

Temporal variation in zebra mussel (*Dreissena polymorpha*) density structure the benthic food web and community composition on hard substrates in Lake Constance, Germany

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Abstract Invasive species often influence existing biocenoses by altering their environment or facilitating the ecology of other species. Here we combined stable isotope analysis with quantitative benthic community sampling to investigate temporal variation in the influence of biodeposition of organic material (biodeposits) by the zebra mussel (*Dreissena polymorpha*) on the benthic food web in hard substrate habitats of Lake Constance, Germany. The accumulation of organic material excreted by zebra mussels (faeces and pseudofaeces) is hypothesised to implement a biodeposition based food web. By means of stable isotope analyses, we found that the feeding strategy of amphipods was dependent on the availability of zebra mussel biodeposits. The proportion of pelagic resources contributing to the diet (by $\delta^{13}\text{C}$) and trophic position (by $\delta^{15}\text{N}$) of amphipods were significantly and positively correlated to the production of zebra mussel biodeposits. Also, the benthic community in Lower Lake Constance showed

a shift towards higher densities of the mayfly *Caenis* spp., Chironominae, and the caddisfly *Ecnomus tenellus*, which might act as links to higher trophic levels when more zebra mussel biodeposits were available. These results demonstrate that temporal variation in zebra mussel density, and thus in organic biodeposition, have a strong impact on the benthic communities and food web structure associated with hard substrates to the extent that there may be dependence on zebra mussel occurrence in such habitats in Lake Constance.

Keywords Stable isotope analysis · Biodeposition · Amphipods · Invasive species · Food web · Benthic-pelagic coupling

Introduction

Trophic relationships significantly affect the structure of aquatic communities and vice versa (e.g. Langeland et al. 1991; Vander Zanden et al. 1999) with each species contributing to the structure of the food web in a different manner. Invasive species often influence native biocenoses and potentially alter the community structure and food web by modifying the existing habitat, providing new food resources or reducing existing ones (Vander Zanden et al. 1999; Ricciardi and MacIsaac 2000; Maguire and Grey 2006). A single invasive species can have a disproportionate role in its surrounding food web and

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community and the effects can even cascade across ecosystem boundaries (Baxter et al. 2004), proving that they can be more harmful to the native biodiversity than their native counterparts (Letnic et al. 2009). Since the introduction, establishment, and distribution of invasive species are promoted by increasing global trade, the topic of invasive species is of increasing global concern (Chandra and Gerhardt 2008).

Invasion of the zebra mussel *Dreissena polymorpha* in North America and Europe has been associated with changes in the structure of benthic habitats of many freshwater ecosystems. Mussel shells increase surface area and structural complexity of the physical habitat, while the filtration activity of mussels deposits organic material to the benthos (Klerks et al. 1996; Silver Botts et al. 1996). Increased structural complexity associated with living mussels and empty shells has been shown to positively affect the abundance of macroinvertebrates via habitat provision (Stewart et al. 1998; Mörtl and Rothhaupt 2003). Furthermore, it is hypothesized that the availability of material biodeposited by zebra mussels may be used as a new food source by other organisms, leading to the development of a biodeposition-based food web (Stewart and Haynes 1994; Mitchell et al. 1996). Such biodeposits were found to be a suitable food source for amphipods and chironomids in laboratory experiments (Izvekova and Lvova-Katchanova 1972; González and Burkart 2004; Gergs and Rothhaupt 2008b).

In natural ecosystems, amphipods may benefit from the new resource either directly by feeding on zebra mussel biodeposits, or indirectly by preying upon other invertebrates consuming the biodeposits. There is some evidence from stable isotope analysis that the natural diet of the amphipod *Gammarus fasciatus* contains zebra mussel biodeposits (Limén et al. 2005), but comparatively little is known about the temporal importance of biodeposit availability under field conditions and its subsequent effects on the benthic macroinvertebrate community. Stable carbon and nitrogen isotope measurements have been used increasingly to investigate such relationships (e.g. Maguire and Grey 2006). The trophic transfer of stable carbon isotopes is relatively conservative with little fractionation, and thus $\delta^{13}\text{C}$ is a good indicator of the energy source of a consumer (Peterson and Fry

1987; Post 2002). Since pelagic primary producers are typically ^{13}C -depleted compared to benthic primary producers, the origin of the carbon in a consumer can be determined (France 1995a, b). Trophic position within a food web can be inferred from organismal $\delta^{15}\text{N}$ values by typical trophic fractionation relative to a known baseline (on average 3–3.5 ‰, e.g. McCutchan et al. 2003).

