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Food web regulation under different forcing regimes in shallow lakes – synthesis and modelling

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Contents

General Introduction

Living organisms grow and reproduce based on autotrophic or heterotrophic assimilation and they are subject to the consumption by other organisms. These trophic interactions form predator-prey pairs, food chains and food webs, with an increasing degree of complexity regarding the underlying regulating processes. The **food web regulation** characterizes processes limiting the biomass or production of its components. The dominant processes are the top-down and bottom-up control, which describes the regulation of the prey through predator feeding and the limited availability of resources or prey for the predator, respectively. Thus, in predator-prey systems the prey is usually top-down and the predator bottom-up controlled. In contrast to biotic predator-prey pairs, the utilization of abiotic resources, such as nutrients and light, may form consumer-resource interactions with bottom-up regulated consumers. A bottom-up regulated population increases in biomass if more resources or prey production is available and decreases if less is available. A top-down regulated population is in general characterized by low biomasses and high production to biomass ratios. Their biomass remains stable if the amount of resources or prey production available to them increases. Solely the production of the top-down regulated population can increase up to their physiologically determined maximum production to biomass ratio. A further increase of resources would remain unconsumed. The concept of top-down and bottom-up regulation is continuously extended e.g. to the trophic cascade concept (Carpenter *et al.*, 1985), by including omnivory, leading to apparent competition or apparent mutualism (Abrams *et al.*, 1998) and intraguild predation (Polis *et al.*, 1989), and by considering a weaker or stronger linked parallel food chain (Wollrab *et al.*, 2012). These extensions of the concept of bottom-up regulated predators and top-down regulated prey enhance its utility for food web analyses. Trophic interactions are ubiquitous, but they not necessarily regulate a population. Beyond trophic interactions also non-trophic interactions are relevant for the food web regulation, e.g. the competition for light between autotrophs, the production of allelopathic substances by macrophytes, which hamper the phytoplankton growth (Hilt and Gross, 2008) and macrophytes providing shelter from fish predation (Jeppesen *et al.*, 1997; Timms and Moss, 1984). Finally, also abiotic conditions limit the production of organisms as e.g. well known for crustaceans in spring. A large amount of food is available during the phytoplankton spring bloom, but crustacean growth is limited by low temperatures which diminishes the trophic regulation of phytoplankton (Straile, 2000). Thus, a variety of processes determines the regulation of the food web components, which consequently results in a specific food web structure.

Alterations of the top-down and bottom-up regulation under different **forcing regimes** have presumably consequences at the species, community and ecosystem scale, such as the dominant species, the community biomass and size spectrum and the prevalent ecosystem state (e.g. turbid or clear-water state). Forcing regimes may arise from external and internal, abiotic and biotic processes and may strengthen, reduce or even reverse the regulating forces of food web components, as exemplified for aquatic ecosystems (Table 1). Effects of the enhanced input of terrestrial organic matter into aquatic ecosystems (chapter I) and persistent low temperatures in winter (chapter II & III) are categorized as external, abiotic forcing regimes. Western civilization is already aware of the problems regarding large nutrient fluxes, e.g. from agriculture into aquatic ecosystems, as another external, abiotic forcing regime and manage to regulate the fluxes for several ecosystems. However, developing countries still face the major problems of eutrophication e.g. for the stable supply of drinking water. In a tri-trophic food chain higher nutrient availability may cause increased phytoplankton production which is not utilized by their top-down controlled predators. Food web theory predicts that the top-predator of this system accumulates biomass until it is sufficient to sustain a further trophic level. Then, this fourth trophic level leads to control changes at each trophic level, i.e. top-down becomes bottom-up and vice versa (Oksanen *et al.*, 1981). Biomanipulation as an ecosystem management tool relies on this concept and aims to enhance the water quality by reducing the phytoplankton biomass with the introduction of a fourth trophic level, namely piscivorous fish (Benndorf, 1995). Biotic, external processes, as feeding by waterfowls, might also regulate trophic food web interactions (Table 1). The predation pressure by waterfowls on a specific ecosystem food web may strongly vary in time, as they are mobile and thus have access to prey from different ecosystems. Waterfowls feeding from aquatic food webs export biomass and therefore, either strengthen the bottom-up control of the organisms' predator or release its prey from top-down pressure. The waterfowls' excrements and organic matter or even living organisms transported within their feathers are an import to aquatic ecosystems, which may again alter the ecosystem food web regulation. Besides external, also internal, abiotic forcing regimes such as the stratification of lakes may affect the food web regulation. Stratification hampers the access to nutrients for phytoplankton and thus their production especially in oligotrophic systems, which may consequently lead to bottom-up regulated predators. Additionally, internal, biotic processes may strongly alter the trophic food web interactions, for example the formation of defense strategies against predation, which can be morphological, chemical or realized by predator avoidance. Defense strategies emerge if a prey encounters strong top-down control, to reduce the predation pressure (Tollrian and Harvell, 1999). These defense mechanisms diminish if the predation pressure is reduced and therefore, are an example for an internal food web regulation. These instances show exemplarily how forcing regimes may alter the trophic food web regulation and that the understanding of these processes is required to predict effects of climate change and to advise ecosystem management.

Table 1. Examples for forcing regimes potentially altering the trophic food web regulation in lakes. Effects of the highlighted forcing regimes were investigated in this dissertation.

forcing regimes	external	internal
abiotic	**terrestrial matter input** **temperature** nutrient inflow	stratification
biotic	mobile external predators	defense strategies

In general, the food web regulation by trophic interactions is stronger within aquatic ecosystems, i.e. a higher proportion of the prey production is consumed by a predator, than in terrestrial ecosystems. This is driven by the inherent aquatic ecosystem properties as increasing body size with trophic level, by a more homogenous environment, which increases the access of the prey production for predators, by primary producers having less structural components thus being more palatable and by having a higher nutritional quality in aquatic ecosystems (Cebrian, 1999; Polis and Strong, 1996). The focus of this dissertation is on **shallow lakes**, which represent the most common type of lakes worldwide (Downing *et al.*, 2006). Shallow lakes have per definition a low depth and are often small leading to a high area to volume and catchment to area ratio. As a consequence, shallow lakes may be highly susceptible to external forcing regimes, as changes in the atmospheric temperature and inputs from the surrounding, compared to larger, deeper lakes. A further typical characteristic of shallow lakes arises from their specific morphology. Their shallowness implies a certain habitat structure, which in turn results in a typical food web, where the benthic compartment is more relevant than in deep lakes. Due to complex trophic and also non-trophic interactions between the food web components, shallow lakes occur in two alternative stable states (Fig. 1; Scheffer and Jeppesen, 2007). This bistability is either characterized by a turbid phytoplankton-dominated state or by a clear-water macrophyte-dominated state, depending on the actual and past nutrient concentrations (Scheffer *et al.*, 1993). The mechanisms stabilizing each state, buffer a certain change in nutrient concentration until the system abruptly switches (Fig. 1). Beyond the internal processes also external forcing regimes may affect the bistability of shallow lakes and due to the sharp transition between the alternative stable states even a small change in the forcing factors may lead to a drastic change in the ecosystem functioning. The ecosystem studies of this dissertation were performed in Schulzensee, occupied by submerged macrophytes and Gollinsee, which had no submerged macrophytes, to account for the alternative stable states of shallow lakes. Both lakes are located in North-East Germany, a temperate region. The lakes are small (3-4 ha), shallow (about 2 m) and eutrophic (average 2010-2011: 32-36 µg total phosphorus L^{-1}). Both lakes were investigated already in 2007 and then intensively in 2010 and 2011, as part of the TerraLac project, which aimed to investigate the effects of an enhanced input of terrestrial particulate organic matter (t-POM) at the scale of whole ecosystems. Thus, both lakes were divided into separate halves and a distinct carbon source was added in autumn 2010 to one of the halves in each lake (Attermeyer *et al.*, 2013; Scharnweber *et al.*, 2014). In line with the TerraLac objectives, the modelling study of this dissertation investigated effects of the t-POM input to shallow lakes (chapter I). Further, the measurements conducted within the TerraLac project were synthesized and analyzed in ecosystem studies focusing on observations beside the t-POM input (chapter II-IV).

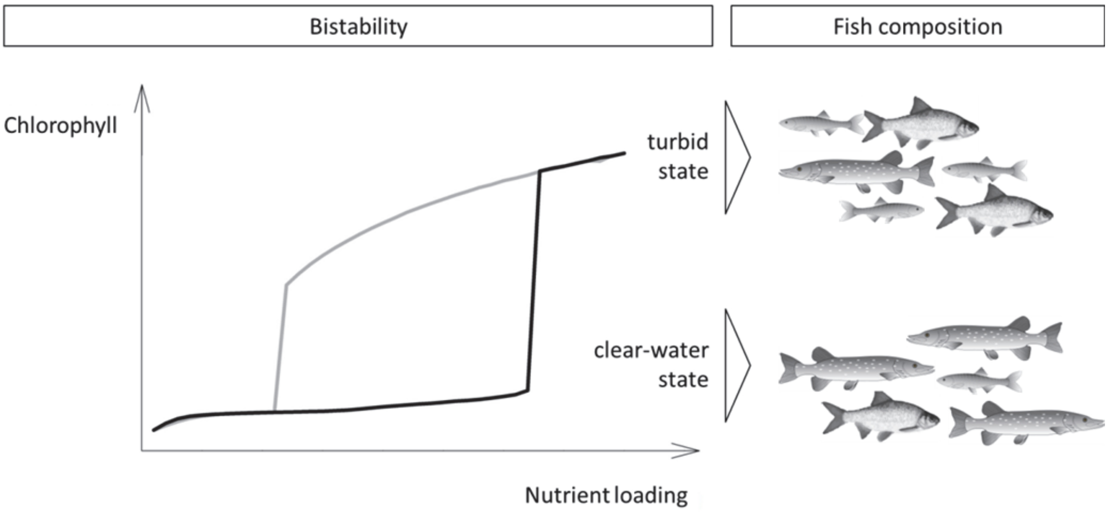

Figure 1. Bistability in shallow lakes resulting in a clear-water and a turbid state. At low nutrient concentrations only the clear-water state is prevalent and the internal feedback mechanisms buffer rising nutrient concentrations until the system switches abruptly into the turbid state (black line). Starting with high nutrient concentrations requires a reduction in nutrient concentrations far below the critical concentrations where the clear-water state crashed, until the turbid state switches back to the clear-water state (grey line). The fish communities of clear-water and turbid lakes are exemplified, showing a higher proportion of piscivorous fish in the clear-water lake than in the turbid lake.

Previously, lakes have been studied from a simplified pelagic perspective focusing on the trophic food chain: phytoplankton – crustaceans – fish. This dissertation goes beyond the traditional perspective and considers further trophic levels and additionally the benthic food web in order to derive a **comprehensive ecosystem** understanding. The zooplankton includes next to crustaceans also rotifers, ciliates and heterotrophic nanoflagellates. All zooplankton groups compete for primary production and are connected via feeding interactions which implies complex dynamics between zooplankton and phytoplankton. Among zooplankton, ciliates are still a largely overlooked group, although, they are an important prey for crustaceans (Adrian and Schneider-Olt, 1999; Sanders and Wickham, 1993) and often the most important phytoplankton grazers in spring (Gaedke and Straile, 1994a; Weisse *et al.*, 1990). Due to their low generation times and high weight specific grazing rates, compared to the metazooplankton (rotifers and crustaceans) (Hansen *et al.*, 1997), they are capable to track phytoplankton dynamics immediately (Berninger *et al.*, 1993) and exert an enormous predation pressure on their prey if ciliates become quantitatively important. The second major step towards more comprehensive ecosystem studies, after considering ciliates as an important organism group, is to account for the benthic food web. Its relevance within lake ecosystems was outlined by Vadeboncoeur *et al.* (2002). The benthic bacterial and autotrophic production was reported to equal or exceed the respective pelagic production (Vadeboncoeur *et al.*, 2002). This benthic production is expected to be efficiently transferred to benthic animal consumer production as known from the pelagic habitat (Gaedke and Straile, 1994b).

Comprehensive ecosystem studies further require the consideration of terrestrial matter inputs if relevant for the respective ecosystem. In small lakes the relevance of **terrestrial inputs** relative to autochthonous sources can be large due to the high catchment to volume ratio. Such terrestrial carbon sources are either dissolved or particulate and enter lakes via e.g. run off, groundwater influx, precipitation, wind and litter fall (Polis *et al.*, 1997 and references therein). Bartels *et al.* (2012) reviewed the effects of terrestrial organic matter input for ecosystem dynamics. Most studies were conducted in lotic systems and the few lentic studies focused on terrestrial dissolved organic matter (t-DOM) effects in the pelagic zone. The dissolved organic carbon concentrations were observed to increase in many aquatic systems (Clark *et al.*, 2010). With climate change heavy precipitation events may occur more often and likely enhance the flux of t-DOM to aquatic systems (Clair *et al.*, 1999). The negative effects of t-DOM on the underwater-light availability and thus the autotrophic production are well known (Ask *et al.*, 2009; Carpenter *et al.*, 1998). However, the utilization of t-DOM by aquatic consumers is under debate. In experiments the bacterial biomass was positively correlated to the concentration of t-DOM (Tranvik, 1988), whereas it remains unclear whether animal consumers receive t-DOM via this pathway (Cole *et al.*, 2006; Grey *et al.*, 2001). The effects of t-POM on lake food webs remained rather unknown although the major input of t-POM to temperate lakes – the autumnal litter fall – is a regular process. The amount of t-POM inputs to lakes as litter is also predicted to increase as temperature and CO_2 concentrations rise due to the ongoing climate change (Amthor, 1995; Zaehle *et al.*, 2007). This strikingly requires the study of t-POM effects on ecosystem dynamics. Enhanced t-POM input may indirectly affect the bistability of shallow lakes via three major pathways: (1) zoobenthos consumption of t-POM, (2) zooplankton consumption of suspended t-POM and (3) effects on light availability within the lake by suspended t-POM. To predict the emerging effect of the several direct and indirect, biotic and abiotic effects of the enhanced t-POM input all major pathways of energy flux need to be considered in whole-lake studies. In chapter I this objective was evaluated using the complex ecosystem model PCLake (Janse *et al.*, 2010). The model meets the requirements for such a study as the benthic and pelagic food web with all relevant pathways are included (Janse, 2005). In addition, the mechanisms, which allow for bistability, are implemented in PCLake. This enables predictions at the community and ecosystem scale due to enhanced t-POM input into lakes.

Beside ecosystem models, comprehensive whole lake studies are useful to identify processes at the ecosystem scale. The external, abiotic forcing factor temperature has the potential to alter the food web regulation, which may have effects at the ecosystem scale. Low temperatures in winter for instance may lead to a persistent ice cover of lakes also in temperate regions (Balayla *et al.*, 2010). As a consequence, oxygen concentration drops to low values in respect to fish requirements which can result in a **winterkill of fish.** Along with an overall reduction of the fish biomass, the severe oxygen depletion is expected to alter the fish community. According to the trophic cascade concept, piscivorous fish facilitate the top-down control of phytoplankton by zooplankton and thus the clear-water state (Jeppesen *et al.*, 1997). In line with that, piscivorous fish are more abundant in clear-water than turbid lakes (Fig. 1; Persson *et al.*, 1991). As they are very sensitive to low oxygen concentrations (Doudoroff and Shumway, 1970) winterkills of fish may align the fish community in clear-water lakes to the fish community typical for turbid lakes which has a lower proportion of piscivorous fish (Fig. 1). Beside effects for the fish community also the trophic level below fish might be affected by the winterkill of fish. The loss of piscivorous fish was suggested to cascade along the food web, resulting in top-down controlled zooplankton and bottom-up controlled phytoplankton which can actually lead to a switch from the clear-water state to the turbid state (Brönmark and Weisner, 1992). This cascade can occur through increased planktivorous fish biomass if piscivorous fish suffer from low oxygen concentrations. In case the overall fish biomass is reduced the recruitment of young of the year (YOY) fish can be enhanced (Ruuhijärvi *et al.*, 2010) which can likewise exert a strong top-down control on metazooplankton (Mehner and Thiel, 1999) and consequently reduce the grazing pressure on phytoplankton leading also to more turbid lakes (Romare *et al.*, 1999). If YOY fish do not benefit from the overall low fish biomass, zooplankton may be released from top-down control, enhance the predation pressure for phytoplankton and facilitate the clear-water state. In line with that, a reduction of the predation pressure by omnivorous and planktivorous fish after winterkills of fish was previously observed to favor large-bodied zooplankton and in turn phytoplankton experienced high grazing losses and lakes became clearer (Balayla *et al.*, 2010; Ruuhijärvi *et al.*, 2010). If metazooplankton is under top-down control by planktivorous or YOY fish protozoan zooplankton, such as ciliates, could be released from predation pressure enhancing their biomass. Consequently, ciliates could maintain the high grazing pressure on phytoplankton and control also the pelagic bacteria by strengthening the top-down control, due to their high weight specific grazing rates (Hansen *et al.*, 1997). As such, winterkills of fish have the potential to alter the pelagic food web regulation at all trophic levels in different ways depending on the resulting fish community. In addition, cascading trophic effects may even alter the ecosystem state. The consequences of the winterkills of fish for the phytoplankton, crustacean and fish community itself, are evaluated in chapter II by means of stable isotope analysis, gut content analysis and biomass measurements. In chapter III changes of the food web regulation and resulting food web structure post winterkills of fish are described at the community scale for all groups of zooplankton, phytoplankton and bacteria by presenting community biomasses. Furthermore, the community composition of crustaceans, ciliates and phytoplankton is illuminated to define effects at the species scale.

The pelagic perspective of chapter II and III is complemented by the benthic organisms to receive a comprehensive understanding of the ecosystem carbon fluxes in chapter IV. The morphology of shallow lakes might induce a larger autotrophic production in the benthic habitat compared to the pelagic habitat (Brothers *et al.*, 2013; Genkai-Kato *et al.*, 2012), if sufficient light reaches the benthic habitat. The relevance of the **benthic production** was depict in a meta-analysis which revealed a dominance of benthic autotrophic and bacterial production over the pelagic ones (Vadeboncoeur *et al.*, 2002). The benthic autotrophs have a strong impact at the ecosystem scale by e.g. stabilizing the clear-water state. However, the trophic interactions in the benthic were rarely investigated due to the pelagic perspective of previous studies. In addition, the quantification of carbon fluxes in food webs requires extensive measurements of biomasses, productions and diet compositions at all trophic levels explaining the rarity of such studies. The few existing quantitative studies focused either on the basis (Althouse *et al.*, 2014; Blindow *et al.*, 2006; Brothers *et al.*, 2013) or the top of the food web (Vander Zanden and Vadeboncoeur, 2002) and usually neglected the bacterial production in the benthic habitat (Andersson and Kumblad, 2006). From these studies, the benthic production turned out to be relevant at either end of the food web, but information on the intermediate pathways are still lacking. The pelagic habitat of Lake Constance is well-known to transfer autotrophic and bacterial production efficiently along the trophic levels (Gaedke and Straile, 1994b). The latter is due to the spatial match of prey production and predator abundance in the pelagic habitat and the high edibility and sufficient food quality of pelagic autotrophs and bacteria. The sediment is a more nutrient rich habitat than the pelagic zone (Sand-Jensen and Borum, 1991) allowing for a sufficient food quality of the dominant benthic autotrophs, the periphyton (Brothers *et al.*, 2013). In addition, the bacterial stoichiometry is rather fixed (Hessen *et al.*, 2013). Thus, the benthic trophic transfer efficiency is expected to be comparable to the pelagic one. To evaluate this hypothesis the benthic and pelagic carbon fluxes were compiled in quantitative food webs and the trophic efficiencies were calculated as presented in chapter IV. The particularity of this approach is that the productions of all benthic autotrophs, the bacterial production and the vast majority of the animal consumers were considered. The production of each group related to the prey production available for ingestion gives further hints on the organisms' regulation. If the majority of available prey production was consumed a bottom-up regulation is likely, whereas a top-down regulated organism group might leave a large amount of prey production unconsumed.

This dissertation presents new insights on the regulation of lake food web components at all trophic levels in different habitats and under different forcing regimes. The mechanisms how enhanced terrestrial organic matter inputs and partial winterkills of fish alter the food web regulation are illuminated. In addition, the carbon fluxes in whole ecosystems were quantitatively described to evaluate the fate of the benthic and pelagic, autotrophic and bacterial production.

Dissertation outline

This dissertation investigates the food web regulation with enhanced t-POM input and after winterkills of fish in shallow lakes. Methodological diverse approaches were used to get insights into the regulation at all trophic levels in the pelagic and benthic habitat. The effects at the species, community and ecosystem scale of altered regulations are displayed.

The four chapters of this dissertation are outlined below:

The foreseen enhanced input of t-POM to shallow lakes may serve as additional food for pelagic and benthic consumers and act on the light availability. Alterations of the food web regulation may affect the resilience of the turbid and clear-water state. The underlying mechanisms affecting alternative stable states are disentangled in **chapter I** using a comprehensive ecosystem model of shallow lakes.

The fish community of lakes with submerged macrophytes is usually characterized by a higher proportion of piscivorous fish than the fish community in lakes without submerged macrophytes. As piscivorous fish are very sensitive to low oxygen concentrations they presumably suffer most from the observed persistent ice coverage on the lakes studied in this dissertation. This would beside an overall reduction of the fish biomass align the fish communities of both lakes. The consequences of the oxygen depletion in winter are illuminated for phytoplankton, crustacean zooplankton and fish in **chapter II**.

The absence of adult fish can drive pelagic food webs to top-down regulation by large crustaceans or YOY fish. In the present study the biomass and community structure of crustaceans indicated that YOY fish were very abundant. They considerably altered the zooplankton community with consequences down to autotrophic and bacterial producers as described in **chapter III**.

The importance of the benthic food web within whole-lake ecosystems was evaluated for two shallow lakes. Therefore, comprehensive quantitative food webs were compiled to characterize the efficiency of carbon fluxes in the pelagic and benthic habitat. The differences in the trophic efficiencies between both habitats and potential underlying mechanisms of those are presented in **chapter IV**.

Declaration of Contributions

Chapter I – Enhanced input of terrestrial particulate organic matter reduces the resilience of the clear-water state of shallow lakes - a model study

Betty Lischke, Sabine Hilt, Jan H. Janse, Jan J. Kuiper, Thomas Mehner, Wolf M. Mooij, and Ursula Gaedke

S. Hilt and I conceived the study supported by T. Mehner and U. Gaedke. I performed the research and received comments by J.J. Kuiper, J.H. Janse and W.M. Mooij. I analyzed the model results assisted by all coauthors. I wrote the manuscript and received comments by all coauthors.

Chapter II – Contrasting response of two shallow eutrophic lakes to a partial winterkill of fish

Sabine Hilt, Thomas Wanke, Kristin Scharnweber, Mario Brauns, Jari Syväranta, Soren Brothers, Ursula Gaedke, Jan Köhler, **Betty Lischke**, Thomas Mehner

The overall experimental design of the whole-lake experiment was conceived by S. Hilt and T. Mehner, assisted by M. Brauns, U. Gaedke, J. Köhler and later K. Attermeyer, S. Brothers and K. Scharnweber. I analyzed the plankton data, supported by U. Gaedke. S. Hilt, M. Brauns, J. Syväranta, T. Mehner, T. Wanke and K. Scharnweber analyzed the fish biomass and the stable isotope data. S. Brothers, K. Scharnweber and T. Wanke took samples and provided data on chlorophyll (S.B.), fish biomass (K.S.) and fish gut content (T.W.). S. Hilt wrote the manuscript and received comments by all coauthors.

Chapter III – Large biomass of small feeders: Ciliates may dominate herbivory in eutrophic lakes

Betty Lischke, Guntram Weithoff, Stephen A. Wickham, Katrin Attermeyer, Hans-Peter Grossart, Kristin Scharnweber, Sabine Hilt and Ursula Gaedke

The overall experimental design of the whole-lake experiment was conceived by S. Hilt and T. Mehner, assisted by H. P. Grossart, U. Gaedke and later K. Attermeyer and K. Scharnweber. I analyzed and synthesized the plankton data counted by S. Donath and the LimSa Gewässerbüro. K. Attermeyer and K. Scharnweber took samples and K. Attermeyer provided data on bacterial biomass and production. G. Weithoff, S. A. Wickham and U. Gaedke supported the data analysis. I wrote the manuscript and received comments by all coauthors.

Chapter IV – Dominance of pelagic carbon fluxes in shallow lakes emerges from inefficient benthic carbon transfer

Betty Lischke, Thomas Mehner, Katrin Attermeyer, Mario Brauns, Soren Brothers, Hans-Peter Grossart, Sabine Hilt, Jan Köhler, Kristin Scharnweber and Ursula Gaedke

The overall experimental design of the whole-lake experiment was conceived by S. Hilt and T. Mehner, assisted by M. Brauns, H. P. Grossart, U. Gaedke, J. Köhler and later K. Attermeyer, S. Brothers and K. Scharnweber. I analyzed and synthesized the whole food web data. K. Attermeyer, S. Brothers and K. Scharnweber took samples and provided data on bacterial biomass and production (K.A.), biomass of benthic primary producers and production of pelagic and benthic primary producers (S.B.) and macrobenthos and fish biomass and production (K.S.). U. Gaedke and T. Mehner supported the data analyses. I wrote the manuscript and received comments by all coauthors.

Further related manuscripts written during my Ph.D. project, which are not included as entire chapters but rather in the general Introduction and Discussion:

During my study described in chapter I I intensively discussed the modelling framework of PCLake with W.M. Mooij, J.J. Kuiper and L.P.A. van Gerven. These discussions inspired two conceptual manuscripts. I contributed to the discussion of their content and assisted in the writing of the manuscripts.

Mooij, W. M., Brederveld, R. J., de Klein, J. J. M., DeAngelis, D. L., Downing, A. S., Faber, M., Gerla, D. J., Hipsey, M. R., 't Hoen, J., Janse, J. H., Janssen, A. B. G., Jeuken, M., Kooi, B. W., **Lischke, B.**, Petzoldt, T., Postma, L., Schep, S. A., Scholten, H., Teurlincx, S., Thiange, C., Trolle, D., van Dam, A. A., van Gerven, L. P. A., van Nes, E. H. and Kuiper, J. J. (2014) Serving many at once: How a database approach can create unity in dynamical ecosystem modelling. *Environmental Modelling & Software,* 61, 266-273.

van Gerven, L. P. A., Brederveld, R. J., de Klein, J. J. M., DeAngelis, D. L., Downing, A. S., Faber, M., Gerla, D. J., 't Hoen, J., Janse, J. H., Janssen, A. B. G., Jeuken, M., Kooi, B. W., Kuiper, J. J., **Lischke, B.**, Liu, S., Petzoldt, T., Schep, S. A., Teurlincx, S., Thiange, C., Trolle, D., van Nes, E. H. and Mooij, W. M. (2015) Advantages of concurrent use of multiple software frameworks in water quality modelling using a database approach. *Fundam.Appl.Limnol.,* 186, 5-20.

I analyzed and provided plankton data for two more manuscripts. I contributed to the discussion of their content and assisted in the writing of the manuscripts.

Brothers, S. M., Hilt, S., Attermeyer, K., Grossart, H. P., Kosten, S., **Lischke, B.**, Mehner, T., Meyer, N., Scharnweber, K. and Köhler, J. (2013) A Regime shift from macrophyte to phytoplankton dominance enhances carbon burial in a shallow, eutrophic lake. *Ecosphere,* 4, art137.

Mehner, T., Attermeyer, K., Brauns, M., Brothers, S., Diekmann, J., Gaedke, U., Grossart, H. P., Köhler, J., **Lischke, B.**, Meyer, N., Scharnweber, K., Syväranta, J., Vanni, M. J. and Hilt, S. (2015) Weak response of animal allochthony and production to enhanced supply of terrestrial leaf litter in nutrient-rich lakes. *Ecosystems*, doi: 10.1007/s10021-015-9933-2.

Chapter I

Enhanced input of terrestrial particulate organic matter reduces the resilience of the clear-water state of shallow lakes - a model study

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Abstract

The amount of terrestrial particulate organic matter (t-POM) entering lakes is predicted to increase as a result of climate change. This may especially alter the structure and functioning of ecosystems in small, shallow lakes which can rapidly shift from a clear-water, macrophyte-dominated into a turbid, phytoplankton-dominated state. We used the integrative ecosystem model PCLake to predict how rising t-POM inputs affect the resilience of the clear-water state. PCLake links a pelagic and benthic food chain with abiotic components by a number of direct and indirect effects. We focused on three pathways (zoobenthos, zooplankton, light availability) by which elevated t-POM inputs (with and without additional nutrients) may modify the critical nutrient loading thresholds at which a clear-water lake becomes turbid and vice versa. Our model results show that (1) increased zoobenthos biomass due to the enhanced food availability results in more benthivorous fish which reduce light availability due to bioturbation, (2) zooplankton biomass does not change, but suspended t-POM reduces the consumption of autochthonous particulate organic matter which increases the turbidity, and (3) the suspended t-POM reduces the light availability for submerged macrophytes. Therefore, light availability is the key process which is indirectly or directly changed by t-POM input. This strikingly resembles the deteriorating effect of terrestrial dissolved organic matter on the light climate of lakes. In all scenarios, the resilience of the clear-water state is reduced thus making the turbid state more likely at a given nutrient loading. Therefore, our study suggests that rising t-POM input can add to the effects of climate warming making reductions in nutrient loadings even more urgent.

Introduction

Small and shallow lakes are the most common lake type worldwide (Downing *et al.*, 2006) and are reported to exhibit alternative stable states (Scheffer and Jeppesen, 2007 and references therein). The clear-water state is stabilized by a number of positive feedback mechanisms facilitated by the presence of submerged macrophytes and resilient to nutrient loading up to a critical threshold (Scheffer *et al.*, 1993). By passing this threshold, the lake switches to a turbid, phytoplankton-dominated state which, in turn, is again resilient to reductions in nutrient loading; a phenomenon known as hysteresis (Scheffer *et al.*, 1993).

The effect of the input of terrestrial organic matter for ecosystem dynamics has rarely been investigated for lentic systems, but some studies have been conducted in lotic systems (reviewed by Bartels *et al.*, 2012b). Due to their high catchment to volume ratio, in particular small and shallow lakes are expected to be influenced by terrestrial organic matter input. Field observations (Solomon *et al.*, 2011) and whole-lake experiments (Cole *et al.*, 2006) have shown that the within-lake production may rely considerably upon terrestrial organic matter fluxes. Hence, terrestrial organic matter can represent an important resource for pelagic and benthic primary consumers, and may even support higher trophic levels (Carpenter *et al.*, 2005; Jones *et al.*, 1998). Most of the studies focused on terrestrial dissolved organic matter (t-DOM) in pelagic food webs. Experiments have revealed a positive correlation between the concentration of humic substances and bacterioplankton biomass (Tranvik, 1988), although the channeling of t-DOM into the production of higher tropic levels via bacteria is still under debate (Cole *et al.*, 2006; Grey *et al.*, 2001). The t-DOM loading affects the pelagic food web further due to its effects on light extinction, physical mixing and primary production (Carpenter *et al.*, 1998; Houser, 2006; Houser *et al.*, 2003). For example, an experiment in an oligotrophic, subarctic lake revealed a shift towards a more heterotrophic food web when t-DOM fluxes were elevated (Forsström *et al.*, 2013). A simple static model showed that an enhanced terrestrial organic matter input reduced the autochthonous primary production, and thus the total basal resource supply, in meso- to eutrophic lakes due to shading (Jones *et al.*, 2012).

In contrast, very little is known on the effect of terrestrial particulate organic matter (t-POM) on food webs of lakes. The main contribution of t-POM in temperate lakes is autumnal litterfall. Within the next decades, the terrestrial primary production is predicted to increase due to rising temperatures and elevated CO_2 concentrations (Amthor, 1995; Zaehle *et al.*, 2007) with the potential to raise the flux of t-POM into lakes. In contrast to t-DOM which leads to brownification (Pace and Cole, 2002), t-POM input is not considered to directly affect the light climate of lakes. Furthermore, a direct subsidy of bacterial production as found for t-DOM cannot be expected due to the particle size of leaves entering the lake, whereas primary consumers such as benthic macroinvertebrate shredders certainly profit from the enhanced resource availability (Bartels *et al.*, 2012a). Accordingly, the food web effects of t-POM input to lakes may differ markedly from those so far described for t-DOM influx.

The studies conducted so far suggest that our knowledge is particularly limited with respect to the indirect effects of terrestrial organic matter on lake ecosystems. Whereas single processes directly affected by terrestrial organic matter (e.g. organic matter consumption, light availability, oxygen dynamics) are often well described, indirect biotic and abiotic effects induced by terrestrial organic matter are often neglected, but can act additively or compensatory in relation to the direct effects. Furthermore, terrestrial organic matter is additionally a source of nutrients (phosphorus, nitrogen) which may stimulate primary production. Only consideration of the entire set of these interactive and feedback processes determines whether terrestrial organic matter inputs may modify the resilience of shallow lake ecosystems. Due to the bistability of small and shallow lakes, even small changes in external factors such as the recent and expected elevated input of terrestrial organic matter into lakes will likely lead to drastic changes in ecosystem functioning.

