicorophium curvispinum	Pontocaspis
Dikerogammarus villosus	Pontocaspis
Dikerogammarus haemobaphes	Pontocaspis
Pontogammarus robustoides	Pontocaspsis
Gammarus tigrinus	North America
Obesogammarus crassus	Pontocaspis
Orconectes limosus	North America
Erichoeir sinensis	East Asia

14.4.4. Management and Conservation

14.4.4.1 Economic Importance

The Oder has been used early for navigation both in north-south and east-west directions, as it has been connected early with the Elbe catchment via two canals, the Friedrich–Wilhelm canal (Spree-Oder waterway, since 1668) and the Finow Canal since 1746. A navigable connection between the Oder and Vistula catchment has existed since 1774 with the opening of the Bydgoszcz (Bromberger) canal. This 26-km long canal connects the Warta tributary Note with the Vistula tributary Brda. This waterway between both river systems is of particular interest from a biogeographic point of view because the Vistula has two connections to the Dnjepr River, and thus to the Black Sea. There is a common floodplain area along the Vistula and Dnjepr headwaters near Svitaz and the Dnjepr–Bug canal (since 1775) between the Vistula tributary Bug and the Dnjepr tributary Pripjat.

The first watermills on the Oder have been documented from the 12th century (Reynolds 1983). Early mill dams and fishing weirs impeded navigation in a way that in 1337 King Johann of Bohemia enacted the so called ‘king measure’, a 9.3-m wide minimum opening in all weirs and dams to allow navigation and fish migration along the Oder between Brzeg (Brieg, Rkm 198) and Krosno Odrzanskie (Krossen, Rkm 514) (Bekmann 1751). Although repeatedly confirmed, this edict has never been fully implemented. In the Silesian part of the Oder, seven weirs are mentioned for the year 1375, and 18 for 1550 (Uhlemann & Eckoldt 1998). When nearly the entire river came under Prussian administration in 1742, several meanders were cut off, the longest being the 21-km long cut-off between the villages Güstebiese and Hohensaaten (1746–1753), which enabled the farming of the Oderbruch floodplain (920 km^2) with its fertile soils (Uhlemann & Eckoldt 1998). In total, the main channel of the Oder has been shortened in the section between Rkm 27 and Rkm 666 from a length of 822–635 km by 1896. In the 19th century, the river channel was fixed and confined by the construction of 5432 perpendicular groynes and 263 km of shoreline embankments (Herrmann 1930). Further, the natural floodplain was reduced from 3709 to 859 km^2 by extensive construction of dikes (Landesumweltamt Brandenburg 1997).

14.4.4.2 Conservation and Restoration

In the lower Oder, floodplain areas were also diked but the polders created have always been flooded at least during winter. Under that extensive management regime, many features of unaltered floodplains have been preserved (Dohle et al. 1999). The German/Polish Lower Oder Valley International Park was established extending along 60 km river with an area of 105 km^2 in Germany and 60 km^2 in Poland. The branched river channels, remnants of the floodplain forest with black poplar, extensive sedge and reed stands, wet meadows and active floodplain areas offer habitats for the breeding, resting and overwintering of many bird species. In total, 161 bird species are breeding there, including, for example white-tailed eagle (*Haliaeetus albicilla*), osprey (*Pandion haliaetus*), lesser spotted eagle (*Aquila pomarina*), goosander (*Mergus merganser*), spotted crake (*Porzana porzana*), corn crake (*Crex crex*), terns, and bluethroat (*Luscinia svecica*). An especially rare species is the aquatic warbler (*Acrocephalus paludicola*), a migratory songbird breeding in short sedge beds, which is endangered globally and has its westernmost breeding population on the lower Oder. In autumn, the park regularly harbours ∼150 000 individuals of migrating geese, duck and swans, as well as 13 000 cranes.

During the great Oder flood in August 1997, many fishes, amphibians, birds and mammals living in the Oder National Park were washed away, could not reproduce, or were eaten by predators when fleeing from the rising waters. After the flooding receded, mass concentrations of birds of prey, herons and wading birds were observed, for example 40 white-tailed eagles were seen in the park. However, the event was not catastrophic for the park, but renewed habitats and eventually sustained populations of some riverine and floodplain species, for example in fish (Bischoff & Wolter 2001).

The Warta Mouth (Ujście Warty) National Park covers an area of 80 km^2 of mostly grassland vegetation mixed with alluvial willow stands. The southern part of the park near the village of Słońsk is subject to a water-level amplitude of up to 4 m. The park harbours species typical of river corridors such as the Baltic toadflax (*Linaria loeselii*), the umbelliferous plant *Cnidium dubium*, elk, beaver, otter, and 254 bird species of which 174 are breeding. In autumn, up to 200 000 migrating birds may temporarily concentrate there. The park is embedded in a highly forested landscape to the north, east and south, which facilitates movement of larger species to neighbouring parks like Drawa National Park.

Like other large European rivers, the Oder has been substantially modified by damming, regulation and other river engineering works. Because the lower Oder forms the border between Poland and Germany, intensive development was limited so that some typical features of large rivers have been preserved. On the other side, the Oder suffers along most of its length from significant inputs of wastewater and diffuses inputs of organic contaminants, nutrients, and heavy metals. The lower Oder and Warta are still free-flowing and are potential sites for the re-introduction of migratory fishes such as salmon and sturgeon. However, such efforts conflict with planned river training works to improve navigation on the Oder during periods of low flow.

14.5. EM

The Em River, with a catchment area of 4460 km^2, is the largest river in southeast Sweden (river mouth at 63°33′N, 15°42′E). The Em originates in the highlands of Småland (∼330 m asl), just north of Lake Storasjön near the city Nässjö. It flows approximately 220 km before entering the Baltic Sea near the city Em at Kalmar Sound. The Em valley is one of the most valuable watersheds in Sweden, as it is of great national interest for nature preservation, cultural history, and outdoor recreation. The lower river contains wetland types that are rare in the European boreal region. The river is well known for its population of European catfish and fast growing Sea trout, and meandering river sections provide valuable habitats for otter.

Early settlements dating back 6000 years have been found near large lakes and along the river. With the onset of agriculture and livestock breeding, settlements expanded and moved to higher areas in the landscape some 2000–3000 years ago. The cattle grazed in large wetlands along the river, where flooding by the river provided nutrients that supported good plant growth. Hay was harvested from meadows as a common way to get winter fodder for cattle, almost until today. Before industrialization in the 19th century and urbanization in the 20th century, humans lived from agriculture and forestry in villages or on small farms. From 1750 to 1880 the population increased markedly (by 135%), and subsequently large land areas like meadows, bogs, and marshes were transformed into agricultural fields, and lake water tables were lowered to gain new land.

The Em has been an important waterway for transportation, both in summer as well as on the ice cover in winter. Hence, the river has been straightened for timber transport, watermills, sawmills, and power stations. The lower river (county of Kalmar) was declared as a general timber route in 1897, being first used in 1912. About 25 000 m^3 of timber was floated down the river each year, and this business lasted until 1963. Timber was also transported on smaller streams, the Sällevadsån, Lillån, and Silverån in particular. Earlier, every village in forested areas had a watermill, thus thousands of watermills existed in the Em catchment. Most of these have disappeared by the 20th century. Today, the river is dammed in >100 locations (Photo 14.6). In total, the streams and rivers in the catchment had 292 fish migration barriers in the mid 1990s.

14.5.1. Physiography, Climate, and Land use

The river basin has a hilly topography with sediment filled valleys. Bedrock in the catchment is dominated by poorly buffered granites with low nutrient content, which is resistant to erosion and results in acidic soils. Sedimentary bedrock occurs in the westernmost part of the basin, thus soils are generally nutrient rich, calcareous, and more fertile compared to the east. In the east, porphyric bedrock can be found, and the soil layer is thin or even absent in some areas. Quaternary deposits covering the valley floor are dominated by tills, glaciofluvial material, and are rich in clay or sandy moraines suitable for agriculture.

Mean annual air temperature ranges from 3 °C in the upper catchment to 7 °C in the lower part. The coldest month is December with mean temperatures ranging from 0 °C near the coast to −2 °C in the upper basin. The warmest month is July, averaging 16–18 °C. Annual precipitation peaks in June and July. Freeze-up of lakes in the catchment begins around mid December to January and ice break-up usually

PHOTO 14.6 Em River with Järnforsens power plant at Järnforsen, municipality of Hulstfred, county of Kalmar. The dam consists a migration barrier, for example for brown trout (Photo: J. Bergengren).

starts around mid April. The growing season is 140–180 days in the north and 180–210 days in the south (Nordic Council of Ministers 1984, Gustafsson & Ahlén 1996). The catchment is located in a mixed deciduous forest region (Illies 1963). This biogeographical region is characterized by mostly spruce and pine forest in the north and deciduous forest in the south. The Em catchment is primarily covered by forest, with coniferous forest dominating at 69%, followed by mixed deciduous forest (19%). Only 12% of the forests consist of pure deciduous tree species, and riparian vegetation is dominated by coniferous trees such as spruce, pine, as well as Silver birch, and Black alder.

14.5.2. Geomorphology, Hydrology, and Biogeochemistry

In the Em catchment, six large lakes can be found along the mainstem of the river, that is Storasjön, Vallsjön, Tjurken, Grumlan, Norrasjön, and Flögen, together with 89 other lakes. The main tributaries of the Em are the Solgenån, Linneån, Silverån, Brusaån, Sällevadsån, Pauliströmsån, Gnyltån, Saljenån, Gårdvedaån, Marån, Morån, Nötån, Tjustaån, and Lillån. The upper tributaries for example Övre Solgenån, Kroppån, and Silverån Övre, had a maximum discharge <10 m^3/s between 1992 and 1997. Tributaries in the middle catchment, for example Silverån Nedre, and Gårdvedaån, had a maximum discharge <16 m^3/s between 1992 and 1997. The mean discharge in the lower catchment near Emsfors at the river mouth was 30 m^3/s between 1926 and 1975. During this period the lowest discharge was 2 m^3/s and the highest was 270 m^3/s (UNESCO 2004). Seasonally, the flow regime follows a general pattern with highest discharge in April after snowmelt and low discharge during summer from July to September. Seasonal variation in flow is quite marked, so that large areas along the river are flooded every year. This large variation in flow creates problems for the biota and people living in the valley. Most tributaries within the catchment are slow flowing (<0.2 m/s), and turbulent or fast-flow sections (>0.7 m/s) are rare.

Bed sediments in the Em main channel as well as its tributaries are dominated by sand, followed by cobble (5–50%). This mix of hard and soft sediments is usually supplemented by vegetation cover, mostly by submerged and floating vegetation and phytobenthos. Pebble or rocky sediments as well as dead wood are relatively rare within the catchment. The load of suspended sediments is relatively low in the river and tributaries, ranging from 0.7 mg/L (Silverån in 2006) to 5.6 mg/L (upper Em in 2006). Suspended loads usually peak in July in the lower and middle river. The river as well as Silverån and Solgenån are generally classified as mesohumic (61 mg Pt/L in Solgenån to 86 mg Pt/L in the upper river). Seasonally, the humic content in the streams is usually highest early in the year due to runoff, and is lowest in September. The humic content in the river is a growing problem, as the water colour has intensified by 100% in the last 10–15 years.

Mean water temperature in the Em ranges from 0.5 °C in winter to 18–20 °C in July, with the lowest temperatures typically occurring in the upper river. Long-term records show a slight increase in water temperature in the lower and upper river as well as in Silverån since the early 1990s. However, a decrease in water temperature has been recorded in Solgeån during the last 20 years. Concentrations of chloride and sulphate are low in the Em and the tributaries Silverån and Solgeån, ranging 4.8 mg/L (Silverån 2004) to 15.1 mg/L (Solgeån 2003) for chloride and 6.6 mg/L (Silverån 2005) to 18.5 mg/L (lower Em 1997) for sulphate. During the last 9 years, both chloride and sulphate concentrations have markedly decreased in the lower and upper river as well as in Silverån. Total ion concentration, measured as conductivity, has also declined during the past 16 years in all streams except for Silverån.

The Em and its tributaries Solgenån and Silverån can be classified as mesotrophic to eutrophic, as they exhibit annual averages of 12–53 μg/L total phosphorous and 503–1389 μg/L total nitrogen. The Solgenån has slightly higher total phosphorous content than the Em, but nitrogen content is on average higher in the river than in the tributaries. Concentrations of total phosphorous and nitrogen generally peak in summer. Long-term trends show an increase in nutrient content in the lower river, but a decrease in the middle part since the mid 1980s. In Solgeån, total nitrogen has strongly increased during the last 30 years. Saturation of stream water with dissolved oxygen (DO) ranges from 95% to 98% in the Em and its tributaries Silverån and Solgenån in December and January, and 81–85% in July and August.

14.5.3. Aquatic and Riparian Biodiversity

Riparian zones are dominated by wetlands, especially in the lower river. Here, the flora is rich and more continental than in the upper catchment. The Alpine bastard toadflax (*Thesium alpinum*), a national redlist species, is found in this area. Royal fern (*Osmunda regalis*), hemp agrimony (*Eupatorium cannabinum*), flowering rush (*Butomus umbellatus*), the nationally redlisted wood fescue (*Festuca altissima*) and great yellowcress (*Rorippa amphibia*) are relatively common plants along the river. The grey cinquefoil species *Potentilla arenaria* also has its largest growing site here. Cryptogam species, for instance, *Usnea florida, Leptogium cyanescens, Dimerella lutea,* and *Dichelyma capillaceum* (EU Habitats directive species) are common in the wetlands (Olevall et al. 2002).

In total, 96 species of higher aquatic plants can be found along the river (Sandin et al. 2003). Water plants are generally sparse and mostly found at sites impacted by nutrient point sources and lack of canopy cover. In the northern and western part of the catchment, mosses like *Fontinalis* spp. dominate, whereas the eastern and middle parts are dominated by submergent and emergen higher plants. Here, *Ranunculus flammula, Potaogeton polygonifolius, Littorella uniflora,* and especially *Batrachospermum* spp. dominate. In the middle northern part, the Yellow pond-lily (*Nuphar lutea*) is the prevailing plant. Recently, two rare aquatic plants have been found in the catchment, that is the slender naiad (*Najas flexilis*) in Lake Södra Vixen and *Nitella mucronata* in lake Norra Vixen. At some western sites, the neophyte species Canadian waterweed (*Elodea canadensis*) occurs.

Since the Em and its tributaries are generally small streams, phytoplankton growth is low. Red and green algae as well as Cyanobacteria are common in the main channel and tributaries. Diatoms have the highest algae taxa richness and abundance; the most common includes *Eunotia* and *Achnanthes* genera as well as *Fragilaria capucina*, *Gomphonema parvulum*, *Tabellaria flocculosa* and *Brachysira neoexilis* (Sandin and others 2003). A study of phytoplankton assemblages in 10 lakes within the catchment showed that *Cryptophyceae* and diatoms were most common. Diatom communities consist mainly of *Aulacoseira* sp., *T. flocculosa*, *Rhizosolenia longiseta*, and *Fragilaria* spp., whereas *Cryptomonas* sp. and *Chromonas* sp. represent the cryptophycean group (Sundberg & Ericsson 2005). Dinophyceans, almost solely represented by *Peridinium*, *Ceratium*, and *Gymnodinium* spp. as well as Cyanobacteria comprised ~10% of the total community composition in the lakes. Filamentous**,** nitrogen-fixing species such as *Anabaena* sp. and *Aphanizomenon* sp. as well as potentially toxic and floating *Microcystis* sp. are common blue-green algae. *Snowella* spp. and *Planktothrix mougeotii* also occur in some lakes, especially in Lake Solgen and Lake Södra Vixen, both have relatively high numbers of Cyanobacteria. Green algae are frequently represented by *Pediastrum* and *Scenedesmus* spp., and *Dinobryon*, *Mallomonas*, and *Synura* taxa are the most common gold algae. *Nostoc zetterstedtii*, an indicator of nutrient poor clear water lakes, has one of its largest populations in the Em catchment.

The nuisance flagellate *Gonyostomum semen* is common in the lakes and comprises ~11% of the total phytoplankton biomass. *G. semen* is invasive in mesotrophic Scandinavian lakes and may form dense blooms in humic lakes with high nutrient content. In most lakes this species is not abundant, but in Lake Grumlan about 70% of total phytoplankton biomass consists of *G. semen*, and can lead to skin reactions in humans. Long-term studies showed that annual total phytoplankton biomass and number of taxa varied little during the last 15 years, ranging from about 0.05–6 mg/L biomass and 20–55 phytoplankton taxa (Sundberg & Ericsson 2005).Zoobenthos in some sections of the river have high diversity. In a study at five sites (three in the mainstem, two in Silverån, and one in Gårdvedaån) (Boström 2005), two sites had high zoobenthos richness compared with a large dataset from southern Sweden. The five sites harboured 43–66 taxa (near the river mouth) and 45–61 taxa (at Kungsbron in the main stem). In 2003, a large inventory of 27 sites was made (Boström & Engdahl 2003), where 9 out of 11 sites sampled in the mainstem contained high taxa richness (41–58 taxa). A number of redlisted and rare species also were found in these studies, for example the amphipod *Gammarus lacustris*, the odonate *Calopteryx splendens*, the ephemeropterans *Baetis buceratus*, *Rithrogena germanica*, the trichopterans *Brachycentrus subnubilus*, *H. contubernalis*, *Oecetis notata*, *P. pusilla*, *Adicella reducta*, *Ceraclea nigronervosa*, the hemipteran *Aphelocheirus aestevalis*, the coleopterans *Stenelmis canaliculata*, *Oulimnius troglodytes*, *Normandia nitens*, the dipteran *Ibisia marginata*, and the gastropods *Gyraulus crista*, *Marstoniopsis scholtzi*, *Bithyna leachii.* In the 22 lake littoral zones studied in 2003, the trichopterans *Goera pilosa* and *Notidobia ciliari* as well as the gastropod *Valvata piscinalis* were found. In the river, seven large mussel species have been found such as the redlisted and protected freshwater pearl mussel (*Margaritifera margaritifera*) and the thick-shelled river mussel *Unio crassus* as well as the depressed river mussel (*Pseudanodonta complanata*). The river also has four other large mussel species, that is painter's mussel (*Unio pictorum*), the duck mussel (*Anodonta anatina*), the swan mussel (*Anodonta cygnea*), and the swollen river mussel (*Unio tumidus*). The Noble crayfish as well as the introduced signal crayfish (*Pacifastacus leniusculus*) are also found in the river.

The ichthyofauna of the Em comprises over 30 fish species, including salmon, asp, chub, and trout. The Em is considered the most important water in Scandinavia for the European catfish. The European catfish, requiring a water temperature of ~22 °C for spawning, is a relict species from a warmer climate period in Sweden and lives on the edge of its climatic range. Its population has declined significantly over the last century in Scandinavia. Today, the catfish occurs only in the lower river, where most are found in quiet parts below the power station dams Karlshammar and Emsfors near the river mouth.Originally, the Em offered extraordinary suitable habitats for Salmon and migratory Sea trout. In the early years of the last century, these fish occurred as high up as Vetlanda in the middle and western part of the catchment. Today, power station dams hinder spawning fish from reaching their original breeding grounds, decreasing access to only ~10% of the river length. A recent study (Andersson & Nilsson 2004) showed that biomass as well as the number of sea trout decreased during the last years, although this fish is still dominant in waters of the catchment (County Administrative Board of Jönköping 2006a). In surveys, cyprinids have been the most common fish in the Em and its tributaries, and include Minnow, Roach, and Tench. Other noteworthy fishes are burbot, Brook lamprey and Alpine bullhead, and the globally redlisted Asp.

14.5.4. Management and Conservation

Water of the Em is abstracted by a number of industries, several municipalities and farmers. Fourty-five dams used for hydropower production are found in the upper catchment. During summer, river discharge can be too low for drinking water supply, industry and irrigation purposes, as well as for fish migration. Flooding of floodplains and farmlands regularly occurs during snowmelt. The Swedish Meteorological and Hydrological Institute therefore implemented a water management plan for the river to regulate its flow by controlling the outflow of dams and to guarantee a minimum flow of 4.5 m^3/s near the mouth.

Since the early 19th century, the lower river has been affected by the release of cadmium, nickel and lead from a battery factory ~20 km upstream of the mouth. Monitoring programs to reduce pollution levels were implemented at the end of the 1970s, and the heavy metal content has decreased, although cadmium levels are still high. Persistent organic compounds (PCBs) contaminate the catchment, especially the upper basin (Johansson 1996; Olevall et al. 2002). While some factories have been closed for >20 years, and local restoration projects have been carried out, high levels of metal and PCBs are still found locally in river sediments. One of the largest sources of PCBs is contaminated sediments still present in rivers and lakes, especially in Lake Järnsjö, which were heavily polluted by emissions from a paper mill in the early 1990s.

PCB is considered to be the major factor for the dramatic decline of the otter population in the Em catchment, as in the rest of Europe. In addition, hydromorphological alterations exert major impacts on river biota. Water control measures conducted in the late 19th century to create additional agricultural land, water pollution and the construction of dams have probably contributed to the decline of the European catfish. The decrease in populations of salmon and migratory Sea trout is probably related to the dam of the Högsby power station that forms the upper limit of migration in the main channel (County Administrative Board of Jönköping 2006a). The salmon population in the lower catchment is one of the few remaining stocks south of the Dalälven River (middle Sweden) which has a significantly natural reproducing population (County Administrative Board of Jönköping 2006b).

14.5.5. Perspectives

The Em River is of national importance for nature conservation, as it is a designated Ramsar site since 1999. Part of the catchment is a European Natura 2000 site, and it contains one of the largest continuous wetlands in Sweden. The Em catchment harbours a high level of both plant and animal diversity. There also are good conditions for recreation and tourism, especially sport fishing in the river. The main environmental problems in the catchment relate to water use, as hydropower plants and irrigation hinder fish migration, and historic pollution by heavy metals and PCBs are evident, especially in lake sediments. In 2002, a water management plan was set up for the catchment to guarantee a minimum flow of 4.5 m^3/s at river mouth. Environmental and economic sustainability in the catchment is maintained through the River Em Catchment Management Association, including municipalities, the county administrative boards, some 200 landowners, and NGOs.

14.6. SKJERN

The Skjern River originates in glacial moraines that cover the center of the Danish Peninsula of Jutland, then flows West before entering the Ringkjøbing Fjord estuary and finally the North Sea. The Skjern is the largest river in Denmark in terms of discharge, draining an area of 2490 km^2 with a length of 94 km from its source in Tinnet. The river network including tributaries is 1526 km long. In the 20th century, the original diverse fauna and flora of Danish streams declined dramatically due to pollution by wastewater from cities, industry and fish farms, and by channelization that aimed to improve drainage of agricultural land. During the 1970s to early 1980s, increasing public awareness of water pollution problems lead to a rapid decrease in discharges of organic matter to surface waters from point sources (Kronvang et al. 2006). Since the mid 1980s, nitrogen and phosphorus loadings of Danish surface waters have been significantly reduced (Kronvang et al. 2005). Since the 1990s, considerable efforts have been made to improve habitat diversity in streams by introducing more environmentally friendly regulations and implementing stream restoration projects. Some of these projects have been carried out locally on short reaches of streams, for example providing spawning gravel for fish. The continuity in some streams was re-established, while in larger projects the restoration included both the stream and adjacent riparian areas, for example by re-meandering streams. A large restoration project was conducted by the National Forest and Nature Agency in the lower Skjern.

14.6.1. Biogeographic Setting

Denmark, which lies completely within one ecoregion, is a small lowland country with the distance of any location in Denmark from the seacoast never exceeds 50 km. For this reason, even the largest streams in Denmark are relatively small. The freshwater flora and fauna is generally species poor when compared to other areas within this ecoregion, partly because of dispersal barriers caused by the sea. The glacial history of Denmark is reflected in the dispersal of freshwater organisms and partly explains the higher diversity in western Jutland that remained ice free during the last glaciation 10,000 years ago.

14.6.2. Physiography, Climate, and Land Use

Three types of landscapes can be identified in the Skjern catchment, including moraine hills, washout plains and post-glacial deposits The washout plains, which consist of deposited sand and gravel, appear as heath plains acting as wider river valleys between old moraine hills. The major river flowing through this landscape is the Skjern. Soils in Danish river valleys are generally dominated by deposits of organic origin, equaling an area of 6700 km^2 (15% of Denmark's area). In the Skjern valley, peat as well as fine particulate organic matter and diatom frustules deposited in shallow waters, making up the so-called gytja layers, are found to a depth of ~10 m. Historically, these soils have been extensively used because when drained they provide excellent nutrient-rich soils for agriculture. In the entire catchment, soils are dominated by sand (70–80%), 15–20% is sandy loam and 4–8% consist of humic soils.

The average yearly measured precipitation in the catchment is 89.2 cm/year (1961–1990) compared with 71.2 cm/year for the entire country. This corresponds to an actual precipitation reaching the catchment surface of 108 cm/year. The climate is oceanic temperate (annual mean temperature 7.6 °C), so that winters are fairly mild (coldest monthly average temperature ~0 °C) and wet, whereas summers are cold (warmest monthly average 15 °C) with high levels of precipitation. Air temperatures have been increasing 1.5 °C since 1874 with half of this increase occurring since the late 1980s.

The floodplains of the Skjern River have been farmed for centuries. The meadows provided nutrient-rich farmland in a part of Denmark otherwise dominated by leached sandy soils of little value. The frequent flooding of the river regularly supplied nutrients and organic matter to meadows and fields. Livestock fed on fresh grass in the summer and in winter on hay harvested from the meadows. Farming in this period was largely sustainable. The purchase of winter feed for livestock is a relatively recent phenomenon, and the use of fodder turnips in the region did not start until the turn of the last century.

The unpredictability of floods often ruined hay making, so that the river was regulated for the first time in 1901–1902 to reduce flooding. The lower main channel was straightened and summer dykes were built. Despite these efforts, farming was still difficult in large parts of catchment due to wet soils and occasional flooding. Hence, in 1962 the largest drainage project in Denmark was initiated, which comprised the straightening of the lower 20 km of the main channel from the town of Borris to the estuary Ringkøbing Fjord (Figure 14.10). The regulation took 6 years to complete at a total cost that today would correspond to EUR 27 million. Flooding was prevented by large dykes and the groundwater table was lowered by installing pumping stations and drainage ditches. After the regulation, 4000 ha of arable farmland resulted from what were previously meadows and wetlands. The area covered by wetlands was reduced to only 430 ha by the end of 1990s (Svendsen & Hansen 1997).

In 1987 the Danish Parliament decided to restore the lower Skjern and its valley. The objectives of the restoration were (1) to restore the nutrient retention capacity of the river and its valley, (2) to restore an internationally valuable wetland and habitats for migratory birds, (3) to promote fisheries in the downstream estuary, and (4) to increase the recreational and tourist values of the area. Most of the project area (19.5 km^2) was purchased from the farmers by the Danish Forest and

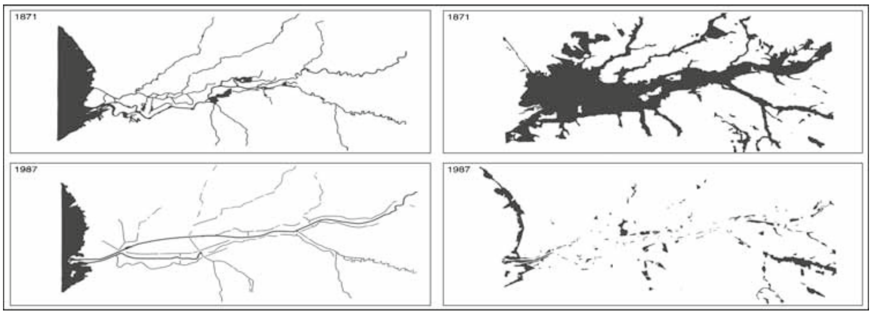

FIGURE 14.10 The course of the lower 20 km of the River Skjern (left) and the extent of meadows and wetlands along the Skjern (right) mapped in 1871 and after river regulation in 1987.

Nature Agency. Local authorities, trade organisations and interest groups covering outdoor life and environmental protection participated in the entire decision process of the project. The restoration project included re-meandering of the river and re-establishment of natural water levels and water level fluctuations in the river and its valley. The main purpose was to enhance living conditions for plants and animals and safeguard high water quality in the river and estuary by enhancing nutrient retention. Construction was initiated in June 1999 and was mostly finished by autumn 2002 with a total cost of EUR 37.7 million; 3.3 million were granted by the EU LIFE program. This corresponds approximately to the costs of land reclamation in the 1960s. The main activities were the excavation of a new meandering river channel that increased channel length from 19 km to 26 km, the removal of existing dykes, the filling of the old channelised reaches, and the construction of bridges and paths. Whenever possible, one of the original riverbanks was used for the restored river channel. In total, 2.7 million m^3 of soil was moved and 40 km of restored river channel was established (Photo 14.7).

PHOTO 14.7 Flooded floodplain of the lower Skjern near its mouth. The bended river course that was newly built in the restoration project, and some remnants of the former straightened channel can be seen (Photo: Poul Toft).

14.6.3. Geomorphology, Hydrology and Biogeochemistry

Before the first regulation in 1901–1902, the Skjern meandered freely across the floodplain. Its width was between 65 and 100 m and the slope was 20 cm/km in the lower reaches (Rambusch 1900). Near the sea, the river formed a delta with several side channels flowing parallel to the mainstem. After the large-scale regulation in 1968, the width of the river channel was fixed at 45 m at the downstream reach below the Omme River confluence and 30 m at the reach below Borris. By installing embankments, the bank height was raised to 3.5–3.8 m along the regulated reach. With the increase in width and bank height, bankfull discharge increased fivefold at the upstream reach at Borris to 178 m^3/ and fourfold to 144 m^3/s at the downstream reach. After construction of the new river channel comprising 46 new meanders, average cross-sectional area was reduced by 20–30%, the dominant depth interval decreased from 100–160 to 40–140 cm (Figure 14.11), and current velocities increased from 30–40 cm/s to around 30–60 cm/s in the middle of the channel. Newly excavated cross sections of the channel were now subject to significant fluvial dynamics.