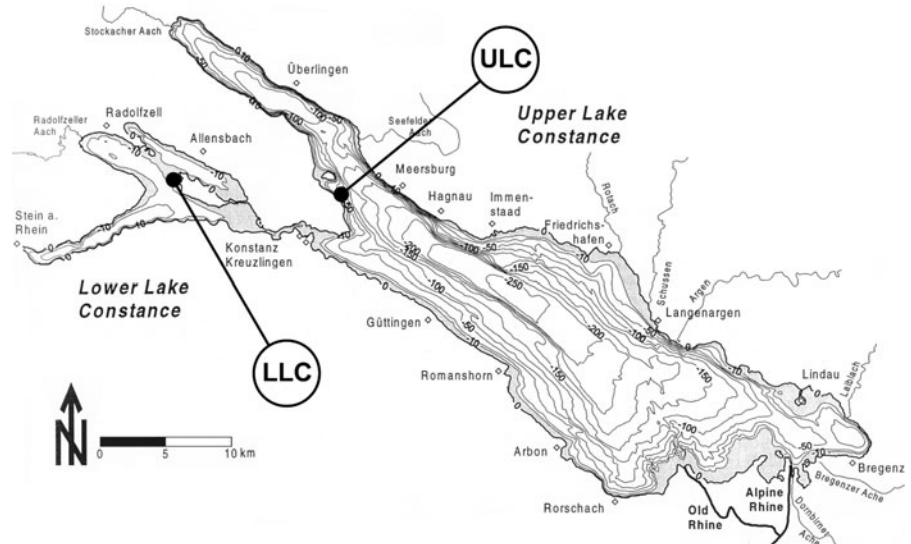
There have been a number of studies determining the repackaging of energy and matter from the pelagic to the benthos by invasive zebra mussels (for an overview see Ward and Ricciardi 2007), but less attention has been paid to studying the ramifications of variable mussel density, and hence biodeposition over time. We hypothesized that the coupling of pelagic primary production to the benthic food web by zebra mussel biodeposition is density dependent. We quantitatively assessed how the benthic community structure and food web on hard substrates depends on zebra mussel biodeposition and epilithon production. Furthermore, we compared data collected from two consecutive years when zebra mussel density was reduced in the second following a cold winter with low water conditions.

Material and methods

Study area and sites

The study was conducted in Lake Constance, a pre-alpine, oligotrophic lake of the unregulated alpine system of the River Rhine, bordering Germany, Switzerland and Austria (Fig. 1). Lake Constance is divided into two major basins which are connected by a river-like part. The major basin, Upper Lake Constance (ULC), has a mean depth of approximately 100 m and covers a large area of 473 km², whereas Lower Lake Constance (LLC) is more shallow (mean depth of approximately 13 m) and smaller (63 km²) (IGKB 2004). Two study sites were located in the western part of ULC (N 47° 41.5'; E 9° 12.2') and in the central part of LLC, near a peninsula (N 47° 42.1'; E 9° 2.4'). Samples at each site were collected from hard substrates (covered with zebra mussels) during mid October 2005 and 2006 at a depth of one metre below mean low-water level (MLL -1 m), respectively.

Fig. 1 Map of Lake Constance, modified after Wessels (1998). Black dots show the sampling sites. Hard substrates at site ULC (Upper Lake Constance) and site LLC (Lower Lake Constance) were sampled in October 2005 and 2006



Benthic sampling

Quantitative macroinvertebrate samples ($n = 5$, each site and year) were collected by scuba divers using an infralittoral suction sampler, which covers a sampling area of 625 cm^2 (Baumgärtner 2004; Mörtl 2004). A sampling frame ($25 \times 25 \text{ cm}$) was placed on the substrate from which rocks were collected in a handnet ($200 \mu\text{m}$ meshsize), and fine substrate was whirled up by hand. Floating matter and macroinvertebrates were collected by suction onto a filter element ($200 \mu\text{m}$ mesh size). In the laboratory, zebra mussels were detached from rocks; other macroinvertebrates were brushed from rocks or separated from inorganic sediments and collected with a $200 \mu\text{m}$ sieve. The organic fraction was fixed in 95% ethanol. All invertebrates were identified to lowest practical taxonomic level (mostly species or genus level) and counted under a stereomicroscope (Zeiss Stemi 2000-C, Jena, Germany). Zebra mussels were divided into two size classes ($>5 \text{ mm}$ and $<5 \text{ mm}$) and counted. All mussels $<5 \text{ mm}$ are the young of the year and thus were described as newly settled juveniles (Cleven and Frenzel 1993).

Similarity of benthic macroinvertebrate communities among sampling sites and dates were analysed by non-metric multidimensional scaling (nMDS) with PRIMER 5 (version 5.2.8). We analysed Bray–Curtis similarities between the communities, which compare ranked similarities for differences between defined groups. Statistical differences between communities

as a function of sampling sites and years were analysed using analyses of similarity (ANOSIM; PRIMER 5). The percentage contribution of single species to the differences between benthic community structures was estimated using SIMPER (PRIMER 5) analyses. Differences between sampling years and sites for zebra mussels $>5 \text{ mm}$ were analysed using a two-way analysis of variance (ANOVA). Homogeneity of variances was checked by F test. Since each of the two dominant amphipod species in Lake Constance was only found in one of the two lake parts (*Dikerogammarus villosus* in ULC, *Gammarus roeselii* in LLC), changes in density of amphipods were only analysed between sampling years by t tests. All statistical analyses were conducted using the statistical software package R (R Development Core Team 2006).

