Effects of the invasive Asian clam *Corbicula fluminea* on the littoral communities of Lake Constance

Dissertation

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Falls Gott die Welt geschaffen hat,
war seine Hauptsorge sicher nicht,
sie so zu machen,
dass wir sie verstehen können

Albert Einstein

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1 General Introduction

The composition of benthic communities in freshwater systems depends on large-scale factors, such as climate, geology, or geographical distribution (Johnson & Goedkoop 2002) and fauna of littoral zones among lakes differs due to diverse abiotic variables such as morphometry, productivity, water chemistry and temperature (Jackson & Harvey 1993, Bailey *et al.* 1995, Tolonen *et al.* 2001). However, habitat structure, waterdepth and disturbance have the greatest impact on the variability of benthic communities (Johnson & Goedkoop 2002, Scheifhacken 2008, Baumgärtner *et al.*, in press). Additionally, the extent of biotic factors such as predation, competition, life-history traits and facilitation can control the patterns in the macroinvertebrate community (Gilinsky 1984, Johnson *et al*. 1996, Jackson & Harvey 1993, Bruno *et al.* 2003, Mörtl *et al.*, in press).

However, in the current times of global trade, biological invasions are predicted to be the major threat in freshwater biodiversity in the future (Sala *et al.* 2000). Anyhow, most exotic species do not successfully establish or do only have little impact on natural communities (Williamson & Fitter 1996). Non-indigenous species, that use so far unoccupied niches or greatly differ from native species in resource use have the greatest potential to change indigenous communities. The impact of established invaders on benthic communities and even the whole ecosystem can be severe (Strayer 1999, Spencer *et al*. 1991). Newly invaded taxa often increase their populations in a spectacular way, but the outcome of such an invasion is difficult to predict (Lodge 1993). On the one hand, invasive species can quickly replace native or previously arrived taxa (Dick & Platvoet 2000, Bachmann *et al.* 2001, den Hartog *et al.* 1992), but on the other hand, established communities can also facilitate from non-indigenous species (Stewart *et al.* 1998, Mörtl & Rothhaupt 2003).

Lake Constance was subject to many substantial biological invasions in the past 50 years. Until 2008, 16 benthic invertebrate species arrived in Lake Constance (Rey *et al.* 2005 and additions). Most important invasions were that of the gastropod *Viviparus ater* in 1956 (Turner *et al.* 1998), the zebra mussel *Dreissena polymorpha* in the mid-1960s (Siessegger 1969), the New Zealand mudsnail *Potamopyrgus antipodarum* in the early 1970s (Frenzel 1979), the crayfish *Orconectes limosus* in the late 1980s (Hirsch *et al.*, in press) as well as the recent arrivals of the amphipod *Dikerogammarus villosus* in 2002 (Mürle *et al.* 2004, Mörtl *et al*. 2005), the Asian clam *Corbicula fluminea* between 2000 and 2002 (Werner & Mörtl 2004), and the mysid *Limnomysis benedeni* in 2006 (Fritz *et al.* 2006).

The zebra mussel invasion to Lake Constance was subject to intensive studies (e.g. Siessegger 1969, Jacoby & Leuzinger 1972, Walz 1973, 1974, 1975, Suter 1982a, b, c, Cleven & Frenzel 1993, Mörtl & Rothhaupt 2003, Werner *et al.* 2005). *D. polymorpha* had severe ecological consequences for the benthic community (Mörtl & Rothhaupt 2003, Mörtl *et al.*, in press) and for mussel-consuming waterbirds that altered their migration pattern (Suter 1982a, b). Apparently in response to the mussel, the waterbird population increased by three- to fourfold since the early 1960s, making Lake Constance one of the most important staging and wintering sites for waterbirds in central Europe (Stark *et al.* 1999). However, further newcomers to Lake Constance remained greatly disregarded in the last century. Only the most recent wave of biological invaders to Lake Constance is focus of several studies including my own work.

Especially newcomers that change substrate qualities, e.g., bivalves that provide persistent and often abundant physical structures via the production of shells (Strayer *et al*. 1999, Gutiérrez *et al*. 2003), have a great impact on benthic communities (Dittman 1990, Karatayev *et al*. 1997, Stewart *et al*. 1998, Robinson & Griffith 2002, Nalepa *et al*. 2003). Bivalves that dominate the biomass of the benthic community can exert control over ecosystem structure and function as dominant filter-feeder (Welker & Walz 1998, Strayer *et al*. 1999). Bivalves of the genus *Corbicula* belong to the most invasive species (Morton 1979) that can largely decrease and control phytoplankton in lakes and rivers and influence the pelagic nutrient cycling (Cohen *et al*. 1984, Hwang *et al*. 2004, Cahoon & Owen 1996, Vaughn & Hakenkamp 2001). The grazing effect of *Corbicula leana* in a mesotrophic and a hypertrophic lake was stronger than that of the zooplankton community (Hwang *et al.* 2004). Further particles such as bacteria and particulate organic matter can also be removed from the pelagial. Filtration, nutrient excretion and bentho-pelagic coupling by biodepositing faeces and pseudofaeces are the main water column processes completed by *Corbicula fluminea* (Lauritsen & Mozley 1989, Vaughn & Hakenkamp 2001).

Despite its tremendous effects on pelagic habitats, only little is know about the influence of *C. fluminea* on nutrient and organic matter cycling in sediments (Hakenkamp & Palmer 1999). Although a high impact of burrowing bivalves on benthic processes is postulated (Vaughn & Hakenkamp 2001), the impact of *C. fluminea* on benthic organisms is rarely studied (c.f. Karatayev *et al*. 2005). Even most recent studies focus on the life cycle of *C. fluminea* (Sousa *et al.* 2008). Anyhow, *C. fluminea* is known to reduce bacteria and flagellates in the sediments by pedal feeding (Hakenkamp *et al.* 2001), but their impact on macroinvertebrates seems weaker (Karatayev *et al.* 2003). The decline of unionids in the United States came along with the invasion and the dominance of *C. fluminea* (Vaughn & Hakenkamp 2001), but evidence that this decline can be attributed to *C. fluminea* is weak (Karatayev *et al*. 2005, Vaughn &

Spooner 2006). Asian clam *C. fluminea* can reach very high densities and can build up to 90% of the biomass of the littoral community (Cherry *et al.* 1980, Meister 1997, Karatayev *et al.* 2003). By this, it could affect native species or even already established invaders.

I hypothesize that *C. fluminea* mediates biotic and structural changes that will influence the benthic community. Therefore, I studied the effect of the newly established bivalve on littoral communities of sandy habitats in lake Constance by field monitoring and by the use of *in situ* and laboratory experiments. I postulated that (1) valves of *C. fluminea* can alter the substrate characteristics; (2) hard substrate preferring taxa are supported by these changes; (3) zebra mussels will colonize so far unsettled sandy substrates by attaching to *C. fluminea* as biogenic hard substrate; and (4) biodeposition of faeces and pseudofaeces of *C. fluminea* can facilitate benthic taxa.

Short invasion history of *C. fluminea*

Originating mainly from Southeast Asia, *Corbicula fluminea* was introduced to North America in the early 20th century (McMahon 1982), where it spread and dispersed widely, now inhabiting freshwaters of nearly the whole USA. In the late 1960s, South America was also colonized by *C. fluminea*, where it is still spreading (Ituarte 1981, Darrigran 2002). Then, in the 1980s *Corbicula* spp. invaded Europe (Mouthon 1981) via ballast of ships from North America. Since the first detection it spread quickly across European waterways (den Hartog *et al*. 1992). In Germany, it quickly replaced the zebra mussel as dominant mollusk in large rivers (Bachmann *et al*. 2001, Tittizer *et al*. 2000). Within 15 years, *C. fluminea* conquered the whole River Rhine up to the border of Switzerland (Turner *et al*. 1998), where cargo shipping ends. *C. fluminea* arrived at Lake Constance (Central Europe) in the early 2000s (Werner & Mörtl 2004). This settlement is isolated from other occurrences.

The first individuals of *C. fluminea* in Lake Constance were discovered at the Rohrspitz (Vorarlberg, Austria) in 2003 (Fig. 1.1). Within one year, the clams spread between the two inlets of the Rhine River into Lake Constance. At that time the first field sampling was conducted. During the low water in winter 2005/2006, further occurrences of *C. fluminea* were discovered at the southern shore in the Bay of Rorschach (Switzerland) and at the northern shore between the cities of Bregenz, Lindau and Langenargen. In 2007, *C. fluminea* spread at the northern shore up to Immenstaad and an isolated appearance in the western part of the lake close to Konstanz-Egg was discovered (Fig. 1.1).

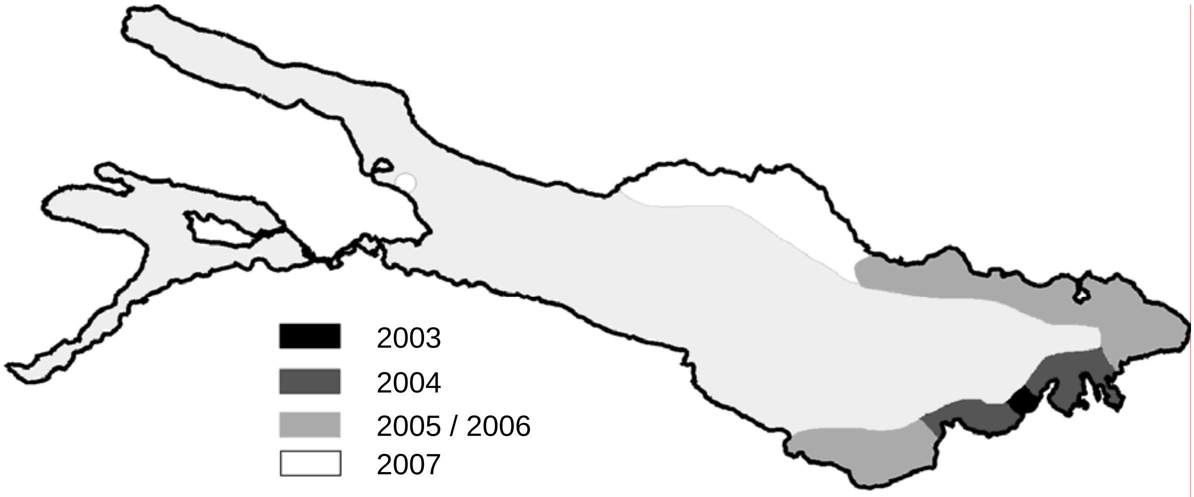

Fig. 1.1. Invasion of *Corbicula fluminea* in Lake Constance. Our study site Rohrspitz was in the area of the discovery of 2003

Study aims

My thesis assesses if the invasion of *Corbicula fluminea* to Lake Constance changes the benthic community and if single taxa respond to the clam. As habitat gradients and seasonal changes in the community can overlap with biological signals (Reid *et al*. 1995), it is important to consider how macroinvertebrates distribute temporally and spatially. Benthic macroinvertebrates show extremely heterogeneous and patchy distributions (Wetzel 2001) and communities among sites differ greatly (Scheifhacken 2008). To exclude horizontal gradients caused by macrophyte stands, lake inflows, different substrates or wind exposure, that can potentially influence the community structure (Röck 1999, Tolonen *et al*. 2001, Strayer & Malcom 2007), we focused on one study site with high densities of *C. fluminea*.

Recent studies in Lake Constance that focused on abiotic and biotic interactions in benthic communities lead to a better knowledge of spatial and temporal patterns (Baumgärtner 2004, Mörtl 2005, Scheifhacken 2008). Baumgärtner & Mörtl developed a quantitative sampling technique that can deal with the methodological problems that occur in the wind-swept littoral of lentic systems through roughly bi-directional water currents. To study the biotic interactions on soft bottomed habitats in Lake Constance, I established an *in situ* monitoring of the benthic community using this sampler. All macroinvertebrate taxa at the study site Rohrspitz were sampled along a depth gradient between 2004 to 2007. Additionally, I analyzed the biotic and structural effects of *C. fluminea* in a field experiment and in laboratory experiments. As unionids became very rare in

Lake Constance, I could not investigate their response to *C. fluminea*.

The thesis starts with two descriptive studies about the results of the field monitoring. During the second study winter, a centennial low water in association with low water temperatures lead to an unexpected mass mortality of *C. fluminea*, what had severe consequences for its population development and dispersal. Based on this event, described in Chapter 2, the structural role of valves of *C. fluminea* became a focal point of this study, as impressive masses of valves of dead clams were scattered on the lake bottom. A mesocosm experiment that excluded predation effects was conducted simultaneously to document the factors responsible for the mass mortality.

The main outcome of the routine sampling programme, that retrieved data on spatial and temporal patterns of *C. fluminea* and the associated macroinvertebrate community, is subject of Chapter 3. Herein, I describe the development and the characteristics of the *C. fluminea* population in respect to different abiotic factors such as water level fluctuations and water temperature. Further, Chapter 3 focuses on the composition of the benthic community and its temporal and spatial patterns. I assumed that different biomasses of *C. fluminea* within the samples will affect the associated macroinvertebrates. For detailed analyzes, I grouped the invertebrates into two groups: (1) epifaunal taxa that live on the surface of the sediments and (2) infaunal taxa living in the sediments.

My first study was an *in situ* experiment that investigated the effects of live *C. fluminea* and their valves on the benthic assemblage compared to bare sand (Chapter 4). I posed the question if the surface increase by the valves, that lie on the sediment, can play a substantial role in structuring benthic communities and if living clams that burrow completely in the sediment have an impact on the settlement of benthic invertebrates.

Chapter 5 describes how each of ten different macroinvertebrate taxa, that are typical for the littoral zone of Lake Constance, respond to *C. fluminea* in habitat choice experiments. I hypothesized that these benthic organisms might prefer *C. fluminea* over sand in pairwise habitat-choice tests. I distinguished between biotic effects of living burrowed *C. fluminea* (without structural effect) and the structural importance of their valves lying on sand. Living clams were either starved (only bioturbation) or fed with algae (biodeposition, bioturbation and nutrient reallocation).

Chapter 6 focuses on interactions between the two invasive bivalves *D. polymorpha* and *C. fluminea.* During the field sampling it became apparent that *D. polymorpha* uses *C. fluminea* as settling core, so I decided to study the effects of this interaction on the individual growth in laboratory experiments. I hypothesized that the infestation by *D. polymorpha* might have negative consequences for the growth of *C. fluminea*, but that the growth of epibiotic *D. polymorpha* will not be affected.

2 Mass mortality of the invasive bivalve *Corbicula fluminea* induced by a severe low water event and associated low water temperatures

Stefan Werner & Karl-Otto Rothhaupt

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Abstract

The Asian clam *Corbicula fluminea*, originating from Southeast Asia, was first recorded in Lake Constance in 2003 and developed local mass occurrences afterwards. Effects of harsh winter conditions in 2005/2006 associated with a strongly decreasing water level were studied at 3 different depths at and below the mean low water level (MLL, MLL -1 m and MLL -3 m). Low winter temperatures produced a massive die-off of the *C. fluminea* population. The mortality of the clams was size-class and depth dependent. At the mean low water level (MLL), all clams died because of lying dry. However, at MLL -1 m and at MLL -3 m, mortality was a consequence of water temperatures around 2 °C for nearly 3 months. At MLL -3 m, clams > 5 mm died later than young clams < 5 mm and later than clams of all sizes at MLL -1 m. But in late spring even the clams > 5 mm at MLL -3 m were dead and only about 1% of the overall population of *C. fluminea* survived the winter conditions until spring 2006.

Lethal effects of low water temperatures on *C. fluminea*, that may become effective only after a time lag, were corroborated in an outdoor mesocosm experiment with constant water level and without predation.

Keywords water level fluctuation, invasive, bivalve, winter mortality, low water, population

Introduction

Originating mainly from Southeast Asia, *Corbicula fluminea* was introduced to North America in the early 20th century (McMahon 1982). Then, in the late 1960s South America was also colonized by *C. fluminea*, where it is still spreading (Ituarte 1981, Darrigran 2002). Europe was invaded in the 1980s (Mouthon 1981, bij de Vaate & Greijdanus-Klaas 1990, den Hartog *et al.* 1992). Due to its meanwhile almost worldwide distribution supported by men and due to its natural dispersal characteristics, clams of the genus *Corbicula* belong to the most invasive taxa (Morton 1979). They mainly establish in the southern parts of the temperate zone, in the subtropics and the tropics, since its northern range is limited by cold temperatures (≤ 2 °C; Britton & Morton 1979, Karatayev *et al.* 2005).

After its invasion, *C. fluminea* became the dominant mollusk in large German rivers (Bachmann *et al.* 2001). The entire River Rhine from the mouth to Switzerland, the upper limit of cargo shipping (~ 850 river km), was colonized within 15 years (Turner *et al.* 1998).

In 2003, *C. fluminea* was first recorded in pre-alpine Lake Constance (Werner & Mörtl 2004), where this clam can meanwhile constitute up to 90% of the biomass of the littoral community (Chapter 3). This settlement is isolated from other occurrences of this species and may therefore be caused by men (Werner & Mörtl 2004).

The catchment area of oligotrophic Lake Constance (Central Europe) is largely dependent on the unregulated alpine system of the Rhine River. Generally, the lake level reaches a minimum at the end of February. Afterwards, the water level is rising due to increased precipitation and snowmelt in spring, leading to a maximum in June/July. By this, the water level annually fluctuates within 2 m (Jöhnk *et al.* 2004). We wanted to observe if clam densities are affected by low temperatures combined with low water levels during winter. The specified sampling period turned out to be particularly interesting, because the winter conditions in 2005/2006 were exceptionally harsh with water levels decreasing below the usual minimum values.

Material and methods

Study area and sampling

For Lake Constance, *C. fluminea* was first recorded in a large, sandy shallow-water zone called Rohrspitz near the city of Bregenz (Werner & Mörtl 2004), where, after two years, the clams occurred in high densities. Therefore, we chose this site (E 9°37′/N 47°30′) for sampling. The substrate consisted of fine sand with a grain size of 200–630 μm (90%) and coarser sand with a grain size of 630 μm–2 mm (10%).

We studied the development of the clam population at 3 different depths related to the mean low water level (264 cm): MLL, MLL -1 m, and MLL -3 m. Sampling dates in 2005/2006 were September 20th, December 13th, March 16th and June 27th. Daily mean water level and water temperatures were continuously received from the water gauge measuring site at the harbor in Bregenz (August 1st 2005 until July 31st 2006; gauge zero is 391,89 m NN). Water temperature was measured 50 cm below the water surface (lowest water depth: 228 - 50 cm).

Field sampling methods and laboratory analyses

The chosen depths were located using GPS and characteristic landmarks. Asian clams were collected by Scuba divers using an infralittoral suction sampler (Mörtl 2005) covering a sampling area of 625 cm^2. Three replicates were taken at each depth. In the laboratory, sampled mussels were fixed in 95% ethanol after each sampling day. Juvenile and adult clams were separated from sediment by the use of sieves with three mesh-sizes (250 µm, 1mm, 2 mm). Clams were grouped into two different size classes: 1. clams < 5 mm (juveniles of the year), and 2. older clams > 5 mm by using an electronic calliper (Preisser, Digi-Met).

Mesocosm Study

To rule out effects of water level fluctuation and predation on survival of *C. fluminea*, we conducted a study at the Limnological Institute in Konstanz-Egg in an outdoor mesocosm with a size of 2 x 2 x 1 m^3 and constant water level. We recorded the impact of natural winter temperatures on a *C. fluminea* population from the study site. We added 1331 *C. fluminea* > 5 mm and, additionally, two individuals of the native unionid *Anodanta cygnea* (shell lengths: 6.3 and 6.9 cm, respectively) to the mesocosm. Water temperatures were recorded by a HOBO Pendant Temperature/Light Data Logger (Part # UA-002-XX) from December 23rd to May 3rd. Living clams were counted on December 23rd, March 15th and June 15th.

Data analyses

Clam abundance was reported as ind. m^{-2} (mean ± standard error). To achieve homogeneity of variances, all values were logarithmically transformed [ln (x + 1)] and checked with the Hartley, Cochran, Bartlett Test (p = 0.05). Data were distributed normally. Mussel density changed with time and water depth. Differences as well as interactions time x depth were tested with two-way ANOVA. Subsequently, Tukey-HSD *post-hoc* tests were conducted. All statistical analyses were conducted with Statistica, Stat. Soft. V. 99.

Results

Field Study

Abiotic factors

Water temperature and water level fluctuated strongly within the year (Fig. 2.1). During January 2006, the shallow water zone at Rohrspitz was covered with ice. Water temperature at Bregenz were below 4 °C for nearly 4 months (Dec – Mar) and only rose slowly in spring. Water achieved the 10 °C threshold as late as April 19th. Mean monthly water temperatures at Bregenz were on average 1.7 °C lower than during the preceding 6 winters (data from Wasserwirtschaftsamt Vorarlberg). In summer, water temperatures reached 25 °C in late July (Fig. 2.1). After a strong increase in August 2005 (55 cm within 24 h), water level continuously decreased until February 15th, when a centennial low water with a level of 228 cm above 391.89 m NN (gauge zero) was recorded. The water level was then only 2 cm above the absolute lowest water level of Lake Constance since the beginning of registration in 1850 (Internationale Gewässerschutzkommission für den Bodensee, 2006). Afterwards, the water level rose until June, when 410 cm were achieved. During the whole sampling period, the water levels remained below the mean monthly water levels of the preceding years.

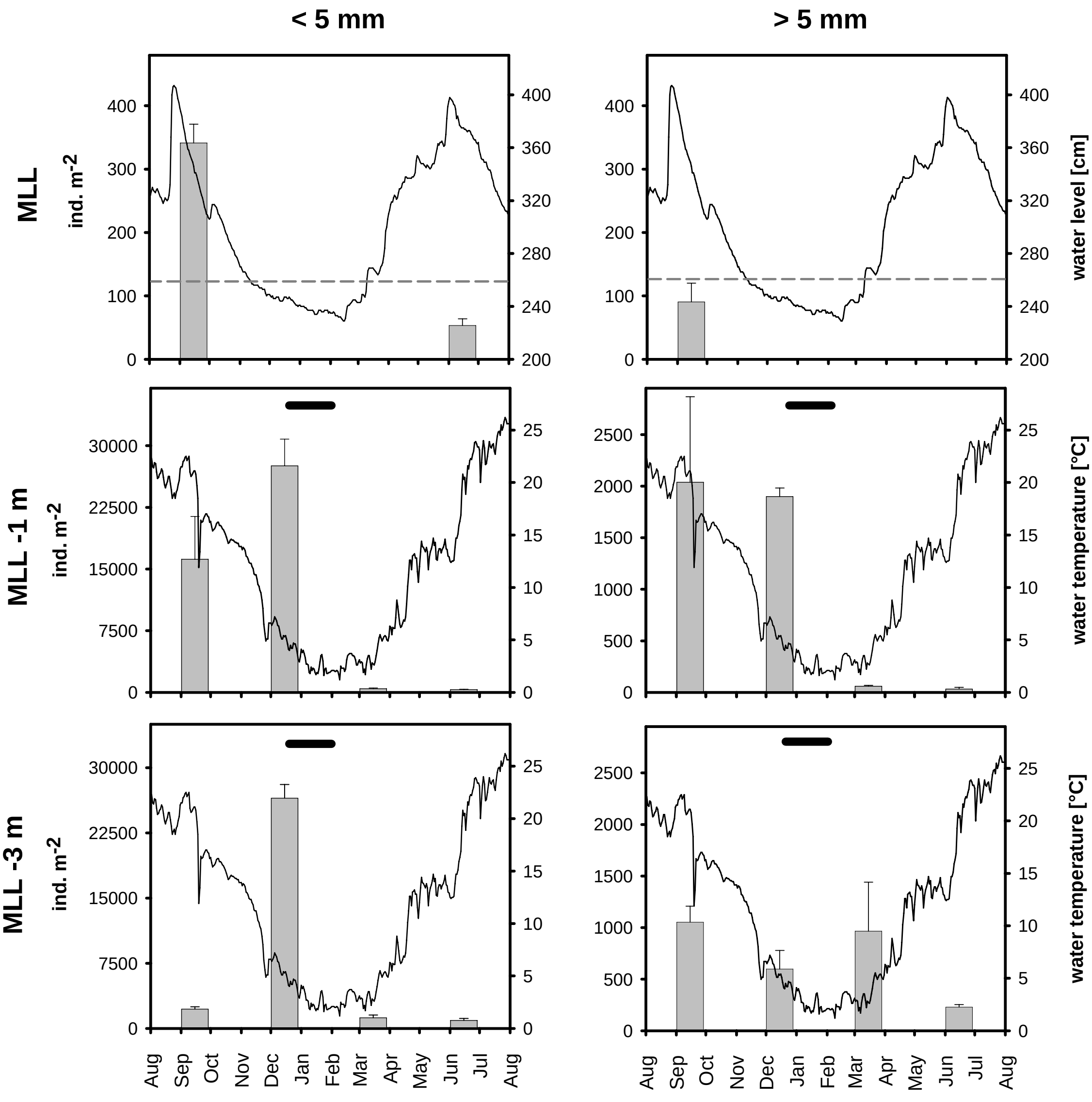

Fig. 2.1. Changes in *Corbicula fluminea* densities + SE for clams < 5 mm and > 5 mm (bars) for the 3 different depths MLL, MLL -1 m and MLL -3 m from Sept 2005 to June 2006. The black lines indicate the water level (upper two graphs) and the courses of water temperatures at Bregenz (lower 4 graphs). Dashed grey line marks water level when MLL fell dry. Solid black bar: ice cover at study site Rohrspitz.

Development of the clam population

In each sampling month population densities of *C. fluminea* were significantly different at the three depths (Tab. 2.1). Therefore, abundance changes over time were regarded separately for different depths. At **MLL,** abundance of *C. fluminea* was the lowest of all depths. In September, 91 ± 30 older clams (> 5 mm) m^{-2} and 341 ± 30 young clams (< 5 mm) m^{-2} were recorded. Then all clams died when the substrate dried up. Until June, juvenile clams re-colonized this site in low densities (53 ± 11 ind. m^{-2}; Fig. 2.1).

At **MLL -1 m,** clams > 5 mm reached the highest mean abundance of the study area in September and December (2037 ± 829 and 1899 ± 83 ind. m^{-2}, respectively). *C. fluminea* < 5 mm increased significantly during autumn ($p < 0.001$) and reached a maximum of 27,563 ± 3234 ind. m^{-2} in December. During winter, MLL -1 m did not dry up, the lowest water depth recorded at this site was at least 65 cm. Nevertheless, in this depth the clam population dropped down significantly (Fig. 2.1, Tab. 2.1). Abundance of both size classes of *C. fluminea* (> 5 mm and < 5 mm) decreased from December to March. Only ~1% of the Asian clam population remained in late spring (32 ± 16 ind. > 5 mm m^{-2} and 331 ± 47 ind. < 5 mm m^{-2} in June). There were no differences between abundances in March and June (Fig. 2.1, Tab. 2.1).

Abundance of clams > 5 mm at **MLL -3 m** did not show significant changes from September (1052 ± 156 ind. m^{-2}) to March (965 ± 475 ind. m^{-2}; Fig. 2.1). However, abundance decreased afterwards (229 ± 23 ind. m^{-2}; $p = 0.014$), and in June, the soft bodies of recently died *C. fluminea* floated in the water. Abundance of small clams < 5 mm significantly increased from 2228 ± 274 ind. m^{-2} in September to 26,491 ± 1589 ind. m^{-2} in December ($p < 0.001$). But then, in contrast to older clams, they significantly decreased already till March (1227 ± 310 ind. m^{-2}) and abundance remained constant till June (928 ± 236 ind. m^{-2}; Fig. 2.1).

Mesocosm study

Abiotic factors

In the mesocosm with constant water level, water temperatures were constantly below 4 °C from December to mid March and for nearly 2 months below 2 °C. An ice cover was observed between Dec 29th and mid February. Temperature began to rise in early April and achieved the 10 °C-threshold on April 15th. Afterwards, water temperature quickly increased (Fig. 2.2).

Development of the clam population

From 1331 clams > 5 mm in mid December only 150 ind. survived till March 15th. Although water temperatures increased afterwards, mortality of residual clams went on as in the lake: only one of the remaining 150 ind. survived till June (Fig. 2.2). Thus, only 0.1% of the exposed *C. fluminea* population survived. In contrast to the Asian clams, the native unionid *A. cygnea* survived these conditions.

Table 2.1. Results of two-way-ANOVA for density differences of young (< 5 mm) and older (> 5 mm) *Corbicula fluminea* over depth and its changes over time (α= 0.05).

