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Strong influences of larval diet history on subsequent post-settlement growth in the freshwater mollusc *Dreissena polymorpha*

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ABSTRACT

Significant seasonal variation in size at settlement has been observed in newly settled larvae of *Dreissena polymorpha* in Lake Constance. Diet quality, which varies temporally and spatially in freshwater habitats, has been suggested as a significant factor influencing life history and development of freshwater invertebrates. Accordingly, experiments were conducted with field-collected larvae to test the hypothesis that diet quality can determine planktonic larval growth rates, size at settlement and subsequent post-metamorphic growth rates. Larvae were fed one of two diets or starved. One diet was composed of cyanobacterial cells which are deficient in polyunsaturated fatty acids (PUFAs), and the other was a mixed diet rich in PUFAs. Freshly metamorphosed animals from the starvation treatment had a carbon content per individual 70% lower than that of larvae fed the mixed diet. This apparent exhaustion of larval internal reserves resulted in a 50% reduction of the postmetamorphic growth rates. Growth was also reduced in animals previously fed the cyanobacterial diet. Hence, low food quantity or low food quality during the larval stage of *D. polymorpha* lead to irreversible effects for postmetamorphic animals, and is related to inferior competitive abilities.

Keywords: Dreissena polymorpha; food quality; fatty acid; life history; metamorphosis; PUFA

INTRODUCTION

Aspects of food quality in terrestrial (Elser *et al.* 2000) and aquatic food webs (Sterner & Schulz 1998) have been major topics of study during the past years. However, reports on life history consequences with regard to food quality for benthic freshwater invertebrates are scarce, even though species such as *Dreissena polymorpha* contribute substantially in the transfer of primary to secondary production.

Information about life history consequences as reported for amphibians, where reduced food availability leads to metamorphosis at smaller than average sizes (Audo *et al.* 1995) are rare for invertebrate species. Knowledge comes mostly from studies of marine filter feeders, where larval food shortage affects metamorphic success (West & Costlow 1987), reduces postmetamorphic growth (Pechenik *et al.* 1996; Pechenik *et al.* 1998), or delays metamorphosis. Delaying metamorphosis substantially alters postmetamorphic growth and performance of marine invertebrate species (Woollacott *et al.* 1989; Wendt 1996; Qian & Pechenik 1998; Wendt 1998). Slow postmetamorphic juvenile growth is related to inferior competitive abilities, as has been shown for marine sessile invertebrates (Connell 1961; Miller & Carefoot 1989). This suggests that postmetamorphic growth could be a key parameter for the competitive strength of also benthic freshwater invertebrates, such as the zebra mussel *D. polymorpha*. In the field, all settled mussels within a patch are exposed to the same food conditions. If all animals possess the same competitive capacity, all individuals should show similar growth. However, if postmetamorphic juveniles differ in growth rate, this probably translates into differences in the competitive capacity of juvenile mussels. These differences in growth could result from differences in larval food conditions.

It has not been investigated whether the planktotrophic larvae of *D. polymorpha,* which metamorphose to sessile juvenile mussels when they exceed a certain size threshold (Lewandowski 1982; Sprung 1989), are able to replenish their internal stores sufficiently when temporarily subjected to suboptimal food conditions. Although effects of low food concentrations and low food quality on growth and reproduction of adult *D. polymorpha* were shown recently (Stoeckmann & Garton 2001), and food quality effects on larval growth are well documented (Vanderploeg *et al.* 1996; Wright *et al.* 1996; Wacker *et al.* 2002), no studies have considered that the food conditions during the larval life stage of *D. polymorpha* might affect its postmetamorphic growth as a benthic animal.

In nature, larvae can be exposed to substantial fluctuations in food supply and composition during their pelagic dispersal, to which they may respond by depletion of internal reserves before metamorphosis. If these reserves are then replenished, there should be no differences in size and growth capacity of postmetamorphic juveniles. If no such entire replenishment of internal energy stores takes place, growth capacities of newly settled daily cohorts should vary over time.

We therefore decided to determine whether daily cohorts of newly settled zebra mussels in Lake Constance differ in their postmetamorphic growth capacity. Growth capacity was defined as growth under saturating food conditions in order to distinguish from effects of food quantity. Since it is not known to what extent the observed differences in the growth capacity are attributable to variations in larval food quantity and quality in the field, the importance of larval food regimes for the growth of postmetamorphic individuals was investigated in controlled growth experiments. While Pechenik *et al.* (1996) studied the influence of food quantity (starvation) experienced during larval life of marine invertebrates, we additionally examined possible impacts of food quality.