Quantification of basal resources

We estimated the daily production rates of zebra mussel biodeposits and epilithon as the two potential available basal resources (i.e. trophic level one) in the hard substrate habitat. Biodeposited material is effectively seston transformed and repackaged by zebra mussels and has a pelagic origin, whereas the carbon fixation of epilithon takes place in the benthic zone resulting in distinct $\delta^{13}\text{C}$ values; the pelagic carbon and hence the biodeposit material is more ^{13}C -depleted (Limén et al. 2005). A large part ($\sim 66\%$) of the ingested seston is not digested by

zebra mussels but directly expelled as biodeposits (Walz 1978a), and therefore the production of biodeposits should not involve any trophic fractionation, simply reflecting the seston $\delta^{13}\text{C}$.

Epilithon samples ($n = 5$, each site and year) were collected with a brush sampler (\varnothing 20 mm) as described by Peters et al. (2005). The sampler was placed onto the stone and fixed with one hand, while the other hand pushes down the plunger and rotates the brush several times. Then, water was suctioned up when the plunger is pulled to the top of the sampler. The brush sampler was then closed with the ball valve by a 90 degree turn of the handle, which minimises sample losses. For further analyses, epilithon was resuspended and adjusted to a defined volume with distilled water. Epilithon production was calculated from its chlorophyll *a* concentration and local water temperature (Morin et al. 1999). For chlorophyll *a* measurements, a sub-sample (10 ml) of each replicate was filtered on precombusted glass-fibre filters (Schleicher and Schuell GF6, \varnothing 25 mm, Dassel, Germany). Chlorophyll *a* concentration ($\mu\text{g}/\text{cm}^2$ stone surface) was measured spectrophotometrically after extraction of pigments from the filters in 90% ethanol for 12 h in the dark at 4°C, and correcting values for pheopigment content (Lorenzen 1967). To calculate area-specific chlorophyll *a* concentration in the field, we estimated the proportion of colonisable stone surface area of the benthos. At each sampling site, the stones from four replicate sampling areas of 625 cm² (depth: MLL -1) were collected, the surface area of each stone was calculated as an oval by length and width, and the total colonisable stone surface area as the sum of stone areas for each replicate.

Zebra mussel biodeposition production at the sampling sites was estimated as the product of daily biodeposition rate per mussel (calculated from seston biomass concentration, see Gergs et al. 2009) and zebra mussel density. Seston from a depth of 2 m below MLL was sampled approximately 300 m from shoreline with a horizontal water sampler. To exclude those particles too large for zebra mussel feeding, lake water was prefiltered through a 200 μm net before further processing (Ten Winkel and Davids 1982). Five sub-samples (750 ml) of seston were filtered on precombusted glass-fibre filters (Schleicher and Schuell GF6, \varnothing 25 mm, Dassel, Germany) for ash-free dry mass (AFDM) and dried at 105°C for 24 h. After weighing (dry mass), the filters were

combusted at 550°C for 8 h and weighed again; the AFDM was calculated by subtraction.

Differences between epilithon production and zebra mussel biodeposition, among sampling years and sites, were analysed using a three-way analysis of variance (ANOVA). Data were $\ln(x)$ transformed to homogenize variances, checked using *F* tests.

Stable isotope analyses

Macroinvertebrates were collected with a handnet (200 μm mesh size) by scuba divers at each site. All invertebrates (see Fig. 5) were maintained alive individually over gauze to allow gut clearance for 24 h. Whole organisms were analysed for stable isotopes, except for zebra mussels and *Bithynia tentaculata*, from which only the soft tissue was used. Single individuals were analysed whenever size allowed. Chironominae (5–15 individuals) and *Centroptilum luteolum* (five individuals) were pooled to provide sufficient material for analyses. Epilithon samples were obtained from the brush samples. Seston was filtered onto pre-combusted glass fibre filters (Whatman GF/F; \varnothing 25 mm, Kent, England). Samples of primary producers were split into two groups. One group was acidified (1 M HCl for Approx. 2 h) to remove carbonate and used for stable carbon analysis; the second group was used without acidification for stable nitrogen analysis. All samples were dried at 55°C, ground, and weighed into tin cups (0.4–0.7 mg for animal material and seston, and 1.5–3.0 mg for epilithon). Five replicates were analysed if no variation is explicitly noted. Isotope ratios were measured using a ThermoFinnigan Delta Plus Isotope Ratio Mass Spectrometer and are presented using the δ notation and units of per mille (‰). The international standards Vienna PeeDee belemnite for carbon and atmospheric N₂ for nitrogen were used as reference. Repeated analyses of an internal standard resulted in typical accuracy ($\pm 1\text{SD}$) of 0.19 and 0.08 ‰ for carbon and nitrogen, respectively.

Differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of macroinvertebrates and primary producers between sampling sites and years were analysed by two-way ANOVAs with *Bonferroni* correction of the significance level for multiple comparisons. To assess the importance of the two basal resources for macroinvertebrate feeding strategy, the dependence of stable isotope values of macroinvertebrates on zebra mussel

biodeposition or epilithon production was examined by regression analyses.