Corbicula	depth	time	effect	F	df	p
> 5 mm	all	all	time x depth	26.845	6	< 0.0001
	all	all	depth	443.593	2	< 0.0001
	all	all	time	91.469	3	< 0.0001
	MLL	all	time	100.957	3	< 0.0001
	MLL -1	all	time	54.422	3	< 0.0001
	MLL -3	all	time	5.675	3	0.0184
	all	Sep	depth	26.891	2	0.0005
	all	Dec	depth	615.269	2	< 0.0001
	all	Mar	depth	127.981	2	< 0.0001
	all	Jun	depth	106.841	2	< 0.0001
< 5 mm	all	all	time x depth	145.279	6	< 0.0001
	all	all	depth	1143.399	2	< 0.0001
	all	all	time	189.771	3	< 0.0001
	MLL	all	time	588.838	3	< 0.0001
	MLL -1	all	time	109.735	3	< 0.0001
	MLL -3	all	time	58.820	3	< 0.0001
	all	Sep	depth	84.674	2	< 0.0001
	all	Dec	depth	6070.548	2	< 0.0001
	all	Mar	depth	298.858	2	< 0.0001
	all	Jun	depth	46.653	2	0.0002

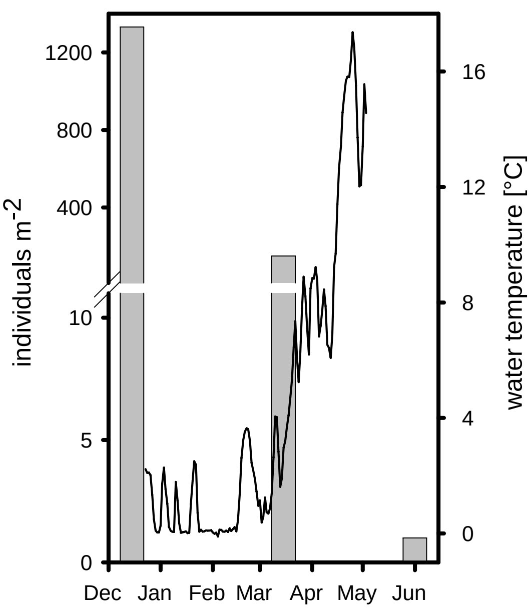

Fig. 2.2. Water temperatures from December 2005 to June 2006 (black line) and survival of *Corbicula fluminea* in mesocosm (bars).

Discussion

During winter 2005/2006 different abiotic factors lead to a mass mortality of *C. fluminea* in Lake Constance, with only ~1% of the population remaining. Whereas in the shallowest water depth (MLL), the drying out directly lead to an extinction of the population (Fig. 2.3), in both other depths low water temperatures for a long period affected the survival of clams. However, the date of mortality depended on clam-size and water depth. Although Corbiculidae can survive short term extreme conditions like cold temperatures (French & Schloesser 1996), drying outs (White & White 1977), and hypoxia (Matthews & McMahon 1999), these events seem to severely hurt the population when they last for weeks (French & Schloesser 1991, and 1996). Nearly all clams died at Rohrspitz between December and March, only clams > 5mm at MLL -3 m survived this period. However, these clams still died at rising water temperatures until late spring. Impressive summer mortalities of *C. fluminea* are known from the rivers Rhine and Saône (Westermann & Wendling 2004, Mouthon & Daufrasne 2006), which could be due to food limitation during heatwaves. Corbiculidae seem to be susceptible to food limitation under unfavorable temperatures (Vohmann & Kureck, personal communication). However, the Chlorophyll a- concentration in Upper Lake Constance (upper 10 m) reaches an annual peak in May (~10 µg Chl a l^{-1}). Although a clear-water phase follows up in June (~3 µg Chl a l^{-1}), phytoplankton-concentration at that time is more than three times higher than during January to March (Roßknecht 1998). Since during preceding winters and summers, clams did not show any mortality (unpublished data) and because *C. fluminea* is additionally able to feed from the sediments by pedal-feeding (Hakenkamp & Palmer 1999), it is unlikely that phytoplankton availability limited the survival of the few remaining *C. fluminea* at MLL -3 m (only 1% of former densities). Probably *C. fluminea* at MLL -3 m were too weakened and stressed to recover from the cold period in winter. Condition indices of *C. fluminea* were reported to decrease significantly after one month of temperatures around 2 °C (French & Schloesser 1996). French & Schloesser (1991) assumed that first year clams are more susceptible to low temperatures than older clams. For perch and ruffe it is shown that bigger and older individuals have a better ability to store energy and therefore have a better resistance against different stressors than small and young (Eckmann 2004). This might also apply for older clams (> 5 mm), that survived longer at MLL -3 m than young clams (< 5 mm).

Furthermore, clams > 5 mm at MLL -3 m survived longer than that at MLL -1 m, maybe because water temperatures during the frost period at MLL -3 m were less extreme than those at MLL -1 m. Water temperature in shallow littoral zones respond faster to air temperature than in deeper water. Therefore, critical temperature for clam survival at MLL -3 m might have occurred later in winter or for a shorter period than at MLL -1 m, what might have delayed mortality of *C. fluminea* until late spring. Unfortunately, two temperature loggers that were exposed at Rohrspitz caused troubles: one logger fell dry after 5 weeks and the another one was stolen. Water temperatures at a mean depth of ~ 40 cm in the phase from Dec 15th to Jan 25th at Rohrspitz were on average 2.77 ± 0.80 °C lower than water temperatures at a water depth of 50 cm in Bregenz. Furthermore, the ice cover recorded at Rohrspitz in January indicated that actual water temperatures

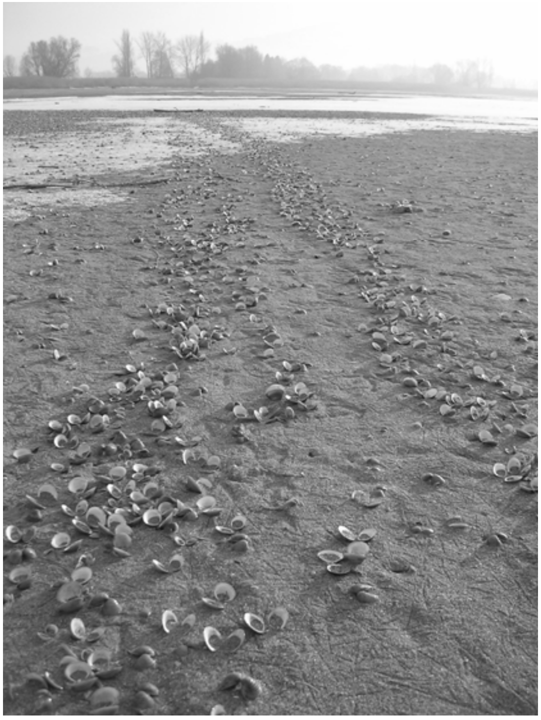

Fig. 2.3. Dead *Corbicula fluminea* during drought at Rohrspitz (MLL).

were lower than that at the ice-free site Bregenz.

Our mesocosm study approved that temperatures around 2 °C for 2 months or longer are lethal for *C. fluminea* (Mattice & Dye 1976, French & Schloesser 1991, and 1996). The native unionids seem to be better adapted to low temperatures than the invasive clam. Although bivalve species differ in metabolism, the survival of both *A. cygnea* is a hint that O_2-limitation and food availability can be excluded as a reason for the observed mass mortality of *C. fluminea.* Cold winters often caused winter mortality of complete *C. fluminea* populations in the United States (French & Schloesser 1991, Morgan *et al.* 2003). By this, the northern boundary of *C. fluminea* dispersal is limited. Beyond winter survival of single individuals, reproduction is limited by water temperature: growth as well as development of *Corbicula fluminea* begins at 10-11 °C (reviewed in Karatayev *et al.* 2005). Schöll (2000) hypothesized that *C. fluminea* would not have established in Germany without heat pollution of rivers by power plants.

Since bivalves have very slow migration rates (some species are sessile), mass mortalities can occur, when water level sinks dramatically. Water level decreases caused massive die-offs of Corbiculidae (White & White 1977, Morgan *et al.* 2003). After 4 days of air exposure 50% mortality occurred (White & White 1977). The study site Rohrspitz is a shallow littoral zone with a very flat ground profile and the zone with water depths of about MLL -1m is nearly 1 km in width. Although clams tried to follow the fast sinking water level, nearly all clams dried up. Some were trapped in rest water holes that ran dry later or froze (personal observation). After this mass mortality, substrate was littered with empty shells (Fig. 2.3). Physical structure of persistent and abundant shells of many bivalves are important for organization of invertebrate communities in aquatic environments (Gutiérrez *et al.* 2003). On soft substrates, empty *C. fluminea* shells can favor populations of benthic invertebrates that prefer hard substrates (Werner & Rothhaupt 2007).

Until June, MLL was resettled by juvenile *C. fluminea* of the year in low densities, most probably descending from adults that survived in greater depths. Compared to this, annual re-colonization of the littoral zone by zebra mussels *Dreissena polymorpha* in Lake Constance after strong predation of wintering waterbirds with only 3 % of the zebra mussels remaining is very quick (Werner *et al.* 2005). In comparison with zebra mussels that have planktonic veliger larvae, the ability of *C. fluminea* to re-colonize areas in lakes without strong currents seems to be limited. *C. fluminea* juveniles do not disperse as plankton, because they are released by the maternal clams in a crawling stage (Britton & Morton 1979, Karatayev *et al.* 2005). However, *C. fluminea* seems to have autonomously moved upstream at least 1.2 km $year^{-1}$ in the Savanna River, USA (Voelz *et al.* 1998).

Conclusion

Harsh winter conditions with water temperatures ≤ 2 °C for weeks strongly limit survival and also dispersal of C*. fluminea*, whereas timing of mortality was depending on size-class and depth. Only few individuals remain that can reproduce and that might establish a resistance against lower winter temperatures. Natural water level decreases can also regulate the population of this invasive clam. Consequently, quick water level decreases in regulated reservoirs could be used as regulation tool against mollusk invaders.

Acknowledgement

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3 The invasive bivalve *Corbicula fluminea* causes changes in the benthic soft-bottom community in the littoral zone of Lake Constance

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submitted

Abstract

The invasive burrowing bivalve *Corbicula fluminea* has become established in freshwater ecosystems worldwide. It invaded Lake Constance, a large, pre-alpine, oligotrophic lake in central Europe, in the early 2000s. Here we studied the impact of *C. fluminea* on the spatial and temporal dynamics of littoral communities of benthic macroinvertebrates in soft sediments of Lake Constance at various depths over 3 years. Benthic soft bottom communities varied greatly seasonally and according to depth. The benthic assemblage was influenced by physical disturbances, e.g., water-level fluctuations, which led to an increase in the number of taxa, density, and biomass at higher depths, i.e., in habitats with greater stability. The *C. fluminea* population grew slowly, had a maximum life span of 4 years, and usually built one cohort per year; during hot summers and in very shallow depths, two cohorts were observed. Densities of infaunal taxa and juvenile *C. fluminea* were independent from *C. fluminea* biomass. The impact of *C. fluminea* depended on the structural complexity of the habitats. On bare sand, densities of *Dreissena polymorpha* and other epifaunal taxa increased with the biomass of *C. fluminea*, whereas in habitats with increased structural complexity owing to dominating macrophytes, *C. fluminea* had no effect. We conclude that on poorly structured sediments, *C. fluminea* increases the surface area and substrate diversity and could thereby lead to an increase in most epifaunal benthic invertebrates. This effect might partly be due to the indirect effect of *C. fluminea* facilitating the settlement of *D. polymorpha*, an important ecosystem engineer.

Key words benthos, littoral zone, Asian clam, ecosystem engineering, macroinvertebrate, *Dreissena polymorpha*, epifaunal, infaunal, water depth

Introduction

The organization of the macroinvertebrate community in the littoral zone of lakes is influenced by many habitat variables and biotic interactions (Macan 1966, Gilinsky 1984, Diehl 1992, Cobb & Watzin 1998). The composition of benthic communities in lakes depends on abiotic factors, such as lake morphometry, productivity, and water chemistry (Jackson & Harvey 1993, Bailey *et al.* 1995). Within large oligotrophic lakes, it is mainly affected by wave action, substrate type, habitat stability, water temperature, geomorphology, and water-level fluctuations (Winnell & Jude 1987, Tolonen *et al.* 2001, Scheifhacken *et al.* 2007, Baumgärtner *et al.*, in press). The density and species richness of benthic macroinvertebrate communities generally increases with the availability of interstitial refuges and habitat complexity (Diehl 1992, Schmude *et al.* 1998, Gjerlov *et al.* 2003). Biotic factors, such as predator–prey interactions, competition, facilitation, and life-history traits, play a major role in the community structure (Gilinsky 1984, Johnson *et al.* 1996, Bertness & Leonard 1997, Harrison & Hildrew 1998, Harrison & Hildrew 2001, Mörtl *et al.*, in press).

In recent history, another factor affecting the community structure has gained in importance: the removal of former macroinvertebrate-dispersal barriers by human activity. Channels now connect river systems that once had different communities separated by land (see, e.g., Bij de Vaate *et al.* 2002) and merchant shipping with boats containing invaders in their ballast have linked continents separated by water (Bailey *et al.* 2007). In the current times of global trade, the presence or absence of an organism in a lake might depend only on human activity and its introduction elsewhere is just a matter of time.

Human-induced biological invasions can cause dramatic changes in communities, ecosystem processes, and biodiversity (Spencer *et al.* 1991, Lövei 1997, Dick *et al.* 2002, Nalepa *et al.* 2003). Especially biological invaders that alter substrate qualities, e.g., bivalves that provide persistent and often abundant physical structures via shell production (Strayer *et al.* 1999, Gutiérrez *et al.* 2003), can have a great impact on biotic communities (Karatayev *et al.* 1997, Stewart *et al.* 1998, Nalepa *et al.* 2003). The invasive epifaunal bivalve *Dreissena polymorpha*, for example, often exerts strong positive effects on the density and biomass of diverse macroinvertebrate communities of littoral habitats (Stewart *et al.* 1998, Nalepa *et al.* 2003, Mörtl & Rothhaupt 2003). In contrast, most infaunal burrowing bivalves seem to have minor effects on benthic assemblages (Karatayev *et al.* 2003, Vaughn & Hakenkamp 2001, Werner & Rothhaupt 2007). However, the impact on benthic communities of the burrowing, Asian bivalve *Corbicula fluminea* — one of the most invasive species (Morton 1979) — remains unclear. *C. flu-*

minea can reduce the amount of benthic bacteria and diatoms on the sediment via pedal feeding (Hakenkamp *et al.* 2001), but whether it also affects macroinvertebrates is largely unknown (c.f. Werner & Rothhaupt 2007).

C. fluminea has been introduced into North and South America (McMahon 1982, Ituarte 1981, Darrigran 2002) and Europe (Mouthon 1981, den Hartog *et al.* 1992). Between 2000 and 2002, *C. fluminea* invaded the pre-alpine Lake Constance in central Europe (Werner & Mörtl 2004).

We aimed to assess the changes in the macroinvertebrate community in the sandy littoral zone of Lake Constance caused by the presence of *C. fluminea* and the seasonal dynamics of the community in relation to water depth and correlated factors. *C. fluminea* occurs on unstructured sandy sediments; without the valves of C. *fluminea,* this surface has only a low potential for settlement of taxa preferring hard substrates. We have hypothesized that *C. fluminea* allows several invertebrate taxa to increase in density, especially epifaunal taxa that positively select for the valves (Werner & Rothhaupt, in press). We also postulated that *D. polymorpha*, which invaded Lake Constance in the 1960s (Siessegger 1969), should be able to use *C. fluminea* as a biological hard substrate on soft bottoms in Lake Constance that have not yet been colonized by *D. polymorpha* (see Werner & Mörtl 2004). If these two postulations hold true, they together could have strong consequences for invertebrates.

Materials and methods

Study site

Lake Constance is a pre-alpine, oligotrophic lake in central Europe. At mean water level, about 15% of its surface area (75 km^2) is classified as a littoral zone. Its largely unregulated water level fluctuates annually within 2 m; the fluctuation is triggered by rainfalls and melting water runoff in the Alps and depends largely on the alpine system of the Rhine River [Internationale Gewässerschutzkommission für den Bodensee (IGKB) 2004b]. The grain size and the proportion of silt and clay of sediments in Lake Constance are related to wave action (Schmieder *et al.* 2004). We conducted our study in the southeastern part of Upper Lake Constance near the city of Bregenz (Austria). The study site "Rohrspitz" (9° 37′ 00.4″ E, 47° 30′ 00.3″ N) is a 2-km-wide, sandy, shallow-water zone that was invaded by *C. fluminea* between 2000 and 2002. The littoral of Upper Lake Constance outside of our study area is dominated by silty sands with a more-or-less packed stony overlay (Fischer & Eckmann 1997).

Sampling design

Macroinvertebrates, including *C. fluminea,* were sampled in September 2004 and then every three months (in March, June, September, and December) from September 2005 to December 2007. Samples were collected from up to four depths; the number of depth zones depended on the water level. Three fixed sampling sites were located using GPS and characteristic landmarks: the zone of the mean low-water level (MLL), which is equivalent to a gauging level of 2.64 m measured at the Konstanz harbor; and two infralittoral stations, 1 and 3 m below the MLL (MLL –1, and MLL –3 m). At these fixed sites, the water depth changed according to the water level of the lake. Since the water level of Lake Constance fluctuates annually, samples were also collected at a constant depth of 0.4 m in the eulittoral zone to study the dispersal of *C. fluminea,* especially juveniles. The sampling site at each depth was randomly chosen within 20 to 30 m of the shoreline.

The substrate at the MLL, MLL –1 m, and MLL –3 m sites consists of fine sand particles with a grain size of 200–630 µm (90%) and of coarse sand particles with a grain size of 630 µm to 2 mm (10%). At MLL –3 m, macrophytes dominated from June to at least December (mainly *Chara* spp., but also *Potamogeton perfoliatus* and *Najas intermedia*) and covered up to 100% of the sediment. At MLL –1 m, no macrophytes occurred. At MLL, some slender-leaved macrophyte species, e.g., *Potamogeton pectinatus,* occurred from June to September and covered up to 30% of the sediment. At 0.4-m depth, the substrate changed with the change in the lake water level from sand to silt and clay with organic matter; no macrophytes were detected.

Sample collection and processing

Benthos was quantitatively sampled by scientific scuba divers using an infralittoral suction sampler (Baumgärtner 2004, Mörtl 2005), which minimized the number of escaping mobile individuals by the use of an artificial current. The sampler had a mesh size of 200 µm and covered a sampling area of 625 cm^2 (25×25 cm^2). Four replicates were taken at each depth; three of the replicates were analyzed. All samples were immediately processed in the laboratory. Each benthos sample was sieved through different mesh sizes (20 mm, 5 mm, 2 mm, and 400 µm) to remove all organisms from the inorganic matter. Fine sediments were stirred up repeatedly, and the floating organisms and debris were collected on a 200-µm sieve. Collected organisms were fixed in 70% ethanol.

Using a dissecting microscope, we identified invertebrates to the species or genus level (except oligochaetes and chironomids) and counted the individuals. Invertebrates were classified into three size classes (small, medium, and large; according to Baumgärtner & Rothhaupt, 2003) for subsequent biomass calculations. For taxa not listed in Baumgärtner & Rothhaupt (2003), values were based on our own extensive length/dry mass calculations following the methods described therein. In contrast to this previous study, all dry mass data for mollusks included their shells because shell production by mollusks is an important process in the physical engineering of habitats. *D. polymorpha* and *C. fluminea* were measured using an electronic calliper (Preisser, Digi-Met) and grouped into cohorts.

Abiotic factors: temperature and gauging level

The daily mean water level and water temperatures were continuously received from the water-gauge measuring site at the Bregenz harbor from June 1, 2004 to February 29, 2008; gauge zero is 391.89 m NN. The water temperature was measured 50 cm below the water surface. The actual water depth fluctuated between 228 cm (February 15, 2006) and 407 cm (August 26, 2005) during our study.

The water temperature at the study sites was measured with a HOBO Pendant Temperature/Light Data Logger (Part # UA-002-XX) at 0.4-m depth from December 15, 2005 to January 25, 2006 and at 0.4-m depth, MLL –1 m and MLL –3 m from March 13, to June 11, 2007. Three other loggers were stolen.

Data processing and statistical analyses

We reported invertebrate density as individuals m^{-2} (ind. m^{-2}) and biomass as g dry weight m^{-2} (g dry wt. m^{-2}) of lake bottom (including shells and macrophytes). The biomass data of *C. fluminea* from the different samples were grouped into four classes (class 1: 0–5 g, class 2: 5–50 g; class 3: 50–500 g, and class 4: >500 g); each sample was then assigned to a biomass class. The similarity of the benthic macroinvertebrate community among the different samples was analyzed by non-metric multidimensional scaling (NMDS) in PRIMER 6.0. We chose a square root (x) transformation to downplay the influence of dominant species and to allow moderately abundant species to contribute almost as much as abundant species to differences in similarity between samples. Each algorithm was re-run 25 times for each plot (Clarke & Gorley 2001). We analyzed Bray-Curtis similarities between the communities in different samples using analysis of similarity (ANOSIM) in PRIMER 6.0 (PRIMER-E Ltd., Plymouth), which compares ranked similarities for differences between defined groups. In theory, *R*-values obtained by ANOSIM can vary from –1 to +1. Large *R*-values imply differences between samples, whereas values close to 0 imply no or little segregation (H_0: hypothesis is true). For interpreting existing differences among groups of samples, we looked at the role of individual species in contributing to the separation between two groups of samples with the SIMPER routine in PRIMER, listing the percentage contribution of single species in decreasing order (Clarke & Gorley 2001). Therefore, Bray-Curtis similarities between samples were decomposed by computing average dissimilarities between all pairs of intergroup samples and then breaking down this average into separate contributions from each species to dissimilarity. Since comparisons between all groups for all factors would lead to extensive sets of tables, we only compared the groups of samples that were attributed to four bio-

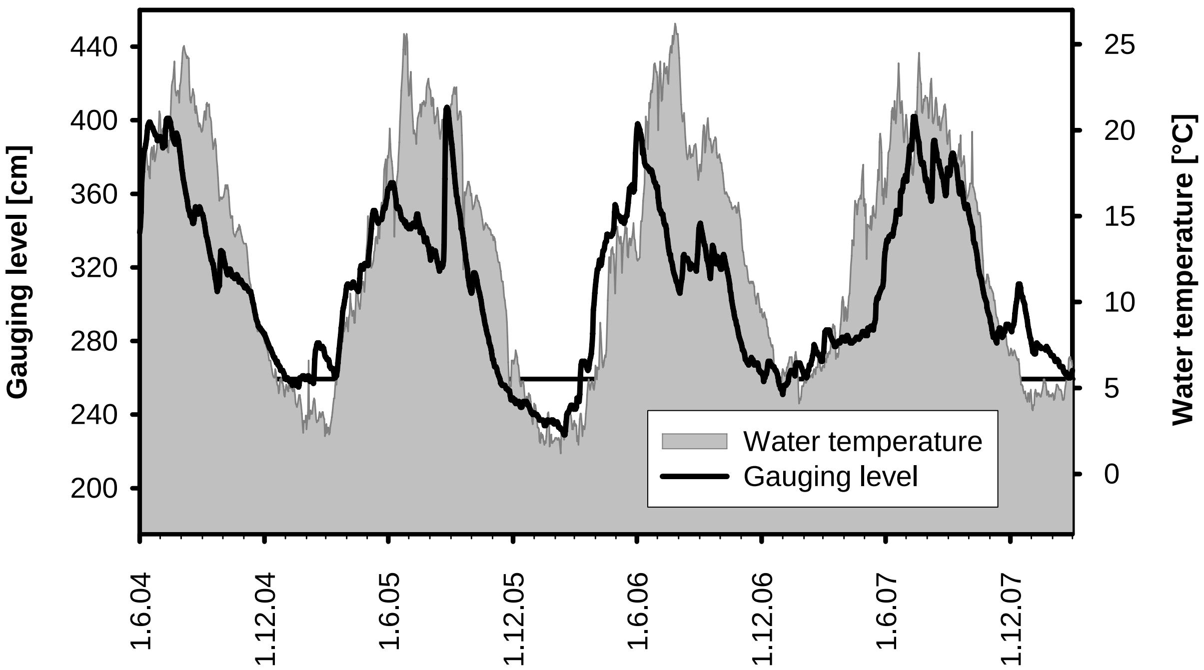


Fig. 3.1. Water temperature and gauging level at Bregenz during the study period (data from Wasserwirtschaftsamt Vorarlberg). The straight black line (background) depicts the mean low-water level of 264 cm.

mass classes of *C. fluminea* to consider the impact of *C. fluminea* on those epifaunal and infaunal taxa, ruling out an impact of depth and season. Using a Spearman-Rank test (Statistica, stat. soft V.6.0), we analyzed whether the biomass classes of *C. fluminea* correlate with the most common epifaunal and infaunal taxa or with those that contributed most to the dissimilarities of groups of samples. We tested epifaunal and infaunal taxa in two separate groups and adjusted the results for each group with a sequential Bonferroni correction (Rice 1989).

Results

Abiotic factors: water temperature and gauging level

Water temperature and water level fluctuated strongly within each year (Fig. 3.1). The water level fluctuated within 1.8 m and showed a basic seasonal pattern with a peak in summer and a trough in late winter. In early spring 2006, a centennial low-water level was reached (IGKB 2006). Except for single days and a flood in August 2005, when the water level rose 55 cm within 24 h, the gauging level remained below the mean monthly water levels of preceding years during

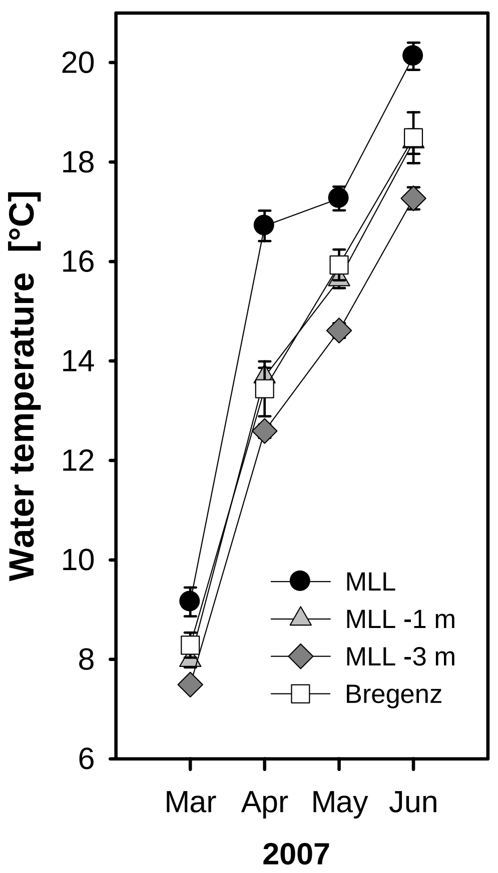


Fig. 3.2. Mean monthly water temperatures ± SE at the three different sampling depths and at the Bregenz harbor.

the entire sampling period. In each late winter, the water level decreased below the MLL of 264 cm. However, in the winters 2004/2005, 2006/2007, and 2007/2008, the water level was always very close to the MLL (Fig. 3.1).

Water temperature at Bregenz ranged from 1.6 to 26.2 °C. The water temperatures in winter 2004/2005 were normal, whereas the mean monthly water temperatures at Bregenz in winter 2005/2006 were on average 1.7 °C lower than during the preceding six winters (data from Wasserwirtschaftsamt Vorarlberg). Water temperatures were below 4 °C for nearly 4 months, and during January 2006, the shallow water zone at Rohrspitz was covered with ice. In winter 2006/2007, the water was very warm (close to 5 °C) and above the long-term average (IGKB 2007). In summer, the water temperatures were always above 20 °C and peaked annually close to 25 °C in late July (Fig. 3.1). The water temperatures at the different sampling depths differed. In winter 2005/2006, the water temperature was 2.77 ± 0.8 °C lower at 0.4 m than at the Bregenz harbor. However, from mid-March to June 2007, the water at MLL was generally warmer than at all other depths and showed the strongest temperature increase and the highest temperature fluctuations. Water temperatures at MLL –1 m and at the Bregenz harbor were similar. At MLL -3 m, the mean monthly water temperatures were lowest in summer (Fig. 3.2), whereas in winter, the water cooled down much more slowly at MLL -3 m than at the shallower depths.

C. fluminea population development

The changes in the *C. fluminea* population biomass over time at each spatially fixed depth were considered separately. At MLL, the *C. fluminea* biomass was the lowest of all depths; only up to 80 ± 25 g dry wt. m^{-2} was recorded in September 2004. All clams died in February 2006 owing to the centennial low-water level. Although single adult clams survived the low water of winter 2006/2007, the population did not recover before September 2007, and thereafter decreased again (Fig. 3.3). At MLL, the clams grew

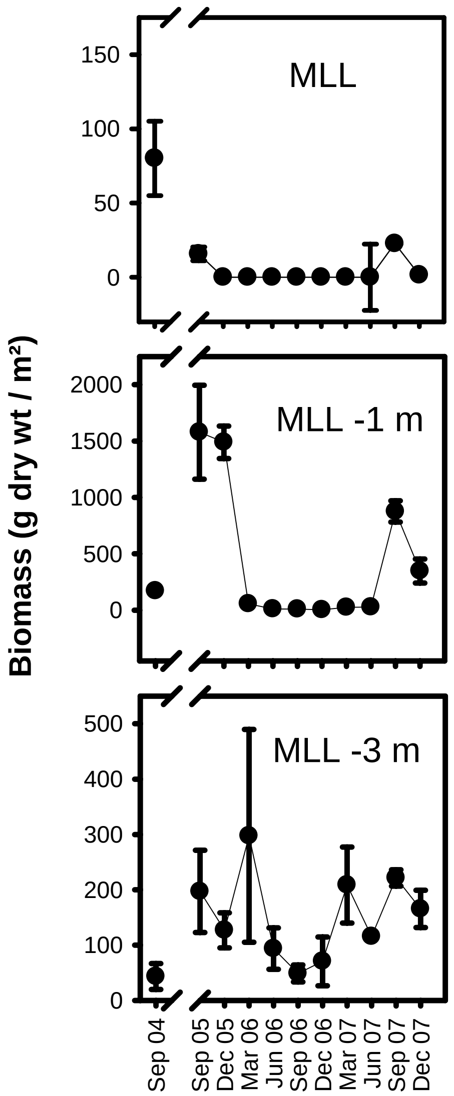


Fig. 3.3. Seasonal changes of *C. fluminea* biomass (mean ± SE) in three different sampling depths.

on average up to 10.7 mm from March to September (1.8 mm per month). Within 15 months, the clam shells reached a length of 22.0 mm; at the maximum, only three different cohorts were recorded (September 2004). Two cohorts of juveniles occurred every year, with the first occurring between March and June and the second occurring between September and December (data not shown).