In our study, we use the integrative dynamic ecosystem model PCLake (Janse *et al.*, 2010) to analyze how rising t-POM inputs pulsed in autumn as sole effect or in combination with additional nutrients may affect shallow lake ecosystems in the context of alternative stable states. PCLake was designed to study the effect of eutrophication and is well established in the field of water quality management (for an overview see Mooij *et al.*, 2010). Recently, PCLake has also been used to predict effects of rising temperatures on shallow lakes (Mooij *et al.*, 2009; Mooij *et al.*, 2007). Their study showed that PCLake can be a useful tool to evaluate complex processes at the ecosystem level because it also includes multiple indirect effects via abiotic and biotic processes beyond the main interactions. We predict that t-POM input affects the transparency of shallow lakes and thereby their resilience to changes in nutrient loading by the combination of directly contributing to light extinction and indirectly by promoting the biomass of consumers. We separated three main pathways (t-POM consumption by zoobenthos, suspended t-POM consumption by zooplankton and suspended t-POM effects on light extinction) and studied them independently to each other and in concert. Hence, we extend previous studies by now also considering the manifold feedbacks at the ecosystem level to enhance our understanding of system dynamics and to facilitate management decisions in response to rising t-POM fluxes into shallow lakes.

Methods

PCLake

We used the well-established dynamical ecosystem model PCLake to identify effects of elevated terrestrial particulate organic matter (t-POM) input on the resilience of shallow lakes. In this context, we refer to ecological resilience as the magnitude of disturbance a system can absorb without shifting to an alternative stable state (Gunderson, 2000). We consider the resilience of the clear-water state as enhanced when the critical threshold of the driving variable increases at which the lake switches from the clear-water to the turbid state or vice versa, and we consider the resilience as reduced when both thresholds decrease.

PCLake was originally developed to study the effects of eutrophication in shallow lakes (Janse, 2005; Janse *et al.*, 1992), and has been used for many study purposes since then, including management options (Fragoso *et al.*, 2011; Janse *et al.*, 1995), littoral-pelagic coupling (Sollie *et al.*, 2008) and climate change (Mooij *et al.*, 2007; ter Heerdt *et al.*, 2007). It is a dynamic model which considers the main food web dynamics within the context of closed cycles of nutrients and matter in a non-stratifying lake. It considers a well-mixed water body and the sediment top-layer (Fig. 1). Spatial heterogeneity is not included. Stocks and fluxes are quantified in units of dry weight (representing carbon), nitrogen, phosphorus and, when relevant, also silicate. The nutrient-to-dry-weight ratios of the organic components are variable. The organisms are aggregated into functional groups. The pelagic food chain comprises three groups of phytoplankton (diatoms, green algae and cyanobacteria) which differ mainly in their nutrient and light requirements, zooplankton and planktivorous fish. The benthic food chain consists of zoobenthos, which consumes sediment organic matter and settled phytoplankton, and benthivorous fish. Both chains are linked by a shared top predator, the predatory fish. Macrophytes compete with phytoplankton for nutrients and light. They are (default) defined as one functional group, with a rooted part taking nutrients from the sediment and a shoot part that takes them from the water column. Cyanobacteria have a higher phosphorus affinity and maximum uptake rate than the other groups. For the green algae, the light dependency of growth is defined by a half-saturation function whereas a Steele function (considering inhibition by high light intensities) is used for the other groups. The light intensity at the water surface which is set by a sine curve (based on long-term averages for Dutch lakes) and the light extinction in the water column (Lambert-Beer’s law) determine the available light for primary production. The amount of macrophytes, phytoplankton, detritus and inorganic matter in the water column as well as the ‘background extinction’ of the water contribute to the light extinction. The temperature is (in the default setting) defined as sine curve with an average of 12°C and a variance of 10°C. Temperature effects on abiotic processes (nitrification, denitrification, mineralization, etc.) are covered by an exponential function. For biotic groups (phytoplankton, zooplankton, zoobenthos, etc.), Gaussian functions with an optimal growth temperature and a temperature variance are used. The cycles of carbon and nutrients comprise processes such as egestion, mineralization, sedimentation and resuspension of the organic and inorganic matter fractions in the water and sediment compartment. Additionally, PCLake comprises numerous other processes and feedbacks that are hypothesized to directly and indirectly control lake ecosystem functioning (Scheffer *et al.*, 1993). Some important ones are: benthivorous fish promote resuspension whereas macrophytes inhibit this process, macrophytes provide shelter and habitat for predatory fish, oxygen dynamics determine the mineralization rate and therefore the internal nutrient loading (for a detailed model description see Appendix 1 and Janse, 2005).

The model was calibrated against a combined data set from > 40 shallow lakes in Western Europe, with different loadings and characteristics (Janse, 2005; Janse *et al.*, 2010); variables used were chlorophyll-a, total P, total N, Secchi depth and macrophyte cover. The default model setting that is also used in this study, uses the characteristics resembling a realistic average shallow lake in the temperate zone (i.e. mean depth = 2 m, areal hydraulic loading = 20 mm d^{-1}, fetch = 1000 m, no infiltration or seepage, no surrounding wetland zone, slightly clayish sediment (30% dry matter, of which 10% is organic and 90% inorganic matter, the latter containing 10% clay particles)). The model outcome is sensitive to these lake characteristics (Janse *et al.*, 2008). However, by using average lake characteristics, our study revealed generic and broadly applicable results.

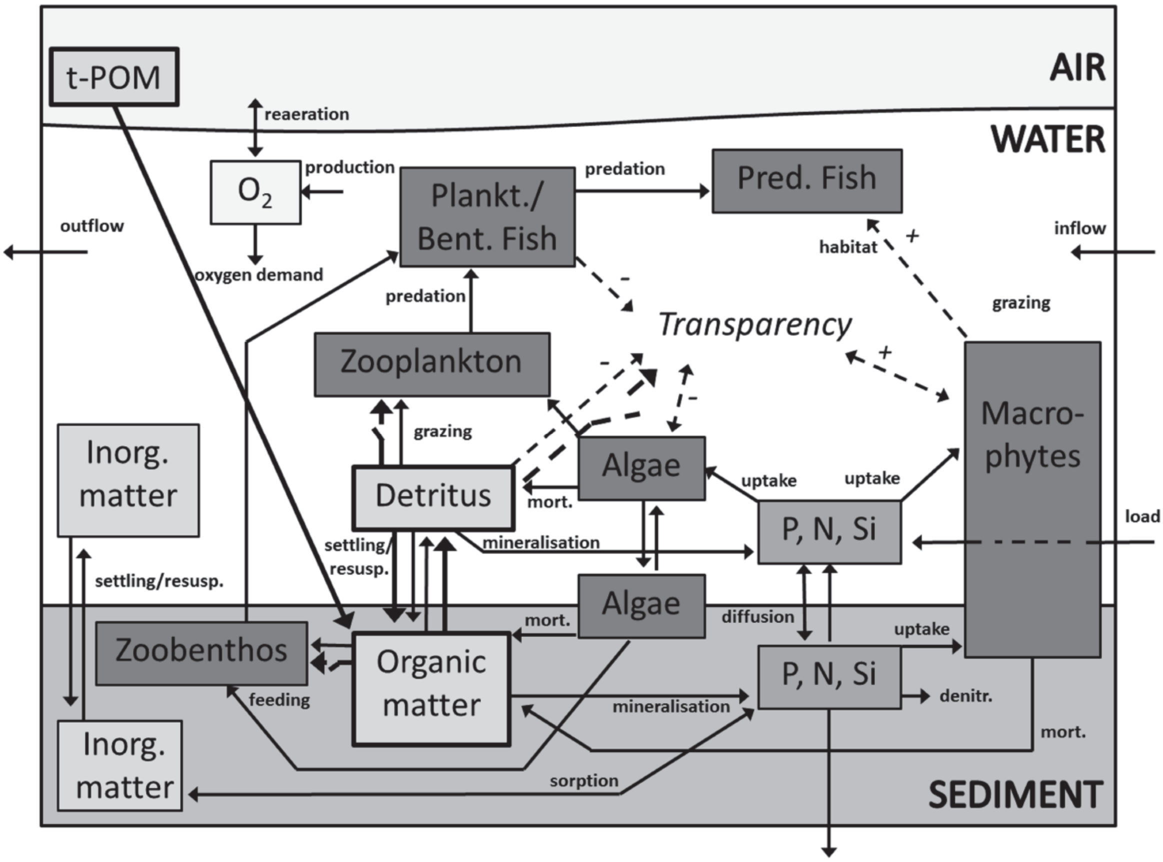

Figure 1. Overview of the main biotic and abiotic components in the open water and sediment compartments of PCLake. Solid arrows represent transfer of matter, dashed arrows represent functional relationships without transport of matter. State variables and processes whose model equations were adapted to separate effects of different pathways of t-POM are highlighted with bold boxes and arrows. The three main pathways of t-POM (via zoobenthos, zooplankton and light) could be switched on and off (extended after Janse *et al*. 2010).

Critical phosphorus loading (CPL)

The lake ecosystem modeled by PCLake shows a highly non-linear response to rising nutrient loadings (Janse, 1997). The phosphorus loading has been considered as driving variable. The modeled lakes are bistable for a wide range of parameterizations (Janse *et al.*, 2008) which means they are in the clear-water, macrophyte-dominated state with low chlorophyll concentrations at low nutrient loadings and in the turbid, phytoplankton-dominated state with high chlorophyll concentrations at high nutrient loadings (Fig. 2). At intermediate nutrient loadings, both states are stable and the prevalent state depends on the foregoing conditions. When enhancing the nutrient loading, the clear-water state switches to the turbid state at a higher critical phosphorus loading (CPL_{eu}) compared to the critical phosphorus loading (CPL_{oligo}) at which the turbid state switches back to the clear-water state during oligotrophication. The two critical phosphorus loadings are defined as the phosphorus (P) loading at which the lake is still clear (CPL_{eu}) starting with a clear lake (eutrophication) and at which the lake is again clear (CPL_{oligo}) starting with a turbid lake (oligotrophication), respectively. The CPL_{eu} and CPL_{oligo} are used to quantify the resilience of the clear-water state.

Bifurcation analysis

To derive the CPL values, we run the model for 30 years at different P loadings, which varied between 0.1 and 4 mg P m^{-2} d^{-1} in steps of 0.1, starting with either an initially clear-water or an initially turbid lake. The nitrogen loading was consistently 10 times the P loading to maintain phosphorus limitation (cf. Janse *et al.*, 2008). We focused for our analyses on the average Secchi depth and chlorophyll concentration during the last year of simulation to quantify the CPLs under eutrophication and oligotrophication. The lake was defined as clear if the whole-year average Secchi depth was > 50% of the lake depth (i.e. > 1 m) and the chlorophyll concentration was below 25 mg m^{-3}. Otherwise, the lake was defined as turbid.

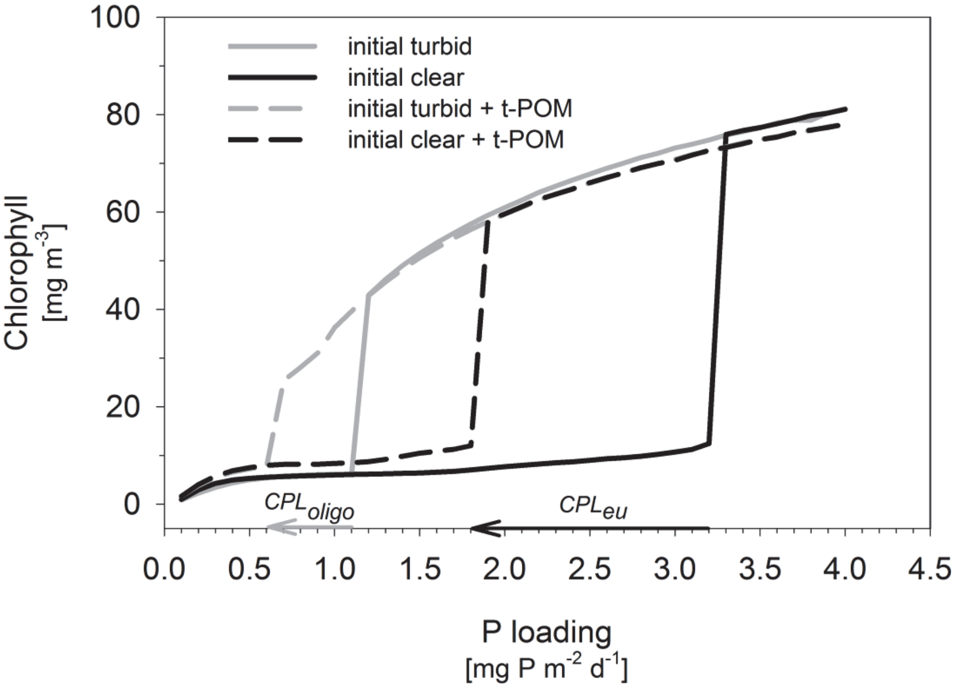

Figure 2. The combined effect of t-POM on the critical nutrient loading (CPL) of the hysteresis curve modeled over a range of P loadings showing switches in the whole-year average chlorophyll concentration. Gray lines indicate simulations for an initially turbid lake and black lines simulations for an initially clear lake. Solid lines present the scenario without t-POM input and dashed lines with the highest t-POM input rate (8 g dw m^{-2} d^{-1} in autumn) without accompanied nutrients. Arrows indicate the shift of the critical nutrient loadings (CPL) at which the clear lake switched to the turbid state (CPL_{eu}) and the turbid lake switched to the clear-water state (CPL_{oligo}).

Terrestrial particulate organic matter

As the majority of the annual t-POM flux will be leaves of terrestrial plants which enter temperate lakes in autumn during litterfall (Dixon, 1976), we simulated an addition of pulsed t-POM during 30 days in autumn (Day 274 – 303) in each of the 30 simulation years. The t-POM entered the lake ecosystem via the organic matter pool in the sediment. Within the modeled lake ecosystem, we studied three main pathways by which t-POM could modify the structure of the lake, its food web and its resilience. The first pathway is the consumption of t-

POM by zoobenthos with several subsequent indirect effects, the second one is the consumption of suspended t-POM by zooplankton with several subsequent indirect effects, and the third one the contribution of suspended t-POM to light extinction and the accompanying changes of other processes (Fig. 1). The model complexity bears the risk that, as in whole-ecosystem studies, the underlying mechanisms of the outcome can hardly be identified (Scheffer and Beets, 1994). Following van Nes and Scheffer (2005), we overcame this difficulty by scrutinizing the model for the sensitivity to nutrient loading and t-POM input. Additionally we slightly simplified the model in considering only the pathways mentioned and modified PCLake to such an extent that we could track the processing of t-POM via each of the three studied pathways separately from each other, and from the pathways of autochthonously produced organic matter (Fig. 1).

Scenarios

Studies evaluating the natural amount of t-POM input by litterfall are rare and vary by one order of magnitude (France and Peters, 1995 and references therein). For a small shallow lake (10 ha), the t-POM input was estimated at 0.3-3 g dw m^{-2} d^{-1} in October. To our knowledge, predictions concerning the elevated t-POM amount are not reported. We accounted for a 2-25 fold elevated t-POM input (0.3 - 8 g dw m^{-2} d^{-1} in autumn) based on the reported autumnal t-POM inputs (France and Peters, 1995 and references therein).

We started our bifurcation analysis by adding 8 g dw m^{-2} d^{-1} t-POM in autumn (carbon only, equals 0.66 g dw m^{-2} d^{-1} t-POM when averaged over the whole year), which adds approximately 50% to the annual average within-lake sediment organic matter pool in the clear-water state and respectively about 100% in the turbid state, and checked how the t-POM addition modified the CPL values when all three pathways were acting simultaneously. Subsequently, in a factorial design, we tested the sensitivity of PCLake to t-POM additions by varying the t-POM input using seven concentrations (0; 0.3; 0.6; 1; 2; 4; 8 g dw m^{-2} d^{-1}) and by using t-POM that consisted of both carbon and nutrients, using a stoichiometric composition of 40 g DW : 1 g N : 0.1 g P or 200 g DW : 1 g N : 0.1 g P (Ostrofsky, 1997). This implies an additional nutrient loading of 20 mg P m^{-2} d^{-1} in autumn for the 8 g dw m^{-2} d^{-1} t-POM loading scenario using the low carbon : nutrient ratio (which equals 1.65 mg P m^{-2} d^{-1} when averaged over the year). Furthermore, to elaborate on the relative importance of each of the three proposed pathways (via zoobenthos, zooplankton and light), we repeated the bifurcation analyses for all t-POM concentrations with and without nutrients but switched each pathway on and off separately to quantify their effects on the CPLs independently. To illuminate the effect of additional t-POM on the biotic functional group level, we inspected biomasses and process rates and compared scenarios with the lowest t-POM addition to scenarios with higher t-POM loadings in the clear-water state (P loading 0.7 mg P m^{-2} d^{-1}) and in the turbid state (P loading 3.3 mg P m^{-2} d^{-1}), using t-POM consisting only of carbon. This enabled us to explain effects of elevated t-POM more mechanistically.

Results

The addition of the highest t-POM amount (8 g dw m^{-2} d^{-1} in autumn) to the modeled ecosystem reduced the CPL_{eu} by 1.5 mg P m^{-2} d^{-1} and CPL_{oligo} by 0.5 mg P m^{-2} d^{-1}, which reduced the range of P loadings along which we observed bistability, i.e. the resilience of the clear-water macrophyte-dominated state was also reduced (Fig. 2). Although the absolute reduction of CPL_{eu} was larger than that of CPL_{oligo}, the relative reductions of CPL_{oligo} (45%) and CPL_{eu} (44%) were very similar.

Increasing t-POM loadings decreased both CPLs for all the t-POM flux rates modeled (Fig. 3a, solid lines), though the decrease of CPL_{eu} was stronger than that of CPL_{oligo}, therefore diminishing the range of P loading across which bistability can occur. In the model, the additional t-POM reduced the CPLs via each of the three studied pathways (Fig. 3b, solid lines), and the reduction of CPL_{eu} and CPL_{oligo} was very similar for the three pathways when considered separately. At the highest t-POM loading, the consumption of t-POM by zoobenthos alone resulted in a CPL_{eu} of 2.7 mg P m^{-2} d^{-1} and a CPL_{oligo} of 0.8 mg P m^{-2} d^{-1}. Considering only the consumption of suspended t-POM by zooplankton, these values became 2.4 and 0.7 mg P m^{-2} d^{-1}, respectively. An analysis of the sole contribution of suspended t-POM to light extinction resulted in values of 2.6 and 0.8 mg P m^{-2} d^{-1}, respectively. This striking resemblance in impact means that the resilience of the clear-water, macrophyte-dominated state was reduced almost equally via each of the three pathways of t-POM. When the highest amount of added t-POM was channeled along all three pathways simultaneously, the CPLs were more strongly reduced (44 – 45%) than when adding the same amount of t-POM to an individual pathway (16 – 36%) (cf. Fig. 3a & 3b).

The addition of t-POM accompanied by nutrients (40 g DW : 1 g N : 0.1 g P) resulted in a both relatively and absolutely stronger reduction of the CPLs via the three pathways separately and the combined effect compared to the addition of t-POM without nutrients (Fig. 3, dotted lines). The range of P loadings along which we observed bistability was reduced more strongly when we added t-POM accompanied by nutrients than when only t-POM consisting of carbon was added (Fig. 3). For the highest t-POM addition accompanied by nutrients, a lake once shifted to a turbid state could not switch back to the clear-water state by any reduction of P loading. Scenarios with lower t-POM DW : nutrient ratios (200 g DW : 1 g N : 0.1 g P) revealed CPL reductions intermediate between scenarios without accompanied nutrient additions and scenarios with high t-POM DW : nutrient ratios (data not shown).

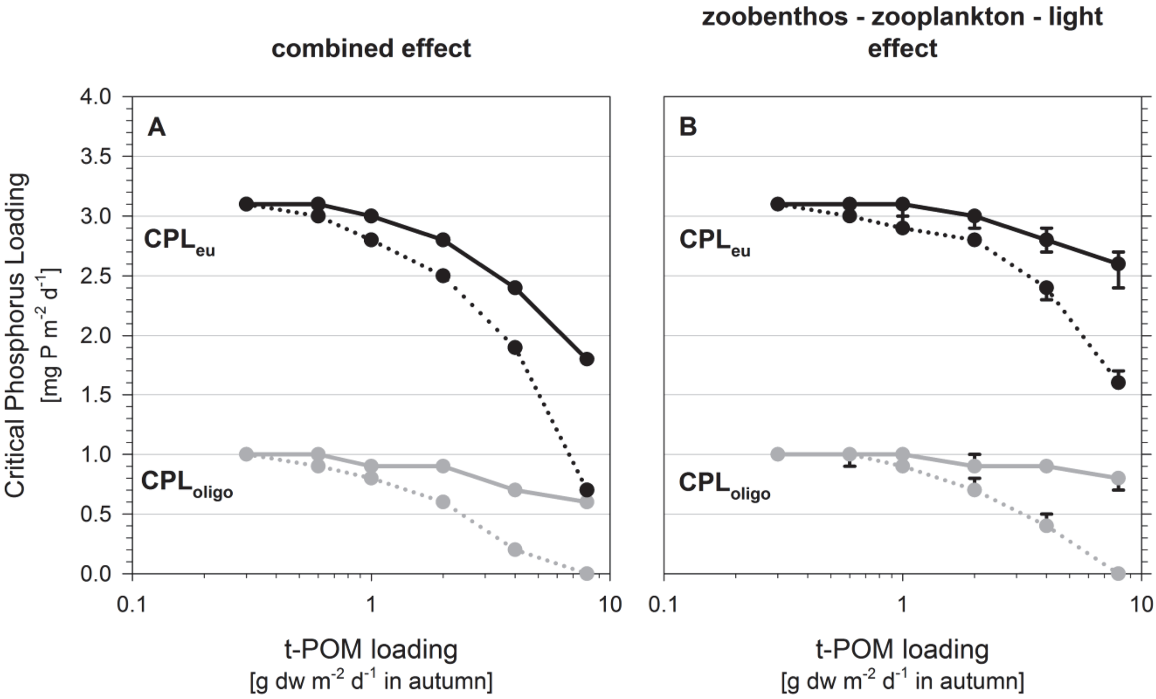

Figure 3. Simulations were done for a broad range of terrestrial particulate organic matter (t-POM) loading in autumn (Day 274 – 303). Black lines indicate the CPLs at which the initially clear lake switched to the turbid state (CPL_{eu}) and gray lines indicate CPLs where the initially turbid lake switched to the clear-water state (CPL_{oligo}). We modeled t-POM loading as sole carbon input (solid lines) and as carbon input accompanied by nutrients (40 g DW : 1 g N : 0.1 g P) (dotted lines). (a) Circles represent the CPL for the combined effect; (b) CPL for the three pathways; circles represent the median CPL of all three effects and vertical bars indicate the range of CPL for the three pathways.

The addition of t-POM (carbon only) with its consumability by zoobenthos ‘switched on’ raised the zoobenthos and benthivorous fish biomass (Fig. 4 – pathway 1, Appendix 2). As benthivorous fish forage at the sediment surface, their increased biomass resulted in a higher bioturbation of autochthonous detritus and inorganic matter which reduced the transparency. This affected the light-sensitive macrophytes more strongly than phytoplankton and thereby reduced the resilience of the clear-water state. The addition of t-POM under the assumption that it can be suspended into the water column and consumed by zooplankton revealed no change in the zooplankton biomass (Fig. 4 – pathway 2; Appendix 2, 3). The amount of food consumed by zooplankton and their production remained rather constant but the food composition switched towards more t-POM. Thereby the consumption of autochthonous detritus in the water column declined, and its quantity increased. This again reduced transparency, suppressed the macrophytes and reduced the resilience of the clear-water state. Finally, the suspended t-POM and its contribution to light extinction reduced directly the available light for primary producers (Fig. 4 – pathway 3, Appendix 2), reducing submerged macrophytes and thus the resilience of the clear-water state.

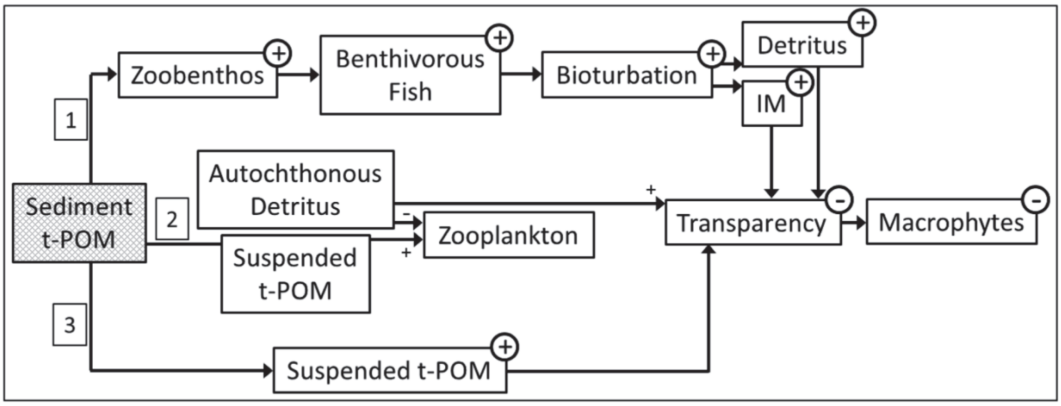

Figure 4. An elevated terrestrial particulate organic matter (t-POM) input affects the resilience via three different pathways. Sediment t-POM is presented as shaded box. Unshaded boxes present compartments in the water. Positive and negative signs at boxes indicate changes in biomasses, bioturbation and transparency. Positive and negative signs at arrows indicate changes in the per capita food consumption for zooplankton or an enhanced contribution of detritus to the transparency reduction (see text for detailed description of the pathways, IM: inorganic matter).

Discussion

Our model study suggests that an enhanced input of terrestrial particulate organic matter (t-POM) pulsed in autumn will reduce the resilience of the macrophyte-dominated clear-water state of shallow temperate lakes. Hence the likelihood that shallow lakes will shift to or stay in the turbid state with all the accompanied problems such as loss of biodiversity and deteriorated water quality (Scheffer *et al.*, 1993) will likely be enhanced by the predicted increasing t-POM input to lakes in the future. Remarkably, all three main processes which we studied separately and in concert finally modified lake transparency, and hence light availability is the key factor which determines the resilience of shallow lakes. This resembles the deteriorating effects of terrestrial dissolved organic matter (t-DOM) on light climate in lakes (Ask *et al.*, 2009; Karlsson *et al.*, 2009), albeit that the presumed underlying mechanisms are somewhat different.

The effect on the critical phosphorus loadings (CPL) when all pathways were considered in concert (combined effect) was, as expected, stronger than each effect separately but less strong than the cumulative reduction of the three effects separately. The addition of the threefold amount of t-POM in the combined effect exceeded the CPL reduction observed via each pathway individually due to differences in the distribution of t-POM into the three pathways. For example, the unused t-POM in the zoobenthos pathway can contribute to the zooplankton and extinction pathway in the combined effect. Therefore, the magnitude of changes in biomasses and process rates via the three separately studied pathways may only be seen as hints for the actual underlying mechanisms (Appendix 2). Nevertheless we were able to identify plausible key mechanisms how t-POM may modify the response of the shallow lake ecosystem to rising nutrient loadings.

In a mesocosm experiment, the addition of t-POM contributed up to 28% to the diet of zoobenthos which was however not reflected in a biomass increase (Bartels *et al.*, 2012a). In contrast, the only available whole-lake experiment testing the effect of t-POM (maize leaves and stems) on two divided shallow lake ecosystems (turbid and clear-water, respectively) (Attermeyer *et al.*, 2013) revealed a significant increase in the biomass of several zoobenthos groups in the treatment sides as compared to the controls (Scharnweber 2013). Our model supports the latter findings, as t-POM consumption by zoobenthos resulted in an increase of its biomass and a subsequent numerical response of benthivorous fish. However, in the model the higher benthivorous fish biomass did not affect the pelagic food chain as top down effects via the predatory fish remained weak. The decisive process influencing the resilience was instead an increase in bioturbation and thus sediment resuspension by more bottom-feeding benthivorous fish which increased turbidity and thus hampered macrophyte growth. This effect may strongly depend on the sediment type and benthivorous fish species present. However, experimental studies in general confirm the positive relation between benthivorous fish biomass and extinction (Adamek and Marsalek, 2013; Breukelaar *et al.*, 1994).

The predatory fish remained largely unaffected by elevated t-POM input and hence little changes in top down effects in the pelagic and benthic food chain were observed. Even a simulation scenario considering a stronger top down control of benthic and pelagic fish by predatory fish did not change the overall results (results not shown). Accordingly, the model reflected the often suboptimal growth conditions of predatory fish in eutrophic lakes (Jeppesen *et al.*, 2000). This result is in line with observations from streams where higher trophic levels were less affected by t-POM subsidies than lower trophic levels due to their higher degree of omnivory and thus a lower contribution of t-POM to their diet (Marczak *et al.*, 2007). Therefore, in shallow eutrophic lakes a biomass increase in the benthic food chain due to an elevated t-POM input is unlikely to become balanced by a strong trophic cascade from high predatory fish biomass in the pelagic zone, and hence a top-down directed control of the resilience of the clear-water state is unlikely.

Zooplankton relies on terrestrial carbon (Cole *et al.*, 2006) and experiments showed a direct consumption of t-POM as well as an indirect consumption via microbes, but without an effect on zooplankton biomass in response to t-POM input (Bartels *et al.*, 2012a). However, the contribution of t-POM to the diet of zooplankton is still under debate (Francis *et al.*, 2011) and, depending on the relevance of t-POM for zooplankton, our model may over- or underestimate effects of rising t-POM via this pathway. A constant biomass despite changes in t-POM input (as found by Bartels *et al.*, 2012a) is in line with our model results and supports our findings that the zooplankton switched its food composition rather than increased overall biomass and consumption. In line with Gulati *et al.* (1982), the food consumption of zooplankton was modeled using a filtering rate which depends on the amount of available food and decreases with the seston concentration. In our model, the per capita consumption of the highly preferred algae remained almost constant but the per capita consumption of the less preferred autochthonous detritus decreased due to food interference when equally preferred suspended t-POM was available as additional food for zooplankton. Hence, the amount of autochthonous detritus in the water increased when suspended t-POM was available as additional food for zooplankton which reduced the transparency and thus hampered macrophyte growth (for further explanation see Appendix 3). In a scenario that did not account for the functional response suggested by Gulati *et al.* (1982), the zooplankton biomass did increase with elevated t-POM fluxes (results not shown).

Our model result provides multiple evidence that t-POM can influence the dominance switch between macrophytes and phytoplankton via light availability. Both resource-mediated pathways ended up in a reduction of the available light via indirect effects which suppressed macrophytes and thus decreased the resilience of the clear-water state. The resilience of the clear-water state was also reduced via the third pathway where detritus suspended from t-POM into the water contributed to light extinction. Previous studies showed that macrophyte growth is hampered by shading through colored dissolved organic matter (Dillon and Molot, 1997; McKnight and Aiken, 1998). The negative effect of the reduction of available light by terrestrial organic matter was shown recently with a static model based on empirically determined parameters and a variety of regressions from the literature (Jones *et al.*, 2012). In their model, especially the benthic primary production (periphyton) decreased due to shading by t-DOM. In PCLake, the macrophytes were those primary producers which were most vulnerable for light availability (Janse *et al.*, 2008). Field measurements revealed a sevenfold greater efficiency of light utilization for phytoplankton than for submerged macrophytes at low light (Sand-Jensen and Madsen, 1991). Thus a reduction in the available light always negatively affects the resilience of the clear-water state. In our model, phytoplankton growth can also be reduced due to lower light availability by additional t-POM as observed in lake ecosystems (Jones, 1992), but if so, this effect is overlaid by the effects on the macrophytes. Other studies have shown that apart from t-POM also increased input of t-DOM can reduce light availability and hence may hamper macrophyte growth. In the model, this effect might be mimicked by an increase of the background extinction, as its definition in the model includes dissolved substances. This has not been elaborated in this study.

Experiments considering a variety of habitats suggested that the subsidy effect of allochthonous resources on the organism level appeared to be largest in systems with low levels of comparable resources as the addition to these systems is large compared to autochthonous resources (Marczak *et al.*, 2007). Whole-lake experiments further showed that the relative use of terrestrial organic matter by aquatic organisms decreased with increasing nutrient concentrations (Carpenter *et al.*, 2005; Cole *et al.*, 2006). From these experimental results we would suggest the rising t-POM input to have a stronger effect during oligotrophication ($\mathrm{CPL}_{\mathrm{oligo}}$) as these systems have less nutrients and a smaller autochthonous matter pool than the systems showing eutrophication ($\mathrm{CPL}_{\mathrm{eu}}$). If we compare the relative change in the CPLs, our model results confirm these former experimental results. However, in absolute terms, our model study revealed a stronger reduction for the system with higher nutrient concentrations and a larger autochthonous matter pool, due to the large amount of unconsumed macrophyte biomass and debris in the clear-water state.

Beyond quantity, also the quality of t-POM may be relevant. Additional nutrient loads may reinforce the effect of t-POM as shown by our study where t-POM inputs of higher quality i.e. a lower carbon : nutrient ratio, primarily favored the phytoplankton and thus reduced the resilience of the macrophyte-dominated state to a larger extent than the addition of t-POM with a high carbon : nutrient ratio. At the global scale, croplands, pastures, plantations, and urban areas still expand (Foley *et al.*, 2005) bearing the risk of increasing loading of nutrient-rich matter to lakes which according to our simulations will reduce the resilience of the clear-water state even stronger than t-POM input with low nutrient contents.