Results

Benthic community structure

Zebra mussel density differed significantly between years (ANOVA, $P < 0.001$), but there were no differences between the Upper (ULC) and Lower Lake Constance (LLC) (ANOVA, $P = 0.48$). For both sites the density of zebra mussels was about 10–20 fold higher in 2005 than in 2006 (Fig. 2a), resulting in a different environment for all the associated macroinvertebrates.

Consequently, the macroinvertebrate community composition (excluding *D. polymorpha*) differed between sampling sites and years (ANOSIM, $P = 0.001$), whereas the five replicates within each year and site were similar (Fig. 3). We also found marked differences in the benthic macroinvertebrate communities between ULC and LLC (dissimilarity $\sim 40\%$ for both years; Table 1). Chironominae and the caddisfly *Ecnomus tenellus* were primarily responsible for the observed differences in 2005,

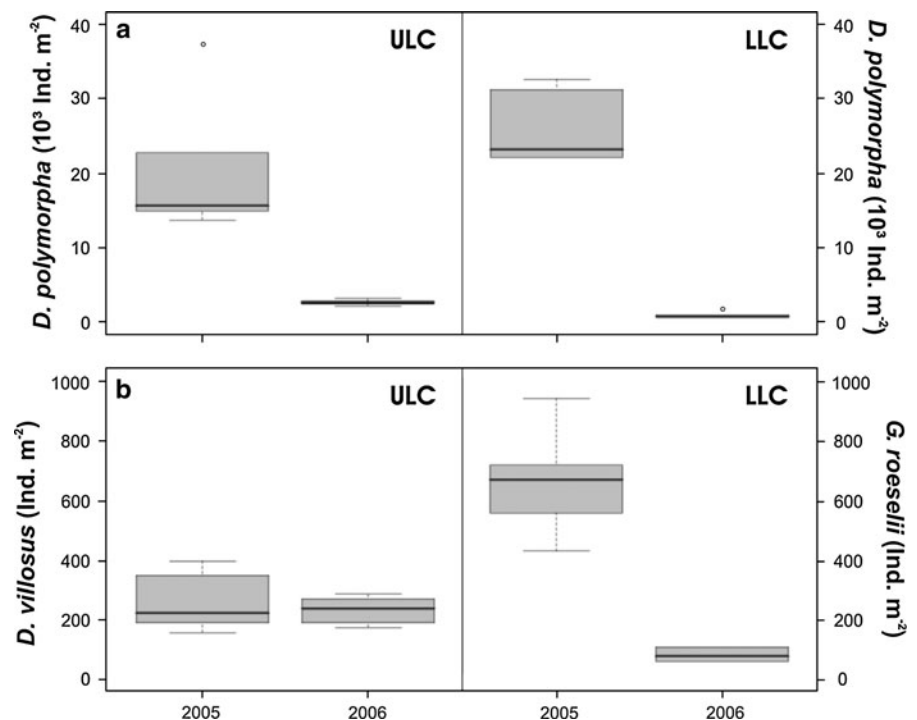
whereas it was the mayfly *Caenis* spp. in 2006 (Table 1). The shift in the benthic community structure between 2005 and 2006 was lower (dissimilarity $\sim 29\%$) for ULC in comparison to LLC (dissimilarity $\sim 35\%$). In LLC, differences between years were mainly caused by the decrease in abundance of Chironominae and *E. tenellus*, while in ULC it was primarily due to the decrease in abundance of *Caenis* spp. in 2006 (Table 1). The density of amphipods showed a similar pattern between years to the community as a whole. In ULC, the density of *D. villosus* was approximately 250 ± 100 individuals m^{-2} in both years (mean \pm SD; t test, $P = 0.56$; Fig. 2b). *G. roeselii* was not abundant at the sampling site in ULC. In LLC, *G. roeselii* decreased from 700 ± 200 individuals m^{-2} in 2005 to 90 ± 25 individuals m^{-2} in 2006 (t test, $P < 0.001$; Fig. 2b).

There was no difference in ambient water temperature between the two sites but there was a slight difference between years (2005: 13.6 to 13.7°C; 2006: 14.9 to 15.0°C).