MATERIALS AND METHODS

(a) Collecting newly settled cohorts

Our study was carried out in Lake Constance, a mesotrophic lake of warm-monomictic character at the northern border of the Alps in Central Europe. This lake consists of two basins, Upper and Lower Lake Constance, connected via the river Rhine.

Flat scourers made of viscose fibre (2-mm thick) were mounted on galvanised frames (20×20 cm) and were fixed to a rope in a horizontal position at 6-m water depth. Three replicate collectors were deployed on three dates between early August and early September 1998, with each deployment lasting 24 h. In mid-August, collectors were additionally deployed in the lower, more eutrophic part of the lake. After each deployment, collectors were lifted carefully and subsequently transported to the laboratory in filtered (<30-µm pore size) lake water. A strong jet of cool tap water was used to detach newly settled larvae from the fibres of the scourers, and mussels were collected by sieves with 350-µm and 55-µm Nitex netting. The collected live zebra mussels were then counted and measured in length (Ackerman *et al.* 1994) under a stereomicroscope (Zeiss, Jena, Germany; 100× magnification) using an image analysis system.

(b) Preparation of food

Algae were obtained from culture collections of the Max-Planck-Institute for Limnology (MPIL, Plön, Germany), the Institute of Freshwater Ecology and Inland Fisheries (IGB, Berlin, Germany), the University of Göttingen (SAG, Germany), the University of Texas (UTEX, Austin, USA), and the IFremer Centre de Brest (IFremer, France). The cyanobacterium *Aphanothece* sp. (IGB Berlin) and the algae *Cryptomonas erosa* (MPIL

Plön), *Cyclotella meneghiniana* (SAG 1020-1a), and *Nannochloropsis limnetica* (SAG 18.99) were cultured semi-continuously in modified WC medium with vitamins (Guillard 1975). *Isochrysis* aff. *galbana* (UTEX 2307) was cultivated semi-continuously in artificial seawater (Starr & Zeikus 1993); for *Chaetoceros calcitrans* (IFremer), diluted seawater medium (50%) was used. Cells were concentrated by centrifugation. Carbon concentrations of solutions were estimated from photometric light extinction (800 nm) using carbon-extinction equations. Aliquots of algal or cyanobacterial solutions were added to filtered lake water (0.45-µm pore-sized membrane filter), and the resulting suspensions were used as food for zebra mussel larvae and juveniles. Suspensions were renewed daily and concentrations kept constant throughout the experiment.

Marine algae were used previously by Wright *et al*. (1996) and were of excellent food quality for *D. polymorpha* larvae. Adding marine algae to filtered lake water did not result in lysis of algal cells (determined as particulate organic carbon after 4 h incubation); therefore, the carbon concentrations remained constant in the food suspensions.

(c) Postmetamorphic growth capacity of larvae that had been feeding in the field

Cohorts of newly settled postmetamorphic juveniles were isolated and, after measurement of length, animals were kept separately in food suspensions in 3-mL multiwell cell-culture plates at 20°C. All animals were fed *C. erosa* (rich in polyunsaturated fatty acids, PUFAs), at an identical food concentration of 3 mg C l^{-1} with daily changes of food suspensions. The growth of the newly settled zebra mussels was determined by measuring the length of each individual at 3, 6, 9, 13, and 16 days after the animals had been brought to the laboratory. Changes in length over time were used to calculate absolute growth rates. For statistical analysis, a postmetamorphic growth rate from settlement until day 16 was calculated for each animal.

(d) Postmetamorphic growth capacity of larvae under different food regimes

Larvae were sampled from the lake using a 100-µm mesh plankton net. Three thousand larvae (120– 140 µm) were picked manually under a stereomicroscope using a Pasteur pipette and were subsequently fed with a mixed diet of four algal species [*I. galbana, N. limnetica, C. meneghiniana,* and *C. calcitrans* (1.6, 1.6, 0.4, and 0.4 mg C l^{-1}, respectively)] for 2 days.