Our simulations revealed that direct interactions among adjacent trophic levels (e.g. the missing transfer of trophic effects via the top predator) were less relevant than indirect, biotic effects (e.g. light limitation as a result of food switch) and non-trophic interactions (e.g. bioturbation) for the impact of elevated t-POM on the bistability of shallow lakes. This is in line with the concept of alternative stable states of shallow lakes. The main interactions between macrophytes and phytoplankton, which determine the prevalent stable state, are defined by abiotic processes like nutrient and light availability whereas trophic interactions are usually of subordinate importance (Scheffer *et al.*, 1993). PCLake did not account for all potential pathways of additional t-POM like periphyton - macrophyte interactions (Jones and Sayer, 2003), direct inhibition of phytoplankton and macrophytes by humic substances (Steinberg *et al.*, 2006) and omnivorous fish showing a short term behavioral and a long term numerical response to the altered resource availability in the littoral food chain. We are aware that the model structure partly dictated a general framework for the results which we did not overcome as we avoided redoing the calibration and validation of PCLake which has been done before by Bayesian statistics (Aldenberg *et al.*, 1995; Janse *et al.*, 2010). However, we are convinced that this model nevertheless promotes our understanding of the functioning of lake ecosystems in response to t-POM input.

Conclusion

We analyzed the effect of the predicted elevated future input pulse of t-POM in autumn into shallow lakes on the bistability of these ecosystems using the integrative ecosystem model PCLake. Each of the three studied pathways declined the water transparency, hampered macrophyte growth and thus reduced the resilience of the clear-water, macrophyte-dominated state. Thus in response to climate change including effects of warming (Mooij *et al.*, 2007) and rising t-POM fluxes, the turbid, phytoplankton-dominated state will become more likely already at intermediate nutrient loadings. Our model analysis thus predicts that a further reduction in nutrient loading is required to maintain the clear-water state in temperate shallow lakes.

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Supporting Information

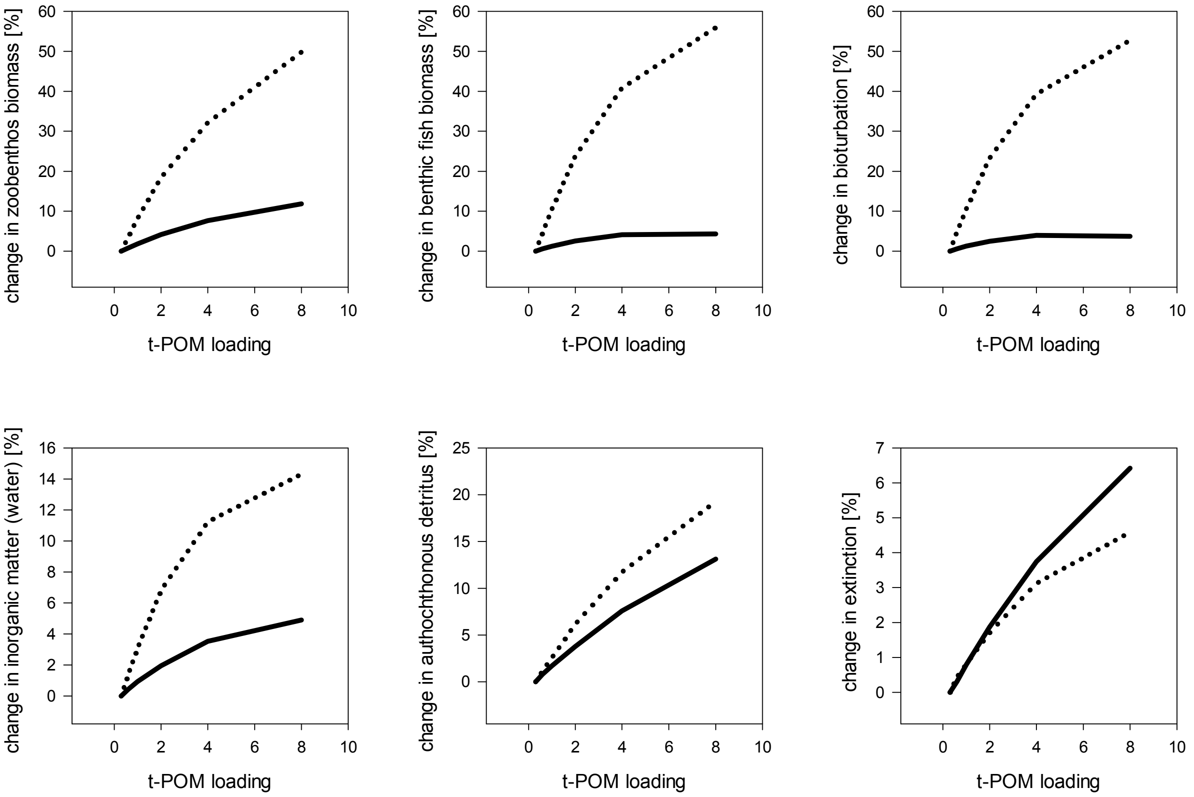
Appendix 1: State variables

Appendix 1 – Table 1. State variables in PCLake.

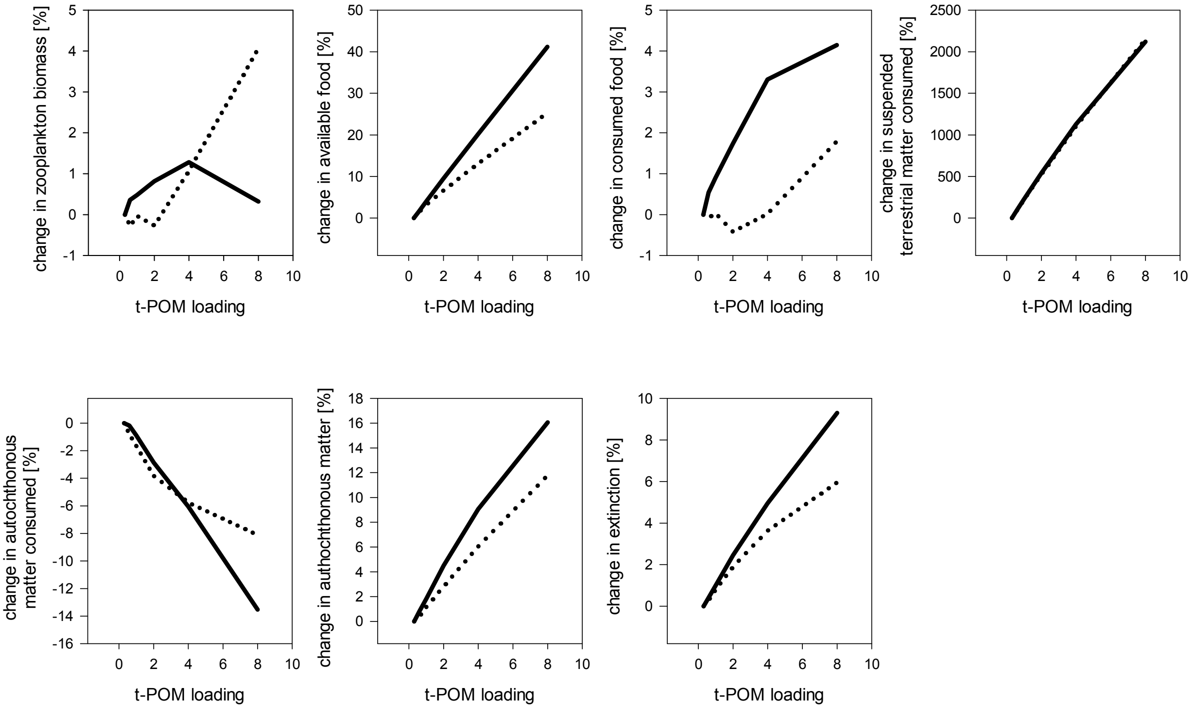
Component (state variable)	In water column	In sediment top layer
Water		
water depth	water	-- (fixed)
Abiotic components		
inorganic matter (IM)	D	D
humus	--	D
detritus	D, P, N, Si	D, P, N, Si
nutrients	PO_4, P_{ads}, NH_4, NO_3, SiO_2	PO_4, P_{ads}, NH_4, NO_3
oxygen	O_2	-- (aerobic fraction)
Phytoplankton		
diatoms	D, P, N, (Si)	D, P, N, (Si)
green algae	D, P, N	D, P, N
cyanobacteria	D, P, N	D, P, N
Vegetation		
submerged vegetation	D, P, N	
Animal groups		
zooplankton	D, P, N	
zoobenthos	D, P, N	
planktivorous fish	D, P, N	
benthivorous fish	D, P, N	
predatory fish	D, (P, N)	

Abbreviations: D = dry weight, P = phosphorus, N = nitrogen, Si =silica, O_2 = oxygen.

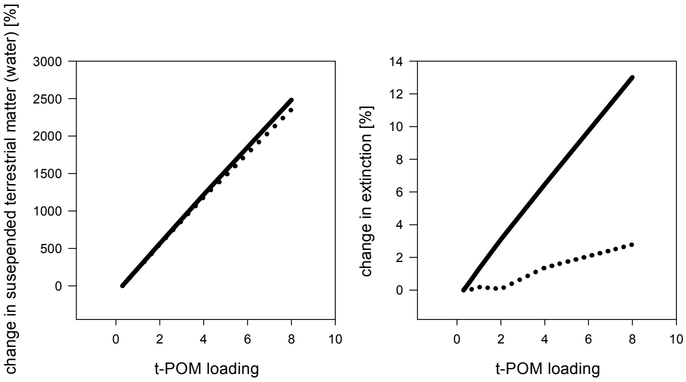
Appendix 2: changes in biomasses and process rates over range of t-POM loading for the three pathways



Appendix 2 – Figure 1. The percental change in variables belonging to the zoobenthos pathway over a range of t-POM loadings [g dw m^{-2} d^{-1} in autumn]. The percental change is based on the lowest t-POM loading. Scenarios in the clear-water state (P load 0.7 mg P m^{-2} d^{-1}) are presented as solid lines and in the turbid state (P load 3.3 mg P m^{-2} d^{-1}) as dotted lines. Consider the different scaling of the y-axes. Read figures from left to right and top to bottom to follow mechanistic sequence of t-POM effects.



Appendix 2 – Figure 2. The percental change in variables belonging to the zooplankton pathway over a range of t-POM loadings [g dw m^{-2} d^{-1} in autumn]. The percental change is based on the lowest t-POM loading. Scenarios in the clear-water state (P load 0.7 mg P m^{-2} d^{-1}) are presented as solid lines and in the turbid state (P load 3.3 mg P m^{-2} d^{-1}) as dotted lines. Consider the different scaling of the y-axes. Read figures from left to right and top to bottom to follow mechanistic sequence of t-POM effects.



Appendix 2 – Figure 3. The percental change in variables belonging to the extinction pathway over a range of t-POM loadings [g dw m^{-2} d^{-1} in autumn]. The percental change is based on the lowest t-POM loading. Scenarios in the clear-water state (P load 0.7 mg P m^{-2} d^{-1}) are presented as solid lines and in the turbid state (P load 3.3 mg P m^{-2} d^{-1}) as dotted lines. Consider the different scaling of the y-axes. Read figures from left to right to follow mechanistic sequence of t-POM effects.

Appendix 3: functional response zooplankton

The functional response for zooplankton is implemented in PCLake according to Gulati *et al.* (1982) who found in a long-term study that an increased amount of an unpreferred food reduced the total amount of food consumption above a certain food concentration. To illuminate this type of functional response we compare it for a system with one prey (A - preferred) and with two prey (A, B - unpreferred). The predator has a certain preference for each prey, pA and pB with pA > pB. Without loss of generality we put pA=1. Both functional responses, $f(A) = \frac{A}{h+A}$ and $f(A+B) = \frac{A+pB*B}{h+A+B}$, have the same half-saturation constant h (Eq. 1). The presence of the additional food B enhances the overall food consumption per predator when A is relatively low and reduces it at high concentrations of A (Appendix 3 – Fig. 1). The threshold value of A when the food consumption is equal with or without B can be determined in the following way:

$$f(A) = \frac{A}{h+A} = \frac{A+pB*B}{h+A+B} = f(A+B) \qquad (1)$$

This equation can be rearranged into:

$$A*(h+A+B) = (A+pB*B)*(h+A)$$

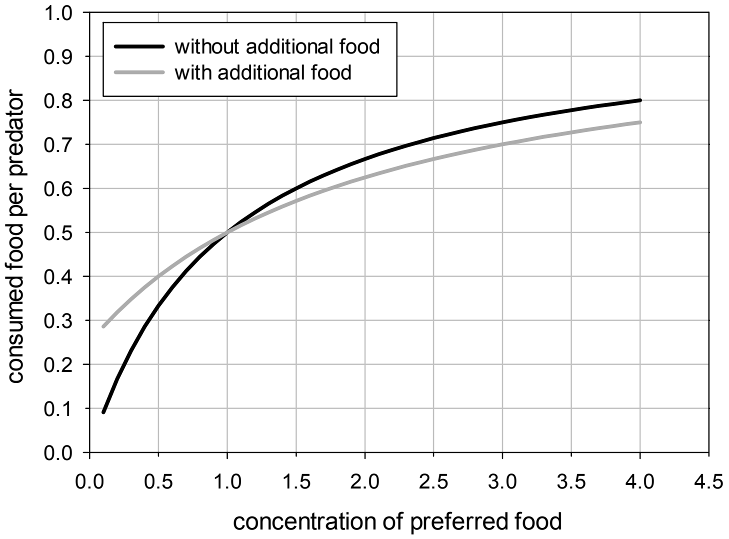
$$A*h+A*A+A*B = A*h+pB*B*h+A*A+pB*B*A$$

$$A*B = pB*B*h+pB*B*A$$

$$\frac{A*B}{B*h+B*A} = pB$$

$$\frac{A}{h+A} = pB \qquad (2)$$

Given that during most of the simulations done with PCLake the equivalent term $\frac{A}{h+A}$ is larger than pB, the additional food B often reduces the overall food consumption (Appendix 3 – Fig. 1).



Appendix 3 – Figure 1. The consumed food per predator increases as a function of the concentration of the preferred food (A) less steep when an additional less preferred food (B) is available. (pB=0.5; B=1; h=1)

Chapter II

Contrasting response of two shallow eutrophic lakes to a partial winterkill of fish

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Abstract

Food-web effects of winterkill are difficult to predict as the enhanced mortality of planktivorous fish may be counterbalanced by an even higher mortality of piscivores. We hypothesized that a winterkill in a clear and a turbid shallow lake would equalize their fish community composition, but seasonal plankton successions would differ between lakes. After a partial winterkill, we observed a reduction of fish biomass by 16% and 43% in a clear-water and a turbid small temperate lake, respectively. Fish biomass and piscivore shares (5% of fish biomass) were similar in both lakes after this winterkill, but young-of-the-year (YOY) abundances were higher in the turbid lake. Top-down control by crustaceans was only partly responsible for low phytoplankton biomass at the end of May following the winterkill in both lakes. Summer phytoplankton biomass remained low in the clear-water lake despite high abundances of YOY fish (mainly roach). In contrast, the crustacean biomass of the turbid lake was reduced in summer by a high YOY abundance (sunbleak and roach), leading to a strong increase in phytoplankton biomass. The YOY abundance of fish in shallow eutrophic lakes may thus be more important for their summer phytoplankton development after winterkill than the relative abundance of piscivores.

Introduction

Temperate shallow lakes can exhibit alternative stable regimes. They can be either turbid and phytoplankton-dominated or clear with abundant submerged macrophytes (Scheffer *et al.*, 1993), with potentially long phases of so-called crashing conditions in between (Hilt *et al.*, 2013). Macrophytes can maintain high water clarity during increased external nutrient loading through mechanisms such as allelopathy, nutrient and light competition with phytoplankton, and the provision of refuges for zooplankton and periphyton grazers (Moss, 1990; Scheffer *et al.*, 1993). Food-web effects exerted by fish can also contribute to contrasting water transparency in shallow lakes. Abundant planktivorous and omnivorous fish feeding on herbivorous crustaceans may reduce grazer control on phytoplankton and hence facilitate the turbid state (Jeppesen *et al.*, 1997). Similarly, benthivorous fish such as bream (*Abramis brama*) may contribute to turbidity by stirring up sediments during the feeding process (Breukelaar *et al.*, 1994; Meijer *et al.*, 1990). In turn, high densities of piscivorous fish may suppress planktivorous, omnivorous and benthivorous fish, and hence may indirectly facilitate the clear-water state (Jeppesen *et al.*, 1997).

Winterkill (the partial or complete eradication of a fish community in the wintertime due to oxygen depletion) is a common phenomenon among shallow lakes in regions with long or severe winters (e.g. Danylchuk and Tonn, 2006; Greenbank, 1945; Ruuhijärvi *et al.*, 2010), but also occurs at intermediate latitudes after exceptionally long durations of ice and/or snow cover, especially in eutrophic shallow lakes (Balayla *et al.*, 2010). As a consequence of reduced predation by planktivorous and omnivorous fish, a higher proportion of large-bodied zooplankton (e.g., *Daphnia*) with a high grazing capacity on phytoplankton has been observed to follow winterkills, inducing higher water clarity (Balayla *et al.*, 2010; Jeppesen *et al.*, 2010; Ruuhijärvi *et al.*, 2010; Schindler and Comita, 1972). However, esocids and other piscivores are reported to be more sensitive to low oxygen levels than omnivorous cyprinids (e.g. Doudoroff and Shumway, 1970) and, further, larger size classes of pike (*Esox lucius*) usually suffer from higher mortality than younger ones (e.g. Casselman and Harvey, 1975; Grimm and Backx, 1990). Therefore, the food-web effects of an enhanced mortality of planktivorous or benthivorous fish during a partial winterkill may be counterbalanced by an even higher mortality of piscivores. The abundance of the piscivorous pike tends to be higher in macrophyte-dominated lakes (Grimm and Backx, 1990; Persson *et al.*, 1991), whereas benthivorous fish such as bream usually dominate in turbid shallow lakes (Persson *et al.*, 1991). Partial winterkills may reduce the abundances of both benthivorous and piscivorous fish. This way they can produce similar fish community compositions in macrophyte- and phytoplankton-dominated shallow lakes, with omnivorous species such as roach (*Rutilus rutilus*) dominating after the partial winterkill. It has been hypothesised that the selective loss of piscivores during partial winterkills may induce a switch of clear-water lakes into the turbid state (Brönmark and Weisner, 1992). In turn, Kosten *et al.* (2009) suggested that a high abundance of submerged plants in regions with cold winters, which was observed in many lakes despite high nutrient levels, could be an indirect result of winterkills, because lowered abundances of planktivorous fish may enhance grazer control of phytoplankton and periphyton. Therefore, massive fish losses after winterkill may also induce a switch from a turbid to a macrophyte-dominated state.

In this study, we hypothesised that a partial winterkill would reduce both total fish biomass and the relative abundance of piscivores within the fish community of clear and turbid shallow lakes. This may result in a similar fish community composition with a dominance of omnivorous species such as roach. We further hypothesised that the presence of submerged macrophytes in the clear lake can prevent a shift to turbid conditions following a partial winterkill. Turbid lakes may become clear at least temporarily due to a lower predation pressure of fish on crustaceans. To test these hypotheses, we compared the abundance and biomass of fish, stable carbon isotope values ($\delta^{13}C$) of roach (the dominant fish species) and crustaceans, and the seasonal development of phytoplankton biomasses in two small, temperate, eutrophic and shallow lakes before (2007) and after (2010) a natural partial winterkill in winter 2009/10. Before the partial winterkill, one lake was characterised by higher water clarity and the presence of submerged macrophytes with a more diverse fish community and a higher share of piscivores as compared to the other, phytoplankton-dominated lake. After the partial winterkill, data on crustacean biomass and gut contents of roach were also available, thus allowing us to assess top-down effects of fish on crustaceans. Being a true omnivore, roach can switch diet preferences between crustaceans and macroinvertebrates, and may thus be a crucial factor for contrasting water turbidity in shallow eutrophic lakes (Christoffersen *et al.*, 1993; Cryer *et al.*, 1986; Persson *et al.*, 1991).

Methods

Study sites

Schulzensee (53°14’N, 13°16’E) and Kleiner Gollinsee (53°01’N, 13°35’E; hereafter referred to as Gollinsee) are small (0.03 -0.04 km^2), shallow (mean depth: 1.7-2.2 m), eutrophic lakes (Table 1) located in forested catchments of northeastern Germany. Both lakes are encircled by alder trees (*Alnus glutinosa*) and a reed belt (*Phragmites australis*) and have some stands of floating-leaved plants (*Nymphaea alba*, *Nuphar lutea*), but only Schulzensee contains submerged macrophytes (*Ceratophyllum submersum*). Schulzensee featured greater water clarity than Gollinsee at similar nutrient concentrations (Table 1) and phytoplankton was the primary biotic determinant of water clarity in both lakes (Brothers *et al.*, 2013). For simplicity, the lakes are hereafter referred to as clear and turbid, respectively. The lakes experienced a strong winter with slightly more than three months of ice coverage (measured daily at Lake Müggelsee, about 100 km south of the study lakes) starting mid-December 2009 (18th of December) and lasting until the end of March 2010. The ice was covered with 1-20 cm of snow for the entire period.

Water sampling and analyses

Pelagic water samples (containing equal parts water from 0.5, 1 and 2 m at the lake centre) were taken monthly from April to August 2007 and from April to September 2010. Measurements of concentrations of soluble reactive phosphorus (SRP), total phosphorus (TP) and total nitrogen (TN) were carried out following standard laboratory procedures (DEV 2009). Monitoring probes (YSI; Xylem Inc., Yellow Springs, OH, U.S.A) were installed at the lake centre from early May 2010 at a depth of 1.2 m (varying with lake level) and recorded temperature every 10 minutes.

Fish abundance

Fish community structure was estimated by carrying out exactly the same fishing effort at each lake, in early September 2007 as well as in early September 2010. Fish were sampled in the pelagic and littoral zone by gill netting, and additionally in the reed-covered part of the littoral zone by electrofishing. Therefore, eight benthic NORDIC multi-mesh gill nets (length: 30 m, height: 1.5 m, mesh size: 5, 6.25, 8, 10, 12.5, 16, 19.5, 24, 29, 35, 43 and 55 mm; Lundgrens Fiskredskapsfabrik AB, Stockholm, Sweden) were set perpendicular to the shore line, with each net covering the pelagic as well as littoral zone. All gill nets were set from dusk until dawn so as to include the likely maximum activity periods for all fish species. In the reed-covered area, fish were sampled by electrofishing, applying a voltage of about 200-300 V DC (20-30 A electrofishing aggregates EFG 4000, Bretschneider Spezialelektronik, Breitenbrunn, Germany) between anodic handnets and a copper cathode. We sampled fish by applying 15 dips at each of six randomly chosen locations. At each dip, the anode was submerged for a maximum duration of 15 s, or shorter if fish already displayed positive galvanotaxis. Between the dips, the boat was punted approximately 10 m. For fish caught by gill netting we determined species, number, total length (measured to the nearest mm) and wet weight (measured to the nearest 0.1 g). For fish caught by electrofishing, only species, number and total length were measured in the field. Wet weight was calculated using length-weight regressions (derived from specimens caught with gill nets). Fish biomass and number of fish caught during the samplings in 2007 and 2010 was calculated by pooling fishes caught by gill netting with those caught by electrofishing. We refer to the sum of catches as fish biomass subsequently.

Table 1. General characteristics of sampled lakes, April to September 2007 and 2010, with standard error of the mean and comparison between lakes; macrophyte coverage from A. Becker (unpublished) and Brothers *et al*. (2013).

	Schulzensee (clear lake)	**Kleiner Gollinsee (turbid lake)**	***P***
Surface area (m^2)	39,000	33,000	-----
Z_{mean} (m)	2.2	1.7	-----
Secchi depth (m)			
2007	1.53 ± 0.1 (*n* =6)	1.17 ± 0.13 (*n* =6)	0.04
2010	1.88 ± 0.1 (*n* = 8)	1.39 ± 0.1 (*n* = 8)	0.01
pH (May-September)			
2007	8.0 ± 0.3 (*n* =6)	8.0 ± 0.3 (*n* =6)	0.84
2010	7.9 ± 0.2 (*n* = 11)	7.8 ± 0.4 (*n* = 11)	0.43
Total phosphorus ($\mu g\ L^{-1}$)			
2007	37 ± 2 (*n* =6)	55 ± 6 (*n* =6)	0.02
2010	33 ± 3 (*n* = 7)	49 ± 8 (*n* = 7)	0.11
Total nitrogen ($mg\ L^{-1}$)			
2007	1.1 ± 0.1 (*n* =6)	1.4 ± 0.1 (*n* =6)	0.04
2010	0.85 ± 0.11 (*n* =6)	0.98 ± 0.11 (*n* = 6)	0.46
Macrophyte coverage (%)			
Emergent (*Phragmites australis*)			
2007	7	4	
2010	10	15	
Floating-leaved (*Nuphar lutea, Nymphaea alba*)			
2007	13	1	
2010	12	3	
Submerged (*Ceratophyllum submersum*)			
2007	9	0	
2010	22	0	

Carbon stable isotope ratios and gut content analysis of roach

For the analyses of $\delta^{13}C$ and gut contents, roach were caught with benthic NORDIC multi-mesh gill nets (as described in the previous section) in spring (May), summer (end of June until beginning of July) and autumn (end of September) 2010. Nets were exposed for three hours and fish were stored on ice until being transferred to a deep freezer. Stable isotope ratios of dorsal muscle tissue (the standard tissue sampled due to its accurate reflection of the diet isotopic composition and its turnover rate of several months (Pinnegar and Polunin, 1999)) were determined as described in Scharnweber *et al.* (2014) and are expressed as parts per thousand (‰) delta values ($\delta^{13}C$), following the international standard for carbon (PeeDee Belemnite) (Peterson and Fry, 1987).

For gut content analyses, the entire intestinal tract was extracted after defrosting and transferred to glass beakers filled with 5% formalin. The anterior third of the gut was removed, and its contents were inspected through a stereo microscope (Leica Wild MZ8, Leica, Bensheim, Germany). The volume proportion (equivalent to area proportion at uniform depth) of each prey category observed in the sample was estimated to the nearest 10% (adapted from Windell, 1968). For means of comparability among samples and to avoid overestimation of single items in almost empty guts, we discarded all samples for which the anterior third of the gut was less than half-filled. Prey items were grouped into three categories: benthic macroinvertebrates (i.e. Trichoptera, Gastropoda, Chironomidae, Bryozoa and Isopoda), algae & detritus and zooplankton (i.e. *Daphnia* sp., *Bosmina* sp., Copepoda, Hydrachnidiae, Ostracoda, Rotifera, Chaoboridae and *Leptodora kindtii*).

Phytoplankton and crustacean biomass

Pelagic chlorophyll *a* (chl *a*) concentrations were estimated monthly from April to August 2007 and April to September 2010 by filtering lake water (100 mL, three replicates) for pigment concentration analysis by high-performance liquid chromatography (HPLC, Waters, Millford, MA, USA) following methods outlined by Shatwell *et al.* (2012). Crustacean biomass was determined monthly from April to September 2010 from 40 L of an epilimnetic mixed water sample taken from the lake centre with a cylindrical water sampler (volume approx. 7 L) around noon and filtered through a 55 µm mesh (data for 2007 not available). The crustacean samples were fixed with 4% sugar formalin (Haney and Hall, 1973), counted at the genus or species level, and length was measured at the LimSa Gewässerbüro (Constance, Germany). We used regressions to calculate the individual carbon content based on size using the conversion factors of Dumont *et al.* (1975) and assumed a carbon content of 50% dry weight (Gaedke, 1992).

Data analysis

$\delta^{13}C$ values of roach were compared between 2007 and 2010 using a Mann-Whitney U test and between seasons in 2010 using Kruskal-Wallis tests (PASW Statistics 17.0). Multivariate analysis of roach gut content data was performed using the statistics software package PAST 3.01 (Hammer *et al.*, 2001). To compare seasonal differences in gut content composition in 2010 we applied one-way analyses of similarities (ANOSIM) based on Bray-Curtis distance measures and with season as a grouping variable for the dataset of each lake. Mean values of water quality parameters (Table 1), phytoplankton (measured as chlorophyll concentration) and crustacean biomass were compared between lakes using Mann-Whitney U tests (PASW Statistics 17.0).

Results

Fish biomass, abundance and community structure after partial winterkill

Partial winterkill reduced the fish biomass by 16% from 19.0 kg in 2007 to 16.0 kg in 2010 in the clear lake and by 43% from 25.6 kg in 2007 to 14.9 kg in 2010 in the turbid lake. Total fish numbers caught in September were similar in the clear lake before and after partial winterkill (1012 and 1334 fish), but more than doubled in the turbid lake (1200 versus 3203 fish). The total number of fish species decreased in both lakes, from 10 (2007) to 5 (2010) in the clear lake and from 9 (2007) to 7 (2010) in the turbid lake (Fig. 1). Perch and bream represented a high proportion of the fish biomass in 2007 (especially in the turbid lake), but were not caught in 2010. Pike biomass decreased markedly, whereas the biomass of roach, rudd (*Scardinius erythrophthalmus*) and tench (*Tinca tinca*) increased in both lakes. Sunbleak (*Leucaspius delineatus*) had a three times higher biomass in the turbid lake in 2010 than in 2007 (Fig. 1). Considering biomass, roach was the dominant species in both lakes after partial winterkill, accounting for almost two thirds of fish biomasses, followed by rudd and tench with more than 10% each (Fig. 1). Sunbleak was highly abundant only in the turbid lake after the partial winterkill. Abundance data (NPUE) was dominated by young-of-the-year (YOY) of roach (78% and 27% in the clear and turbid lake, respectively) and sunbleak (64% in the turbid lake) in 2010. All other species together contributed less than 6% to the total NPUE in both lakes after partial winterkill.

Fish communities of both lakes were almost equally structured in their biomass after partial winterkill. Piscivorous pike, which had a twice as high proportion in the clear lake as compared to the turbid lake before winterkill in 2007 (29% and 14%, respectively), declined to about 5% in both lakes afterwards. Benthivores (bream, white bream (*Blicca bjoerkna*) and tench) dominated the fish community biomass in the turbid lake before winterkill (42%), but declined strongly to 16% due to the extinction of bream after partial winterkill. The lake-wide proportion of omnivorous fish (roach, perch (*Perca fluviatilis*) smaller than 15 cm and ruffe (*Gymnocephalus cernuus*)) rose from about 40 to 60% in both lakes, and omnivores became the dominant guild after the partial winterkill.

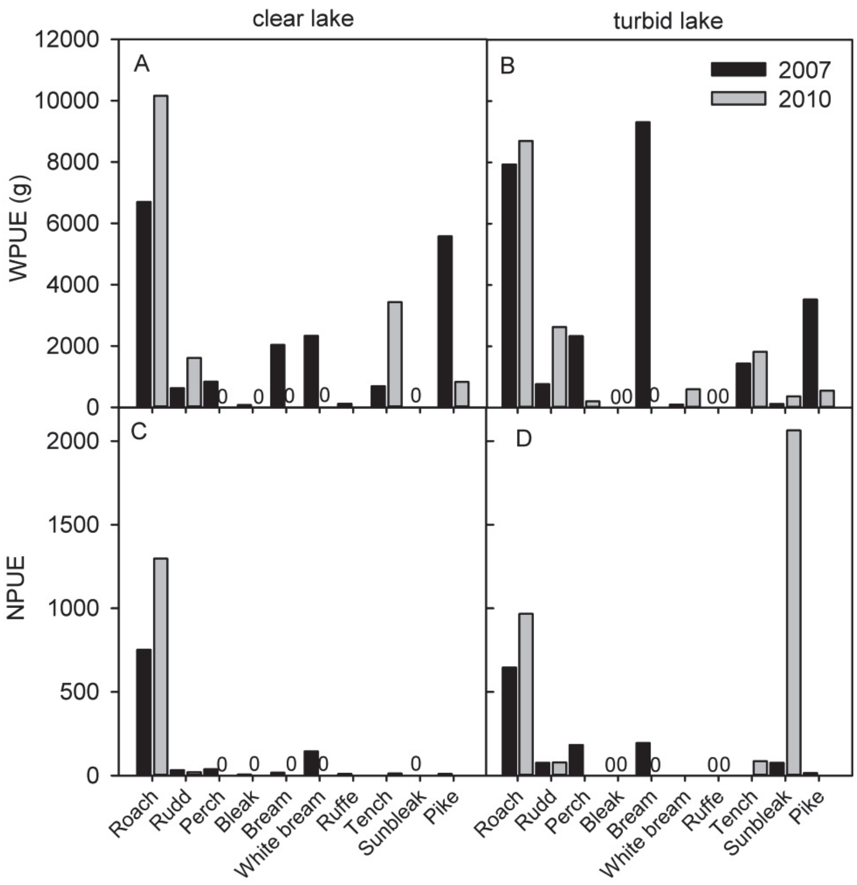

Figure 1. Fish community composition (WPUE: weight per unit effort, NPUE: numbers per unit effort) in a clear-water and a turbid shallow eutrophic lake before (2007) and after (2010) partial winterkill of fish. Fishing effort (gillnet and electro fishing) was the same in 2007 and 2010.