At MLL –1 m, the highest biomass of the entire study period was reached in September 2005 and in December 2005 (up to 1578 ± 417 g dry wt. m^{-2}). The population then decreased, with less than 3% of the biomass remaining for the next year (Fig. 3.3). The biomass increased again from June to September 2007 owing to rapid growth (Fig. 3.3). Thereafter, the biomass further decreased until December 2007. At MLL –1 m, *C. fluminea* grew more slowly than at MLL; the maximum average growth rate was 7.3 mm from June to December 2005, corresponding 1.2 mm per month. After the severe winter 2005/2006, three cohorts disappeared completely and the numbers of individuals in the cohort of 2004 became scarce. Individuals that survived this winter grew very slowly afterwards (Fig. 3.4). For example, the second cohort of 2005 only grew 5.8 mm within 15 months, until June 2007, and then had a growth spurt, with a shell length increase of 5.7 mm by December 2007. In comparison, the cohort of 2006 grew 7.4 mm in 12 months until September 2007. Five different cohorts were present in the samples before the winter 2005/2006 (December 2005); thereafter, only two or three cohorts were present (Fig. 3.4). In 2002, 2003, 2004, and 2006, only one cohort of juveniles was present, whereas in 2005, two cohorts of juveniles occurred — the first between June and September and the second between September and December 2005. The first cohort, consisting of only a few individuals, did not survive the harsh winter of 2005/2006 (Fig. 3.4).

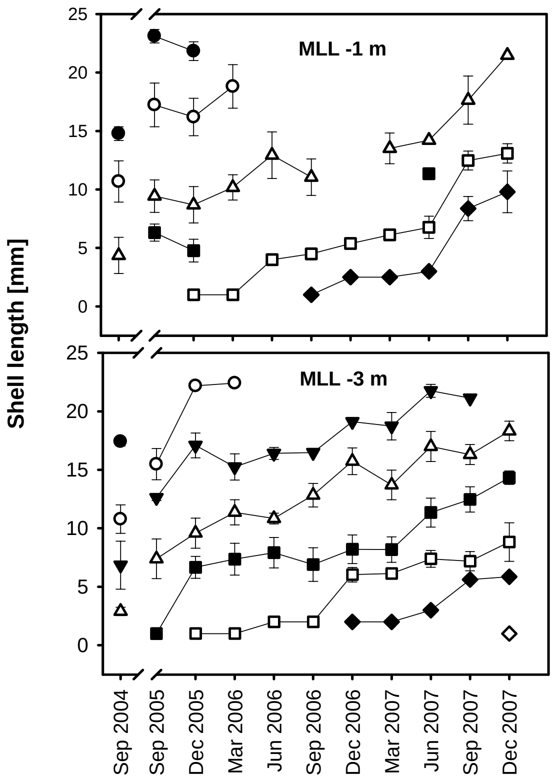


Fig. 3.4. Mean shell lengths of different *C. fluminea* cohorts ± SE. ● first cohort 2001, ○ first cohort 2003, ▼ second cohort 2003, △ first cohort 2004, ■ first cohort 2005, □ second cohort 2005, ◆ first cohort 2006, and ◇ first cohort 2007.

The biomass at MLL –3 m fluctuated during the 3-year study period, but never showed such a distinct decrease as populations in the shallower depths MLL and MLL –1 m did (Fig. 3.3). After a decrease in spring 2006, the population recovered steadily until autumn 2007. However, *C. fluminea* never reached as high a biomass as at MLL –1 m (maximum: 298 ± 192 g dry wt. m^{-2}). At MLL – 3 m, *C. fluminea* grew up to 2.8 mm within 6 months (0.5 mm per month). In contrast to the shallower depths MLL and MLL –1 m, no cohort at MLL –3 m disappeared after the harsh winter of 2005/2006, but the growth of the first cohort from 2005 stagnated for 15 months (December 2005 to March 2007; Fig. 3.4). The clams then started to grow again. In comparison, the first cohort of 2004 grew 5 mm within the same period. At MLL –3 m, two cohorts of juveniles were present in 2003 and 2005, one in September and one in December; in 2002, 2004, 2006, and 2007, only one cohort was present, in December. At MLL –3 m, at least four and usually five different cohorts were present (Fig. 3.4). The upper limit of life span was 4 years.

Community composition

We distinguished 62 taxa in 124 benthic samples. The number of taxa increased with depth: 27 taxa at 0.4 m depth, 28 taxa at MLL, 37 taxa at MLL –1 m, and 41 taxa at MLL –3 m. The frequency of occurrence, mean density, and dry weight of the 45 most common taxa (on average over season and depth) are shown in Annex 1. The most frequently occurring taxa in more than 95% of all samples were Nematoda, Ostracoda, Chironominae, Oligochaeta, and *Pisidium* spp. Three other taxa were present in more than 75% of all samples: Orthocladinae, *D. polymorpha*, and *C. fluminea*. Twelve taxa occurred in more than 50% of all samples (Annex 1). The ten taxa with the highest densities were (in decreasing order) *D. polymorpha*, Nematoda, *C. fluminea*, Chironominea, Ostracoda, Oligochaeta, *Potamopyrgus antipodarum, Pisidium* spp., *Bithynia tentaculata*, and Orthocladinae (Annex 1). Seven mollusk species were among the ten taxa

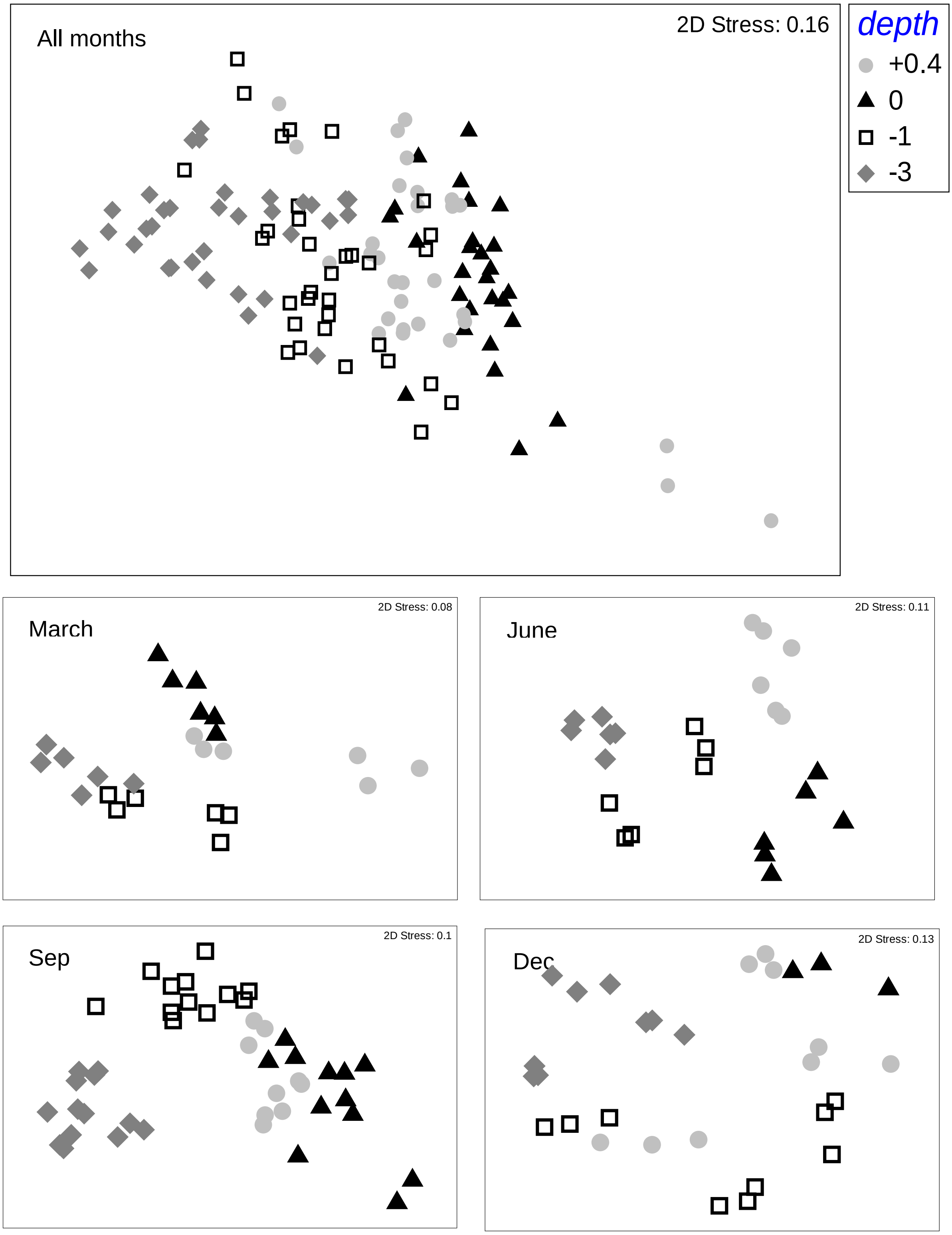


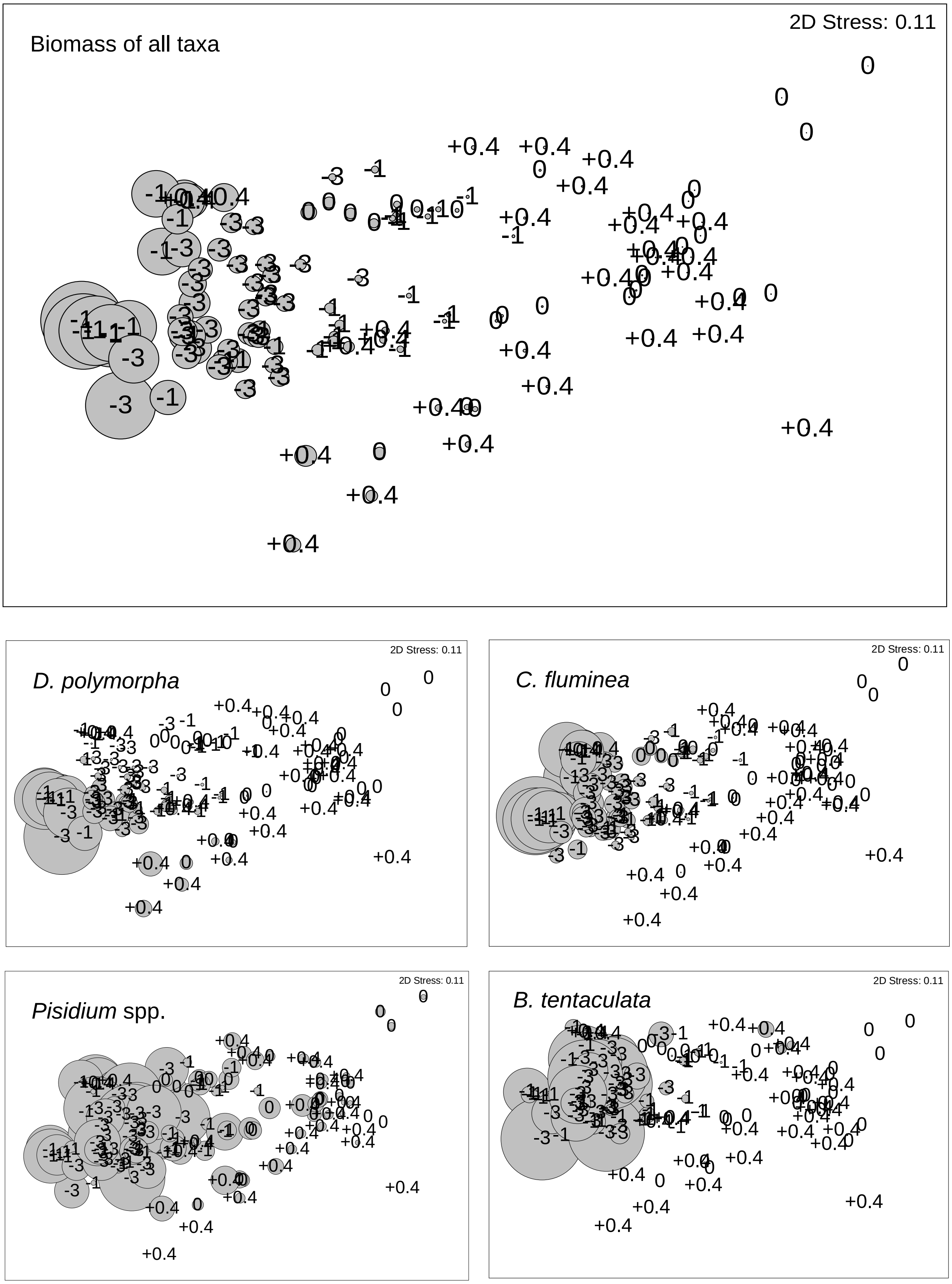
Fig. 3.5. NMDS plots of vertical zonation of the benthic community including all taxa (density) at Rohrspitz in general and for each of the four different sampling months. +0.4: 0.4 m depth; 0: MLL; -1: MLL –1; -3: MLL –3.

with the highest biomass, i.e., the benthic community biomass was clearly dominated by mollusks (weight includes shell). These species were (in decreasing order): *C. fluminea*, *D. polymorpha*, *B. tentaculata*, *P. antipodarum*, *Pisidium* spp., *Pisidium amnicum*, *Radix auricularia*, Chironominae, Nematoda, and *Helobdella stagnalis*.

The soft-bottom community at our study site was dominated by invasive species. Seven invaders made up 11.3% of the total species number: *C. fluminea*, *D. polymorpha*, *Potamopyrgus antipodarum*, *Gyraulus parvus*, *Branchiura sowerbyi*, *Dikerogammarus villosus*, and *Limnomysis benedeni.* They contributed 96.3% of the mean biomass to the total weight of the benthic community; 56.3% of the mean biomass consisted of *C. fluminea* and 38.9% consisted of *D. polymorpha*. The five non-bivalve invaders contributed < 1% to the total biomass of the benthic community; however, if we exclude the biomass of the two invasive bivalves *C. fluminea* and *D. polymorpha*, the non-bivalve invaders then contribute at least 23% to the total biomass of the community. Although biomass was dominated by invasive species, density was not. The invasive species made up 43.2% of the total abundance; the invasive bivalves *C. fluminea* and *D. polymorpha* made up 17.6 and 22.1% of the total abundance, respectively. *P. antipodarum* reached high densities of up to 16,768 individuals m^{-2}.

Vertical zonation

In general, the depth distribution patterns of benthic taxa biomass and density were similar (Table 3.1). Benthic assemblages at the four different depths differed significantly (Table 3.1, Fig. 3.5). However, if each of the four sampling months is considered separately, the segregation of the samples is more pronounced. The samples from 0.4-m depth occupy the largest area in the NMDS plots (Fig. 3.5). Since the sampling sites at this depth were not fixed, the samples sometimes overlap with those from MLL and MLL –1 m. This resulted in insignificant biomass differences between MLL and 0.4-m depth; however, samples between MLL and 0.4-m depth regarding density data differed significantly (Table 3.1). The samples from the three fixed depths (MLL, MLL -1 m, and MLL –3 m) separated well. Adjacent sampling depths were more similar to each other than to samples further away. Within single sampling months, samples from the four different depths were even better separated, especially in March, June, and September (Fig. 3.5, Table 3.1).


Biomass of all taxa
2D Stress: 0.11
D. polymorpha
2D Stress: 0.11
C. fluminea
2D Stress: 0.11
Pisidium spp.
2D Stress: 0.11
B. tentaculata
2D Stress: 0.11

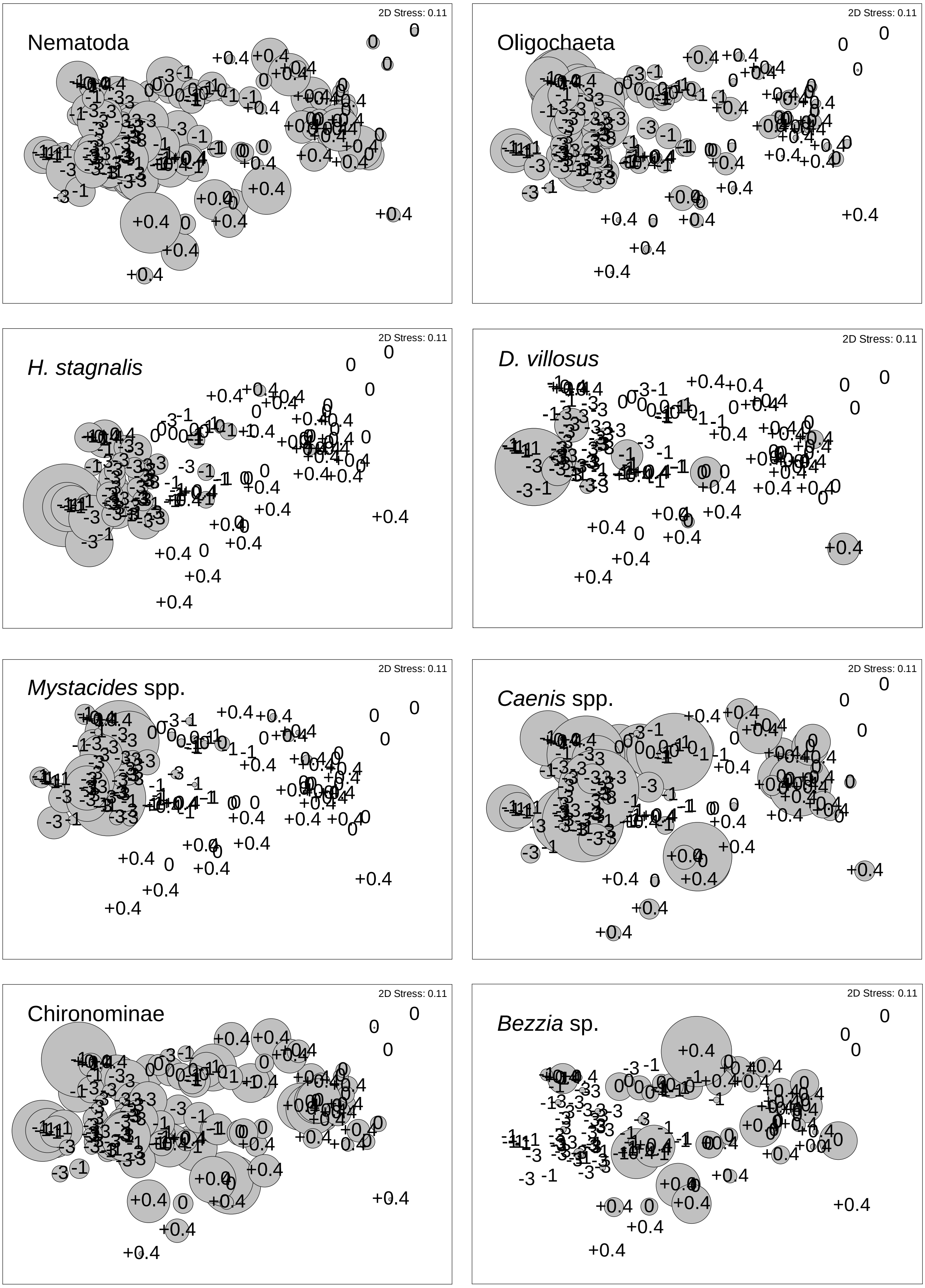


Fig. 3.6. Bubble plots of biomass and depth zonation of the total soft-bottom community and the individual taxa at Rohrspitz. Bubble size corresponds to biomass within each sample. Biomass among taxa is not to scale. +0.4: 0.4 m depth; 0: MLL; -1: MLL –1; -3: MLL –3.

In December, the samples from 0.4-m depth did not differ from samples from MLL and MLL –1 m owing to the water level.

The total biomass of all taxa was highest at MLL –3 m and MLL –1 m (Fig. 3.6). At 0.4-m depth and MLL, the total biomass was low. Most taxa preferred the greater depth zones. The biomasses of *C. fluminea, D. polymorpha, Pisidium* spp., *B. tentaculata, H. stagnalis, D. villosus, Mystacides* spp., and *Oligochaeta* were highest predominantly at MLL –3 m and also at MLL –1 m; at both shallower depths (MLL and 0.4 m) the biomasses of all the taxa listed above were low. In contrast, the density of chironomid larvae *Bezzia* sp. was highest at 0.4-m depth and MLL; the larvae avoided the two greater depths MLL –1 m and MLL –3 m (Fig. 3.6). The biomass of *Caenis* spp. was also highest at MLL –3 m and MLL –1 m, but reached high values even at 0.4-m depth. Nematoda and Chironominae were distributed throughout all depths but had the lowest biomass at MLL (Fig. 3.6).

Seasonal variability

Season had significant effects on benthic communities at different depths, whereas the ordination of all samples from different sampling months in one plot resulted in an overlap of most samples (*R*-values < 0.5; Fig. 3.7, Table 3.2). The densities at each of the four depths differed significantly for at least two different sampling months (Table 3.2, Fig. 3.7). Except for MLL, the biomass data were less different; at MLL –1 and at MLL –3 m, the biomass data among the sampling months did not differ significantly. The biomass data from the September samples at MLL –1 m and MLL –3 m did not differ from those of the December samples, even considering the *p*-values, which were influenced by the high number of samples (Table 3.1). The biomass data from the September and June samples among the various years were more similar to each other than were samples from adjacent months within the same year. The biomass data from the December and March samples varied more among the different years (Fig. 3.7).

Some taxa reached an annual peak in autumn, followed by a decrease in spring, e.g., *D. polymorpha, C. fluminea*, *B. tentaculata*, *H. stagnalis*, and *D. villosus* (invaded the study site in 2004). However, the patterns of Oligochaeta, *Caenis* spp., *Mystacides* spp., and *Bezzia* sp. were less clear (Fig. 3.8). Oligochaeta and *Mystacides* spp. each showed just one distinct peak in autumn 2006, whereas *Caenis* spp. showed two peaks, one in December 2005 and one in June 2006. *Bezzia* sp. had two peaks, one in winter

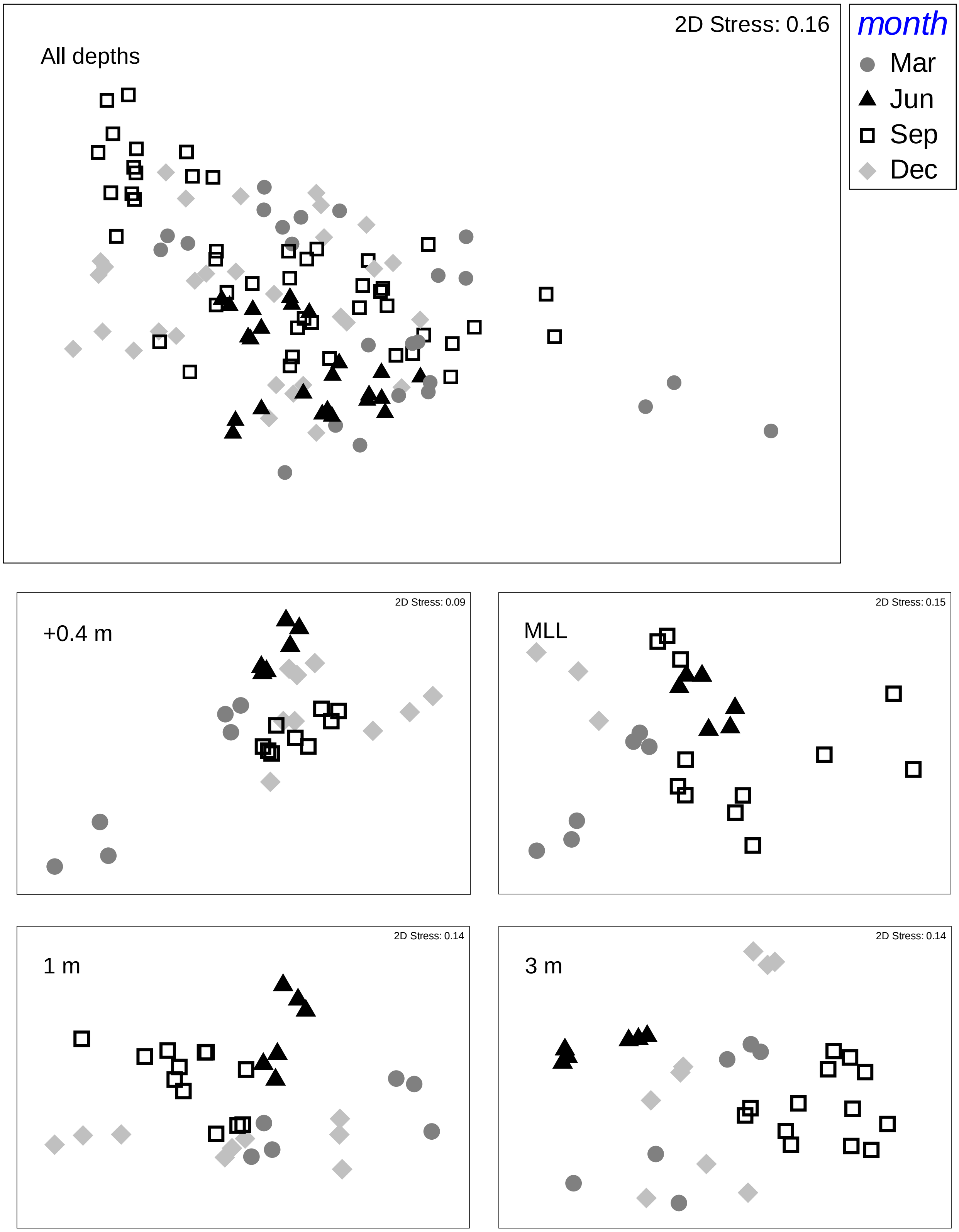


Fig. 3.7. NMDS plots of seasonal variability of the benthic community including all taxa (density) at Rohrspitz in general and for each of the four different depths.

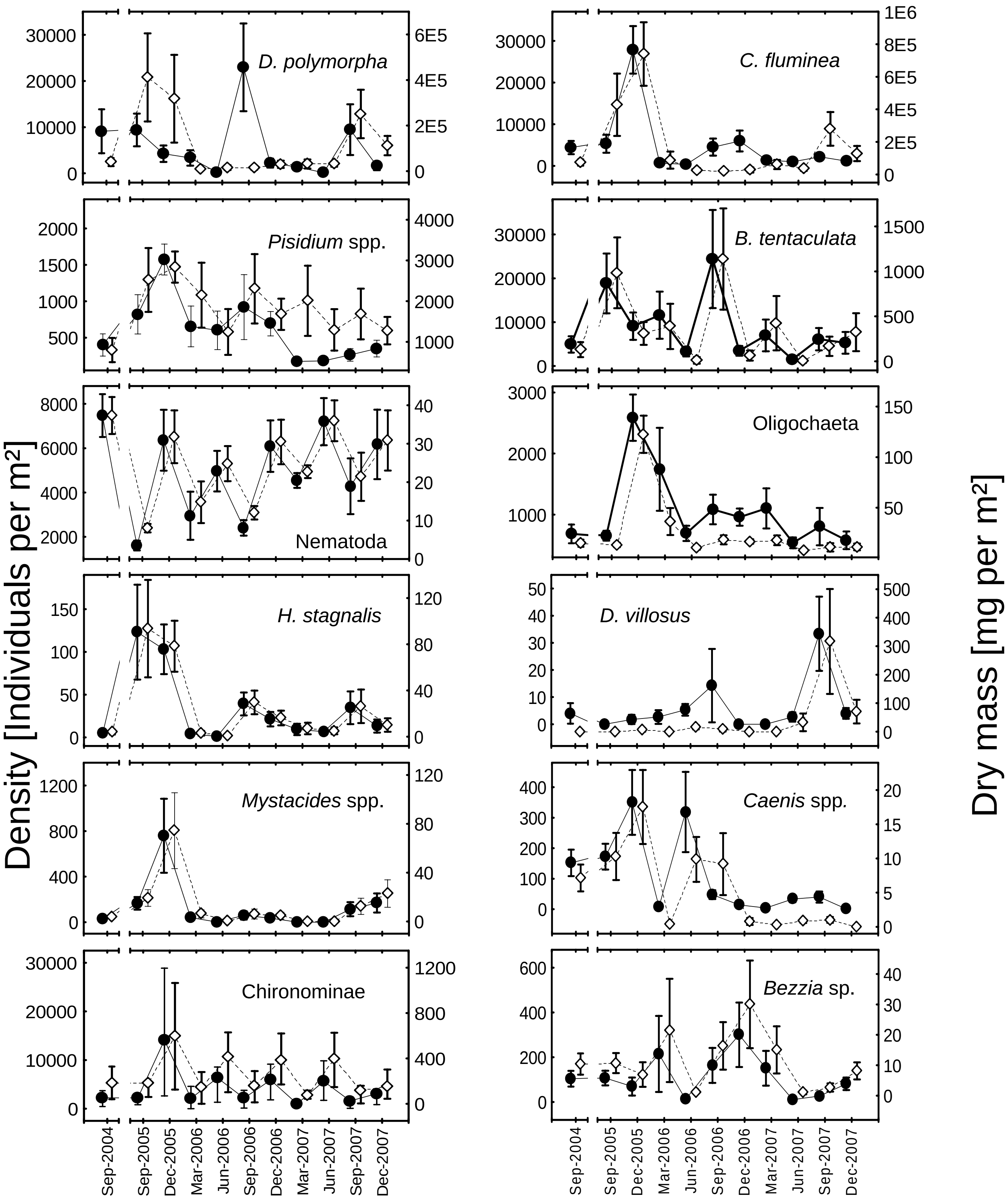


Fig. 3.8. Seasonal variation in taxa occurrence averaged about all depths (mean ± SE). –●– density, –◇– biomass.