After 2 days on the mixed diet, the animals were transferred to three sets of flow-through systems (3.75-l volume, 100-µm screen, three replicates each), and fed (i) the mixed diet (4 mg C l^{-1}), (ii) the cyanobacterium *Aphanothece* sp. (4 mg C l^{-1}), or (iii) no food. Food suspensions were renewed every other day. After 6 days, artificial substrates (flat scourers, 5 cm in diameter) were added to the flow-through chambers (24 h). Newly attached mussels were isolated and measured. The size of the animals at settlement on the collectors was determined as the mean length of animals collected from each of the three replicates. The animals from all treatments were then reared individually in 3 ml of the mixed diet (4 mg C l^{-1}) in multiwell plates, with algal suspensions being renewed daily. In order to assess juvenile growth rates, the mussels were measured at day 3 and day 16 after settlement, and growth rates were calculated from the attachment date until day 16. All larvae and juveniles were cultured at a temperature of 20°C.

(e) Particulate parameters

Particulate organic carbon (POC), nitrogen (PON), and phosphorus (P_{part}) of algal or cyanobacterial food was analysed according to Wacker and Von Elert (2001). For analysis of POC in newly settled mussels, 50 animals were collected on a GF/F filter. For determination of fatty acids, aliquots of food suspensions corresponding to approximately 1.0 mg POC were extracted, transesterified, and analysed according to Von Elert & Stampfl (2000) using an HP 6890 GC (Agilent Technologies, Waldbronn, Germany).

(f) Data analysis

Each individual juvenile growth rate was considered as a replicate within the originally settled cohort of each replicate collector (n=3) or replicate flow-through system. The collector or the flow-through system was used as an additional factor (block factor) in analysis of variance (ANOVA). The size of the animals at settlement on the collectors was determined as the mean value of animals collected from three deployed collectors. For POC-values, for size at settlement and for larval growth rates ANOVA was used. Because juvenile growth is affected by size at settlement (table 1), analysis of covariance (ANCOVA) was used when testing for significant effects of attachment date and different larval treatments. Adjusted mean growth rates were calculated using size at settlement as a covariate. In no case were interactions of covariate with treatments significant. POC values were log(1+x)-transformed to meet assumptions for ANOVA; all other raw data met assumptions. All analyses were carried out using STATISTICA 5.5 (StatSoft Inc., Tulsa, Okla., USA).

RESULTS

(a) Postmetamorphic growth capacity of larvae that had been feeding in the field

Newly settled animals from different dates differed significantly in size (figure 1*a,* ANOVA, $F_{2,6}$=9.1, p<0.05). Animals attached to the substrates deployed in the upper basin of Lake Constance showed a significant size variability over time (figure 1*a,* Tukey's HSD multiple-comparison test, p<0.05), and animals isolated from the lower basin, a more shallow and eutrophic part, were on average 19 µm larger than animals from the upper basin.

In order to assess the postmetamorphic growth capacity of different daily cohorts from the lake, newly settled animals were isolated and reared under controlled food conditions.

The growth of freshly settled larvae was linear for 16 days of postmetamorphic life **(**figure 1*b***)**, and the juvenile growth rate was significantly influenced by attachment date (figure 1*c,* table 1*a*). The cohort attaching on the 11th of August had higher adjusted mean growth rates than individuals attaching towards the end of the recruitment season (Spjotvoll/Stoline multiple-comparison test $p<0.001$).

(b) Postmetamorphic growth capacity of larvae under different food regimes

Individually collected *D. polymorpha* larvae isolated from the lake were 130±11.2 µm in size. When the animals were reared on a mixed diet of four algal species (*I. galbana, N. limnetica, C. meneghiniana,* and *C. calcitrans*), they increased in size to 162.7±12.1 µm (figure 2) within 2 days. Subsequently, the animals were divided into groups for three different 6-day food regimes.

Effects of food were already apparent in the premetamorphic growth rates (figure 3*a*). Larvae starved for 6 days showed significantly lower growth rates (9.5±0.26 µm d^{-1}) than larvae either continuously fed the mixed diet (13.0±0.68 µm d^{-1}) or grown on *Aphanothece* sp. (12.7±0.23 µm d^{-1}; ANOVA, $F_{2,6}=19.2$, Tukey's HSD, $p<0.01$).