Size-frequency distributions of fish changed markedly in both lakes between 2007 and 2010 (Fig. 2). After the partial winterkill during the winter of 2009/10 (ice-off: end of March 2010), large fish ($\geq$25 cm) were solely represented by tench and pike. In both lakes, the abundance of all fish $\leq$ 8 cm (young-of-the-year fish and adult sunbleak) was several times higher in 2010 as compared to 2007 (Fig. 2). Small fish frequencies in 2010 were higher in the turbid than in the clear lake.

Seasonal changes in roach diet after partial winterkill

Roach (only >10 cm), the dominant fish species in both lakes, had significantly lower δ^{13}C values in September 2007 before the partial winterkill event compared to after (September 2010) (Mann-Whitney U-test, $p = 0.001$, Fig. 3). The seasonal development in δ^{13}C values in 2010 differed between lakes. In the clear lake, median δ^{13}C values ranged from -30.7 to -31.1 ‰ and did not change between spring and autumn (Kruskal-Wallis test, H=0.63, df=2, p=0.72) (Fig. 3). In the turbid lake, median δ^{13}C values significantly increased from -29.1 ‰ in spring by almost 2 ‰ in summer and autumn (Kruskal-Wallis test, H=57.2, df=2, p<0.001) (Fig. 3). Gut content analyses indicated that seasonal changes in the diet composition of roach were less pronounced in the clear lake (one-way ANOSIM, R=0.17, p=0.0001) than in the turbid lake (one-way ANOSIM, *R*=0.33, *p*=0.0001) in 2010. The diet of roach in the clear lake consisted of 47% and 36% crustaceans in spring and summer, respectively, and this proportion only declined in autumn (Fig. 4). In contrast, crustaceans were an important food source of roach in the turbid lake only in spring, but not in summer and autumn (Fig. 4). Benthic macroinvertebrates were an important food source of roach in both lakes in spring. In the clear lake, they also remained important in summer and autumn, but chironomids in roach guts were less abundant than in the turbid lake. In the turbid lake, mean proportions of macroinvertebrates in roach guts rose in summer, when chironomids dominated the gut contents, and declined afterwards. In autumn, algae and detritus contributed about 85% to the diet of the roach sampled in the turbid lake (Fig. 4).

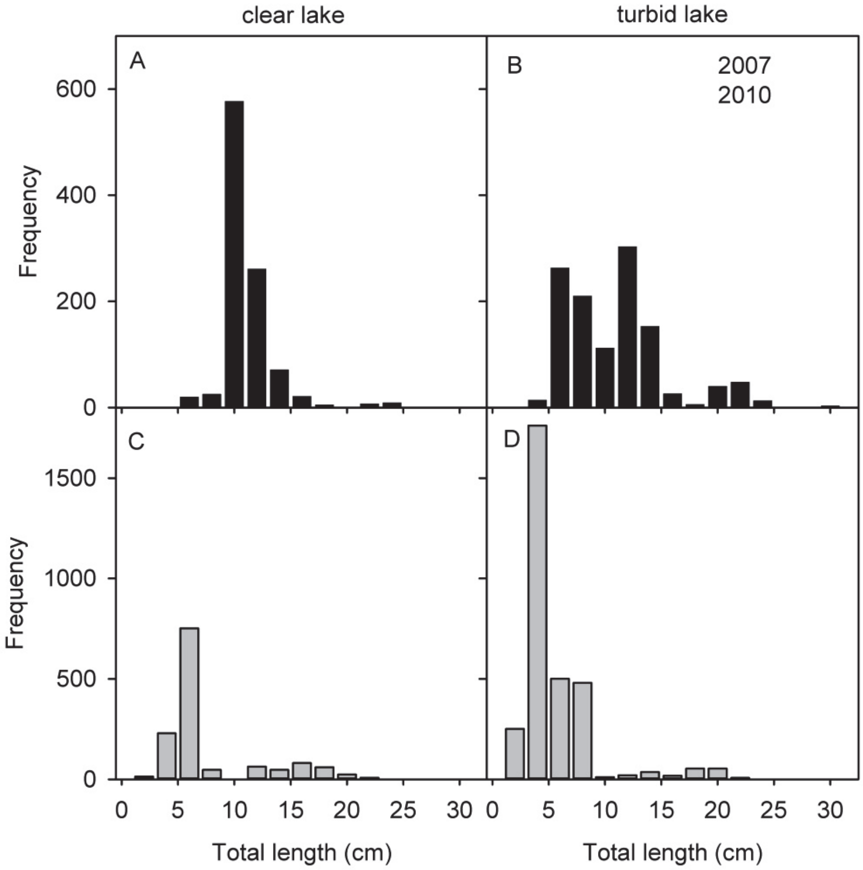

Figure 2. Size-frequency distribution of fish in a clear-water and a turbid shallow eutrophic lake before (2007, A, B) and after (2010, C, D) a partial winterkill of fish (0: no fish).

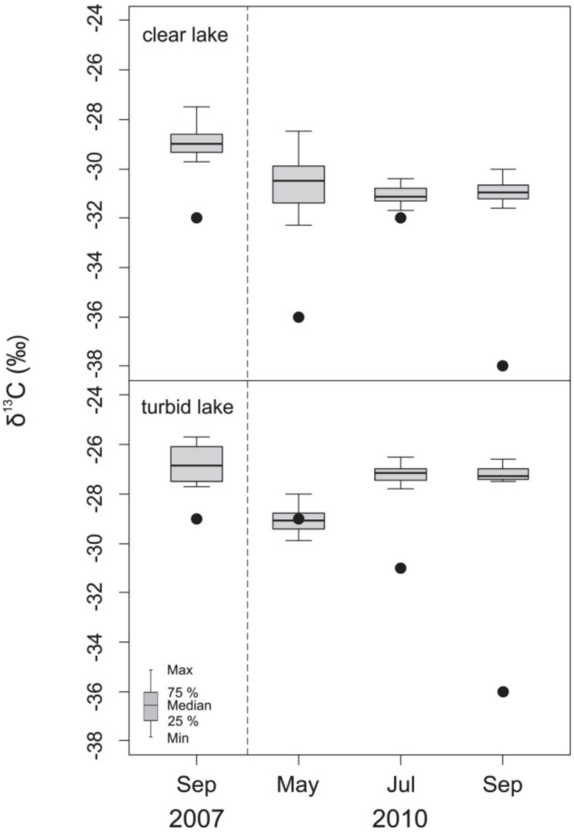

Figure 3. Seasonal changes in the stable carbon isotope values ($\delta^{13}C$) of roach (>10 cm) in a clear-water and a turbid shallow eutrophic lake prior (2007) and after a partial winterkill of fish (2010). Black dots denote the mean $\delta^{13}C$ of crustaceans plotted for comparison.

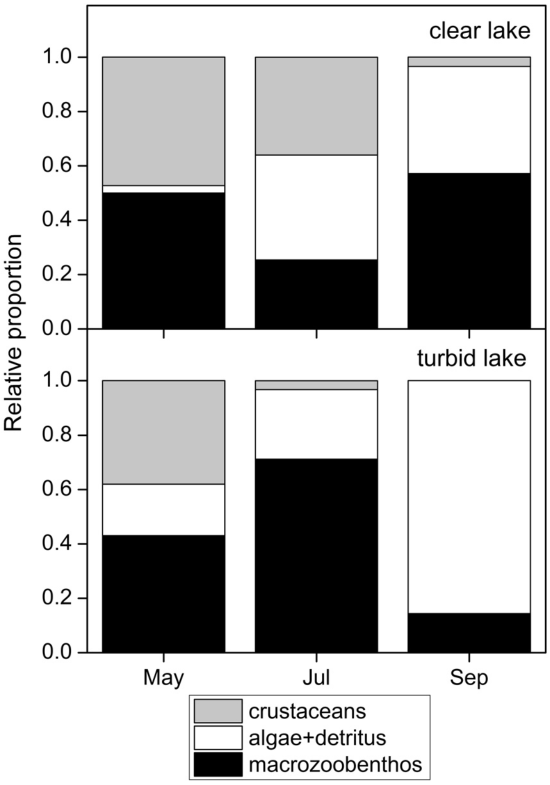

Figure 4. Mean volume proportions of diet components observed in the guts of roach in a clear-water and a turbid shallow eutrophic lake after a partial winterkill of fish in 2010 (numbers of fish were 44, 50 and 32 in the clear and 35, 40 and 25 in the turbid lake, in May, July and September, respectively).

Seasonal development of phytoplankton and crustacean biomass before (2007) and after partial winterkill

Phytoplankton development was similar before and after partial winterkill in the clear lake, but differed strongly in the turbid lake (Fig. 5). In 2007 in the turbid lake, phytoplankton biomass increased strongly from April to June when it reached maximum values (Fig. 5). In 2010, phytoplankton biomasses differed between the lakes in April, but decreased to similar values by the beginning of June (Fig. 5). Strong differences were detected in the development of phytoplankton biomass during the subsequent summer. The phytoplankton biomass of the clear lake remained low throughout June and July, and later increased only slightly. In contrast, a steep increase in phytoplankton biomass was detected in the turbid lake in 2010 (Fig. 5). Phytoplankton biomass was significantly lower in the clear lake than in the turbid lake between April and September 2010 (Mann-Whitney-U, p=0.02).

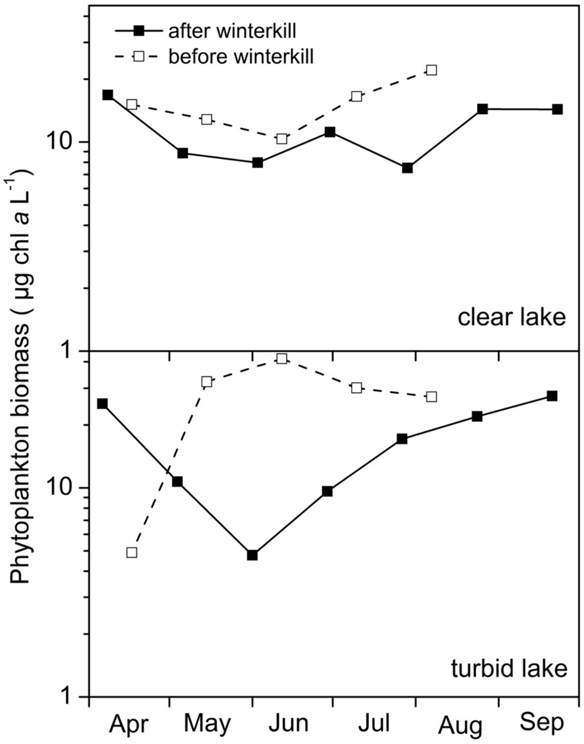

Figure 5. Seasonal development of phytoplankton mean chl *a* concentrations (± standard error) in the pelagic of a clear-water and a turbid shallow eutrophic lake before (2007) and after (2010) a partial winterkill of fish during the winter of 2009/10.

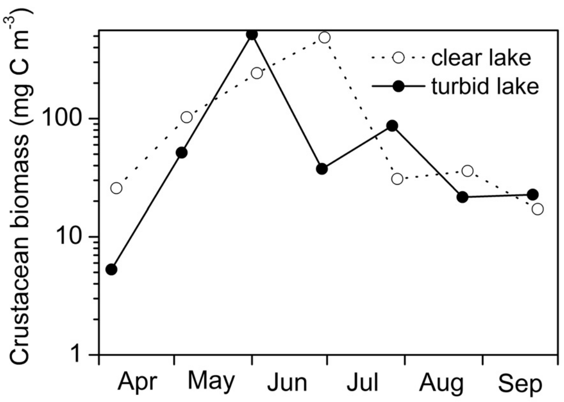

Figure 6. Seasonal development of crustacean biomass in the pelagic of a clear-water and a turbid shallow eutrophic lake in 2010 after a partial winterkill of fish in the winter 2009/10.

The biomasses of crustaceans are only available for 2010. They initially increased strongly in the pelagic zones of both lakes and peak biomasses were observed around late May or June (Fig. 6). Afterwards, a strong decrease of crustacean biomasses was observed in the pelagic zones of both lakes (Fig. 6). Crustacean biomass was not significantly different between lakes (Mann-Whitney-U, p=0.71). Copepods dominated the crustacean biomass in both lakes (turbid lake 61%, clear lake 82% (seasonal average)). Cyclopoid copepodites and nauplii composed the main biomass within the copepods. In the turbid lake, cladocerans composed on average 39% of the crustacean biomass with *Daphnia cucullata* being the dominant species. In the clear lake, different cladoceran species contributed on average 18% to the crustacean biomass.

Discussion

Effects of the partial winterkill on fish biomass and community composition

The partial winterkill reduced the fish biomass in both lakes, with a higher reduction in the turbid lake (43%) than the clear lake (16%) leading to similar fish biomasses in both lakes in 2010. Despite the similar fish biomass and species composition, the seasonal succession of crustaceans and phytoplankton differed between both lakes from May onwards. Possible explanations for this difference are lower frequencies of YOY fish and a potential refuge effect for crustaceans or other effects of submerged macrophytes on phytoplankton (nutrient competition, allelopathy) in the clear lake (see below).

In contrast to the findings in 36 Danish lakes (Balayla *et al.*, 2010), our lakes showed a higher proportion of small fish (<10 cm) in the summer following the partial winterkill. Increases in the abundance of YOY fish were often observed after strong reductions of adult planktivores during biomanipulation experiments (Hansson *et al.*, 1998; Meijer *et al.*, 1999; Romare and Bergman, 1999) and were attributed to decreased competition from adult roach, making food resources (zooplankton) available to YOY fish (Persson and Greenberg, 1990). As hypothesised, piscivores, which initially represented a higher proportion of the clear lake fish community, were more strongly affected by the partial winterkill than omnivores, resulting in similarly composed fish communities in both lakes. Piscivorous perch (>15 cm) were killed off, and pike was only represented by a few small specimens in both lakes, confirming the sensitivity of these species to hypoxia (Grimm and Backx, 1990; Rimoldi *et al.*, 2012). Benthivorous bream, which represented a high proportion in the turbid lake fish community before the winterkill, died out completely. This may have contributed to a decrease in water turbidity due to lower sediment resuspension and nutrient transfer from the benthic to the pelagic zone (Breukelaar *et al.*, 1994). TP concentrations, however, were not significantly different between 2007 and 2010 (Table 1).

Differences in phytoplankton development after a partial winterkill

The seasonal phytoplankton biomass development in 2010, the year following the partial winterkill, differed between both lakes despite their similar fish biomasses, community composition and relative abundances of piscivores. By the end of May 2010, both lakes showed a low phytoplankton biomass, suggesting strong top-down control by large-bodied zooplankton, which were released from fish predation after winterkill (Balayla *et al.*, 2010). However, studies in other lakes have shown that herbivorous crustaceans can have a marked impact on edible phytoplankton when their biomass exceeded several hundred mg C m^{-2} (Gaedke *et al.*, 2004; Gaedke and Straile, 1998). This condition was met in both of our lakes only at peak times of crustaceans (220-300 mg C m^{-2}) at the end of May or in June. In April and May, however, top-down effects of crustaceans on phytoplankton were unlikely due to the low crustacean biomass. Alternatively, the small edible phytoplankton fraction may have been grazed down to low biomasses by ciliates and rotifers which were abundant in both lakes (B. Lischke, unpublished data).

In the clear lake, phytoplankton biomass remained low in summer despite a significant decline of pelagic crustacean biomass sampled during the daytime. There are different potential explanations for this. Crustaceans still represented about one third of the roach gut content in July and mean $\delta^{13}C$ values of roach also did not indicate major diet changes. Crustaceans thus may have been more abundant than indicated by the data sampled in the pelagic of the clear lake during the daytime due to the presence of submerged macrophytes.

These are known to provide shelter from fish predation (Jeppesen *et al.*, 1997; Timms and Moss, 1984) and support diel horizontal migration of crustaceans (Burks *et al.*, 2002). The dominant macrophyte species (*C. submersum*) typically develops its peak biomass rather late in the season (July) (Sayer *et al.*, 2010) and thus could provide shelter from late June onwards. Predation pressures on crustaceans inside the submerged vegetation would likely be low if YOY roach dominate, as they co-occur with crustaceans in the vegetation during the day much less than YOY perch (Burks *et al.*, 2002). Jacobsen and Perrow (1998) and Jacobsen *et al*. (2004) found that roach in a clear lake stayed near the vegetation during the day but tended to move into the pelagic zone at night. In addition, the clear lake had a lower frequency of YOY fish in 2010 than the turbid lake (Fig. 2). Crustacean grazing pressure thus could at least partly have been responsible for keeping phytoplankton biomasses lower in the clear lake than in the turbid lake during the summertime. Summer phytoplankton suppression in the clear lake may also partly be explained by allelopathic effects of macrophytes, as *C. submersum* is known for inhibitory effects (Hilt and Gross, 2008), and/or by nutrient limitation as the rootless *C. submersum* plants take up nutrients from the water column (Mjelde and Faafeng, 1997). SRP concentrations were below detection limits (3 µg L^{-1}) in the clear lake from June to early August 2010, whereas average concentrations of 5 ± 1 µg SRP L^{-1} were measured in the turbid lake from July to September 2010. Average TP (clear: 30 ± 2 µg L^{-1}, turbid: 56 ± 15 µg L^{-1}) and TN (clear: 0.73 ± 0.08 mg L^{-1}, turbid: 0.95 ± 0.22 mg L^{-1}) concentrations from July to September 2010 were not significantly different between lakes.

In contrast to the clear lake, summer phytoplankton biomass increased in the turbid lake and by September had returned to pre-winterkill (2007) concentrations. A low crustacean biomass from June onwards signalled a low top-down grazing control on phytoplankton. In contrast to the clear lake, the share of crustaceans in the guts of roach > 10 cm long in the turbid lake was negligibly low. Furthermore, mean $\delta^{13}C$ values of large roach increased from May to July, indicating a diet shift towards benthic prey items. This is a typical pattern of adult roach, which can successfully exploit crustaceans but switch to benthic food sources when crustacean densities are reduced by planktivorous juveniles (Crowder, 1985). Furthermore, predation pressures on crustaceans may have been higher in the turbid lake due to the additional high abundance of YOY sunbleak. We did not study gut content of sunbleak, but a previous study showed a strong dominance of crustaceans in the diet of later juvenile phases of sunbleak (Pinder *et al.*, 2005).

Implications for climate effects on temperate small eutrophic shallow lakes

Interannual variability in the total duration of winter ice cover is large in the studied north temperate region. Intermittent ice cover during winter is the rule, but long periods (up to four months) of continuous ice cover, and thus winterkills, can occur during extremely cold winters (Livingstone and Adrian, 2009). In contrast to suggestions by Brönmark and Weisner (1992), our study indicates that the chance for shifts of clear shallow lakes with submerged vegetation into turbid conditions due to winterkill-related reductions in piscivores is low. Although the share of piscivores was strongly reduced to 5% in both lakes, macrophyte effects on top-down and bottom-up control of phytoplankton seemed to maintain a lower phytoplankton biomass during the subsequent season in the clear-water lake. In contrast, many shallow lakes of the studied region and other north temperate lakes have shifted to the turbid, phytoplankton-dominated state by eutrophication during the last century (e.g. Hilt *et al.*, 2013; Körner, 2002; Timms and Moss, 1984). In order for a return to the clear-water state to be induced by a winterkill, two conditions seem to be necessary. First, fish biomass must be reduced by about 75% for significant effects on water clarity, as found in biomanipulation case studies (Meijer *et al.*, 1999). Fish biomass reductions may also be important due to their direct impacts on submerged macrophytes (Hilt, 2006; Körner and Dugdale, 2003). Secondly, the re-establishment of submerged macrophytes seems to be important for a longer-term stabilisation of clear-water conditions. Efficiently biomanipulated lakes with low algal biomass in summer showed macrophyte coverages of more than 25% of the lake surface area. The re-establishment of macrophytes after winterkills may be especially difficult in lakes that featured a turbid state for longer periods, and hence lack a viable propagule bank (Bakker *et al.*, 2013; Hilt *et al.*, 2006). Ultimately, any local positive (or negative) effects of a winterkill on water clarity will become less likely because projected climate changes predict warmer winters and less snow coverage for the studied region (Kreyling, 2010). Although winterkills are predicted to occur with lowered frequencies, a better understanding of their ecological role and relationship to water clarity and stable regimes is still important for many regions which will continue to feature such winterkills for the foreseeable future. Similarly, some of the ecological outcomes of winterkills here described may be analogous to summer anoxia fish kills, which may become more widespread as projected warmer water temperatures and increases in dissolved organic carbon concentrations result in higher stratification and community respiration rates and lower benthic primary production (Brothers *et al.*, 2014).

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Chapter III

Large biomass of small feeders: Ciliates may dominate herbivory in eutrophic lakes

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Abstract

The importance of ciliates as herbivores and in biogeochemical cycles is increasingly recognized. An opportunity to observe the potential consequences of zooplankton dominated by ciliates arose when winter fish kills resulted in strong suppression of crustaceans by young planktivorous fish in two shallow lakes. On an annual average, ciliates made up 38% to 76% of the total zooplankton biomass in both lakes during two subsequent years. Consequently, ciliate biomass and their estimated grazing potential were enormously high compared to other lakes of various trophic states and depths. Grazing estimates based on abundance and size suggest that ciliates should have cleared the water column of small (<5 µm) and intermediate (5-50 µm) sized phytoplankton more than once a day. Especially small feeders within the ciliates were important, likely exerting a strong top-down control on small phytoplankton. Particle-attached bacteria were presumably strongly suppressed by intermediate-sized ciliate feeders. Contrary to other lakes, large phytoplankton was proportionately very abundant. The phytoplankton community had a high evenness, which may be attributed to the feeding by numerous fast growing and selective ciliate species. Our study highlights ciliates as important trophic link and adds to the growing awareness of the role of winter processes for plankton dynamics.

Introduction

Ciliates have been known to be important components of zooplankton communities for more than two decades (Beaver and Crisman, 1989). Nevertheless, trophic cascade studies still focus mainly on the classical food chain: phytoplankton, crustaceans and fish. However, ciliates and rotifers may also be highly relevant for trophic cascades, in that ciliates are known to be often the most important grazers in spring (Gaedke and Straile, 1994; Weisse *et al.*, 1990) and an important food source for large zooplankton (Adrian and Schneider-Olt, 1999; Sanders and Wickham, 1993) and in general their biomass increases with the trophic state (Beaver and Crisman, 1982). The updated version of the Plankton Ecology Group Model explicitly considers ciliates as important grazers of bacteria and small phytoplankton, influencing the phytoplankton composition but less the seasonal patterns (Sommer *et al.*, 2012). Ciliates have short generation times and thus may, in contrast to crustaceans, track phytoplankton developments within 1-2 weeks even at low temperatures (Tirok and Gaedke, 2007b) or even without a time lag (Berninger *et al.*, 1993). Among freshwater zooplankton, they have the highest weight specific grazing rates (Hansen *et al.*, 1997), which may lead to a strong top-down control of their prey if ciliates become important in terms of biomass. As cyclopoid copepods and cladocerans can exert strong top-down control on ciliates (Wickham, 1998; Wickham and Gilbert, 1993), ciliates often contribute little to the total zooplankton biomass of lakes. They may gain in importance within the pelagic zooplankton community when their predators or competitors fail to build up large biomasses and hence to control ciliate development.

Cyclopoids and cladocerans themselves are typically influenced by the abundance of their predators, which are usually fish. Especially in shallow lakes, a long period of ice cover and snow may reduce oxygen concentrations up to the point of anoxia resulting in a winter fish kill (Tonn *et al.*, 1990), with consequences for the whole food web during the following years. Such a loss of planktivorous fish was observed to reduce the predation pressure on metazooplankton which may increase metazooplankton biomass, mean species size and individual body mass of crustaceans (Balayla *et al.*, 2010; Iglesias *et al.*, 2011) at least on a short time scale (Ruuhijärvi *et al.*, 2010).

Concurrent with reduced biomasses in planktivorous fish, winter fish kills can result in young of the year (YOY) fish gaining in importance and exerting a strong predation pressure on metazooplankton (Ruuhijärvi *et al.*, 2010). YOY fish have been observed to graze strongly on cladocerans, typically reducing grazing on phytoplankton and often resulting in more turbid lakes (Romare *et al.*, 1999). Various studies reported the structuring effect of YOY fish in lake food webs (Cryer *et al.*, 1986; Mills and Forney, 1983): In years with strong fish recruitment, cladocerans were less abundant (Mills and Forney, 1983) and rotifers and copepods dominated the zooplankton community (Cryer *et al.*, 1986). These early studies focused on effects on crustaceans and rotifers. However, ciliates may substantially contribute to the top-down control on phytoplankton and bacteria as well as the transfer efficiency of organic matter and energy within the planktonic food web (Gaedke *et al.*, 2002; Sanders and Wickham, 1993). Cascading effects of a winter fish kill, as described for crustaceans and rotifers, are very likely to also affect the protozoan zooplankton; however, knowledge about such specific effects is still rather limited.

We observed a low biomass of adult fish due to partial winter fish kills in two well-studied, small, temperate, shallow lakes (Attermeyer *et al.*, 2013; Brothers *et al.*, 2013; Scharnweber *et al.*, 2014a; Scharnweber *et al.*, 2014b) in two consequent winters (Hilt *et al.*, 2015) and a high abundance of YOY fish particular during the second year. We investigated the zooplankton and phytoplankton communities to unravel their regulation in these lakes and hypothesize that crustaceans and, in particular the large forms, were under severe grazing pressure by YOY fish. In turn, low crustacean biomass was expected to favor ciliates and rotifers. We further hypothesize that ciliates with their high weight specific grazing rates exert a strong grazing pressure on specific phytoplankton species, promoting a species-specific density dependence of loss rates and thus a diverse phytoplankton community. The emerging strong top-down control by ciliates may result in low phytoplankton and bacterial biomass. This was evaluated by calculating the potential grazing pressure by ciliates based on abundance and size of ciliates and comparing it to measured production rates of phytoplankton and bacteria. We expected that these cascading effects would be more pronounced in the second year given the second partial winter fish kill in a row. The results were further related to measurements from selected lakes of differing trophic states and depths.

Our results reveal that crustaceans were under severe predation pressure as indicated by a low biomass and the dominance of nauplii and copepodites. Ciliates benefited enormously from the reduced top-down control. They dominated the zooplankton community in terms of biomass, which exceeded values reported from various lakes. The calculated estimates of the grazing rates suggest that ciliates exerted a strong predation pressure on small phytoplankton and particle-attached bacteria. Consequently large, grazing resistant, slow growing species accumulated within the phytoplankton community.

Methods

Study site

Field observations were conducted for two very similar small, shallow eutrophic lakes in the North-Eastern part of Germany differing mainly in their composition of primary producers (Table 1). The Schulzensee (SS, 53°14'N, 13°16'E) has a well-developed submerged macrophyte community (predominantly *Ceratophyllum submersum*), whereas submerged macrophytes are absent in the Kleiner Gollinsee (GS, 53°01'N, 13°35'E) (Brothers *et al.*, 2013). Both lakes are surrounded by a reed belt. Samples for zooplankton, phytoplankton and bacteria were taken every 4 weeks at nearly the same sampling dates in both lakes in 2010 and 2011, whereby the actual sampling period differed between the plankton groups (see below). In autumn 2010 both lakes were divided by a plastic curtain to conduct an experiment on the fate of terrestrial organic carbon in the food web (Attermeyer *et al.*, 2013; Scharnweber *et al.*, 2014a; Scharnweber *et al.*, 2014b). Thus, in 2011 we analyzed only the samples of the reference half of both lakes.

Table 1. Characteristics of Gollinsee and Schulzensee. For Secchi depth, chlorophyll, total phosphorous (TP) and soluble reactive phosphorous (SRP) monthly mean values (± SD) for the years 2010 and 2011 are shown. TP, SRP and chlorophyll are mean values from samples taken in pelagic and littoral habitats. The number of samples is indicated by N. *SRP values below the detection limit were set to half the detection limit (0.01 µmol L^{-1}).

	Gollinsee	**Schulzensee**
Surface area (m^2)	33,200	39,130
$Z_{\mathbf{mean}}$ (m)	1.8	2.2
$Z_{\mathbf{max}}$ (m)	2.9	4.2
Secchi depth (m)	1.3 ± 0.4 (N = 19)	1.8 ± 0.3 (N = 18)
Chlorophyll (µg L^{-1})	25.3 ± 16.1 (N = 17)	14.6 ± 8.3 (N = 17)
TP (µmol L^{-1})	1.2 ± 0.3 (N = 19)	1.0 ± 0.2 (N = 19)
SRP (µmol L^{-1}) *	0.11 ± 0.05 (N = 19)	0.10 ± 0.06 (N = 19)
Surface area covered by submerged macrophytes	0%	20-25%

Zooplankton

Zooplankton samples were taken from April to October 2010 and from February to December 2011 from littoral and pelagic locations in each lake. An epilimnetic mixed water sample of 40 L was taken and 50 mL of it was fixed with acidified Lugol's solution (Hoehn *et al.*, 1998). Ciliate samples were quantitatively analyzed with inverted microscopy (Hund Labovert, >100 cells per species and sample counted) as in Müller (Müller, 1989) and Gaedke and Wickham (Gaedke and Wickham, 2004). They were identified to the genus or species level (Curds, 1982; Foissner, 1991; Foissner *et al.*, 1999; Lynn and Small, 2002). Note, that the identification of ciliates below the genus level is possible only for a few species in Lugol-preserved samples. Length and width of 10-20 individuals of each species were measured to calculate the species-specific cell volume (Barthelmeß, 1995; Boit and Gaedke, 2014 and literature cited therein; Tittel, 1997). We used linear regressions to calculate the individual carbon content based on cell volume using the specific conversion factors for ciliates (Müller and Geller, 1993).

The remaining water was filtered through a 55 µm mesh, and these rotifer and crustacean samples were fixed with 4% sugar formalin (Haney and Hall, 1973). Rotifers and crustaceans were quantitatively analyzed and length and width for rotifers and length for crustaceans were measured. We used power regressions to calculate the individual carbon content based on the volume of rotifers (Telesh *et al.*, 1998) and the length of crustaceans (Dumont *et al.*, 1975). A carbon content of 50% dry weight was assumed (Gaedke, 1992 and references therein). In close cooperation the zooplankton samples were quantified at the LimSa Gewässerbüro (Constance, Germany, by Dr. S. Schmidt-Halewicz) after the detailed descriptions by Schmidt-Halewicz *et al.* (2012).

Phytoplankton

Littoral and pelagic water samples were taken from April to November 2010 and from January to December 2011. Pelagic samples included equal portions of water from 0.5 m, 1 m, and 2 m depth at the middle of the lake, while littoral samples of subsurface water (Z = 0.5 m) were pooled from three locations within the reed belt. Samples were stored in 500 mL glass jars and fixed with an acidified Lugol's solution. The jars were stored in the dark until laboratory analysis. The samples were analyzed with inverted microscopy distinguishing 70 different morphotypes. The size of at least 20 cells from each morphotype was measured. The average width and length of the cells were used to calculate the morphotype-specific cell volume allowing for the respective shape (Hillebrand *et al.*, 1999) which was converted into the cell specific individual carbon content (Menden-Deuer and Lessard, 2000). Phytoplankton gross primary production was estimated from monthly Phyto-PAM and HPLC measurements as described by Brothers et al. (Brothers *et al.*, 2013) and was converted to net primary production assuming 40% respiration of gross primary production (Platt *et al.*, 1991).

Bacteria

From June to November 2010 and April to December 2011 pelagic and littoral samples were taken and separated by filtration through 5 µm polycarbonate membranes (Nuclepore) for particle-attached bacteria (>5 µm) and free-living bacteria (<5 µm; >2 µm). Bacteria were SYBR gold-stained and counted with an epifluorescence microscope. The volume of about 100 cells was measured and converted to biomass (Simon and Azam, 1989). Bacterial production of both bacterial fractions was measured by incorporating L-^{14}C-leucine (Attermeyer *et al.*, 2013).

Data analysis

The pelagic and littoral locations of the phytoplankton, zooplankton and bacteria samples were less than 50 m apart from each other. Comparing the species composition we concluded that these small lakes had horizontally well mixed water bodies as species biomass and composition were similar in the pelagic and littoral and thus we arithmetically averaged the samples from both habitats.

Phytoplankton diversity was calculated using the Shannon-Wiener Index (H):

$$H = -\sum_{i=1}^{n} \frac{b_i}{b} ln \frac{b_i}{b}$$

where b_i is the biomass of the *i*th morphotype, *b* the total phytoplankton biomass and *n* the number of all morphotypes. The diversity was calculated per sampling day and averaged over each sampling year. The evenness was determined as diversity (*H*) divided by the maximum diversity of the respective community (ln(*n*)).