Quantification of basal resources

The availability of the two major basal resources for the benthic food web, zebra mussel biodeposits

Fig. 2 Comparison of the median densities (\pm the upper and lower quartile) of **a** zebra mussels >5 mm; and **b** amphipods in Upper (ULC) and Lower Lake Constance (LLC) between the sampling years. The invasive *D. villosus* was only abundant in ULC, and the indigenous *G. roeselii* in LLC between sampling years



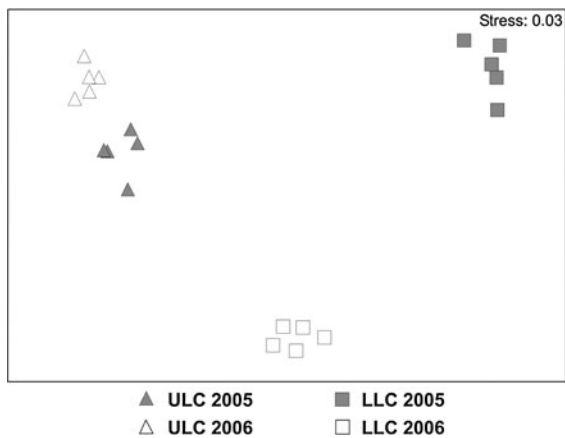


Fig. 3 Non-metric multidimensional scaling (nMDS) ordination plot of invertebrate densities, representing the benthic community structure (without *Dreissena polymorpha*) in the hard substrate habitat at both sampling sites and years

(based on the zebra mussel density) and epilithon, varied significantly between the two years (ANOVA: $P < 0.001$; Fig. 4; Table 2). Differences between sampling site were significant too (ANOVA: $P = 0.04$), but with a similar trend between the two years: in 2005, the calculated production of biodeposition material was three to five times higher than epilithon production (Fig. 4a), which implies that most of the available basal resource was provided by zebra mussel biodeposits. In 2006, the production of biodeposits was considerably lower at both sampling sites than in the previous year because of a lower

zebra mussel density (Fig. 2a). The epilithon production was more than three times higher than the biodeposition production, and thus the majority of basal resource was epilithic (Fig. 4b).

Stable-isotope analyses

We found a clear distinction between pelagic (i.e. seston) and benthic (i.e. epilithon) primary production stable carbon isotope values for both sampling sites and years, with a lower $\delta^{13}\text{C}$ value for seston because of reduced algal discrimination against ^{13}C in benthic habitats (France 1995a); $\delta^{15}\text{N}$ values were comparable between seston and epilithon (Fig. 5). The feeding strategy of Chironominae was comparable between the two years; the $\delta^{13}\text{C}$ did not vary and although the $\delta^{15}\text{N}$ was statistically different, the difference was $< 1\text{‰}$ (Fig. 5; Table 3). Differences in Chironominae stable isotope values between the sampling sites were significant, indicating slight differences in their feeding strategy. Due to the filter feeding of the mussels, zebra mussel $\delta^{13}\text{C}$ tracked that of the seston at both sampling sites and among years (Fig. 5). However, zebra mussel $\delta^{15}\text{N}$ decreased significantly at both sites from high values in 2005 to a level of primary consumer in 2006 (Table 3). Amphipods showed marked differences between years, but a similar pattern between the two sampling sites. Amphipods were ^{13}C -depleted, tracking the seston in 2005, but in 2006 reflected the

Table 1 Contribution of macroinvertebrate species/groups to measures of dissimilarity, and their densities (round to hundreds, mean \pm SD) in Upper Lake Constance (ULC) and

Lower Lake Constance (LLC) for two sampling years revealed by SIMPER analyses

| Site | Year | Dissimilarity (%) | Tax. group | Contribution (%) | Density (Ind./m ²) | |
|-------------------|------------------|-------------------|--------------------|------------------|--------------------------------|--------------------|
| | | | | | 2005 | 2006 |
| ULC | 2005 versus 2006 | 28.8 | <i>Caenis</i> spp. | 41.9 | 9,400 \pm 1,800 | 1,200 \pm 600 |
| | | | Chironominae | 22.5 | 11,900 \pm 2,900 | 15,700 \pm 2,200 |
| LLC | 2005 versus 2006 | 35.4 | Chironominae | 40.2 | 29,300 \pm 5,500 | 17,500 \pm 1,400 |
| | | | <i>E. tenellus</i> | 16.5 | 5,900 \pm 500 | 1,200 \pm 200 |
| | | | <i>Caenis</i> spp. | 14.7 | 7,100 \pm 2,900 | 1,000 \pm 100 |
| | | | | | LLC | ULC |
| ULC versus LLC | 2005 | 41.7 | Chironominae | 50.2 | 29,300 \pm 5,500 | 11,900 \pm 2,900 |
| | | | <i>E. tenellus</i> | 14.8 | 5,900 \pm 500 | 800 \pm 200 |
| | | | <i>Caenis</i> spp. | 51.6 | 1,000 \pm 100 | 1,200 \pm 600 |
| | 2006 | 39.0 | | | | |

Only species with a contribution $>10\%$ were included in the table to refer to the most important macroinvertebrates