The Skjern is a typical lowland, low energy river with a mean discharge at its mouth of 35.6 m^3/s (1920–95), ranging between 35.6 m^3/s (1929) and 319 m^3/s (extreme snowmelt event in 1970). As most of the catchment is builtup by sandy deposits, most precipitation infiltrates. Hence, the river is mostly fed by groundwater and shows a relatively mitigated flow regime, with minimum flows rarely less than half of mean flow. Mean flow velocity is 0.49 m/s (measured at Ahlergaarde, 1994–1998). In the period from 1925 to 1995, mean discharge increased significantly (Larsen et al. 2005), likely explained by the increase in average precipitation of ~0.1 cm/year since 1874 (Cappelen 2007), increased tile drainage and increase in impervious areas (roads, towns). Annual average river temperature is ~8 °C, and typically ranging during the year between 2 and 16 °C. The average (1965–1995) annual suspended sediment load in the river is 5.0 tons/km^2/year (Andersen & Svendsen 1997) compared to 9.5 tons/km^2/year on average in 14 Danish rivers (Kronvang et al. 2006). The suspended matter is fine-grained, and is an important carrier of environmentally harmful adsorbed substances such as phosphorus, heavy metals, and pesticides. The movement of coarse sediment on the streambed (bed load) averaged during the same time period was 6.5 tons/km^2/year.

Nitrate transport in the river measured at Ahlergaarde was ~1500 tons/year from 1979 to 1995. Nitrate constitutes ~80% of the nitrogen in transport. Despite the reduction of nitrate emissions from sewage treatment plants, there was a significant increase in nitrate from 1979 to 1995, reflecting that the main source of nitrogen was diffuse pollution from farmlands. In contrast to nitrogen, phosphorous transport was halved in the same period from around. 80 to 40 tons/year, corresponding to a concentration of 70–80 μg P/L and reflecting the decrease in sewage inputs. Phosphorous levels in the river in the 1990s were only half of those found in other Danish streams in an agricultural landscape, partly explained by the presence of ochre sediments (FeO(OH)) within the river that result in the formation of ferrous phosphate ($FePO_4$) particles that settle in the channel.

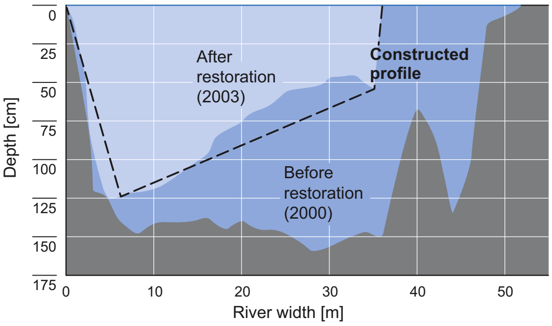

FIGURE 14.11 Example of the changes to the cross-sectional profiles in Skjern River. The cross sectional area has generally decreased by approximately 30%. The morphology of the profiles has changed from the constructed rectangular shape to a more natural physical appearance.

Channelisation of the lower Skjern resulted in large amounts of soluble iron (85 000 tons of Fe between 1966 and 1995) being released when the pyrite rich soils in the floodplain were drained and oxidized. This was paralleled by soil shrinking of 1.5 m as organic matter decomposed and was further compressed by heavy farm machinery that rendered soils wetter and more anoxic. After completion of the restoration project, monitoring of the concentrations of nitrogen and phosphorus showed that the retention of N and P is likely to be <10% of the total riverine input to the project area. No effect of the restoration of the river channel could be detected so far. Approximately 4.5 km^2 of the river valley will be flooded regularly after restoration, equaling around one month per year. Sedimentation on the floodplain during flooding was measured in winter by means of artificial grass mats, and sedimentation was estimated to add 8 g/m^2 total phosphorous and 280 g/m^2 of total nitrogen. An annual basis, it is estimated that typical deposition is 5 tons P/year and 13 tons N/year (Ovesen & Damgaard 2005). In the adjacent permanent Lake Hestholm and in flooded parts of the river valley, nitrate from the river water is denitrified to atmospheric nitrogen, which is estimated at 45 tons N in flooded riparian areas and 150 tons N in Lake Hestholm in normal years (Kronvang et al. 2001; Jessen & Andersen 2005).

14.6.4. Aquatic and Riparian Biodiversity

14.6.4.1 Terrestrial Fauna

Historically, the lower catchment harboured a rich bird diversity because of the extensive reed beds and wetlands that occurred in the floodplain. Despite changes due to drainage measures, the area remained a bird protection area of international importance as an integral part of Ringkjøbing estuary, which is protected by the Ramsar Convention on wetlands since 1977. It was estimated that >1% of the total international population of whistling swan, whooper swan and pink-footed goose rested in the Skjern River floodplain (Nøhr 1988), and the area was identified as the main resting area for dotterel (*Charadrius morinellas*) in north Europe. In 1994, 124 bird species were registered in the lower Skjern River valley.

Of the 17 species of mammals registered for the Skjern River valley, otter is a key species listed in the Danish Red Book. Prior to the floodplain drainage, the river was considered the primary otter locality in Denmark. In surveys in 1979/1980 and 1991 otters were registered only at a few locations along the river (Madsen et al. 1992). Since then, a marked increase in the occurrence of otter in the restored area has been documented, which parallels the general spreading of otter from northwest Jutland to the rest of the Jutland Peninsula (Madsen et al. 2005).

In 1976, eight species of amphibians were found in the catchment as well as all five Danish reptiles (Fog 1993). Habitat loss from extensive drainage of rivers, wetlands and ponds in the catchment probably has had a detrimental impact on both amphibians and reptiles. It appears that the restoration project has improved both the breeding and terrestrial habitats for Common frog and Moor frog, whereas the response of common toad and natterjack toad to restoration remains unclear (Madsen et al. 2005). The habitat improvements are primarily due to the creation of shallow ponds surrounded by non-cultivated land.

14.6.4.2 Terrestrial Vegetation

Prior to the drainage, the lower catchment had a high diversity of plants on the wet meadows (Baagøe & Ravn 1895; Mentz 1906). The differences in soil humidity created a range of different habitats and hence a variety of plant communities. The wet meadows were dominated by smooth black sedge (*Carex acuta*), beaked sedge (*Carex rostrata*), creeping bent grass (*Agrostis stolonifera*) and reed sweetgrass (*Glyceria maxima*), and in open stagnant waters the floating water-plantain (*Luronium natans*) occurred, but is today highly endangered. This changed completely in the 20th century when meadows were converted into arable farmland. As a consequence, the original flora was lost with the exception of a few areas such as the two bogs Raadensig kær and Albæk, but which were negatively affected by draining and fertilization of adjacent lands. A number of rare plant species such as the water lobelia (*Lobelia dortmanna*), whitish bladderwort (*Utricularia ochroleuca*), slender cottongrass (*Eriophorum gracile*) and string sedge (*Carex chordorrhiza*) also were impacted. After the restoration project, most of the valley was converted back into meadows and wetlands. The area is grazed by cattle to prevent reed stands or black alder and willow forests from taking over. In total, an area of 12 km^2 is grazed by ~800 cattle, while an additional 3 km^2 are mechanically cut. There is an on-going evaluation of the grazing pressure targeted towards achieving an attractive breeding habitat for birds characteristic of meadow ecosystems and an optimal habitat for migratory water birds, according to the designation of the Skjern River valley as a Natura-2000 area.

14.6.4.3 Fish

Based on large-scale fish surveys in the 1980–1990s, 26 fish species were found in the Skjern River. In Denmark, Siberian sculpin, a IUCN red list species, is only found in the Skjern catchment. Similarly, the Skjern harbours the largest natural populations of grayling and salmon in Denmark. Common whitefish occurs in Jutland and can be found in high densities in the Skjern. Two non-native fish, rainbow trout and brook trout, were found in the river and were probably introduced by accidental releases from Denmark's ~400 fish farms. The Skjern is one of five Danish rivers where original salmon populations still exist, as shown by comparisons of DNA analyses of preserved salmon scales from fish caught in 1913, 1930s and 1950s (Nielsen et al. 1997). In 1989, the number of spawning salmon was estimated at 125–2000 ind./year (Dieperink & Wegner 1989). By rod catches, about 300–500 salmon were caught per year in the 1950s, while this number decreased to ~10 per year from 1977 to 1985 (Miljøstyrelsen 1994). Sea trout followed the same downward trend as salmon, with rod catches decreasing substantially from 500–700 to ~50 per year in the same period.

The reasons for the decline in salmon populations in the catchment are a general degradation in water quality as a consequence of high concentrations of ochre, habitat loss through dredging, channelisation, and fishing pressure, especially in the estuary. To reduce fishing pressure, commercial fishing in the estuary and river was substantially restricted since 1996, and fishing is now prohibited during winter in the river. Over the last 20 years, the number of salmon returning from the sea to the Skjern to spawn has increased from about 100 to 1000 salmon annually (Figure 14.12). This increase was primarily caused by stocking of juveniles and by restrictions on commercial fishing rather

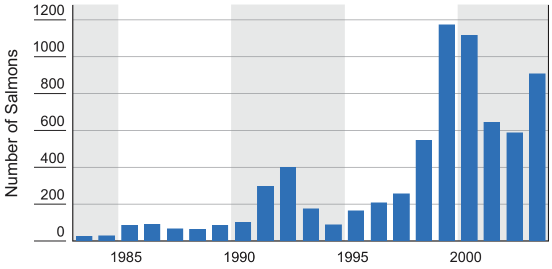

FIGURE 14.12 Annual spawning migration of salmon into Skjern River from 1984 to 2004 (modified from Koed et al. 2006).

than by the restoration project. The number of migrating salmon smolts was estimated at 5800 and 26 200 in 2000 and 2002, respectively, and for trout smolts at 7100 and 8500 using tagging-recapture methods (Koed and Baktoft Bak 2006). The mortality of radio-tagged smolts during their migration in the Skjern was estimated at ~50% for salmon and 25% for brown trout. Great cormorants and grey herons caused, respectively, 16% and 14% of the mortality of radio-tagged salmon and trout smolts in 2002.

14.6.4.4 Aquatic Macroinvertebrates

The first recorded macroinvertebrates samples from the Skjern can be dated back to 1912. When comparing samples through time, there has been a marked change in taxonomic composition (Jensen 1995). Three species of mayflies (*Ephemeralla ignita, Caenis rivulorum* and *Heptagenia fuscogrisea*) have become more abundant over time, while all other mayfly species have declined and four species have not been recorded since 1957 (*Baetis buceratus, B. digitatus, Paraleptophlebia werneri* and *Siphlonurus alternatus*). A similar trend can be seen with respect to stoneflies where *Isoperla grammatica* and *Taeniopteryx nebulosa* have become increasingly more abundant, while most other species have decreased in abundance (e.g. *Perlodes microcephala)* or completey disappeared (*Siphonoperla burmeisteri*). The decline in populations of mayflies and stoneflies likely reflect the increased pollution and habitat degradation that occurred in the Skjern through the 20th century. Despite these species declines and losses, the Skjern is today considered to harbour one of the most taxa-rich macroinvertebrate faunas in Denmark. Mayflies (Ephemeroptera) and stoneflies (Plecoptera), and to some degree caddisflies (Trichoptera), include species that are rare or absent from other parts of the country. Several species such as the mayfly *Brachycercus harrisella* and the stonefly *Isoptena serricornis* have good populations in the river but are threatened by extinction at a national level. The Skjern is also the main locality for the green club-tailed dragonfly (*Ophiogomphus cecilia*).

After completion of the restoration project, the short-term effects of restoration on river habitats, macrophytes and macroinvertebrates were examined in surveys within the restored section of the river, while upstream reaches that remained unaltered were used as a control. Two years after the restoration, macroinvertebrate diversity and abundance had reached pre-restoration levels. Species richness was 63 before the restoration in 2000 and 76 after the restoration in 2003. Before restoration, blackflies (Simuliidae) was the dominant taxon, and about twofold more abundant than non-biting midges (Chironomidae). In 2003, the three most dominant taxa, Orthocladiinae, the caddisfly *Brachycentrus maculatus*, and the mayfly *Heptagenia sulphurea,* were almost equally abundant. The riffle beetle *Elmis aenea* and the mayflies *Baetis* spp. (six species including the dominant *B. rhodani* and *B. niger*) and Heptageniidae (two genera and five species including the dominant *Kageronia fuscogrisea*, *H. sulphurea*, and *H. flava*) increased in numbers after the restoration.

14.6.4.5 Aquatic Macrophytes

Most streams in the catchment are vegetated by emergent and submergent macrophytes. Of these, the Atlantic/subatlantic species Flowing water-plantain and the river water-Dropworth are both nationally and internationally regarded as being endangered and have their main Danish populations in the Skjern River. Historically, river water-dropworth occurred in most reaches in the lower river (Baagøe & Ravn 1895). After large-scale regulation in the 1960s, river water-dropworth was lost from the mainstem but remained in tributaries. Similarly, the number of Pondweed species found in the lower river declined from 13 species in the 1890s to only two in the 1970s (Wiberg-Larsen 1978). The decline of Pondweed species has been a general trend in Danish rivers and can be directly related to eutrophication, disturbance by channelisation, and weed cutting in channels (Riis & Sand-Jensen 2006). After restoration, the species richness of aquatic macrophytes increased from 28 in 2000 to 40 in 2003. Reed Sweet-grass and Floating Sweet-grass and reed dominated the macrophyte community before restoration. The re-meandered channel and the edge habitat were dominated by Canadian waterweed and burreed (*Sparganium emersum*).

14.6.5. Perspective

The history of the Skjern River and its catchment shows similarities to the majority of streams and rivers in the northern lowlands of Europe. Large-scale changes in land use have increased the loads of nutrients and organic matter in streams. The hydrological regime and hydromorphology have been impaired directly through channel modifications to secure drainage of fields and prevent flooding. Some of the impacts date back to human activities at a time when food scarcity was a significant problem for rural populations. When industrialised farming was introduced, the view was deeply imbedded in society from farmers to policy makers that the only service that the Skjern River should provide was to transport water to the sea as efficiently as possible. A number of scientists predicted the negative consequences even before the channelisation work was initiated, estimating the economic gain of the reclaimed land to be small compared to the loss of ecological integrity and services. The lower Skjern differs from other lowlands rivers of its size in the respect that it has been restored by the largest project of its kind to date in Europe. It will probably never be fully known what irreversible losses in biodiversity were caused by the short period of intensive agricultural use.

14.7. SPREE

The Spree River is in the east Elbe catchment and borders the Oder catchment. With a length of 380 km, the Spree is a small river, but rather well known as the governmental center in Berlin lies on its banks. It shows typical hydrological and ecological features of a lowland river of the central plains, which though has undergone severe transformations by its use for production of lignite and drinking water, the removal of wastewater, as well as for navigation and recreation. The multiple uses of the Spree contrast with low water availability in the catchment, from both natural and anthropogenic reasons. Therefore, and stimulated by major concerns about the integrity of the river ecosystem, the hydrology and ecology of the Spree have been intensively studied for decades. The Spree constitutes today one of the best known and most intensively managed rivers of the world (Köhler et al. 2002a).

14.7.1. Physiography, Climate, and Land Use

14.7.1.1 Physiography

The Spree's source is in the Lusatian highlands near the boundary triangle of Germany, the Czech Republic and Poland at ~480 m asl on the slope of Mount Kottmar (583 m asl) only 6 km from the Czech border. Mount Kottmar, which lies east of the small city of Ebersbach, seems to have been a holy place in early medieval times. The river's name was first mentioned in the year 965, and probably is related to the indogermanic linguistic root 'spread'. The Lusatian highlands are made up of granite partially overlain by tertiary and quaternary deposits (Driescher 2002). Within its catchment of 10,105 km^2, the general flow direction of the Spree is northwest. As the mouth of the Spree at Berlin-Spandau is at 30 m asl, the average slope along its 380-km long channel is around 1. The Spree loses 300 m in altitude along its upper segment that ends at the city of Bautzen. The historic skyline of this city is mirrored in the Spree that passes the city walls in a steep valley before entering the Bautzen reservoir. Once the river enters the lowlands, the slope decreases from 5 in the highlands to 0.09. Concomitantly, the aspect gradually changes from a rushing upland stream to a slow-flowing lowland river downstream of the city of Cottbus. In the highlands, the catchment comprises a dense, multiple-branched network of streams. In contrast, in the lowlands, which mostly consist of sandy glacial deposits, precipitation easily infiltrates so that the density of stream channels is much lower.

After leaving the highlands, the middle Spree first crosses the Wrocław-Magdeburg glacial valley produced by the meltwaters of the Saale glaciation period. There, the Spree joins with its second largest tributary, the Schwarzer Schöps, that drains an area adjacent the Neisse River. In the Lusatian lignite mining region near Boxberg, the stream network has been largely altered or even lost, first through lowering groundwater levels on an area of 250 km^2 and second by physically removing these landscape elements by huge excavators used to remove the sandy deposits that cover the lignite layers. Mining pits square kilometres in size and depths up to 120 m have been created to access the 10–16 m thick layers of lignite. The Spree flows by the small city of Spremberg and then breaches through a major moraine produced by the Weichsel glacial period, regionally called 'Lausitzer Grenzwall'. There, the Spree has been dammed to create Spremberg reservoir.

After passing the 'Lausitzer Grenzwall', the Spree enters the Glogów-Baruth glacial valley, thereby by changing to northwest flow direction. In this section, the river slope reaches a minimum, as the difference in river altitude between the city of Cottbus und Lake Neuendorfer See (~70 km channel length) is only 15 m. Due to the low slope, the river forms a unique network of anastomosing channels with a total length of 1300 km within an extensive wetland area, the Spreewald. Any agricultural and other transports performed on this channel network used traditional wooden barges until the early 20th century. The Spreewald is also fed by the third largest tributary to the Spree, the Malxe River.

In its lower segment, the Spree changes its direction several times, as it again follows glacial valleys or is guided by the arrangement of sandurs and glacial ground moraines. The river crosses several lakes such as Lake Neuendorfer See, the northern tip of Lake Schwielochsee, Lake Dämeritzsee and Lake Müggelsee. Additionally, the river closely flows by a number of smaller lakes that are connected to the river. Just downstream of Spreewald, the Spree originally split into two branches for ~10 km, the main Spree and the Pretschener Spree. The latter historically may have had more flow than today's main Spree channel. Downstream of Lake Neuendorfer See is the Krumme Spree ('bended Spree'), which had extensive meanders before it became straightened and channelized from 1906 to 1912. After the river passes the northern tip of Lake Schwielochsee, it follows glacial meltwater channels northward and reaches the Berlin glacial valley east of the city of Fürstenwalde.

In the section between Fürstenwalde and Berlin, called 'Müggelspree', (Photo 14.8) several large paleo-meanders can be seen, which were used by a precursor river of the Spree that received glacial meltwaters, and nearly being the size of today's Elbe River as deduced from meander radii. In the area of Lake Dämeritzsee, the Spree originally split again, this time forming three branches that discharged not only into Lake Müggelsee (the only route today), but southwest into Lake Seddinsee and Lake Wernsdorfer See (Driescher 2002). The Spree then merges with the largest tributary of the Spree, the Dahme River (catchment size = 2186 km^2) that enters the Spree in Berlin–Köpenick. The city of Berlin, and its former twin city of Cölln on Fischerinsel Island, were founded at a place where the Spree split into two channels, which facilitated the use of a ford,

PHOTO 14.8 The Spree upstream of Berlin in summer of the dry year 2003, when discharge in this reach (called Müggelspree) fell below a level of 5 m^3/s for 2 months. Due to extensive gowth of aquatic macrophytes that create hydraulic roughness, the water level in the river remains constant even if flow velocity decreases to ~10 cm/s (Photo: M. Pusch).

and later the construction of a bridge. Even today, Berlin still boasts more bridges than Venice. After crossing Berlin from east to west, the Spree joins the Havel River near the citadel of Berlin-Spandau, which flows to a large extent within riverine lakes. Despite the fact that the length of the Havel and its discharge are <50% of that of the Spree (mean discharge 15 m^3/s versus 38 m^3/s at the confluence at Berlin-Spandau), the resulting river is called Havel. The Havel then flows through the city of Potsdam, heads west and northwest to its confluence with the Elbe River near the city of Havelberg.

14.7.1.2 Climate

Climate in the catchment is mostly sub-continental with relatively low annual precipitation and hot and dry summers. Mean annual temperature at Cottbus, which is on the middle Spree, was 8.9 °C (time period 1961–1990), with only 564 mm of mean annual precipitation and maximum precipitation in summer. Within the catchment, precipitation decreases from 600 to 1000 mm in the headwaters to 500 mm near the northeast margin of the catchment, including the lower Spreewald, and is one of the driest regions within Germany. Climatic water balance in this region is negative from April to September (Kaden et al. 2002). Due to limited water availability and multiple uses of its water, the Spree is seen as especially susceptible to climate change. This assumption became evident during a recent sequence of dry years (2000, 2003, 2006) that significantly affected the hydrology, ecology and public uses of the river.

14.7.1.3 Land Use

In the early medieval age, the Spree catchment was mainly inhabited by Slavic tribes that mainly built their villages and fortifications near rivers and lakes, for example at the confluence of the Dahme and Spree Rivers in Berlin–Köpenick. Slavic identity, culture and language are still maintained by the minority of the Sorbs settling along the Spree in upper and lower Lusatia. Most of the pristine forest in the catchment was cleared with the German immigration wave during the 12th and 13th centuries, so that in the 14th century the catchment became even less forested than today (Driescher 2002). Deforestation probably caused substantial increases in erosion in the catchment, sediment and nutrient exports from the catchment, as well as in river discharge. In contrast to many other rivers in Central Europe, the floodplain along the lower Spree was not covered by a clay layer due to anthropogenically enhanced erosion, as the transported sediments were retained in the Spreewald wetland as well as in riverine lakes. Today, the Spree catchment upstream of Berlin has a population density of 100 inhabitants/km^2, and thus represents a relatively sparsely populated region within Germany. The population density decreases from 150 to 200 in the upper catchment to 55 inh./km^2 in the lower catchment near Berlin (Driescher & Behrendt 2002). The Spree catchment upstream of Berlin has a relatively high percentage of forest at 41.5%, 43.4% crop fields, 4.6% settlements and 2.2% surface waters. In the upper river, over one third of the agricultural areas are drained.

Most of the Spree has been profoundly influenced by lignite mining activities in the Lusatia region. The production of lignite was forced during World War II, and afterwards was further developed to be the main energy resource of the former German Democratic Republic. The mining industry was accompanied by power plants and other industries. Large-scale mining involved the digging of pits at depths up to 120 m, which was possible only after the lowering of the groundwater. This resulted in the creation of a large-scale groundwater lowering funnel with an extent of 2100 km^2 and the removal of 9 km^3 of static groundwater (Pusch & Hoffmann 2000; Kaden et al. 2002). For the production of 1 ton of lignite, 8 tons of water had to be pumped out of the mining region. This resulted in an artifically increased discharge in the Spree for several decades until the political change 1990. Then the demand for lignite and electricity produced from it dramatically decreased with the shrinkage of east German industry. Abandoned mining pits refilled with groundwater with a pH of ~2.5 produced by sulphuric acid originating from mine remnants. The pits are refilled as much as possible with water from the Spree to increase the chemical buffering capacity in the new lakes. Water is abstracted at a large scale from the middle segment and redirected into the pits, that is the emerging Lusatian Lakeland. Hence, the discharge of the Spree has been transformed from an artificially enhanced discharge until 1990 to an artificially lowered discharge regime since the mid-1990s.

14.7.2. Geomorphology, Hydrology, and Biogeochemistry

14.7.2.1 Geomorphology

In its upper segment, the Spree flows through relatively steep upland valleys where it is impounded by numerous mill weirs still partially used for hydropower generation. Only short reaches are preserved that give an impression of the original features of an upland stream. After entering the lowlands, extended sections of the Spree have been trained or even shifted to adapt the river course to the needs of lignite mining. Historic maps show that branched river channels had developed in the section of Cottbus. The Spreewald wetland originally consisted of a huge forest of black alder in lowland forest peat up to 2.5 m thick. The bog area encompassed by the numerous river channels was frequently flooded and impeded agricultural use. This situation was profoundly changed by the creation of reservoirs and canals in the 20th century that prevented flooding.

In the lower river reaching from the Spreewald to Berlin, the river course originally formed large meanders. Aerial photographs of the Müggelspree floodplain revealed that the radii of abandoned meanders that are still visible varied between 50 and 250 m, indicating varying discharge conditions that might be linked with changes in climate or land use, for example with the clearcutting of forests in the medieval age. From meanders that were cut off in historical times, and from some historic records, it can be deduced that the natural river channel was much shallower than today. The lowest areas of the channel bottom incised by ~2.0 m into the floodplain. Fallen trees and macrophyte stands probably created a diverse flow pattern within the channel and created high hydraulic roughness (Hilt et al. 2008). Therefore, sediment transport probably was low. The lower Spree does not receive a sediment load from its upper catchment because of the disruptions by the Spreewald and riverine lakes. Floods carrying driftwood, or drifting ice in winter, probably favoured bank erosion and provided sources of sediment in the lower river. It is still a matter of speculation what proportion of the river bottom was covered originally by gravel entrained by bank erosion, and which would have provided valuable habitat for invertebrates and fish.

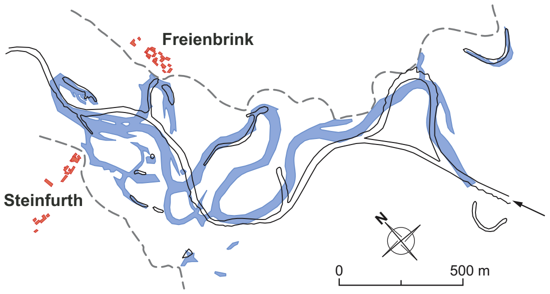

FIGURE 14.13 Course of the Spree River 10 km upstream of Berlin based on maps from 1779 (blue) and today (black lines), floodplain margins shown as dashed line (Historic map 'Brouillon Plan ', Staatsbibliothek Berlin).

To shorten the duration of annual flooding of floodplain meadows, meanders of the Spree have been cut since the late 18th century (Figure 14.13). In the 20th century, in the river downstream of Spreewald >40 meanders of the Spree were cut to increase the river's flow capacity, which shortened the river by ~20 km. The shortening of the channel resulted in significant incision of the riverbed, and a subsequent lowering of the floodplain aquifer by 1.0–1.5 m on the 'Krumme Spree' section. Channelization enabled more reliable use of floodplain areas for meadows, but the lowering of the groundwater table caused by the channelization made agricultural use of areas neighbouring the floodplain impossible (Andreae 1956). Today, a large portion of the riverbed is covered by shifting sands, which are only sparsely populated by benthic invertebrates. In summer, the river is dominated by masses of submergent aquatic macrophytes, which thrive because of high nutrient concentrations, the lack of floods that would potentially uproot them, and the lack of riparian trees in many places.

14.7.2.2 Hydrology

Based on the average amount of precipitation in the Spree catchment (678 mm, years 1951–1996), it is estimated that 87% of that amount may be lost through potential evapotranspiration. Hence, the relatively high proportion of

TABLE 14.3 Shift in the mean discharge of the River Spree at several gauging stations during the 1990s

Gauging station	Location	Discharge (m^3/s)		Specific runoff l/km/s 1997–2007
		1971–1997	1997–2007	
Bautzen	Upstream of mining region	2.6	2.5	9.5
Cottbus	Downstream of mining region	18.7	9.4	4.1
Beeskow	Lower catchment	25.8	13.2	2.4
Berlin-Sophienwerder	Near river mouth	36.4[a]	25.1	2.7

The shift was caused by a large reduction in groundwater production in the lignite mining region and concomitant start of water abstraction to fill abandoned mining pits.

[a] ***1981–1997.***

surface waters in the catchment does not reflect high water availability, but rather the long residence time of the surface waters. Due to the flat orography and unconsolidated bedrock in most of the catchment, the flow regime of the Spree is highly mitigated in comparison to other rivers of similar size in Central Europe (Kaden et al. 2002). Any quantitative hydrological analyses of the Spree are hampered by the fact that there are several sites of water abstraction, redirection and input in the catchment, which have changed over time and thus give inconsistent gauging records. The large-scale pumping of groundwaters from the Lusatian mining region has increased mean discharge at Cottbus by ~6 m^3/s.

With the sharp decrease in lignite production in the early 1990s, hydrological conditions in the lower Spree have profoundly changed because former inputs of groundwater to the river were replaced by water abstractions. While mean discharge of the upper Spree at Bautzen (Saxony) did not significantly change, the mean discharge at Cottbus (Brandenburg), which is directly downstream of the mining region, was reduced by half from 18.7 m^3/s (1971–1997) to 9.4 m^3/s (1997–2007) (Table 14.3). Due to low runoff in the lower catchment, the gauging station at Beeskow 100 km downstream showed a similar reduction in discharge. Even at its mouth to the Havel River in Berlin-Spandau, the mean discharge of the Spree decreased by 31% (Table 14.3).