To estimate the consumption of bacteria and phytoplankton by ciliates, ciliates were grouped according to their known feeding preferences from literature (Kivi and Setälä, 1995; Sanders, 1988; Simek *et al.*, 1995) and phytoplankton according to their longest linear dimension (LLD) into the groups small (<5 µm), intermediate (5-50 µm) and large (>50 µm). Free-living bacteria were allocated to the small plankton and particle-attached bacteria to the intermediate plankton. We calculated estimates of the grazing pressure by ciliates based on their abundance and biovolume. The potential filtering rate for each ciliate group was estimated using regressions of specific filtering rates against ciliate cell size for each species, corrected for the ambient temperature using a Q_{10} value of 2.8, then summing the rates for all individuals in each feeding group (Hansen *et al.*, 1997). In a second approach estimates of the maximum ingestion rates were calculated similarly, using both the ciliate cell size and the median prey size within each ciliate feeding group (Hansen *et al.*, 1997). Ultimately, we calculated the proportion of the total available prey which was consumed by each ciliate group per day given our estimates of grazing rates. This potential loss rate by predation was related to the measured growth rate of the prey group given as the production to biomass ratio.

To evaluate the size-selective feeding impact by ciliates we generated biomass size spectra for phytoplankton by summing the biomass of each $\log_2$ size class (based on individual carbon content). As described by Gaedke (1992), the biomass of each size class was distributed over the adjacent size classes by allocating 25% of the biomass to the upper and lower size class and leaving 50% within the respective size class.

Data for cross lake comparisons

To evaluate the generality of our findings, we compiled data from lakes of various trophic states and depths (Table 2). Cross lake comparisons can be problematic due to differences in sampling procedures, species identification and data processing. To overcome this problem, we used only lakes where the data were gathered and/or processed by the same group of people (GS, SS, the Königssee, Lake Constance, the Arendsee and the Müggelsee (for sampling see Gaedke *et al.*, 2004)). We further used zooplankton community measurements averaged across 12 lakes of different trophy and morphometry from North America (Pace, 1986) and rotifer and crustacean data from the Großer Vätersee (Steiner, 2002). We compared the copepod age structure as reflected by the portion of nauplii of the total copepod biomass in GS and SS with those of the Königssee and the Großer Vätersee, for which ratios were calculated using the compiled data. For Lake Constance we calculated the respective ratio from measurements in 1988 (Wölfl, 1989).

Table 2. Characteristics of the lakes used for comparison. Sampling was conducted either twice a week (tw), weekly (w) or biweekly (bw). *For this lake only rotifer and crustacean data were available.

lake	**trophy**	**depth [m]**		**sampling period**	**reference**
		mean	**max**		
Königssee	oligotroph	98	190	1992 (tw)	Barthelmeß, 1995
Lake Constance	mesotroph	101	252	1987-1996 (w)	Boit and Gaedke, 2014 and literature cited therein
Arendsee	eutroph	30	49.5	1994 (w)	Tittel, 1997
Müggelsee	hypertroph	4.9	8	1988-1990 (w)	Gaedke et al., 2004 and literature cited therein
Großer Vätersee *	mesotroph	5.2	11.5	1997-1999 (bw)	Steiner, 2002

Results

Gollinsee (GS) and Schulzensee (SS) were both characterized by low crustacean biomass, high total phytoplankton biomass and a remarkably high ciliate biomass. Literature estimates of size-specific grazing rates suggest that the enormous ciliate biomass was sufficient to exert strong predation pressure on small phytoplankton and particle-attached bacteria, as described in detail below.

Metazooplankton biomass and composition

In GS and SS the volume specific crustacean community biomass amounted to 33-119 mg C m^{-3} and fell into the range found in deep Lake Constance, the Königssee and the Arendsee (Fig. 1, Appendix 1). However, it was an order of magnitude lower than in the shallow highly eutrophic Müggelsee and the crustacean biomass per area was much higher in the deep lakes than in the shallow GS and SS. The average crustacean biomass was still lower in both lakes in the second year (Fig. 1, Appendix 1). Within the community, cladocerans were relevant only in summer 2010 and copepods dominated otherwise (61-83%). In particular cyclopoid copepodites (mean length 490 µm) and small (mean length 200 µm) and large nauplii (mean length 400 µm) were present, whereas hardly any adult copepods were found. The contribution of nauplii to the copepod biomass was extremely high in both lakes (GS: from 16% to 51%, SS: from 31% to 52%). Predacious metazooplankton such as carnivorous cladocerans and *Chaoborus* sp. which may have reduced the biomass of crustaceans, was not relevant in neither lake. The rotifer biomass was lower in 2011 than in 2010 (GS 2010: 72 mg C m^{-3}, 2011: 18 mg C m^{-3}; SS 2010: 44 mg C m^{-3}, 2011: 20 mg C m^{-3}; Appendix 1) and was mainly attributable to biomass peaks in July 2010 which did not develop in 2011. The volume specific rotifer biomass was in range of those found in the Müggelsee and the Großer Vätersee and about an order of magnitude larger than in lakes Constance, Arendsee and Königssee (Appendix 1).

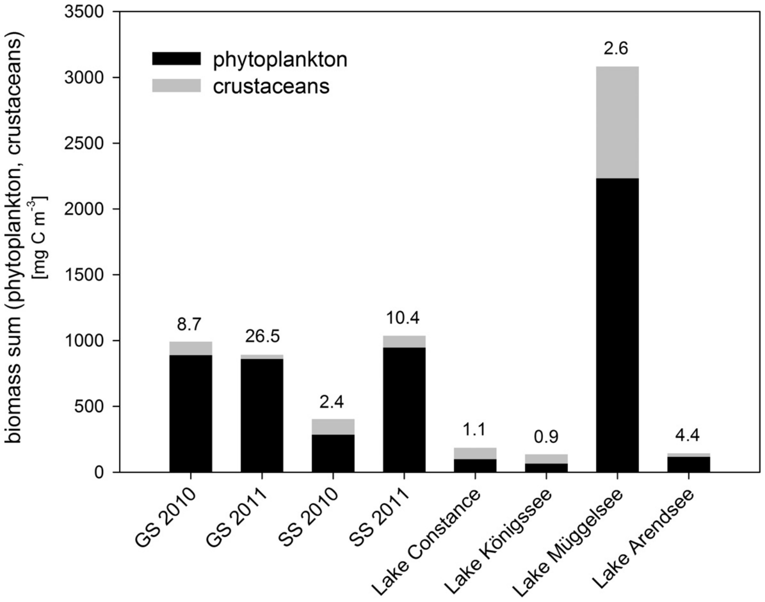

Figure 1. Whole-year arithmetic averaged biomass of phytoplankton and crustaceans for GS and SS in 2010 and 2011. For comparison, measurements from other lakes were included. Numbers on the bars are the average phytoplankton to crustacean biomass ratios.

Phytoplankton biomass and composition

Along with the low crustacean zooplankton biomass, the volume specific average phytoplankton biomass was relatively high (Fig. 1, Appendix 1). In comparison to the deep lakes Constance, Königssee and Arendsee, GS and SS had almost 10 times more phytoplankton biomass and only about two times less than the shallow, hypertrophic Müggelsee. The phytoplankton : crustacean biomass ratio was three to four times larger in 2011 than in 2010, and especially in 2011 much higher than in the lakes we used for comparison (Fig. 1). The phytoplankton community was diverse in respect to size (see below and Fig. 2) and composition (Appendix 3). The Shannon-Wiener Index ranged between 1.8 and 2.2 with 24-34 morphotypes (yearly average, Appendix 2). The evenness varied between 56% and 65%. Diatoms were often the most important group with respect to biomass, especially in spring but also during other months, whereas cyanobacteria were of minor importance in both lakes.

A large part of the phytoplankton biomass accumulated in the intermediate and larger size classes. The highest biomasses occurred in the size classes 7-8 (128-256 pg C cell^{-1}, 12.0-15.3 µm equivalent spherical diameter) which were dominated by pennate diatoms (Fig. 2, for details on the species composition see Appendix 3). In GS and SS large phytoplankton of the size class 12 (mainly *Peridinium* sp.) contributed high amounts to the total phytoplankton biomass. The relative contribution of very small phytoplankton (≤ 2 pg C cell^{-1}) was low and the absolute biomass in these size classes was 10-100 mg C m^{-3}.

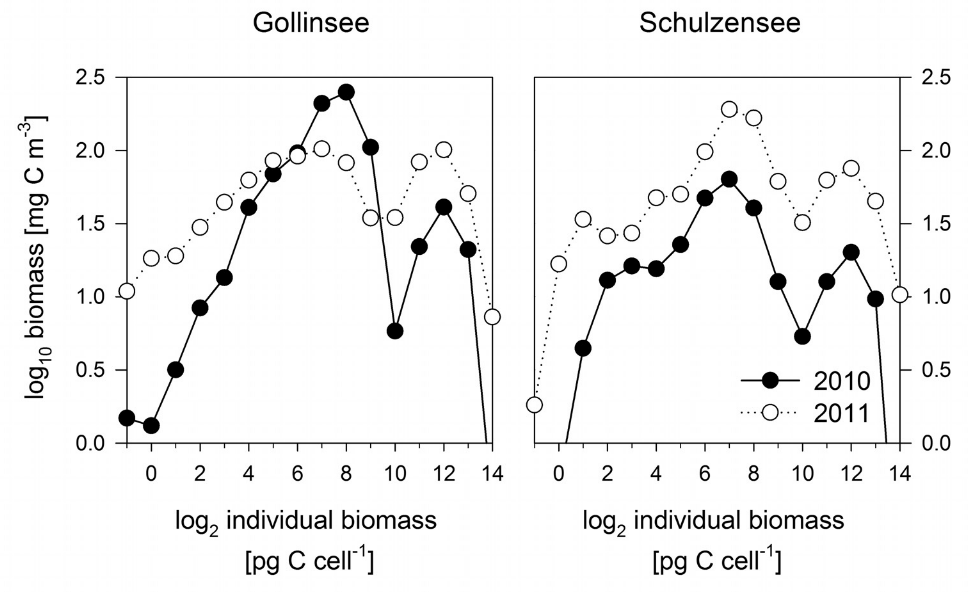

Figure 2. Absolute phytoplankton biomass per size class in GS and SS in 2010 and 2011.

Ciliates biomass and composition

The very low abundance of adult crustaceans was accompanied by a remarkably high ciliate abundance in 2010 and even higher numbers in 2011 (GS 2010: 42 cells mL^{-1}, 2011: 164 cells mL^{-1}; SS 2010: 54 cells mL^{-1}, 2011: 117 cells mL^{-1}). Likewise, ciliates built up enormously large biomasses (GS 2010: 151 mg C m^{-3}, 2011: 161 mg C m^{-3}; SS 2010: 100 mg C m^{-3}, 2011: 120 mg C m^{-3}, Appendix 1). Accordingly, ciliates dominated the zooplankton community in terms of biomass in 2010 in GS (47% of total zooplankton biomass) and in both lakes in 2011 (GS: 76%; SS: 52%). Such a relative contribution of ciliates is extremely high in comparison to various lakes of differing trophic state and depths (Fig. 3). In absolute terms, the ciliate biomass was 10 to 100 times larger than in the deep lakes we used for comparison, and similar to the hypertrophic Müggelsee (Appendix 1). Ciliate biomass peaked in spring and autumn in both lakes in 2010 and 2011 (Appendix 4). The ciliate to rotifer biomass ratio was roughly two in 2010 and six to nine in 2011 and thus in 2011 also higher than in the reference lakes.

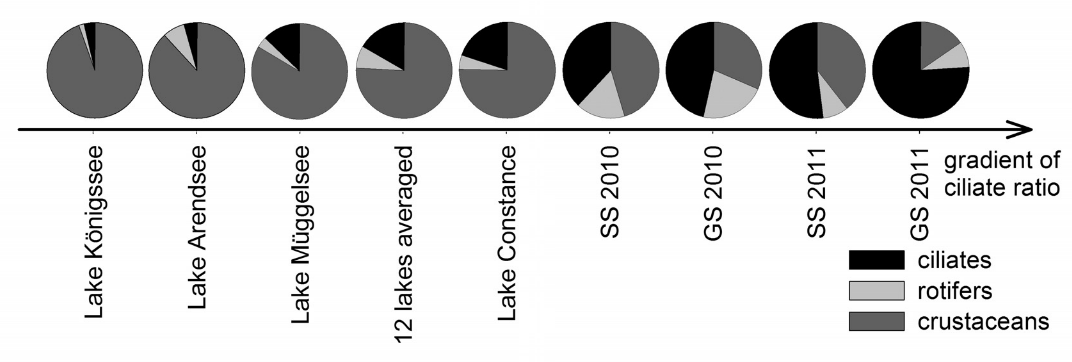

Figure 3. Ratios of arithmetically averaged ciliate, rotifer and crustacean biomasses in GS and SS for 2010 and 2011 and of various lakes for comparison (see Table 2 for details).

The ciliate community was composed of an average number of 12 to 18 different morphotypes per sampling date in both lakes and was rather similar in both lakes. The morphotypes belonged to the taxonomic groups Choreotrichia (36% abundance, 45% biomass), Scuticociliatia (28% abundance, 8% biomass), Prostomatea (21% abundance, 21% biomass) and Peritrichia (1% abundance, 11% biomass). Representatives of the Choreotrichia were typified by members of the genus *Strobilidium*, as were the Scuticociliates by *Cyclidium* and the Prostomatea by *Urotricha* and *Coleps*. The peritrich *Vorticella* is typically epibenthic, as it attaches to a substrate, but when filamentous algae are present, it is also found in the pelagic zone, as was the case in GS and SS. The small *Strobilidium* sp. (individual size: 4.500 µm³), the large *Strobilidium* sp. (15.000 µm³) and *Coleps hirtus* (21.000 µm³) were on average the most important ciliate morphotypes in terms of biomass and made up more than 40-51% of the total ciliate biomass (except GS 2010: 26%). Especially in early spring, large, predatory species as *Monodinium* sp. (50.000 µm³), *Didinium nasutum* (75.000-200.000 µm³), *Stentor* sp. (980.000 µm³) and *Bursaridium* sp. (370.000-570.000 µm³) gained in importance. Small sized ciliates (cell volume: 10^3-10^4 μm^3) made up 30% of the total ciliate biomass on average in 2010 in both lakes and 48% in GS and 43% in SS in 2011. Medium sized ciliates (cell volume: 10^4-10^5 μm^3) contributed on average the largest proportion to the ciliate biomass (48-59%, except for GS 2011 with 40%). Ciliates having a cell volume larger than

10^5 µm^3 made up the smallest proportion. The largest ciliates were of the same size (in units of carbon) as nauplii and small cladocerans. Thus ciliates had the potential to graze on the whole size spectrum of phytoplankton.

Bacterial biomass

The total volumetric biomass of bacteria ranged between 60 and 142 mg C m^{-3}, thus the phytoplankton biomass was 5 to 15 times larger. It was dominated by free-living bacteria (about 2 to 5 times higher than particle-attached bacteria), whereas cell-specific biomasses were higher in the attached fraction compared to the free-living fraction (about 2 times). However, as particle-attached bacteria clump the effective prey size was several times larger.

Ciliate top-down effects on phytoplankton and bacteria

Ciliates were categorized according to their feeding type into feeders of small, intermediate and large particles, and phytoplankton and bacteria were grouped according to their edibility for these ciliate groups. Small and intermediate feeders had the largest biomass within the ciliates whereas large feeders were of minor importance (about 20% or less, Fig. 4). The pattern was different within the prey. On average, the small prey contributed the least to the prey biomass and the portion of large prey varied strongly between lakes and years (10-71%). Over the course of the years, the biomass ratio prey : ciliates was usually above 1 and declined along with the groups “large”, “intermediate” and “small”. The average prey : ciliates ratio ranged from 38 to 203 for large particles, from 5 to 24 for the intermediate prey, and from 2 to 5 for the small groups.

The estimated proportion of the water column filtered daily by ciliates was calculated based on the abundance and size of ciliates and suggests a huge impact by small feeders. Except for a few dates, the small feeders achieved the highest estimated proportion of the filtered water column, on average 0.8 to 1.1 times per day in 2010 and 1.9 to 3.5 times per day in 2011, followed by the intermediate feeders filtering the water 0.7 to 1.8 times per day for GS and SS. The calculated ingestion rate of phytoplankton and bacteria by ciliates was related to the actual amount of prey to estimate the proportion of prey potentially consumed by ciliates per day (Fig. 5). The median proportion of small phytoplankton grazed by small ciliate feeders is above 1, implying that based on our estimates more than 100% of the actual biomass could be grazed by the ciliates per day. Median values for intermediate sized phytoplankton were usually one order of magnitude lower than for small phytoplankton. The production : biomass ratios of the entire phytoplankton were in the range of the calculated consumed proportion of intermediate sized phytoplankton, suggesting production sufficient to sustain the ingestion rates by intermediate ciliate grazers (Fig. 5). However, the average phytoplankton production : biomass ratios were too low to maintain constant phytoplankton biomasses when taking the large calculated ingestion rates by small feeders into account. The opposite pattern was found for bacteria (Fig. 5). According to the calculated estimates of the grazing rates, the proportion of particle-attached bacteria consumed by intermediate feeders was much larger than the proportion of free-living bacteria consumed by the respective ciliates. The bacterial production : biomass ratio was in the range of the calculated proportion of bacterial biomass consumed by small feeders and much lower than for intermediate feeders. Thus the growth rate of the prey (indicated by the production to biomass ratio) was much lower than the enormously high ingestion we calculated for small phytoplankton and particle-attached bacteria.

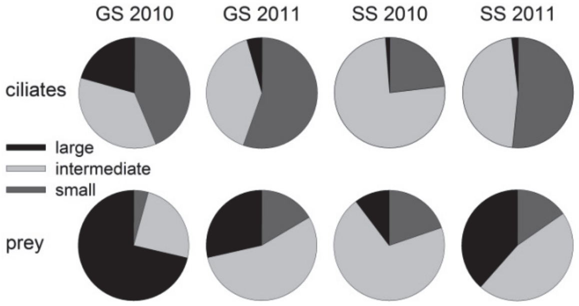

Fig. 4: Average biomass ratio of large, intermediate and small feeders within the ciliates and their prey (phytoplankton and bacteria) in GS and SS in 2010 and 2011. Free-living bacteria were allocated to the small plankton and particle-attached bacteria to the intermediate plankton.

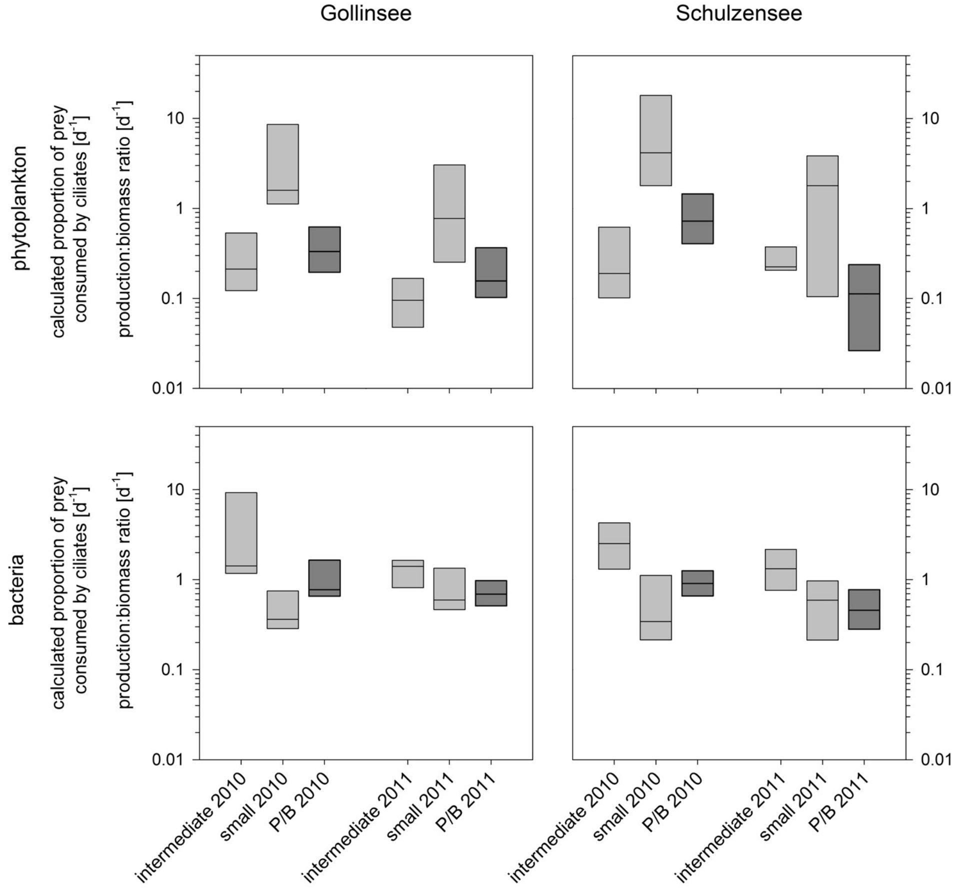

Figure 5. Calculated proportion of potentially ingested prey (phytoplankton: upper panels; bacteria: lower panels) by ciliates of feeding type intermediate and small in GS and SS in 2010 and 2011. P/B indicates the production to biomass ratio of the entire phytoplankton or bacteria community and allow a comparison between phytoplankton growth and potential grazing losses. Intermediate ciliate feeders graze on particle-attached bacteria and small ciliate feeders graze on free-living bacteria. The median is given as line within each box which represents the middle 50% of the values of the respective year.

Discussion

The winter fish kill revealed several important aspects about the role of ciliates in pelagic food webs. First, low biomasses of crustaceans, arising through grazing by very high densities of young of the year (YOY) fish, released ciliates from otherwise effective predation pressure. Second, when released from predation pressure, ciliates attained remarkably high biomasses, even in moderately eutrophic lakes such as those in our study. We conclude that this high ciliate biomass and the accompanying high estimated grazing pressure on various phytoplankton size classes altered the phytoplankton size structure, but were only partially successful in suppressing phytoplankton (Fig. 6). Finally, the release of ciliates from grazing pressure only moderately changed their community structure, with the same small species typical for many pelagic systems also dominating in the lakes of our study.

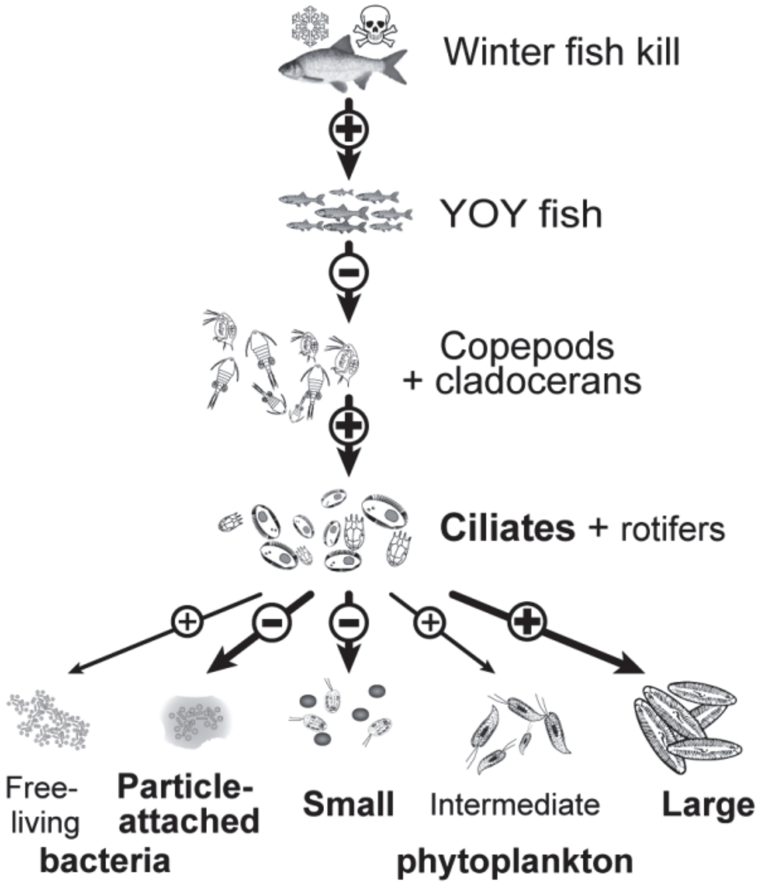

Figure 6. Cascading effects of the winter fish kill for the pelagic food web. + indicates positive effects; − negative effects. Effects were more pronounced within groups highlighted by bold letters and large signs.

Metazooplankton under severe grazing pressure

Due to the partial winter fish kills prior to our sampling campaign and in between both years, the adult fish biomass was reduced and YOY fish dominated in respect to abundance, being several times more abundant than before the fish kills (Hilt *et al.*, 2015). A severe top-down control of crustaceans by YOY fish was indicated by low biomasses and their composition

(Fig. 6). In their review, Mehner and Thiel (Mehner and Thiel, 1999) concluded that in temperate regions, YOY fish have the largest impact on zooplankton in late summer and autumn. This is in line with our observation that in 2011 adult crustaceans were almost absent and nauplii and copepodites dominated the crustacean community during the respective time. The ratio of nauplii to total copepod biomass was unusually high (about 50% in 2011) compared to other lakes (Königssee: 7%, Großer Vätersee: 6%, Lake Constance: 2-7%; Table 2) and confirmed the high predation pressure on adult copepods and the potential benefit for nauplii from cannibalistic predator release (Van Den Bosch and Santer, 1993). The cladoceran biomass was reduced even more strongly than the copepod biomass from 2010 to 2011 which can be explained by the fact that copepods are able to escape more efficiently from fish predation (Winfield *et al.*, 1983).

Effects on phytoplankton

Phytoplankton was released from predation pressure by crustaceans and thus built up large biomasses compared to the deep lakes. In both study lakes the phytoplankton : crustacean ratio was even higher than reported from the hypertrophic Müggelsee which is characterized by cyanobacteria blooms. In the Arendsee, however, where planktivorous fish stocking released phytoplankton from its top-down control (Tittel *et al.*, 1998), the phytoplankton : crustacean ratio was closest to those measured in GS and SS, which is in line with an exceptionally low crustacean biomass in the two lakes (Fig. 1).

The phytoplankton community in GS and SS was as diverse as reported for shallow Danish lakes of similar trophy (Jeppesen *et al.*, 2000). However, phytoplankton diversity in the Danish lakes was driven by a high species number, whereas in GS and SS the fewer phytoplankton species were more evenly distributed, resulting in a similar Shannon-Wiener Index. In our ciliate dominated zooplankton communities, consumers were more selective than in communities dominated by e.g. filter feeding *Daphnia*, which likely promoted a relatively even distribution of the biomass across the different morphotypes and size ranges.

Phytoplankton often escapes zooplankton grazing pressure by accumulating in forms which are beyond the preferred size spectra of the consumers. In GS and SS ciliates potentially grazed on a broad range of phytoplankton sizes classes. However, the shape of phytoplankton size spectra (Fig. 2) did not deviate very much from those in Lake Constance (Gaedke, 1992) and the Müggelsee (Gaedke *et al.*, 2004). A remarkable exception was the high proportion of large phytoplankton species which increased over the study period, especially in GS (Fig. 6). This may be attributed to the strong decrease in crustacean biomass controlled by high YOY fish abundances. The biomass peak of the size spectra was constituted by pennate diatoms. The majority of the ciliates could presumably neither graze on these pennate diatoms nor on other large phytoplankton (mainly *Peridinium* sp.).

Severe top-down control by ciliate dominance

Ciliates, which are usually suppressed by metazooplankton grazing (Adrian and Schneider-Olt, 1999; Hansen, 2000; Jürgens *et al.*, 1999; Wickham, 1998; Wickham and Gilbert, 1993), dominated the zooplankton community in our study lakes where high abundance of YOY fish released the ciliates from top-down control by crustaceans (Fig. 3). Not only the proportional contribution of ciliates to total zooplankton biomass, but also their absolute biomass was much higher than reported from various other lakes. Ciliate numbers ranged up to 350 cells mL^{-1} and the yearly average ranged between 42 and 164 cells mL^{-1}. In another temperate eutrophic lake the maximum density reached 9 cells mL^{-1} (Laybourn-Parry *et al.*, 1990) and average densities of 56 cells mL^{-1} were reported for eutrophic tropical lakes (Beaver and Crisman, 1982). In shallow eutrophic Lake Võrtsjärv ciliates also dominated (66% of zooplankton biomass) within the zooplankton community because metazooplankton grazing was inhibited by filamentous algae and strong, continuous resuspension (Zingel and Noges, 2010). Thus, maximum densities reached 285 cells mL^{-1} and yearly average densities were 52 cells mL^{-1}. In another study in Lake Võrtsjärv, sampling was conducted for several years during the annual abundance peaks at eight different sites in the lake and ciliate abundances were observed to range between 80 and 123 cells mL^{-1} (Karus *et al.*, 2014a). In our study, the ciliates seemed to benefit exceptionally from the absence of crustaceans, which were fully controlled by YOY fish, exhibiting a positive feedback on ciliates via a trophic cascade. The ciliate abundance in GS and SS was on average 10 times larger than previously observed in an experimental removal of metazooplankton in the Schöhsee (Wickham, 1998), which may be attributed to the higher productivity in GS and SS.

In GS and SS ciliates rather than rotifers dominated when crustaceans failed to build up. Although the contribution of rotifers to the total zooplankton biomass in GS and SS was larger than in other lakes of various depth and trophic state, the ratio of ciliate to rotifer biomass was still up to 15 times higher in GS and SS than in other lakes. Thus, ciliates benefited proportionally more from crustacean absence than rotifers. Rotifers are competitors and predators of ciliates, but the actual strength of interaction is species specific (Weisse and Frahm, 2002). The dominant rotifer species, *Keratella cochlearis* is small and thus more likely a competitor of ciliates, feeding on small and intermediate phytoplankton, rather than preying on ciliates. The egg ratio of *K. cochlearis*, i.e. the number of eggs per female, serves as an indicator of food limitation (Gonzalez and Frost, 1992; Weithoff *et al.*, 2000). It was below 0.2 in early summer and autumn suggesting a severe food limitation for rotifers. Given the large overlap in the feeding niches of small ciliates and rotifers, this suggests that also the small feeders within the ciliates were food limited, at least part of the year.

Interestingly, the release from grazing pressure did not radically change the ciliate species composition. The ciliate community was dominated by Choreotrichia, Scuticociliatia, Prostomatea and Peritrichia, including species typical for the pelagic zone of lakes with crustacean zooplankton present in sizable numbers such as *Halteria*, *Strobilidium* and

Cyclidium (Foissner *et al.*, 1999; Gaedke and Wickham, 2004 and references therein). Small ciliates dominated along with some large, predatory species potentially feeding on the small ciliates. Some, such as *Stentor* and *Bursaridium*, are capable of ingesting algae, ciliates and small rotifers, while *Didinium* is specialized on other, larger, ciliates (Hewett, 1988; Jiang and Morin, 2005). In an experiment where metazooplankton was removed, predacious ciliates comprised 63% of the total ciliate biomass and a decline in abundance of small ciliates along with an increase in predacious ciliates suggested a strong top-down control (Agasild *et al.*, 2013). In contrast, in SS the biomass of predacious ciliates can be neglected and in GS, apart from a peak in spring 2010, they contributed on average only 10% of the total ciliate biomass. While the size of predaceous ciliates was large by ciliate standard (200 x 10^3 µm^3 – 800 x 10^3 µm^3), the size was well within the preferred size range of many cyclopoid copepods (Brandl and Fernando, 1975). Cyclopoids are capable of remarkably high ingestion rates on ciliates (Wickham, 1995), and large, unarmored, relatively slow-swimming species such as *Bursaridium* and *Stentor* may represent the preferred prey of the few cyclopoids (adult and copepodites) present in the two study lakes. Thus, the inability of predacious ciliates to fully exploit an open niche may have been due to their only partial release from predation pressure. Overall, for whatever reason, the absolute biomass of predacious ciliates was too low to suppress ciliates and thus predation within ciliates was of minor importance most of the year in both lakes, GS and SS.