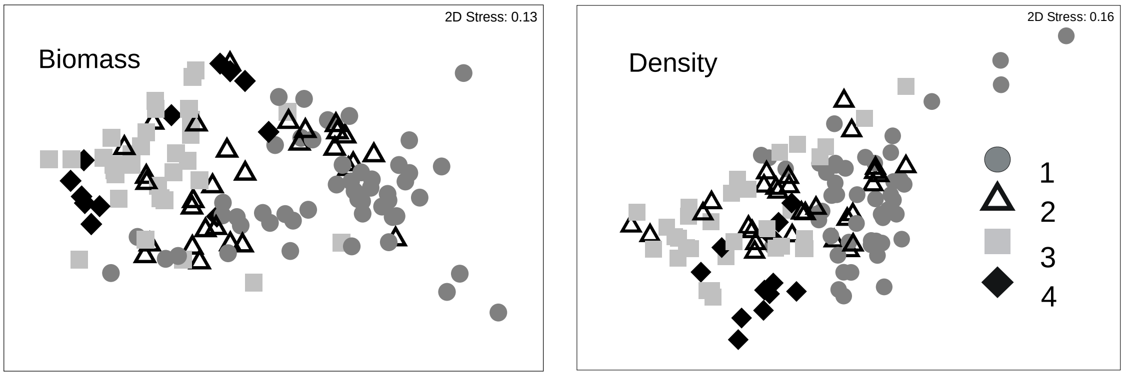


Fig. 3.9. NMDS plots of the response of total community (biomass and density) in dependence of biomass size classes of *C. fluminea* (all samples without *C. fluminea*). See Materials and methods for the definition of the size classes.

2005/2006 and one in winter 2006/2007. *Pisidium* spp., Chironominae, and Nematoda showed no obvious seasonality (Fig. 3.8), although the two latter taxa seemed to have two annual peaks. The seasonal variations in biomass and density of the two invasive bivalve species *D. polymorpha* and *C. fluminea* were not congruent. *D. polymorpha* biomass reached a peak in autumn 2005 even though the density decreased. In September 2006, *D. polymorpha* density but not biomass showed a distinct peak. A less clear aberration of the two population size parameters occurred for *C. fluminea* in autumn 2006, with a small density peak despite low biomass, and in September 2007, when biomass but not density increased. *D. villosus* density also showed a small peak in September 2006, when biomass was low (Fig. 3.8).

Impact of *Corbicula fluminea*

The biomass and density of the overall benthic community is related to the biomass of *C. fluminea* (Table 3.3). *C. fluminea* samples categorized in the higher biomass classes (3 and 4) differed from those assigned to biomass class 1 (Table 3.3, Fig. 3.9). The pronounced differences in the NMDS ordination and ANOSIM analyses of all samples together could be due to correlations with the vertical zonation of the benthic taxa since most of the samples showed highest densities in MLL –1 m and MLL –3 m, and low biomasses in both shallow depths (0.4 m and MLL). A separate consideration of the depth with samples containing all four biomass classes of *C. fluminea* revealed differences between samples of biomass class 1 and 4 at MLL –1 m for biomass data and differences between

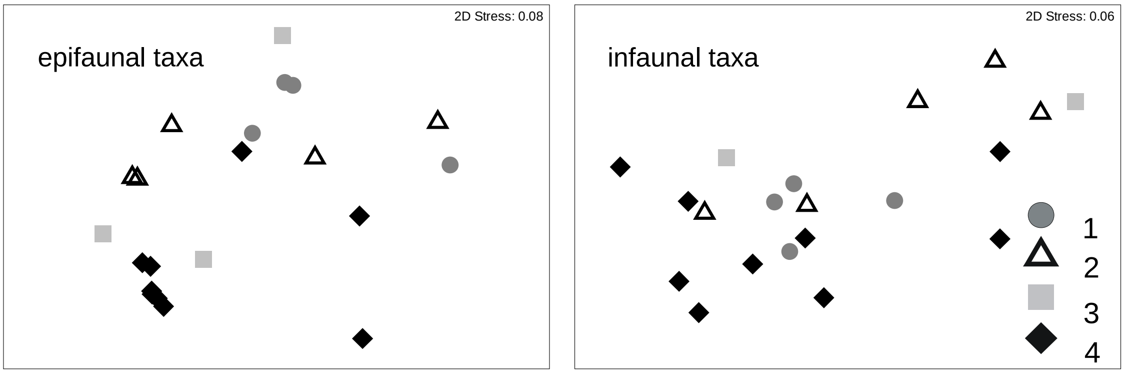


Fig. 3.10. NMDS plots of the response of epifaunal and infaunal taxa (biomass data without *C. fluminea*) at MLL –1 m to biomass size classes of *C. fluminea.* September and December-data were pooled since there were no seasonal differences between the two months. See Materials and methods for the definition of the size classes.

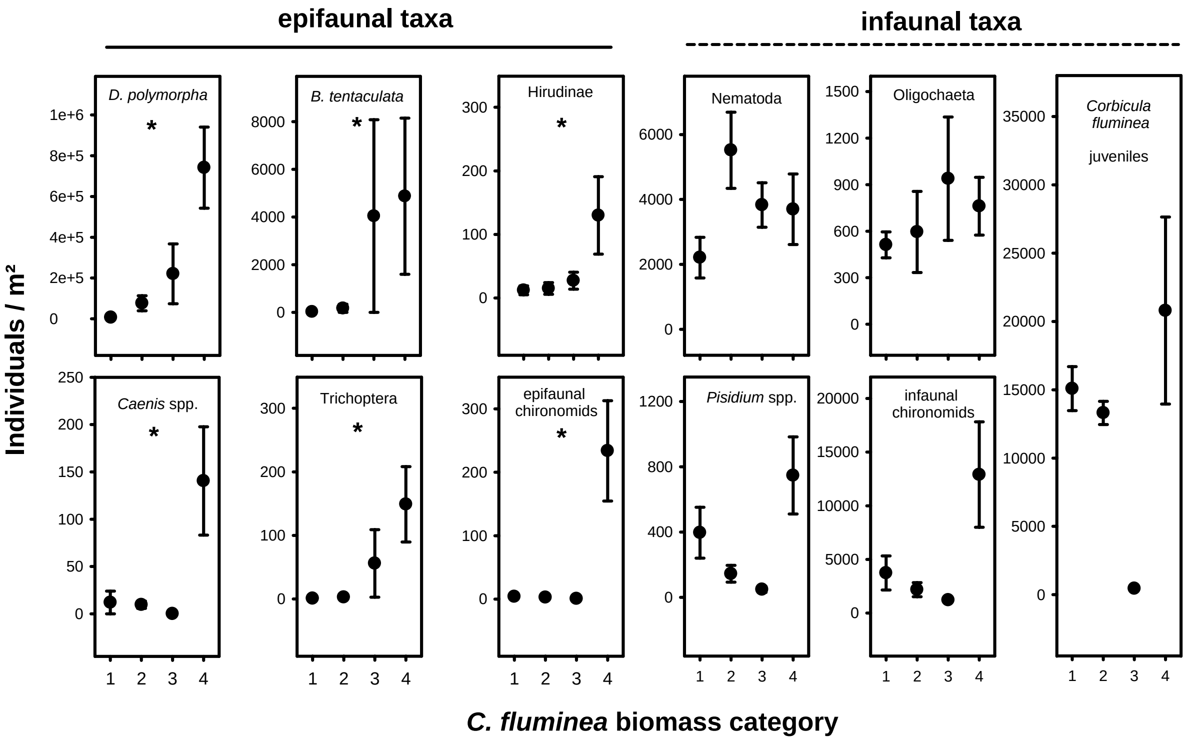


Fig. 3.11. Response of different taxa to biomass of *C. fluminea.* All samples are from MLL –1 m sampled in September and December; there were no significant differences between the two sampling dates. See Materials and methods for a definition of the classes. *: significant correlation.

samples of biomass class 3 and 4 for density data at MLL –1 m. However, at MLL –3 m, no differences among samples assigned to the different biomass classes were found (Table 3.3).

Most taxa show a depth zonation similar to that of *C. fluminea,* with highest biomass in MLL –1 m and MLL –3 m, e.g., *D. polymorpha, Pisidium* spp., *B. tentaculata, H. stagnalis, D. villosus, Mystacides*

Table 3.1. ANOSIM results. The depth-dependent differences were separated for each sampling month. Pronounced differences are in bold.

Depth	Test	Density		Biomass	
		R	p	R	p
All months	Global	0.431	0.001	0.419	0.001
	MLL, 0.4	0.067	0.014	0.039	0.067
	MLL, MLL –1	0.244	0.001	0.361	0.001
	MLL, MLL –3	**0.799**	**0.001**	**0.882**	**0.001**
	0.4, MLL –1	0.214	0.001	0.154	0.002
	0.4, MLL –3	**0.660**	**0.001**	**0.628**	**0.001**
	MLL –1, MLL –3	**0.516**	**0.001**	0.337	0.001
March	Global	**0.650**	**0.001**	**0.743**	**0.001**
	MLL, 0.4	0.419	0.004	**0.830**	**0.002**
	MLL, MLL –1	**0.846**	**0.002**	**0.956**	**0.002**
	MLL, MLL –3	**0.985**	**0.002**	**0.996**	**0.002**
	0.4, MLL –1	0.478	0.004	0.385	0.017
	0.4, MLL –3	**0.739**	**0.002**	**0.744**	**0.002**
	MLL –1, MLL –3	**0.550**	**0.004**	**0.811**	**0.002**
June	Global	**0.910**	**0.001**	**0.727**	**0.001**
	MLL, 0.4	**0.922**	**0.002**	0.287	0.015
	MLL, MLL –1	**0.933**	**0.002**	**0.867**	**0.002**
	MLL, MLL –3	**1**	**0.002**	**0.996**	**0.002**
	0.4, MLL –1	**0.789**	**0.002**	**0.750**	**0.002**
	0.4, MLL –3	**1**	**0.002**	**0.924**	**0.002**
	MLL –1, MLL –3	**0.789**	**0.002**	**0.574**	**0.006**
September	Global	**0.844**	**0.001**	**0.549**	**0.001**
	MLL, 0.4	0.267	0.004	0.277	0.005
	MLL, MLL –1	**0.860**	**0.001**	0.420	0.001
	MLL, MLL –3	**0.982**	**0.001**	**0.628**	**0.001**
	0.4, MLL –1	**0.772**	**0.001**	**0.786**	**0.001**
	0.4, MLL –3	**1**	**0.001**	**0.867**	**0.001**
	MLL –1, MLL –3	**0.942**	**0.001**	0.360	0.001
December	Global	0.443	0.001	0.281	0.001
	MLL, 0.4	0.067	0.255	–0.130	0.827
	MLL, MLL –1	0.421	0.014	0.349	0.023
	MLL, MLL –3	**0.913**	**0.005**	**1**	**0.005**
	0.4, MLL –1	0.159	0.071	0.043	0.251
	0.4, MLL –3	**0.599**	**0.002**	0.350	0.001
	MLL –1, MLL –3	0.477	0.003	0.376	0.001

spp., and Oligochaeta (Fig. 3.6). The seasonal patterns of most of these taxa were also similar to that of *C. fluminea,* with a peak in late autumn, especially in 2006 (Fig. 3.8). Therefore, the pronounced differences in the NMDS ordination and ANOSIM analyses could also be due to correlations with the seasonal distribution of benthic taxa. To exclude possible correlated effects, we analyzed September and December samples from MLL –1 m.

We pooled these samples to increase the number of replicates; the samples did not show seasonal differences for biomass data (with respect to *R*- and *p*-values). Samples from 0.4-m depth, MLL, and MLL –3 m were excluded from the analyses because only the two lowest biomass classes of *C. fluminea* were present in samples from September and December. When we considered all taxa together, samples containing high biomasses of *C. fluminea* (classes 3 and 4)

Table 3.2. ANOSIM results. The seasonal differences were separated for each sampling month. Pronounced differences are in bold.

Season	Test	Density *R*	Density p	Biomass *R*	Biomass p
All depths	Global	0.165	0.001	0.050	0.017
	Dec, Mar	0.134	0.001	0.096	0.011
	Dec, Jun	0.251	0.001	0.160	0.001
	Dec, Sep	0.156	0.001	0.010	0.287
	Mar, Jun	0.333	0.001	0.107	0.015
	Mar, Sep	0.151	0.004	0.044	0.102
	Jun, Sep	0.128	0.009	0.002	0.432
0.4 m	Global	0.497	0.001	0.233	0.003
	Dec, Mar	**0.542**	**0.001**	–0.007	0.425
	Dec, Jun	0.371	0.010	0.346	0.017
	Dec, Sep	0.282	0.003	0.292	0.008
	Mar, Jun	**0.680**	**0.002**	**0.526**	**0.011**
	Mar, Sep	**0.620**	**0.001**	0.430	0.003
	Jun, Sep	**0.943**	**0.002**	0.004	0.383
MLL	Global	0.334	0.002	0.387	0.002
	Dec, Mar	**0.512**	**0.024**	**0.710**	**0.012**
	Dec, Jun	**0.870**	**0.012**	**0.938**	**0.012**
	Dec, Sep	0.415	0.035	–0.097	0.655
	Mar, Jun	0.485	0.004	**0.604**	**0.002**
	Mar, Sep	0.386	0.006	**0.572**	**0.001**
	Jun, Sep	0.166	0.105	0.286	0.020
MLL –1 m	Global	0.419	0.001	0.199	0.008
	Dec, Mar	0.102	0.143	0.192	0.059
	Dec, Jun	0.310	0.023	0.298	0.018
	Dec, Sep	0.319	0.002	–0.006	0.447
	Mar, Jun	**0.604**	**0.002**	0.244	0.008
	Mar, Sep	**0.596**	**0.001**	0.252	0.023
	Jun, Sep	**0.657**	**0.001**	0.391	0.007
MLL –3 m	Global	**0.691**	**0.001**	0.132	0.023
	Dec, Mar	0.253	0.022	0.239	0.039
	Dec, Jun	**0.569**	**0.001**	0.187	0.075
	Dec, Sep	**0.776**	**0.001**	0.067	0.171
	Mar, Jun	**0.691**	**0.002**	0.322	0.022
	Mar, Sep	**0.568**	**0.001**	0.043	0.308
	Jun, Sep	**0.983**	**0.001**	0.183	0.076

were separate from samples of the lowest biomass class (Table 3.4). This is due to epifauna because epifaunal taxa samples containing the highest *C. fluminea* biomass differed pronouncedly from samples of biomass class 1 (Table 3.4). In contrast, infaunal taxa did not respond to the different biomass classes of *C. fluminea* (Table 3.4, Fig. 3.10). The three species that contributed most to the epifaunal taxa differences in MLL –1 m (September and December) among the four examined biomass classes of *C. fluminea* were *D. polymorpha*, *P. antipodarum*, and *B. tentaculata* (SIMPER, Table 3.5).

The epifaunal taxa *D. polymorpha* (Spearman-Rank test; $p = 0.005$), *Potamopyrgus antipodarum* ($p < 0.001$), *Bithynia tentaculata* ($p = 0.003$), Hirudinae ($p = 0.007$), *Caenis* spp. ($p = 0.009$), Trichoptera ($p = 0.004$), and epifaunal chironomids ($p = 0.014$) showed a significant positive correlation with the increasing biomass of *C. fluminea*, whereas the infaunal taxa Nematoda ($p = 0.520$), Oligochaeta ($p = 0.994$), juveniles of *Corbicula fluminea* ($p = 0.515$), *Pisidium* spp. ($p = 0.849$), and infaunal chironomids ($p = 0.303$) did not (Fig. 3.11).

Table 3.3. ANOSIM results. The differences of benthic community in relation to *C. fluminea* biomass were separated for each sampling depth. Pronounced differences are in bold.

		Density		Biomass	
	Test	*R*	p	*R*	p
All depths	Global	0.315	0.001	0.349	0.001
	1, 2	0.126	0.003	0.177	0.001
	1, 3	**0.513**	**0.001**	**0.587**	**0.001**
	1, 4	**0.509**	**0.001**	**0.570**	**0.001**
	2, 3	0.192	0.001	0.215	0.001
	2, 4	0.336	0.001	0.250	0.001
	3, 4	0.145	0.029	0.220	0.002
MLL –1 m	Global	0.261	0.003	0.254	0.004
	1, 2	–0.118	0.858	–0.051	0.654
	1, 3	0.213	0.087	0.463	0.024
	1, 4	0.309	0.027	**0.638**	**0.001**
	2, 3	0.112	0.210	0.110	0.186
	2, 4	0.406	0.001	0.340	0.003
	3, 4	**0.784**	**0.001**	0.306	0.055
MLL –3 m	Global	–0.178	0.988	–0.031	0.593
	2, 3	–0.139	0.951	–0.017	0.562
	2, 4	–0.355	0.963	–0.252	0.875
	3, 4	–0.469	1	–0.093	0.704

Table 3.4. ANOSIM results. The differences of benthic community in relation to *C. fluminea* biomass were separated for each sampling depth (data from September and December are pooled). Pronounced differences are in bold.

			Biomass	
		Test	*R*	p
All taxa	MLL –1 m	Global	0.313	0.011
		1, 2	0.125	0.039
		1, 3	**0.648**	**0.029**
		1, 4	**0.604**	**0.003**
		2, 3	–0.036	0.554
		2, 4	0.272	0.039
		3, 4	0.307	0.114
	MLL –3 m	Global	–0.014	0.486
Epifauna	MLL –1 m	Global	0.361	0.007
		1, 2	0.075	0.286
		1, 3	0.407	0.086
		1, 4	**0.648**	**0.003**
		2, 3	0.077	0.304
		2, 4	0.280	0.042
		3, 4	0.225	0.173
	MLL –3 m	Global	0.012	0.405
Infauna	MLL –1 m	Global	0.048	0.193
	MLL –3 m	Global	–0.071	0.682

Table 3.5. Contribution of individual species to the dissimilarities between two groups of samples classified into different biomass classes of *C. fluminea* in SIMPER-analyses for biomass data of epifaunal taxa at MLL –1 m (September and December samples were pooled; data were square-root transformed). See Materials and methods for the definitions of the classes.

Species	Average dissimilarity	Dissimi-larity/ SD	Contribution (%)	Cumu-lative (%)
C. fluminea biomass class 1 & 2 Average dissimilarity = 63.15				
D. polymorpha	48.9	1.7	77.5	77.5
B. tentaculata	3.7	0.8	5.8	83.4
M. minutissima	2.7	0.7	4.3	87.7
P. antipodarum	2.2	1.4	3.5	91.1
C. fluminea biomass class 1 & 3 Average dissimilarity = 75.87				
D. polymorpha	45.5	1.7	60.8	60.8
R. auricularia	9.5	1.0	12.6	73.4
P. antipodarum	7.4	0.8	9.9	83.3
B. tentaculata	4.7	0.9	6.4	89.7
L. benedeni	2.7	1.0	3.6	93.3
C. fluminea biomass class 1 & 4 Average dissimilarity = 80.47				
D. polymorpha	56.4	2.2	70.1	70.1
P. antipodarum	10.6	0.9	13.2	83.3
B. tentaculata	5.8	1.1	7.2	90.4
C. fluminea biomass class 2 & 3 Average dissimilarity = 64.96				
D. polymorpha	39.7	1.4	61.1	61.1
R. auricularia	6.7	1.0	10.3	71.4
P. antipodarum	6.6	0.8	10.2	81.6
B. tentaculata	4.2	0.8	6.5	88.0
L. benedeni	1.9	0.9	2.9	90.9
C. fluminea biomass class 2 & 4 Average dissimilarity = 69.72				
D. polymorpha	50.1	2.3	71.9	71.9
P. antipodarum	8.6	1.0	12.3	84.3
B. tentaculata	4.6	1.0	6.5	90.8
C. fluminea biomass class 3 & 4 Average dissimilarity = 61.77				
D. polymorpha	40.0	1.6	64.8	64.8
P. antipodarum	7.5	1.1	12.2	76.9
B. tentaculata	4.6	1.2	7.5	84.4
R. auricularia	3.6	0.9	5.8	90.2

Discussion

C. fluminea population development

In the United States, cold winters with water temperatures around 2 °C for at least 2 months have often destroyed complete *C. fluminea* populations (French & Schloesser 1991, and 1996, Morgan *et al.* 2003, Mattice & Dye 1976). In Lake Constance, low water temperatures strongly influenced the population development and shell growth of *C. fluminea*. During winter 2005/2006, a centennial low-water level associated with very low water temperatures caused a mass mortality of *C. fluminea*, with only ~3% of their biomass remaining (Fig. 3.3). The dead soft bodies of *C. fluminea* floated in the water, and their empty valves increased the surface area of the lake bottom considerably (Werner & Rothhaupt 2007, Werner & Rothhaupt 2008). Such a production of bivalve shells can play a major role in the organization of invertebrate communities in aquatic environments, i.e., through ecosystem engineering (Gutiérrez *et al.* 2003).

Generally, dispersal of both adult and juvenile *C. fluminea* in our study area was limited. We found them only in very low densities in shallow depths (MLL and 0.4-m depth). After the mass mortality, juvenile *C. fluminea* of the year, which are released by the remaining maternal clams in a non-planktonic crawling stage (Britton & Morton 1979, Karatayev *et al.* 2005), resettled orphaned areas in low densities. It took 18 months for the *C. fluminea* population to recover completely. In contrast, the *D. polymorpha* population in Lake Constance recovers annually after the strong predation (> 90%) by wintering waterbirds (Werner *et al.* 2005, Mörtl *et al.*, in press), possibly because their planktonic veliger larvae disperse much better than juvenile *C. fluminea* (Karatayev *et al.* 2005).

Although no conspicuous mortality of *C. fluminea* occurred after the mass mortality in winter 2005/2006, the *C. fluminea* population at MLL –1 m decreased again between September and December 2007. This decrease could have been caused by predation by wintering waterbirds, which discovered infaunal *C. fluminea* as a new substantial food source just a few years after the invasion. Waterbird faeces at our study site contained ground valves of *C. fluminea* (personal observation), and the gut of a Tufted Duck *Aythya fuligula* drowned in a fishing net in January 2008 contained one *C. fluminea* (> 10 mm in length) along with zebra mussels (Matuszak & Werner, personal observation). *C. fluminea* is the main food item of the diving duck *Aythya affinis* in South Carolina (Hoppe *et al.* 1986).

Reproduction and growth of *Corbicula fluminea* begins at 10–11 °C (reviewed in Karatayev *et al.* 2005), and our results support these observations. *C. fluminea* shell growth stopped during winter (December to March), and growth rates decreased with depth in the warmer seasons, probably because the water temperatures declined with depth (Fig. 3.2). At MLL –3 m, water takes longer to warm up, but in autumn, it retains the warmth much longer than shallower depths. Therefore, shell growth of *C. fluminea* at MLL –3 m was better between September and December than at MLL -1 m. The growth rates at MLL –1 and MLL –3 m were lower than those of other populations of *C. fluminea* because during their first year, individuals only reached an average size of 5–7 mm. Under normal conditions, they are able to reach 16–30 mm (discussed in Mouthon 2001); we found such growth rates at MLL. Slow growth rates can be caused by unfavorable conditions, such as low mineral content (Ca^{2+}), slightly acidic water, low water temperature, low food availability, and an adverse hydraulic regime (see Mouthon 2001). In our study, we can exclude only the two former factors (IGKB, 2004b).

Water temperature also strongly influenced the recruitment of *C. fluminea*. We usually found one cohort of juveniles at the more densely populated depths of MLL –1 m and MLL –3 m, except during the exceptionally warm summers of 2003 and 2005, when two cohorts appeared. The water temperatures in June 2003 were 6.4 °C above the long-term average, and in June 2005, they were 2.1 °C higher (IGKB, 2004a and 2006). In contrast, at the quickly warming depth MLL, we usually found two annual cohorts of juveniles. Although the number of cohorts at this depth was usually higher, these fast-growing cohorts are at high risk of extinction when the lake at this level regularly dries up.

After winter 2005/2006, with water temperatures close to the survival limit, the shell growth of the remaining individuals was interrupted, even though *C. fluminea* can use various food sources, by, e.g., filtering algae and feeding from sediments (Reid *et al.* 1992, Hakenkamp & Palmer 1999, Hakenkamp *et al.* 2001). Mouthon (2001) reported a particularly long period of reduced shell growth rates of *C. fluminea* after a snow melt.

The physical stability of the different depths was reflected by the mean number of *C. fluminea* cohorts recorded per sampling (Fig. 3.4), as the number of cohorts increased with decreasing hydraulic stress, which can affect the life cycle of *C. fluminea* (Mouthon 2001).

The maximum life span of *C. fluminea* was 4 years, which compares well with that of other *C. fluminea* populations (reviewed in McMahon 1999).

Community patterns

Vertical gradients, such as sheer stress caused by wave action, light attenuation, water temperature, substrate particle size, and macrophyte stands, can influence the benthic community (Scheifhacken *et al.* 2007, Strayer & Malcom 2007, Zbikowski & Kobak 2007). The assemblage at our sampling site showed a high spatial and temporal variability. Samples from adjacent depths were more similar to each other than were samples from more distant depths, which is accounted for by gradual changes of invertebrate communities with water depth (Baumgärtner *et al.*, in press). Although the influence of dominant taxa on the NMDS ordination was downplayed by square-root-transformed data, density and biomass changes of the most common species contributed more to the differences than an exchange of species. This indicated that different depth zonation might be caused by sheer stress and the therewith-linked habitat stability (c.f., Death & Winterbourn 1995).

Owing to our sampling design, the largest variation in the community structure at a single depth occurred at 0.4 m, where sampling sites varied spatially with the water level. In summer, the 0.4-m depth was in the eulittoral zone, but in December and March, it was deeper than the MLL, which fell dry. At the two eulittoral depths of 0.4 m and MLL, the variation in the benthic assemblage was not only caused by seasonal differences, but also differed depending on whether the water level was sinking or rising prior to sampling. At the study site Rohrspitz, a minor increase in the water level leads to flooding of large areas that are barely reachable for less-mobile taxa, such as mollusks, because the MLL depth zone can attain several hundred meters in width. Re-flooded areas were very poor in species composition, total abundance, and especially biomass. The re-colonization of re-flooded areas by macroinvertebrates depended on the duration of the flooding and on the different abilities of taxa to spread and to use the poorly available food sources in recently flooded habitats, such as the scarce episamnic algae and coarse particulate organic matter (Baumgärtner *et al.*, in press). Short-term variations in species arrival can influence the outcome of interspecific interactions (Morin 1999). As the water levels decreased, less-mobile taxa also had problems retreating from droughts; for example, taxa that burrowed into the sand, such as *C. fluminea,* did not survive (Werner & Rothhaupt 2008).

Compared to the eulittoral zone, the infralittoral zone provides a more stabile habitat for colonization because sediment relocations are less frequent and less intensive at greater depths (Röck 1999), which enables more-competitive species to increase their dominance in the community (Death & Winterbourn 1995). In our study, biomass, density, and number of species generally increased with depth. Thus, we can assume that the therewith-linked habitat stability increased productivity. In a survey of ten streams and a wind-swept lake, species richness and density were markedly higher at more-stable sites, but species evenness peaked at sites of intermediate stability (Death & Winterbourn 1995). In streams, disturbance is important for species diversity (Townsend *et al.* 1997, Cowie *et al.* 2000), as it can reduce the dominance of single taxa. Compared to assemblages of the soft-bottoms, assemblages of the stony littoral zones at Upper Lake Constance had the highest biomass, density, and diversity of taxa at MLL and MLL –1 m; values decreased at both deeper and shallower water depths (Baumgärtner 2004, Mörtl 2005). The authors of these studies assumed that this pattern might be due to the intermediate disturbance hypothesis by Connell (1978), although the substrate above MLL –2 m (stones on sand) was more diverse than in the infralittoral zone below MLL –2 m (sand and clay). Compared to a rocky habitat, spatial heterogeneity was less pronounced at our soft-bottomed study site and distribution of taxa was less patchy. Our results further show that abundance, biomass, and taxa number increased with depths and associated habitat stability when sediment qualities were consistent across all depths. Therefore, we assume that the availability of space, e.g., in terms of hard substrates or macrophytes providing habitat and refuge for invertebrates, is more important for community organization than the intermediate occurrence of disturbances. This supports the hypothesis of Quinn *et al.* (1998), which states that space is a limited resource in the littoral zone of lakes.

The benthic assemblages between June and September differed significantly at 0.4-m depth, MLL –1 m, and MLL –3 m, but the communities within each of the two months in consecutive years were relatively similar to each other. In contrast, in March and December, benthic communities showed a higher variability among years. MLL was even dry twice during sampling. These patterns may be due to different abiotic and biotic factors that annually recur during the same period, such as recruitment of juveniles, age-related mortality, and predation by wintering waterbirds, which could cause higher variability during winter (Mörtl *et al.*, in press).