Larvae that had settled within 24 h in the experimental flow-through systems were of the same size (approximately 250 µm) when fed the mixed diet or the cyanobacterium (figure 2). However, starved animals attached to substrates were approximately 20 µm smaller than their fed conspecifics. The starved larvae exhibited less but still significant growth at the expense of their internal stores: newly attached animals that were starved during their larval stage were only 8% smaller than fed larvae, but contained one third of carbon compared with animals fed the mixed diet (figure 3*b*, ANOVA, $F_{2,6}=8.5$, Tukey's HSD, $p<0.05$). Larvae that had been feeding on *Aphanothece* sp. had a carbon content higher than that of starved larvae (figure 3*b*), which indicated that the cyanobacterial carbon was assimilated. The carbon content of larvae fed *Aphanothece* sp. did not differ from those fed the mixed diet, but growth diverged after metamorphosis even though identical food was offered to all postmetamorphic animals (figure 2).

Adjusted mean growth rates after settlement were significantly affected by the different larval food sources (table 1*b*). The juvenile cohorts continuously fed the mixed diet showed the highest adjusted mean growth rate (figure 3*c*; 14.2±1.07 µm), twofold higher than that of individuals evolved from larvae previously fed *Aphanothece* sp. (7.1±1.43 µm) or starved (6.4±1.05 µm, Spjotvoll/Stoline HSD, $p<0.01$).

DISCUSSION

The present study demonstrates convincingly that even brief periods of poor diet have persistent and lingering influences on subsequent size at settlement, energy stores and post-metamorphic growth rates. Size at settlement was in the same range as reported by Martel *et al.* (2001) and growth of freshly settled larvae was linear for 16 days of postmetamorphic life (this study), as is known for other bivalves (Bayne 1964). We found that size at settlement and postmetamorphic juvenile growth capacity of *D. polymorpha* varied considerably among individuals recruiting to a particular population on different dates. These results are consistent with results of Jarrett & Pechenik (1997), who observed temporal variations in growth capacity of field-collected daily cohorts of marine barnacles. Since all of their and our postmetamorphic animals were reared at constant temperatures and food concentrations, and divergent postmetamorphic growth was found, we conclude that these distinctions are due to intrinsic differences in the animals' physiological growth capacity.

The postmetamorphic growth rates found in our study are in accordance with growth rates of newly settled *D. polymorpha* in Lake Erie (Martel 1993), suggesting that juvenile animals in our laboratory were reared under conditions similar to those found in nature.

Although the observed significant differences in postmetamorphic growth capacity among cohorts recruiting on different days could have a genetic basis (Bertness & Gaines 1993; Hilbish *et al.* 1999), these differences in growth capacity may ultimately result in considerable variation among daily cohorts in survival and recruitment success because individual size can influence vulnerability to predation (Kornobis 1977) as well as the outcome of competitive interactions (Connell 1961; Bertness 1989).

In order to assess whether larval food conditions lead to the differences in size at settlement and in postmetamorphic growth observed with daily cohorts from the field, we tested the influence of low food quantity (larvae temporarily starved) and low food quality (larvae temporarily fed *Aphanothece* sp.) in comparison with food of high quality and quantity (algal mixture). The effects of these different treatments were already apparent in the larval growth rates: temporarily starved animals grew more slowly at the expense of their internal stores, which were not restored before metamorphosis, and settled at a smaller size. Temporary low food quality did not affect the increase in larval size, but, as in the starvation treatment, body size increased through the consumption of internal stores. The result of the starvation treatment is in accordance with findings for non-feeding bryozoan larvae, which reduce internal stores when prolongating their larval stage (Wendt 2000). In consequence the depletion of internal stores of bryozoan larvae during larval swimming dramatically affected later juvenile performance in the laboratory (Wendt 1996) and in the field (Wendt 1998). Our finding that the animals showed

reduced postmetamorphic growth rates when larvae were starved are consistent with results of Pechenik *et al.* (1996), who have reported that postmetamorphic juvenile growth rates of a marine gastropod decrease when larvae were starved for a few days. In contrast, other species (e.g. the polychaete *Capitella* sp.) do not reduce postmetamorphic growth after an unfavourable larval period (Pechenik & Cerulli 1991). While Pechenik *et al.* (1996) studied the influence of food quantity (starvation) during larval life on postmetamorphic growth of marine invertebrates, we additionally examined possible impacts of food quality. The animals fed the mixed diet and the animals fed *Aphanothece* sp. were reared at identical food concentrations; therefore, the reason for the difference in postmetamorphic growth capacity was not food quantity, but rather food quality. Cyanobacteria are known to be of low food quality for freshwater zooplankton owing to toxicity (Lampert 1981), mechanical interference (Porter & McDonough 1984), or nutritive deficiencies in fatty acid composition (Von Elert, in press). Since the larvae of *D. polymorpha* fed *Aphanothece* sp. grew significantly better than starved larvae, ingestion and assimilation of this cyanobacterium is obvious. However, these processes might be less efficient than with the mixed algal diet, so that the relative influence of toxicity, mechanical interference and lack of PUFAs cannot be separated.