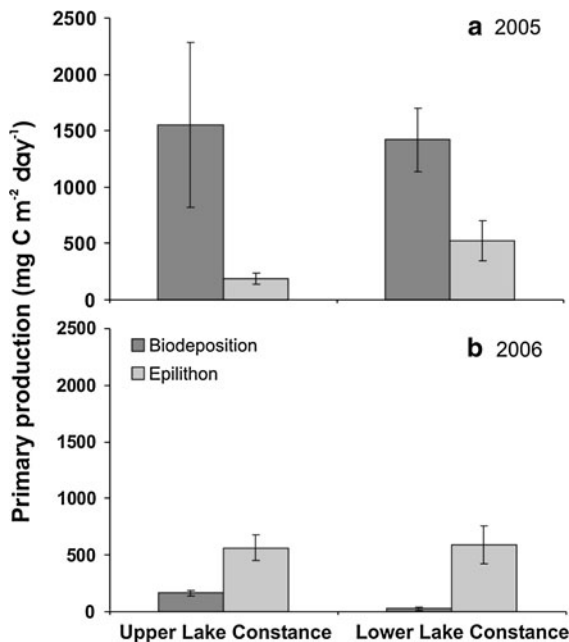


Fig. 4 Daily production rates (mean \pm SD) of zebra mussel biodeposition and epilithon, the two main benthic resources available in the hard substrate habitat. Values were estimated according to the current conditions at both sites during sampling in 2005 and 2006

Table 2 Results of analysis of variance (ANOVA) comparing type of production (biodeposition and epilithon), sampling site and sampling year; differences depending on these factors and their interactions were analysed

| Effect | F | Df | P |
|--------------------------|-------|----|---------|
| Production | 8.5 | 1 | 0.007* |
| Sampling site | 4.5 | 1 | 0.04* |
| Sampling year | 185.9 | 1 | <0.001* |
| Production * site | 70.5 | 1 | <0.001* |
| Production * year | 388.7 | 1 | <0.001* |
| Site * year | 53.2 | 1 | <0.001* |
| Production * site * year | 5.5 | 1 | 0.03* |

* Significant differences

values of epilithon more closely. The $\delta^{15}\text{N}$ of the amphipods decreased from ~ 15 to 7‰ from 2005 to 2006, equivalent to a decrease of two to three trophic levels (Fig. 5; Table 3). Both amphipod species showed a clear shift in their feeding strategy from an apparently high trophic position stemming from pelagic primary production in 2005 to a relatively lower trophic position based on benthic primary production in 2006 (Fig. 5; Table 3).

Dependence of feeding strategies on available basal resources

Combining the results, the stable isotope analyses and the estimation of the availability of the two basal resources demonstrated that the stable isotope composition of amphipods was positively related to the production of zebra mussel biodeposits, but not to the epilithon production (Table 4). The higher biodeposition production rates of zebra mussels in 2005 caused enriched nitrogen and a more pelagic signature in the amphipods. In contrast, regression analysis revealed no significant relationship between biodeposition or epilithon production and the stable isotope composition of Chironominae and *D. polymorpha*, respectively. This result indicates a strong dependence of the feeding strategy of the amphipods on the availability of zebra mussel biodeposits.

Discussion

Food web structure on hard substrates

Filtration by zebra mussels increases the amount of organic matter in the benthic zone, which has been suggested to lead to higher abundances of benthic macroinvertebrates (Stewart and Haynes 1994; Stewart et al. 1998). We hypothesized that the benthic food web structure would depend on temporal variation of the zebra mussel density, and that the organic matter biodeposited by zebra mussels represents a major resource for benthic invertebrates on hard substrates. In fact, the feeding strategy of amphipods depended on the availability of zebra mussel biodeposits; when most available, the stable isotope composition clearly reflected a pelagic-derived source. Hence, amphipods benefited significantly from zebra mussel biodeposits.

Previous studies have demonstrated that biodeposited material affects habitat choice and growth of amphipods (González and Burkart 2004; Gergs and Rothhaupt 2008a, b). In nature, the benefit to macroinvertebrates has been recorded as increased density in the presence of increased structural substrate complexity (mussel shells) and living mussels (Stewart and Haynes 1994; Silver Botts et al. 1996; Mörtl and Rothhaupt 2003). It has been shown that the diet of the amphipod *G. fasciatus* can be based, at least

Fig. 5 Stable isotope bi-plots ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of primary producers and macroinvertebrates in the hard substrate habitat of Upper and Lower Lake Constance in 2005 and 2006. *Errors bars* indicate standard deviation