Species patterns and impact of *C. fluminea*

C. fluminea or *D. polymorpha* dominate the benthic community in lakes in which they occur and comprise more than 95% of the biomass (see Karatayev *et al.* 2003). Our results confirmed this also for Lake Constance. In the soft-sediment environment of our study site, *C. fluminea* and *D. polymorpha* comprised 95.2% of the total biomass and 39.7% of the total abundance of the benthic community. On hard substrates, *D. polymorpha* builds more than 90% of the biomass of the total community (Mörtl 2005). Living infaunal *C. fluminea* can influence benthic invertebrates mainly by biotic effects, such as nutrient reallocation, bioturbation, and organic matter production by biodeposition of faeces and pseudofaeces (Vaughn & Hakenkamp 2001, Werner & Rothhaupt, in press). However, *C. fluminea* valves that lie on the soft sediment provide physical habitat and interstitial refuges (Werner & Rothhaupt 2007). *D. polymorpha* and other hard-substrate-preferring species have not yet been able to gain ground on fine particulate substrates in the shallow water zone of Lake Constance (Werner & Rothhaupt 2007), even though *D. polymorpha* is known to settle even on mudflats (Berkman *et al.* 1998). Since its invasion, the burrowing *C. fluminea* and their valves act as biogenous hard substrate on soft bottoms, which builds a settling core for *D. polymorpha* aggregations (druses); *D. polymorpha* even settles on completely burrowed living *C. fluminea.* This explains why *D. polymorpha* densities at MLL –1 m increased significantly with the biomass of *C. fluminea* (Fig. 3.11). Since epifaunal bivalves have a greater potential to change benthic communities than infaunal clams (Karatayev *et al.* 2003), we cannot differentiate between effects of *C. fluminea* and *D. polymorpha* on the epifaunal benthic taxa, which also showed a significant positive correlation with increasing biomass of *C. fluminea* at MLL –1 m (Fig 3.11). *D. polymorpha* is an ecosystem engineer (Strayer *et al.*, 1999) that causes severe changes in invertebrate communities (Ricciardi *et al.* 1997, Stewart *et al.* 1998, Karatayev *et al.* 1997, Mörtl & Rothhaupt 2003). Especially epifauna facilitates from the presence of *D. polymorpha* because of the enhanced complexity of the settlement surface provided in the form of valves and because of biodeposition of organic matter (Botts *et al.* 1996, Karatayev *et al.* 1997, Stewart *et al.* 1998, Nalepa *et al.* 2003, Ward & Ricciardi 2007).

Infaunal taxa such as Nematoda, Oligochaeta, *Pisidium* spp., and Chironominae did not respond to the increasing biomass of *C. fluminea* (Fig. 3.11). Infauna does not profit from *D. polymorpha* (Ward & Ricciardi 2007) because structural diversity of surfaces does not facilitate infaunal invertebrates. Additionally, the number of juvenile *C. fluminea* did not correlate with the biomass of conspecifics. Our former findings have shown that juveniles of *C. fluminea* settle at lower densities when living adult *C. fluminea* are present than when valves on sand or only bare sand are present (Werner & Rothhaupt 2007). The settlement of many juvenile bivalve species is negatively influenced by chemical cues of adult conspecifics (Butman 1987, Dodson *et al.* 1994, Anderson 1996).

While most invertebrates preferred only the deeper section of the littoral zone, Nematoda, *Caenis* spp., and Chironominae occurred over a broader part of the depth gradient and *Bezzia* sp. inhabited mainly the shallow part of the littoral zone (Fig. 3.6). *D. polymorpha*, *B. tentaculata*, *H. stagnalis*, and *D. villosus* showed a seasonal pattern similar to that of *C. fluminea,* with a peak in September, and they showed the same depth distribution as *C. fluminea.* These similar patterns could, on one hand, be attributed to the combined effects of *C. fluminea* and *D. polymorpha*, but, on the other hand, they might also be driven by factors that act simultaneously on the total benthic community, such as water temperature, water-level fluctuations, or predation by wintering waterbirds. For example, the seasonal dynamics of *D. polymorpha* in Lake Constance are regulated by waterbird predation in winter and by re-colonization during summer (Werner *et al.* 2005, Mörtl *et al.*, in press). Since waterbirds positively select for food particles > 7 mm in length or >4 mm in diameter (Suter 1982a) and up to 40,000 diving ducks and coots regularly occur in the surroundings of our study site (Heine *et al.* 1999), all larger benthic taxa might be directly subjected to strong predation. The infaunal taxa Oligochaeta, *Pisidium* spp., Chironominae, and Nematoda, as well as the smaller taxa *Caenis* spp., *Mystacides* spp., and *Bezzia* sp. showed no clear seasonality. This may be in part due to a more difficult perceptibility for preying birds, but the aggregation of several species to one taxon may also conceal seasonal patterns. For example, Chironominae seem to show two annual peaks, which may actually be the emergence of different species at different times. Except for the emergence of *Bezzia* sp. between March and June 2006, we did not observe the emergence of insect larvae in spring and predation by benthivorous fish, such as perch and ruffe during summer (Dieterich *et al.* 2004, Scheifhacken 2008).

Seasonal changes in biomass were slighter than seasonal changes in density. Biomass was less susceptible to population recruitment than density because juveniles of low weight could be extremely abundant. For example, the high density yet low biomass of *D. polymorpha* in autumn 2006 illustrates the lack of older individuals. Differences between abundance and biomass of the invasive amphipod *D. villosus* among the seasons also point to the occurrence of different life stages. Although *D. villosus* favors hard substrates (Hesselschwerdt *et al.*, in press), it has occurred at our soft-bottomed study site, dominated by *C. fluminea,* since September 2004. Amphipods facilitate from *D. polymorpha*-mediated effects (Gonzalez & Downing 1999, Mörtl & Rothhaupt 2003). The predacious *D. villosus* arrived at Lake Constance in 2002 and quickly repelled other amphipods throughout the lake (Mürle *et al.* 2004, Mörtl *et al.* 2005). *D. villosus* causes massive changes in benthic communities (Dick *et al.* 2002, van Riel *et al.* 2006). The negative consequences of *D. villosus* on benthic assemblages reveal the threat of biological invasions. Not all biological invasions are as harmless as that of *D. polymorpha* in Lake Constance, which facilitated most indigenous species (Mörtl & Rothhaupt 2003). Seven species of biological invaders at our study site, including *C. fluminea, D. polymorpha,* and *D. villosus,* have been recorded to date. The invasive gastropod *Potamopyrgus antipodarum,* has reached high densities of up to 16,768 individuals m^{-2}; however, the impact of this species on benthic assemblages seems to be unimportant compared to the impact of bivalve invaders.

Structure-dependent influence of *C. fluminea*

Infaunal taxa were neither impacted by *C. fluminea* nor by the therewith-correlated presence of *D. polymorpha* because they do not facilitate from increasing sediment surfaces. On the contrary, we would expect them to decrease in number when bivalves settle in high densities

(Ward & Ricciardi 2007) because of the loss of infaunal habitat close to the substrate surface. However, such high densities of bivalves did not occur at our study site.

In marine systems, epifauna is unable to occupy soft sediments lacking mussel beds (Dittman 1990, Robinson & Griffith 2002). Ward and Ricciardi (2007) found that effects of *D. polymorpha* are greatest on fine sediments and that *Dreissena*-associated communities on soft sediments include organisms more typical for rocky substrate; biotic effects seem to be of less importance for the community composition (Stewart *et al.* 1998). Karatayev *et al.* (2003) found no correlation between densities of *C. fluminea* and other benthic invertebrates, but the part of the reservoir that was dominated by *C. fluminea* had a variety of substrates. In our study, densities of most epifaunal invertebrates increased with the biomass of *C. fluminea,* but only at MLL –1 m, where only bare sand without macrophytes is found. In contrast, taxa at MLL –3 m showed no correlation with increasing *C. fluminea* biomass. The MLL –3 m depth was dominated by highly structured macrophyte species, such as charophytes and broad-leafed *Potamogeton perfoliatus*, from June to at least December. The macrophytes greatly increased the available settlement area for invertebrates compared to the bare substrates at MLL –1 m. Macroinvertebrate densities in plant beds are several-fold higher than non-vegetated sediments (Strayer & Malcom 2007). The effect of the valves at MLL –3 m was negligible compared to the macrophyte-mediated surface increase, whereas at MLL –1 m, the increase in structural diversity and surface caused by *C. fluminea* (Werner & Rothhaupt 2007) and associated *D. polymorpha* strongly enhanced settlement area for epifaunal invertebrates on the otherwise unstructured bare sand. High densities of *C. fluminea* additionally may stabilize the sediment at the more sheer-stressed depth MLL –1 m, and thus facilitate colonization of different benthic taxa or even macrophytes. Increased habitat stability is positively linked with the density of invertebrates (Death & Winterbourn 1995).

Conclusions

Pronounced similarities of samples within a depth zone and significant differences between adjacent zones support the hypothesis that water depth is a key factor in the structuring of the littoral community. The benthic assemblage is influenced by physical disturbance, such as water-level fluctuations or the impact of wave action, since the number of taxa as well as their density and biomass increased with water depth and the therewith-linked habitat stability. Temporarily changing abiotic and biotic factors co-determine the structure of the benthic community, which resulted in a seasonal variability with a yearly recurring pattern. Additionally, the community structure differences were largely the result of dominance structures, mainly of the two invasive bivalves *C. flumi-*

nea and *D. polymorpha*. Therefore, biotic interactions are also of particular importance in organizing community structures in the littoral zone. Although *C. fluminea* and *D. polymorpha* often co-occur in the same freshwater bodies, they are claimed to have a contrasting distribution (Karatayev *et al.* 2005); however, at our study site, *D. polymorpha* uses *C. fluminea* as a settling substrate. Before the invasion of *C. fluminea,* taxa typical for rocky substrates did not inhabit soft bottoms in the littoral zone of Lake Constance. Now, the physical and biotic effects of *C. fluminea* facilitate *D. polymorpha* and most epifaunal taxa in an otherwise unstructured sandy zone. Biotic effects of bentho-pelagic coupling by the invasive bivalves seemed to be of less importance for community structure, since in habitats with high structural diversity, e.g., mediated by macrophytes, *C. fluminea* had no effect on benthic communities. It remains unclear whether the positive correlation of epifaunal taxa with *C. fluminea* biomass is direct or whether it is due to the increase of *D. polymorpha* mediated by *C. fluminea*. Nevertheless, our study provides a basis for a better understanding of biotic invasions and the ecological consequences that drive spatial and temporal patterns in the littoral community.

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Annex 1. The 45 most common taxa at our study site in Lake Constance and their frequency of occurrence, biomass, and density, averaged over all samples.

Taxon	Frequency of occurrence [%]	Density [ind. m^{-2}]	± SE	Bio mass [mg dry wt. m^{-2}]	± SE
Nematoda	100.0	4883.5	355.0	24.4	1.8
Oligochaeta	96.8	998.5	103.8	23.4	3.3
Turbellaria	2.4	0.4	0.2	0.0	0.0
Erpobdella octoculata	25.0	22.6	6.6	19.7	5.7
Helobdella stagnalis	36.3	32.0	7.7	24.3	5.8
Glossiphonia complanata	9.7	2.8	0.9	4.3	1.4
Other Hirudinea	15.3	3.9	1.2	3.2	1.0
Bithynia tentaculata	49.2	362.5	71.6	8301.4	1670.5
Gyraulus albus	0.8	0.3	0.3	0.0	0.0
Gyraulus parvus	12.1	6.3	2.8	12.3	5.3
Potamopyrgus antipodarum	61.3	867.6	222.1	3279.6	839.4
Radix auricularia	16.1	8.1	2.5	642.1	195.5
Valvata piscinalis	16.9	12.1	3.4	19.3	5.4
Other Gastropoda	1.6	0.8	0.5	0.8	0.6
Dreissena polymorpha	83.9	5570.7	1214.0	116894.7	30179.5
Corbicula fluminea	80.6	4427.6	831.4	169037.6	33438.5
Sphaerium corneum	0.8	0.3	0.3	14.9	14.9
Pisidium amnicum	32.3	12.3	2.3	764.3	141.8
Pisidium spp.	95.2	558.1	72.3	1006.5	130.4
Ephemera danica	11.3	3.1	0.9	1.2	0.4
Caenis spp.	57.3	101.9	19.6	5.0	0.9
Centroptilum luteolum	5.6	1.4	0.6	1.4	0.8
Athripsodes spp.	29.0	36.4	12.6	5.1	1.5
Ceraclea spp.	16.9	9.2	2.4	1.3	0.4
Hydroptila spp.	0.8	0.1	0.1	0.1	0.1
Mystacides spp.	40.3	114.1	31.6	4.2	1.1
Oecetis lacustris	21.8	15.2	5.5	8.6	3.0
Orthotrichia	3.2	0.6	0.3	0.0	0.0
Tinodes waeneri	0.8	0.1	0.1	0.0	0.0
Leptoceridae, juveniles	36.3	49.4	15.8	2.2	0.7
Other Trichoptera	0.8	0.1	0.1	0.1	0.1
Micronecta minutissima	63.7	256.4	56.4	2.7	0.5
Dikerogammarus villosus	14.5	6.2	2.0	14.5	6.8
Gammarus roeselii	1.6	0.3	0.2	0.0	0.0
Limnomysis benedeni	7.3	3.6	1.7	2.7	1.2
Ostracoda	98.4	2199.6	422.9	4.4	0.8
Chironominae	98.4	3971.1	496.7	82.0	7.5
Chironomidae pupae	47.6	33.5	5.9	7.7	1.4
Corynoneura sp.	1.6	0.3	0.2	0.0	0.0
Orthocladinae	87.1	324.1	60.2	18.4	4.3
Tanypodinae	45.2	41.9	9.6	0.5	0.1
Bezzia sp.	45.2	108.0	23.9	10.8	2.4
Coleoptera	3.2	0.5	0.3	0.1	0.0
Acari	69.4	147.4	22.5	15.5	2.4
Hydra sp.	2.4	0.5	0.3	0.1	0.0
Non-indigenous species	**91.9**	**10,882**	**16,869**	**289,241**	**625,540**
Indigenous species	**100.0**	**14,313**	**11,031**	**11,020**	**21,127**
Total sum	**100.0**	**25,195**	**25,792**	**300,261**	**631,785**

4 Effects of the invasive bivalve *Corbicula fluminea* on settling juveniles and other benthic taxa

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Abstract

The Asian clam *Corbicula* has become established worldwide in a wide range of freshwater ecosystems. *Corbicula fluminea* invaded Lake Constance (Central Europe) between 2000 and 2002 and has reached densities up to 3520 individuals > 5 mm in length per m^2 in sa ndy areas. However, whether this species affects other benthic invertebrates remains unclear. Here, we show that ecosystem engineering via shell production by *C. fluminea* in Lake Constance considerably increases availability of hard surfaces in primarily soft-bottomed habitats. We studied effects of *C. fluminea* on littoral communities of sandy habitats using boxes containing bare sand, sand with *C. fluminea* shells (2000 m^{-2}), and sand with live clams (1000 m^{-2}). After 2 month of exposure, the overall benthic community did not differ among treatments, but density of the mayfly *Caenis* spp. increased in boxes containing shells compared to the boxes containing sand or sand with live clams (analysis of variance [ANOVA], $p < 0.0001$). The density of shells greatly increases after mass mortality of *C. fluminea* populations. Our results indicate that shells can provide valuable hard surfaces for species preferring structured habitats, especially in unstructured soft-bottomed habitats. In addition, density of juvenile *C. fluminea* was lower in boxes containing live adult clams than in boxes containing sand or sand and shells (ANOVA, $p = 0.0048$), possibly because of a chemical cue that might hinder settlement of juveniles in areas with high intraspecific concurrence.

Key words Asian clam, ecosystem engineering, hard substrate, macroinvertebrate, chemical cue, *Dreissena polymorpha*, Ephemeroptera

Introduction

Nonindigenous bivalves can alter community structure and ecosystem processes considerably (Stewart *et al.* 1998, Nalepa *et al.* 2003). Invasive bivalves, when present, often dominate the biomass of the benthic community in littoral zones of lakes and lake outlets and exert control as dominant filter feeders over ecosystem structure and function (Strayer *et al.* 1999, Vaughn & Hakenkamp 2001). Among the most invasive species are clams of the genus

Corbicula (Morton 1979). Originating from southeast Asia, *Corbicula fluminea* was introduced into North and South America (McMahon 1982, Ituarte 1981, Darrigran 2002) and Europe (Mouthon 1981, den Hartog *et al.* 1992). In Germany, it quickly replaced the zebra mussel as the dominant mollusk in large rivers (Bachmann *et al.* 2001). Within 15 years, the clam colonized the entire River Rhine up to the Swiss border (Turner *et al.* 1998).

Between 2000 and 2002, *C. fluminea* invaded the pre-alpine Lake Constance (Werner & Mörtl 2004), where it reaches local densities of up to 3520 individuals > 5 mm in length per m^2 and can constitute up to 90% of the biomass of the littoral community (see Chapter 3). Temperatures < 2 °C (French & Schloesser 1991) and low water levels (White & White 1977) can kill *Corbicula*; thus, severe conditions during winter have caused periodic mass mortalities with only 1% of the littoral *C. fluminea* population remaining in Lake Constance (Werner & Rothhaupt 2008). After such mass mortalities, soft substrates are littered with shells of dead clams. In aquatic environments, shells of many bivalve species are persistent and often abundant physical structures that are important for invertebrate community organization (Gutiérrez *et al.* 2003).

Organisms that create, modify, and maintain habitats — such as mollusks via shell production — are ecosystem engineers (Jones *et al.* 1994). In addition to engineering effects of empty shells, live burrowing bivalves can influence benthic communities by bioturbation and biodeposition of faeces and pseudofaeces, which produces organic matter (Vaughn & Hakenkamp 2001). Therefore, effects of empty shells and living clams might influence populations of other species. However, interactions between *Corbicula* and benthic invertebrates have rarely been studied (Vaughn & Hakenkamp 2001, Karatayev *et al.* 2005).

Our objective was to determine whether living buried *C. fluminea* and their empty shells could influence benthic macroinvertebrate populations. We studied the effect of *C. fluminea* on littoral communities of sandy habitats in Lake Constance in boxes containing live clams, shells, or bare sand, respectively. We postulated that *C. fluminea* shells would alter substrate characteristics and generate a habitat for taxa preferring hard substrates, thereby allowing these taxa to increase in density. Furthermore, we hypothesized that deposition of organic matter by *C. fluminea* would increase the density of many invertebrates that feed in sediments. In addition, because of the ability of *C. fluminea* to invade unsettled areas quickly, we postulated that juvenile *C. fluminea* would colonize areas without competing conspecifics faster than areas already settled by conspecifics.

Methods

Study area

Lake Constance is a pre-alpine, oligotrophic lake in Central Europe bordering Germany, Switzerland, and Austria. Water levels fluctuate annually within 2 m, depending largely on the unregulated alpine system of the Rhine River. Lake Constance features 2 ecologically distinct basins: 1) the shallow, nutrient-rich Lower Lake Constance that covers 63 km^2 and 2) the larger, deeper, nutrient-poor Upper Lake Constance (maximum depth: 254 m, mean depth: ~100 m) that covers 473 km^2 (Internationale Gewässerschutzkommission für den Bodensee 1999).

We conducted our study in the south-eastern part of Upper Lake Constance near the city of Bregenz. The study site (lat 9°37′00.4″E, long 47°30′00.3″N) is a large, sandy, shallow-water zone that was invaded by *Corbicula fluminea* between 2000 and 2002. Clam densities fluctuate annually depending on water level and temperature variations. We carried out our experiment in summer 2005 at a depth of 3 m, where the substratum consists of fine sand particles with a grain size of 200 to 630 μm (90%) and of coarse sand particles with a grain size of 630 μm to 2 mm (10%). We chose this depth to avoid disturbance by wave action and bathers. The actual water depth fluctuated between 3.5 and 4.5 m during the experiment because of a flood in late August.

Experimental design

To detect effects of *C. fluminea* on the macroinvertebrate community, we used boxes containing: 1) bare sand (control), 2) sand with empty *C. fluminea* shells arising from 1000 dead individuals at a naturally occurring density of 2000 single shells m^{-2} (to detect ecosystem engineering effects caused by increased surface area and substrate diversity), and 3) sand with live adult *C. fluminea* at a naturally occurring density of 1000 ind. m^{-2} (to detect effects of organic matter deposition and bioturbation). Four replicate samples of each treatment (a total of 12 boxes) were used so that the standard error of replicate samples averaged 20% for invertebrate taxa with a density of 300 ind. m^{-2}. A ccording to Downing (1984), 3 replicates would be required to meet this criterion.

We randomly chose live clams > 5 mm in length from the study site a week before placing the boxes; mean shell length was 15.5 ± 3.2 mm. We collected shells of dead clams > 5 mm from the drift line at the study site and dried them; mean shell length was 15.1 ± 2.7 mm.

In late July, we exposed 12 open plastic boxes (37 × 26.7 × 17 cm) at the study site. We half filled each box with dry sand (9.42 ± 0.22 kg) originating from the study site. We sieved the sand with a 2-mm mesh to exclude hard substrata, such as stones, pebbles, wood, and mollusk shells, especially of *C. fluminea*. Scuba divers exposed the boxes in a 3 × 4 rectangular formation in a randomized block design, leaving a space of ~1 m between the boxes. They buried the boxes so that the sand in the boxes was level with the surrounding sediment and added shells or live clams according to treatments. The tops of the boxes were open to allow settlement of macroinvertebrates. We marked the position of the experimental site with GPS.

Sampling methods and laboratory analyses

We terminated the experiment after 2 month in late September. Scuba divers closed the boxes with a lid to keep all organisms inside and placed the boxes in a net (mesh size = 200 µm) before lifting them to the surface. On deck, we poured the water in each box into a net with a mesh width of 200 µm to concentrate benthic organisms. We had to store samples overnight at 4 °C because sampling required a full day (12 h) and health regulations forbid formalin fixation on the lake. Former experience at our institute shows that decomposition of organisms does not start within 24 h. In the laboratory, we separated the inorganic sediment and organic matter fractions, including benthic organisms, with various mesh sizes of sieves (20, 5, 2, and 0.2 mm). As soon as possible, we fixed samples in 95% ethanol. We identified invertebrates under a dissecting microscope to the species or genus level (except oligochaetes and chironomids) and counted the individuals.

Estimation of surface area of clam shells

We wrapped and fitted 30 shells in aluminum foil (mean shell length: 12.27 ± 0.31 mm, including shells < 5 mm in length) to estimate the surface area provided by *C. fluminea* shells. We fitted the outside and the inside of each shell separately. We plotted a foil mass-to-area regression curve from 9 different-sized foil pieces with a range of 1 to 25 cm^2 (foil area = 0.3247 × foil mass – 0.1362; R^2 = 0.999).

We used this equation to calculate the area provided by 2000 shells m^{-2}, a density occurring *in situ* after winter mortalities; e.g., in winter 2005/2006, the density of *C. fluminea* at 1 m depth dropped from 1899 ± 143 ind. m^{-2} in December to 53 ± 9 living ind. m^{-2} in March. We assumed that, by chance, 50% of the shells would lie on the sediment with the inner side up and 50% would lie on the sediment with the outer side up. We calculated the area of shells lying with the inner side up as the surface of the inside of the shell plus the area of the outside of the shell minus the bearing surface, measured from the shell print in soft sediment. We calculated the area of shells lying with the outer side up as the surface of the outer side only.

Data processing and statistical analyses

We reported invertebrate density as ind. m^{-2} of lake bottom. We used analysis of variance (ANOVA) to identify effects of treatments for taxa with mean densities (over all treatments) > 1% of mean total

Table 4.1. Density of taxa with mean densities (over all treatments) >1% of mean total density.

Taxon	Density Mean	SE	% of total density
Nematoda	1000	107	5.3
Oligochaeta	590	76	3.1
Hirudinea	184	18	1
Bithynia tentaculata	2077	209	11.1
Potamopyr. antipodarum	357	41	1.9
D. polymorpha juv.	7184	906	38.3
C. fluminea juv.	5486	1051	29.3
Pisidium spp.	727	113	3.9
Caenis spp.	283	27	1.5
Chironomidae	9972	933	53.2
Total (excl. postveliger of *C.fluminea* and *D. polymorpha*)	18,737	1687	100
Total	29,871	2179	

density (excluding newly settled postveliger larvae of *Corbicula* and *Dreissena*). In addition to juvenile *C. fluminea* (≤ 3 mm), we tested 9 other taxa: Nematoda, Oligochaeta, Hirudinea, *Bithynia tentaculata* (Gastropoda), *Po tamopyrgus antipodarum* (Gastropoda), *Pisidium* spp. (Bivalvia), *Dreissena polymorpha* < 5 mm (Bivalvia), *Caenis* spp. (Ephemeroptera), and Chironomidae. We used Tukey's Honestly Significant Difference (HSD) *post-hoc* tests to identify significant effects of the different treatments. We checked density values of taxa for normality and homogeneity of variance with the Hartley, Cochran, and Bartlett test (p = 0.05). Data did not require transformation. Coefficients of variation (CV) of density estimates of invertebrates ranged between 0.1 and 0.75 with a median of 0.36. Our statistical power to detect a 2-fold difference at the median CV was 0.84 (www. math.yorku.ca/SCS/Online/power). For ANOVA statistics, we used a sequential Bonferroni adjustment (Rice 1989) to obtain an experiment-wise error rate of p = 0.05 across all dependent variables.

We analyzed similarity of the benthic macroinvertebrate community between different treatments by nonmetric multidimensional scaling (NMDS). We chose a sqrt (x) transformation to allow moderately abundant species to contribute almost as much as abundant species to differences in similarity between samples, and reran every algorithm 50 times for each plot (Clarke & Gorley 2001). We analyzed Bray–Curtis similarities between the communities in different treatments with analysis of similarity (ANOSIM) in PRIMER 5.0, which compares ranked similarities for differences between defined groups. In theory, R-values obtained by ANOSIM can vary from –1 to +1. Large R-values imply differences between samples, whereas values close to 0 imply no or little segregation (H_0: hypothesis is true).

Results

Corbicula fluminea shells in naturally occurring densities (2000 m^{-2}) nearly doubled the surface area of soft substrata. The shells (mean shell length: 12.27 ± 0.31 mm) expanded a 1-m^2 area of sand by 0.95 ± 0.05 m^2. The bearing surface of the shells lying with the inner side up in the sediment was 13.98 ± 0.5% of the total area of the outer sides of the shells.

Table 4.2. Analysis of variance results for benthic taxa (> 1% of total density). (*) = not significant after sequential Bonferroni adjustment; * = significant with 0.05 > α > 0.01, *** = α < 0.001.

Taxon	*F*	df	*P*
Nematoda	0.7902	2	0.4829
Oligochaeta	0.0286	2	0.9719
Hirundinea	4.757	2	0.0395(*)
Bithynia tentaculata	0.7832	2	0.4857
Potamopyr. antipodarum	0.0648	2	0.9377
Dreissena polymorpha juv.	0.1282	2	0.8813
Corbicula fluminea juv.	10.2688	2	0.0048*
Pisidium spp.	0.3237	2	0.7316
Caenis spp.	39.0393	2	< 0.0001***
Chironomidae	1.1919	2	0.3474

After 2 month of exposure, the overall density of benthic invertebrates inside the boxes (29,871 ± 2179 ind. m^{-2}; Table 4.1) was similar to their *in situ* density (54,412 ± 3455 ind. m^{-2}). During the experiment, clams grew an average of 3 mm, and no mortality was observed in the boxes containing live *C. fluminea*. Ten taxa had mean densities (over all replicates) ≥ 1% of the mean total density, excluding newly settled postveliger larvae of bivalves (Table 4.1). Seven of these taxa (Nematoda, Oligochaeta, *Bithynia tentaculata*, *Potamopyrgus antipodarum*, juvenile *Dreissena polymorpha*, *Pisidium* spp., and Chironomidae; Table 4.2) were unaffected by treatments. Density of Hirudinea (leeches) did not differ across treatments after sequential Bonferroni adjustment, but they showed increased densities in boxes containing *C. fluminea* shells (p = 0.0395, sequential Bonferroni critical p-value: 0.0063) before data correction (Table 4.2, Fig. 4.1A). Density of the mayfly, *Caenis* spp., was significantly higher in boxes containing shells than in the other treatments (Table 4.2, Fig. 4.1B). Abundance of juvenile *C. fluminea* was significantly lower in boxes with live adult clams than in the other treatments (Fig. 4.1C).

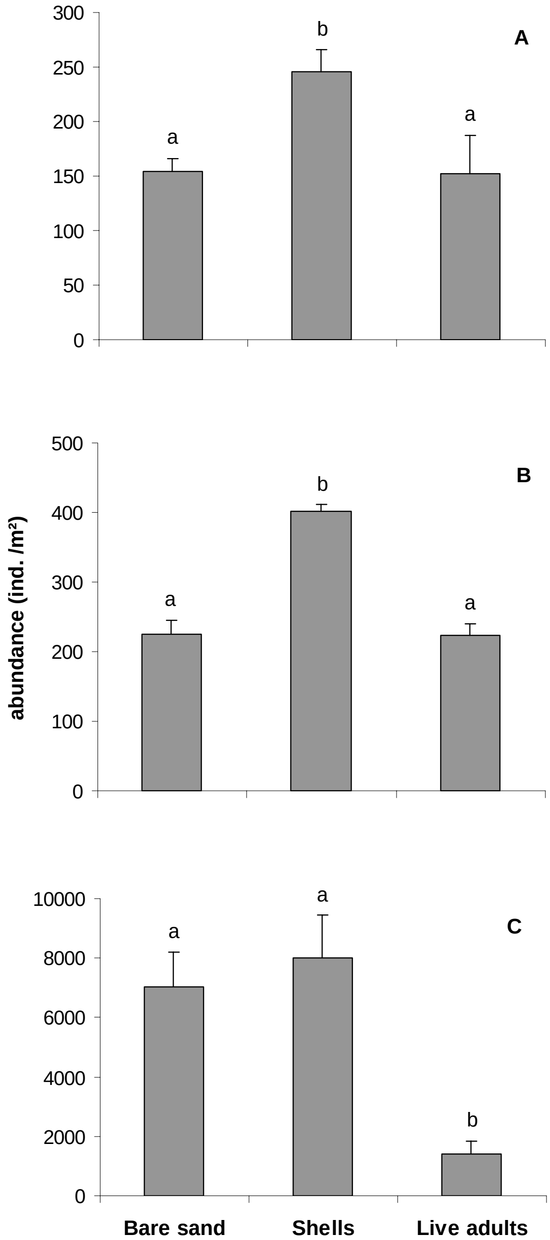

Fig. 4.1. Effects of treatments on Hirudinea (A), *Caenis* spp. (B), and *Corbicula fluminea* juveniles (C). Differences for Hirudinea were not significant after sequential Bonferroni adjustment.