Since PUFAs are essential for many vertebrates and invertebrates (Stanley-Samuelson *et al.* 1988), a deficiency in PUFAs could provide an explanation for the low food quality of *Aphanothece* sp. for *D. polymorpha* larvae. When feeding food poor in PUFAs, internal PUFA stores of larvae are exhausted and growth of *D. polymorpha* larvae will be affected by food quality, in particular by defiencies of long-chained PUFAs e.g. eicosapentaenoic (EPA, 20:5n-3) and docosahexaenoic acid (DHA, 22:6n-3), which is discussed by Vanderploeg *et al*. (1996), Wright *et al*. (1996), and Wacker *et al*. (2002). This is consistent with findings of marine aquaculture (e.g. Brown *et al.* 1997), which have demonstrated a requirement for (n-3) long-chained PUFAs, in particular eicosapentaenoic (EPA, 20:5n-3) and docosahexaenoic acid (DHA, 22:6n-3). In the present study, animals continuously reared on the mixed diet showed high growth rates, indicating that the mixed diet met metabolic demands. In the mixed diet, 9.5% of total fatty acids were (n-3) PUFAs and 3.3% were (n-6) PUFAs. The portion of (n-3) long-chained PUFAs (>C18) amounted to 23.7% and (n-6) long-chained PUFAs (>C18) to 3%. In contrast to the mixed diet, *Aphanothece* sp. is deficient in PUFAs (Wacker *et al.* 2002). The larvae fed the cyanobacterium for 6 days therefore had to use internal PUFA stores originating from the previously fed mixed diet; the reduced growth in their postmetamorphic life possibly started after they had exploited these fatty acid reserves.

To summarise, we found that larval food quality as well as larval food quantity influenced the postmetamorphic growth of *D. polymorpha*. Although we cannot exclude genetic or maternal effects on postmetamorphic growth (Zielinski *et al.* 1996), the importance of larval food conditions is supported by our results: the decrease of postmetamorphic growth rates was in the same order of magnitude when larvae were starved or when larval food quality was limited for only a few days, in comparison to the variation of the postmetamorphic growth capacity of newly settled larvae from the field. Hence, low food quantity or low food quality during the larval stage of *D. polymorpha* may lead to irreversible effects for postmetamorphic animals.

We do not know exactly how frequently larvae of *D. polymorpha* are affected by fluctuations in food quantity or quality that are comparable in magnitude and duration to those tested in our study. However, typical algal summer blooms in eutrophic lakes mainly consist of low-food-quality green algae and cyanobacteria (Kenyon 1972; Sommer *et al.* 1986). Since *D. polymorpha* reproduces from June to August (Walz 1978; Garton & Haag 1993), the low biochemical quality of algal and cyanobacterial summer blooms may affect the planktonic larvae of *D. polymorpha.* Hence, food quality has obvious implications for the growth of the larvae and postmetamorphic juveniles and therefore for the recruitment to form adult populations in nature.

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Table 1. Results [degrees of freedom (*df*), F-value, and probability (*p*)] of statistical analysis of covariance (ANCOVA) for postmetamorphic growth capacity of juvenile mussels from *(a)* larvae feeding in the field (upper basin of Lake Constance), and *(b)* larvae fed differently, using size at settlement as a covariate (covar).