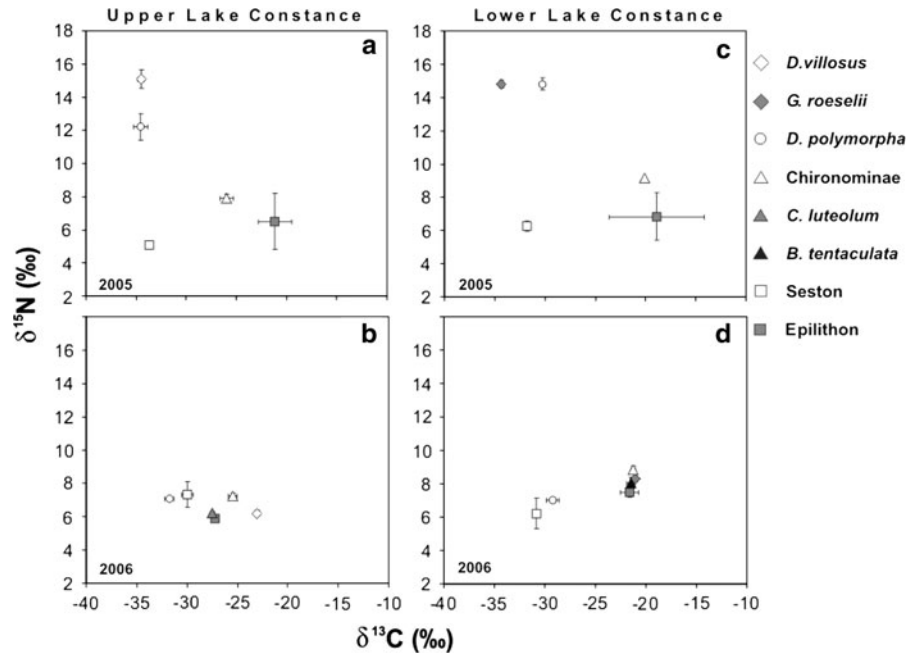


Table 3 *P* values for comparison of mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data ($n = 5$) between the two sites in Upper (ULC) and Lower Lake Constance (LLC) and sampling years; differences were

analysed by two-way ANOVAs and significance levels were adjusted by *Bonferroni* correction for multiple comparisons

| Species | <i>P</i> values [$\delta^{13}\text{C}$ (‰)] | | | <i>P</i> values [$\delta^{15}\text{N}$ (‰)] | | |
|----------------------|--|---------|-----------|--|---------|-----------|
| | Site | Year | Site*Year | Site | Year | Site*Year |
| Amphipoda | <0.001* | <0.001* | <0.001* | <0.001* | <0.001* | <0.001* |
| <i>D. polymorpha</i> | <0.001* | <0.001* | 0.02 | <0.001* | <0.001* | <0.001* |
| Chironominae | <0.001* | 0.13 | <0.001* | <0.001* | <0.001* | 0.07 |
| Epilithon | 0.02 | 0.007* | 0.22 | 0.14 | 0.99 | 0.17 |
| Seston | <0.001* | <0.001* | <0.001* | 0.54 | <0.001* | <0.001* |

* Significant differences after correction. All epilithon samples and seston samples from ULC were replicated four times, seston samples from LLC three times

Table 4 Dependence of amphipod feeding strategy on the available basal resources in the hard substrate habitat

| Dependent variable | Biodeposition [$\text{mg C m}^{-2} \text{day}^{-1}$] | | | Epilithon [$\text{mg C m}^{-2} \text{day}^{-1}$] | | |
|---------------------------|--|-------|----------------|--|-------|----------------|
| | Regression coefficient | r^2 | <i>P</i> value | Regression coefficient | r^2 | <i>P</i> value |
| $\delta^{13}\text{C}$ [‰] | -0.99 | 0.99 | 0.003* | 0.69 | 0.47 | 0.31 |
| $\delta^{15}\text{N}$ [‰] | 0.97 | 0.94 | 0.03* | -0.68 | 0.46 | 0.32 |

There was a significant dependence of the $\delta^{13}\text{C}/\delta^{15}\text{N}$ of amphipods upon zebra mussel biodeposition production, but not epilithon production indicated by linear regression analyses. Regressions for Chironominae and zebra mussels resulted in non significant results

* Significant regression

partly, on zebra mussel biodeposits (Limén et al. 2005). This is strongly supported by our data, demonstrating that organic matter biodeposited by

zebra mussels forms the basis of amphipod diet under natural conditions but is clearly a function of zebra mussel density. High zebra mussel biodeposition rates

increased the availability of resources for the benthic invertebrates, resulting in a greater secondary production. As a possible consequence, higher abundances of predators can be found when zebra mussels comprise a part of the benthic community (Dusoge 1966). Our stable isotope analyses have provided new insights into the feeding strategies of amphipods under field conditions. In particular, the low $\delta^{15}\text{N}$ of the invasive *D. villosus* in 2006 was similar to the values of a typical primary consumer (e.g. the mayfly *C. luteolum* or the snail *B. tentaculata* in 2006; Fig. 5). This is in contrast to other studies, where *D. villosus* is characterised as a strong predator (Dick and Platvoet 2000; Dick et al. 2002; Kinzler and Maier 2003). Predation by amphipods also tends to increase with water temperature (van der Velde et al. 2009). However, we could not ascribe the decline in amphipod $\delta^{15}\text{N}$ from 2005 to 2006 to water temperature. Furthermore, the specific prey organisms of amphipods remain unclear, because no other benthic primary consumers with a ^{13}C -depleted carbon value except for *D. polymorpha* were found in autumn 2005. Even if *D. villosus* appeared one trophic level higher than the zebra mussel in 2005, it is unlikely that the invasive amphipod fed on the mussels directly because *D. villosus* is strongly associated with *D. polymorpha* as a habitat (Hesselschwerdt et al. 2008).