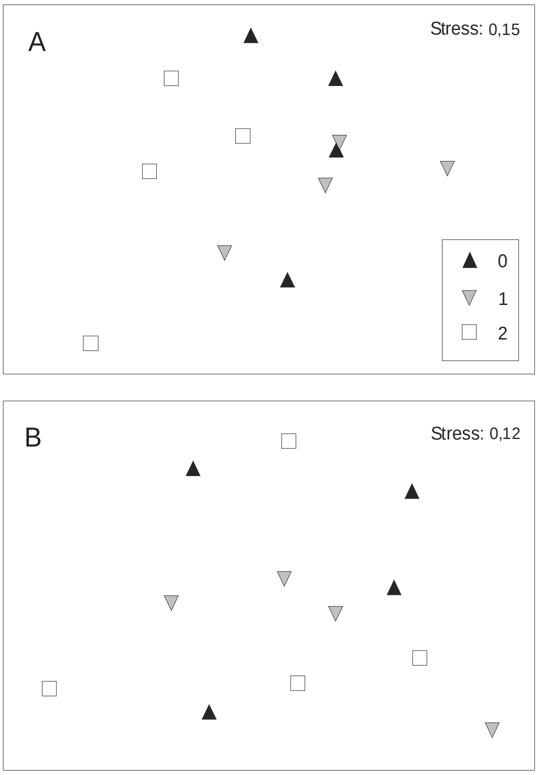

Fig. 4.2. Non-metric multidimensional scaling ordination plot of invertebrate densities including juvenile *Corbicula* (A) and excluding juvenile *Corbicula* (B). Treatment codes are: 0 = bare sand, 1 = shells, and 2 = live adults.

Multivariate community measures (ANOSIM)

Ordination of the macroinvertebrate communities by NMDS revealed that the invertebrate community within boxes containing live adult clams could be separated from the other 2 treatments (Fig. 4.2A). However, the differences were caused mainly by juvenile *C. fluminea*. When we reran the analysis without juvenile clams, the invertebrate communities were very similar (Fig. 4.2B).

Differences in community structure among the treatments were tested with ANOSIM. Global differences among the 3 treatments including all taxa were not significant (p = 0.073). The benthic communities in boxes with bare sand and with shells were very similar, whereas benthic invertebrate densities in boxes with live clams were almost significantly different (p = 0.057) than in boxes with bare sand and with shells (Table 4.3). Communities were more similar when juvenile *C. fluminea* were excluded from the analysis (Table 4.3).

Discussion

Interspecific effects

Mollusks act as ecosystem engineers (Jones *et al.* 1994, Jones *et al.* 1997, Crooks 2002, Gutiérrez *et al.* 2003) by altering sediment structure and providing additional habitat on empty shells after mortality. Furthermore, bivalve biodeposition enriches the benthic substrata with organic matter (Stewart *et al.* 1998, Vaughn & Hakenkamp 2001, Mörtl & Rothhaupt 2003). Most populations of benthic invertebrates benefit from these bivalve effects (Stewart *et al.* 1998, Karatayev *et al.* 1997, Nalepa *et al.* 2003, Karatayev *et al.* 2005). On soft substrata, *Dreissena* increases structural complexity (Berkman *et al.* 1998, Werner *et al.* 2005) and reduces predation efficiency of benthivorous fish (Mayer *et al.* 2001, Dieterich *et al.* 2004); hence, macroinvertebrate communities differ depending on zebra mussel abundance (Ricciardi *et al.* 1997). Here we showed that *C. fluminea* could act as an ecosystem engineer on sandy substrata by providing empty shells. To our knowledge, this aspect of

Table 4.3. Results of analysis of similarity (ANOSIM) for differences in community composition between treatments.

Comparison	Juvenile *Corbicula* included *R*	Juvenile *Corbicula* included *P*	Juvenile *Corbicula* excluded *R*	Juvenile *Corbicula* excluded *P*
All treatments	0.19	0.073	–0.109	0.766
Bare sand vs shells	–0.156	0.857	–0.208	0.943
Bare sand vs live adults	0.344	0.057	–0.156	0.686
Shells vs live adults	0.417	0.057	0	0.486

C. fluminea ecology has not yet been studied (cf. Karatayev *et al.* 2005).

In Lake Constance, empty *C. fluminea* shells can reach numbers as high as those of living clams because of mass mortality during cold winters and droughts. Therefore, the engineering effects of these clams are important for, at least, some taxa in Lake Constance.

The density of the mayfly *Caenis* spp. on soft substrates was enhanced by *C. fluminea* shells. This result agrees with earlier findings of our working group, which show that the density of *Caenis* spp. larvae increases with structural diversity (Mörtl & Rothhaupt 2003). We also showed that, on sandy substratum, the loss of ecosystem engineering effects of zebra mussels results in a decline of *Caenis* spp. (Mörtl *et al.*, in press) because bare sand is not a suitable habitat for *Caenis* spp. (Malzacher 1986). Shells of *C. fluminea* might support other species that prefer hard substrates in fresh waters with relatively unstructured sandy areas. Our study could not provide support for this hypothesis, probably because *Corbicula* colonized the sandy study area so recently that taxa preferring hard substrata have not had enough time to colonize. However, we found increased densities of mayflies and leeches on the shells, and this result suggests that a gradual colonization of the sandy littoral zones by hard-substrate species might be occurring now that *C. fluminea* is present. On the other hand, the engineering effects of *C. fluminea* might be negligible in habitats with diverse substrate structure including hard substrata.

In addition to their ecosystem engineering effects, bivalves such as *Corbicula* deposit faeces and pseudofaeces, which enrich the organic content of benthic sediments (Vaughn & Hakenkamp 2001) and provide an additional food resource for benthic invertebrates (Roditi *et al.* 1997, Gergs & Rothhaupt, unpublished data). However, no effects of live clams on other benthic invertebrates were observed in our study or previous studies (Hakenkamp & Palmer 1999, Karatayev *et al.* 2005). A possible explanation for this result lies in the ability of the clams to filter feed and to pedal feed (Reid *et al.* 1992, Hakenkamp & Palmer 1999). Pedal feeding reduces the amount of benthic bacteria and diatoms on the sediment (Hakenkamp *et al.* 2001); therefore, the clams might use their own deposited matter, making it unavailable for other benthic taxa. Our experimental design had modest statistical power. Therefore, we cannot fully exclude the possibility that a lack of significant differences could be the result of a Type II error. However, biodeposition and bioturbation of live burrowing Asian clams has seemed to play only a minor role in other studies (Hakenkamp & Palmer 1999, Karatayev *et al.* 2005). By comparison, the nonburrowing zebra mussel *Dreissena polymorpha* changes benthic communities considerably (Karatayev *et al.* 1997, Nalepa *et al.* 2001, 2003), possibly because live zebra mussels simultaneously provide substrate structure, bioturbate, and biodeposit, and thereby have a greater potential to change invertebrate communities than *Corbicula.* Live *Corbicula* are buried, and thus, do not change the surface of sediments. They can exert effects only by bioturbation and biodeposition, whereas shells of dead clams lie on the sediment and can have only a structural influence. This decoupling of effects might be responsible for less pronounced effects of *C. fluminea* on macroinvertebrates than those observed for *D. polymorpha*.

Intraspecific effects

Density of juvenile *C. fluminea* was higher in both treatments lacking live adult *C. fluminea* than in the treatment with live clams. This result indicates that adults influenced settlement of juveniles. Bare sand and sand with shells were colonized by juveniles at similar densities. Therefore, structural diversity plays a minor role during larval settlement. *Corbicula* can colonize unsettled areas rapidly (Voelz *et al.* 1998), so juveniles might invade areas without competing conspecifics faster than they colonize areas with competing conspecifics, and these areas might be made identifiable by chemical cues (Butman 1987, Dodson *et al.* 1994, Turner *et al.* 1994, Anderson 1996, Tamburri *et al.* 1996).

Other possible explanations for the lower density of juvenile *C. fluminea* in the presence of adult clams could be competition for food or mortality of juveniles caused by the filtering activity of adults. Cannibalism is a regulatory mechanism in zebra mussel settlement (MacIssac *et al.* 1991), but it is unlikely for *C. fluminea* because the released postveligers have a shell length of 250 µm (Meister 1997, Werner, personal observation), which exceeds the upper limit of the adult food particle size of 170 µm (Boltovskoy *et al.* 1995). Competition for food in areas with high densities of adults might decrease the survival rates of postveligers (Chase & Bailey 1996). However, if competition had led to starvation of juvenile *C. fluminea*, then their shells should have occurred in our samples, which was not the case. Therefore, the release of a chemical cue that might deter juveniles from settling in areas with high intraspecific concurrence seems to be the most likely explanation for the lower density of juvenile *C. fluminea* in the presence of adult clams.

In conclusion, engineering effects of *C. fluminea* via shell production can be more important for benthic invertebrates than nonengineering effects. The ecosystem engineering of *C. fluminea* shells increased density of the mayfly *Caenis* spp. and, possibly, of Hirudinea. Both taxa prefer hard substrates in fresh waters and avoid unstructured sandy areas. We could not detect a biotic or a structural effect of burrowed live clams on other benthic macroinvertebrates, but the presence of burrowed live clams did reduce the number of their own recruits, possibly because of a chemical cue. To our knowledge, ours is the first study to provide direct evidence that *Corbicula* affects benthic macroinvertebrate populations (Karatayev *et al.* 2005).

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5 Effects of the invasive Asian clam *Corbicula fluminea* on benthic macroinvertebrate taxa in laboratory experiments

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Abstract

The invasive burrowing bivalve *Corbicula fluminea* has an impact on ecosystem processes and on organic matter dynamics in sediments. However, little is known about its effect on benthic communities, especially on macroinvertebrates. In laboratory experiments, we determined the effect of naturally occurring densities of *C. fluminea* (1012 ind. m^{-2}) on ten macroinvertebrate taxa typical for the littoral zone of Lake Constance: two species of leeches, three species of gastropods, two amphipod species, one isopod, and two taxa of insect larvae (a stonefly and chironomids). We hypothesized that these benthic organisms might prefer *C. fluminea* over sand in pairwise habitat-choice experiments because of structural and biotic effects of the bivalves. We distinguished between biotic effects of living infaunal *C. fluminea* that were either starved (only bioturbation) or fed with algae (biodeposition, bioturbation, and nutrient reallocation), and we tested the importance of their structural role using *C. fluminea* valves lying on sand. No benthic taxa avoided areas with live *C. fluminea* or their valves. The detritivorous gastropod *Lymnaea stagnalis* and the amphipod *Gammarus roeselii* were found in higher numbers in areas with fed *C. fluminea* than in areas with sand. Starved clams were only preferred over sand by the amphipod *Dikerogammarus villosus*. The epifaunal taxa *Erpobdella octoculata*, *Glossiphonia complanata* (Hirudinea), *D. villosus*, *G. roeselii* (Amphipoda), *Asellus aquaticus* (Isopoda), and *Centroptilum luteolum* (Ephemeroptera) preferred areas with *C. fluminea* valves to areas with sand. The crustacean species and the leeches preferred valves over sand more than they preferred fed or starved living clams over sand. *C. luteolum* was the only taxon that responded differently to *C. fluminea* in the three experiments, whereas gastropods and chironomids did not show differences. We conclude that on poorly structured sediments, valves of *C. fluminea*, which increase the surface area and substrate diversity, could lead to an increase of most epifaunal benthic invertebrates.

Key words biodeposition, bioturbation, ecosystem engineering, exotic bivalve, benthos

Introduction

The composition of benthic communities in large oligotrophic lakes is mainly affected by abiotic factors, including hydrodynamics, which can impact the size-class structure of substrates, geomorphology, and water-level fluctuations (Scheifhacken *et al.* 2007). The density and species richness of benthic macroinvertebrate communities is positively linked to the availability of interstitial refuges and habitat complexity (Diehl 1992, Schmude *et al.* 1998, Gjerlov *et al.* 2003). Considerable changes in community structure and ecosystem processes can be caused by biotic effects, e.g., biological invasions (Spencer *et al.* 1991, Dick *et al.* 2002, Nalepa *et al.* 2003). Biological invaders that alter substrate qualities can have a great impact on biotic community (Karatayev *et al.* 1997, Stewart *et al.* 1998, Nalepa *et al.* 2003).
Bivalves are important ecosystem engineers (Strayer *et al.* 1999, Gutiérrez *et al.* 2003), and many are successful invaders, reaching high densities and dominating the biomass of the benthic community (Stewart *et al.* 1998, Karatayev *et al.* 2003). In freshwater ecosystems, the invasive zebra mussel *Dreissena polymorpha* reallocates nutrients from pelagic to benthic habitats and increases habitat complexity by providing physical structure in the form of valves; both these factors exert positive effects on the abundance and biomass of diverse macroinvertebrates (Karatayev *et al.* 1997, Stewart *et al.* 1998, Nalepa *et al.* 2003). Compared to structural effects of the epifaunal zebra mussels, the infaunal Asian clam *Corbicula fluminea* has no physical effect, because it burrows completely in sediments (Werner & Rothhaupt 2007). They therefore exert only biotic effects, such as biodeposition, bioturbation and nutrient reallocation. In contrast, the valves of dead clams that lie on the sediment surface have only abiotic effects by providing physical habitats and interstitial refuges (Werner & Rothhaupt 2007). Nevertheless, each of the separate biotic and structural effects of burrowing bivalves and their empty shells could affect macroinvertebrates in marine and freshwater systems (reviewed in Vaughn & Hakenkamp 2001).
Although only a few studies have demonstrated that *C. fluminea* influences other benthic organisms (meiofauna: Hakenkamp *et al.* 2001, macroinvertebrates: c.f. Karatayev *et al.* 2005 and Werner & Rothhaupt 2007), we hypothesize that *C. fluminea* can affect benthic macroinvertebrates, especially taxa preferring hard substrates, via the empty valves. Between 2000 and 2002, *C. fluminea* invaded Lake Constance (Werner & Mörtl 2004), a large oligotrophic lake in central Europe, where it spread quickly and reached local densities of up to 3520 individuals > 5 mm in length per square meter and constitutes on average more than 90% of the biomass of the littoral

soft bottom community (Chapter 3). Therefore, we carried out habitat-choice experiments in order to assess whether living *C. fluminea* and their empty valves influence various macroinvertebrate taxa that are characteristic and important representatives of benthic communities in Lake Constance. The shallow littoral zone of this pre-alpine lake is dominated by hard substrates (Schmieder *et al.* 2004, Scheifhacken *et al.* 2007), and the diversity of its benthic community is positively correlated with surface area and physical complexity of substrates (Mörtl *et al.*, in press). However, *C. fluminea* occurs on unstructured sandy sediments; this surface would have only a very low potential for settlement of taxa preferring hard substrates if the valves of this clam are absent. We tested whether *C. fluminea* influences the habitat choice of benthic taxa using empty valves (abiotic structural role), starved clams (biotic effect: bioturbation), and clams fed with algae (biotic effects: biodeposition, nutrient reallocation and bioturbation).

Material and methods

Study design

The response of different macroinvertebrates to *C. fluminea* was studied in pairwise laboratory habitat-choice experiments. Ten benthic taxa > 5 mm that are typical for Lake Constance and important representatives of its benthic communities were tested: *Lymnaea stagnalis* (Gastropoda), *Bithynia tentaculata* (Gastropoda), *Radix auricularia* (Gastropoda), *Erpobdella octoculata* (Hirudinea), *Glossiphonia complanata* (Hirudinea), *Dikerogammarus villosus* (Amphipoda), *Gammarus roeselii* (Amphipoda), *Asellus aquaticus* (Isopoda), *Centroptilum luteolum* (Ephemeroptera), and infaunal Chironominae (Diptera). The invertebrates were collected from stones on sandy sediment in the littoral zone near the city of Konstanz in spring 2006 and in spring 2007. *C. fluminea* was kept in a flow-trough-system in the laboratory for the whole study period, whereas all further animals were kept only for up to two weeks in 20-l flow-through systems flushed with filtered (30 μm pore size) lake water. The number of replicates and individuals of the different macroinvertebrate taxa varied according to their size and their *in situ* availability (Table 5.1).

The distribution of these benthic taxa with respect to *C. fluminea* was tested in a two-choice setup in aquaria (37.5 × 19.5 × 25 cm; L × W × H). We had to choose a pairwise rather than a four-way comparison, because algae that were added to test the effects of biodepostion by living *C. fluminea* would have distributed equally in an aquarium with four choice areas and, by this, ruled out the treatment with starved clams. Each aquarium had a removable partition, which allowed the two habitat halves to be separated at the end of the experiment to record the distribution of the invertebrates in each half. Living clams were kept on one side of the aquarium by a second partition inserted into the sediment flush with the sediment surface. This partition was also used in the treatments with valves and sand only. To exclude the invertebrates from the channel for the partition, it was covered with sliced rubber tubing. Each aquarium contained 2 kg of dried sand (105 °C for 24 h), corresponding to a sediment layer with a height of about 3 cm, allowing *C. fluminea* to burrow completely. Sand was obtained from our study site Rohrspitz at Lake Constance and was sieved through a 630 μm mesh. The aquaria were filled with 10 l of filtered (30 μm) lake water. As lake water was slightly aerated to keep algae in suspension (in the treatment with fed *C. fluminea*), in every treatment, aerators were hanging in the free water column in the centre of each aquarium. They had no contact to any surface of the aquarium. Experiments were conducted in a climate chamber at 16 ± 1 (SD) °C and a 10 h dark phase (light: dark: light: 7 h: 10 h: 1 h). Each experiment ran 18 h; the experiments were conducted overnight and terminated 1 h after the light was turned on. *C. fluminea* and valves, respectively, were added to the aquaria 2 h before the experiment. After each trial, sand and aquaria were fully cleaned.

The possible abiotic and biotic effects of *C. fluminea* on benthic invertebrates were tested against bare sand: 1) structural effects of empty valves (abiotic), 2) biotic effects of starved, living clams burrowed in the sand (bioturbation), and 3) biotic effects of living clams burrowed in the sand and fed with algae (biodeposition, bioturbation, and reallocation of 'pelagic' nutrients). In each case, 36 *C. fluminea* individuals or 72 empty valves arising from 36 individuals, corresponding to a density of 1012 individuals m^{-2}, were placed in one half of each aquarium. This density was chosen as the mean density of *C. fluminea* at 1 m depth at our study site in Lake Constance was 931 ± 289 (SE) individuals m^{-2} (unpublished data). *C. fluminea* was reused during the experiments as filtering activity was not affected by handling. The mean shell lengths ± SD of the valves and the living clams were 17.5 ± 1.5 mm and 17.6 ± 1.3 mm, respectively. The increase in surface provided by the valves was calculated according to Werner & Rothhaupt (2007). Non-starved *C. fluminea* were fed the algae *Scenedesmus obliquus* at 1 mg C per clam. This amount of food algae led to the production of pseudofaeces and faeces within the first few hours of the experiment (own observations). Algae were applied to the entire aquarium 30 min before adding the invertebrates. Only algae processed by *C. fluminea* (pseudofaeces) were an ingestible food source for invertebrates (except for *B. tentaculata* which is able to filter algae). The deposited algae were situated close to the clams and were not found on the side with bare sand. The orientation of the area with *C. fluminea* within the aquaria alternated to exclude bias of the distribution of the macroinvertebrates owing to effects of spatial orientation. Furthermore, we determined whether all ten benthic taxa distributed equally in an aquarium with sand on both sides.

All three treatments (valves vs. sand, starved *C. fluminea* vs. sand and fed *C. fluminea* vs. sand) were conducted for every macroinvertebrate taxon each. Macroinvertebrates were used for 2 experiments. At the beginning of each experiment, the macroinvertebrates were placed on the partition line in the middle of each aquarium. At the end of each experiment, all invertebrates in each half of each aquarium were counted. No mortality occurred during our short term study.

Statistical analyses

Invertebrate distribution data were calculated as percentages and were angular transformed ($x' = \arcsin \sqrt{x}$; $0 \leq x \leq 1$) to homogenize variances. When individuals were not recovered or when they could not be assigned to a specific half of the aquarium for technical reasons, i.e., when they were found within 1 cm of the partition, the data were excluded from statistical analyses. When > 30% of the tested individuals could not be allocated, the replicates were removed from the analyses (Table 5.1).

Analyses were performed separately for each macroinvertebrate taxon. To check for equal distribution in controls individuals were counted on both sides (both of which contained sand). The preference for one side (front half of each control aquarium) was compared with equal distribution (50%) using a single sample t-test (Statistica V.6.0, Statsoft Inc.). Moreover, we analyzed with a t-test for single means how every taxon distributed in the three habitat-choice experiments (valves vs. sand, starved *C. fluminea* vs. sand and fed *C. fluminea* vs. sand). We checked if the percentage of every taxon found in the aquarium halves with *C. fluminea* differed from equal distribution. If invertebrates preferred valves over sand, we further tested if the number of individuals increases in proportion to the amount of available surface area, which was 2.475 times higher in the side with valves.

To test for differences between the three habitat-choice experiments for all taxa, the data were analyzed with one-way ANOVA (Statistica, Statsoft V.6.0). Both assumptions, normality (Kolmogorov-Smirnov test with Liliefors´ correction; $\alpha = 0.05$) and homogeneity of variance (Levene's test; $\alpha = 0.05$), were checked. Tukey's Honestly Significant Difference (HSD) *post-hoc* test was used to identify significant effects of the different habitat-choice experiments.

Because data were used for four analyses (3 t-tests and ANOVA), the results were sequentially Bonferroni corrected.

Results

All ten benthic invertebrate taxa distributed equally in the control aquaria (sand vs. sand; Table 5.1). In the test aquaria, living (starved or fed) clams burrowed within five minutes and empty valves were on the sand surface. Since living clams burrow completely, with only their siphons protruding from the substrate, they barely influenced the

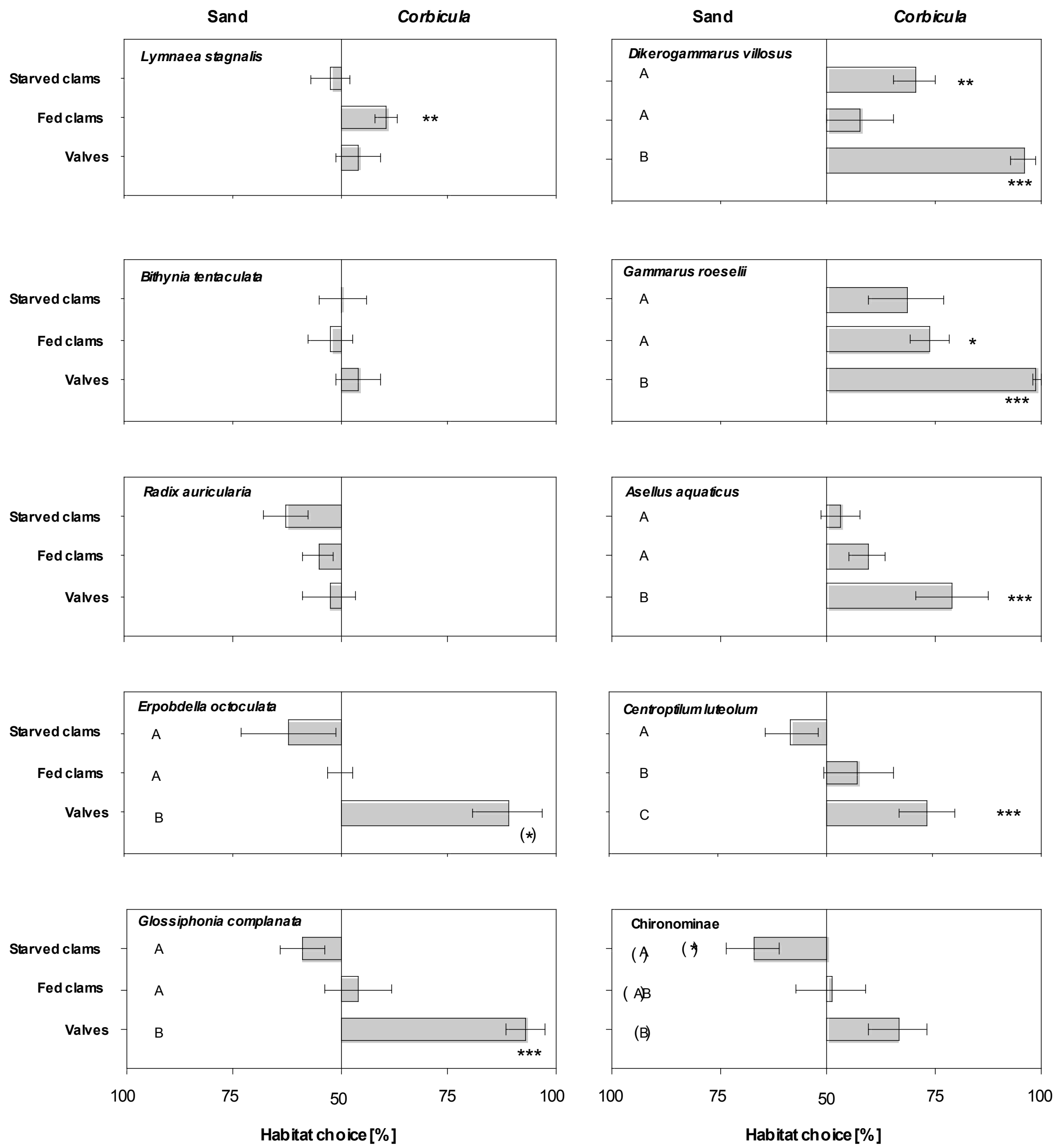

Fig. 5.1. Habitat choice of ten benthic taxa ± SE. Capital letters indicate differences between the three experiments: starved live clams, live clams fed with algae, and valves in a *post-hoc* test after the ANOVA. Asterisks indicate differences between the distribution in the experiment and equal distribution (50%): * = 0.05 ≥ □ > 0.01, ** = 0.01 ≥ □ > 0.01, *** = □ ≤ 0.001. ( ): not significant after sequential Bonferroni correction.

surface area. By contrast, the empty valves greatly increased the surface area from 366 cm^2 (sand only) to 905 ± 26 (SD) cm^2 (sand plus valves).

The gastropods *Bithynia tentaculata* and *Radix auricularia* distributed equally within the aquaria in all habitat-choice experiments. In contrast, the gastropod *Lymnaea stagnalis* preferred living clams fed with algae over sand (t = 4.296, df = 5, p = 0.008; Fig. 5.1), but this distribution did not result in significant differences (ANOVA) among the three habitat choice experiments (Tab. 5.2). *B. tentaculata* and *R. auricularia* also showed no differences among the three habitat-choice experiments (ANOVA, Tab. 5.2). Both species of leech, *Erpobdella octoculata* and *Glossiphonia complanta*, distributed equally in aquaria with starved and fed clams, but *G. complanata* favored valves over bare sand (t = 9.813, df = 7, $p < 0.001$). *E. octoculata* only showed a trend to prefer valves (t = 4.847, df = 2, $p = 0.040$; □ = 0,017). For both leeches, significantly more individuals were found on valves than on living clams (ANOVA, Table 5.2, Fig. 5.1). The amphipod *Dikerogammarus villosus* preferred valves over sand (t = 15.970, df = 7, $p < 0.001$) and starved clams over sand (t = 4.273, df = 5, $p = 0.008$), and distributed equally on fed clams. *Gammarus roeselii* preferred clams fed with algae (t = 5.046, df = 5, $p = 0.004$) and valves (t = 59.573, df = 7, $p < 0.001$) over sand. Owing to the high standard deviation, the distribution of *G. roeselii* on starved living clams did not differ from that on sand (Fig. 5.1). The isopod *Asellus aquaticus* also strongly preferred the valves over sand (t = 28.481, df = 4, $p < 0.001$), but distributed equally in the aquaria with starved or fed clams. These three crustacean species, like the leeches, preferred valves over sand more than they preferred fed or starved living clams over sand (ANOVA, Table 5.2, Fig. 5.1).

Larvae of the stonefly *Centroptilum luteolum* preferred valves over sand (t = 9.658, df = 7, $p < 0.001$), but they distributed equally in the two living clam habitat-choice experiments. *C. luteolum* was the only taxon whose distribution significantly differed among the three habitat-choice experiments (ANOVA, Table 5.2, Fig. 5.1). The distribution of *Chironominae* numbers were not significantly different in the three experiments using Bonferroni corrected *p*-values, but there was a trend ($p < 0.05$) of higher number in areas with valves than starved clams (Table 5.2, Fig. 5.1).

Table 5.1. Taxa length (mm ± SD), number of individuals added to each replicate, and number of replicates with *Corbicula fluminea*, and t-test for single means of the control (sand vs. sand).