A shift towards dominance of ciliates as observed in our study implies an increase of the total grazing pressure by zooplankton despite an overall constant zooplankton biomass as ciliates consume per biomass approximately 3-4 times more than crustaceans (Tirok and Gaedke, 2006). Species-specific ciliate filtration rates are typically in the range 0.5 – 10 µL h^{-1} $cell^{-1}$, at temperatures 10 - 20°C (Jonsson, 1986; Simek *et al.*, 1995). Simply applying a median literature filtration rate, e.g. 2 µL h^{-1} $cell^{-1}$, multiplied by the average ciliate abundances for the two studied lakes (42 – 164 cells mL^{-1}) gives a rough estimate of the potential community filtration rate, e.g. 2 µL h^{-1} $cell^{-1}$*24h*70 cells mL^{-1}=3.4 times per day filtering the water volume. Using Hansen *et al.*'s (1997) cell-volume-specific formulas, corrected to the ambient temperatures in the lakes, allowed more accurate estimates for each sampling date, delivering yearly average values in the range of 0.7-3.5 d^{-1} for the community filtration rate. These calculated estimates of the filtration rate by ciliates indicated that small feeders were the most important ciliate group for phytoplankton grazing. This resulted in very high calculated ingestion rates on a restricted size range of the phytoplankton size spectrum, leading to an accumulation of large phytoplankton species (Fig. 2, 4). The phytoplankton to ciliate biomass ratio increased along with the groups of small, intermediate, and large feeders, further supporting a large predation pressure by small feeders (Fig. 4). In theory, a certain amount of prey can sustain the same amount of predator biomass if the prey has a substantially larger weight specific production than the predator (Boit and Gaedke, 2014; Gaedke *et al.*, 2002). Additionally, the actual biomass ratio for the small feeders may be larger as we did not measure autotrophic picoplankton (APP; length < 2 µm) as potential prey. In general, the share of APP on phytoplankton decreases with eutrophication. Therefore, we assume a moderate biomass increase of small prey. For example, in the eutrophic Arendsee the APP contributed on maximum 4% to the total autotrophic biomass (Tittel, 1997). Adding this overall small amount of prey to the small size classes raises the biomass of the small prey by about 25%. This rough estimate, however, still implies a biomass of small phytoplankton in GS and SS between 10-100 mg C m^{-3}, which is considered as the threshold for positive population growth for various ciliate species (Tirok and Gaedke, 2007a; Weisse, 2006). Thus, ciliates were presumably not able to lower the biomass of small phytoplankton further. In line with that estimate, the calculated ciliate ingestion rates strongly exceeded the growth rates of small phytoplankton, even if considering that small phytoplankter are more productive than the average community. Mass-balanced fluxes of the pelagic food web indicate that the phytoplankton and bacteria production was sufficient to maintain the large ciliate biomass, but did not allow for their maximum potential growth rates (unpublished data). Consequently, these calculations deliver further evidence that ciliates were likely bottom-up controlled, as reported for another shallow eutrophic lake where the grazing impact by metazooplankton was low (Zingel and Noges, 2010). However, the monthly sampling restricts the generality of our conclusions as ciliates, but also phytoplankton and bacteria, have generation times on the order of one day, and tight coupling between ciliate and algal dynamics has previously been reported (Berninger *et al.*, 1993; for seasonal dynamics see Appendix 4). Thus opposed dynamics might have been overlooked. Nevertheless, by sampling in two lakes for two years we received consistent results of four replicates, which lower the chance for undetected opposed effects.

The distinction between free-living and particle-associated bacteria enabled us to also investigate the grazing pressure on both bacteria fractions separately. Accordingly, the highest grazing pressure by ciliates was presumably exerted on particle-attached bacteria, which had a much higher cell-specific biomass than free-living bacteria (Fig. 6). Particle-associated bacteria seem to be easier to ingest by ciliates because of their generally larger size and association to particles which can be well ingested by ciliates (Gonzalez *et al.*, 1990). As a consequence, free-living bacteria may have been released from ciliate predation (Fig. 5). Omnivorous ciliates as e.g. *Halteria* are generally efficient grazers of suspended bacteria (Jürgens and Simek, 2000; Simek *et al.*, 1996). Unfortunately, the role of heterotrophic nanoflagellates was not considered in our study, but the calculated enormous grazing pressure of ciliates on nanophytoplankton would imply top-down control by ciliates on heterotrophic nanoflagellates as well. Thus free-living and smaller bacteria were likely released from flagellate grazing in the studied lakes. This is supported by the observation that ciliates instead of nanoflagellates became the main bacterial grazers after the experimental addition of juvenile planktivorous fish to an otherwise fishless pond (Karus *et al.*, 2014b). It is certain that the observed winter fish kill resulted in a concomitant decrease in crustaceans and increase in ciliates. Therefore, the microbial loop greatly gained in importance for organic matter and nutrient cycling and thus represents an exceptionally important component in the lake's food web under such environmental conditions.

Conclusions

Due to partial winter fish kills followed by a very high density of YOY fish, the zooplankton community composition largely deviated from that in other lakes. A ciliate dominance came along with strongly reduced biomasses of adult crustaceans, whereas nauplii and copepodites gained in relative importance. According to the estimated grazing pressure small sized phytoplankton and particle-attached bacteria were likely top-down controlled by the small and intermediate particle feeders within the ciliates (Fig. 6). Ciliates have a narrower feeding niche than an equivalent biomass of crustacean zooplankton, preventing them from controlling the larger phytoplankton size classes, in which biomass accumulated. We strongly emphasize the importance of more detailed measurements of ciliates as they can be an important trophic link in the pelagic food web, especially if crustaceans are reduced. Additionally, our measurements add to the recently recognized importance of winter processes for fish and plankton development during subsequent years, which are far beyond a simple reset.

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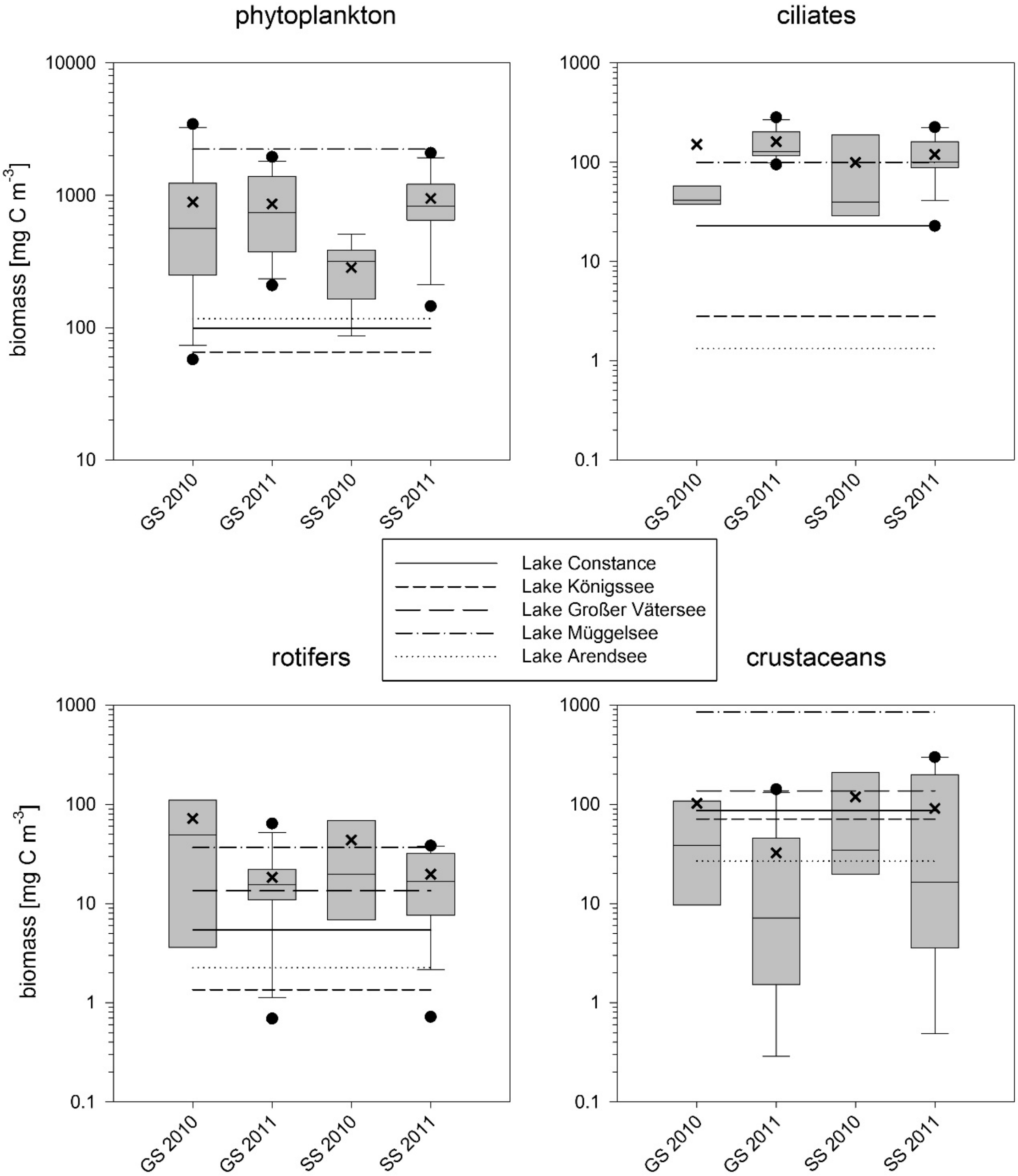
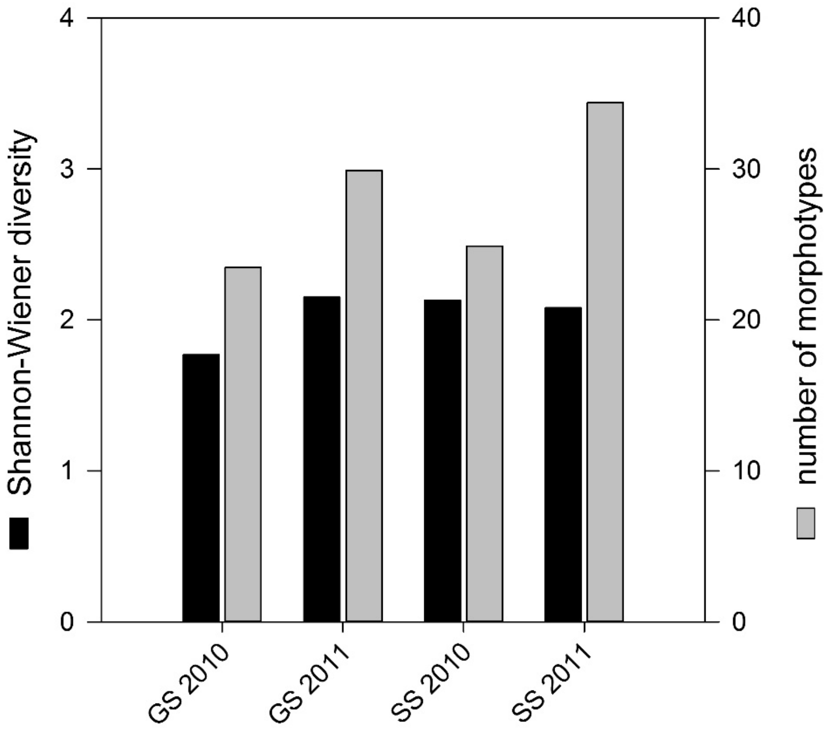
Supporting Information

Appendix 1: Phytoplankton and zooplankton biomass



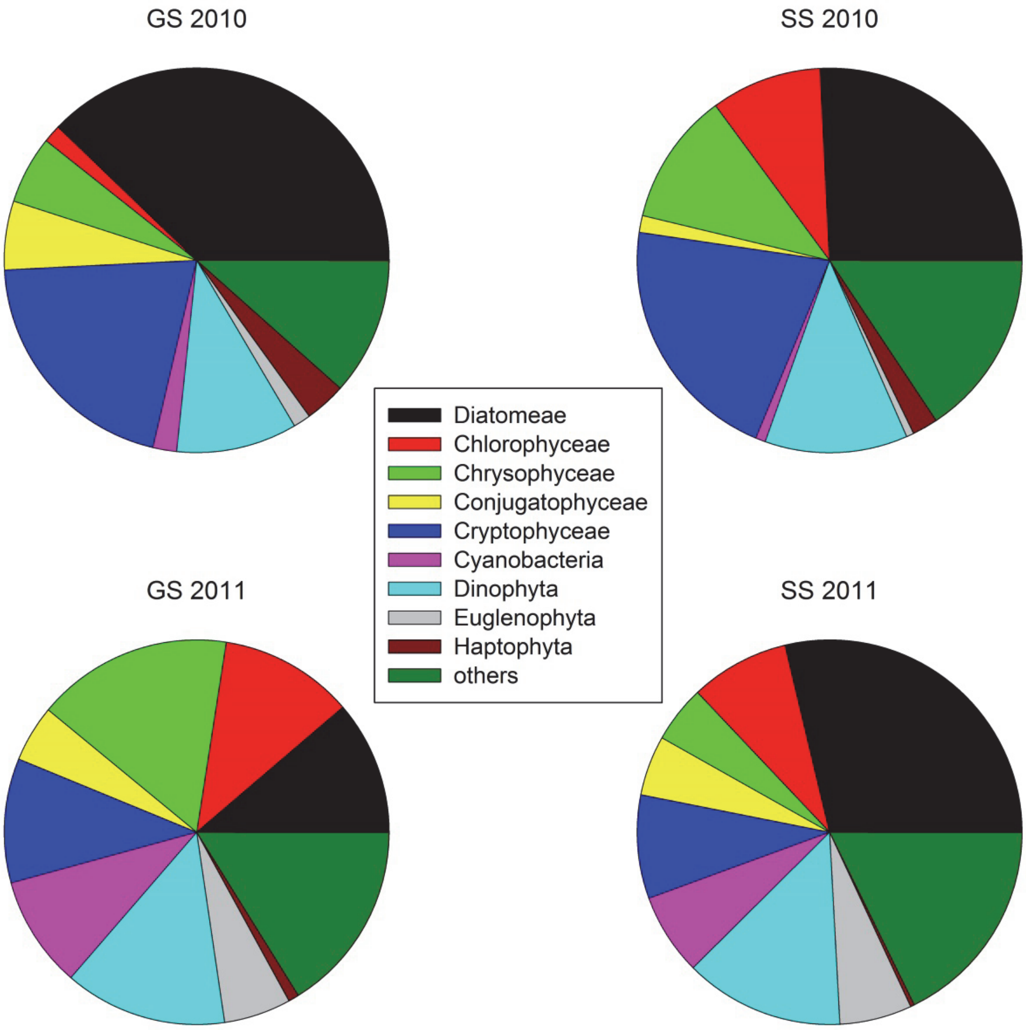
Appendix 1 – Figure 1. Boxplots representing the phytoplankton, ciliate, rotifer and crustacean biomass measurements for GS and SS in 2010 and 2011 in comparison with other lakes. The lower edge of the box represents the 25% quartile, the upper edge the 75% quartile and the line within the box the median. Whiskers depict the 5% and 95% range and were only drawn if sufficient data were available. Crosses represent the respective whole year arithmetic average biomass. The average ciliate biomass was far larger than the median in GS in 2010 due to a biomass peak (912 mg C m^{-3}). Two extremely low values were excluded from the figure (24.02.2011 crustaceans: GS 0.03 mg C m^{-3}, SS 0.01 mg C m^{-3}). For comparison arithmetic average biomasses from various lakes were included as horizontal lines (see Table 2 for details). Note the different y-axes for phyto- and zooplankton.

Appendix 2: Phytoplankton diversity



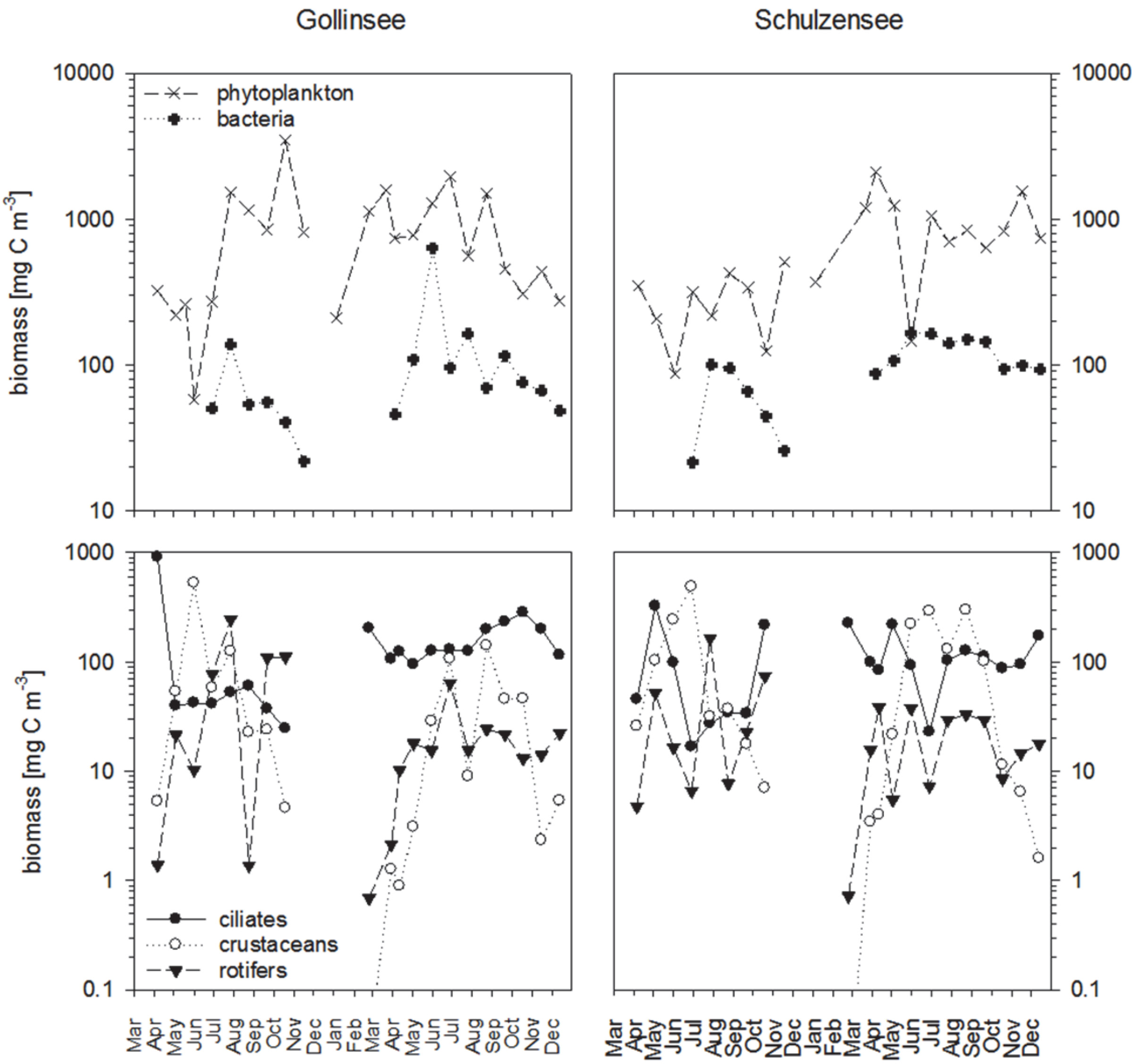
Appendix 2 – Figure 1. Phytoplankton Shannon-Wiener diversity and average number of morphotypes in GS and SS per sample in 2010 and 2011.

Appendix 3: Phytoplankton composition



Appendix 3 – Figure 1. The Diatomeae, Cryptophyceae and Dinophyta represented proportionally the largest biomass. Representatives of the Diatomeae were typified by large pennate morphotypes, as were the Crytophyceae by *Cryptomonas* and the Dinophyta by *Peridinium* and *Gymnodinium*. In GS 2011 Chrysophyceae, Dinophyta, Chlorophyceae and Diatomeae contributed almost equally to the phytoplankton community. Among the Chrysophyceae *Ochromonas* and *Dynobryon* were dominant.

Appendix 4: Seasonal dynamics of phytoplankton, bacteria and zooplankton



Appendix 4 – Figure 1. Seasonal course of phytoplankton, bacteria, ciliate, rotifer and crustacean biomass in Gollinsee (GS) and Schulzensee (SS) from April 2010 to December 2011. The phytoplankton biomass peaked in spring, summer and autumn. The maximum biomass peak in GS in mid-October 2010 was due to a bloom of one large (200 µm) pennate diatom which did not develop in 2011. The bacterial biomass peaked in summer in both lakes in 2010 and additionally in spring and autumn in GS in 2011 whereas in SS the biomass remained high from summer to autumn. In both lakes the peak biomass was larger in 2011 than in 2010. In 2010 in GS and SS, ciliates peaked in spring (100-900 mg C m^{-3}) and persisted at relative low levels during summer (15-60 mg C m^{-3}), whereas in 2011 the ciliate biomass ranged between 100-300 mg C m^{-3} all over the year except for one outlier in summer in SS (45 mg C m^{-3}). The ciliate biomass varied less over the course of the year in 2011 in both lakes. The rotifer biomass showed little variation over the course of the years and remained at most of the sampling dates far below 100 mg C m^{-3} except for July 2010 in both lakes and in GS in autumn 2010. The crustacean biomass remained low until May and peaked in June in 2010 whereas in 2011 it remained at an intermediated level for a longer period during summer. Peaks did not exceed 100-500 mg C m^{-3}. All over the zooplankton, phytoplankton and bacteria biomasses were quite constant over the course of the year. Two outliers have been excluded from the figure (24.02.2011 crustaceans: GS 0.03 mg C m^{-3}, SS 0.01 mg C m^{-3}). Consider the differing y-axes for phyto- and zooplankton.

Chapter IV

Dominance of pelagic carbon fluxes in shallow lakes emerges from inefficient benthic carbon transfer

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Abstract

Benthic autotrophic and bacterial production rates often exceed pelagic rates, making them a potentially important component in food webs, especially in shallow lakes. It can be expected that their quality is comparable to the one of the respective pelagic producers, which are efficiently utilized by animal consumers. Thus, we hypothesize similar efficiencies for the pelagic and benthic habitat. We performed whole ecosystem studies in two shallow eutrophic lakes, one with and one without submerged macrophytes, by measuring or estimating pelagic and benthic biomass and production rates for all food web components including bacteria, to derive quantitative food webs. Benthic organisms dominated the bacterial and autotrophic production, whereas the animal consumer production was mainly pelagic. Consequently, the benthic carbon transfer, i.e. from benthic bacterial and autotrophic production to macrobenthos production, was an order of magnitude less efficient than that of the pelagic food web, i.e. from pelagic bacterial and autotrophic production to rotifer and crustacean production. This holds true when considering several aspects influencing benthic transfer efficiencies, such as (1) the food quality of producers, (2) further consumer production by pelagic and benthic protozoa and meiobenthos at an intermediate or the pelagic and benthic top consumer level and (3) pelagic-benthic links, being unlikely according to the consumer community composition. (4) Oxygen may limit benthic consumers in the profundal zone, resulting in lower whole-lake benthic than pelagic efficiencies. But, benthic efficiencies in the more oxygenated littoral remain a tenth of the pelagic efficiencies.

Introduction

Ecosystems can be composed of spatial compartments, which may exhibit fundamental differences with respect to resource availability, habitat structure and food web components. Lakes feature both pelagic (open-water) and benthic (sediment surface) habitats. So far, research in lakes has focused primarily on the pelagic zone, but benthic habitats are increasingly recognized to contribute substantially to whole-lake functions and processes (Althouse *et al.*, 2014; Vander Zanden and Vadeboncoeur, 2002). Vadeboncoeur and others (2002) compiled data from several studies to show that the production of benthic autotrophs, heterotrophic bacteria and invertebrates approximates or exceeds the pelagic production and accordingly demanded the reintegration of benthic pathways in food web models. Especially in shallow lakes with their high area to volume ratio, benthic autotrophic and bacterial production rates can be greater than pelagic rates (Brothers *et al.*, 2013b; Genkai-Kato *et al.*, 2012). However, the entire food webs in both habitats have rarely been quantified simultaneously (Andersson and Kumblad, 2006; Jia *et al.*, 2012; Rowland *et al.*, 2015). The few studies comparing the pelagic and benthic habitats have either focused only on autotrophic producers (Althouse *et al.*, 2014; Blindow *et al.*, 2006; Brothers *et al.*, 2013b) or only on top predators (Vander Zanden and Vadeboncoeur, 2002). In both trophic levels, a high relevance of benthic organisms was confirmed. However, it is not clear whether the high contributions of benthic organisms to the diet of top predators (Vander Zanden and Vadeboncoeur, 2002) originate from the high contribution of benthic producers to the lake-wide autotrophic production (Althouse *et al.*, 2014; Brothers *et al.*, 2013b); hence little is known about the relative efficiencies of the energy transfer from producers to animal consumers in both lake habitats.

The transfer efficiency is expected to be high if prey and predators co-occur in the same habitat and if a large part of the prey production is edible for the predator. These requirements are fulfilled for example in the pelagic habitat of the large, oligotrophic Lake Constance, where the phytoplankton and bacterial production was efficiently transferred to animal consumers (Boit and Gaedke, 2014; Gaedke and Straile, 1994). Benthic autotrophs and bacteria have access to a larger nutrient pool in the sediment compared to pelagic producers in the open-water (Sand-Jensen and Borum, 1991). Periphyton, typically the dominant benthic autotroph (Brothers *et al.*, 2013b), and bacteria aggregates are of suitable size for invertebrate grazing. Thus, the nutritional quality and edibility of the dominant pelagic and benthic autotrophs and bacteria is suggested to be equivalent (Hessen *et al.*, 2013; Sand-Jensen and Borum, 1991). Consequently, we postulate that the benthic autotrophic and bacterial production are equally efficiently transferred to animal consumers as in the pelagic food web.

Obtaining reliable information on the energy transfer in spatially different compartments of lakes is, however, often hampered by the large effort to reliably measure or estimate biomasses, production rates and diet compositions of all relevant groups of organisms. Accordingly, no study has yet achieved to comprehensively compare trophic transfer efficiencies in the two spatial compartments of lakes. We provide here an integrated view on the pelagic and benthic food webs of two shallow eutrophic lakes, one with and one without submerged macrophytes. Our quantitative approach relies on detailed measurements of biomass and production of all basal producers including the rarely investigated pelagic and benthic (sediment) bacteria, and biomass and production measurements or estimates of various animal consumer groups. We calculate the trophic efficiencies of autotrophic and bacterial production to animal consumers for the full lake, as well as separately for the pelagic and benthic habitats of both lakes and hypothesize similar pelagic and benthic efficiencies.

Methods

General overview

We studied two shallow lakes, Schulzensee and Kleiner Gollinsee (hereafter referred to as Gollinsee), both located in northeastern Germany. The lakes have a similar size (3-4 ha), mean depth (about 2 m), and nutrient concentrations (on average: 32-33 µg total phosphorus L^{-1}), but 20-25% of the area of Schulzensee was occupied by submerged macrophytes (*Ceratophyllum submersum*), whereas Gollinsee had no submerged macrophytes during the period of our investigation (Brothers *et al.*, 2013b). In 2011, we measured the biomass and production rates of bacteria and autotrophs, the biomass of consumers, and either measured or calculated consumer production rates in both, the pelagic and benthic zones to construct a fully quantitative food web model for each lake. Samples were taken from the beginning of April to the end of October 2011 (213 days). We averaged the biomass measurements and summed the production measurements and estimates to obtain seasonal data. Bacteria, phytoplankton, epipelon and zooplankton were sampled in the pelagic and littoral zone. As their biomasses, production rates, and community composition were similar at both sampling locations, the lakes were considered to be horizontally mixed. Pelagic and littoral measurements were thus arithmetically averaged for whole-lake values. The lakes were divided by a plastic curtain since October 2010 and maize leaves were added to one half of each lake as part of an unrelated experiment (Attermeyer *et al.*, 2013; Scharnweber *et al.*, 2014). We use only the data from the reference halves for this study, but refer to them as whole lakes as the proportions of pelagic and benthic habitats were similar between entire lakes and divided lake halves.

Autotrophs

Phytoplankton were sampled monthly in the pelagic zone at three depths and in the littoral zone at three locations. Samples from each habitat were pooled, fixed with acidified Lugol's solution, and analyzed with inverted microscopy. The size of at least 20 cells of each morphotype was measured to calculate the cell volume (Hillebrand *et al.*, 1999) and converted into the cell-specific individual C content (Menden-Deuer and Lessard, 2000). Submerged plastic strips were exposed to measure epiphyton and epipelon biomass monthly, as described by Brothers and others (2013b). We measured the maximum submerged macrophyte biomass, occurring in July as further outlined by Brothers and others (2013b). Epiphyton, epipelon and submerged macrophyte biomasses were measured in 2010, but were not expected to differ systematically in 2011.

The gross primary production (GPP) of autotrophs was measured using a fluorometric approach, which did not provide plant respiration rates (see Brothers *et al.*, 2013b for details). Phytoplankton and submerged macrophytes were thus assumed to have lost, respectively, 40% and 60% of their GPP due to respiration (following Best, 1982 and references therein; Platt *et al.*, 1991). Epiphyton and epipelon respiration rates were calculated using a seasonal relationship between their biomass and respiration rates (Liboriussen and Jeppesen, 2006). For Schulzensee, we did not consider the cyanobacterial population of *Aphanothece stagnina* in this study, as it contributed only a minor fraction (< 5%) of the whole-lake primary production rates and the uncertainty in estimating its NPP is large (Brothers *et al.*, 2013b). Emergent and floating macrophytes were not considered as aquatic autotrophs, because they derive inorganic carbon directly from the atmosphere, but they are significant contributors to the lakes' organic carbon pools (see below).

Bacteria

The water samples for phytoplankton were also used to measure free-living and particle-attached bacterial biomasses and production rates. To measure the biomass and production rates of sediment bacteria, the first upper centimeter of three sediment cores were taken monthly with a sediment corer in the profundal and littoral zones. 1–2 mL of the water and 40–50 µL of the sediment samples were filtered onto a 0.2 µm polycarbonate filter. Bacterial abundance and cell volume were determined by epifluorescence microscopy after staining with SYBR gold (Shibata *et al.*, 2006). Bacterial cell volume was converted to biomass using the relationship of Simon and Azam (1989). Bacterial production rates were measured by the incorporation of L-^{14}C-leucine into the protein fraction using the protocols of Simon and Azam (1989) for water samples and Buesing and Gessner (2003) for sediment samples (for details see Attermeyer *et al.*, 2013).

Zooplankton

The monthly zooplankton samples were split to fix ciliate samples with acidified Lugol's solution (Schmidt-Halewicz *et al.*, 2012) and to filter (55 µm mesh) and fix (Haney and Hall, 1973) rotifer and crustacean samples. The samples were quantitatively analyzed, identified to the genus or species level, and size was determined as volume (ciliates, rotifers) or length (crustaceans) after Schmidt-Halewicz and others (2012). Individual C contents were calculated using regressions with specific conversion factors for each zooplankton group (Dumont *et al.*, 1975; Müller and Geller, 1993; Telesh *et al.*, 1998) and assuming that 50% of the dry weight was C (Gaedke, 1992 and included references).

Ciliate production was estimated following Montagnes and others (1988), accounting for species biomass, cell volume and temperature, which provided values similar to those obtained using the equations of Hansen and others (1997). We followed previous studies also based on Montagnes and others (1988), in recognizing that these were maximum estimates which may not always be reached due to food shortages. Thus, the calculated values were reduced by 75-80% in the previous studies (Gaedke *et al.*, 2002). We restricted ciliate production estimates according to the available C for ciliate consumption, assuming a growth efficiency of 33% (see further explanations below), and ultimately reduced the maximum production by about 60%. Rotifer production rates were estimated using a linear regression model, which accounted for total biomass and temperature (Shuter and Ing, 1997). Production estimates for crustaceans considered the individual size and biomass of each species using two sets of specific parameters for below and above 10°C (Stockwell and Johannsson, 1997).

Macrobenthos

Macrobenthos biomass values were obtained from monthly samples of the eulittoral, sublittoral and profundal zones at two transects in each lake (for details see Brothers *et al.*, 2013a). The annual production of macrobenthos was estimated using the allometry-based approach of Plante and Downing (1989) accounting for the seasonal average biomass and the maximum individual size for each habitat (for details see Mehner *et al.*, 2015).

Fish

To estimate the biomass and production of fish, abundance data were derived from a mark-recapture approach as described in Brothers and others (2013a). Individual growth was estimated by a scale analysis of the predominant fish species roach (*Rutilus rutilus*). Length at age was back-calculated following the approach of Fraser (1916) and Lee (1920). Biomass and weight increment of the different cohorts, and hence production in 2011, were estimated using our own length-weight regressions. Production for the whole fish community was extrapolated according to the proportion of roach to the total biomass estimated from a standardized fishing campaign. Young of the year (YOY) fish were very abundant (Hilt *et al.*, 2015), but we were unable to quantify their biomass and production.

PDOC pool

Dead particulate and dissolved organic carbon (PDOC) originates from several sources (Fig. 1) and is taken up by the pelagic and sediment bacteria. PDOC results from the exudation of all autotrophs, which was assumed to amount to 4% of macrophyte GPP (Wetzel and others 1972 in Hough and Wetzel, 1975) and 15% of the GPP for all other autotrophs (Gaedke and Straile, 1994). We assumed that all consumers assimilate 67% of the ingested prey, the remains being excreted and entering the PDOC pool (Fig. 1). Animal consumers having lower assimilation efficiencies ingest more C to achieve similar production rates. Thus, less C remains unconsumed, but the consumers excrete more C (Fig. 1). The sum of C entering the PDOC, originating from unconsumed and excreted C, is equivalent. The trophic efficiencies are not sensitive towards these growth efficiencies as long as there remains C unconsumed. The assimilated C was assumed to fuel animal production (50%) and respiration (50%) equally. We thus estimated the C demand of the consumers to equal three times their production (Boit and Gaedke, 2014; Gaedke *et al.*, 2002). The difference between the C available to the consumers, i.e. the sum of the respective prey production, and the consumer's C demand was termed unconsumed C and was allocated to the PDOC pool (Fig. 1). The rotifers and crustaceans production, left over by omnivorous fish, was considered to be consumed by YOY fish. In addition, allochthonous C originating from emergent and floating macrophytes, leaf litter, and DOC from groundwater input and precipitation, contributed to the PDOC pool (Brothers *et al.*, 2013a), which was quantified only in 2010, but we were unaware of any reason for systematic deviations in 2011.