Chironomids are often assumed to benefit from zebra mussel invasion and are supposed to provide a link to higher trophic levels (Mitchell et al. 1996; Silver Botts et al. 1996). However, our stable isotope data show that pelagic resources contributed approximately 20–50% to diet of chironomids (see Fig. 5), i.e. rather little dependence on zebra mussel biodeposition material in autumn. However, differences in the importance of the mussels to chironomids might occur on a shorter temporal scale than investigated in our study. It is most likely that the importance varies seasonally and is greatest during summer, when zebra mussel biodeposition rate is highest (Gergs et al. 2009). Mörthl and Rothhaupt (2003) found an increased chironomid density on substrates with living zebra mussels in comparison to substrates with empty mussel shells in a field experiment during summer. In LLC, the differences in the benthic macroinvertebrate community structure between the two years were mainly caused by Chironominae, the mayfly *Caenis* spp., and the caddisfly *E. tenellus*, with higher abundances in 2005 than in 2006

(Table 1). This strongly suggests that these latter two taxa were also linked to a *Dreissena*-biodeposition based food web.

Stable isotope analyses of zebra mussels revealed unexpectedly high $\delta^{15}\text{N}$ in 2005. The diet of zebra mussels can contain considerable amounts of detritus (>50%), beside the filtered seston (Garton et al. 2005), which could lead to an ingestion of detrital material. For example, the microbial activity and bacterial density in biodeposited material of zebra mussels can increase within a few days and accelerate its degradation (Izvekova and Lvova-Katchanova 1972; Roditi et al. 1997). Simultaneously, a microbiocenosis consisting of ciliates, nematodes and rotifers may develop (Walz 1978b). Hence, we speculate that the increased nitrogen cycling subsequently resulted in an elevation of zebra mussel $\delta^{15}\text{N}$ by feeding on their own biodeposits.

Comparison of the lake basins

The benthic community structure changed markedly in both lake parts between the two years in response to zebra mussel density. That mussel density is normally controlled through predation by diving ducks in some habitats, reducing biomass by 90% in Lake Constance during winter. Juvenile mussels suffer less from diving duck predation, maintaining populations in shallow areas, and constitute the upcoming summer population (Werner et al. 2005). However, the major decline in the zebra mussel density between 2005 and 2006 was due to an atypical low water level of the unregulated Lake Constance during a particularly cold and dry winter. As a consequence, parts of the littoral area were exposed to desiccation and caused mortality of the attached zebra mussels (R. Gergs, personal observation). However, our sampling sites at one metre below mean low-water level were flooded all the winter, and should consequently harbour a more stable community (Baumgärtner et al. 2008). Even if the impact of the low water level during the winter 2005/2006 cannot be excluded completely, the difference in the benthic communities in our study are for the most part attributed to effects caused by the zebra mussels (i.e. shelter and biodeposits).

In many studies, the density of gammarid amphipods was found to be positively related to zebra mussels (e.g. Wisenden and Bailey 1995). We found

the density of the dominant amphipod *G. roeselii* was also related to the production of zebra mussel biodeposits only in LLC (Figs. 3, 5), whereas in ULC, the density of the invasive amphipod *D. villosus* was constant and not connected to the production of zebra mussel biodeposits. *D. villosus* demonstrates trophic plasticity (Platvoet et al. 2009) and thus, is likely to be better able to cope with changing conditions (independent of deposition rate) when compared to *G. roeselii*.

Changes in the whole macroinvertebrate community were also observed (Fig. 3; Table 1). In comparison to LLC, differences between years were low in ULC. As zebra mussel density was similar for both sites within year, other factors besides the impact of zebra mussels, were important in determining community structure in both lake basins. The sampling site in ULC on a northwest shore is relatively sheltered. In comparison, the sampling site in LLC on an east shore is more wind-exposed, and therefore more turbulent, which influences the benthic community structure (Scheiffhacken et al. 2007). Zebra mussels can tolerate and stabilize turbulent conditions simply by the physical presence of their shells, which may facilitate settlement of other invertebrates on soft as well as on hard substrates (Dusoge 1966; Wisenden and Bailey 1995; Bially and MacIsaac 2000). The differences in the benthic community in LLC were an interactive effect of zebra mussel density (via stabilisation) and wind exposure, whereas the stabilising effect of zebra mussels was of less importance in the more sheltered sampling site in ULC.

Conclusion

Our study clearly reveals the significance of variation in zebra mussel density and biodeposits for the benthic food web structure and benthic invertebrate community under natural conditions in Lake Constance. The feeding strategy of amphipods was significantly related to the availability of zebra mussel biodeposits. The higher biodeposition production rates of zebra mussels caused a higher trophic level and a more pelagic stable isotope signature in the amphipods. Additionally, at the wind-exposed sampling site in LLC, the benthic community showed a clear shift to high densities of *Caenis* spp.,

Chironominae and *E. tenellus* at high availability of zebra mussel biodeposits, suggesting they benefitted from biodeposit resource use. Hence, our results strongly support the hypothesis that the biodeposition of organic matter by zebra mussels provides a basis of a benthic food web dependent upon mussel density (Stewart and Haynes 1994; Mitchell et al. 1996).

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