The entire lower section, that is 250 km of river, has been affected by this shift from an artificially elevated discharge regime to an artificially lowered discharge regime. In some aspects, this large-scale flow reduction can be taken as a model case study on the effects of flow reduction expected for other rivers due to climate change. The ecological integrity of the river is especially affected by the concomitant decrease in minimum flows (Pusch & Hoffmann 2000; Pusch & Köhler 2002). During hot summers, the evapotranspiration rate of the Spreewald biosphere reserve causes a reduction in river discharge by up to 7 m^3/s in this area. This reduction results in flows approaching zero for several weeks in the downstream river reach called ‘Krumme Spree’ (Figure 14.14). Further downstream, evaporation of water in Lake Müggelsee and indirect abstraction of drinking water from river via bank filtration results in a similar situation in Berlin. As urban reaches of the Spree receive treated wastewater, even a reversal of flow direction may occur locally. The hydrological situation has been especially tense in the recent series of dry and hot years (2000, 2003, 2006).

14.7.2.3 Nutrients and Pollution

The Spree was historically polluted by urban sewage, by wastewater produced by the many small factories (cloth industry) in the upper catchment, and by the effluents from the mining industry along the middle river. For some time groundwater pumped from the lignite mining area was discharged directly into the river, which was heavily polluted by flocculating iron oxides that covered the riverbed with an inorganic mud layer. Additionally, the river was loaded by nutrients released from fish ponds and agriculture. Today, the discharge of poorly treated wastewater has been largely reduced, but locally still causes critical loadings in impounded headwaters. Following the political change in 1990, total inputs of total phosphorous and total nitrogen into the Spree were 68% and 46% lower, respectively, than in the 1980s (Behrendt 2002). Based on the river catchment model MONERIS, it is estimated that non-point pathways of nutrient input are still prevailing for phosphorous and nitrogen. Within the river, these nutrients are subject to sedimentation and intensive biological metabolism. Thus, around 50% of the phosphorous and nitrogen inputs are retained, with the actual

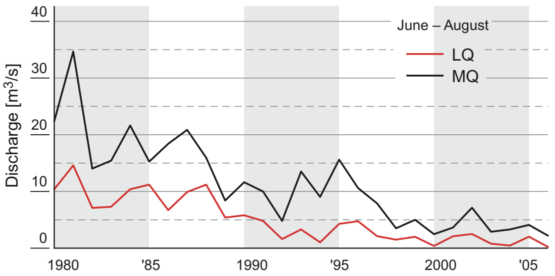

FIGURE 14.14 Long-term decrease of the Spree River discharge in summer due to gradual abandonment of lignite mining activities in the catchment, with recent minima in 2000, 2003 and 2006 additionally caused by extraordinary dry and hot years.

retention efficiency dependent on hydraulic properties, loads, and biological metabolic activities (Gücker & Pusch 2006). The present concentration of total phosphorous, averaging ~100 μg/L is still two- to threefold higher than estimated background concentrations (Gelbrecht et al. 2002), and allows intensive growth of aquatic plants.

During the period of artificially elevated discharge and highest nutrient loading, the Spree was a plankton-dominated river (Böhme 1994), but shifted around 1995 to a macrophyte-dominated river. The production of large amounts of autochthonous biomass due to eutrophication is regarded as a 'secondary pollution' of the river. This biomass fuels intensive metabolism of organic matter, which mainly takes place in the uppermost sediments (Fischer 2002; Fischer et al. 2002a, 2002b). Suspended particles are retained, depending on discharge, – at a rate of 9–33% per river kilometer (Wanner & Pusch 2001, 2002), and may be even higher in reaches with dense macrophyte stands. In the Krumme Spree section, a population of 5 million unionid mussels together with 120 million zebra mussels caused a significant improvement in water quality by removal of suspended algae and other particles from the water column (Pusch et al. 2001). However, the mussel populations have decreased by 93% since then, probably due to the reduction in flow.

With reduced flows, phytoplankton can grow better in riverine lakes and be retained more efficiently within the river channels downstream of the lakes. Enhanced retention of organic matter is followed by increased microbial degradation, which may produce severe deficiencies in dissolved oxygen (DO). Reduced flow velocity and DO availability can lead to the loss of sensitive lotic invertebrate and fish species. Hence, flow reduction due to water abstraction and climate change aggravates existing problems of water quality that arise from the secondary pollution produced by eutrophication (Pusch & Köhler 2002).

14.7.3. Aquatic and Riparian Biodiversity

14.7.3.1 Terrestrial Fauna

Although being subject to multiple pressures, the Spree and its floodplain still harbour many rare birds that depend on aquatic and semi-aquatic habitats such as kingfisher (*Alcedo atthis*), crane (*Grus grus*), bittern (*Botaurus stellaris*), black tern (*Chlidonias niger*), white stork, black stork (*Ciconia nigra*), osprey, marsh harrier (*Circus aeruginosus*) and corn crake (Beutler 2002). Besides breeding species, the Spree valley and its floodplains flooded in spring offer resting areas for migratory birds such as bean goose (*Anser fabalis*), white-fronted goose (*Anser albifrons*), whooper swan (*Cygnus cygnus*), goldeneye (*Bucephala clangula*) and goosander. The lower Spree, tributaries, and associated lakes harbour a stable population of otter (*Lutra lutra*). For otters, the river has special importance during cold winters when lakes entirely freeze and some spots remain open on the river. In the 1970s, American mink (*Mustela vison*) that escaped from fur farms colonized the Spree. The presence of this invasive species makes the potential reintroduction of the European mink (*Mustela lutreola*) difficult. Another invasive species, the bisam rat (*Ondatra zibethicus*), lives on the Spree, partially feeding on aquatic macrophytes and unionid mussels (Beutler 2002).

In the lower Spree, 12 species of amphibians and six species of reptiles have been recorded (Beutler 2002). Among them, a relict population of European pond turtle (*Emys orbicularis*) and scattered populations of firebellied toad are most noteworthy. The European pond turtle need sunny water bodies with dead wood present near the shores to allow them to warm themselves. A sunny sandy hillslope should be nearby where they can lay eggs. Adult turtles are long-lived, but are regrettably often killed in fish traps. The firebellied toad is a continental species that needs sunny floodplain areas that are flooded during May and June for the development of tadpoles. Due to the drainage of most floodplains, the firebellied (*Bombina bombina*) toad now rarely occurs in its original habitats, but does in man-made ponds and other types of waterbodies.

14.7.3.2 Aquatic Fauna

Originally, the upper Spree were classified as a trout and grayling zone, the middle and part of the lower river as barbel zone, and some of the lowermost sections as bream zone. Even after the recent improvement in water quality, the construction of numerous impoundments and other alterations in hydromorphology limits the restoration of the natural zonation of fish species today (Wolter et al. 2002). In addition, the numerous weirs prevent the longitudinal migration not only of former migratory species but also potamodromous species (Baade & Fredrich 2005). Today, the most abundant fishes in the Spree are roach, perch, silver bream, bleak, common bream, gudgeon, rudd, pike, European eel and ruffe. Six species of the river's original fishes are missing. Rheophilic fishes have declined substantially with the receding discharge, and recently represent only 4–21% of the fish assemblages in the middle and lower Spree (Wolter et al. 2002).

In the river and adjacent waterbodies, 440 species of benthic macroinvertebrates have been identified (including chironomids; Pusch et al. 2002). Due to sparse historic records, losses in this inventory can be estimated only for some groups. The invertebrate fauna clearly differs between the highland segment, the Spreewald section, the lower river, and the urban section in Berlin. Rheophilic species make up ~70% of the fauna in the upper river, 50% in the middle segment, and 20% in the lower river. Invertebrate assemblages are still affected by pollution in some headwaters. In most of the river sections, flow velocity, availability of stable bottom substrates and secondary pollution by eutrophication are the most important habitat factors (Brunke et al. 2001, 2002). In sections most severely affected by the reduction in flow, lotic fauna may be almost totally replaced by lentic fauna that tolerate reduced dissolved oxygen content.

In the Spree, the large populations of unionid mussels and zebra mussels can significantly improve water quality in the river by the removal of suspended particles, including planktonic algae, from the water column (Pusch et al. 2001). Filtration activity of some unionid mussels (especially *Unio tumidus, U. pictorum* and *A. anatina*) may be significantly hampered by the colonization of their shells by zebra mussels. However, zebra mussels and unionids seem to coexist in the Spree. Infestation of unionid shells by zebra mussel seems to be limited by the fact that unionids spend a major part of the year fully buried in sediments, which is not tolerated by zebra mussels (Schwalb & Pusch 2007). Despite the human alterations of the river, a number of rare invertebrate species have survived, especially in the Spreewald biosphere reserve, such as the thick-shelled river mussel, the European fingernail clam, the Asian dragonfly, and the green club-tailed dragonfly.

14.7.3.3 Aquatic Vegetation

The river, riverine lakes, and oxbow lakes are inhabited by 55 species of submerged or floating aquatic macrophytes (Körner & Pusch 2002). The middle and lower river have been dominated by macrophytes since the mid-1990s. Here, aquatic vegetation is dominated by arrowhead (*Saggitaria sagittifolia*), strapweed (*Sparganium emersum*), yellow water-lily, common water-crowfoot (*Ranunculus aquatilis*) and sago pondweed (*Potamogeton pectinatus*). Water chestnut (*Trapa natans*) and water soldier (*Stratiotes aloides*) are of special cultural and ecological interest (Körner 2002). Water chestnut reaches its northern limit in distribution here. Historically, water chestnut occurred in large populations on the river and its floating rosettes even hampered navigation on the river. The nuts produced by this plant were harvested by monks, and more recently also fed to pigs. Today, the riverine Lake Neuendorfer See again holds a significant population of water chestnut. The sword-like leaves of the water chestnut are half-submerged, half-emerged during summer, and its stands may be used for nesting by black tern. This plant also hosts the aquatic caterpillars of the butterfly *Paraponynx stratiotarum* and serves the southern hawker (*Aeshna viridis*) as exclusive substrate to lay its eggs (Körner 2002).

Phytoplankton development in the Spree is favoured by the fact that the river, including riverine lakes, exhibits a travel time of up to several weeks, which enables phytoplankton with a doubling time of one to several days to reach significant populations (Köhler 1994; Köhler et al. 2002b). The river is constantly inoculated by phytoplankton flushed from Spremberg reservoir, as well as by phytoplankton from riverine lakes. During periods of low flow, phytoplankton development may be reduced due to deposition of diatoms and grazing by zooplankton. During summer, filtration activity of mussels, shading by aquatic macrophytes, and retention by epiphytic biofilms lead to significant decreases in phytoplankton downstream of riverine lakes (Welker & Walz 1998).

14.7.4. Management and Conservation

14.7.4.1 Economic Importance

Since the 13th century, hydropower of the Spree and its tributaries was used by numerous water mills. In later centuries, the Spree gained major importance as a navigational waterway. With improved construction, the river channel was deepened and canals built to connect it to other navigational waterways. The annual flood period of floodplain meadows also was shortened during winter or spring. Due to low precipitation, there is substantially less water available for each inhabitant than for other Central European rivers (Figure 14.15). Each cubic meter of river water of the Spree is subject to multiple uses, all managed by the regional environmental agencies of Berlin and Brandenburg. Three major reservoirs have been built in the catchment, which serve to mitigate water shortages during summer, to control flooding (especially in Spreewald), to provide cooling water for lignite powerplants, and for recreation. The Bautzen reservoir holds 49 million m^3 of water. On the tributary Schwarzer Schöps, the Quitzdorf reservoir retains 25 million m^3 of water. The dam of the Spremberg reservoir is at the site where the Spree cuts into the glacial moraine called ‘Lausitzer Grenzwall’. The dam is 20 m high and retains a 7-km long lake holding 42 million m^3 of water (Driescher 2002). In numerous places within the catchment, tributaries have been impounded to create fishponds, for example in upper Lusatia or near Peitz/Cottbus where a pond of 7.2 km^2 is found (Driescher & Behrendt 2002). These fishponds need a certain net supply of water that is evaporated and also release water enriched with nutrients.

In the river crossing the Lusatian mining area, water is abstracted to refill mining pits, and a constant minimum discharge of 8 m^3/s is left for the river at Cottbus, except

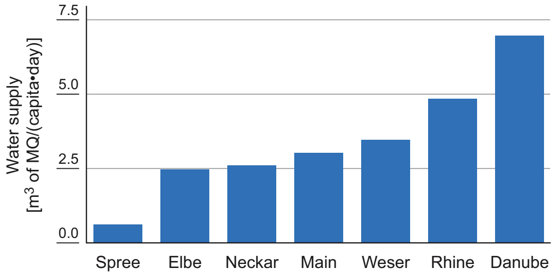

FIGURE 14.15 Potential water resources available for citizens living in various river catchments in Germany, expressed as mean river discharge per capita.

during major floods that cannot be fully redirected into mining pits. In the Spreewald biosphere reserve, boating on the river is a major tourist attraction and supports a major business. The luxuriant wetland forest within the Spreewald biosphere reserve has an evapotranspiration potential of 5–8 m^3/s, so that on hot summer days – together with water abstractions for agriculture – the minimum discharge of 8 m^3/s at Cottbus is reduced to 1 m^3/s or less downstream of Spreewald. Near the city of Fürstenwalde, a 19-km reach of the Spree is used as a part of the Oder-Spree navigational canal, where a significant part of the river discharge is abstracted even during drought periods to allow shipping on the canal. The Müggelspree, which is the section of the Spree directly upstream of Berlin, and lakes downstream are favourite sites for anglers and boating, including motorboats, sailing boats and kayaks.

Within the city of Berlin, the river is again used as a navigational waterway for cargo and tourist ships, which significantly affect littoral biota by the hydrodynamic effects of ship-induced waves (Gabel et al. 2008). The inland harbour of Berlin (Berlin–Westhafen) can be reached through canals from the Oder as well from the Elbe, Weser and Rhine systems, and thus links Berlin with ocean harbours, for example at Hamburg. Berlin gets two thirds of its drinking water supply from the Spree and Havel, which is produced from wells built along the shores, for example Lake Müggelsee via bank filtration. To assure the quality of drinking water, the removal of wastewater, and the use as cooling water, a minimum discharge of 8 m^3/s in the Spree at its inflow to Berlin is necessary (Rehfeld-Klein 2002). In recent years, this value has not been reached for several weeks or even months due to the flow reduction in the river. The urban reach of the Spree is used as cooling water for electric power generation, and it still receives some tertiary-treated wastewater with relatively low residual concentrations (Gücker et al. 2006) and stormwater runoff from the streets (Rehfeld-Klein 2002). Due to the design of the canals of Berlin, most treated wastewater enters the Havel River downstream of Berlin. It is envisioned to reopen the upstream part of the urban Spree for bathing after further progress in the retention of stormwater runoff.

14.7.4.2 Flood Control

Even though infiltration capacity of the sandy soils dominating the lowlands is high, the Spree can produce significant winter or spring floods from snowmelt or heavy rains. Large summer floods may also occur. Such flood risks in the catchment have been managed in multiple ways, such as by deepening river channels, building levees, construction of the Bautzen, Quitzdorf and Spremberg reservoirs, use of some lakes in the newly created Lusatian lake district for water retention, and by the construction of several canals that can serve as additional discharge routes (flood canals in the Spreewald, Dahme flood canal connecting the Spree to the Dahme River, and Oder-Spree canal).

14.7.4.3 Conservation and Restoration

The hydrological and ecological characteristics of the Spree are different than any other river in the region, a fact giving high priority to its conservation. Valuable habitats within the Spree floodplain and adjacent wetland areas, including areas linking these habitats, have been assigned legal conservation status. From the Spree highland valley upstream of the city of Bautzen down to Berlin, 40 nature reserves and Natura 2000 areas occur and are legally protected (Zimmermann et al. 2002). These protection zones mainly cover the river channel, adjacent oxbow lakes and ponds, lowland bogs, remnants of softwood and hardwood floodplain forests, reed areas, wet meadows with diverse vegetation, and dryland vegetation in dune areas. The preservation of aquatic and terrestrial biological diversity in these areas will largely depend on the future management of the river, especially flood dynamics, and minimum flow rates and water levels during drought periods. Hydrological dynamics not only provide aquatic habitat diversity, but also shape floodplain vegetation. For many reserves, stabilization of groundwater levels by closure of drainage ditches would be necessary to stop degradation of bogs, or to even re-initiate peat growth. In the Spreewald UNESCO biosphere reserve, as on many other reserves along the Spree, a special challenge is the protection of valuable habitats that were created by former agricultural practices, such as wet meadows that are extensively grazed or mowed only once a year.

Recent reductions in river discharge influenced the structure and function of the river ecosystem for a distance of 230 km in various ways (Pusch & Köhler 2002). Reduced flow velocity and DO availability has lead to the loss of sensitive lotic invertebrate and fish species from that reach. In free-flowing river reaches, lower discharge is paralleled by lower water levels, which are followed by lower groundwater levels in the floodplain up to a distance of several hundred meters. Water levels in the river also affect floodplain habitats. Management and restoration strategies must be developed to mitigate the ecological effects of flow reduction (Grünert et al. 2002; Pusch & Köhler 2002). The restoration approach is based on (i) an ecologically defined minimum flow level, supplemented by (ii) ‘ecological’ floods in the river to provide minimum discharge dynamics, and (iii) the restoration of a shallower river bed. The restoration of a shallower riverbed would counteract most of the problems produced by flow reduction that have been mentioned above. With a shallower riverbed, flow velocity would be higher even at low flows, and physical reaeration would be more efficient. In contrast, an alternative strategy that foresees the construction of more impoundments, as discussed for the Spreewald biosphere reserve, would only stabilize groundwater levels in the floodplain, but worsen problems concerning water and habitat quality.

14.7.5. Perspective

For many people in Berlin seeking recreation, for example by swimming or boating in the lower Spree, the river represents a piece of 'pure nature'. This impression has arisen by the green river margins with lush vegetation and clear water. Only with good knowledge of the system is it recognized that the lush stands of common reed and cat-tail root within rip–rap stones protecting the shores from erosion were rarely present before 1995 and do not represent a typical shoreline vegetation of a dynamic river. Similarly, mass development submerged macrophytes clearly indicates eutrophication and lack of shading by riparian trees. The large plant biomass may produce critical depletion of dissolved oxygen (DO) during the night. Anglers will notice that typical riverine fishes are lacking. A synopsis of the ecological situation of the river reveals the unexpected situation that even after significant efforts and success to improve its water quality after 1990 the ecological integrity of Spree system today is again at the brink. Due to flow reduction, there is a real risk that the river will lose basic riverine features such as a mixed water column providing DO to benthic assemblages, a typical riverine invertebrate fauna contributing to the 'self-purification' of the river, and a self-reproducing lotic fish fauna. It seems that the decrease in river discharge – in combination with significantly altered channel morphology – may produce as severe ecological effects as pollution did earlier. Hence, the Spree gives an impressive example of how the unsustainable exploitation of a resource – which in this case was the static groundwater resources in the Lausitz region – may hide existing socio-ecological problems but inevitably produces an unwelcome legacy for future generations. These then must find ways to reinstatel a self-regulating system that includes key features of hydrology, geochemistry and ecology.

14.8. DRAWA

The Drawa River in northwest Poland is one of the few lowland rivers in the ecoregion that still exhibits many natural features along major portions of the river. These include fluvial dynamics of the river channel, connectivity to many natural lakes, extensive surrounding forests that are not managed on the riverbanks, and a diverse aquatic fauna. As the river flows through scenic lake areas and steep moraine valleys, it is considered to be one of the most beautiful rivers in Poland. These features are protected and further developed by the Drawa National Park, which has the otter as its symbol. As there are no dams present between the lower Drawa and the Baltic Sea, the Drawa forms an important potential site for the reintroduction of endangered migratory fish such as salmon and sturgeon.

14.8.1. Physiography, Climate, and Land Use

The Drawa flows roughly southward through northwest Poland, draining a catchment area of 3289 km^2 (Kondracki 1994). It discharges into the Noteć River near the small city of Krzyż Wielkopolski, which runs west and enters the Warta River near Gorzów Wielkopolski, a large tributary to the Oder River. Along its course of 199 km, the Drawa flows through the Polish provinces (voivodhips) of West Pomerania, Wielkopolska and Lubuskie. The Drawa basin comprises 472 lakes with a total area of 156 km^2 (Pasławski 1981), many of them in glacial troughs. Of these lakes, 178 exceed a surface area of 10 ha each, 25 lakes 100 ha each (Jańczak 1996), and 390 are interconnected by streams and rivers.

The Drawa originates in Krzywe Lake (53°42′33″N, 16° 8′46″E) at 160 m asl in the Drawa lake district, a scenic landscape comprising 47 lakes >1 ha. Downstream of the source, the river is mostly bordered by agricultural areas, while the bottom of the small river valley is little used. The upper river until the small city of Drawno changes the direction of flow several times and thereby joins 18 lakes (Kaczanowska et al. 2004, Rzętała and Jaguś 2007), the largest ones being Lake Drawno (surface area 18 km^2, max. depth 80 m, second deepest lake in Poland) and Lake Lubie (14 km^2, 46 m) (Pasławski 1996). Additional numerous lakes are connected through tributaries. The lower river meanders through a deeply incised valley lacking fluvial lakes. This section is within the Drawa National Park and its adjacent buffer zone dominated by the Drawa forest (~800 km^2), while the valley bottom is often used as meadows. Here the river receives its major tributaries Korytnica and Płociczna (left side) and Mierzęcka Struga (right side) (Jańczak 1996).

The Drawa catchment was formed by glacial and periglacial processes in the Weichsel Glacial period. The highest altitude (223 m asl) is reached at its northernmost edge by the moraines of the Pomeranian stage. There, the Drawa rises in a small glacial valley, the so-called Valley of Five Lakes (near the road Połczyn-Zdrój-Czaplinek), and subsequently flows through various clear lakes. The Drawa then drains the western part of a vast outwash plain (sandur) that developed south of the moraine belt. This plain that gently slopes to the south is locally interrupted by loamy moraine deposits formed as post-lake hummocks (Rzętała and Jaguś 2007). Isolated ice masses produced numerous thaw hollows as well, which are now often filled by kettle lakes or peat bogs. Near postglacial channels, sediments filling cracks in the dead ice formed kames ridges (Wnuk-Gławdel et al. 2006). Hence, the catchment now exhibits a diverse orography, which is partially reflected in the diversity of lake types. Shallow lakes situated in the ground moraine and oval kettle lakes contrast with the deep ribbon lakes Drawsko, Lubie and Siecino that exhibit complex morphometry, long shore lines and many peninsulas and islands, for example Lake Drawsko with 74 km of shoreline and 14 islands.

Forced by some smaller morain belts, the Drawa first flows west, but then follows the general slope of the sandur to the south. Together with several other rivers neighbouring to the east, the Drawa is an exception in the central and east European lowlands where most river systems flow directly to the North and Baltic Seas. As the middle part of the Drawa's valley is accompanied to the west by a section of the Pomeranian stage moraines, the valley was probably pre-formed by postglacial meltwater. The valleys of the Drawa and Płociczna Rivers are incised in their lower courses by up to 30 m into the surrounding sandur. The glacial gullies formed parallel to them by glacial scour or outwash beneath the ice sheet are now partially filled with lakes, including the gullies of the Lakes Płociowe, Marta, Jamno and others. The lowermost section of the Drawa valley breaches through a local moraine belt bordering the Toruń-Eberswalde postglacial stream valley, where the Drawa then discharges into the Noteć River (Kondracki 1994)

The Drawa catchment lies in a transition zone between the sub-atlantic and sub-continental climate types, having relatively low annual temperature amplitudes and moderate drought periods, but late springs with ground frosts and long warm autumns. Average annual temperature is 7.9 °C. The warmest months are July and August with average temperatures of 17 °C, the coolest month is January at −2 °C. On average, there are 32 days with an average temperature below 0 °C, and five days of 30 °C or more (Wnuk-Gławdel et al. 2006). Annual precipitation is 592 mm, and there is rain on 172 days per year on average. The length of the growing season varies between 200 and 230 days from north to south (Koźmiński et al. 2001).

In 1237, the Drawa was mentioned for the first time in a deed of the Duke of Great Poland Vladislav Odonic under the name *Drava.* German settlers who subsequently moved in called it *Drage*. The linguistic sources of the name are traced back to Indo-European and early Slavonic sources meaning 'to be in a hurry', referring to the rushing flow of the river. From the late 14th century to 1772, the lower Drawa and its tributary Płociczna formed the borderline between the German Electorate of Brandenburg and the Kingdom of Poland, a situation that may have contributed to the preservation of the area. The Drawa also served as military defensive line, as German fortifications were built both in the 14th century and before World War II. Today the Drawa still forms the borderline between three voivodhips.

The wilderness along the Drawa was first colonized to a significant extent by Cistercian monks in the 14th century, who cut parts of the forest, drained marshes and built water mills. In the 16th century, a local squire founded a dozen small villages to populate the area, leading to a mosaic of fields, pastures and forest. Tar distilleries (e.g. at Dragetheerofen 10-km upstream of the river mouth) and glass smelting works (from the 17th century on) were run near the river (Wnuk-Gławdel et al. 2006). From the medieval ages until 1979, the Drawa served as a waterway for timber rafting (Wnuk-Gławdel et al. 2006). In 1662, its banks were stabilized, the riverbed was deepened in shallow reaches, and tree trunks were removed. From about 1850, timber rafting mostly supplied a sawmill operating on the lower Drawa (Drageschneidemühl). Today, remains of rollways used as river ports for preparing timber rafting can be seen on the banks (Rzętała and Jaguś 2007). In the 19th century, a system of irrigation canals was built to bring water to the meadows in the valley. Today, the river is used for hydropower and tourist purposes.

At the end of the 19th century, a long-term decrease in the population started and pasture land formerly used for sheep farming as well as fields on poor soils were abandoned. Today, the population density is relatively low, and farmlands are found only on patches of moraine clays (e. g. in the region of Drawno). As abandoned farmland was transformed into pine plantations, and because of historical forestry strategies, pine forests now cover extensive areas (Kujawa-Pawlaczyk and Pawlaczyk 1997). In the Drawa catchment, there are numerous small point sources and diffusive inputs of nutrients threatening water quality (Woźniak 2000). Despite new sewage treatment plants and existing ones being refurbished, inputs of domestic sewage still enter the river. Additionally, a pig farm near Drawno as well as crop fields situated adjacent to the river channel are still threats to water quality. Tourism may also impair water quality by camping in uncontrolled places, excessive development of tourist facilities, for example at Lake Lubie, or through disposing bait used for angling.

14.8.2. Geomorphology, Hydrology, and Biogeochemistry

Surface features are composed of Quaternary siliceous sandy deposits 140 to 180 m thick, which overlay Tertiary and older bedrock layers (Nowacki 1999). These porous sediments, which exhibit a filtration rate of 3×10^{-4}–1×10^{-4} m/s, contain a 10, −20 m thick usable uppermost water bearing horizon. This aquifer is usually well protected by covering layers some 10–50 m thick, which increase in thickness to the north and also comprise clay layers. Within the aquifer, there exist regional channel structures from north to south. Due to the high infiltration capacity of deposits and a high evapotranspiration rate, parts of the catchment lack surficial drainage systems.

The average slope of the river channel is 0.61, ranging between 0.79 in the uppermost section until Lake Lubie to 0.47 in the lowermost section downstream of the hydropower station Kamienna. Channel slope locally peaks for ~1 km at

2.67 within the gorge called ‘hell’ below Lake Lubie. In the upper catchment, the river network is rather irregular and joins the subcatchments of several lakes. In total, the river flows for 38.5 km within lakes. Hence, the slope of fluvial sections is somewhat higher than lentic sections, reaching 1.07 in the uppermost section (Pasławski 1996). In the southern part of the cachment, the drainage system is better developed with less flow through lakes and having two large tributaries, the Płociczna (catchment area 450 km^2) and the Mierzęcka Struga (585 km^2). The Drawa flows through 18 lakes with a total area of 42 km^2 and capacity of $>700 \times 10^6$ m^3.

The Drawa catchment supplies an area-specific runoff of 6–8 L/km^2/s (mean value for Poland is 5.5 L/km^2/s). Numerous springs can be found in the upper Płociczna and Korytnica Rivers (delivery 7–29 L/s), and numerous smaller ones in the area of Drawa National Park along the Płociczna and Drawa rivers that drain the first water bearing horizon (Nowacki 1999). Infiltration of water has been observed in the area of Lake Czarne and Lake Ostrowieckie. River discharge (mean, minimum and maximum annual flows 1961–2000) increases longitudinally from 0.46 (0.05–0.5) m^3/s at Stare Drawsko on Lake Drawsko to 4.2 (0.4–18.8) m^3/s in Drawsko Pomorskie near Lake Lubie, to 9.3 (2.6–9.3) m^3/s in Drawno, and to 21.5 m^3/s (8.0–46.0) at the gauging station Drawina near the mouth (Pasławski 1981; Nowacki 1997). The largest tributary, the Płociczna, has a discharge of $\sim$3 m^3/s at its mouth.

The annual flow regime is a rainy oceanic type, with maximum flow occurring in April and May, and minimum flow in July and August (Pasławski 1981; Nowacki 1997). The Drawa’s flow regime shows the least seasonal variation among all rivers in the Oder basin. This stable flow regime is due to the fact that the river is mainly fed by groundwater from numerous springs. Further, hydrological extremes are significantly mitigated by subsurface storage as well as by surficial storage within the numerous lakes connected to the fluvial system. Interannual variation in water levels at the gauging station Drawina also are quite moderate. Maximum, mean and minimum water levels vary between wet and dry years by 100, 49 and 38 cm, respectively (Pasławski 1996). Water levels in the Drawa may significantly increase (up to 120 cm upstream of Drawno) by the luxuriant growth of aquatic plants during summer, so that maximal water levels can be observed even at minimum flows during summer.