Taxon	Length (mm)	N per replicate	no of actual replicates				*t*	*df*	*P*
			valves	starved	fed	control			
Lymnaea stagnalis	21.8 ± 3.0	20	8	8	6	6	0.048	5	0.963
Bithynia tentaculata	7.2 ± 0.5	50	8	6	6	6	1.154	5	0.301
Radix auricularia	12.3 ± 0.8	24	8	8	8	8	1.531	7	0.17
Erpobdella octoculata	20.7 ± 7.4	20	3	3	3	3	–0.169	2	0.881
Glossiphonia complanata	15.6 ± 1.7	20	7	8	8	8	–0.404	7	0.698
Dikerogammarus villosus	14.5 ± 2.4	20	8	6	6	6	1.649	5	0.16
Gammarus roeselii	11.8 ± 2.1	20	8	6	6	5	–1.553	4	0.195
Asellus aquaticus	9.9 ± 3.2	30	5	6	6	6	–0.163	5	0.877
Centroptilum luteolum	5.4 ± 0.7	40	8	6	6	5	–0.081	4	0.939
Chironominae	11.3 ± 1.3	36	4	6	6	4	0.88	3	0.444

Probably the leech *G. complanata,* the crustaceans, and the stonefly preferred the side of the aquarium with valves over the side with sand purely because of the 2.475-fold increase in surface area. Thus, we would expect 71% of the individuals to prefer the side with valves. This value was reached by the stonefly *C. luteolum*, but was exceeded by all three crustacean species (*D. villosus*: $t = 8.598$, $df = 7$, $p < 0.001$; *G. roeseli*: $t = 33.640$, $df = 7$, $p < 0.001$; *A. aquaticus*: $t = 15.440$, $df = 4$, $p < 0.001$) and the leech *G. complanata* ($t = 4.996$, $df = 6$, $p = 0.002$).

Discussion

Structural effects

Substrates with a greater heterogeneity, surface complexity, and interstitial space support more diverse and abundant macroinvertebrate communities in lakes than less-complex, two-dimensional substrates (Schmude *et al.* 1998). On soft substrata in marine and freshwater systems, substrate heterogeneity is increased by the ecosystem engineering of bivalves through the production of valves (Strayer *et al.* 1999, Gutiérrez *et al.* 2003). In the Laurentian Great Lakes, for example, the increase in density of almost every benthic invertebrate taxon as a consequence of zebra mussel invasion was mainly attributed to the surface area increase caused by the mussels (Stewart *et al.* 1998). The shells of bivalves also provide interstitial refuges, which support benthic macroinvertebrates by, e.g., reducing predation efficiency of fish (Dieterich *et al.* 2004). Valves of *C. fluminea* can considerably increase the surface area available for invertebrate settlement (Werner & Rothhaupt 2007). In our study, valves increased the surface area ~2.5-fold over sand alone, whereas living clams, which burrowed, did not change the surface area.

In our habitat-choice experiments, none of the tested benthic taxa avoided *C. fluminea*. All epifaunal taxa except the three species of gastropods preferred valves over sand. That the result for *E. octoculata* was no longer significant after data correction is due to the statistical power, as it was the only taxon with just three replicates. The preferences of the leech *G. complanata*, the amphipods *G. roeselii* and *D. villosus*, the isopod *A. aquaticus*, and the stonefly *C. luteolum* for valves were significantly stronger than those for burrowed living clams (ANOVA) and those for sand (t-test). This fits well with their natural habitat preference, as they all favor hard substrata and other structured habitats, such as macrophytes (Colling & Schmedtje 1996, Karatayev *et al.* 1997, Kley & Maier 2005, Lods-Crozet & Reymond 2006). *G. roeselii* in Lake Constance favored living zebra mussels over their shells and bare substrate (Mörtl & Rothhaupt 2003). Here, compared to their shells, living zebra mussels had structural and biotic impacts. Amphipods avoid low-complexity substrates (Gonzalez & Downing 1999). This explains why the amphipods preferred valves of *C. fluminea* compared to living infaunal clams.

Table 5.2. Analysis of benthic taxa by ANOVA. The distributions in the three different habitat-choice experiments are compared. *Post hoc* comparison was done with Tukey´s HSD test. Valves: treatment with valves vs. sand; fed: treatment with infaunal living *C. fluminea* fed with algae vs. sand; starved: treatment with infaunal starved *C. fluminea* vs. sand.

Taxon	*F*	*df*	df_{err}	*P*	post hoc comparison
Lymnaea stagnalis	1.938	2	19	0.171	
Bithynia tentaculata	0.4	2	17	0.677	
Radix auricularia	0.875	2	21	0.431	
Erpobdella octoculata	10.896	2	6	**0.01**	Valves > fed = starved
Glossiphonia complanata	19.311	2	20	**< 0.001**	Valves > fed = starved
Dikerogammarus villosus	15.385	2	17	**< 0.001**	Valves > fed = starved
Gammarus roeselii	10.271	2	17	**0.001**	Valves > fed = starved
Asellus aquaticus	33.856	2	14	**< 0.001**	Valves > fed = starved
Centroptilum luteolum	21.599	2	17	**< 0.001**	Valves > fed > starved
Chironominae	4.916	2	13	0.0257	

In 3-month *in situ* experiments, we previously found increased densities of the stonefly *Caenis* spp. on valves of *C. fluminea,* but at the community level, no ecosystem engineering effect was detectable (Werner & Rothhaupt 2007). However, the sandy study site had a naturally low potential for settlement of benthic taxa that prefer hard substrates. For four of the six taxa tested in our study reported here, the preference for valves was not only due to the increase in surface area. The other factors leading to this preference are not known, but could be the surface structure or chemical composition of the valves.

The general habitat demands of our three tested gastropod species (Colling & Schmedtje 1996) are reflected by our results and a study in Lake Erie, in which the density of four of five gastropod species did not increase on zebra mussel shells (Stewart *et al.* 1998). This study was conducted on cobbles, with a naturally high potential for shelter. But, in an *in situ* study performed on sandy sediments with single stones, *B. tentaculata* favored zebra mussel shells over bare substrate (Mörtl & Rothhaupt 2003). In this study, organic matter that accumulated between the interstices of the shells might have attracted *B. tentaculata* as well as other taxa. However, no organic matter aggregated between the valves of *C. fluminea* in our study. But this could also be an important effect in lakes, especially, as the ecosystem engineering effects of valves can persist even after mass mortalities of *C. fluminea* (Werner & Rothhaupt 2008).

Biotic effects

Biodeposits of mussels are a suitable food source for benthic organisms (Roditi *et al.* 1997) and bioturbation of sediments and nutrient allocation are ecosystem functions performed by burrowing bivalves that potentially influence benthic communities (Vaughn & Hakenkamp 2001). Although the burrowing activity of the mobile amphipods *D. villosus* and *G. roeselii* partly exposed some infaunal *C. fluminea* (personal observation), both amphipod species showed a preference for living clams that is probably not only due to structural effects. *D. villosus* preferred starved living clams over sand, but the variance in the habitat choice of *G. roeselii* on starved clams was too large to result in significant differences (Fig. 5.1). Apart from this possible biotic effect on amphipods, burrowing activity (bioturbation) of the clams did not influence the habitat choice of other benthic taxa in our short-term experiments. Long-term bioturbation through bivalve movements, in contrast, increases the oxygen and water content of sediment (Vaughn & Hakenkamp 2001), which could affect infaunal invertebrates.

G. roeselii preferred fed infaunal *C. fluminea*, whose siphons protrude from the sand. Because of this structural effect, it remains unclear to what extent the biotic effects of *C. fluminea* are responsible for the habitat choice of *G. roeselii*. It is unknown why *D. villosus* did not respond similarly. However, we found more individuals of the gastropod *L. stagnalis* on the area were living *C. fluminea* produced deposited pseudofaeces. This organic matter acted as a food source for these gastropods (own observations), which are epiphyton and detritus feeders as well as scavengers (Colling & Schmedtje 1996). Generally *Dreissena* is associated with an increase in gastropod density in field experiments and surveys (Ward & Ricciardi 2007). However, in contrast to burrowing bivalves like *C. fluminea*, zebra mussels exert simultaneous biotic and abiotic (physical structure) effects. It is most likely that *L. stagnalis* selected the pseudofaeces as food more than the living *C. fluminea,* because they did not respond to unfed *C. fluminea*.

Although the stonefly *C. luteolum* did neither favor fed nor starved *C. fluminea* over sand, the responses between both these habitat choice experiments were significantly different (Fig. 5.1). There was a trend to avoid starved and to prefer fed clams. *C. luteolum* is mainly a grazer, but also a gatherer (Colling & Schmedtje 1996); therefore, biodeposited algae should be a suitable food source. In our study, chironomids seemed to prefer starved living *C. fluminea* over bare sand, although the data were not significant after sequential Bonferroni adjustment. Uncertain results for chironomids could be caused by their unknown species composition: even morphologically similar species could have different habitat preferences. Since zebra mussel density is positively correlated with chironomid density (Karatayev *et al*. 1997, Stewart *et al*. 1998, Botts *et al*. 1996), *C. fluminea* might also support some chironomid species, especially epifaunal taxa via production of valves.

Even though the short-termed design of our study limits the power of conclusions, especially about the impact of bioturbation and nutrient reallocation, three species responded to the living clams. In comparison, during our longer termed *in situ* experiments, we did not detect any effects of living *C. fluminea* on benthic invertebrates (Werner & Rothhaupt 2007). One reason why benthic taxa barely respond to living *C. fluminea* could be that *C. fluminea* is able to filter and pedal feed (Reid *et al.* 1992). Thus, the clams might use their own deposited pseudofaeces and faeces, making it unavailable to other benthic taxa. When conditions favor pedal-feeding, *C. fluminea* significantly reduces the organic content of stream sediments by this means (Hakenkamp & Palmer 1999). In contrast, filter-feeding promotes biodeposition of organic matter as faeces and pseudofaeces, which enriches the organic content of sediments (Hakenkamp & Palmer 1999) and thereby enhances the conditions for deposit-feeding organisms (Ricciardi *et al.* 1997). Furthermore, in our habitat choice experiments, mobile and fast-moving taxa, such as amphipods, might have distributed the pseudofaecal and faecal pellets of the clams and thus resuspended and homogenized the algae in both halves of the aquaria. In this way, the conditions for habitat choice on both sides of the aquaria could have been equal. However, slower taxa, such as leeches, chironomids, and gastropods did not seem to affect the algal pellet distribution because we found deposited algae covered with a mucus casing only close to *C. fluminea*. Therefore, the presence of living *C fluminea* seems to be less important for the habitat choice of most taxa than the physical presence of valves. However, we cannot determine from this short-termed study whether biotic effects (pseudofaeces and faeces production as well as bioturbation and nutrient allocation) are marginal in natural habitats.

Conclusions

C. fluminea has the potential to change the surface quality of soft-bottomed sediments through the presence of their valves (Werner & Rothhaupt 2008). Since all epifaunal taxa except gastropods showed a clear preference for *C. fluminea* valves, many species that prefer hard substrates might invade sandy areas settled by *C. fluminea* in the future. Even taxa that are not directly affected by the occurrence of *C. fluminea* could be influenced indirectly by predators that spread because of the increase in structural diversity. One such species is the invasive amphipod *D. villosus*, a predator that can cause considerable changes in invertebrate communities (Dick *et al.* 2002). The density of *D. villosus* that attaches to diverse substrates and avoids unstructured habitats like sand (Hesselschwerdt *et al.* accepted) significantly increased on soft substrates with valves of *C. fluminea* in

Lake Constance (unpublished data). Our study implicates that structural effects of *C. fluminea* facilitate epifaunal benthic invertebrates more than biotic effects, but longer termed studies should confirm this conclusion.

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6 Substrate-dependent shifts from facilitation to competition between two invasive bivalve species

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submitted

Abstract

In dynamic interactions between individuals or species, facilitation and competition can occur simultaneously. Here we studied the effects of intraspecific and interspecific interactions of the Asian clam *Corbicula fluminea* and the zebra mussel *Dreissena polymorpha* on the growth of both invasive bivalve species in laboratory experiments. After 30 days with limiting food, the growth of both *C. fluminea* and *D. polymorpha* in high densities was lower than that of controls containing one individual, providing evidence for intraspecific competition. When food was not limiting, the growth of *D. polymorpha* and *C. fluminea* was unaffected by the density of conspecifics. However, when the two species were kept together (one *C. fluminea* and four attached *D. polymorpha*), the growth rate of *C. fluminea* on sand was higher than under all other conditions, even when food was not limiting, which indicated that *C. fluminea* facilitated from biodeposits produced by the associated zebra mussels. This effect did not occur when *C. fluminea* grew on pebbles, even with the same amount of food, because the *D. polymorpha* biodeposits fell into the substrate interstices and were unavailable to *C. fluminea*. Our results indicated that biodeposition and the organic content of sediments play a major role in the outcome of the interaction (competition or facilitation) between the two species of invasive bivalves. The successful co-existence of the two species in freshwaters may therefore be a reflection, at least in part, of facilitative interactions between them.

Key words pedal feeding, biodeposition, organic content, growth, intraspecific interaction, interspecific, zebra mussel, Asian clam, *Corbicula fluminea*, *Dreissena polymorpha*

Introduction

The outcome of interspecific and intraspecific interactions is strongly influenced by the availability of resources. According to most modern ecological concepts and theories, interactions between individuals, populations, or species lead to competition, predation, or physiological stress, and abiotic factors deplete populations and remove species; however, the importance of facilitation in these interactions has been neglected (Bertness & Leonard 1997, Bruno *et al.*

2003). Interactions between individuals and species can be dynamic, with facilitation and competition co-occurring in time and space (Walker & Chapin 1987, Callaway *et al*. 2002). The consequences of these interactions can be influenced by abiotic factors.

Both the zebra mussel *Dreissena polymorpha* (Pallas 1771) and the Asian clam *Corbicula fluminea* (Müller 1774) can dominate the benthic communities of colonized freshwaters and control physical and functional processes in freshwater ecosystems (Karatayev *et al.* 2005, Karatayev *et al.* 1997, Phelps 1994, Cohen *et al.* 1984). Both bivalves are among the most invasive freshwater species worldwide and can reach very high densities (Karatayev *et al.* 2005). The epifaunal zebra mussels can facilitate most species in benthic communities mainly by physical engineering and biodeposition (Karatayev *et al.* 1997, Stewart *et al*. 1998, Nalepa *et al*. 2003), but they also are responsible for the decline of most native unionid species in North America (biofouling) (Schloesser *et al.* 1997; Ricciardi *et al.* 1998, Strayer 1999, Nalepa *et al.*, 2001). The evidence that infaunal *C. fluminea* affects native bivalves is much weaker (Vaughn & Spooner 2006), and their impact on benthic communities is probably limited to epifaunal taxa on soft substrates (Werner & Rothhaupt 2007, Werner & Rothhaupt, 2008).

The effects of *D. polymorpha* and *C. fluminea* on different taxa, communities, and processes are known to various degrees, but to our knowledge, the interactions between these two species have not been examined (cf. Karatayev *et al.* 2005). Since *C. fluminea* burrows in soft sediments and *D. polymorpha* attaches with byssal threads to hard substrates, Karatayev *et al.* (2005) stated that they have contrasting distributions, even when they occur in the same water body. However, since *D. polymorpha* uses *C. fluminea* as a biogenic hard substrate, the two species coexist, for example, on the soft bottom areas of Lake Constance not yet colonized by *D. polymorpha* alone (personal observation). *D. polymorpha* invaded the rather deep, pre-alpine, and oligotrophic Lake Constance in Central Europe in the 1960s (Siessegger 1969), and *C. fluminea* arrived in the early 2000s (Werner & Mörtl 2004). We tested the outcome of their interactions in laboratory experiments with various food concentrations, sediment grain sizes, and sediment organic contents to determine whether the growth of *C. fluminea* affects or is affected by attached *D. polymorpha*.

Methods

Bivalves and algal diet composition

We collected *D. polymorpha* and *C. fluminea* from the littoral zone of Lake Constance (Central Europe) near the cities of Konstanz and Bregenz in September 2006 and in September 2007. Until the experiments started, the juveniles of both bivalve species were kept in a climate chamber at 20 °C with a 20-l flow-through system flushed with 30-µm-filtered lake water (*C. fluminea* on sand, *D. polymorpha* on pebbles). Bivalves grown in the experiment with inorganic sand and unlimited food (Oct 2006) and those grown in the experiment on inorganic sand with limited food (Oct 2007) were kept for one month, those for further experiments for two months [pebbles with unlimited food (Nov 2006); organic sand with limited food (Nov 2007)].

For growth experiments, we used young bivalves with shell lengths of 3–7 mm. Mussels and clams of this size class do not yet reproduce and therefore show a distinct somatic growth (Aldrige & McMahon 1978, Walz 1978). In every experiment, we used new bivalves that were fed with a mixture of four species of algae grown under constant illumination: *Scenedesmus obliquus* (SAG 276-3a; Sammlung von Algenkulturen Göttingen, Germany, 130 µmol quanta m^{-2} s^{-1}), *Chlorella* sp. (isolate from Lake Con stance, 215 µmol quanta m^{-2} s^{-1}), *Chlamydomonas klinobasis* (isolate from Lake Constance, 215 µmol quanta m^{-2} s^{-1}), and *Cryptomonas erosa* (from Plön, Germany, 65 µmol quanta m^{-2} s^{-1}). These algae were chosen because *C. fluminea* grows optimally with this mixture (Foe & Knight 1986) and because *D. polymorpha* positively selects *Cryptomonas* (Ten Winkel & Davids 1982). All algae were 2–10 µm in

Table 6.1. Actual replicate numbers of *C. fluminea* and *D. polymorpha* in the experiments. *: one moldy but living *C. fluminea* was excluded. *C*: one *C. fluminea* individual, *5C*: five *C. fluminea* individuals, *C-4d*: one *C. fluminea* individual with four attached *D. polymorpha, C-4d*†: one *C. fluminea* individual with four attached valves of *D. polymorpha; D*: one *D. polymorpha* individual, *5D*: five *D. polymorpha* individuals, *c-4D*: four *D. polymorpha* individuals attached to one *C. fluminea* individual

Substrate	Food limitation	Experiment	$n_{started}$	$n_{analyzed}$
Pebbles	No	*C*	10	10
		5C	10	10
		C-4d	5	5
		C-4d †	10	10
		D	10	9
		D	5	5
		c-4D	5	5
Sand inorganic	No	*C*	10	8
		5C	10	10
		C-4d	10	9*
		C-4d †	10	9
		D	10	9
		D	10	10
		c-4D	10	10
Sand inorganic	Yes	*C*	10	10
		5C	10	8
		C-4d	10	10
		C-4d †	10	10
		D	10	10
		D	10	10
		c-4D	10	10
Sand organic	Yes	*C*	10	10
		5C	10	10
		C-4d	10	10
		C-4d †	10	9
		D	10	9
		D	10	10
		c-4D	10	10

length and are easily digested by both bivalve species (Way *et al.* 1990, Sprung & Rose 1988). Algae were grown in semi-continuous batch cultures at 20 °C in aerated 5-l vessels. The dilution rates were 0.25 d^{-1} for *Chlorella* sp. and *Chlamydomonas klinobasis*, 0.33 d^{-1} for *Cryptomonas erosa*, and 0.5 d^{-1} for *S. obliquus*. The green alga *S. obliquus* was grown in Cyano medium (Jüttner *et al.* 1983); the flagellate *Cryptomonas erosa*, the motile green alga *Chlamydomonas klinobasis*, and the green alga *Chlorella* sp. were grown in modified Woods Hole (WC) medium containing vitamins (Guillard 1975). Stock solutions of these organisms for the growth experiments were prepared by concentrating the cells by centrifugation and resuspending the cell pellet in WC or Cyano medium lacking vitamins, as appropriate. Carbon concentrations of the food suspensions were estimated from photometric light extinction (800 or 480 nm, *S. obliquus*) and from carbon-extinction equations determined previously. The food stock contained four equal parts of carbon from each species of algae.

Experimental design

We expected that interspecific and intraspecific interactions would affect the growth rates of both bivalve species. To test intraspecific interactions, we used five *C. fluminea* clams (*5C*), with one clam (C) as the control or five *D. polymorpha* mussels (*5D*), with one mussel (*D*) as the control. Interspecific interactions were studied with either four living *D. polymorpha* or four valves *of D. polymorpha* glued (UHU® two-component epoxy adhesive) onto one *C. fluminea*. With the four attached living *D. polymorpha*, we tested whether they biotically or physically affected the growth of *C. fluminea* (*C-4d*) and vice versa (*c-4D*). The four valves of *D. polymorpha* were used to test only physical effects that might influence the growth of *C. fluminea* (*C-4d*†), such as ballast of weight and steric challenge. To achieve the approximate weight of living mussels, we glued small pebbles into the *D. polymorpha* valves.

Each experiment was run in a separate aerated 1.5-l Weck® vessel filled with 1 l of filtered (0.45 µm) lake water at 20 °C. The filtration excluded ingestible organisms, and aeration kept the added algae in suspension. The water was changed every second day. The algal mixture was added after every water exchange. Vessels with *C. fluminea* were filled with sediment to a height of 1.5 cm (~50 ml). The highly mobile *D. polymorpha* individuals were glued onto small pebbles (2.0–6.3 mm) with UHU® two-component epoxy adhesive to prevent mobility. The experiments were conducted in a climate chamber at 20 °C (optimal growth; Foe & Knight 1986), and each set of growth experiments lasted for 30 days. If mortality occurred, the bivalves were removed. The planned and analyzed replicate numbers are shown in Table 6.1. In treatments with more than one bivalve, every individual was marked with an Edding® text marker. All animals were measured and weighed before and after the experiments. Shell length was measured under a binocular with an image-processing program (precision: ± 0.05 mm), and fresh mass was determined with a scale (Mettler AE 240; precision: ± 0.1 mg). Bivalves were dried with a non-woven cloth before weighing.

Effect of organic content and grain size

Since *C. fluminea* favors sand over pebbles (Belanger *et al.* 1985, Schmidlin & Baur 2007), we wanted to determine whether intraspecific and interspecific interactions on coarser sediments results in reduced shell growth rates. We used inorganic sand (0.2–0.63 mm) and pebbles (2.0–6.3 mm) as sediment; both were ignited at 550 °C for 5.5 h. Sediment was collected from the littoral zone of Lake Constance and was not changed during the 30-day experiment. Hence, if the carbon fraction of inorganic and organic sediment increased during the experiment, this was due to biodepostion. This carbon input was used to quantify the possible advantage of pedal feeding of *C. fluminea* compared to *D. polymorpha.*

Furthermore, we determined whether the organic carbon content of sand influences the interaction between the two invasive bivalves. We used autoclaved organic sand (13 ± 1.3 mg organic carbon per g sand) and inorganic sand. *C. fluminea* would be able to take up nutrients by pedal feeding on organic sand but not on inorganic sand.

All experiments with *C. fluminea* (*C, 5C, C-4d = c-4D, C-4d*†) were repeated ten times. Control experiments with *D. polymorpha* (*D, 5D*) were repeated five times and were always conducted on pebbles.

Effects of food particle concentration

Unlimited food (controls) was provided with 0.5 mg carbon per individual living bivalve in the form of algae (e.g., *5C* were fed with 2.5 mg carbon, and *C-4d*† were fed with 0.5 mg carbon). Food limitation was achieved by adding 0.5 mg carbon per vessel, independent of the number of living bivalves.

Analyses

For each bivalve, growth was calculated from the changes in size and weight that occurred during the experiment. Growth data are reported as the total increase in shell length (mm) and fresh mass (mg) during the 30-day study period. For experiments with more than one bivalve (*5C, 5D*, and *c-4D*), we calculated the mean growth of each replicate. Differences between experiments were analyzed with the non-parametric Kruskal-Wallis-ANOVA (Statistica, stat. soft V.6.0); the assumptions for ANOVA (homogeneity of variance) could not be achieved by data transformation. When results were significant, Tukey-HSD *post-hoc* tests (for unequal n) were conducted. Experiments were compared pair-wise with non-parametric Mann-Whitney U-tests.

Table 6.2. Effects of substrate and food limitation. Results of Kruskal-Wallis-ANOVA are shown. $\alpha = 0.017$.

Species	Growth parameter	Substrate	Food limitation	$\_^2$	*df*	*P*
C. fluminea	Shell length	Pebbles	No	3.775	3	0.287
		Inorganic sand	No	12.4	3	**0.006**
		Inorganic sand	Yes	23.2	3	**< 0.001**
		Organic sand	Yes	16.897	3	**0.001**
	Biomass	Pebbles	No	6.977	3	0.073
		Inorganic sand	No	14.711	3	**0.002**
		Inorganic sand	Yes	27.2	3	**< 0.001**
		Organic sand	Yes	16.897	3	**0.001**
D. polymorpha	Shell length	Pebbles	No	7.947	2	0.019
		Inorganic sand	No	14.711	2	0.413
		Inorganic sand	Yes	27.2	2	**< 0.001**
		Organic sand	Yes	18.829	2	**< 0.001**
	Biomass	Pebbles	No	6.164	2	0.046
		Inorganic sand	No	1.768	2	0.413
		Inorganic sand	Yes	12.8	2	**< 0.001**
		Organic sand	Yes	6.351	2	0.042

Some data from single experiments were used three times; thus, we conducted a Bonferroni adjustment to obtain an experiment-wise error rate of $p = 0.05$ across all dependent variables ($\alpha = 0.05/3 = 0.017$).

Results

Growth differences within the experiments

In all experiments, both the shell length and fresh mass, i.e., the growth parameters, of *C. fluminea* and *D. polymorpha* showed the same pattern, except for *D. polymorpha* on organic sand, which significantly differed in shell length, but not in fresh mass (Table 6.2).

With *C. fluminea* on inorganic pebbles (2.0–6.3 mm) and with unlimited food, the shell growth and biomass in all four experiments (*C*, *5C*, *C-4d,* and *C-4d*†) did not significantly differ. With *D. polymorpha* (*D*, *5D,* and *c-4D*) on pebbles, no significant differences were observed after Bonferroni adjustment (Table 6.1, Fig. 6.2).

On inorganic sand (0.2–0.63 mm) with unlimited food, the shell and biomass growth rates of *C. fluminea* differed (Fig. 6.1, Table 6.2). *C-4d* grew significantly better than *C*, *5C,* and *C-4d*† (Fig. 6.1, Table 6.2). The increase in shell length and biomass of *D. polymorpha* in all experiments (*D*, *5D*, and *c-4D*) did not differ (Fig. 6.2). *D* and *5D* grew on single pebbles, and *c-4D* grew on sand.

The growth rates of both bivalve species on inorganic sand with food limitation strongly differed. *C* and *C-4d*† had higher growth rates than *C. fluminea* in both experiments with a higher number of individuals (*5C* and *C-4d*; Fig. 6.1). Under food limitation, single zebra mussels (*D*) showed significantly higher growth rates than *5D* and *c-4D* (Fig. 6.2).

Table 6.3. Results of Mann-Whitney U-Test for *C. fluminea*. In the comparisons *pebbles vs. inorganic sand* and *inorganic vs. organic sand*, the sediment was changed in all experiments. In the comparison *limited vs. unlimited food on inorganic sand* (2.5 and 0.5 mg C, respectively), the amount of food differed only for *5C* and *C-4d*. In the controls, single *C* and *C-4d*† were fed with 0.5 mg C in both experiments. $\alpha = 0.05$; after data correction: $\alpha = 0.017$. P = pebbles; iS = inorganic sand; oS = organic sand; U = unlimited food; L = limited food. *C*: one *C. fluminea* individual, *5C*: five *C. fluminea* individuals, *C-4d*: one *C. fluminea* individual with four attached *D. polymorpha* individuals, *C-4d*†: one *C. fluminea* individual with four attached valves of *D. polymorpha.*

Comparison	Growth parameter	Experi-ment	*U*	*n1*	*n2*	*P*		Effect
P vs. iS; U	Shell length	*C*	25.5	8	9	0.312		
		5C	46	10	10	0.762		
		C-4d	2	5	9	**0.006**	P < iS	Facilitation
		C-4d †	22.5	10	9	0.066		
	Fresh mass	*C*	34	8	9	0.847		
		5C	44	10	10	0.65		
		C-4d	0	5	9	**0.003**	P < iS	Facilitation
		C-4d †	30	10	9	0.221		
L vs. U; iS	Shell length	*C*	11.5	8	10	**0.011**	U < L	Cohort
		5C	2	10	8	**0.001**	U > L	Intraspecific competition
		C-4d	4	9	10	**0.001**	U > L	Interspecific competition
		C-4d †	15	9	10	**0.014**	U < L	Cohort
	Fresh mass	*C*	19	8	10	0.068		
		5C	0	10	8	**< 0.001**	U > L	Intraspecific competition
		C-4d	0	9	10	**< 0.001**	U > L	Interspecific competition
		C-4d †	22	9	10	0.065		
oS vs. iS; L	Shell length	*C*	8	10	10	**0.001**	oS < iS	Captivity
		5C	12	10	8	**0.013**	oS > iS	Intraspecific competition
		C-4d	48.5	10	10	0.91		
		C-4d †	18	10	9	0.027		
	Fresh mass	*C*	15	10	10	**0.008**	oS < iS	Captivity
		5C	5	10	8	**0.002**	oS < iS	Captivity
		C-4d	17	10	10	**0.013**	oS < iS	Captivity
		C-4d †	10	10	9	**0.004**	oS < iS	Captivity

The growth rate of *C. fluminea* on organic sand with food limitation differed only in one comparison of the four experiments (*C*, *5C*, *C-4d* and *C-4d*†; Table 6.2, Fig. 6.1); *C* grew significantly better than *5C*. Comparisons of all other experiments revealed no differences. As expected from the experiment with food limitation, single zebra mussels (*D*) on organic sand had significantly higher shell growth rates than *5D* and *c-4D*. However, when we consider biomass, these differences are not significant after Bonferroni correction.