Food web

We compiled the measurements and estimates described above into a quantitative food web for each lake. The C fluxes between organismal groups depict the available production to the respective consumer group rather than the actual consumption, which was not directly measured. If multiple consumers shared one prey, the production of this prey was distributed according to the relative production of each consumer group. The pelagic food web structure is complex as ciliates, rotifers and crustaceans compete for phytoplankton as prey and simultaneously are linked by predator-prey interactions. We consider metazooplankton (rotifers and crustaceans) as pelagic top consumer and calculate efficiencies based on their production. The pelagic and benthic food webs were linked by omnivorous fish, which feed on both pelagic and benthic organisms (Scharnweber *et al.*, 2013), and by the PDOC pool, which is shared by pelagic and sediment bacteria. Otherwise, the pelagic and benthic food webs were displayed separately as we assume trophic links to be minor, due to e.g. relatively few filter feeders in both habitats (for details see Discussion). We derive trophic efficiencies by dividing the consumer production by the prey production in a stepwise manner with an increasing degree of detail.

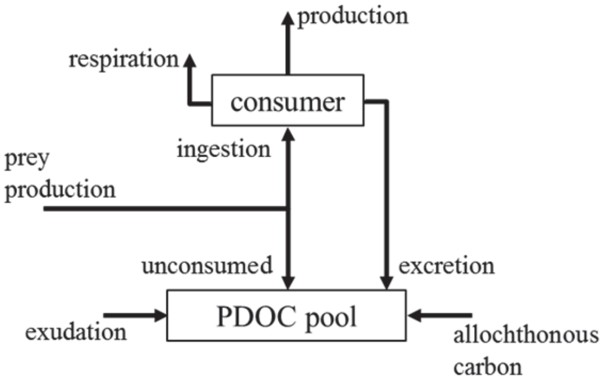

Figure 1. Fluxes to the pool of dead particulate and dissolved organic carbon (PDOC) originate from exudation by all primary producers, unconsumed prey production, consumer excretion and allochthonous carbon inputs.

Results

Biomass patterns and carbon fluxes between food web components

The compilation of all different measurements and estimates revealed mass-balanced food webs. The autotrophic and bacterial production was sufficient to sustain the production of the animal consumers (Fig. 2). Furthermore, the amount of carbon (C) entering the PDOC pool from exudation, excretion, C unconsumed by animal consumers and allochthonous inputs was sufficient to allow for the measured bacterial production.

The main patterns in absolute biomasses and the C fluxes between the organismal groups were similar in both lakes (Fig. 2). Within the pelagic food web, phytoplankton dominated the biomass, having about seven times more biomass than pelagic bacteria and roughly four times more biomass than the zooplankton, which was dominated by ciliates. Phytoplankton production was roughly twice the pelagic bacterial production. Ciliate production dominated the consumer production of the entire zooplankton community. If split according to the estimated consumer production rates, the majority of the phytoplankton production (70% and

86% in Schulzensee and Gollinsee, respectively) was used by ciliates, while 50% and 74% (respectively) of the C available to metazooplankton (rotifers and crustaceans) originated from ciliates (Fig. 2).

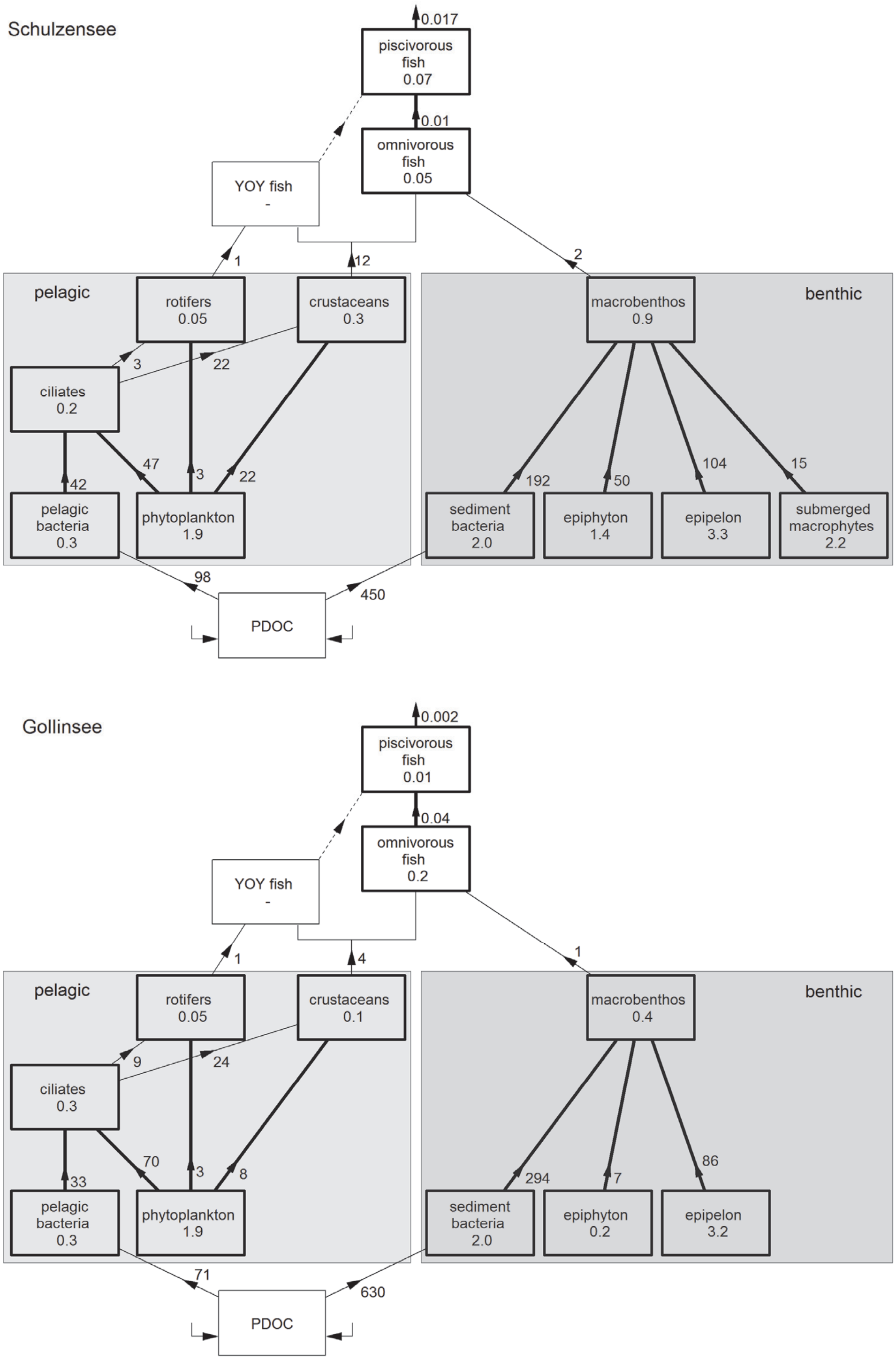

Figure 2. Quantitative food web of Lake Schulzensee and Gollinsee for the period 1 April to 31 October 2011. Each organismal group is represented by a box including its average biomass [g C m^{-2}] and by an arrow indicating the flux of the production [g C m^{-2} $season^{-1}$] potentially available to consumers. Bold boxes and arrows indicate measured biomasses and production rates whereas boxes and arrows in thin lines were calculated. All fluxes to the PDOC pool are indicated by the arrows entering the PDOC pool (cf. Fig. 1). The presumably high biomass and production (dashed line) of YOY fish could not be estimated (see Discussion).

The benthic autotrophs (epiphyton, epipelon and submerged macrophytes) accumulated together the highest biomass of any group in the food webs of both lakes, whereas benthic (sediment) bacteria dominated the food webs of both lakes in terms of production (Fig. 2). The biomass of macrobenthos was in the same order as that of zooplankton, but the zooplankton production exceeded that of macrobenthos by factors 16 and 31 in Schulzensee and Gollinsee, respectively. Accordingly, more than 80% of the C available for fish originated from the pelagic zone (Fig. 2).

The food webs differed between both lakes in some details. In Schulzensee, the benthic autotrophic production was almost twice as high as in Gollinsee due to the presence of submerged macrophytes and epiphyton, whereas the benthic bacterial production in Gollinsee exceeded that of Schulzensee by 50%. The crustacean and macrobenthos biomasses and accordingly the production estimates were at least twice as high in Schulzensee as in Gollinsee. Omnivorous fish biomass and production measurements were almost four times higher in Gollinsee than in Schulzensee, while piscivorous fish biomass and production were roughly an order of magnitude lower in Gollinsee than in Schulzensee (Fig. 2).

Pelagic vs. benthic carbon fluxes

Benthic bacteria contributed 82% and 90% to the entire bacterial production in Schulzensee and Gollinsee, respectively and benthic autotrophs dominated the total autotrophic production (70% and 53%, respectively) (Fig. 3). In contrast, the sum of the estimated production of metazooplankton and macrobenthos was mainly pelagic (84% and 81% in Schulzensee and Gollinsee, respectively, Fig. 3). Considering the large ciliate production in addition raises the pelagic contribution to the whole-lake animal consumer production to 94% and 97%, respectively.

To estimate the amount of unconsumed C in both pelagic and benthic food webs, we compared the total autotrophic and bacterial production in the pelagic and benthic zones with estimates of the C demands of metazooplankton and macrobenthos (Table 1). Both, the absolute amount and the ratio of unconsumed to total C available were much larger in the benthic (98% and 99% in Schulzensee and Gollinsee, respectively) than in the pelagic food webs (66% and 86%). The majority of the C unconsumed by metazooplankton was potentially utilized by pelagic ciliates (Fig. 2).

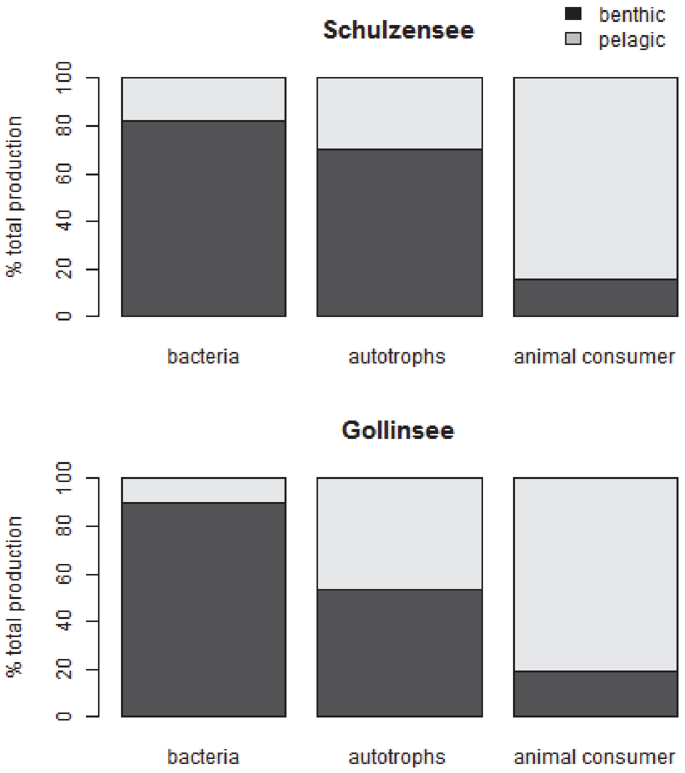

Figure 3. Relative contribution (in %) of pelagic (grey) and benthic production (black) to the total production of bacteria, autotrophs and animal consumers (metazooplankton, macrobenthos) in Schulzensee (top) and Gollinsee (bottom).

Table 1. Carbon (C) budget of pelagic and benthic animal consumer in Schulzensee (top) and Gollinsee (bottom). We assumed their C demand to equal three times the respective production to account for losses by excretion and respiration. The C demand was related to the total available C (autotrophic+bacterial production) separately for the pelagic and benthic habitat by calculating the difference between demand and available C, named unconsumed C by metazooplankton and macrobenthos. Further consumer such as pelagic ciliates, benthic protozoa and meiobenthos may have utilized the unconsumed carbon (see Fig. 2 and Discussion). All values in g C m^{-2} $season^{-1}$.

lake	**C budget**	**pelagic consumer (metazooplankton)**	**benthic consumer (macrobenthos)**
Schulzensee	*C demand*	4+35	7
	C available	114	360
	unconsumed C	75	353
Gollinsee	*C demand*	4+12	4
	C available	114	387
	unconsumed C	98	383

Pelagic, benthic and food web efficiencies

The trophic efficiencies (consumer production/autotrophic production) of metazooplankton were much higher (4.7-18%) than those for macrobenthos (0.3-1.4%) in both lakes (Fig. 4). They were lower when including the bacterial production (BP) in addition to the autotrophic production (AP), resulting in a pelagic efficiency (metazooplankton production (P)/pelagic (AP+BP)) of 11% (Schulzensee) and 4.7% (Gollinsee), which was more than an order of magnitude higher than the efficiency in the benthic zone (macrobenthos P/benthic (AP+BP); Schulzensee 0.7%, Gollinsee 0.3%, Fig. 4). Pelagic and benthic efficiencies were consistently higher in Schulzensee than in Gollinsee. The food web efficiency at the level of the pelagic and benthic top consumers (metazooplankton+macrobenthos P/whole lake (AP+BP)) was 3.3% in Schulzensee and 1.3% in Gollinsee. At the level of omnivorous fish (omnivorous fish P/whole lake (AP+BP)) the efficiencies were low (0.002% or 0.008% in Schulzensee and Gollinsee, respectively) as were the overall food web efficiencies (piscivorous fish P/whole lake (AP+BP)) with Schulzensee 0.004% and Gollinsee 0.0004%.

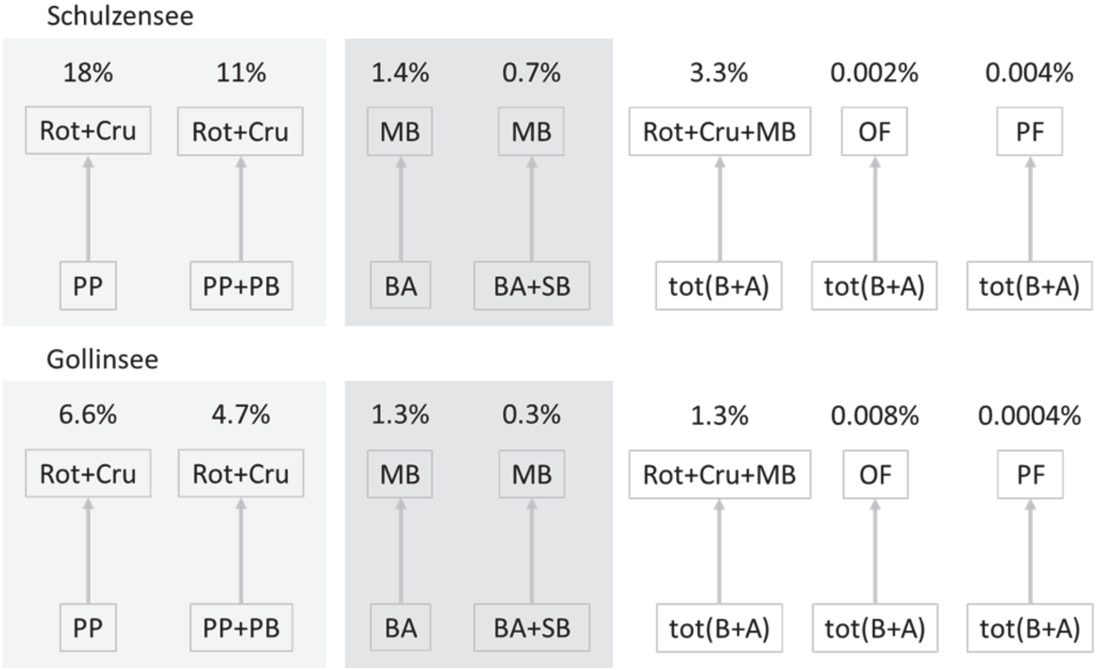

Figure 4. Food chain efficiencies (consumer production/prey production in %, numbers on top of food chain) for different pairs of prey and consumers in the pelagic (left), benthic (middle) and total food web (right) in Schulzensee (top) and Gollinsee (bottom). PP=Phytoplankton, PB=pelagic bacteria, BA=benthic autotrophs (epiphyton, epipelon and submerged macrophytes; the latter only in Schulzensee), SB=sediment bacteria, Rot=Rotifers, Cru=Crustaceans, MB=Macrobenthos, tot(B+A)=total bacterial and autotrophic producers, OF=omnivorous fish, PF=piscivorous fish.

Discussion

We demonstrate here a striking discrepancy between the benthic autotrophic and bacterial production and their utilization by animal consumers. The lake-wide autotrophic and bacterial production was dominated by benthic organisms in both shallow lakes, in line with the findings of Vadeboncoeur and others (2002) that benthic organisms contribute substantially to the whole-lake production. In contrast, the dominant animal consumer production occurred in the pelagic zone, because metazooplankton (crustaceans and rotifers) production was much higher than macrobenthos production. The benthic efficiency (macrobenthos production/benthic autotrophic and bacterial production) was at least an order of magnitude lower than the pelagic efficiency (metazooplankton production/pelagic autotrophic and bacterial production). Thus, the vast majority of the benthic autotrophic and bacterial production remained unconsumed by animal consumers, which is counterintuitive. As a consequence, our data suggest that even shallow lakes are primarily pelagic systems, at least according to the animal consumer production. This conclusion is based on repeated and detailed measurements of pelagic and benthic biomasses combined with measurements and estimates of production rates in pelagic and benthic habitats in two lakes, and hence seems to be a reliable result.

The resulting food webs were internally consistent with respect to the mass balance of two pools and rates. First, the sum of autotrophic and bacterial production was sufficient to sustain the estimated animal consumer production. Second, there was sufficiently dead organic matter to fuel the measured bacterial production. When assuming a bacterial growth efficiency of 50% (del Giorgio and Cole, 1998), about 80 g C m^{-2} $season^{-1}$ and 50 g C m^{-2} $season^{-1}$ of the dead organic carbon would have remained unconsumed by sediment bacteria in Schulzensee and Gollinsee, respectively. This amount is in the range of the carbon burial rates estimated from sediment cores for Schulzensee (Brothers *et al.*, 2013a). The burial rates estimated from sediment cores for Gollinsee were higher than 50 g C m^{-2} $season^{-1}$, but this mismatch between both approaches falls into the range of uncertainty arising e.g. from the measurements of the bacterial production, the estimate of the bacterial growth efficiencies and measured burial rates presented as average values over 60-100 years. Therefore, we are convinced that our conclusion on the disparity of pelagic and benthic efficiencies is a real phenomenon and not attributable to missing or imprecise data acquisition.

The pelagic efficiencies in both lakes were exceptionally low due to low crustacean biomasses (Lischke and others in press). The adult fish biomasses were crashed after partial winterkills of fish, whereas the YOY fish released from competition exerted a strong predation pressure on crustaceans (Hilt *et al.*, 2015; Lischke and others in press). Thus, the discrepancy between the pelagic and benthic efficiencies could have been even larger when calculated for the situation before the winterkill of fish. The low overall food web efficiencies (fish production/whole-lake (autotrophic and bacterial production)) are also attributable to the low fish biomasses after the winterkills. However, the biomass of YOY fish could not be quantified, which restricts the validity of the overall food web efficiencies.

Comparisons with other studies revealing higher benthic efficiencies than in our study are limited by the fact that efficiencies were calculated in an inconsistent way and included different groups of producers and consumers (Jonasson, 1992; Lindegaard, 1994; Vander Zanden *et al.*, 2006). Additionally, the efficiencies derived by artificially assembled communities (Rowland *et al.*, 2015) need to be distinguished from those of natural lake communities. To our knowledge, our study is the first to quantify natural pelagic and benthic efficiencies within the same ecosystems, considering the production of all trophic groups including bacteria. In particular the benthic bacterial production was equal to or three times greater than the benthic autotrophic production in Schulzensee and Gollinsee, respectively. Hence, without considering benthic bacteria production, we would have severely overestimated the benthic efficiencies, and would not have detected the fundamental disparity between pelagic and benthic habitats.

Four processes may contribute to lower efficiencies in the benthic than in the pelagic habitat: (1) In the benthic habitat production of diverse quality is provided to benthic animal consumers, including bacterial production, partly based on allochthonous matter, periphyton (epiphytes and epipelon) and macrophyte production. Allochthonous organic matter is expected to be of lower nutritional quality than autochthonously produced matter, but was assumed to be processed by bacteria before reaching benthic animal consumers. In addition, allochthonous organic carbon contributed only 19% and 32% in Schulzensee and Gollinsee, respectively, to the total dead organic carbon pool. Macrophytes have high carbon to phosphorous ratios (Duarte, 1992), but contributed in Schulzensee only 4% of the autotrophic and bacterial production. Periphyton and sediment bacteria are expected to be of equal or higher nutritional quality as their pelagic counterparts, as the sediment is a more nutrient rich habitat than the pelagic habitat and the bacterial stoichiometry is in general rather constant (Hessen *et al.*, 2013; Sand-Jensen and Borum, 1991). Consequently, the majority of the carbon available to benthic consumers is of suitable nutritional quality, which rejects nutrient limitation as determinant for the disparity of the pelagic and benthic efficiencies.

(2) For pelagic habitats it is well established that formerly neglected consumer groups, such as ciliated protozoa, have to be embedded into the food web as a decisive component e.g. regarding the feeding of pelagic autotrophic and bacterial production (Sommer *et al.*, 2012). For the two lakes studied here, the calculated pelagic carbon fluxes and efficiencies reveal that rotifers and crustaceans derived the majority of the pelagic autotrophic and bacterial production via ciliates. Generally, additional intermediate trophic levels, such as ciliates, lower the overall food web efficiency due to losses by excretion and respiration. Analogously to the pelagic habitat, we can speculate that the benthic food webs appear inefficient because we neglected additional trophic levels, e.g. benthic protozoa and meiobenthos, which are much less studied than pelagic protozoa or benthic macroinvertebrates (Robertson *et al.*,

2000). Unfortunately, we were likewise not able to quantify biomasses and production rates of benthic protozoa and meiobenthos in this study. By assuming a stringent benthic food chain of autotrophic and bacterial production, protozoa, meiobenthos and macrobenthos, the benthic food chain would have had one more trophic level than the pelagic food chain, and hence this additional trophic level may explain the lower benthic than pelagic efficiencies. However, the majority of the macrobenthos production arises from herbivorous organisms, feeding directly on autotrophic producers, thus a predominantly short food chain is more likely. In addition, neglected consumer biomass at the same trophic level as macrobenthos would enhance the benthic efficiency. We compiled the few available studies, which reported the production of benthic protozoa, meiobenthos and macrobenthos (Appendix 1). The resulting average values suggest that the sum of benthic protozoan and meiobenthos production is about twice as high as the macrobenthos production. Accordingly, total benthic consumer production would be three times the rates estimated for macrobenthos alone, and applying this ratio to our lakes would result in three times higher benthic efficiencies (2.1% in Schulzensee and 0.9% in Gollinsee, by assuming that all benthic consumers occupy the same trophic level). Therefore, even by considering that we may have missed to measure potentially significant parts of the benthic consumer production (protozoa and meiobenthos), the overall benthic efficiencies remain low and are still substantially below the pelagic efficiencies.

(3) Habitat-specific trophic efficiencies do not reflect that pelagic and benthic habitats may be energetically linked. Multichannel feeding is described for different organismal groups in all types of ecosystems, but it is in general less common in lakes than in other ecosystems (Polis and Strong, 1996). In small lakes, crustaceans and some macrobenthos can be considered as sufficiently mobile to transfer carbon between habitats. *Daphnia* were reported to graze on epiphytes, if the phytoplankton production was low (Mahdy *et al.*, 2014). However, in our lakes, the crustacean community was dominated by juvenile copepods (Lischke and others in press), which are predominantly pelagic consumers. Consequently, benthic contributions to pelagic consumers were unlikely. Macrobenthos feeding on pelagic autotrophs and bacteria would increase the discrepancy between pelagic and benthic efficiencies.

(4) Finally, the macrobenthos production can be limited by several additional factors. The larger benthic consumers have lower biomass turnover rates than their pelagic counterparts (Banse and Mosher, 1980). To achieve similar efficiencies in both habitats, low turnover rates can be compensated for by higher biomasses of consumers in benthic than in pelagic habitats. However, the macrobenthos and metazooplankton biomasses did not differ much and consequently the production of macrobenthos in our lakes was substantially below the amount required to achieve equally efficient pelagic and benthic food webs. However, the macrobenthos biomasses in Schulzensee and Gollinsee were comparable with those from other lakes in north-east Germany (Brauns *et al.*, 2011; pers. comm. O. Miler, IGB Berlin) and in the northern USA (Craig *et al.*, 2015). Accordingly, the low macrobenthos production

rates in both lakes were not attributable to unexpectedly low macrobenthos biomasses. Our data show that the macrobenthos production was not limited by the carbon availability, i.e. the benthic autotrophic and bacterial production and the food quality. As recently proposed by Craig and others (2015), oxygen limits the available habitat for macrobenthos. In a survey of ten shallow north temperate lakes, the macrobenthos production correlated positively with the benthic autotrophic production, but the highest predictive power for macrobenthos production was found when oxygen concentration alone was considered (Craig *et al.*, 2015). Our study lakes are characterized by muddy sediments, which is a less suitable habitat for zoobenthos due to its fine texture and tendency to be oxygen depleted (Lindegaard, 1994). Indeed, the oxygen concentration above the profundal sediments dropped to anoxic levels several times in 2011 in both lakes (Brothers *et al.*, 2014 and further unpublished data). We thus conclude that the macrobenthos and likely other benthic consumers were oxygen limited in the profundal sediments of both lakes, and this may be similarly the case in many comparable lakes in north-east Germany. In contrast, benthic bacteria were able to cope with low oxygen concentrations and hence may have utilized the unconsumed benthic autotrophic and bacterial production, resulting in a benthic bacterial loop. However, there are no studies having elucidated the structure and efficiency of benthic bacterial loops in lake sediments. A study of river biofilms suggested that abiotic constraints had a greater influence on the bacterial community than predation by protozoa indicating that a benthic bacterial loop may be prevalent also under more suitable conditions (Wey *et al.*, 2012). The more extended littoral zone with abundant submerged macrophytes in Schulzensee improved the habitat heterogeneity and oxygen availability and resulted in a twofold higher macrobenthos biomass and higher benthic efficiencies than in Gollinsee. However, the benthic efficiencies considering area-based productions in the more oxygenated littoral of Schulzensee remain a tenth of the pelagic efficiencies in this lake, as there is per area a 1.5-2 times higher macrobenthos production but also a 1.25 times higher autotrophic production in the littoral. Thus, the littoral-based benthic efficiencies remain surprisingly low and factors other than oxygen and benthic autotrophic and bacterial production appear to limit the macrobenthos production.

Conclusion

We quantified the fluxes in the pelagic and benthic food webs in extensive whole-ecosystem studies in two lakes and demonstrated that the pelagic energy transfer was substantially more efficient than the benthic one. This holds true even if the food quality, further benthic consumers, pelagic-benthic links and the oxygen concentrations as determinants of the benthic efficiency were considered. Sediment bacteria turned out to be of major importance at the producer level and seem to form a bacterial loop in the anoxic profundal by utilizing the otherwise unconsumed benthic autotrophic and bacterial production. The discrepancy between the pelagic and benthic efficiencies was a persistent phenomenon in two shallow lakes, and we suggest that it may be true for lakes in general. Testing the generality of these findings requires follow-up studies in a variety of aquatic ecosystems with differences in the pelagic and benthic food web structure and autochthonous productivity.

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Supporting Information

Appendix 1: Zoobenthos production

Appendix 1 – Table 1. Zoobenthos production in various freshwater ecosystems. Production is given in g C m^{-2} y^{-1}, dw was converted to C by the factor 0.45 (Wetzel, 2001). § Production estimates using different methods. ~ Average of literature values, based on maximum values.

ecosystem	**protozoa**	**meiobenthos**	**macrobenthos**	**reference/comment**
Mirror Lake		3	3	Strayer and Likens 1986
3 Swedish lakes		4.6-10		Schroeder and others 2012
Eutrophic stream	4.2	4.2	4.2	Reiss and Schmid-Araya 2010
Stream (Breitenbach)	20	10	30	Marxsen 2006
Stream		1.3	1.3	Stead and others 2005
oligotrophic lake	22	1.6-1.7§	3.1-6.7§	Bergtold and Traunspurger 2005
average~	15.4	5	9	average literature values

General Discussion

This dissertation examined the food web regulation of shallow lakes from **different perspectives**: effects of an enhanced terrestrial matter input, emerging effects after winterkills of fish and energetic comparisons of carbon fluxes in pelagic and benthic compartments. The presented studies focused on the regulation of several groups of lentic organisms, as phytoplankton, periphyton (epiphyton and epipelon), macrophytes, bacteria in the pelagic and benthic habitat, ciliates, rotifers, crustaceans, macrobenthos and omnivorous and planktivorous fish. The emerging consequences of their regulation were displayed at the species, community and ecosystem scale. Thereby models and the analyses of ecological studies up to the scale of whole-lake studies were used to identify the effects of the regulating forcing regimes. After a general discussion of the studies comprised in this dissertation and further studies to which I also contributed within my dissertation project, the attained insights into the regulation of each organismal group are discussed more specifically. Finally, the ecological relevance of the presented studies and their respective findings are described.

The study of carbon fluxes within food webs requires large-scale investigations using very different approaches to capture the various organism groups at different time and spatial scales. The **natural lake studies**, as performed in chapter II-IV, have a certain advantage compared to experiments on a smaller scale e.g. in mesocosms or on laboratory scales, as natural dynamics in its full complexity can be observed under natural forcing regimes. However, they have also inherent disadvantages as they are uncontrollable, require a huge effort, have a limited number of replicates and it is difficult to reveal a mechanistic understanding. Those disadvantages can be overcome if complex ecosystem models are used to examine the food web regulation, as performed in chapter I. In case the ecologist finds an applicable model and keeps in mind the model inherent assumptions and restrictions, models can be a useful tool along with experiments.

The application of **ecosystem models** is often restricted to a limited group of scientist cooperating with the responsible modelers. A ubiquitous use of ecosystem models is desirable as it decreases the modelling effort and therefore, the scientific use gets more into focus (Mooij *et al.*, 2010). The collective use of models is mainly hampered by the fact that modelers differ in their programming framework in favor and most non-modelers balk the complexity of programming. In Mooij *et al.* (2014), we proposed a concept to overcome these difficulties with the database approach towards modelling (DATM). Through DATM, models are reduced to their ecological meaningful components (Mooij *et al.*, 2014); in the case of aquatic models usually differential equations for organism groups and nutrients. The equations, parameter settings and initial conditions are listed separately in a table format (e.g. Microsoft's Excel) and are thus framework independently stored, broadly available and easily modifiable (Fig. 2). Certain routines, which are model independent, are required to translate the information automatically into programming language to run the model. The translating routine must be written only ones for each framework and can be easily shared as long as the structure of the database is similar. Thus, DATM facilitates the share of models between modelers and increases the model disposability for ecologists in general as the user will not necessarily get in touch with the required framework and rather focuses on the equations. We established the DATM for the complex ecosystem model PCLake and its twin model PCDitch (van Gerven *et al.*, 2015). This approach was applied to several frameworks and large differences in the speed of the calculations and the tools available for analyzation, e.g. for calibration, validation and sensitivity and bifurcation analyses, have been found between the frameworks (Fig. 2). Thus, although ecologist can stick to the ecological meaningful pure description of the model by using DATM, the suitable framework with the required analysis tools needs to be identified. Accordingly, ecologists should prevent "reinventing the wheel" (Mooij *et al.*, 2010) by sharing and using existing and future models for ecological modelling studies using DATM.

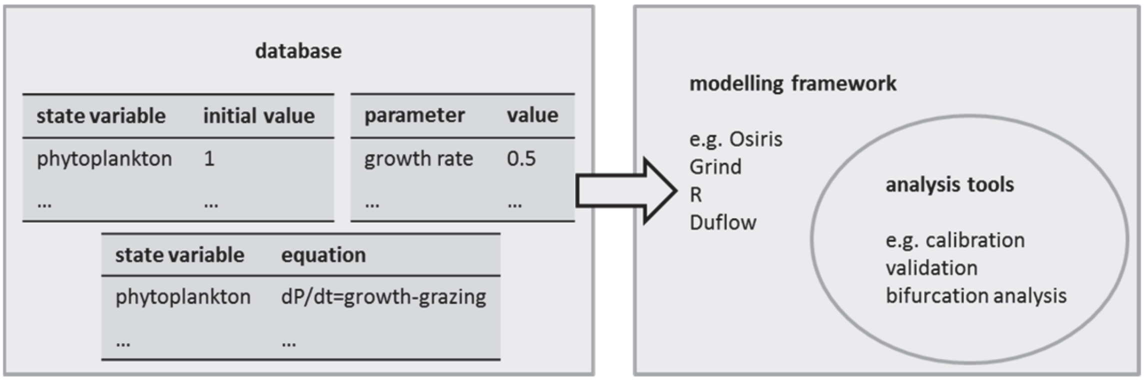

Figure 2. The concept of DATM defines the model using a database in which at least state variables with their initial values, parameters with their values (all in a defined unit) and the equation of each state variable are stored. The database can be linked to various frameworks to run the model. The frameworks provide different analysis tools.