Despite its stable hydrology, the Drawa, and especially its tributaries Płociczna and Korytnica, exhibit significant fluvial morphodynamics that shape the valley slopes and the relief of the riverbeds. River bends frequently cut the erodible moraine slopes, producing sandy scarps or sheer walls of morainal clay (Photo 14.9). The riverbed alternates between shallow rapids and pools with depths from 1.5 to 2.5 m, and backwaters are frequently encountered. Sediments consist of stones, gravel, sand or organic mud (Woźniak 2000). Fallen trees, which are mostly not removed, play a special role in diversifying streambed

PHOTO 14.9 The Drawa seen from one of the steep erosional banks formed in the area of the National Park where the river broke through glacial moraines (Photo: M. Bylina).

morphology. The lowermost section between the confluence of the Prostynia to the Drawa's mouth shows special fluviomorphological diversity, with depth varying from 0.5 m in riffles to 2.5 m in pools at a channel width of 20–30 m (Nowacki 1997). Water temperatures are mitigated by the high proportion of subsurface runoff contributing to river flow. For the same reason, ice rarely forms on the Drawa. Maximal water temperatures in the Drawa are in July (22.6 °C in July 1952), and the lowest (0.2 °C) in December, January, and February. The highest changes in water temperatures within one month occur in May (11.0 °C), and the lowest in February (0.4 °C) (Pasławski 1981; Nowacki 1997).

In the second half of the 19th century, large-scale land reclamation efforts were started to drain meadows, irrigate dry areas, and build fishing ponds. Today, the remains of dry reservoirs, dikes, barrages and culverts can be seen, as well as canals several kilometers long such as the Kanał Siciński between lakes Sitno and Głusko. The Drawa was also influenced by the channelization of the Noteć River conducted in the years 1891–1896, when the river was shortened by 23.2 km. As a result, a considerable decrease in the water table and an enlargement of the Drawa catchment were observed. The drainage of wetlands first resulted in increased agricultural productivity for some years, which then fell again as a result of soil mineralisation, ground lowering by 0.4–0.8 m, and subsequent secondary swamping (Nowacki 1999).

Water quality in the Drawa was significantly affected by the input of domestic sewage from the villages along the Drawa, for example from the small cities of Złocieniec and Drawsko Pomorskie, which also caused pollution of cadmium and carbolic acids that affected the water quality of Lake Lubie. Downstream of Drawno, water quality was less affected. According to monitoring surveys conducted by the Chief Inspectorate for Environmental Protection in Szczecin, water quality has remarkably improved since the 1990s in terms of concentrations of bacteria and nitrate (Nowacki 2002). At present, many reaches of the Drawa are assigned to the first water class, although lake outflow reaches are significantly loaded by algae flushed from lakes. Below the small cities of Złocieniec, Drawsko Pomorskie and Drawno, the Drawa is still moderately loaded with bacteria as well as phosphorus and nitrogen, and effluent standards are partially not met. Just downstream of Drawno, water quality is threatened by a large pig farm where liquid manure is poured on fields in the immediate vicinity of the Drawa.

Water quality, which is also monitored by the Chief Inspectorate for Environmental Protection, is moderately impaired by eutrophication in lakes on the Drawa and its tributaries. The mesotrophic lakes in the area, which hold populations of the stoneworts *Chara aspera, Chara fragilis, Chara jubata, Chara rudis* and *Chara tomentosa*, are all groundwater-fed, including lakes Marta, Piaseczno, and Duże within the Drawa National Park (Nowacki 2002). Several lakes in the park are dystrophic. Lake Czarne, which is surrounded by forest, is meromictic. There are many lakes that are strongly eutrophic and develop phytoplankton blooms. The medium-sized lakes Mąkowarskie downstream of Kalisz Pomorski and Wąsosze near Złocieniec even have bad water quality (Nowacki 2002).

Monitoring of water quality in groundwaters conducted by the Polish Geological Institute at some scattered observation wells show that the first level of groundwaters contains not only significant concentrations of iron (0.5–3.5 mg/L) and manganese (0.1–3.6 mg/L), but also elevated concentrations of nitrates and nitrites. These waters directly supply water to rivers, lakes, swamps, and springs. Deeper groundwaters contain waters of the highest quality, as these are protected against pollution by thick clay layers, and thus are used for drinking water supply (Nowacki 2002).

14.8.3. Aquatic and Riparian Biodiversity

In the extensive protected areas in the Drawa catchment, rare species still occur that depend on habitats maintained by the dynamic natural processes that are limited outside protected areas, such as slumps and landslides on river banks or dead trees falling into the river channels that shape the river channel and enhances the diversity of aquatic habitats.

14.8.3.1 Flora

The Drawa valley exhibits a high diversity of plant communities. The area of the Drawa National Park has nearly 80 plant communities mentioned in the European Habitat Directive. These are, among others, rich beech and swamp alder forests, marsh meadows, parts of coniferous forests and marsh birch woods, wet and fresh meadows, fens, stonewort meadows in lakes, pond weeds of eutrophic lakes, spring vegetation, stands of great fen-sedge, and peat fens (Wnuk-Gławdel et al. 2006). The Drawa forest, which extends from Lake Lubie to the Noteć River, mainly consisted of beech, while today pine dominates and beech forests may be encountered in the valley of the Drawa and west. Fragmented remains of beech and oak-beech forests are now actively managed in the area of Drawa National Park, while some other parts are completely left to natural processes. The shores of lakes and rivers are accompanied by alder forests, which often grow on former meadows, and in some cases rare riparian elm forests (*Ficario-ulmetum minoris*).

One of the most precious natural features in the Drawa valley are peat bogs of several types, which – even if formerly used as meadows – still harbour their characteristic flora (Woźniak 2000) such as menyantes, cranberry, cottongrass species, white beak-sedge (*Rhynchospora alba*), sundew species, marsh violet, dwarf marsh violet (*Viola epipsila*), fen orchid (*Liparis loeselii*), lesser panicled sedge (*Carex diandra*), stands of great fen sedge (*Cladium mariscus*), acid bog springs with common sedge and sedges forming hummocks including fibrous tussock sedge (*Carex appropinquata*) and *Carex caespitosa*. The peat bog called 'Sicienko' on the southern edge of Sitno Lake is one of seven locations in Poland where the inconspicuous boreal shrub leather leaf (*Chamaedaphne calyculata*) grows, which marks its most south-western distribution point in Europe (Wnuk-Gławdel et al. 2006). The Drawa and its tributaries are often colonized by water buttercup species, arrowhead, burreed and pondweeds. In sections of the Drawa with stony bottoms and fast current, stones are frequently overgrown by the rare red alga *Hildebrandtia rivularis*, which indicates good water quality (Wnuk-Gławdel et al. 2006).

14.8.3.2 Fauna

Among the 40 species of mammals recorded in the park, many are related to aquatic or wet habitats. This holds especially true for the numerous beaver and otter, the European water shrew (*Neomys fodiens*), European polecats (*Mustela putorius*), and for elk (*Alces alces*) that sporadically walk through the park (Kujawa-Pawlaczyk 2004; Wnuk-Gławdel et al. 2006). The presence of 10 species of bats is remarkable, as well as a small population of wolves in the Drawa Lakeland that use the Drawa valley as a migration corridor to reach a neighbouring population in the Noteć Forest.

More than half of Polands avifauna can be observed in the Drawa valley. Some 150 species were recorded in the Drawa National Park only, with 120 of them nesting there (Kujawa-Pawlaczyk 2004). In the forests along the Płociczna, there are populations of Tengmalm's owl (*Aegolius funerus*), red-breasted flycatcher (*Ficedula parva*) and crane, and near Ostrowieckie Lake nests of eagle owls, white-tailed eagles and ospreys can be found. Near their preferred types of waterbodies green sandpiper (*Tringa ochropus*), kingfisher (*Alcedo atthis*), dipper (*Cinclus cinclus*), grey wagtail (*Motacilla cinerea*), mallard (*Anas platyrhynchos*), goosander, common goldeneye (*Bucephala clangula*) as well as great crested crebe (*Podiceps cristatus*) have stable populations (Wnuk-Gławdel et al. 2006). The Nature 2000 Protection Area established in the middle and lower Drawa constitutes one of the most important refuges for eagle owls (*Bubo bubo*) and some other birds of prey, and is used as a wintering area by whooper swans (up to 150 individuals) and as resting habitat in autumn for migrating cranes.

The herpetofauna of the Drawa National Park includes 20 species, 13 species of amphibians and seven species of reptiles, which are most of the species found in Poland. The most remarkable species found are great crested newt, smooth snake and the very rare European pond turtle (Wnuk-Gławdel et al. 2006).

The ichthyofauna is the most precious natural element harboured by the Drawa basin. In the Drawa and tributaries, 41 fish species from 11 families (incl. *Cyclostoma*) are found, which is among the richest fish fauna in Poland (Wnuk-Gławdel et al. 2006). In the Drawa River alone, 27 fish species were recorded, and 28 in the Płociczna. Moreover, the Drawa is one of the few rivers in the country that harbours all three biological forms of trout, such as brown trout (*S. trutta m. fario* in rivers and *S. trutta m. lacustris* in lakes) and sea trout (*S. trutta m. trutta*). Apart from extremely threatened species, such as river lamprey and brook lamprey, salmon and sea trout, there are numerous and relatively stable populations of species that are rare at the national scale, including brown trout, grayling, minnow and bullhead. Among the most interesting fish living in Ostrowieckie Lake (the largest lake of the park) are lake trout, vimba, common whitefish and vendace.

The Drawa was the natural spawning ground of one of the last native populations of salmon until it became extinct in the 1980s as a consequence of habitat loss due to flushing the reservoir at Kamienna, as well as by overharvesting and possibly by a viral disease (M75). Within the nation-wide migrating fishes regeneration programme, fry and smolts of this species are released into the lower Drawa and Płociczna every year. Their return to the places of spawning grounds is evident by spawning nests of adults that are annually catalogued by ichthyologists. Two years after the reintroduction had been started in the Drawa, the presence of 37 nests was observed. The numbers of nests have decreased since 2003 with only four nests observed in 2006. The decline is mainly attributed to intensive marine and coastal fisheries as well as to poaching in the Noteć and Drawa Rivers. In 2007, the reintroduction of Baltic sturgeon (*Acipenser oxyrinchus*) was started, which reproduced in the river until 1936. The first release was carried out with the cooperation between Inland Fisheries Institute in Olsztyn and the Institute of Freshwater Ecology and Inland Fisheries in Berlin (Gessner & Bartel 2000). The reintroduction of sturgeon into the Drawa is a long-term process requiring international cooperation, as the first returns of sturgeons from the Baltic Sea to the Drawa for spawning are expected not earlier than 10 years after release (Kolman et al. 2007).

Among invertebrates, 65 species of caddisflies (Trichoptera) have been described in Drawa National Park. One of the recorded subspecies *H. contubernalis borealis* is new for Poland, whereas three species *Crunoecia irrorata, Ceralea annulicornis* and *C. dissimilis* have been noted for the first time in the Pomeranian Lakeland. The most precious communities of caddisflies inhabit springs, rivers and dystrophic lakes (Wnuk-Gławdel et al. 2006). In the middle and lower course of the Drawa, a rich fauna of mayflies (Ephemeroptera) has been noted, for example this is the site where *Rhithrogena semicolorata* and *C. rivulorum* are found in the Polish lowlands. The presence of the sensitive *Baetis calcaratus* indicates good water quality (Agapow 1998). The dragonfly and damselfly (*Nehalennia speciosa*) (Odonata) fauna of the park comprise 47 species, the most valuable ones colonizing peat bogs and lakes with low trophic status such as the pygmy damselfly (*Nehalennia speciosa*), subarctic darner (*Aeshna subarctica elisabethae*) and Siberian winter damsel (*Sympecma paedisca*) (Wnuk-Gławdel et al. 2006).

Aquatic molluscs are represented in the National Park by 20 species of water snails and 19 bivalves. The fingernail clams *Sphaeriidae* are especially rich, represented by the pea mussels *Pisidium hibernicum* and *Pisidium moitessierianum* (Agapow 1998). Six native species of unionid mussels have been found, such as the swollen river mussel that dominates in rivers, but also endangered species like the thick-shelled river mussel, swan mussel and depressed river mussel.

14.8.4. Management and Conservation

14.8.4.1 Economic Importance

For many centuries, the Drawa has been an economically important transport route for timber. At present, it is only used for tourist purposes (canoeing) and for small-scale hydropower production. On its whole course, the Drawa is a well-known tourist attraction for kayaking and canoeing (Rzętała and Jaguś 2007), although mostly used only for weekend tourism. Any boating is forbidden in the National Park from 15th March to 30th June to protect nesting birds. Intensive kayaking tourism and the development of holiday resorts on the riverbanks are major threats to the river. Additionally, the excavation of sand and gravel from the Drawa channel (Woźniak 2000) and fish farming ponds may affect the integrity of the river ecosystem.

On the river there exist two hydropower stations at Borowo (downstream of Lake Lubie, built in 1917, storage height 9 m) and at Kamienna (just upstream of the confluence of the Drawa and Plocicna rivers, built in 1899, storage height 8 m), with an installed capacity of about 1 MW each. Both stations interrupt sediment transport and form serious migration barriers for fish and other water organisms. At the Kamienna station, the existing fish ladder does not work because the lower entrance is too far from the turbine outlet. Downstream migration is hampered, as a significant proportion of fish do not survive passage through the turbine of Kamienna (Bartel et al. 2002). A possible emergency flushing of the sediments accumulated upstream of the Kamienna stations forms a serious pending threat to the river. As the Drawa and its tributaries exhibit a rather stable discharge regime, there is little risk of flooding, so that no preventive activities are undertaken.

14.8.4.2 Conservation and Restoration

Major parts of the Drawa catchment are protected by the Drawa National Park, the Drawski Landscape Park, the European ecological network Natura 2000, or by other categories foreseen by the Polish Environmental Protection Act. A major goal of these conservation activities is to stop eutrophication processes in surface waters. Within the Drawa catchment, there exist 15 nature reserves covering an area of 5.5 km^2 that mainly protect wetlands and peat bogs harbouring stands of rare plants or nesting sites of birds. Additionally, eight protected landscape areas covering 2574 km^2 have been established to protect ecological corridors (Kaczanowska et al. 2004).

The Drawa National Park, which covers an area of 114 km^2 plus 356 km^2 of buffer zone, was created in 1990 as one of 23 national parks present in Poland today (Matczak et al. 2004; Wnuk-Gławdel et al. 2006). It is mainly dedicated to protect the pristine forest, wetland and freshwater habitats that remain along the valleys of the Drawa and Płociczna, and fulfils the requirements of IUCN II category. Among these habitats, 14 are included in the Annex I to Habitat Directive as 'biotopes of special importance of Europe' (Matczak et al. 2004). These habitats include meso-oligotrophic lakes with stonewort, natural eutrophic lakes with pondweed, dystrophic lakes, rivers with water buttercup, wet and fresh meadows, *Corynephorus* grasslands and heathlands, raised bogs**,** calcareous fens with great fen sedge and Davall's sedge, acidophilous beech forest (*Luzulo-Fagetum)*, rich beech forest (*Asperulo-Fagetum*), alluvial forests (*Alno-Padion*), and *Cratoneuron* petrifying springs. Among the 924 species of vascular plants recorded in the park (Pawlaczyk & Łukaszewski 1997), some of the greatest botanical peculiarities are water-dependent, such as leather leaf and fen orchid. The ichthyofauna constitutes another precious natural element, which includes 42 species of fish from 11 families and two species of jawless fish. Eight species are under strict protection.

The Drawski Landscape Park, which covers an area of 414 km^2 in the area of Lake Drawsko, was established in 1979 and is dedicated to protect the most valuable parts of the Drawa Lake District having the highest moraine hills of that region, geological peculiarities, cultural monuments, and 48 lakes partially surrounded by pine and beech forests (Kaczanowska et al. 2004). The precious flora of the park includes the rare aquatic and semi-aquatic plant species *Lobelia dortmanna*, *Isoetes lacustris*, *Litorella uniflora*, *Myriophyllum alterniflorum* and *Nuphar pumila.* It also harbours 140 species of breeding birds and rich vertebrate and invertebrate faunas, and the ichthyofauna is especially remarkable.

In the Drawa catchment, there are four protected areas within the European Ecological Network 'Natura 2000'. The 'Wilderness Forests upon Drawa' area (Lasy Puszczy nad Drawą, 1868 km^2) embraces a part of a large forest complex on the sandur plain in the middle and lower Drawa and is one of the most important habitats for birds in Poland. The 'Drawa Mainstem' area (Ostoja Drawska, 1407 km^2) comprises a part of the Drawa Lakeland with over 50 lakes offering habitats for least 23 bird species from the Annex I to the Birds Directive. The 'Lake Lubie and the Drawa Valley' area (Jezioro Lubie i Dolina Drawy, 132 km^2) comprises Lake Lubie as well as portions of the Drawa and Studzienica valleys with a variety of swamp forests and wetland areas, including scattered Sphagnum mires and dystrophic lakes. Lake Lubie harbours *Mysis relicta* and *Pallasea quadrispinosa*, two crustacean species that represent rare post-glacial relicts. The 'Drawa Forest Ranges area (Uroczyska Puszczy Drawskiej, 658 km^2) covers a partially nearly pristine forest complex accompanying the near-natural river courses of the middle and lower Drawa and Płociczna.

14.9. SYNOPSIS

Most catchments in the Central Highlands and Plains were remodelled by the Weichselian glaciation, which covered Scandinavia and a major part of the Central European lowlands bordering the Baltic Sea. It ended 17 000 years before present in the area of Berlin and around 10 000 years before present in central Sweden. Biological colonization that followed the re-warming took several thousands of years, so that, for example beech arrived in the described region clearly after humans. Further, the salt content of the Baltic Sea remained unstable until 4000 years before present. At that time, man already populated the area and influenced inland waters and coasts increasingly, as these were preferred sites for settlement. There, migratory fishes were a source of valuable food that appeared regularly and was relatively easy to catch. In the medieval age, riverine systems were significantly altered by deforestation, contruction of mills and fishing weirs, heavy fishing pressure especially on migratory fishes, and by partial extinction of large mammals foraging in floodplains such as wisent and aurochs. Large-scale deforestation led to massive changes in hydrology, nutrient budgets, particulate transport, and charactristic riverine and riparian habitats. In major regions of east Germany, deforestation peaked in the 13th century, which resulted in the formation of a clay layer of 1.5 m height on average (max. 4.0 m) and which still covers the floodplain along the lower Elbe.

In the modern era, cities started to massively pollute the rivers flowing through them, and straightening of river channels increasingly became technically feasible. The latter resulted in the drainage of vast wetlands and the channelization of most streams and smaller rivers in the lowlands. With the introduction of industrialised farming methods in the 20th century, it became a deeply imbedded view in society from farmers to policy makers that the major service that streams and rivers should provide was to transport water and wastewater to the sea as efficiently as possible. Streams and rivers also became heavily polluted by the discharge of urban wastewaters, with the regional situation depending on population density and the mode of industrial development. A collation of historic data shows that the Oder and Danube rivers were never as heavily polluted as the Rhine or Elbe (Figure 14.16).

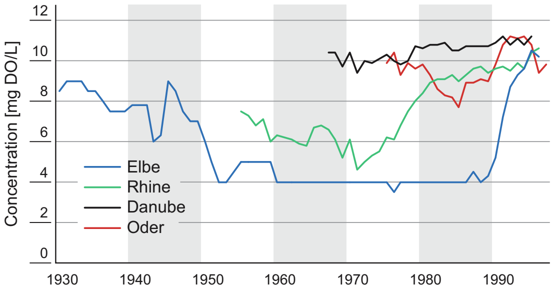

FIGURE 14.16 Historic course of dissolved oxygen concentrations in major rivers of central Europe (Graph: F. Schöll, BfG).

Preservation efforts were mostly restricted to the construction of wastewater treatment plants to avoid massive impairment in water quality, which would have also jeopardised drinking water supply in some places. Only since the last quarter of the 20th century have further ecosystem services and protection aspects become more considered in the management of streams and rivers, including the retention of floods, the preservation of active flood plains, the provision of habitats and migration routes for fish, and the metabolic functions of rivers leading to their 'self-purification'. In many catchments, the problems of pollution with heavy metals, organic micropollutants, or eutrophication from diffuse agricultural inputs are still unresolved or even considered. Moreover, the importance of Central European rivers for aquatic biodiversity is often not seen, especially concerning large rivers that contain rare ecosystems, but underlie various uses and modifications. As the large rivers in Central Europe are all connected by shipping canals, these form avenues for invasive species that are able to cope with the disturbed habitat conditions (Figure 14.17). The example of the restoration project on the Skjern River is to date the largest of its kind in Europe was initiated because it was seen that the economic gain of the reclaimed land was small compared to the loss of ecological integrity and nature values. Many of the negative impacts are now being reversed, although it is still unknown if the restoration succeeded in the

FIGURE 14.17 Spread of the invasive crustacean *Dikerogammarus villosus* in Germany, which especially benefited from the opening of the navigational canal between the Danube and Main rivers in 1992 (Schöll 2007).

long-term stabilization of endangered populations or if lost species will recolonise the catchment from other refuges.

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http://www.ikse-mkol.org – International Commission for the Protection of the Elbe River (ICPER).

www.pla.cz – Povodí Labe, Czech Elbe Catchment Authority.

http://www.arge-elbe.de/ – Working Committee Elbe, with monitoring data on the Elbe segment in Germany.

http://www.mkoo.pl/index.php – International Commission on the Protection of the Oder against Pollution (ICPOaP).

http://www.eman.se – Emåförbundet (Em river committee).

http://swamp.osu.edu/Academics/PDFs/EcoE07.pdf – Description of the Skjern River restoration project.

http://www.berlin.de/sen/umwelt/wasser/ogewaesser/index.shtml – Monitoring data of the Spree in Berlin.

http://www.dpn.pl/ – Drawa National Park.

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USE OF MESOHABITAT-SPECIFIC RELATIONSHIPS BETWEEN FLOW VELOCITY AND RIVER DISCHARGE TO ASSESS INVERTEBRATE MINIMUM FLOW REQUIREMENTS

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ABSTRACT

The benthic macroinvertebrate community in the sixth order lowland River Spree (Germany) was investigated in order to assess ecological effects of a flow reduction. The benthic habitat was composed of visually distinguishable mesohabitats. Eight mesohabitats were delineated, *Dreissena*-bank, unionid mussel bed, rip-rap, coarse woody debris (CWD), alder roots, stable sand, shifting sand and mud. The mesohabitats differed in their physical structure and hydraulic nature. These functional habitats were partly inhabited by distinct invertebrate assemblages. The use of mesohabitat-specific relationships between flow velocity and discharge seemed the most appropriate approach in order to assess the impact of flow reduction on lotic fauna. In combination with the species-specific optima and tolerances for flow velocity, this approach can be used to develop a minimum flow level that mitigates the effects of flow reduction and enables the persistence of rheophilic invertebrates in their specific mesohabitat. Copyright © 2001 John Wiley & Sons, Ltd.

KEY WORDS: flow abstraction; lowland river; macroinvertebrates; mesohabitat; minimum flow assessment

INTRODUCTION

Owing to the increasing use of river systems by man (Dynesius and Nilsson, 1994), motivations for water abstractions in fluvial systems are manifold. Thus, alterations of the discharge regime display several temporal patterns of reduced flow on hourly and daily to multi-annual scale (e.g. Bretschko and Moog, 1990; Gore, 1994; Petts and Maddock, 1994). Human influences on hydrology encompass aspects of water volume, i.e. frequency of floods, duration of low, mean and high flows, and water level, i.e. frequency and duration of inundation or dewatering (Petts and Amoros, 1996). The response of aquatic invertebrate communities to water abstractions appears to be difficult to predict, in general, owing to regional ecological controls (Castella *et al.*, 1995).

In northeastern Germany, the River Spree has been affected by an altered flow regime owing to open-cast lignite mining since the middle of the 20th century. This type of mining requires the removal of ground water to prevent its exfiltration into pits; the ground water was pumped away and transported via canals into the River Spree. Thereby, a ground water deficit of 12 km^3 was produced, which markedly altered the regional water regime. Since 1989, mining has been reduced substantially. Now the river water is used to fill the huge abandoned pits, which have a depth of up to 70 m. Water balance calculations indicate that the water abstraction from the River Spree would last for about 3 decades. During that time, the River Spree will receive a reduced flow, which is markedly below its natural flow, and far below the artificially increased flow of the past decades.

In order to mitigate the impacts of the newly altered flow regime on aquatic biota, a minimum flow level has to be assessed. The diversity of the river bottom owing to visually distinct meso-scale habitats prevented us finding a representative reach which is necessary for physical habitat simulation. Therefore,

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we focused on instream habitat structures and invertebrate assemblages (Harper *et al.*, 1995; Armitage and Cannan, 1998). The specific objectives were then (1) to test whether invertebrate assemblages collected from meso-scale habitats were distinct and, therefore, if the various types of mesohabitats were of significance for the invertebrate community, and (2) to identify rheophilic invertebrate assemblages in this lowland river. Based on that information, we intended to determine a minimum acceptable flow level for species that depend on high flow velocities (rheophilic species), because this group is most likely to be affected by flow reduction.

MATERIALS AND METHODS

Study site

The River Spree is a 6th order lowland river in northeastern Germany. It originates at 390 m above sea level (asl) in the Lusatian Mountains (Figure 1). The river flows through several lakes on its 380 km long course to Berlin. The study section, the so-called 'Krumme Spree', is 21.1 km long, and connects two lakes, the Neuendorfer See (upstream) and the Schwielochsee (downstream). Five sampling sites were chosen within this section, which has a mean width of 25 m, a mean depth of 1.53 m and a mean slope of 0.01%.

The mean discharge at gauging station Luebben was 22.4 m^3/s (pre-mining times from 1921 to 1958), whereas during the peak years of mining (1981–1990), mean discharge was 31.5 m^3/s. In 1997, mean discharge was already reduced to 12.2 m^3/s.

Sampling

We distinguished eight types of mesohabitats, *Dreissena*-bank, unionid mussel bed, rip-rap, alder roots, coarse woody debris (CWD), shifting sand, stable sand and mud. The mussel habitats were distinct parts of the river bottom, and formed a specific habitat for other invertebrates because of their rugged structure

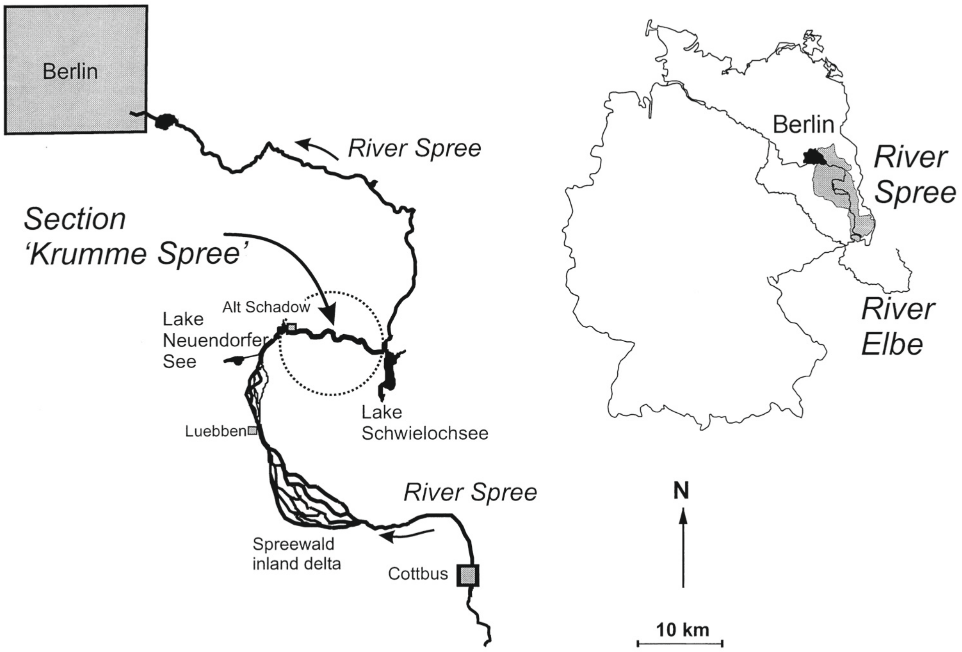

Figure 1. Map of the River Spree showing its catchment and the location of the study section

and the excretions of fine organic matter by the mussels (Silver Botts *et al*., 1996). *Dreissena*-banks consisted of extensive stable areas formed by dense aggregations of zebra mussels *(Dreissena polymorpha*) on most sandy solid sediment. Unionid beds stretched linearly along the flow direction and were inhabited by four species of unionid mussels (*Anodonta anatina*, *Unio tumidus*, *U. pictorum* and *Pseudanodonta complanata*).

The invertebrates within the mesohabitats were sampled by using a box sampler (0.09 m^2, 0.5 mm mesh size) on seven dates between April 1997 and August 1999. On each date, samples were taken from five cross-sections for replicate sampling of mesohabitat types. Because of the bottom heterogeneity, not all types of mesohabitats were present on each cross-section; on average, three types of mesohabitats were investigated on each site and date. Thus, 103 mesohabitat-level samples were collected, which were based on 307 replicate samples in total. For sampling, a scuba diver placed the box sampler on the river bottom and the area delineated by the box was disturbed by hand down to 5–10 cm sediment depth, depending on substratum grain-size. In areas either dominated by small grain-sizes and/or mussels, the uppermost 5 cm of the substrate layer were entirely transferred into the net. Larger stones and larger woody debris were carefully scrubbed off in the net under water. In the laboratory, macroinvertebrates were removed from the samples and preserved in 70% ethyl alcohol for later analysis. Invertebrates were identified to species level, except for Tanypodinae and Orthocladiinae (both Chironomidae, Diptera) and Oligochaeta.