(a)

factor	*df*	*F*	*p*
size at settlement (covar)	1, 183	11.1	<0.001
date of attachment	2, 183	21.4	<0.001
collector	2, 183	0.03	0.96
date×collector	4, 183	0.10	0.98

(b)

factor	*df*	*F*	*p*
size at settlement (covar)	1, 64	11.5	<0.01
food	2, 64	14.8	<0.001
larval replicate	2, 64	0.01	0.99
food×larval replicate	4, 64	0.49	0.74

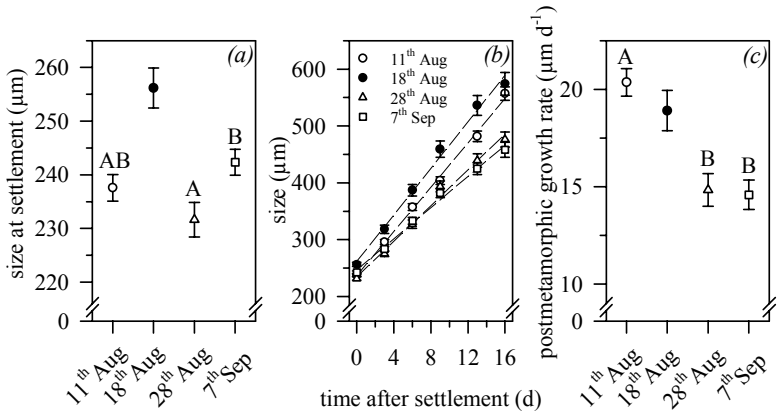

Figure 1. *(a)* Size at settlement (±SE, n=3), *(b)* development of mean shell size (±SE), and *(c)* juvenile growth rates (adjusted least-squares mean ±SE) for four daily cohorts isolated from the lake upper basin [11th of Aug. (n=76), 28 th of Aug. (n=37), 7 th of Sep. (n=62)] and lower basin [(●): 18 th of Aug. (n=55)] and grown under controlled food conditions in the laboratory. Symbols with identical letters represent nonsignificant groupings based on Spjotvoll/Stoline HSD following ANCOVA (p<0.05); data of lower basin are excluded from statistics.

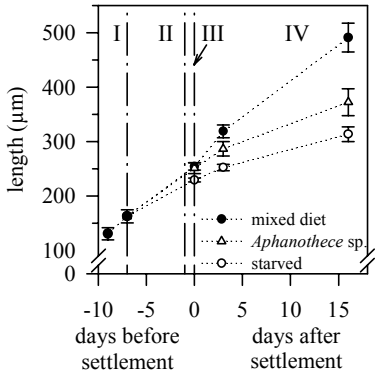

Figure 2. Mean size (±SE) of *Dreissena polymorpha*. I) Time period where all larvae were reared on a mixed diet; II) 6 days: fed a mixed diet, fed *Aphanothece* sp., or starved; III) 24-h deployment of artificial substrates; IV) all postmetamorphic mussels fed a mixed diet.

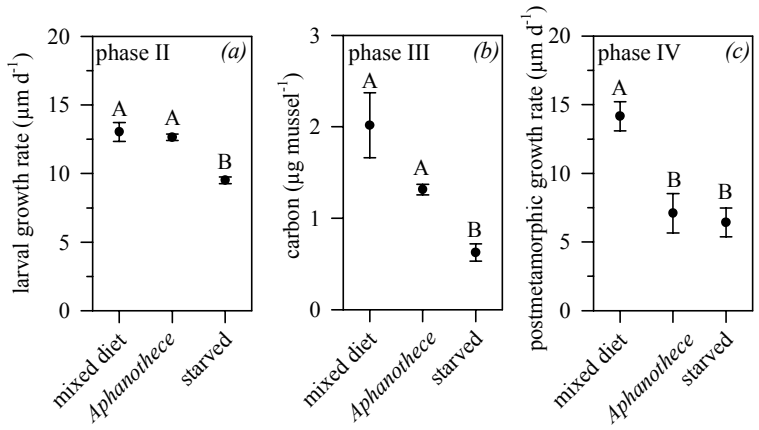

Figure 3. *Dreissena polymorpha* larvae that had been reared on a mixed diet (phase I) were subsequently fed a mixed diet, fed *Aphanothece* sp., or starved (phase II). After deployment of artificial substrates (phase III), all postmetamorphic mussels were fed a mixed diet (phase IV). *(a)* Larval growth rates (mean ±SE, n=3) during phase II, *(b)* organic content of newly settled mussels (mean ±SE, n=3) during phase III, and *(c)* postmetamorphic growth rates (adjusted mean ±SE, n_{mixed}=28, $n_{Aphanothece}$=15, $n_{starvation}$=31) during phase IV. Symbols with identical letters are not significantly different at p<0.05 (Spjotvoll/Stoline HSD following ANCOVA).