In chapter I DATM was applied for the complex ecosystem model PCLake to test for effects of the external, abiotic forcing regime, enhanced **terrestrial particulate organic matter** (t-POM) inputs to shallow lakes. T-POM affected the food web via three pathways: (1) As resource for macrobenthos, (2) suspended in the water as resource for zooplankton and (3) suspended in the water influencing the transparency. The underlying mechanisms were firstly an increase in macrobenthos biomass with more resources available, followed by an increase in benthic fish biomass which than reduced the transparency as the more abundant benthic fish enhanced the bioturbation. Secondly, suspended t-POM substituted autochthonous dissolved organic matter (DOM) in the zooplankton diet as the overall amount of consumed food remained constant. The unconsumed autochthonous DOM reduced the transparency. And thirdly, suspended t-POM also directly reduced the transparency of the lakes. Thus, the lake transparency and consequently the light availability for the autotrophic production were reduced via each of the pathways. The transparency is directly related to the resilience of the alternative stable states in shallow lakes as a reduced light availability limits macrophyte stronger than phytoplankton growth (Scheffer *et al.*, 1993). It can be concluded, that the predicted enhanced input of t-POM will reduce the resilience of the macrophyte-dominated clear-water state of shallow temperate lakes by negative effects on the transparency (chapter I). Moreover, rising temperatures were predicted to reduce the resilience of the clear-water state, too (Mooij *et al.*, 2007). Accordingly, reductions in nutrient loadings are required to maintain the clear-water state with changing climate. However, a switch towards the phytoplankton-dominated state would result in higher burial efficiencies (Brothers *et al.*, 2013a), i.e. less of the additional carbon entering the lakes will be respired. Shallow turbid lakes may also store the projected rising t-DOM input to lakes and thus, might be considered as a carbon sink in terms of climate change. The results of the modelling study presented in chapter I were based on the model inherent assumptions, such as the food web structure and the emerging carbon fluxes. These assumptions on trophic and non-trophic interactions were carefully derived in PCLake and the model has been calibrated and validated by a large dataset (Janse, 2005; Janse *et al.*, 2010). However, recent studies debate on the general contribution of terrestrial matter to aquatic consumers (Cole *et al.*, 2011; Cole *et al.*, 2006; Francis *et al.*, 2011). The relevance of the food web pathways in PCLake may diminish if the consumers rely to a lesser extent on terrestrial matter, following e.g. conclusions by Brett *et al.* (2009). Thereby, only the direct negative effects of the enhanced t-POM input on the light availability remain, which are comparable to the effects of t-DOM (Jones *et al.*, 2012). The consumer allochthony depends on various aspects e.g. the lake morphometry, the catchment of the lake, the autochthonous production, the trophic level of the consumer and the type of consumer group (Marczak *et al.*, 2007). In Schulzensee and Gollinsee stable isotope analyses were conducted and mixing models were used to quantify the contribution of natural terrestrial carbon and experimentally added carbon to crustaceans, macrobenthos and fish (Mehner *et al.*, 2015). The results were compared to a quantitative carbon budget of the consumer production based on autochthonous and terrestrial carbon sources. We observed an increase in the production based on terrestrial carbon for crustaceans, macrobenthos and fish after its addition (Mehner *et al.*, 2015). However, the total production did not respond which suggests a replacement of naturally available carbon sources by the added terrestrial carbon. Crustaceans, macrobenthos and fish were thus likely not bottom-up controlled in the study lakes.

Next to terrestrial carbon inputs the temperature is an important external forcing regime of shallow lake dynamics. In Schulzensee and Gollinsee long lasting ice covers in cold winters resulted in oxygen depleted water inducing partial fish kills in two subsequent years (chapter II). These partial **winterkills of fish** strongly affected the structure of the food webs and thus the regulation within the food web communities of both lakes as described in chapter II and III. Piscivorous fish, which were more abundant in the macrophyte-dominated Schulzensee, were proportionally more harmed by low oxygen concentrations than omnivorous fish. The fish communities of both lakes were aligned due to the partial winterkills of fish along with an overall reduction in fish biomasses (chapter II). YOY fish were in favor when biomasses of adult fish and the predation pressure for them were low. Consequently, crustaceans were under severe predation pressure by the large amounts of YOY fish. In turn, ciliates were released from crustacean grazing and became the dominant zooplankton group (chapter III). Ciliates exerted a strong predation pressure on parts of the phytoplankton and bacteria. In the light of climate change, long-lasting ice covers on temperate lakes and their resulting consequences may become less frequent (Kreyling, 2010). However, lakes closer to the poles will still face periods of winter anoxia also with global warming. Temperate lakes may be confronted by prolonged periods of summer anoxia in the future, e.g. due to enhanced inputs of dissolved organic carbon increasing the bacterial respiration (Brothers *et al.*, 2014). Fish kills may also arise due to elevated ammonia concentrations as observed in a tropic shallow lake (Iglesias et al., 2011) or by fungal infection of fish (Nagdali and Gupta, 2002). Thus, the phenomenon of fish kills keeps its relevance for lake ecology.

The pelagic food web was in focus of former aquatic studies, but especially in small and shallow lakes like Schulzensee and Gollinsee the **benthic autotrophic and bacterial production** exceeded the respective pelagic production (chapter IV; Brothers *et al.*, 2013b), which is in line with the findings of Vadeboncoeur *et al.* (2002). However, pelagic organisms disproportionately contributed to the consumer production (macrobenthos vs. metazooplankton (rotifers and crustaceans)) as presented in chapter IV. Consequently, the benthic transfer efficiency was a tenth of the pelagic efficiency. Accounting for food quality aspects, further trophic levels as ciliates, benthic protozoa and meiobenthos, a pelagic-benthic link and potentially limiting oxygen concentrations for macrobenthos production did not diminish the disparity in pelagic and benthic efficiencies. Thus, benthic producer and consumer are only weakly linked by trophic interactions and at least at the consumer level, even shallow lakes appear as pelagic systems.

Concerning the regulation of lentic food web components plenty of studies already exist and this dissertation adds new insights and confirms or contrasts existing knowledge at all trophic levels in the pelagic and benthic habitat. The following paragraphs discuss the insights gained into the regulation of each organism group (for a summary see Fig. 3).

The **Phytoplankton** production can be limited through nutrients and light availability, but in both eutrophic lakes, Schulzensee and Gollinsee, soluble reactive phosphorous measurements suggested that nutrients were most of the time not a limiting factor and as light usually reached the bottom of those shallow lakes it also might not have been a crucial factor for the phytoplankton production. Therefore, phytoplankton was unlikely to be bottom-up controlled. The top-down regulation of phytoplankton was traditionally meant to be realized by crustaceans (Sommer *et al.*, 1986). However, in the early 1980’s the relevance of the microbial loop was recognized (Azam *et al.*, 1983) which also raised more attention on the ciliates (Müller, 1989; Pace, 1982; Taylor and Heynen, 1987). Meanwhile, ciliates are known to be important grazers of phytoplankton, especially in spring (Sommer *et al.*, 2012). Chapter III shows that under certain environmental forcing regimes, e.g. partial winterkills of fish, ciliates can exert a strong predation pressure on parts of the phytoplankton all over the year, with seasonal average grazing rates larger than the phytoplankton growth rates. Especially small phytoplankton (<5 µm in longest linear dimension) was grazed to biomasses which are considered as threshold for the positive growth of various ciliate species (Weisse, 2006), indicating that ciliates could not further lower the phytoplankton biomass. In contrast, large phytoplankton accumulated when the grazing pressure by crustaceans was reduced due to the partial winterkills of fish followed by high numbers of YOY fish (chapter II and III). Thus, this specific zooplankton community led to a phytoplankton community characterized by a broad size spectrum with a disproportionately high amount of large species. The regulation of phytoplankton by ciliates has further consequences for the overall community composition. In both study lakes, the phytoplankton community was diverse in respect to size and composition as observed also in Danish lakes (Jeppesen *et al.*, 2000). The underlying mechanism was presumably the highly selective feeding by the diverse ciliate community evoking an even phytoplankton community in Schulzensee and Gollinsee (chapter III). Although, the crustacean predation pressure on phytoplankton was reduced after the partial winterkill of fish, the conglomerate of other determinants kept the phytoplankton biomass at a level, which prevented Schulzensee to switch to the turbid state (chapter II). Relevant determinants were presumably the top-down control by ciliate grazing, allelopathic effects of macrophytes (Hilt and Gross, 2008) and a low nutrient concentration by the time of the peak biomass of the macrophyte *Ceratophyllum submersum*.

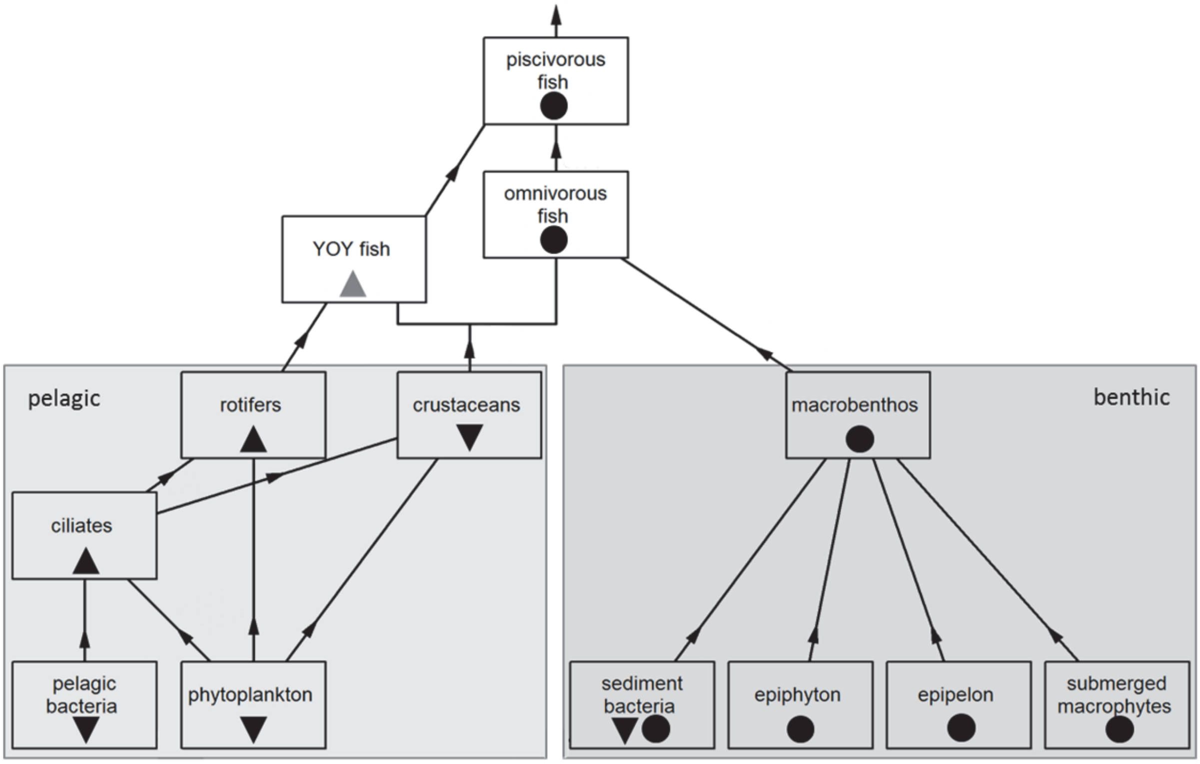

Figure 3. The food web regulation of Schulzensee and Gollinsee revealed by whole-lake ecosystem studies presented in chapter II-IV. Groups of organisms are displayed as boxes and arrows between the boxes indicate trophic interactions. The regulation of each group is depicting within its box. Upward arrows show bottom-up control and downward arrows show top-down control. Circles indicate others than trophic limiting factors (see text). YOY fish were not quantified, thus the indication of bottom-up control should be treated cautious.

According to the compiled carbon fluxes in the benthic zone the **benthic autotrophic** community was not top-down controlled (chapter IV). The estimated consumption by macrobenthos demanded less than 2% of the benthic autotrophic and bacterial production. By considering the estimated consumption of benthic protozoa and meiobenthos still the largest proportion of the benthic primary production remained unconsumed by animal consumers (>90%). The limitation of the benthic autotrophic production by nutrients seems unlikely in these eutrophic study lakes (Sand-Jensen and Borum, 1991). However, light is known to be a crucial determinant for their production as the benthic autotrophs are less efficient in light utilization compared to phytoplankton (Sand-Jensen and Madsen, 1991). In Schulzensee and Gollinsee light availability seemed to be sufficient during the study period, as light reached the bottom of the lakes. Thus, space limitation might have been the regulating force for the study lakes. However, due to rising water levels in 2012 the lakes received large amounts of t-DOM, which strongly reduced the available light and thus eliminated most of the benthic autotrophic production (Brothers *et al.*, 2014). In line with that the model study presented in chapter I revealed that the reduced transparency by the enhanced input of t-POM harmed the benthic production the most and thus reduced the resilience of the clear-water state.

The pelagic **bacteria** and especially the particle-attached bacteria, which are in the preferred size of ciliates, were under severe grazing pressure by ciliates (chapter III). This was indicated by high calculated ciliate ingestion rates compared to the growth rates of pelagic bacteria (chapter III) and high production to biomass ratios of pelagic bacteria (chapter IV). The results presented in this dissertation clearly show a top-down regulation of pelagic bacteria by ciliates. In contrast, the increase of the pelagic bacterial production after the experimental addition of t-POM in autumn suggested a carbon limitation and thus bottom-up control during parts of the season (Attermeyer *et al.*, 2013). The sediment bacteria in the benthic habitat had the largest production rate of all food web components (chapter IV). Unfortunately, their grazers were not included in the extensive food web studies and also from literature only very few data of benthic protozoan production exist (Bergtold and Traunspurger, 2005; Marxsen, 2006; Reiss and Schmid-Araya, 2010). The estimated protozoan production based on these literature data suggested that less than 4% of the sediment bacterial production was consumed, if all protozoans were bacterivorous. Contrarily, the production to biomass ratios of sediment bacteria were as high as those of the top-down controlled pelagic bacteria. Top-down control of sediment bacteria cannot be ruled out due to the latter finding. Furthermore, the sediment bacteria production remained unchanged after the experimental addition of terrestrial organic carbon, which indicated that they were at least in autumn not bottom-up controlled (Attermeyer *et al.*, 2013). By measurements of carbon burial rates in sediment cores in both lakes we detected a loss of carbon from the aquatic ecosystem being permanently buried in the sediment (Brothers *et al.*, 2013a). Bottom-up regulated benthic bacteria may have utilized this carbon. Thus, none of the studies indicated a bottom-up control of sediment bacteria and the top-down control seems to be very weak. Consequently, other factors such as habitat availability might have limited the sediment bacteria community.

In Schulzensee and Gollinsee the **ciliate** abundances and biomasses were much larger than previously reported for eutrophic lakes (Karus *et al.*, 2014; Laybourn-Parry *et al.*, 1990; Zingel and Noges, 2010). They were almost entirely released from top-down control by the partial winterkill of fish (chapter III). In addition, the competition for food was reduced as the biomass of crustaceans was low. Thus, ciliates became the dominant zooplankton group and due to their high weight-specific grazing rates compared to metazooplankton (Hansen *et al.*, 1997) they exerted a strong predation pressure on parts of the phytoplankton and bacteria (chapter III). Ciliates are usually under severe top-down control by crustaceans (Adrian and Schneider-Olt, 1999; Hansen, 2000; Wickham, 1998; Wickham and Gilbert, 1993) but under the circumstances, which arose after the partial winterkill of fish; they were bottom-up controlled. This can be concluded from their ingestion rates, which exceeded the growth rates of their prey, and the estimated ciliate production rates falling below their potential maximum rates (Gaedke *et al.*, 2002; Montagnes *et al.*, 1988). In Lake Võrtsjärv the top-down control of ciliates was reduced as metazooplankton grazing was inhibited by filamentous algae and strong resuspension, which gave rise to predacious ciliates (Zingel and Noges, 2010). In Schulzensee and Gollinsee the ciliate community did not differ substantially from typical ciliate communities in eutrophic lakes. Thus, species effects of the altered food web regulation could not be detected.

Rotifers build up larger biomasses than observed in various other lakes indicating a low top-down control (chapter III). Although, released from predation by crustaceans, rotifers were likely grazed by YOY fish at least part of the season (Mehner and Thiel, 1999; Zingel *et al.*, 2012). Accordingly, the predation pressure on rotifers seemed low at a seasonal scale and rotifers were rather bottom-up controlled. The latter was indicated by low egg-ratios measured for the dominant rotifer species, *Keratella cochlearis* (chapter III).

Winterkills of fish in two subsequent years lead to high numbers of YOY fish exerting a strong top-down control on **crustaceans**. The strong top-down control was reflected in an overall low crustacean biomass and a crustacean community dominated by juvenile life stages, nauplii and copepodites (chapter III). Cladocerans were at low numbers after the first fish kill and their proportion within the crustaceans decreased further after the second fish kill. This confirms that cladocerans are more vulnerable to fish predation than copepods (Winfield *et al.*, 1983). The well-known strategies of crustaceans to build up defenses such as spines and helmets (Tollrian and Harvell, 1999) were seemingly useless in the light of this strong predation pressure by YOY fish. As a consequence of the top-down control, crustaceans were not bottom-up regulated as also found by the quantitative approach of Mehner *et al.* (2015) testing for effects of the enhanced input of t-POM. Their study revealed, that crustaceans substituted naturally available carbon by the added terrestrial carbon in their diet, as it was also suggested by the model study described in chapter I. In line with these results a recent investigation suggests that terrestrial carbon is not a subsidy to zooplankton, in the sense that it enhances the consumers production (Kelly *et al.*, 2014). They suffer rather from enhanced terrestrial matter inputs due to light limitation of autotrophic production and consequently habitat degradation.

Efficiencies were overall low in the benthic habitat, suggesting that **macrobenthos** was not bottom-up controlled (chapter IV), particularly as the positive effect on their production after a carbon addition held off (Mehner *et al.*, 2015). In contrast, the model study described in chapter I revealed a bottom-up control of macrobenthos as their biomass increased when more food was available. Top-down control can be also ruled out as determining factor due to low fish biomasses after the partial winterkills of fish in both study lakes (chapter II). Thus, macrobenthos was not controlled by the quantity of prey or predators. Pelagic animal consumers efficiently used the pelagic autotrophic and bacterial production suggesting a sufficient food quantity and quality. Sediments are a more nutrient rich habitat than the pelagic habitat (Sand-Jensen and Borum, 1991) and the bacterial stoichiometry is rather constant (Hessen *et al.*, 2013). This indicates that the food quality of benthic autotrophs and bacteria is comparable to the respective pelagic food quality and also not limited the macrobenthos community. Likely a low oxygen concentration in the muddy sediments of Schulzensee and Gollinsee limited the settlement by macrobenthos in the profundal zone (Lindegaard, 1994). This can be interpreted as habitat limitation, which was recently suggested by Craig *et al.* (2015) as a very common phenomenon. However, there is no indication for low oxygen concentrations in the littoral. Thus, it remains open for further studies to identify the limiting factors of the macrobenthos community.

Fish were strongly affected in terms of biomass and community composition by the low oxygen concentrations in winter (chapter II). Especially piscivorous fish suffered from the low oxygen concentrations confirming their high oxygen-sensitivity (Doudoroff and Shumway, 1970). Consequently, YOY fish became very abundant, which has been observed previously after reductions in adult fish biomasses (Romare and Bergman, 1999). YOY fish might have been bottom-up limited as they reduced the crustaceans to low numbers, but adult fish were at such low biomasses that they were presumably not limited by the prey availability. The experimental addition of carbon did not enhance the fish production confirming the absence of bottom-up control (Mehner *et al.*, 2015). The fish community was rather in a transient state towards natural fish stocks, which takes more time than the period of study due to the low generation rates of fish. In PCLake the benthivorous fish increased in biomass when more food was available, they were thus displayed as bottom-up controlled in the model (chapter I). This effect did not propagate to the pelagic food web via the piscivorous fish as they were rather unaffected by biomass changes in their prey. In contrast, a model study of food webs with alternative pathways of differing food chain length observed that effects of an enrichment to one chain were mediated to the other chain by the top predator (Wollrab *et al.*, 2012). Thus, PCLake may resemble the often suboptimal growth conditions for piscivorous fish in eutrophic lakes (Jeppesen *et al.*, 2000). Also in experimental studies piscivorous fish were much less affected by additional resources (e.g. t-POM) than lower trophic level consumers, which might be attributed to the larger degree of omnivory at higher trophic levels (Marczak *et al.*, 2007). In line with this study, the addition of a distinct t-POM resource to Schulzensee and Gollinsee revealed a stronger enhancement of the stable isotope values for macrobenthos than for fish, indicating a stronger reliance on the additional t-POM source for macrobenthos (Scharnweber *et al.*, 2014).

Conclusion

Understanding food web regulation is crucial to get better insights into the dynamics of lake ecosystems and to predict climate change effects and to advise ecosystem management under different forcing regimes. The methodological approach using a complex ecosystem model and comprehensive ecosystem measurements were adequate to identify the regulation for most of the organism groups and the resulting carbon fluxes under two external forcing regimes. The enhanced input of t-POM will reduce the resilience of the clear-water state of shallow lakes as revealed by a complex ecosystem model study. Long-lasting low temperatures in winter led to partial winterkills of fish. The pelagic food web structure and the regulation of the pelagic organisms were determined by the resulting alterations of the fish community and abundance. Ciliates were key players in the pelagic habitat of both study lakes. At the whole ecosystem scale benthic autotrophic and bacteria production exceeded the respective pelagic rates, whereas the animal consumer production was dominated by pelagic organisms leading to much lower benthic than pelagic trophic transfer efficiencies. It turned out, that both study lakes were resistant to the restructuring of the pelagic food web after the winterkill of fish, i.e. they remained stable in their previous state. In contrast, the enhanced input of t-POM reduced the resilience of the clear-water state. However, the period of the t-POM study was much longer than the winterkill of fish study period. These observations at the ecosystem scale require more time than studying the dynamics at the species or community scale, as the underlying ecosystem processes are buffered within the food webs and alterations occur time-delayed. Effects of the studied external forcing regimes at the species or community scale, such as community biomass and production, community composition in respect to size and species and the grazing pressure, were representatively determined also for the short time period of the study. These measurements complemented the understanding of the food web regulation. Future studies should not hesitate to invest enormous study efforts or the use of complex ecosystem models to enhance the understanding of the food web regulation especially for formerly less studied organism groups such as sediment bacteria and macrobenthos.

Summary

The standing stock and production of organismal biomass depends strongly on the organisms' biotic environment, which arises from trophic and non-trophic interactions among them. The trophic interactions between the different groups of organisms form the food web of an ecosystem, with the autotrophic and bacterial production at the basis and potentially several levels of consumers on top of the producers. Feeding interactions can regulate communities either by severe grazing pressure or by shortage of resources or prey production, termed top-down and bottom-up control, respectively. The limitations of all communities conglomerate in the food web regulation, which is subject to abiotic and biotic forcing regimes arising from external and internal constraints. This dissertation presents the effects of alterations in two abiotic, external forcing regimes, terrestrial matter input and long-lasting low temperatures in winter. Diverse methodological approaches, a complex ecosystem model study and the analysis of two whole-lake measurements, were performed to investigate effects for the food web regulation and the resulting consequences at the species, community and ecosystem scale. Thus, all types of organisms, autotrophs and heterotrophs, at all trophic levels were investigated to gain a comprehensive overview of the effects of the two mentioned altered forcing regimes. In addition, an extensive evaluation of the trophic interactions and resulting carbon fluxes along the pelagic and benthic food web was performed to display the efficiencies of the trophic energy transfer within the food webs. All studies were conducted in shallow lakes, which is worldwide the most abundant type of lakes. The specific morphology of shallow lakes allows that the benthic production contributes substantially to the whole-lake production. Further, as shallow lakes are often small they are especially sensitive to both, changes in the input of terrestrial organic matter and the atmospheric temperature. Another characteristic of shallow lakes is their appearance in alternative stable states. They are either in a clear-water or turbid state, where macrophytes and phytoplankton dominate, respectively. Both states can stabilize themselves through various mechanisms.

These two alternative states and stabilizing mechanisms are integrated in the complex ecosystem model PCLake, which was used to investigate the effects of the enhanced terrestrial particulate organic matter (t-POM) input to lakes. The food web regulation was altered by three distinct pathways: (1) Zoobenthos received more food, increased in biomass which favored benthivorous fish and those reduced the available light due to bioturbation. (2) Zooplankton substituted autochthonous organic matter in their diet by suspended t-POM, thus the autochthonous organic matter remaining in the water reduced its transparency. (3) T-POM suspended into the water and reduced directly the available light. As macrophytes are more light-sensitive than phytoplankton they suffered the most from the lower transparency. Consequently, the resilience of the clear-water state was reduced by enhanced t-POM inputs, which makes the turbid state more likely at a given nutrient concentration. In two subsequent winters long-lasting low temperatures and a concurrent long duration of ice coverage was observed which resulted in low overall adult fish biomasses in the two study lakes – Schulzensee and Gollinsee, characterized by having and not having submerged macrophytes, respectively. Before the partial winterkill of fish Schulzensee allowed for a higher proportion of piscivorous fish than Gollinsee. However, the partial winterkill of fish aligned both communities as piscivorous fish are more sensitive to low oxygen concentrations. Young of the year fish benefitted extremely from the absence of adult fish due to lower predation pressure. Therefore, they could exert a strong top-down control on crustaceans, which restructured the entire zooplankton community leading to low crustacean biomasses and a community composition characterized by copepodites and nauplii. As a result, ciliates were released from top-down control, increased to high biomasses compared to lakes of various trophic states and depths and dominated the zooplankton community. While being very abundant in the study lakes and having the highest weight specific grazing rates among the zooplankton, ciliates exerted potentially a strong top-down control on small phytoplankton and particle-attached bacteria. This resulted in a higher proportion of large phytoplankton compared to other lakes. Additionally, the phytoplankton community was evenly distributed presumably due to the numerous fast growing and highly specific ciliate grazers. Although, the pelagic food web was completely restructured after the subsequent partial winterkills of fish, both lakes were resistant to effects of this forcing regime at the ecosystem scale. The consistently high predation pressure on phytoplankton prevented that Schulzensee switched from the clear-water to the turbid state. Further mechanisms, which potentially stabilized the clear-water state, were allelopathic effects by macrophytes and nutrient limitation in summer. The pelagic autotrophic and bacterial production was an order of magnitude more efficient transferred to animal consumers than the respective benthic production, despite the alterations of the food web structure after the partial winterkill of fish. Thus, the compiled mass-balanced whole-lake food webs suggested that the benthic bacterial and autotrophic production, which exceeded those of the pelagic habitat, was not used by animal consumers. This holds even true if the food quality, additional consumers such as ciliates, benthic protozoa and meiobenthos, the pelagic-benthic link and the potential oxygen limitation of macrobenthos were considered. Therefore, low benthic efficiencies suggest that lakes are primarily pelagic systems at least at the animal consumer level.

Overall, this dissertation gives insights into the regulation of organism groups in the pelagic and benthic habitat at each trophic level under two different forcing regimes and displays the efficiency of the carbon transfer in both habitats. The results underline that the alterations of external forcing regimes affect all hierarchical level including the ecosystem.

Zusammenfassung

Die Produktion neuer Organismenbiomasse bildet die Grundlage allen Lebens und hängt von zahlreichen Faktoren, wie den trophischen Interaktionen, ab. Diese limitieren Organismengemeinschaften entweder durch starken Fraß oder begrenzte Ressourcenverfügbarkeit, genannt top-down beziehungsweise bottom-up Kontrolle. Die Nahrungsnetzregulation umfasst die trophischen Interaktionen des Nahrungsnetzes. In dieser Dissertation wurde die Beeinflussung der Nahrungsnetzregulation durch die externen, abiotischen Einflussfaktoren (1) erhöhter Eintrag terrestrischen Kohlenstoffs und (2) lang anhaltende niedrige Temperaturen im Winter in Flachseen untersucht. Flachseen sind aufgrund ihrer Morphometrie sensitiv gegenüber diesen Einflussfaktoren, durch einen erheblichen Anteil benthischer Produktion an der Gesamtseeproduktion gekennzeichnet und treten im trüben oder klaren Zustand auf.

Der erhöhte Eintrag terrestrischen Kohlenstoffs in Flachseen verringerte die Resilienz des klaren, Makrophyten dominierten Sees. Unter Nutzung eines komplexen Ökosystemmodells konnten verschiedene Wirkmechanismen dargestellt werden, die jeweils die Lichtverfügbarkeit für Makrophyten reduzierten. Dabei wirkte der zusätzliche terrestrische Kohlenstoff als Nahrungszuschuss für bottom-up kontrollierte benthische Konsumenten, wohingegen top-down kontrollierte pelagische Konsumenten autochthone Nahrungsquellen durch terrestrischen Kohlenstoff ersetzten. Niedrige Temperaturen im Winter verursachten lang anhaltende Eisbedeckung und somit ein Sauerstoffdefizit in beiden Untersuchungsseen. Dies führte zu einem Fischsterben, bei welchem der Anteil piscivorer Fische des Makrophyten dominierten Sees überproportional stark abnahm. Die Fischgemeinschaft beider Seen wurde ähnlicher und war insgesamt von 0+ Fischen gekennzeichnet, welche eine starke top-down Kontrolle auf die Crustaceen ausübten, was diese dezimierte und Ciliaten vom Fraßdruck befreite. Die Zooplanktongemeinschaft wurde von Ciliaten dominiert, welche durch hohe Fraßraten den Biomasseaufbau von Teilen des Phytoplanktons und den Bakterien limitierten. Die energetische Weitergabeeffizienz der pelagischen autotrophen und bakteriellen Produktion zu tierischen Konsumenten war trotz des erheblichen Einflusses des Fischsterbens um ein zehnfaches höher als im benthischen Nahrungsnetz, wie die Synthese von umfangreichen Messungen in Ganzseenexperimenten auf allen trophischen Ebenen zeigte. Die benthischen Konsumenten scheinen weder bottom-up, noch top-down und nur zum Teil Habitat limitiert zu sein, womit ihre Regulation noch unklar bleibt.

Die untersuchten Einflussfaktoren wirkten regulierend auf der Art-, Gemeinschafts- und Ökosystemebene. Beide Seen waren resistent gegenüber der drastischen Nahrungsnetzrestrukturierung nach dem Fischsterben, wohingegen der Eintrag terrestrischen Kohlenstoffs die Resilienz des Makrophyten dominierten Zustands verringerte. Dies verdeutlicht die weitreichenden Folgen externer Einflussfaktoren und zeigt, dass methodisch diverse Analysen der Nahrungsnetzregulation entscheidend zum Verständnis der ablaufenden Prozesse beitragen.

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Erklärung

Ich versichere, dass ich die vorliegende Arbeit selbständig angefertigt und keine anderen als die angegebenen Hilfsmittel und Quellen verwendet habe.

Die Arbeit wurde an keiner weiteren Hochschule im In- oder Ausland vorgelegt.

Die geltende Promotionsordnung der Mathematisch-Naturwissenschaftlichen Fakultät der Universität Potsdam ist mir bekannt.

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Education

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Oct 2009 – Sep 2011	M. Sc. Ecology, Evolution, Nature Conservation at the University of Potsdam “Einfluss von Makrophyten und allochthonen Einträgen auf die Bistabilität aquatischer Nahrungsnetze – eine Modellstudie“
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List of Publications

Reviewed publications

Brothers, S. M., Hilt, S., Attermeyer, K., Grossart, H. P., Kosten, S., Lischke, B., Mehner, T., Meyer, N., Scharnweber, K. and Köhler, J. (2013) A Regime shift from macrophyte to phytoplankton dominance enhances carbon burial in a shallow, eutrophic lake. *Ecosphere,* 4, art137.

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Manuscripts in preparation

Lischke, B., Mehner, T., Hilt, S., Attermeyer, K., Brauns, M., Brothers, S., Grossart, H. P., Köhler, J., Scharnweber, K. and Gaedke, U. Dominance of pelagic carbon fluxes in shallow lakes emerges from inefficient benthic carbon transfer.

Scientific Contributions

Tagung der Deutschen Gesellschaft für Limnologie (DGL) 2011 in Freising, Deutschland: Einfluss von Makrophyten und allochthonen Einträgen auf die Bistabilität aquatischer Nahrungsnetze – eine Modellstudie (Poster)

Workshop der Young Modellers in Ecology (YoMo) 2012 in Craheim, Deutschland: Bistability in shallow lakes – top down controlled? (Vortrag)

Tagung der American Society of Limnology and Oceanography (ASLO) in Otsu, Japan (2012): Terrestrial organic matter affects the resilience of shallow lakes – a modeling study (Vortrag)

Tagung der Deutschen Gesellschaft für Limnologie (DGL) 2012 in Koblenz, Deutschland: Terrestrisches organisches Material beeinflusst die Resilienz der stabilen Zustände in Flachseen – eine Modellstudie (Vortrag)

Tagung des Symposium for European Freshwater Sciences (SEFS) 2013 in Münster, Deutschland: Enhanced input of allochthonous matter reduces the resilience of the clear state of shallow lakes - a model study (Vortrag)

Tagung der Deutschen Gesellschaft für Limnologie (DGL) 2013 in Potsdam, Deutschland: The fate of additional allochthonous organic matter in the pelagic food chain (Vortrag)