The following environmental variables were measured in association with each box sample: nearbed flow velocity (3 cm above substratum) (MiniAir2, Schildknecht Co., Switzerland), water depth and dominant sediment grain-size in mm. The amount of loosely deposited detritus was assessed on a categorical scale (four levels). The discharge was measured continuously at the gauging station *Alt Schadow*. The downstream distance of the sampling sites from the gauging station ranged between 0.9 and 13.5 km. No significant tributary enters the River Spree between the sites. To assess the potential role of evaporation and exchange with ground water, we conducted additional discharge measurements at each sampling site, but could not detect significant differences.

Data analyses

Kruskal–Wallis tests were conducted to test for differences of taxa richness and abundances between seasons. Invertebrate taxa were classified with regard to their flow preferences into seven categories, according to Colling and Schmedtje (1996). Correspondence analysis was performed on faunal presence/absence data using ADE 4 (Thioulouse *et al*., 1997). Three different statistical methods, according to Jongman *et al*. (1995), were used to assess the response of rheophilic species to flow velocity: (1) weighted average (WA), (2) logistic regression, and (3) log-linear regression. The WA disregards absences, and so the value indicates the flow velocity at which most individuals could be found at the sites. Logistic regression models were used to test the effect of flow velocity on the presence of rheophilic species. Log-linear regressions were used to model flow velocity optima and tolerances of rheophilic species based on quantitative data according to Jongman *et al*. (1995). Species abundance data were log-transformed for log-linear regression models.

Polynomial regressions were calculated for a description of relationships between flow velocity and discharge in the mesohabitats. The discharge values that correspond to the species-specific preferences of flow velocity were calculated by using log-linear regression functions.

RESULTS

Invertebrate assemblages of mesohabitats

A total of 103 taxa was recorded, while 43 taxa were only found in less than 4% of the samples. Most taxa were collected from unionid bed (56), rip-rap (53) and CWD (52) mesohabitats. Intermediate amounts of taxa were found in *Dreissena*-bank (46) and alder roots (45). Total taxa richness was lowest in the fine sediment habitats: stable sand (37), mud (27), and shifting sand (25). Taxa richness and abundances in mesohabitats did not differ between the seasons (Table I).

Table I. Results of Kruskal–Wallis tests (p-values) on the effect of season on variations in taxa richness and invertebrate abundances for each mesohabitat, as well as standard deviations (S.D.) of site scores for correspondence analysis factors 1 and 2 for each mesohabitat

Mesohabitats	Taxa richness	Abundance	F1 (S.D.)	F2 (S.D.)
Dreissena-bank	0.16	0.10	2.81	1.1
Unionid bed	0.27	0.25	3.18	1.0
Rip-rap	0.53	0.31	1.59	1.34
Roots	0.23	0.15	0.76	2.56
CWD	0.18	0.26	1.36	2.1
Shifting sand	0.73	0.33	0.74	0.32
Stable sand	0.75	0.16	1.38	1.04
Mud	0.51	0.26	2.56	0.92

The factorial map of the correspondence analysis (CA) revealed three groups of mesohabitats based on faunal composition (Figure 2). Mesohabitats characterized by woody substrate were at the opposite ends of the axis, compared with mussel beds and rip-rap along factor 1. Mesohabitats characterized by fine substrate were displayed along factor 2 and, therefore, did not correlate in their faunal composition to the former. Alder roots and CWD were clearly separated from other mesohabitats. Rip-rap was relatively closely located to mussel fields, but there was only a small overlap between the scores of these mesohabitats. *Dreissena*-bank and unionid bed could not be separated by their faunistic composition. Some scores of the unionid bed showed an overlap with fine substrate mesohabitats. Stable and shifting sand had a similar faunal composition. Mud was separated from the former along factor 2.

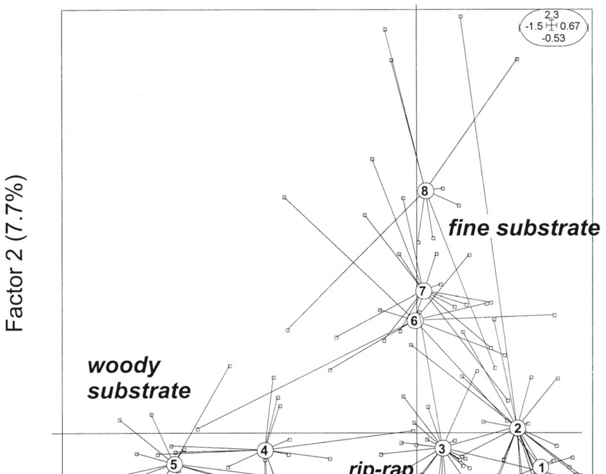

Figure 2. Ordination diagram (factor 1 × factor 2) of a correspondence analysis of invertebrates. The factorial scores of the samples from each mesohabitat were grouped, and the centre of each group is depicted. 1 = *Dreissena*-bank, 2 = unionid bed, 3 = rip-rap, 4 = CWD, 5 = alder roots, 6 = stable sand, 7 = shifting sand, 8 = mud. Percentages in parentheses are the amount of variation explained by factors 1 and 2

Intra-mesohabitat variation based on taxonomic composition was highest for the mussel beds and mud along Correspondence Analysis (CA) factor 1 and for alder roots and woody substrate along factor 2. The lowest intra-mesohabitat variability was recorded for shifting sand. Stable sand and rip-rap showed an intermediate variability.

Most rheophilic taxa and highest rheophilic abundances were found in the *Dreissena*-bank and alder roots, but the variability was high. Fewest rheophilic taxa and individuals were found in fine substrate mesohabitats (Figure 3). The most frequent rheophilic and rheo-limnophilic species were the caddis flies *Neureclipsis bimaculata* (32%) and *Hydropsyche contubernalis* (25.2%), and the mussels *Dreissena polymorpha* (63.9%) and *Unio tumidus* (37.8%). *Neureclipsis bimaculata* was found in high densities in the mussel beds and CWD. *Hydropsyche contubernalis* occurred in highest densities in the *Dreissena*-bank and in lower densities in the unionid bed, rip-rap and CWD. The two mussel species inhabited other mesohabitats in only minor proportions (Figure 4).

Relationships between discharge and flow velocity

The relationships between discharge and flow velocities differed between mesohabitat types (Figure 5). The increase of flow velocity with discharge was steepest for shifting sand at a discharge range between 11 and 14 m^3/s. In contrast, in the *Dreissena*-bank, flow velocity altered markedly within a very low discharge range (6–9 m^3/s). The relationships between flow velocity and discharge for unionid bed and CWD were similar to that of the shifting sand, but slopes were flatter. For rip-rap and all mesohabitats pooled, these relationships appeared to be weak, and in trend to be linear.

Optima and tolerances

The logistic regression models of presence/absence of these species versus flow velocity were highly significant ($p < 0.0001$). *Neureclipsis bimaculata* and *Hydropsyche contubernalis* occurred in highest densities in mussel beds and CWD. The WA of flow velocity derived from field measurements and the modelled optima and tolerances for flow velocity of these species are summarized in Table II. The two mussel species have markedly lower optima and ranges of the confidence limits for flow velocity than the two caddis fly species. The ranges are about three times higher for the mussels compared with the caddis flies. The inferred WA and optima and tolerances for discharge in the River Spree of these species are summarized in Table III.

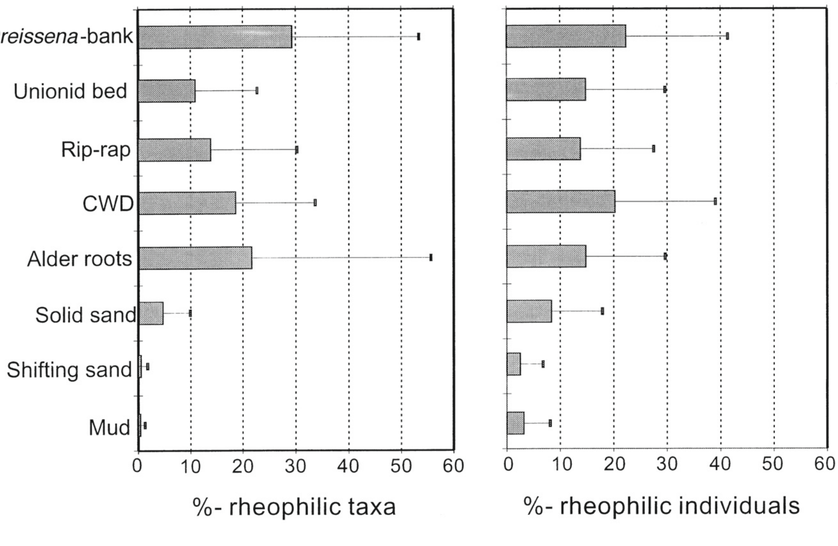

Figure 3. Percentages of rheophilic species in taxa richness and abundances in the various mesohabitats (means and S.D.)

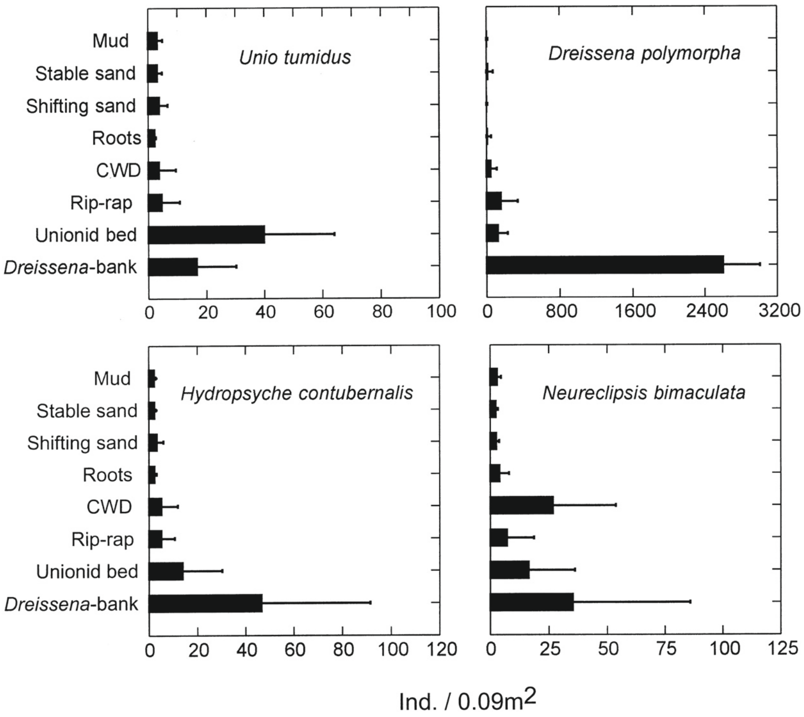

Figure 4. Mean abundances of *Unio tumidus*, *Dreissena polymorpha* (both Bivalvia), *Hydropsyche contubernalis*, and *Neureclipsis bimaculata* (both Trichoptera) for each mesohabitat. Error bars represent S.D.

DISCUSSION

The benthic habitat in the lowland River Spree was composed of various mesohabitats. These functional habitats in terms of biodiversity (*sensu* Harper *et al*., 1998) were colonized by distinct faunal assemblages (see also Armitage *et al*., 1995). As the fauna of different mesohabitats might be affected differentially from a reduction in flow, the effects of water abstractions on invertebrates have to be evaluated on the scale of mesohabitats. In parallel, Wood (1998) found in another lowland stream that average flow velocity differed between mesohabitats, and that these substrate-flow velocity gradients were of relevance for the distribution of specialized species, such as *Brachycentrus subnubilus* (Trichoptera). We have shown, for the River Spree, that the relationships between local flow velocity and discharge varied between mesohabitat types. Hence, the use of mesohabitat-specific relationships in conjunction with flow requirements of rheophilic species appeared to be necessary in order to assess an invertebrate-related minimum discharge level. The modelled minimum discharges for these rheophilic species would range between 6 and 9.4 m^3/s, when using values of lower tolerances (Table III). A minimum discharge of 7.8 m^3/s appeared to be necessary to protect adults of the endangered mussel *Unio tumidus*.

The caddis fly species prefer higher flow velocities than the mussels, and also have broader optima and wider tolerances. Higher flow velocities interfere with the active filtration of mussels (e.g. Ackerman 1999). However, the long life span, especially of unionid species, make mussels more susceptible to critical conditions created by extended low flow periods compared with insects with terrestrial life cycle stages.

The mesohabitat methodology integrates an array of environmental factors that act on local fauna, and allows an assessment of the effects of regulation at the reach scale (Armitage and Pardo, 1995). Based on the definition that mesohabitats are functional units, the spatial and structural delineation of ‘patches’ depends on the faunal group in mind (Pringle *et al*., 1988). Thus, the description of mesohabitats might differ: geomorphic descriptors have been used for fish, i.e. different types of pools, riffles and runs (e.g. Bisson *et al*., 1981; Frissell *et al*., 1986; Kershner *et al*., 1992; Vadas and Orth, 1997), whereas substrate

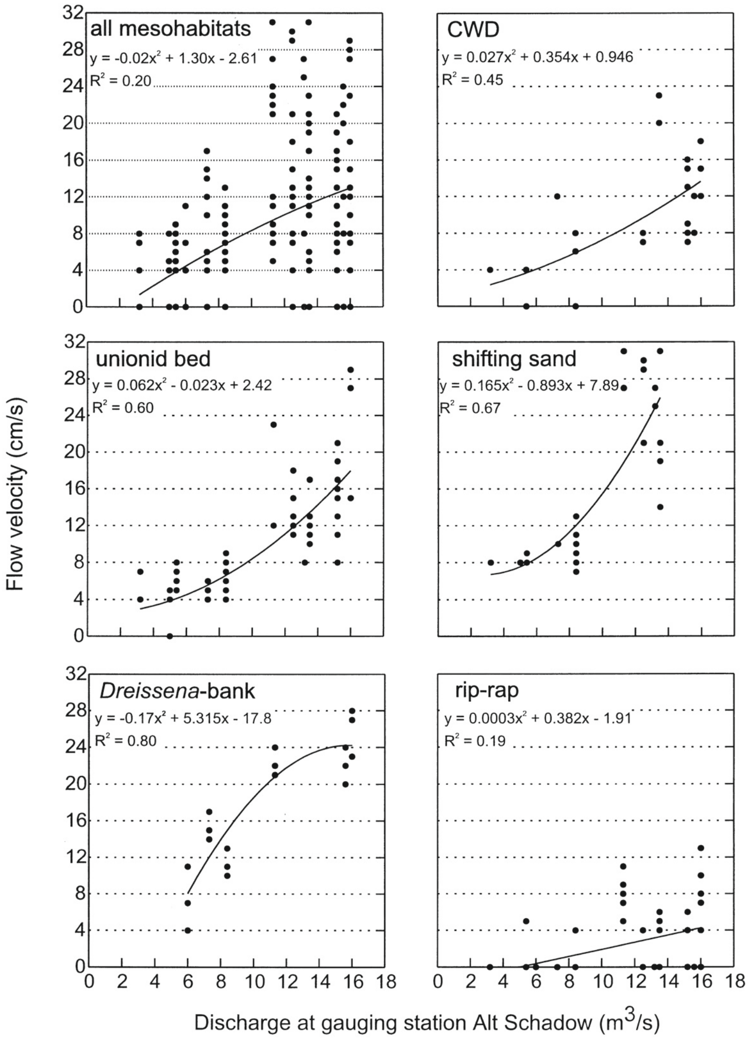

Figure 5. Relationships between flow velocity and discharge for *Dreissena*-bank, unionid zones, CWD, shifting sand, rip-rap, and all mesohabitats combined. Individual polynomial functions and coefficients of determination are displayed in plots left corner

Table II. WA as well as optima (with lower and upper 95% confidence interval), lower and upper tolerances of flow velocity (cm/s), calculated by log-linear regressions for four rheophilic or rheo-limnophilic species

Species	WA	Optimum	Confidence limits for optimum	Lower tolerance	Upper tolerance
Unio tumidus	10.2	16.9	14.0–19.0	6.0	27.8
Dreissena polymorpha	13.6	16.1	13.2–19.0	7.9	24.3
Hydropsyche contubernalis	14.2	23.3	15.2–31.5	8.3	38.3
Neureclipsis bimaculata	12.8	23.4	14.5–32.4	8.8	38.0

characteristics were commonly used for macroinvertebrates, i.e. various inorganic sediment types, submerged plants, woody debris, tree roots, mussel banks (e.g. Anderson and Day, 1986; Armitage *et al.*, 1995; Beisel *et al.*, 1998; Harper *et al.*, 1998). Important constraints for invertebrate distribution patterns are likely to include grain-size distributions, specific substrate properties, small-scale complexity, and hydraulic factors.

Table III. WA and optima (with lower and upper 95% confidence interval), and lower tolerance of mesohabitat-specific discharge (m^3/s) for four rheophilic or rheo-limnophilic species, calculated from relationships between flow velocity and discharge for mesohabitats (Figure 5) and flow preferences (from Table I)

Species	WA	Optimum	Confidence limits for optimum	Lower tolerance
Unio tumidus	11.3	15.3	13.7–16.4	7.8
Dreissena polymorpha	7.8	8.9	7.7–10.2	6.0
Hydropsyche contubernalis	13.6	19.7	14.4–24.7	8.9
Neureclipsis bimaculata	12.6	19.8	13.9–25.2	9.4

The mesohabitat approach and physical habitat simulation models rely on niche theory; the species response to a resource gradient is considered to be a bell-shaped curve. However, there are inherent difficulties in inferring response curves under field conditions; for discussions on the validity of species response shapes and preference curves see Austin (1999) and Morin *et al.* (1986), respectively. A difference of the mesohabitat approach, compared with the physical habitat simulation approach, is that it is not based on selected reaches, which have to be representative for the whole impacted river section. The selection of reaches representative of an extended river section poses many difficulties (Minshall, 1988; Kershner *et al.*, 1992; Armitage and Cannan, 1998). In contrast, the mesohabitat approach circumvents this difficulty, as it focuses on smaller units that are of functional relevance for riverine invertebrate communities.

However, any modelling and prediction of instream habitat requirements are incomplete when critical time periods or essential localities during the life cycle of the target species are not recognized, as has been demonstrated for brown trout by Mäki-Petäys *et al.* (1999). For example, we do not know anything about the requirements of juvenile unionid mussels that live for 2–3 years within the sediment. These young stages are likely to be endangered by excessive sedimentation and oxygen depletion in the sediment (Buddensiek *et al.*, 1993; Brim Box and Mossa, 1999). We assume that the use of the mesohabitat methodology, in general, reduces the risk of overlooking critical factors, as the functional approach integrates various factors. In addition to derivations of an organism-related minimum discharge levels a flow regime has to be developed that preserves mesohabitat diversity as has been discussed for other rivers (Cogerino *et al.*, 1995; Fruget *et al.*, 1996; Humphries *et al.*, 1996). In the case of the River Spree, mesohabitat diversity might be endangered by continuous flows, which lead to siltation, especially of mussel mesohabitats. Thus, flushing flows that remove fine sediment (Kondolf and Wilcock, 1996) are of further importance for the maintenance of the ecological integrity of this lowland river.

CONCLUSIONS

We emphasize the recognition of mesohabitats in lowland rivers as functional units instead of reaches, because mesohabitats were inhabited by characteristic assemblages. This is of practical relevance in the management of lowland rivers which are impacted by a regulated flow regime. For the development of an ecologically-based flow regime, several aspects have to be considered, such as minimum acceptable flows, flushing flows and floodplain-maintenance flows (Petts and Maddock, 1994). Minimum acceptable flows for rheophilic species can be derived by combining species-specific tolerances for flow velocity and mesohabitat-specific relationships between flow velocity and discharge. We recommend this approach in applied studies where it is not possible to select representative river reaches owing to a high instream between-habitat diversity based on biotic (e.g. macrophytes, large woody debris, roots, mussel beds) and abiotic (e.g. different inorganic sediments) structures.

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Conservation concept for a river ecosystem (River Spree, Germany) impacted by flow abstraction in a large post-mining area

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Abstract

In the Lusatia region of northeastern Germany, dewatering for mining activities has resulted in an 8-km^3 deficit in the groundwater balance. In order to refill aquifers and empty lignite pits, water will be abstracted for several decades from the River Spree which drains this region. This affects the ecological integrity of a 230 km river section including the floodplain in several aspects. Ecological consequences are shown for fishes, the aquatic invertebrate fauna, the retention of suspended matter, and oxygen concentrations. Therefore, an ecologically based minimum discharge has to be instituted. Current concepts on the assessment of minimum flow requirements in streams are reviewed. A multiple compartment method (MCM) for the assessment of flow requirements in extended river sections is suggested. Using the MCM, it can be shown that the minimum discharge that is required to preserve the river ecosystem is largely influenced by ambient channel morphology and nutrient concentration. This means that the ecological impacts of water abstraction could be abated by measures of morphological restoration of the river as well as of nutrient input restriction. Also, instream minimum flow requirements would be reduced, so that more river water could be abstracted, and the restoration of the water balance in the post-mining area in Lusatia accelerated.

Keywords: Opencast mining; River system; Minimum flow requirements; Habitat quality; Dissolved oxygen; Invertebrates

1. Introduction

As with most mining activities, opencast mining of lignite is performed after dewatering of the worked seams down to the pit floor. In water-permeable rock strata, this local dewatering entails the formation of a much larger funnel of the groundwater table in the surrounding landscape. Such large-scale perturbations of the natural hydrogeologic settings heavily impact the ecological integrity of the running waters draining mining areas, both during operation and after abandonment of the pit (Younger and Harbourne, 1995; Grzybkowska et al., 1996).

In the Lusatia region in northeastern Germany, which covers parts of the states of Brandenburg and Saxony, opencast lignite mining was initiated in the beginning of the 20th century. During the time of the German Democratic Republic (1949–1989), mining activities were intensive. Lignite seams were exploited down to 120 m below the original ground surface. In the year 1989, 195 × 10^6 metric tons of raw lignite

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were extracted in the Lusatia region. In this way, about 110 lignite pits were created in total. For each ton of lignite, 6.3 m^3 of water had to be raised, with 44% of that being taken from the static groundwater store (Möbs and Maul, 1994). As the lignite seams are imbedded into porous sandy deposits, groundwater extraction near the pits significantly affected groundwater levels in the surrounding landscape due to the funnel effect. In an area of 2500 km^2, groundwater was lowered 2 m and more (in 1990; Fig. 1). As a result, up to 1990, a hydrological deficit of 13 km^3 of water had been produced, which was made up by 9 km^3 of empty aquifer space, and of 4 km^3 within the huge empty mining pits (Möbs and Maul, 1994).

On account of groundwater pumping of up to 33 $m^3\,s^{-1}$ (in 1990) (Möbs and Maul, 1994), the discharge of the main river draining that region, the River Spree, increased significantly during the time of intensive mining, although most of the pumped water infiltrated into the dewatering funnel region again (Fig. 1). At the gauging station of Leibsch, which is

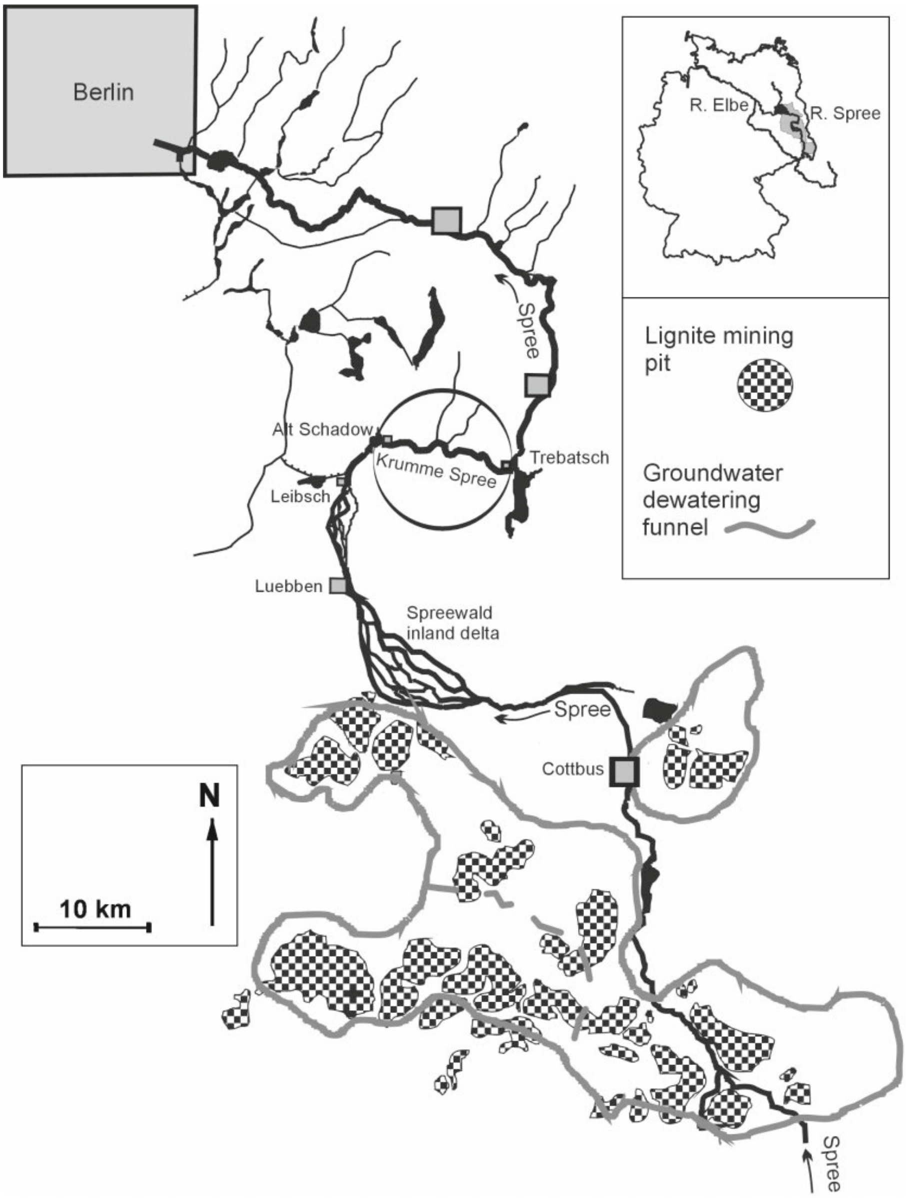

Fig. 1. Map of the lower catchment of River Spree (Germany) with mining pits and dewatering funnels in the Lusatia region.

situated downstream of the mining region, about 15 m^3 s^{-1} consisted of raised groundwater (Jahnke and Glos, 1991), which made up more than 50% of the river flow at low-stage conditions. As a consequence of the artificially elevated discharge of the River Spree, and of channel straightening, the river bottom has been incised by about 1 cm per year (Grünewald et al., 1994), which caused a drop in the adjacent minimum groundwater altitudes of >1.5 m in total (Andreae, 1956; PROWA, 1993).

Since the unification of the two German states in 1990, lignite mining has been substantially reduced, and many lignite pits have been closed. Groundwater extraction declined to a third of former rates up to 1995, so that groundwater altitudes in the Lusatia region are currently slowly returning (Fyson et al., 1998). However, the volume of the groundwater deficit in the River Spree catchment contrasts with the deficient natural water resources of that region. For comparison, annual groundwater recharge rate on that area is about 0.3 km^3 of water (H. Behrendt, personal communication). If an increase in evaporation rates during refilling is taken into considerations, the time period needed for refilling in this way is estimated at the least at three decades. The newly formed groundwater bodies and lakes tend to be highly acidic with a pH value down to 2.4 (Fyson et al., 1998). In order to increase the pace of refilling of the aquifers and abandoned lignite pits, and to counteract acidification, water from River Spree will be partially used for refilling (Luckner and Eichhorn, 1996).

As can be derived from hydrological balances, water has to be abstracted from River Spree over several decades in order to refill the groundwater funnel and pits. Thus, the discharge of the River Spree, which had been artificially elevated in the past, will not only be reduced to its natural level, but even substantially lowered in the future (Jahnke and Glos, 1991) (Fig. 2). The annual mean of discharge at the station of Leibsch probably will decrease from 33 m^3 s^{-1} (years 1981–1990) to a predictable 12 m^3 s^{-1} in 2000 (Hanuschka and Jakubik, 1997). About 230 km of a 6th order river will be affected by severe changes in the ecology of the river (Fig. 3). Vast areas will have to suffer a further drop in groundwater altitude of about half a meter (PROWA, 1993), which means strong effects on vegetation in sandy soils. The time period for flow abstraction will form an ecological bottleneck for the persistence of riverine biota and connected ecological functions, which can only be protected if the ecological integrity of the whole river ecosystem is preserved. As local water authorities have to decide very specifically on the allocation of river flow, ecologically based minimum-flow requirements have to be instituted (Pusch, 1997). The city of Berlin is particularly interested in a stable riverine

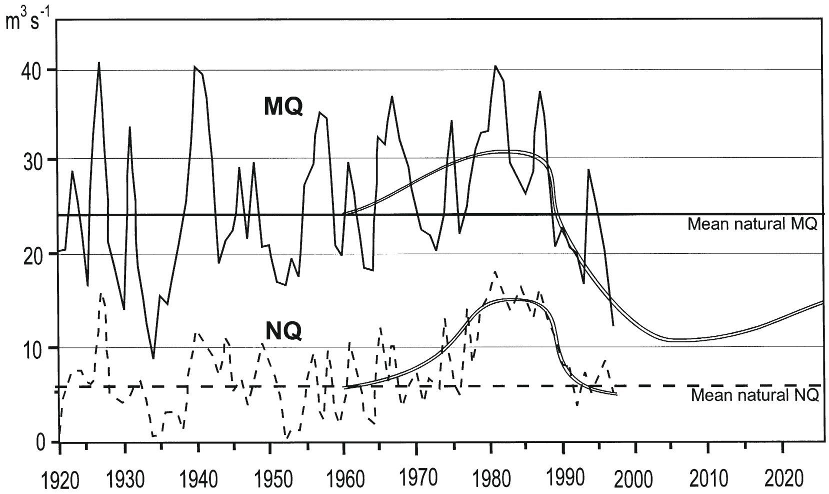

Fig. 2. Changes in the hydrological regime of River Spree at the gaging station of Luebben (Spreewald) due to mining activities (data by Landesumweltamt Brandenburg). The straight and the dotted lines show the course of mean (MQ) and the yearly minimum discharge (NQ), respectively. The average levels for MQ and NQ before they were affected by mining activities are given. Double lines show the trends since the hydrological regime is affected by mining (including current forecast for MQ).

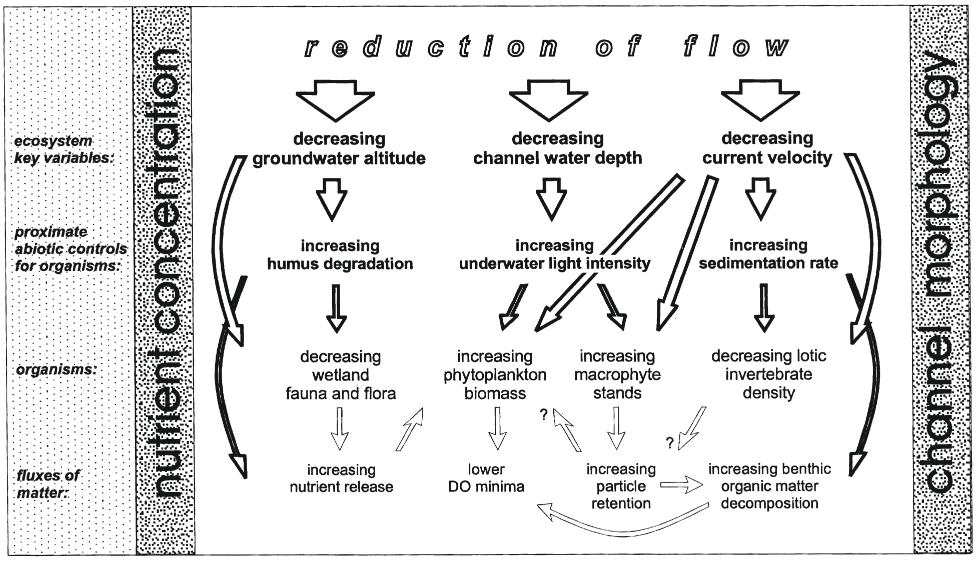

Fig. 3. Conceptual model of most important effects of flow reduction on a plankton-loaded river ecosystem including the floodplain. Effects are organized in four spheres of action with the predictions getting successively more insecure in lower spheres. All effects may be modified if framework conditions, such as channel morphology and nutrient concentrations, are altered.

discharge of water of a good quality, as it obtains most of its drinking water by bank filtration.

Concepts for assessment of specific flow requirements have been developed for hydroelectric power plants that abstract water from the main river channel in some section (e.g. Giesecke and Jorde, 1997; Jowett, 1997). However, most of them cannot be applied in this case for several reasons. Hence, we studied the specific ecological conditions in that lowland river, and developed a method suitable for that large-scale water abstraction.

2. Study site and methods

The River Spree is the main river draining the Lusatia mining region. Downstream of the mining region, it is a typical lowland river, with the bottom sediments mainly consisting of sand and organic detritus. Flow is highly mitigated by geomorphologic factors, and by the construction of several impoundments. Flow-velocity maxima range seasonally between 0.1 and 0.6 m s^{-1}. Concentrations of total phosphorus are typically about 100 g P l^{-1}. During spring and summer, the river is heavily loaded with planktonic algae (Köhler, 1994) which are partially retained and microbially decomposed during riverine transport. These processes cause significant daily amplitudes in dissolved oxygen (DO) (Böhme, 1994).

Field studies were conducted from 1994 to 1998 in a 22-km section of the river known as the ‘Krumme Spree’ (‘Bended Spree’), which connects Lake Neuendorfer See (13 56′E, 52 07′N) and Lake Schwielochsee (14 12′E, 52 06′N). Due to high rates of evapotranspiration in the upstream inland delta ‘Spreewald’, the ‘Krumme Spree’ river section is the one most affected by flow reduction (Pusch, 1997), which has been led to a significant decrease of flow in recent years (Fig. 4). Natural mean discharge of the river in pre-mining times was about 22 m^3 s^{-1} at the gaging station of Leibsch. Due to straightening works in 1906–1912, the river channel now is about 28 m wide and 2.3 m deep on average, with a gradient of 0.010% (PROWA, 1993). Former channel meanders remain as 37 oxbow lakes in the floodplain. At the beginning of this river section near the village of Alt Schadow, and at the end of the section near the village of Trebatsch, water samples and oxygen concentration recordings were taken biweekly between 8 and 12 a.m. Benthic invertebrates were sampled on four transects in April, August, and November 1997 using a modified Surber sampler. In each transect, between 8 and 12 samples were taken, covering a river bottom area of 0.1 m^2 each. Colonization density of unionid clams was also

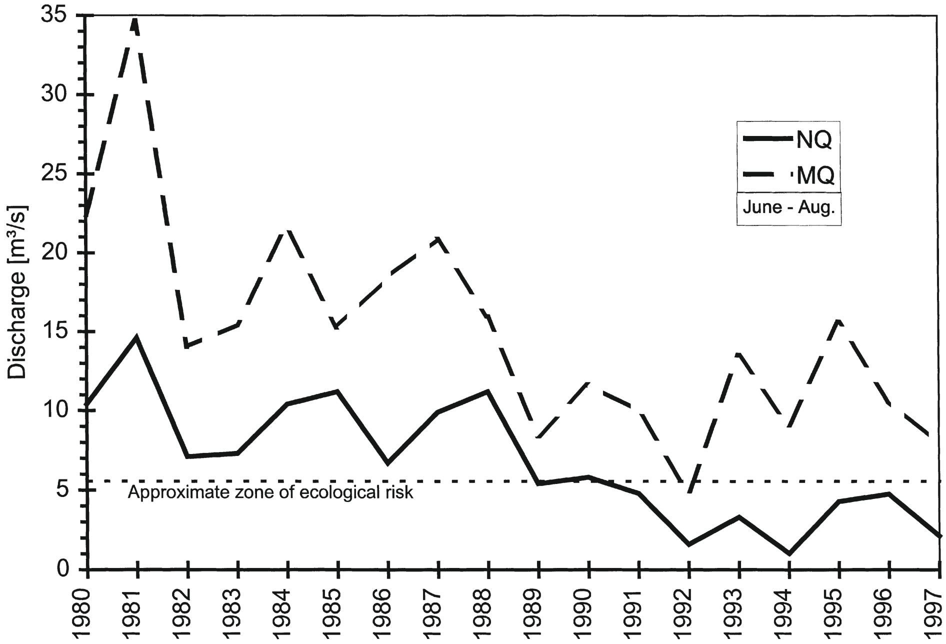

Fig. 4. Mean and minimum discharge of the River Spree during the high summer months (June–August) at the station Leibsch UP for the period 1980–1997. Data by Landesumweltamt Brandenburg.

counted using a gridded 1.0 m × 1.0 m metal frame. Juvenile fish were caught on five dates in summer 1998 in several parts of the ‘Krumme Spree’ by electric current fishing in order to obtain information on the autochthonous fish population.

3. Results

3.1. Fishes

In total, 345 juvenile fishes were caught and determined. Dominant species were roach (*Rutilus rutilus* (L.)) with a 40% share, bleak (*Alburnus alburnus* (L.) 19%), gudgeon (*Gobio gobio* (L.) 9%, rudd (*Scardinius erythrophtalmus* (L.) 8%, and perch (*Perca fluviatilis* (L.) 6%). Besides gudgeon, few individuals of some other lotic species, as chub (*Leuciscus cephalus* (L.)), orfe (*Leuciscus idus* (L.)) and spined loach (*Cobitis taenia* L.) were recorded. However, only 16% of total individuals could be attributed to lotic species.

3.2. Invertebrate fauna

In the study section, 78 species of invertebrates were recorded. Only 17 of them (=22%) are known to occur predominantly in lotic habitats (Moog, 1995). Numerically, the most abundant species was a non-indigenous amphipod, *Corophium curvispinum* Sars 1895, reaching over 120 000 individuals m^{-2} on suitable hard substrates (average colonization density: 1800 individuals m^{-2}). Densities of *Hydropsyche contubernalis* McLachlan 1865 (Hydropsychidae; Trichoptera), and *Neureclipsis bimaculata* (L. 1758) (Polycentropodidae; Trichoptera), two net-building caddisflies typical for lowland rivers, averaged 3.1 and 4.3 individuals m^{-2}, respectively. The highest densities (190 individuals m^{-2}) of *H. contubernalis* occurred in marginal areas dominated by rip-rap, peak densities (220 individuals m^{-2}) of *N. bimaculata* were found on woody debris.

Invertebrate biomass was dominated by the filter-feeding molluscs *Dreissena polymorpha* (Pallas 1791) (zebra mussel; Dreisseniidae; Bivalvia), *Unio tumidus* Retzius (in: Philipson 1788), *Unio pictorum* (L. 1758), *Anodonta anatina* (L. 1758) (all Unionidae; Bivalvia), and *Viviparus viviparus* (L. 1758) (Viviparidae; Gastropoda), and amounted to 40.2 g m^{-2} (dry mass of soft tissue) in total. Highest density of clams and mussels was recorded in the uppermost parts of the ‘Krumme Spree’. Colonization density in this stretch peaked at 180 individuals m^{-2} of unionid clams and 12 500 individuals m^{-2} of *Dreissena p.*

in the same area, which form a 'mussel bank' where the original river bottom is completely covered by the clams and mussels, including some empty shells.

Community filtration rate of this mussel bank can be estimated at about 70 l $m^{-2}\,h^{-1}$ in midsummer months (Kryger and Riisgård, 1988; authors' unpublished results). At a discharge value of 5 $m^3\,s^{-1}$ and a corresponding flow velocity of 0.12 $m\,s^{-1}$, it can be estimated that a stretch of 1 km of that clam and mussel bank would be able to filter about 15% of the water volume of the river.

3.3. Retention of suspended matter

The concentration of seston (suspended solids) remained nearly constant in April, and even increased substantially in May 1997 (Fig. 5). During the summer months, June–August, however, the seston concentration at Trebatsch averaged at only 53% of that recorded at Alt Schadow. This means that a load of particulate organic matter (POM) of 1.4 metric tons per day was retained in that river section. This figure is not corrected for phytoplankton growth on the way, which would raise the retention estimate substantially. This POM load decline equals an areal POM retention rate of 105 mg POM $m^{-2}\,h^{-1}$.

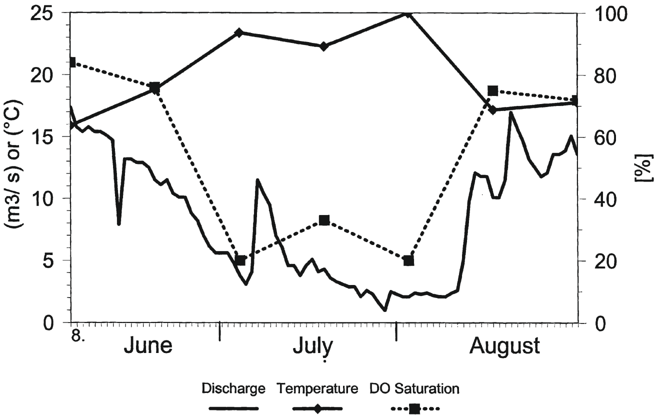

Fig. 6. Discharge, temperature and dissolved oxygen (DO) saturation in the River Spree at Trebatsch in the summer of 1994. Discharge data at the station Leibsch UP by Landesumweltamt Brandenburg.

3.4. Oxygen concentrations

Oxygen concentrations at the downstream end of the 'Krumme Spree' river section may drop to very low values during the summer months. In 1994, DO saturation fell as low as 20% (1.6 mg l^{-1} O_2) at least twice within one month (Fig. 6). Low DO concentrations were paralleled by very low discharge levels of <3 $m^3\,s^{-1}$, and a high water temperature of up to 25 C.

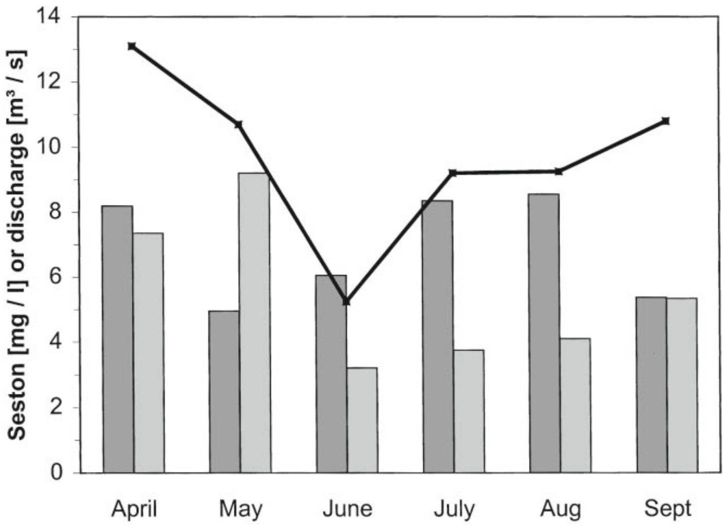

Fig. 5. Discharge (line) and concentrations of suspended solids in the River Spree at the stations Alt Schadow (dark columns) and Trebatsch (light columns) in 1997. Discharge data were collected daily by the Landesumweltamt Brandenburg, seston data biweekly by the authors' institution.

4. Discussion of field studies

The fish fauna in the 'Krumme Spree' section of Spree River is clearly impoverished, especially for lotic species. This is clearly evident when the results are compared to those from a nearby section of the R. Spree ('Kossenblatter Schlossspree'), which is a shallow side channel with a higher flow velocity. There, chub and orfe were more abundant, and other lotic species such as dace (*Leuciscus leuciscus* (L.)) and asp (*Aspius aspius* (L.)) were present (Walz et al., 1994). The barbel (*Barbus barbus* L.), a fish species that has long been typical for the Spree River, has been nearly extinct for several decades due to poor water quality, partially produced by the discharge of untreated lignite mining tailing water at that time.

The 'Krumme Spree' river section still possesses a riverine invertebrate fauna, including lotic invertebrate species typical for lowland rivers. However, in comparison to other river sections (unpublished results), the fauna is somewhat impoverished in terms of species richness and colonization density. The river is still inhabited by a high biomass of mussels and clams. These exert significant influence in the seston budget of the river. In addition to clam and mussel filtration, seston is retained by physical sedimentation. On the other hand, substantial primary production by planktonic algae occurs during passage through this river section. Therefore, we probably underestimated the rate of seston retention in this section.

A high retention of suspended matter in this section, however, is followed by the microbial decomposition of the organic components (Pusch et al., 1998). We suspect that this was the main reason for the heavy DO undersaturation in the downstream parts of the 'Krumme Spree' river section. This suspended matter is mainly generated through algal photosynthesis upstream, especially in Lake Neuendorfer See (unpublished results). Thus, the high nutrient concentrations in the Spree River, which are the basis of phytoplankton growth, aggravate the DO undersaturation that is created in the downstream parts of the river section at extremely low flow conditions. Physical re-aeration of river water through the water surface is impeded by the relative high depth of the river channel and low turbulence of flow due to the large cross-sectional area of the river channel. Before the river had been straightened, mean depth had been 0.5 to 0.7 m at low flow conditions, and 1.1 to 1.2 m at mean flow (Elbstromverwaltung, 1898).

It can be concluded that in the 'Krumme Spree' river section, there is a clear relationship between river discharge and possible deterioration of habitat quality during summer months. However, the ecological impacts of flow reduction could probably be significantly mitigated by the reduction of key nutrient (P) concentrations in the river water, or by improving natural re-aeration of river water (Grünewald et al., 1994; Fischer et al., 1996). The latter could be performed by creating a shallower river channel, which would restore the natural morphological setting that had existed before the historic incision of the river bottom. Such a raise of the river bottom would also produce a second positive ecological effect: During time periods of low flow, the water level could not drop as much in a shallower river channel. This would have a significant effect on the groundwater altitudes in the floodplain. Due to highly permeable sands that form the ground, and because of the flat topography in the surroundings, changes in river altitude may cause changes in vegetation and possible land use up to a distance of 4 km (Andreae, 1956).

5. Current concepts on the assessment of flow requirements in streams

5.1. General procedure

In the upland and mountain regions of Europe, there are several thousand hydropower plants where a high proportion of river flow is diverted from the main channel for some 100 m or kilometers in order to feed the turbines. The most important ecological effect of flow abstraction in these diverted river channel sections is the reduction of flow velocity, which restricts the bottom area that may serve as a habitat for lotic organisms, such as invertebrate or fish species. The second most important effect is the reduction of water depth, and the diminution of the total area of the aquatic habitat. Both effects cause a quantitative decline of biota, and a reduction in diversity (Giesecke and Jorde, 1997; Jowett, 1997). In particular, lotic species disappear, while ubiquitous species remain. In addition, flow reduction causes other ecological consequences, such as the warming of the waters in summer, the increased light penetration to the river bottom, which enhances algal growth, and the lowering of the groundwater altitude in the adjacent floodplain (Länderarbeitsgemeinschaft, 1995).

Conservational strategies aim to save the most important ecological functions despite flow reduction (Länderarbeitsgemeinschaft, 1995; Jowett, 1997; Richter et al., 1997). According to the Austrian guidelines ÖNORM M 6232 (1995), this ecological functioning ability is defined as "*the ability to maintain the interrelation network between the habitats in a water body and its riparian zones and its organismic colonization, according to the natural characteristics of the respective water body type* (*preservation of regulation, resilience and resistence*)." As a consequence, in a specific case it has to be assessed which ecologically important structures and functions are affected. Then, the threshold flow rate values have to be assessed, where important ecological functions cease as flow rates drop below them. As these threshold values usually differ for various ecological functions, all aspects, including the cost–benefit balance, have to be evaluated in a final step (Länderarbeitsgemeinschaft, 1995). However, such a complex optimization procedure cannot be performed for each case of stream flow divertion. Therefore, much simpler methods are currently used for the establishment of minimum flow rates.

5.2. Methods based on hydrological parameters

In that simple type of methods, characteristic hydrological values of the stream or river are taken in order to fix minimum flow rates. These values can be the mean or mean minimum discharge values, duration curves of flow, catchment area, channel depth or flow velocity. In most cases, this results in a minimum flow rate with no annual variation, but some approaches even include a certain variability depending on the natural flow dynamics (see e.g. Richter et al., 1997) (Table 1). However, as this method lacks any ecological basis (with the exception of flow velocity based procedures), the results obtained are questionable (DVWK, 1996).

5.3. Methods based on cost–benefit or efficiency analyses

In these methods, various aspects of environmental protection, and the multiple use of running waters are

Table 1
Comparison of current methods for the assessment of minimum flow requirements concerning the data bases needed, and their applicability for lowland rivers[a]

Features	Hydrological evaluation	Efficiency analysis	Optimization models			
			IFIM	CASIMIR	BfG	MCM
Hydrological characteristics	+	(+)	–	(+)	+	(+)
Channel morphology characteristics	–	(+)	+	(+)	–	+
In-stream ecological characteristics						
Hydraulic habitat	–	(+)	+	+	–	+
Physical habitat	–	(+)	+	(+)	–	+
Velocity preference curves	–		+	+	–	–
In-stream ecological processes						
Sedimentation	–	–	–	(+)	–	+
Ecosystem metabolism/water quality	–	(+)	–		–	+
Floodplain hydrology, flora and fauna	–	–	–	–	+	+
Applicability						
Running water type	H	H[b]	H	H[b]	H, L	H, L
Longitudinal range	Stream, river	Stream, river	Stream	Stream	Floodplain	River

[a] Symbols: – no consideration of the specific feature in the method; (+) partly consideration of the specific feature in the method; + feature is a key parameter in the method; (H) highland streams or rivers; and (L) lowland streams or rivers.

[b] Also partially applicable in lowland streams or rivers

evaluated, for example water quality, landscape ecology, recreational use, power generation. By use of a rating system, the varying effects of specific minimum flow rates on these aspects can be compared. This method, which is used for rivers in Bavaria, Germany (Schmid, 1997), has been criticized, as subjective judgments on the relative importance of the various aspects may largely influence the result (DVWK, 1996).

The following methods are optimization models that are based on ecological field data:

5.4. IFIM (instream flow incremental methodology)

The *I*nstream *F*low *I*ncremental *M*ethodology (IFIM, Bovee, 1982) is widely used in North America in order to predict changes in habitat structure at varying discharge levels caused by water abstraction. It comprises a number of computer models which aid in determining changes in the habitat availability for benthic macroinvertebrates and fishes. On the basis of field data on water depth, substratum type and current velocity, the changes in current velocity and habitat area in a specific stream section are simulated by the module PHABSIM (*P*hysical *Hab*itat *Sim*ulation). The suitability of specific combinations of physical habitat characteristics is evaluated by comparison with species-specific preferences, which are extracted from the literature. In a final step, hydraulic and habitat data are combined, so that the weighted usable area (WUA) for specific key species can be calculated.

5.5. Simulation model CASIMIR

The simulation model CASIMIR (*C*omputer *A*ided *Si*mulation *M*odel for *I*nstream Flow *R*equirements in diverted streams) (Jorde, 1997; Giesecke and Jorde, 1997) is based on field data on the temporal and spatial variability of bottom flow conditions. These are described by FST hemisphere measurements (Statzner and Müller, 1989). From these measurements, the distribution of near-bottom shear stress and its dependence on discharge level are estimated. In the next step, this areal hydaulic pattern is combined with the natural discharge regime and the standardized preferences of selected organisms. In similar fashion to the IFIM, estimates on changes in the population size of key species in the diverted stream are possible. In addition, the economic costs for the owner of a hydroelectric power plant can be simulated.

5.6. BfG floodplain model

The German Bundesanstalt für Gewässerkunde (BfG, Federal Hydrographic Agency) has developed a test model that may predict the ecological impact of long-term changes in the mean river altitude on the river's floodplain (Fuchs et al., 1995). The model is based on field data on the hydrogeology, soils, vegetation and faunistic colonization of that floodplain. Eventually, changes in the species composition of specific habitat types are simulated.

6. A new multiple compartment method (MCM) for the assessment of flow requirements in rivers

The methods for the assessment of minimum flow requirements reviewed above are not suitable in the case of the Spree River for several reasons (Table 1). A fundamental difference from most flow diversion channels is that here flow reduction extends to a much larger river section, so that none of the various ecological effects can be compensated in adjacent unimpacted river sections (cf. Ferrington, 1993; Grzybkowska et al., 1996). One consequence of this extraordinary flow abstraction problem is the large-scale lowering of the groundwater altitude in the alluvial floodplain of the river section that is affected by flow reduction (cf. Bornette et al., 1996). In all but one of the methods reviewed above, the impacts of flow reduction on floodplain ecology are not assessed.

A further fundamental difference is the fact that the Spree River is a typical lowland river. Therefore, invertebrate species which react sensitively to changes in current velocity contribute only a very small share to total riverine fauna. Therefore, any method focusing on this group is inadequate. Even if some sensitive species occur for which a velocity preference curve has been determined, it is questionable as to whether that information can be applied to the largely differing ecological context of lowland streams (e.g. DO concentration). New preference curves which are compatible to existent ones are hard to measure, as FST hemispheres (Statzner and Müller, 1989) are too insensitive for application in lowland streams.

In addition, flow reduction causes ecological consequences which are not considered in the methods reviewed above. In lowland rivers, current velocity and drag forces are often lower than in upland stream sections. Bottom sediments consist mainly of various types of sand or fine gravel. These may be transported even at relatively low flow conditions, so that they readily alter their distribution pattern on flow reduction. If current velocity is reduced, suspended particles tend to settle at the river bottom, which considerably alters habitat characteristics for benthic invertebrates. Due to the increase in the travel time of water with flow reduction, phytoplankton growth may lead to a significant concentration of suspended particulate organic matter. Photosynthesis of algae during the day and their respiration activity at night cause substantial daily fluctuation of DO concentration. Subsequent aerobic microbial degradation of organic matter may cause heavy DO undersaturation which may be catastrophic for both invertebrate and fishes. Therefore, additional criteria for the assessment of instream minimum flow requirements must be considered (Länderarbeitsgemeinschaft, 1995; Grünewald et al., 1994; Muhar, 1996).

We, therefore, suggest a *M*ultiple *C*ompartment *M*ethod (MCM) for the assessment of flow requirements in rivers. This conservation concept considers all the compartments of a river ecosystem which are substantially impacted by flow reduction in the floodplain and in the benthic and pelagic zones (Fig. 7). As a first step, field data are collected. In the floodplain, the spatial and temporal extension of the groundwater lowering as well as its consequences for the quality of water-dependent habitats (as wetlands or oxbow lakes) and target animal taxa (as amphibians or some large bird species) have to be assessed qualitatively. In the benthic zone, the distribution of most typical macroinvertebrate species is assessed, and co-occurring near-bottom current velocities and substratum types are determined. In addition, the areal extension of the most important colonization substratum types is estimated at various discharge levels, so that the effect of sedimentation of suspended solids on benthic habitat quality can be derived. In the pelagic zone, physical

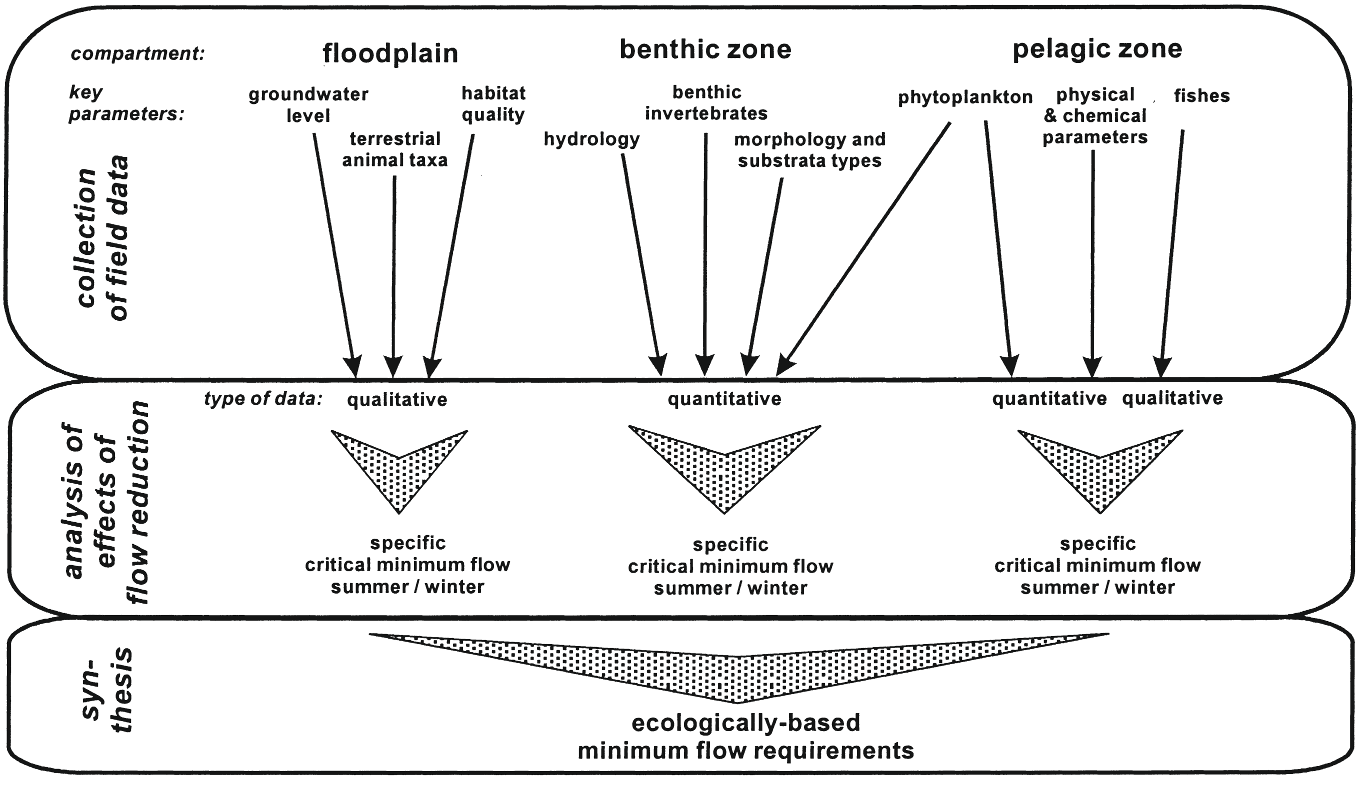

Fig. 7. Schematic representation of the assessment of minimum flow requirements using the multiple compartment method (MCM).

and chemical parameters are monitored at two stations at least, with a focus on DO concentrations during low flow periods. Longitudinal and seasonal dynamics of phytoplankton must be determined. Water quality parameters and phytoplankton dynamics give insight into riverine river community metabolism. Fishes have to be sampled, aiming to determine the presence of lotic species with specific habitat demands.

As a second step, the effects of flow reduction on these parameters are analyzed, which is done partly quantitatively and partly qualitatively. Changes in floodplain ecology may be predicted by comparison to other places with varying groundwater altitudes. The simulation of changes in macroinvertebrate habitat areas is performed based on species-specific information on preferences concerning current velocity, substratum, and DO concentration, which can be derived statistically from local field data. The changes in sedimentation rate with decreasing flow velocity may be simulated using the sedimentation and transport model PAMIR (*Pa*rticulate *M*atter *I*n *R*ivers, Prochnow et al., 1998). Changes in phytoplankton concentration may be predicted from changes in the travel time of the river. From this information, threshold values for river discharge can be derived at which the essential environmental conditions for the persistence of populations of typical riverine biota are fulfilled with high statistical certainty (cf. Länderarbeitsgemeinschaft, 1995). Thus, critical minimum flow levels for each season can be fixed based on data on floodplain, benthic, and pelagic ecology. In a synthesizing step, these have to be combined, so that minimum flow requirements for the whole ecosystem are produced.

7. Conclusion

River Spree has been impacted by the lignite mining activities in the catchment in two ways: First, by the artificial rise of river discharge due to the input of pumped groundwater, which resulted in the deterioration of water quality, and in the erosion of the river bottom. Second, after the closure of most lignite pits, river discharge is decreased artificially in order to refill the pits, which also results in a deterioration of water quality and aggravates the problem of groundwater lowering. The MCM shows that the threshold level of river discharge at which the ecological integrity of the river ecosystem is preserved largely depends upon riverine nutrient concentration and channel morphology, which are controlling ecological factors (Grünewald et al., 1994).

In this way, a strategy emerges that allows both the abatement of the ecological impacts of flow reduction and higher rate of water abstraction from the river (cf. Statzner and Sperling, 1993; Pusch et al., 1998): If nutrient concentrations could be lowered by reduction of point and non-point sources, and if a more natural, shallower channel morphology could be restored, instream minimum flow requirements would be significantly reduced. It is assumed that current velocity would increase due to a smaller cross-sectional area of the channel, that DO minima would be mitigated because of reduced phytoplankton biomass and a more intense physical re-aeration, and that groundwater altitudes in the floodplain would rise due to a higher water level in the river at low flow conditions. Thus, more river water could be taken to refill the deficit in the water balance in the post-mining area in Lusatia so that its hydrological restoration could be accelerated.

Acknowledgements

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4. Diskussion

4.1 Konnektivität als strukturierender Habitatfaktor des Makrozoobenthos in Fließgewässern und Seen

Diesem Kapitel zuzuordnende Publikationen:

1. *Garcia, X.-F., Schnauder, I.,* ***Pusch, M.T.*** (im Druck): How does the complex hydromorphology of river meanders contribute to benthic invertebrate diversity in rivers? *Hydrobiologia*
2. *Schwalb, A.,* ***Pusch, M.T***. (2007): Horizontal and vertical movements of unionid mussels (Bivalvia: Unionidae) in a lowland river. *Journal of the North American Benthological Society 26: 261–272*
3. *Brauns, M., Gücker, B., Wagner, C., Garcia, X.-F., Walz, N.,* ***Pusch, M.T.*** (2011): Human lakeshore development alters the structure and trophic basis of littoral food webs. *Journal of Applied Ecology 48: 916–925*
4. *Donohue I., Jackson A.L.,* ***Pusch M.T.****, Irvine K.* (2009): Nutrient enrichment homogenizes lake benthic assemblages at local and regional scales. *Ecology 90: 3470-3477*
5. *Gabel, F, Garcia, X.-F. , Brauns, M., Sukhodolov, A., Leszinski, M.,* ***Pusch, M.T.*** (2008): Resistance to ship-induced waves of benthic invertebrates in various littoral habitats. *Freshwater Biology 53, 1567–1578*
6. *Brauns, M., Garcia, X.F.,* ***Pusch, M.T.*** (2008): Potential effects of water level fluctuations on littoral invertebrates in lowland lakes. *Hydrobiologia 613: 5-12*
7. *Brauns, M., Garcia, X.-F., Walz, N.,* ***Pusch, M.T.*** (2007a): Effects of human shoreline development on littoral invertebrates in lowland lakes. *Journal of Applied Ecology, 44, 1138-1144*
8. *Brauns, M., Garcia, X.-F.,* ***Pusch, M.T.****, Walz, N.* (2007b): Eulittoral macroinvertebrate communities of lowland lakes: discrimination among trophic states. *Freshwater Biology 52: 1022-1032*

Die Lebensgemeinschaft der mit bloßem Auge sichtbaren wirbellosen Tiere der Gewässersohle (Makrozoobenthos) entstammt einem breiten Spektrum von Tiergruppen des zoologischen Systems, das von Schwämmen über Plattwürmer und Insekten bis hin zu Moostierchen reicht. Im Längsverlauf eines Fließgewässersystems unterliegen die Makrozoobenthosgemeinschaften einem mehr oder weniger kontinuierlichen Wandel. Dieser ist auf die Veränderung der verfügbaren Nahrungsressourcen zurückzuführen, wie bereits im River Continuum Concept betont (VANNOTE et al. 1980), sowie auch auf Veränderungen der hydrodynamischen Verhältnisse im Benthal (STATZNER et al. 1988) und der mittleren Sedimentkorndurchmessers während des Sedimenttransports. Ein ähnlicher, aber wesentlich kleinräumigerer Gradient der Zusammensetzung von Makrozoobenthosgemeinschaften erstreckt sich vom Litoral zum Profundal von Seen, der entsprechenden steilen Gradienten wichtiger abiotischer Faktoren folgt, wie Menge und Qualität der Nahrungsressourcen, räumliche Komplexität des Lebensraums, hydrodynamischer Stress und Lichteinfall.

4.1.1 Konnektivität als strukturierender Habitatfaktor des Makrozoobenthos in Fließgewässern

Die Zusammensetzung der Makrozoobenthosbesiedlung in einem bestimmten Teil eines Fließgewässers wird durch die abiotischen Habitatbedingungen sowie die Nahrungsverfügbarkeit bestimmt. Die lokal vorhandenen Habitatcharakteristika lassen sich über hierarchisch in einander geschachtelte hydromorphologische Einheiten definieren (FRISSELL et al., 1986, POOLE, 2002), die durch Interaltionen zwischen Morphologie und Hydraulik auf mehreren Betrachtungsebenen entstehen. Die dadurch entstehende Habitatheterogenität bestimmt wesentlich die Verteilung und Diversität des Makrozoobenthos (DAHL & GREENBERG 1996, LAMOUROUX et al. 2004, MERIGOUX & DOLEDEC 2004). Während die artspezifischen Fließgeschwindigkeits- und Substratpräferenzen empirisch bereits recht gut bekannt sind, gibt es kaum Kenntnisse darüber, durch welche hydromorphologischen Bedingungen die Diversität von Makrozoobenthosgemeinschaften bestimmt wird. Da die Diversität in Flussbiegungen erfahrungsgemäß besonders hoch ist, wurde in der Habilitationspublikation Nr. 1 (GARCIA, SCHNAUDER & PUSCH, im Druck) zusammengefasst, welche räumlich-zeitlichen Faktorenkombinationen nach dem bisherigen Kenntnisstand die hohe Diversität der Wirbellosen in Flusbiegungen ermöglichen.

In Flussbiegungen bestehen diskrete Beziehungen zwischen hydraulischen Prozessen und flussmorphologischen Elementen sowie deren Dynamik, die auf kleinem Raum eine besonders große Spanne von vielfältigen Kombinationen von Schlüsselfaktoren von Fließwasser-Habitaten erzeugen (HAWKINS et al. 1993). Das primäre Strömungsfeld wird in Flussbiegungen durch erhebliche Sekundärströmungen überlagert, so dass helikale Fließtrajektorien entstehen (THOMSON 1876) und komplexe Sortierungsvorgänge der transportierten Sedimentkorngrößen stattfinden. Das stark asymmetrische Strömungsfeld erzeugt an der Außenkante hohe Sohlschubspannungen und in der Folge erosive Mesohabitate, während die Habitate an der Innenkante durch anhaltende Sedimentation von Feinpartikeln gekennzeichnet sind (WANNER et al. 2002). Infolge der hoch turbulenten Strömung entstehen kurz stromab des Apex einer Flussbiegung Kolke, so dass eine typische bathymetrische Heterogenität entsteht, die auch ein entsprechendes Muster des Lichteinfalls, der benthischen Primärproduktion und der Ablagerung transportierten partikulären organischen Materials erzeugt, wodurch das Muster der Gewässerstruktur die räumliche Verfügbarkeit von autochthon versus allochthon produzieren Kohlenstoffressourcen prägt. Horizontale und vertikale räumliche Muster der sind beispielsweise für die Verteilung von Großmuscheln (Unionidae) bedeutsam, die feinkörnige Siedlungssubstrate bevorzugen (SCHWALB & PUSCH 2007)

Die dadurch definierten Habitateigenschaften werden in der Zeitachse durch unterschiedlich ausgeprägte Störungsdynamik weiter differenziert, da das bei Niedrig- und Mittelwasser vorherrschende Muster hoher und niedriger Strömungsgeschwindigkeiten sich bei Hochwasser umkehren kann, und während des Sommerhalbjahrs durch das Wachstum aquatischer Makrophyten auch das bei niedrigwasser vorherrschende Strömungsmuster massive verändert werden kann. Die starke Diversifizierung der Habitate im durch die Schlüsselfaktoren aufgespannten Raum ermöglicht die Ausbildung entsprechend segregierbarer Wirbellosengemeinschaften in diesen Mesohabitaten (PARDO & ARMITAGE 1997). Da die Habitatpräferenzen aquatischer Wirbelloser sowie von Jungfischen mit zunehmender Größe oft mehrfachen Veränderungen unterliegen (HILDREW et al. 2007), und helikale Strömungstrajektorien zwischen den mosaikartige angeordneten Meso- und Mikrohabitaten aktive oder passive Driftmigration zwischen diesen unterstützt, wird das Vorkommen von Arten mit komplexen Lebenszyklen begünstigt, die an die saisonalen und abflussdynamischen Bedingungen des Gewässers adaptiert sind. Die zu den größten Makrozoobenthostaxa gehörenden Großmuscheln (Unionidae) führen mithilfe ihres Fußes dabei auf der Gewässersohle sowohl horizontale als auch vertikale Wanderungen durch. für die es mehrere Erklärungsmöglichkeiten gibt, wie etwa als Reaktion auf Wasserstandsschwankungen, die aber kaum näher untersucht wurden. Die durch den Mosaikcharakter und die Strömungstrajektorien vermittelte räumliche Konnektivität trägt somit erheblich zur Ausbildung charakteristischer Makrozoobenthosgemeinschaften bei.

In der **Habilitationspublikation Nr. 1** (GARCIA, SCHNAUDER & **PUSCH**, im Druck) wird somit die Bedeutung von Flussbiegungen für die Diversität von lotischem Makrozoobenthos erklärt, indem – ausgehend von den durch die „Intermediate Disturbance Hypothesis (IDH) (CONNELL 1978) aufgestellten Vorhersagen – erstmals die konkret in Flussbiegungen anzutreffen den Zusammenhänge zwischen Gewässerstruktur, Dynamik und Diversität hinsichtlich ihrer Bedeutung für die Wirbellosen-Diversität analysiert werden.

In der **Habilitationspublikation Nr. 2** (SCHWALB & **PUSCH** 2007) wird erstmals die horizontale und vertikale Migration von mehreren Großmuschelarten in einem Flachlandfluss dokumentiert und mit saisonalen Veränderungen von Umweltfaktoren korreliert. Die Ergebnisse legen eine Verbindung mit dem Reproduktionsverhalten nahe, sowie auch mit dem kürzlich nachgewiesenen Ernährungsmodus von Großmuscheln mithilfe ihres Fußes (BRENDELBERGER & KLAUKE 2009). Außerdem konnte erstmals gezeigt werden, dass dieses Verhalten die Beeinträchtigung von Großmuscheln durch aufsitzende Zebramuscheln (*Dreissena polymorpha*) reduziert.

4.1.2 Konnektivität als strukturierender Habitatfaktor des Makrozoobenthos in Seen

Die Zusammensetzung der Makrozoobenthosbesiedlung im Litoral von Seen wird prinzipiell durch dieselben Faktoren bestimmt wie oben für Fließgewässer beschrieben, die dort allerdings in deutlich andersartiger Weise ausgeprägt sind. In uferparalleler Richtung sind litorale Habitate vielfach eher großräumig strukturiert, was u.a. auf die vereinheitlichende Funktion uferparalleler, windgetriebener Strömungen zurückgeführt werden kann.

Entlang des Tiefengradienten nimmt mit abnehmender hydraulischer Dynamik der Anteil von Feinsedimenten regelmäßig zu, und die dadurch bedingte Veränderung der Habitatbedingungen für Makrozoobenthos mit der Tiefe wird durch die Zonierung der aquatischen Makrophyten weiter verstärkt. Die Makrozoobenthosbesiedlung des Eulitorals wird durch die Ausprägung der Konnektivität mit dem terrestrischen Umland stark beeinflusst, da ins Gewässer gestürztes Totholz die Etablierung von obligaten Hartsubstratbesiedlern ermöglicht, ohne die viele Seeufer ausschließlich Weichsubstrat aufweisen würden. Die Falllaub-Einträge aus den Uferzonen ins Gewässer stellen aus qualitativer wie quantitativer Sicht eine wichtige Komponente der organischen Nahrungsressoucen dar, da sie eine zeitlich nur langsam schwankende Nahrungsressource darstellen, sowie die präferierte Nhrungsressource von Zerkleinerern (shredders).

Neben der Morphologie beeinflussen auch die hydrologischen und hydraulischen Verhältnisse an Seeufern deren Makrozoobenthosbesiedlung. Jahreszeitlich bedingte Schwankungen des Seespiegels schließen immobile benthische Arten von der Besiedlung des Eulitorals aus. Die Makrozoobenthosgemeinschaften an windexponierte Ufern zeigen eine deutlich andere Artenzusammensetzung als die an windgeschützten Ufern. Noch wesentlich stärker sind die Effekte von bootsinduziertem Wellenschlag.

Da Seen sich – insbesondere in anthropogen überformten Landschaften – in ihrem Trophiegrad stark unterscheiden, wird die Zusammensetzung des eulitoralen Makrozoobenthos außerdem durch die unterschiedliche Verfügbarkeit autochthon produzierten organischen Materials bestimmt. Die artspezifische Fährigkeit, die mit dem Trophiegrad variierenden Quantitaten und Qualitäten der Bioproduktion durch aquatische Algen und Makrophyten zu nutzen, hat eine stark strukturierende Wirkung auf die Zusammensetzung des litoralen Makrozoobenthos, die aber wissenschaftlich wenig untersucht ist.

In der **Habilitationspublikation Nr. 3** (BRAUNS, GÜCKER, WAGNER, GARCIA, WALZ & **PUSCH**, 2011) wurde erstmals die Bedeutung der Uferstruktur von Seen, und damit auch der aquatisch-terrestrischen Konnektivität für die Struktur und Energiefluxe durch ein litorales Wirbellosen-Nahrungsnetz gezeigt. An anthropogen strukturell überformten Uferabschnitten war die Nutzung terrestrischen Fallaubs durch das Wirbellosen-Nahrungsnetz um die Hälfte reduziert, und die trophischen Verknüpfungen waren sogar um eine Größenordnung verringert. Die Arbeit legt somit Grundlagen für den Schutz von Ökosystemfunktionen an Seeufern.

In der **Habilitationspublikation Nr. 4** (DONOHUE, JACKSON & **PUSCH**, 2009) wurde zum ersten Mal die Wirkung verschiedener trophischer Niveaus von Seen auf die ataxonomische Populationsstruktur von litoralem Makrozoobenthos von Seen dargestellt. Speziell wurde gezeigt, dass die Heterogenität der Zusammensetzung der Zoobenthoszönosen mit zunehmendem Trophiestatus abnahm, d.h. dass der Trophiegrad als „Filter“ für die Diversität fungiert. Dieser Zusammenhang ließ sich sowohl innerhalb von der untersuchten irischen Seen als auch im Vergleich mehrerer Seen nachweisen. Darüber hinaus wurde die β-Diversität durch weitere Faktoren, wie Seegröße, Konnektivität und Alkalinität beeinflusst.

Die **Habilitationspublikation Nr. 5** (GABEL, GARCIA, BRAUNS, SUKHODOLOV, LESZINSKI & **PUSCH**, 2008) ist die erste, die die Wirkung von durch Schiffe induziertem Wellenschlag auf litorales Makrozoobenthos beschreibt und quantifiziert. Hierbei wurden in einem interdisziplinären hydraulisch-ökologischen Ansatz sehr gut reproduzierbare sigmoide Reaktionsmuster von fünf Makrozoobenthosarten gefunden. Darüber hinaus konnte gezeigt werden, dass die Verdriftungswirkung der Wellen mit zunehmender räumlicher Komplexität der Uferhabitate stark abnimmt, da diese die Wellenenergie stärker dissipieren, und andererseits auch den Tieren bessere Anheftungsmöglichkeiten bieten.

In der **Habilitationspublikation Nr. 6** (BRAUNS, GARCIA, **PUSCH** 2008) wird zum ersten Mal untersucht, welche Auswirkungen der Klimawandel auf die eulitorale Makrozoobenthosfauna nordostdeutscher Seen haben kann. Die zu erwartenden stärkeren Seespiegelschwankungen werden dazu führen, dass die von Makrozoobenthos besonders reich besiedelten Unterwasserwurzeln von Uferbäumen trocken fallen. Die Untersuchungen zeigten, dass für dieses räumlich sehr komplexe Habitat bei Seespiegelabsenkung ein Ersatzhabitat im Infralitoral zur Verfügung steht, falls der Schilfgürtel bis in entsprechende Tiefe vordringt. Das Schilfhabitat ist im Gegensatz zu den anderen noch vorhandenen Habitaten von taxonomisch und hinsichtlich der Ernährungstypen ähnlich besiedelt wie die Unterwasserwurzeln.

In der **Habilitationspublikation Nr. 7** (BRAUNS, GARCIA, WALZ & **PUSCH** (2007a) wird zum ersten mal dargestellt, welche Auswirkungen die morphologische Veränderung von Seeufern auf die Zusammensetzung des litoralen Makrozoobenthos im Eulitoral und Infralitoral hat. Die Auswirkungen von Uferbau wurden durch den Umfang der Reduktion der Habitatkomplexität bestimmt, so dass sich überraschenderweise die taxonomische Zusammensetzung der Besiedlung in Steinschüttungen nicht von der an natürlichen Ufern unterschied. Die Auswirkungen von morphologischen Uferveränderungen beschränkten sich auf das Eulitoral, während sich die Auswirkungen von Freizeitnutzung bis ins Infralitoral erstreckten. Mit zunehmendem Uferverbau nahm die Gesamtabundanz und der Anteil der Chironomidae in den Seen zu, und der Anteil der anderen taxonomischen Gruppen ab.

In der **Habilitationspublikation Nr. 8** (BRAUNS, GARCIA, WALZ & **PUSCH** (2007b) wird zum ersten Mal die relative Bedeutung von Umweltfaktoren der Landnutzung, der Wasserqualität und des Habitatangebots für die Zusammensetzung eulitoraler Makrozoobenthosgemeinschaften auf der Ebene von Seen sowie auf der Ebene von Habitaten untersucht. Es konnte nachgewiesen werden, dass der Phosphatgehalt, die elektr. Leitfähigkeit und das Vorhandensein räumlich komplexer Habitate die Zusammensetzung des litoralen Makrozoobenthosam stärksten bestimmten, wobei die Bedeutung dieser Faktoren habitatspezifisch stark variierte, so dass etwa der Phosphatgehalt in Stein- und Schilfhabitaten keine Bedeutung hatte.

4.2. Longitudinale Spiralen – Stoffretention in Fließgewässern

Diesem Kapitel zuzuordnende Publikationen:

9. *Gücker, B*, ***Pusch, MT.*** (2006): Regulation of nutrient uptake in eutrophic lowland streams. *Limnology and Oceanography: 1443-1453*
10. *Fischer, H., Sachse, A., Steinberg, C.,* ***Pusch, M.*** (2002): Differential retention and utilization of dissolved organic carbon (DOC) by bacteria in river sediments. *Limnology and Oceanography 47: 1702-1711*
11. *Wanner, S.C.,* ***Pusch, M.*** (2000): Use of fluorescently labelled Lycopodium spores as a tracer for suspended particles in a lowland river. *Journal of the North American Benthological Society* 19: 648-658

12. ***Pusch, M.,*** *Fiebig, D., Brettar, I., Eisenmann, H., Ellis, B.K., Kaplan, L.A., Lock, M. A., Naegeli, M. W. & W. Traunspurger* (1998): The role of micro-organisms in the ecological connectivity of running waters. *Freshwater Biology* 40: 453-494.

In Bächen (Fließgewässern der Ordnungen 1-3 nach STRAHLER) finden Retention und biologische Umsetzungen von anorganischen Nährstoffen und organischen Kohlenstoffs überwiegend in durchströmten Sedimenten statt (HENDRICKS 1993, PUSCH & SCHWOERBEL 1994, SOBCZAK et al. 1998), die sich unter der Bachsohle (hyporheisches Interstitial) und seitlich unter den Ufern (Parafluvial) befinden. Die durchströmten Sedimente besitzen eine große innere Oberfläche, die regelmäßig von einem heterotrophen Biofilm ausgekleidet sind und eine große Speicherkapazität für gelöstes und partikuläres organisches Material besitzen (BRUNKE & GONSER 1997, PUSCH et al. 1998, FISCHER 2003). In solchen Bächen findet über 99% der Gesamtrespiration in den Sedimenten statt, und nur ein vernachlässigbarer Anteil in der Wassersäule (FUSS & SMOCK 1996, NAEGELI & UEHLINGER 1997). Die in den Sedimenten kleiner Fließgewässer ablaufenden Stoffumsetzungen sind für einige Gewässertypen bereits relativ gut untersucht (MARXSEN 2006, siehe dort Tab. 8), während die Stoffretention in Flüssen bisher nur wenig bearbeitet wurde.

Retention ist dabei definiert als eine Verlängerung der Aufenthaltszeit von Stoffen innerhalb eines festgelegten Fließgewässerabschnitts im Vergleich zur Aufenthaltszeit des Wassers (temporäre Retention), oder die absolute Verringerung der Stofffracht im Längskontinuum (terminale Retention). Die zu Stoffretention führenden Mechanismen sind:

a) die Erhöhung der Aufenthaltszeit durch Verweilen der Stoffe in sogenannten hydrodynamischen Totzonen („transient storage zones“) mit stark verringerter Fließgeschwindigkeit, vor allem in Ausbuchtungen des Gewässers und im hyporheischen Interstitial,

b) die Sedimentation von Schwebstoffpartikeln in strömungsberuhigten Gewässerbereichen (REYNOLDS et al. 1990, PETTICREW & KALFF 1992, CUSHING et al. 1993, SAND-JENSEN 1998, WANNER & PUSCH 2001, BUNGARTZ & WANNER 2004),

c) die Ausfiltrierung von Schwebstoffpartikeln in Interstitialräumen der Flusssohle unter Infiltrationsbedingungen (HUETTEL et al. 1996).

d) die Adsorption von gelösten Stoffen und von Schwebstoffpartikeln an Biofilmen (LOCK et al. 1984, FISCHER 2003, BATTIN et al. 2003)

e) die Filtration von Schwebstoffen durch wirbellose Tiere (WOTTON et al. 1996, WELKER & WALZ 1998, STRAYER et al. 1999, PUSCH et al. 2001, 2002), sowie

f) die biochemische Umwandlung partikulärer oder gelöster Stoffe durch Mikroorganismen, wie etwa der aerobe Abbau organischen Materials oder Denitrifikation.

Dabei sind die unter a)-d) aufgeführten Retentionsmechanismen reversibel (temporäre Retention), während die Prozesse e) und f) irreversibel sind, das heißt die Stoffe verschwinden, indem sie in andere Stoffe umgewandelt werden (terminale Retention).

In den aufgeführten Habilitationspublikationen wurde die Retention von gelösten anorganischen Nährstoffen, gelöstem organischem Material und partikulärem organischem Material sowie die Rolle von Biofilmen bei dieser Retention untersucht.

Die **Habilitationspublikation Nr. 9** (GÜCKER & **PUSCH** 2006) war weltweit unter den ersten, die dabei eutrophierte, anthropogen deutlich beeinflusste Bäche untersuchte, und die erste, die die Retention der Pflanzennährstoffe Stickstoff und Phosphor in Flachlandbächen bestimmte. Durch diese Arbeit wurde erkannt, dass die Nährstoffretention in Flachlandbächen auch wesentlich durch den biologischen Kohlenstoffumsatz mitbestimmt wird, so dass gelöste Stickstoffkomponenten nicht nur dissimilativ, sonderen in wesentlichen Anteilen auch assimilativ metabolisiert werden. Die festgestellten hohen flächenspezifischen Retentionsraten reichten jedoch nicht aus, um die hohen Nährstofffrachten wesentlich zu reduzieren, da die Nährstoffaufnahmelängen im Bereich von mehreren Kilometern lagen.

Die **Habilitationspublikation Nr. 10** (FISCHER, SACHSE, STEINBERG & **PUSCH** 2002) zeigte als erste, dass beim mikrobiellen Abbau des natürlichen gelösten organischen Kohlenstoffs (DOC) eines Flusses auch die Metabolisierung der hochmolekularen Fraktion zur Biomasseproduktion von Bakterien genutzt wird, und somit die Bioverfügbarkeit weitgehend unabhämgig von der Molekülgröße ist, was vorher angenommen wurde. Die Studie machte außerdem deutlich, dass der Biofilm, der die sandigen Sedimente der Spree bedeckt, die Fracht und Zusammensetzung des DOC in der Spree wesentlich beeinflusst.

Die **Habilitationspublikation Nr. 11** (WANNER & **PUSCH** 2000) zeigte als erste, dass die Einflussfaktoren auf den vertikalen Transfer von in Flusswasser suspendierten organischen Partikeln zur Flusssohle über die Verwendung von Bärlapp-Sporen in quantitativer Weise untersucht werden kann. Die Bärlapp-Sporen dienen dabei als partikuläre Tracer mit ähnlichen Sinkeigenschaften wie sie das Seston eines planktonführenden Flusses wie die Spree aufweist. Mit diesen partikulären tracern wurde erstmals die Partikelretentionsrate in einem Fließgewässer mit einem Durchfluss von mehr als 1 m^3/s bestimmt, so dass die bereits bekannte Abhängigkeit der mittleren Partikeltransportdistanz vom Durchfluss um eine Zehnerpotenz erweitert werden konnte.

Die **Habilitationspublikation Nr. 12** (**PUSCH** et al. 1998) erstellte als erster Reviewartikel eine Übersicht über die Rolle der Mikroorganismen des Biofilms in Ufersedimenten für die ökologische Konnektivität von Fließgewässern. Dieser Biofilm beeinflusst wesentlich die Inhaltsstoffe des exfiltrierenden Grundwassers, insbesondere durch die mikrobielle Umsetzung gelöster organischer Stoffe und von gelösten Stickstoffkomponenten, und ist somit selbst Teil einer interstitiellen mikrobiellen Schleife im Nahrungsnetz dar. Diese subterrane Komponente der lateralen Konnektivität von Fließgewässern stellt somit eine grundlegende Eigenschaft von Fließgewässern dar.

4.3 Benthisch-pelagische Kopplung als Schlüsselfaktor für mikrobielle Stoffumsetzungen in Flüssen

Diesem Kapitel zuzuordnende Publikationen:

13. *Wilczek, S., Fischer, H.,* ***Pusch, M.T.*** (2005): Regulation and seasonal dynamics of extracellular enzyme activities in the sediments of a large lowland river. *Microbial Ecology 50, 253–267*
14. *Fischer, H., Kloep, F. Wilczek, S. &* ***Pusch, M.T.*** (2005): A river's liver – microbial processes within the hyporheic zone of a large lowland river. *Biogeochemistry 76: 349–371*
15. *Craft, J.A., Stanford, J.A.,* ***Pusch, M.*** (2002): Microbial Respiration within a Flood-plain Aquifer of a Large Gravel-bed River. *Freshwater Biology 47: 251-262*
16. *Fischer, H.,* ***Pusch, M.*** (2001): Comparison of bacterial production in sediments, epiphyton and the pelagic zone of a lowland river. *Freshwater Biology* 46: 1335-1348
17. *Fischer, H**., Pusch, M.*** (1999): Use of the [14C]leucine incorporation technique to measure bacterial production in river sediments and epiphyton. *Applied Environmental Microbiology* 65: 4411-4418

In Flüssen nimmt der Anteil durchströmter Sedimente am gesamten Gewässerquerschnitt ab, und parallel dazu die Retentionseffizienz für organischen Kohlenstoff (MINSHALL et al. 1983). Es wird daher angenommen, dass mit zunehmender Flussordnung nach STRAHLER der Beitrag der benthischen, hyporheischen und parafluvialen Kompartimente am gesamten Ökosystem-Metabolismus abnimmt (VANNOTE et al. 1980). Insbesondere in mittelgroßen Flüssen, wo die mäßige Wassertiefe autochthone Produktion begünstigt, kann eine hohe pelagische Primärproduktion auftreten (REYNOLDS & DESCY 1996). Kohlenstoffressourcen aus autochthoner Produktion können aber auch noch in großen Flüssen dominieren, wenn infolge steiler Ufer allochthones Material dort nur in geringem Umfang eingetragen wird (THORP & DELONG 1994, 2002). Dieses allgemeine longitudinale Muster wird durch den künstlichen Aufstau von Flüssen verändert (WARD & STANFORD 1983), sowie auch durch natürliche Seen, die in das Gewässernetz eingestreut sind und als Planktonquellen fungieren (SCHWOERBEL 1994; ALLAN 1995).

Allgemein sind jedoch den Stoffbilanzen von Flüssen – im Vergleich zu denen von Bächen – wissenschaftlich wenig untersucht worden. Daher gab es für die oben dargestellten longitudinalen Veränderungen von Kohlenstoffbilanzen wenig empirische Evidenz. An einem beispielhaft gut untersuchten Fluss, dem Schwarzwasserfluss Ogeechee River, trugen Bakterien 97 % der Gesamtrespiration des Flussökosystems, wovon wiederum 97 % auf benthische bakterielle Respiration entfiel (EDWARDS et al. 1990). Um entsprechende Vergleichszahlen für große Flüsse zu generieren, wurden vom Habilitanden in den zwei Flachlandflüssen Spree (oberhalb Berlins) und Elbe (bei Coswig, Sachsen-Anhalt) die Kohlenstoffpools sowie mehrere Parameter mikrobieller Aktivität schwerpunktmäßig in Kompartiment der Sedimente untersucht. Ziel der Untersuchungen war es, die Intensität der stattfindenden mikrobiellen Stoffumsetzungen zu messen, mögliche Orte und Jahreszeiten besonders hoher Aktivität zu erkennen und die Auswirkungen auf das Flussökosystem abzuschätzen. Der Anteil des Sediments am gesamten Stoffumsatz im Flussökosystem wurde dabei anhand zweier Methoden bestimmt, die beide vorher kaum auf Proben aus Fließgewässers angewendet worden waren, nämlich die Bestimmung der extrazellulären Enzymaktivitätspotenziale und der bakteriellen Produktion. Mit diesen beiden Methoden konnte gezeigt werden, dass in beiden Flüssen diese Stoffumsetzungen ganz überwiegend im Sediment stattfinden (Spree Winter 94%, Sommer 95%, Elbe Winter 96%, Sommer 90%). Die beiden mit verschiedenen Methoden an verschiedenen Flüssen durchgeführten Berechnungen des Anteils der Sedimente zeigen eine bemerkenswerte Übereinstimmung. Somit wurde anhand der beiden Flüsse klar nachgewiesen, dass die Sedimente die bei weitem wichtigsten Orte heterotropher mikrobieller Stoffumsetzungen in diesen Sandflüssen darstellen.

Die in der Elbe gemessenen Aktivitätsraten von vier extrazellulären Enzyme wiesen allgemein folgende Reihung auf: Leucin-Aminopeptidase > alkalische Phosphatase > beta-Glucosidase > Exo-1,4-beta-Glucanase. Daraus ist abzuleiten, dass ein hoher Anteil der dort mikrobiell abgebauten Biomasse aus Algenproduktion stammte, was für benthische Biofilme in Fließgewässern typisch ist (CHAPPELL & GOULDER 1994; ROMANÍ & MARXSEN 2002). Da sonst nur wenige Studien zu extrazellulären Enzymen in Fließgewässersedimenten publiziert sind (MARXSEN & FIEBIG 1993; SINSABAUGH et al. 1997), konnten mit diesen Ergebnissen Vorhersagen des (überarbeiteten) Riverine Productivity-Modells (RPP; THORP & DELONG 2002) hinsichtlich des Überwiegens von Kohlenstoffquellen aus autochthoner Produktion in großen Flüssen erstmals durch direkten Nachweis bestätigt werden.

In der Spree wurde die bakterielle Aktivität anhand der bakteriellen Biomasseproduktion bestimmt. Für diese Messungen wurde zunächst die Leucin-Inkorporationsmethode hinsichtlich der Extraktionseffizienz, Substratsättigung, Isotopenverdünnung und anderer methodischer Randbedingungen für Proben aus verschiedenen Kompartimenten adaptiert und überprüft (FISCHER & PUSCH 1999). Die Messungen ergaben im Freiwasser eine bakterielle Produktion von 0.9-3.9 µg C L^{-1} h^{-1}. Im Epiphyton auf submersen Wasserpflanzen, die 40°% des Gewässerbetts bedeckten und dadurch durchschnittlich eine Blattoberfläche von 2,8 m^2 pro m^2 Sedimentoberfläche bereitstellten, wurden 5-58 ng C cm^{-2} h^{-1} produziert, und in den obersten 2 cm des Sediments von 1-8 µg C cm^{-3} h^{-1}. Umgerechnet auf eine Flächeneinheit der Gewässersohle bedeutet dies, dass das Pelagial eine leicht höhere Produktion aufwies als das Epiphyton, und die bakterielle Produktion in den obersten 2°cm des Sediments flächenbezogen 17 – 35°mal höher lag als im Pelagial, FISCHER & PUSCH 2001). Die bakterielle Biomasse in den Sedimenten überstieg die pelagische bakterielle Biomasse um das 6-22-fache. Die bakterielle Produktion war auch deutlich höher als die Primärproduktion. Somit war das Flussökosystem der Spree eindeutig heterotroph geprägt, wobei die heterotrophen Prozesse des Benthals dominierten.

Entgegen früherer Annahmen sind auch produktive Flachlandflusssysteme, die nicht übermäßig anthropogen überformt sind, somit vermutlich allgemein als Kohlenstoffsenken anzusehen (vgl. BATTIN et al. 2008). Das Vorhandensein solcher Flussabschnitte innerhalb eines Flusssystems reduziert vermutlich die Stoffausträge aus dem Einzugsgebiet in erheblicher Weise (BATTIN et al. 2009). Bilanzmäßig lässt sich die Stoffretention in der Elbe wie folgt quantifizieren:

- Sestonsedimentation in Buhnenfeldern: ca. 2,5 t pro Stromkilometer und Tag im Winter.
- Im Sommer wird ca. 1,4 % der Fracht an organischem Kohlenstoff (OC) pro Stromkilometer mikrobiell umgesetzt, d. h. die Spiralenlänge von OC beträgt in der Elbe im Sommer nur ~ 50-100 km.
- Denitrifikation ca. 10-20 t NO_3-N pro Stromkilometer und Jahr.

Die für die Elbe abgeschätzte Umsatzlänge für OC ist deutlich kürzer als im Vergleich mit anderen hierauf untersuchten Fließgewässern (WEBSTER & MEYER 1997) zu erwarten, daher scheint der Kohlenstoffumsatz hier besonders effizient zu sein.

In der **Habilitationspublikation Nr. 13** (WILCZEK, FISCHER & **PUSCH** 2005) wird zum ersten Mal die saisonale Dynamik der dominierenden mikrobiellen Stoffumsetzungen in einem großen Fluss dargestellt. Die mikrobiellen Stoffumsetzungen wurden dabei durch die potenziellen Aktivitäten von fünf extrazellulären Enzyme perameterisiert. Diese Enzyme zeigten jeweils typische jahrenszeitliche Schwankungen, die durch entsprechende Sequenzen von Abläufen des flussinternen Stoffumsatzes erzeugt werden. Insbesondere ließen sich die Perioden dominierender Nutzung autochthoner und allochthoner organischer Substanz erkennen, sowie eine Zeitverzögerung der zeitlichen Muster im Sediment gegenüber der Wassersäule. Die Ergebnisse ergeben ein konsistentes Bild der heterotrophen Funktionalität eines großen Flusses, das die Annahmen des „Revised Riverine Productivity Model“ stützt.

In der **Habilitationspublikation Nr. 14** (FISCHER, KLOEP, WILCZEK & **PUSCH** 2005) wird zum ersten Mal die Rolle der mobilen Sedimente in der Mitte des Flussbetts eines großen Flusses durch in-situ-Messungen dargestellt. Die Messungen der Bakterienabundanz, Bakterienproduktion, potenziellen Enzymaktivitäten, Nitrifikations- und Denitrifikationsraten zeigten, dass die mikrobielle Aktivitäten sich dort wegen ihrer Erstreckung bis in größere Sedimenttiefen erhebliche Raten erreichen, die diejenigen in den Ufersedimenten erheblich übersteigen. Die belebten, metabolisch aktiven Sedimente der Flussmitte repräsentieren somit eine „Leberfunktion“ im Stoffumsatz des Flusses.

Die **Habilitationspublikation Nr. 15** (CRAFT, STANFORD & **PUSCH** 2002) quantifizierte mittels einer innovativen Expiositionstechnik zum ersten Mal die aerobe Respiration und damit die Umsatzrate organischen Kohlenstoffs durch mikrobielle Biofilme in den hyporheischen und phreatischen Sedimenten eines Geschiebe führenden Flusses. Die Ergebnisse erlauben die Abschätzung, dass die mikrobielle Produktion in interstitiellen Biofilmen einen großen Anteil an der gesamten Kohlenstoffproduktion in einem Geschiebe führenden Flusssystem einnimmt.

Die **Habilitationspublikation Nr. 16** (FISCHER & **PUSCH** 2001) verglich zum ersten Mal die Beiträge der verschiedenen Kompartimente eines Flusssystems zur gesamten bakteriellen Produktion in diesem System. Dabei zeigte sich, dass die bakterielle Produktion in den Sedimenten vielfach höher ist als in der darüber liegenden Wassersäule, und auch wesentlich höher als im Periphyton auf Wasserpflanzen. Die benthische bakterielle Kohlenstoff-Produktion war auch höher als die Primärproduktion durch Algen, so dass der untersuchte Plankton-dominierte

Flachlandfluss Spree – entgegen gängiger Theorie – netto ein heterotrophes Ökosystem darstellt.

Die **Habilitationspublikation Nr. 17** (FISCHER & **PUSCH** 1999) erarbeitete die methodischen Grundlagen für den Einsatz der ^{14}C-Leucin-Inkorporationstechnik zur Bestimmung der bakteriellen Biomasseproduktion in Flussökosystemen. Hierzu wurden mehrere Schlüsselschritte dieder Technik systematisch untersucht und optimiert, wie die Extraktion des bakteriellen Proteins, die anzustrebende Substratsättigung und die Isotopenverdünnung. Zur Bestimmung der bakteriellen Biomasseproduktion in Flusssedimenten wird die Methode durchströmter Sedimentkerne empfohlen, um den Artefakt der Ausbildung eines vertikalen Gradienten innerhalb des Sediments zu vermeiden.

4.4. Vom Einzugsgebiet zum Mikrohabitat – anthropogene Kaskadenwirkungen in Gewässern

Diesem Kapitel zuzuordnende Publikationen:

18. ***Pusch, M.****, Andersen, H.E., Bäthe, J., Behrendt, H., Fischer, H., Friberg, N., Gancarczyk, A., Hoffmann, C.C., Hachoł, J., Kronvang, B., Nowacki, F., Peder-sen, M.L., Sandin, L., Schöll, F., Scholten, M., Stendera, S., Svendsen. L.M., Wnuk-Gławdel, E., Wolter, C. (*2009): Rivers of the Central Highlands and Plains. *In: Tockner, K., Uehlinger, U. and Robinson, C. T. (Eds): Rivers of Europe. Elsevier, London, 525-576*

19. *Brunke, M., A. Hoffmann,* ***Pusch, M.*** (2001): Use of mesohabitat-specific relationships between flow velocity and discharge to assess invertebrate minimum flow requirements. *Regulated Rivers: Research and Management* 17: 667-676

20. ***Pusch, M.,*** *Hoffmann, A.* (2000): Conservation concept for a river ecosystem (River Spree, Germany) impacted by flow abstraction in a large post-mining area. *Landscape and Urban Planning* 51: 165-176

Gewässer werden durch die menschliche Zivilisation hinsichtlich ihrer Wasserführung, ihrer Wasserqualität, ihrer Morphologie und/oder ihres biologischen Inventars verändert (MALMQVIST & RUNDLE 2002). Die im globalen Maßstab wichtigsten Treiber von Beeinträchtigungen sind Wasserverschmutzung und Habitatveränderungen (Abb. 8).

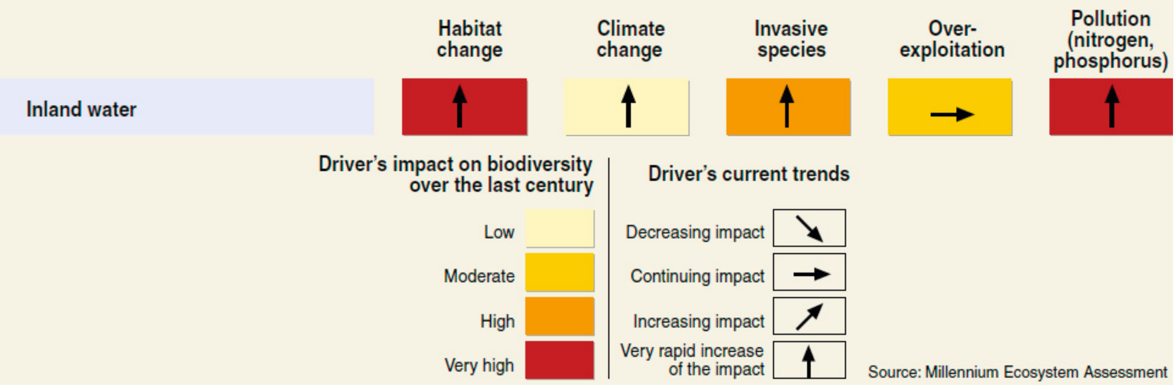

Abb. 8: Hauptsächliche direkte Ursachen von Veränderungen der Biodiversität und Ökosysteme, Auszug aus einer Grafik des Millenium Ecosystem Assessment Report (MA 2005)

Fließgewässer werden am schwerwiegendsten beeinträchtigt, wenn sie zeitweise oder permanent trocken fallen infolge Wasserausleitung für landwirtschaftliche Bewässerung, Trinkwassergewinnung oder Wasserkraftnutzung. Daneben werden Fließgewässer häufig aufgestaut, wobei ihr Fließcharakter, der diese Ökosysteme grundlegend formt, weitgehend entfällt. Weltweit existieren derzeit bereits 50 000 Großstaudämme mit einer Dammhöhe von mehr als 15 m (LEHNER et al. 2011). Für alle geschätzten 16,7 Millionen Stauseen wird angenommen, dass sie mit einem Inhalt von 8069 km^3 etwa ein Sechstel des jährlichen Wasserabflusses zu den Ozeanen enthalten (HANASAKI et al. 2006). Ihre Wasserfläche beträgt etwa 306 000 km^2 (LEHNER et al. 2011), und nimmt jährlich um etwa 10 000 km^2 zu.

Diese Stauseen beeinflussen vor allem die großen Flüsse anteilig in erheblichem Umfang, da innerhalb der Kategorie großer Flüsse mit einem mittleren Durchfluss von mehr als 1000 m^3/s fast die Hälfte (47%) in ihrer Durchflussdynamik durch Stauseen merklich verändert sind (LEHNER et al. 2011). Bereits 19% dieser Flüsse enthalten in ihrem Einzugsgebiet eine Rückhaltekapazität von mehr als der Hälfte ihrer jährlichen Wasserführung, was mit einer entsprechend gravierende Veränderung ihrer jahreszeitlichen Durchflussdynamik (LEHNER et al. 2011)und ihres Sedimenttransports verbunden ist (VÖRÖSMARTY et al. 2003).

Die Umwandlung eines großen Anteils der Flüsse der Erde wird mit den Erfordernissen zur Energiegewinnung, Bewässerung und Trinkwassergewinnung und für die Versorgung einer noch weiter wachsenden Erdbevölkerung und ihres zunehmenden Wohlstands begründet (LEHNER et al. 2011). Allerdings verursachen Stauseen nicht nur erhebliche ökologische sondern auch ökonomische Schäden, abgesehen von den oftmals großen sozialen und kulturellen Schäden durch Umsiedlung der Bevölkerung und Überstauung von Siedlungsgebieten. Sie tragen durch Emission von 4% der anthropogenen Treibhausgasen auch erheblich zum Klimawandel bei, führen durch die Sedimentrückhaltung zur Erosion der Mündungsdeltas durch das Meer (VÖRÖSMARTY et al. 2003), und verringern den Ertrag an Meeres- und Flussfischen.

Diese Zerstörungen und Nachteile werden bei Staudammbauten in Kauf genommen, obwohl Stauseen wegen der ständigen Verlandung durch den Sedimentrückhalt nur für eine begrenzte Zeit genutzt werden können, und ihre Nutzbarkeit bereits nach wenigen Jahrzehnten stark verringert sein kann. Bereits heute übertrifft weltweit der jährliche mittlere Verlust an Speichervolumen durch Verlandung die jährliche Volumenzunahme durch den Bau von neuen Stauseen. In Asien beispielsweise wird bis 2035 rund 80% des bestehenden Stauraums von Wasserkraftwerken verlandet sein (SCHLEISS et al. 2010).

Derartige morphologischen und hydrologischen Veränderungen von Fließgewässern verursachen eine Kaskade ökologischer Veränderungen, die teils erst weit stromab der Veränderung auftreten können und daher oft übersehen oder vernachlässigt werden. Durch die Eingriffe werden wichtige abiotische Umweltfaktoren verändert, was zu einem Wechsel der aquatischen und wasserabhängigen Biozönosen führt, woduch sich wiederum ander Stoffflüsse und biologische Interaktionen ausbilden (MALMQVIST & RUNDLE 2002, Tab. 1, Kap. 1.6). So führt etwa jede Veränderung der Fließgeschwindigkeit und damit der Aufenthaltszeit des Wassers in einem Flusssystem zu einem veränderten Sedimenttransport, sowie gegensinnig veränderter Planktonentwicklung und Nährstoffumsetzungen im Flusssystem.

Solche Kaskaden- und Fernwirkungen sind z.B. im Flusssystem der Elbe gutes dokumentiert (Tab. 1, , Kap. 1.6). Dort legt das Flusswasser in dem zu einer Staukette umgewandelten gebirgigen Mittellauf bei Mittelwasser pro Tag nur 27 km zurück, während es in dem auf auf deutschem Gebiet gelegenen überwiegend durch Flachland führenden Unterlauf pro Tag 73 km zurücklegt (PUSCH et al. 2009). Dort wurde im 19. und 20. Jahrhundert der Strom zugunster der Schifffahrt begradigt und Buhnen und Längsbauwerke gebaut. Die geringe Fließgeschwindigkeit im staugeregelten Oberlauf ermöglicht dort das Wachstum von Phytoplankton, das dann im relativ flachen, gut durchlichteten frei fließenden Abschnitt auf deutschem Gebiet schnell weiter wächst und im Frühjahr und Sommer regelmäßig sehr hohe Algendichten erreicht (PUSCH et al. 2009). Ohne diesen Effekt der„Animpfung“ hätte die Elbe somit eine deutlich bessere Wasserqualität.

Die vollständige Rückhaltung des Sedimenttransports der Elbe aus ihrem oberen Einzugsgebiet in Kombination mit dem Uferverbau im Unterlauf bewirkt dort im Abschnitt von Mühlberg (Elbe-km 120) bis zur Mündung der Saale (Elbe-km 290) eine Tiefenerosion des Flussbetts von 1-2 cm/Jahr, so dass der Fluss seine Sohle seit 1888 um 1,60 m erodiert hat (FAULHABER & ALEXY 2005, SCHOLTEN et al. 2005). Diese Tiefenerosion hält trotz laufender künstlicher Sedimentzugabe an, wird durch die nun deutlich zu hoch liegenden Buhnen sogar beschleunigt, und führt somit zu einer fortschreitenden Austrocknung der Auen, sowie zu geringerem Hochwasserrückhalt (PUSCH & FISCHER 2006).

Eine ähnliche Fernwirkung haben Stauhaltungen von Flüssen in bezug auf das Auftreten der Dreikantmuschel *Dreissena polymorpha*, die nur in Flusssystemen wie der Spree, der Elbe oder dem Rhein Populationen aufbauen kann, die in ihrem Oberlauf entweder einen natürlichen See oder aber (wesentlich häufiger) eine Stauhaltung aufweisen, die von dieser dauerhaft Muschel besiedelt wird, wobei die Persistenz stromab auf der Fließstrecke lebenden Populationen von der Zufuhr planktischer Larven aus der Seepopulation abhängt (PUSCH et al. 2002).

Die Nutzung einer kleinen Auswahl von Ökosystemleistungen der Flüsse und Seen durch den Menschen hat somit vielerorts zu starken Verlusten bei anderen Ökosystemleistungen geführt. Adaptives Gewässermanagement sollte daher die Entwicklung einer neuen Multifunktionalität der Gewässer anstreben, und somit vor allem die verkümmerten Ökosystemleistungen unterstützen (CARPENTER et al. 2006). Wie im Rahmen der vorliegenden Habilitationsschrift gezeigt werden konnte, spielt bei einem solchen integrierten Gewässermanagement die Entwicklung der horizontalen und vertikalen Konnektivität der Gewässer eine Schlüsselrolle. Eine solche ist vielerorts durch gezielte Veränderung begrenzender Rahmenbedingungen möglich, wenn diese im Rahmen des sozioökonomischen Wandels nicht mehr als prioritär gesehen weren.

Da die Bewirtschaftung der Gewässer in der dicht besiedelten Kulturlandschaft oftmals kaum veränderbaren Zwängen sowie unumkehrbaren Veränderungen unterliegt, müssen Ökosystemleistungen gegebenenfalls in neuartigen Ökosystemen durch abiotische und biologische

Strukturen erbracht werden, die deutlich von den ursprünglichen abweichen. Der nachhaltige Erfolg von Revitalisierungsprojekten wird somit erhöht, wenn man die Gewässer der Kulturlandschaften als gekoppelte sozial-ökologische Systeme begreift und alle relevanten gesellschaftlichen Interessen und Entwicklungen bereits bei der Konzeption mit einbezieht (CARPENTER et al. 2009). Von wissenschaftlicher Seite kann die Untersuchung, Entwicklung und Implementierung von Strategien zum integrierten Management solcher komplexer sozial-ökologischer Systeme unterstützt werden, indem die Ökosystemleistungen bewertet und gegebenenfalls monetarisiert werden, indem Indikatoren für ihre Ausprägung erstellt werden, und indem inter- und transdisziplinäre Verbundprojekte durchgeführt werden, die in von allen Beteiligten akzeptierte Entscheidungsgrundlagen münden (CARPENTER et al. 2006).

Es bestehen somit Hinweise, dass die Gewährleistung horizontaler und vertikaler Konnektivität in der Regel mit räumlich komplexeren, diverseren, zeitlich und strukturell resilienteren sowie leistungsfähigeren Ökosystemen einhergeht, die somit intensiver und sicherer nachhaltig genutzt werden können. Die Erarbeitung weiterer Evidenzen wird jedoch als wünschenswert erachtet. Eine Reihe von Zusammenhängen von Ökosystemfunktionen mit ökologischer Konnektivität und anthropogenen Belastungen wurden im Rahmen der vorliegenden Habilitationsschrift durch Labor- und Feldexperimente sowie durch gezielte Feldmessungen von Parametern funktionaler Zusammenhänge wie Stoffretention, Enzymaktivität und Isotopenzusammensetzung in ausgewählten Gewässerteilen in quantitativer Weise dargestellt.

Die **Habilitationspublikation Nr. 18** (**PUSCH** et al. 2009) fasst in einem entsprechend strukturierten Kapitel eines internationalen Handbuchs der Flussökologie die Kenntnisse zu den großen und einiger ausgewählter kleinerer Flüsse der biogeographischen Region der mitteleuropäischen Mittelgebirge und Tiefländer zusammen. Die großen Flüsse Weser, Elbe und Oder sowie die Spree und drei kleineren Flüsse werden jeweils separat hinsichtlich ihrer geographischen, hydrologischen, biochemischen Eigenschaften dargestellt, ebenso wie die aquatische und wasserabhängige Biodiversität und schließlich Aspekte des Managements und Naturschutzes. Es handelt sich – abgesehen von den selbst mit herausgegebenen Monographien zu Spree und Elbe – jeweils um die ersten zusammenfassenden Darstellungen der Ökologie dieser Flüsse.

Die **Habilitationspublikation Nr. 19** (BRUNKE, HOFFMANN & **PUSCH** 2001) wurden zum ersten Mal die Mesohabitat-spezifischen Makrozoobenthosgemeinschaften eines Flachlandflusses mit den dort bei verschiedenem Durchflussniveaus herrschenden Fließgeschwindigkeiten verknüpft, und damit Grundlagen zur Festsetzung einer Mindestwasserführung für einen Flachland-Flussabschnitt erarbeitet. Da in dem untersuchten Flussabschnitt verringerte Wasserführung zu einer Homogenisierung der benthischen Habitate und zu einem Rückgang lotischer Taxa führt, wurden für vier lotische Makrozoobenthostaxa untere Toleranzgrenzen hinsichtlich der Flusswasserführung abgeleitet.

In der **Habilitationspublikation Nr. 20** (**PUSCH** & HOFFMANN 2000) wurde erstmals aus gewässerökologischer Sicht die Folgen der Veränderung der Wasserführung der Spree durch die großräumige Bergbautätigkeit in ihrem Einzugsgebiet dargestellt, insbesondere die Durchflussreduktion aufgrund der Wiederauffüllung der Tagebaulöcher. Die gewässerökologischen Auswirkungen der Durchflussreduktion werden konzeptionell hierarchisch dargestellt, und ein ökologisch basiertes Multikompartiment-Verfahren zur Ableitung einer Mindestwasserführung vorgeschlagen.

5. Zusammenfassung

Gewässer werden traditionellerweise als abgeschlossene Ökosysteme gesehen, und insbesondere das Zirkulieren von Wasser und Nährstoffen im Pelagial von Seen wird als Beispiel dafür angeführt. Allerdings wurden in der jüngeren Vergangenheit wichtige Verknüpfungen des Freiwasserkörpers von Gewässern aufgezeigt, die einerseits mit dem Benthal und andererseits mit dem Litoral, der terrestrischen Uferzone und ihrem Einzugsgebiet bestehen.

Dadurch hat in den vergangen Jahren die horizontale und vertikale Konnektivität der Gewässerökosysteme erhöhtes wissenschaftliches Interesse auf sich gezogen, und damit auch die ökologischen Funktionen des Gewässergrunds (Benthal) und der Uferzonen (Litoral). Aus der neu beschriebenen Konnektivität innerhalb und zwischen diesen Lebensräumen ergeben sich weitreichende Konsequenzen für unser Bild von der Funktionalität der Gewässer.

In der vorliegenden Habilitationsschrift werden am Beispiel von Fließgewässern und Seen des nordostdeutschen Flachlandes eine Reihe von interne und externe funktionale Verknüpfungen in den horizontalen und vertikalen räumlichen Dimensionen aufgezeigt. Die zugrunde liegenden Untersuchungen umfassten zumeist sowohl abiotische als auch biologische Variablen, und umfassten thematisch, methodisch und hinsichtlich der Untersuchungsgewässer ein breites Spektrum. Dabei wurden in Labor- und Feldexperimenten sowie durch quantitative Feldmessungen ökologischer Schlüsselprozesse wie Nährstoffretention, Kohlenstoffumsatz, extrazelluläre Enzymaktivität und Ressourcenweitergabe in Nahrungsnetzen (mittels Stabilisotopenmethode) untersucht.

In Bezug auf Fließgewässer wurden dadurch wesentliche Erkenntnisse hinsichtlich der Wirkung einer durch Konnekticität geprägten Hydromorphologie auf die die aquatische Biodiversität und die benthisch-pelagische Kopplung erbracht, die wiederum einen Schlüsselprozess darstellt für die Retention von in der fließenden Welle transportierten Stoffen, und damit letztlich für die Produktivität eines Flussabschnitts.

Das Litoral von Seen wurde in Mitteleuropa jahrzehntelang kaum untersucht, so dass die durcheführten Untersuchungen zur Gemeinschaftsstruktur, Habitatpräferenzen und Nahrungsnetzverknüpfungen des eulitoralen Makrozoobenthos grundlegend neue Erkenntnisse erbrachten, die auch unmittelbar in Ansätze zur ökologischen Bewertung von Seeufern gemäß EG-Wasserrahmenrichtlinie eingehen.

Es konnte somit gezeigt werden, dass die Intensität sowohl die internen als auch der externen ökologischen Konnektivität durch die Hydrologie und Morphologie der Gewässer sowie durch die Verfügbarkeit von Nährstoffen wesentlich beeinflusst wird, die auf diese Weise vielfach die ökologische Funktionalität der Gewässer prägen. Dabei trägt die vertikale oder horizontale Konnektivität zur Stabilisierung der beteiligten Ökosysteme bei, indem sie den Austausch ermöglicht von Pflanzennährstoffen, von Biomasse sowie von migrierenden Organismen, wodurch Phasen des Ressourcenmangels überbrückt werden.

Diese Ergebnisse können im Rahmen der Bewirtschaftung von Gewässern dahingehend genutzt werden, dass die Gewährleistung horizontaler und vertikaler Konnektivität in der Regel mit räumlich komplexeren, diverseren, zeitlich und strukturell resilienteren sowie leistungsfähigeren Ökosystemen einhergeht, die somit intensiver und sicherer nachhaltig genutzt werden können.

Die Nutzung einer kleinen Auswahl von Ökosystemleistungen der Flüsse und Seen durch den Menschen hat oftmals zu einer starken Reduktion der ökologischen Konnektivität, und in der Folge zu starken Verlusten bei anderen Ökosystemleistungen geführt. Die Ergebnisse der dargestellten Forschungen zeigen auch, dass die Entwicklung und Implementierung von Strategien zum integrierten Management von komplexen sozial-ökologischen Systemen wesentlich unterstützt werden kann, wenn die horizontale und vertikale Konnektivität gezielt entwickelt wird.

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