Comparisons of sets of experiments

Since the growth experiments were conducted consecutively, the shell length and fresh mass differed (Table 6.3 and 6.4). When pebbles and inorganic sand were compared, food was not limiting in all experimental pairs. *C. fluminea* showed significant differences in growth only on pebbles and inorganic sand in *C-4d* (Table 6.3). In this case, *C. fluminea* was significantly larger and heavier when grown on inorganic sand than on pebbles. *C*, *5C*, and *C-4d*† showed no sub-

Table 6.4. Results of Mann-Whitney U-Test for *D. polymorpha*. In the comparisons *pebbles vs. inorganic sand* and *inorganic vs. organic sand*, the sediment was changed only for *c-4D*. *D* and *5D* were kept on pebbles as controls. The amount of food in the comparison *limited vs. unlimited food* differed only for *5D* and *c-4D* (2.5 and 0.5 mg C, respectively). Single *D* was fed with 0.5 mg C in both experiments. $\alpha = 0.05$; after data correction: $\alpha = 0.017$. P = pebbles; iS = inorganic sand; oS = organic sand; U = unlimited food; L = limited food. *D*: one *D. polymorpha* individual, *5D*: five *D. polymorpha* individuals, *c-4D*: four *D. polymorpha* individuals attached to one *C. fluminea* individual.

Comparison	Growth parameter	Experi-ment	*U*	*n1*	*n2*	*P*		Effect
P vs. iS; U	Shell length	*D*	22	9	9	0.102		
		5D	13.5	5	10	0.159		
		c-4D	20.5	5	9	0.789		
	Fresh mass	*D*	12	9	9	0.027		
		5D	5	5	10	**0.014**	P > iS	**?**
		c-4D	11	5	9	0.125		
L vsU; iS	Shell length	*D*	29.5	9	10	0.205		
		5D	11	10	10	**0.003**	L < U	Intraspecific competition
		c-4D	8	10	9	**0.003**	L < U	Interspecific competition
	Fresh mass	*D*	38	9	10	0.568		
		5D	14	10	10	**0.007**	L < U	Intraspecific competition
		c-4D	35	10	9	0.414		
oS vs. iS; L	Shell length	*D*	8	10	9	**0.003**	oS > iS	Captivity
		5D	33	10	10	0.199		
		c-4D	10.5	10	10	**0.003**	oS < iS	Interspecific competition
	Fresh mass	*D*	15	10	9	0.041		
		5D	5	10	10	0.023		
		c-4D	17	10	10	**0.001**	oS < iS	Interspecific competition

strate-dependent growth differences. The shell lengths of *D. polymorpha* did not differ between each experimental pair, but the fresh mass of *5D* grown on pebbles was higher than *5D* grown on sand (Table 6.4). The shell lengths of *C. fluminea* grown on inorganic sand with limited or unlimited food differed in all four experiments (Table 6.3). In experiments with single living clams (*C* and *C-4d*†) fed with the same amount of algae, *C. fluminea* grew significantly better in the trial for limited food than in the trial for unlimited food. However, in experiments with five living bivalves (*5C* and *C-4d*), the shell length of *C. fluminea* was significantly lower with limited food than with unlimited food. In comparisons of fresh mass, only the differences for *5C* and *C-4d* were significant. The shell lengths of single *D. polymorpha* (*D*) did not differ from that of the control (both on pebbles), whereas the growth rate of mussels in the control *5D* (on pebbles) with limited food was lower than the growth rate of *5D* with unlimited food (Table 6.4). The shell lengths of *c-4D* were significantly lower when fed with limited food than with unlimited food. The fresh mass of *D. polymorpha* in these three experimental pairs differed only in *5D*.

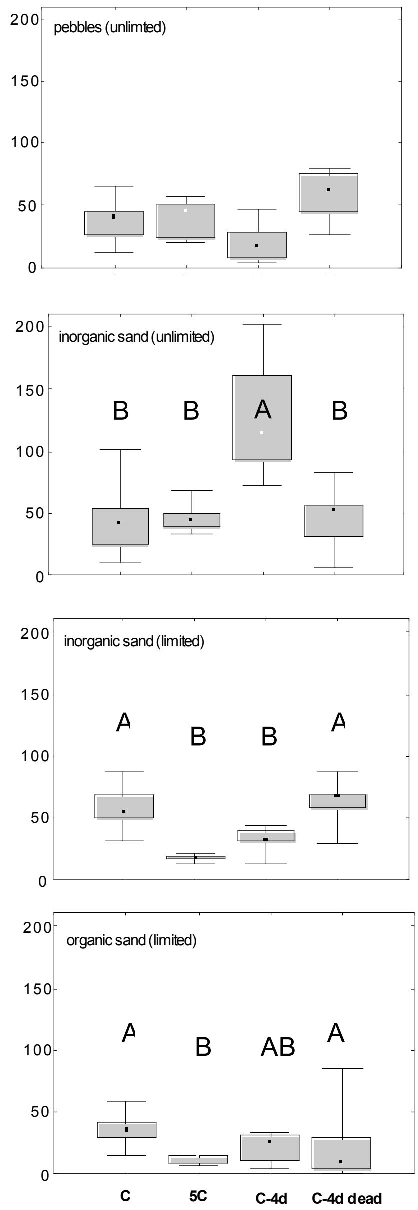

Fig. 6.1. Increase in fresh mass of *Corbicula fluminea* depending on the substrate and food availability (median and interquartile range). C: one *C. fluminea* individual, 5C: five *C. fluminea* individuals, C-4d: one *C. fluminea* individual with four attached *D. polymorpha* individuals, C-4d dead: one *C. fluminea* individual with four attached valves of *D. polymorpha*

The different organic content of sediments with limited food led to shell length differences of *C. fluminea* in only two experiments: *C* and *5C*. Single *C. fluminea* (*C*) were larger on inorganic sand, whereas *5C* were larger on organic sand (Table 6.3). However, in all four experiments, the fresh mass of *C. fluminea* was higher on inorganic sand than on organic sand. The opposite results were obtained with *5C*: although shells were smaller when grown on inorganic sand than on organic sand, *C. fluminea* was heavier when grown on inorganic sand. The shell length of *D. polymorpha* in the control *D* (on pebbles) was larger when grown in the trial for organic sand (also on pebbles). The shell length of *5D* (on pebbles) did not differ, but the shell length of *c-4D* was larger when grown on inorganic sand. For fresh mass, only that of *c-4D* was significant (Table 6.4).

Discussion

In the four different experiments, the growth of *D. polymorpha* fed with 0.5 mg C per individual and liter was independent from the conspecific density and was neither affected by sediment grain size nor by the presence of *C. fluminea* (*c-4D*). *C. fluminea* fed with 0.5 mg C per individual and liter (*C*, *5C*, and *C-4d*†) also grew independently of sediment grain size. Thus, the food regime (0.5 mg per individual and liter) in our experiments did not limit the growth of *D. polymorpha* and *C. fluminea*. However, when we compare the growth rates among the experi-

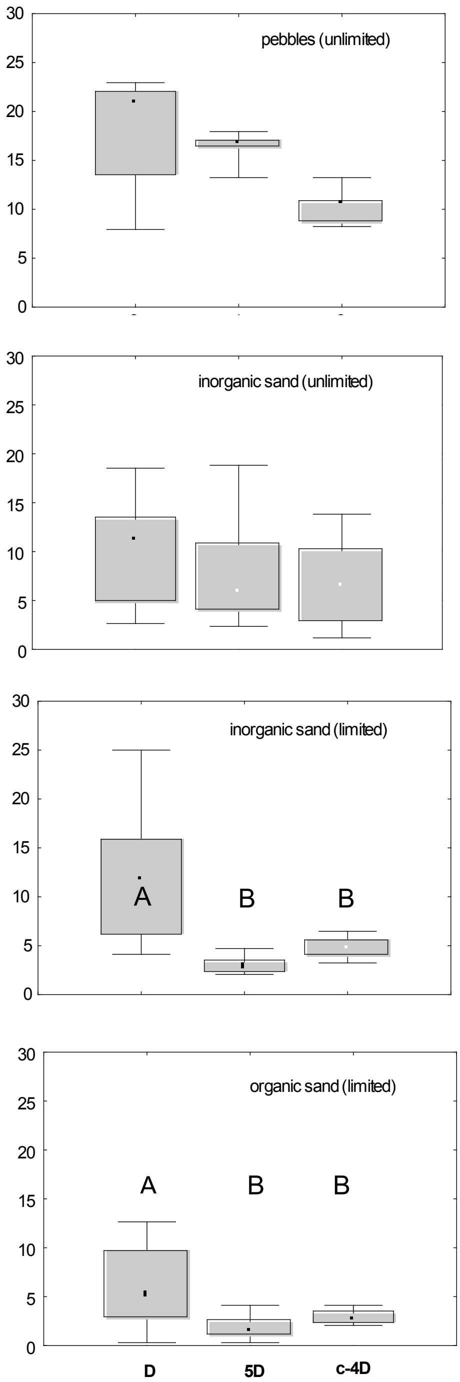

Fig. 6.2. Increase in fresh mass of *Dreissena polymorpha* depending on the substrate and food availability (median and interquartile range). D: one *D. polymorpha* individual, 5D: five *D. polymorpha* individuals, c-4D: four *D. polymorpha* individuals attached to one *C. fluminea* individual

ments, it becomes apparent that the duration of captivity and also different cohorts of the two bivalve species from two different years led to different growth rates in the experiments and also to differences in the biomass and shell length increases (Table 6.3 and 6.4). Individuals fed with the same amounts of food had lower growth rates when they were kept for one month longer than the bivalves in the other experiments. Bivalves greatly reduce fresh mass in aquaria, but not *in situ*; this is called the container effect (Britton 1979, Meister 1997, Lamm 2007). Biomass changes rapidly in a changing environment and is more susceptible to changes than shell length. *C. fluminea* collected in September 2007 had significantly lower shell growth rates than *C. fluminea* collected in September 2006 (Table 6.3). However, this interannual difference in shell length was overlaid by the effects of limited vs. unlimited food on biomass. It remains unknown why *5D* with unlimited food were larger in the trials for pebbles than in those for organic sand, although they were kept for a longer time and had the same substrate (both *5D* treatments were conducted on pebbles).

With unlimited food, interspecific interactions led to substrate-specific growth differences. On sand, the biotic effects of attached *D. polymorpha* facilitated the growth of *C. fluminea*, whereas on pebbles, this facilitation did not occur (Fig. 6.1, Table 6.2). The four attached *D. polymorpha* individuals biodeposited algae as pseudofaeces, which on sand was gathered from the surface by *C. fluminea* via pedal feeding (own observation). Pedal feeding by burrowing bivalves such as *C. fluminea* can supply more than 50% of the energy demand; the remainder is supplied by filter feeding (Reid *et al.* 1992, Cahoon & Owen 1996). On pebbles, in contrast, the biodeposited matter produced by the attached *D. polymorpha* was not available to *C. fluminea* because it fell into the interstices of the substrate (own observations). Pseudofaeces of *D. polymorpha* is a high quality food source (Roditi *et al.* 1997). Collecting these highly concentrated algal pellets by pedal feeding may have been more energy efficient for *C. fluminea* than filtering single algae out of the water column. If the energy saved by pedal feeding was invested in somatic growth, it would explain why *C-4d* grew significantly better than *C. fluminea*, which could only filter or feed on their own biodeposits (*C, 5C, C-4d†*). In contrast, *C. fluminea* (*C-4d*) on pebbles could only filter feed since the biodeposited food was not available, which resulted in a growth rate as in the other experiments (Fig. 6.1).

Food limitation (0.1 mg C per individual and liter) on inorganic sediment led to intraspecific and interspecific competition in all experiments with five bivalves (*5C, 5D* and *C-4d* = *c-4D*). These bivalves had a significantly lower growth rate than single bivalves (*C, D,* and *C-4d†*) and *5C, 5D,* and *C-4d* = *c-4D* grown with unlimited food. With limited food, *D. polymorpha* and *C. fluminea* (*c-4D*) produced no pseudofaeces. *C. fluminea* could then only filter feed and therefore needed to compete with the associated *D. polymorpha*, which in turn had to compete with conspecifics and *C. fluminea.* These interactions resulted in reduced growth rates of both bivalve species.

With limited food, *C. fluminea* and *D. polymorpha* competed on inorganic sand, on which both species could only filter feed. However, the organic content of sediment seemed to compensate for the competition, as *C. fluminea* was able to use the organic content of sediments by pedal feeding. Interestingly, five *C. fluminea* (*5C*) competed with conspecifics in filter and pedal feeding. They grew significantly less than *C*, whereas there were no differences in all other experiments (especially *C-4d*) (Fig. 6.1). Unfortunately, the duration of captivity had stronger effects on the biomass of *C. fluminea* — the more susceptible growth parameter — than the conditions in the different experiments.

The ballast of *D. polymorpha* shells (*C-4d†*) on its own neither affected the growth rates of *C. fluminea* on sand nor on pebbles. Therefore, we conclude that under food limitation, the biotic effects of *D. polymorpha* reduce the growth of infested *C. fluminea*. Unionids infested with *D. polymorpha* also show reduced growth (Burlakova *et al.* 2000) and have a lower lipid content (Hebert *et al.* 1991) and a higher mortality rate (Ricciardi *et al.* 1996) than unsettled unionids. *D. polymorpha* grows faster on live unionids than on stones, which suggests that *D. polymorpha* uses food provided by the filter current of the unionid, resulting in the negative effects for the ‘host’ bivalve

(Hörmann & Maier 2006). The feeding current produced by the living blue mussel *Mytilus edulis* leads to faster growth of the attached epibiotic barnacle *Balanus improvisus* than when it is attached to empty shells. However, in contrast to the situation with unionids, the presence of barnacles has no effect on the growth of *M. edulis* (Laihonen & Furman 1986). The different results and the severity of effects for infested bivalves might be due to density differences of attached epibionts. In their study, Laihonen and Furman (1986) used one *B. improvisus* individual, and we used four juvenile *D. polymorpha*. Denser colonization should have affected the growth of these 'host' bivalves, as observed for unionids (Ricciardi *et al.* 1996).

Conclusions

Although unionids have decreased growth rates and suffer from zebra mussel colonization (Schloesser *et al.* 1997, Ricciardi 1998, Strayer 1999, Nalepa *et al.* 2001, Burlakova *et al.* 2000), it was not known whether biofouling of *D. polymorpha* also affects the growth of *C. fluminea* (Karatayev *et al.* 2005). We showed that *C. fluminea* can facilitate from a low level of *D. polymorpha* settlement (in this case, four individuals), when the attached mussels produce pseudofaeces. Coarser substrate, lower food amounts, and probably also denser colonization by epibionts (not tested here) turns these positive effects into competition. We conclude that biodeposition and the organic content of sediments play major roles in the outcome of the interaction (competition or facilitation) between the two invasive bivalves. Our results are not the first to show facilitation by epibionts; however, the bivalves in the study of Manning and Lindquist (2003) were only indirectly affected by an epibiotic hydroid that facilitates a marine burrowing bivalve by reducing the predation efficiency of a fish species.

Facilitation of *C. fluminea* from pseudofaeces produced by a low level of zebra mussel colonization might occur on sandy substrates in lakes. In contrast, biodeposits would be removed by the water current in streams and rivers. *D. polymorpha* facilitated from biogenic hard substrates provided by physical engineering of *C. fluminea* on soft substrata. But, if both kinds of facilitation exist *in situ*, they could be superimposed by predation. Manning and Lindquist (2003) have shown that the settlement of the epibiotic hydroid *Lovenella gracilis* simplifies the detection of the marine infaunal bivalve *Donax variabilis* by predacious crab species. *C. fluminea* covered with *D. polymorpha* project well outside the sediment and are thereby much easier to detect for visual and tactile predators than infaunal *C. fluminea* without *D. polymorpha*. This increased predation risk, e.g., by wintering waterbirds that consume up to 95% of the *D. polymorpha* population in the littoral of Lake Constance (Werner *et al.* 2005), could overrule the key benefits of the facilitative effects between the two invasive bivalve species.

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7 Conclusions and perspectives

Corbicula fluminea

Densities

In lakes, the abundance of *C. fluminea* increases with trophic level, but densities are generally rather low (Beaver *et al.* 1991, Karatayev *et al.* 2005). In oligotrophic lakes, densities reach only 39 ± 17 Ind. m^{-2} (Beaver *et al.* 1991). In mesotrophic lakes these authors found 368 ± 328 Ind. m^{-2} and in eutrophic lakes 1278 ± 1047 Ind. m^{-2}. The densities of *C. fluminea* in Lake Constance can be very high, although it is a large oligotrophic lake with an actual phosphorus concentration of 8 mg m^{-3} (IGKB 2007). We recorded a maximum of 66,416 ind. m^{-2} including 64,608 juveniles < 5 mm in December 2005 (MLL -1m) and a maximum of 3696 ind. > 5 mm m^{-2} in September 2005 (MLL -1 m), what corresponded to the highest biomass (1578 g dry mass m^{-2} including valves). These densities compare more to those in natural lotic systems than to those in lakes. In rivers, mean densities generally range from 40 to 3502 individuals m^{-2} with a maximum of 10,000 to 20,000 Ind. m^{-2} (reviewed in Meister 1997 and in Karatayev *et al.* 2005). However, under special conditions – in thermal loaded water of the New River – up to 269,000 Ind. m^{-2} were recorded (80% < 1 mm; Cherry *et al.* 1980). McMahon (2004) also found very high densities of up to 12,000 *C. fluminea* m^{-2} in oligotrophic lentic habitats in Texas; but after that peak, populations declined quickly. A comparison of biomass data for *C. fluminea* is not possible, as these data are very rare in the literature (Meister 1997). As species of streaming waters occur in the windswept littoral of large lakes it is similar to lotic systems (c.f. Death & Winterbourn 1995, Baumgärtner 2004, Scheifhacken 2008). The currents in the littoral zone of Lake Constance may allow such high densities of *C. fluminea*, since they could provide constant food supply with phytoplankton from the huge pelagic zone. At the moment, it is unclear if *C. fluminea* densities will remain on a high level, which is far above the predicted densities for oligotrophic lakes (Beaver *et al.* 1991). Invaders to new ecosystems often reach an early very high peak and than stabilize on a lower level due to the beginning of e.g. predator-prey and parasite-host interactions (Kowarik 2003, McMahon 2004).

Growth parameters

C. fluminea begins to grow and to reproduce at 10-11 °C (Karatyev *et al.* 2005). Thus, the individual rich populations in Lake Constance (at MLL -1 m and deeper) annually only have about 7 months for somatic growth and reproduction. One reproductive period per year, reduced growth rates resulting in a reduced maximum size (rarely larger than 20 mm) characterize the *C. fluminea* population in oligotrophic Lake Constance. Life span of the clams compares with other studies and was not impacted by water temperature (Chapter 3 and citations therein). Climate change with increasing temperatures will enhance the reproductive success of *C. fluminea* in Lake Constance, as in the heat summers of 2003 and 2005, a second reproductive period occurred at the greater depths of our study site. Apart from effects of the water temperature, growth rates of *C. fluminea* can depend on food supply (Chapter 6) and probably also on disturbances such as wave action. After a very strong cohort, *C. fluminea* populations in oligotrophic lentic Texas habitats had the same population characteristics as those in Lake Constance. McMahon (2004) attributed the reduced growth rates in Texas to decreasing nutrients. Mean shell length of the *C. fluminea* population in Texas was 43.4 mm, but after very strong cohorts (up to 12,000 Ind. m^{-2}) had reduced the organic content of sediments, the mean shell length of subsequent cohorts was only 17.4 mm (McMahon 2004). With enough food supply in tropical and semi-tropical regions or under artificial situations with constant water temperatures between 20 and 25 °C, *C. fluminea* can grow very fast and build up to 3 generations per year (Doherty *et al.* 1987, reviewed in Meister 1997); this can lead to impressive densities (Cherry *et al.* 1980).

However, water temperatures do not only limit growth parameters, they can even limit the survival of *C. fluminea.* The population of *C. fluminea* at Rohrspitz nearly vanished completely due to water temperatures ≤ 2 °C for weeks in winter 2005 /2006. Only few reproducing individuals remained after the mass mortality described in Chapter 2, and densities were low until September 2007, when a new density peak was achieved with 1904 Ind. > 5 mm m^{-2}. Thus, the re-establishment of the *C. fluminea* population lasted much longer than that of *D. polymorpha*. After the annual depletion by wintering waterbirds, that consume more than 95% of the individuals, the *D. polymorpha* populations in Lake Constance recover completely during one subsequent summer (Werner *et al.* 2005).

Predation

The observed decline of *C. fluminea* between September and December 2007 could be a hint that waterbirds now discovered the new substantial food source. Personal observations showed that waterbirds consume *C. fluminea* at Lake Constance (Chapter 3). Infaunal clams are more difficult to detect for visual and tactile predators than epifaunal taxa. So, how could the birds have discovered the new food source? At our study site, about 100 wintering Whooper swans (*Cygnus cygnus*) consume tubers of macrophytes by digging in the sediments (Heine *et al.* 1999, personal observation). The burrowing activity of the herbivorous swans may expose prey – such as infaunal bivalves – that can be foraged by diving ducks such as Pochards (*Aythya ferina*), that closely associate to swans as commensals (personal observation).

Further, the infestation with *D. polymorpha* will increase the risk of predation for *C. fluminea* due to better perceptibility. Once the mussel-consuming waterbirds have discovered *C. fluminea* as resource, the food is easily accessible, as *C. fluminea* does not attach to surfaces. Nearly 50% of the diet of the diving duck Lesser Scaup (*Aythya affinis*) in South Carolina was *C. fluminea* (Hoppe *et al*. 1986). Further studies at Lake Constance should deal with the question if *C. fluminea* is an efficient resource for preying organisms; my own attempts in cooperation with the Max Planck Institute for Ornithology failed due to problems with the keeping of diving ducks. The thick-walled clams have a low energy content as valves contribute more than 95% to the total dry mass (unpublished data), what could be compensated by its high densities. In comparison, valves of zebra mussels build up 90% of the total dry mass, what is at least sufficient for wintering waterbirds (Werner 2002).

Anyhow, to date, it remains unclear if waterbird predation will play as an important role for *C. fluminea* in Lake Constance as it plays for *D. polymorpha* and associated invertebrates (Mörtl *et al*., in press). If predation pressure will be substantial, it is doubtful whether the life cycle of *C. fluminea* in Lake Constance and the predation of wintering waterbirds will lead to a well-rehearsed cycle. Without co-evolution, high annual predation would reduce the Asian clams lastingly, as the present life cycle of *C. fluminea* is to slow to compensate severe losses during one subsequent summer.

Conclusion

At present, the population of *C. fluminea* in Lake Constance is mainly limited by water temperature. Schöll (2000) postulated that *C. fluminea* could only establish in German Rivers because of thermal loading. This does not hold true for Lake Constance; but in fact, low water temperatures can reduce the success of *C. fluminea* invasions. Climate change with increasing water temperatures at Lake Constance (Arbeitskreis KLIWA 2007, Anneville *et al.* 2005) will reduce winter mortalities of *C. fluminea* and increase its reproductive success and its somatic growth during summer. Additionally, increasing winter temperatures due to climate change may allow *C. fluminea* to spread into freshwater systems further north. In future, predation by waterbirds may displace water temperature as limiting factor for the *C. fluminea* population in Lake Constance.

Benthic communities

Community patterns

A key factor in structuring littoral communities is water depth (Chapter 3). The benthic assemblage is further influenced by physical disturbance, such as water-level fluctuations (Chapter 2 and 3, Baumgärtner *et al.*, in press) or the impact of wave action (Scheifhacken 2008). The number of benthic taxa as well as their density and biomass increased with water depth and the therewith-correlated habitat stability (Chapter 3). Seasonal variability of abiotic and biotic factors such as water level fluctuation, life cycle, and predation can result in yearly recurring patterns in the benthic community. Additionally, the biomass of the benthic community is dominated by the two invasive bivalves *C. fluminea* and *D. polymorpha*; their population development strongly influences the community structure. Therefore, biological invasions are also important for community organization in the littoral zone (Chapter 3).

Corbicula fluminea* and *Dreissena polymorpha

At our study site, *D. polymorpha* settles on *C. fluminea*, although the two bivalves often have a contrasting distribution in the same freshwater bodies (Karatayev *et al.* 2005). Unionids suffer from zebra mussel colonization and infested unionids have decreased growth rates (Schloesser *et al.* 1997, Ricciardi *et al.* 1998, Strayer 1999, Nalepa *et al.* 2001, Burlakova *et al.* 2000). Anyhow, it was unknown whether the growth of *C. fluminea* is also affected by biofouling of *D. polymorpha* (Karatayev *et al.* 2005). In Chapter 6, I show that the outcome of interactions with the epibiont *D. polymorpha* depends on grain size and organic content of substrate and on food amount. On sand, *C. fluminea* can facilitate from a low level of *D. polymorpha* settlement, when the attached mussels produce pseudofaeces. Coarser substrate, lower food amounts (no production of biodeposited matter), and probably also denser colonization by epibionts (not tested) turn the facilitation into competition. Whether this facilitation of *C. fluminea* from pseudofaeces production by epibiotic *D. polymorpha* also occurs *in situ* should be subject to further studies. I would soonest suspect these effects on sandy substrates in lakes, where biodeposits are not removed by water currents. I have proved that *D. polymorpha* facilitated from ecosystem engineering of *C. fluminea* on soft substrata. However, if the mutual facilitation between both bivalve species exists *in situ*, it could be superimposed by predation, as Manning and Lindquist (2003) found that epibionts (hydroids) simplify the detection of an infaunal bivalve by predacious crab species.

***C. fluminea* and benthic community**

Before *C. fluminea* invaded, soft bottoms in the littoral zone of Lake Constance were not colonized by taxa typical for rocky substrates. Now, *C. fluminea* changes the surface quality of soft-bottomed sediments through the presence of their valves what facilitated the strong ecosystem builder *D. polymorpha* (e.g. Stewart *et al.* 1998) and most epifaunal taxa (Chapter 3 and 4). Epifaunal taxa except gastropods preferred *C. fluminea* valves in habitat choice experiments (Chapter 5). Thus, many hard substrate preferring species will continue their colonization of sandy areas that are settled by *C. fluminea* (Chapter 5). Taxa that are not directly affected by the occurrence of *C. fluminea* or associated *D. poly-*

morpha could be influenced by predators such as the invasive amphipod *D. villosus*, that considerably changes invertebrate communities (Dick *et al.* 2002, Chapter 3).

Benthic communities in habitats with high structural diversity were not affected by the presence of *C. fluminea* (Chapter 3) and in habitat choice experiments, only three out of ten taxa preferred living clams compared to sand. This implicates that structural effects of *C. fluminea* are more important for community organization than biotic effects such as benthopelagic coupling; this pattern was confirmed in the field monitoring, in the *in situ* experiment and in the laboratory.

In the field monitoring (Chapter 3), I could not separate whether the positive correlation of epifaunal taxa with *C. fluminea* biomass is direct or if it is due to the increase of *D. polymorpha* that is closely associated with the biomass of *C. fluminea*. Nonetheless, *C. fluminea* invasion had ecological consequences: it enhanced density and biomass of most epifaunal invertebrates. So far, no negative impact of *C. fluminea* was detectable. The structural diversity and surface increase mediated by the valves of *C. fluminea* and by associated *D. polymorpha* leads to an increase of biodiversity on soft substrates. But the positive effects could be scale-dependent. Although the benthic communities at study site Rohrspitz become more 'diverse', they also become more similar to the rest of the littoral zone. On a lake wide scale the ecosystem engineering by valves threatens substrate diversity and therewith linked biodiversity. The physical structures of the mollusk valves could lead to a loss of littoral soft substrates, and to an associated decline of soft bottom specialists and infaunal species within the lake (c. f. Ward & Ricciardi 2007). The unification of substrates and the loss of different biotic habitats within a lake could have a similar effect as the global abolition of barriers has for dispersal of biota. Global exchange of species could create a `supercontinent`, what leads to a loss of more than half the number of (mammalian) species (Lövei 1997). Lövei (1997) states that much of the global diversity of mammalian species is due to the isolation of separate biotic regions. When *C. fluminea* has spread within whole Lake Constance, a lake wide study should be conducted to test this hypothesis.

***Corbicula fluminea* and macrophytes**

Filtration of phytoplankton by *C. fluminea* increases water transparency and, by this, the photic zone for macrophytes greatly increases (Karatayev *et al.* 2005). However, in oligotrophic Lake Constance this effect seems to be of less importance. However, the physical presence of burrowing bivalves stabilizes sediments (Vaughn & Hakenkamp 2001), what may facilitate settlement and growth of macrophytes in the windswept littoral, where substrate re-allocations could be more frequent without clams. Increased macrophyte coverage would enhance benthic invertebrates considerably (Strayer & Malcom 2007). In Chap-

ter 3, I showed that macrophyte-mediated structure decreased the impact of *C. fluminea* on epifauna. Further, the increased macrophyte coverage may decrease habitat availability for *C. fluminea* (Karatayev *et al.* 2005). At our study sites, densities of *C. fluminea* at the macrophyte-dominated depth MLL -3 m were lower as in MLL -1 m (no macrophytes).
Depending on nutrient concentration, *C. fluminea* can whether decrease or enrich organic content of sediments (Vaughn & Hakenkamp 2001), what could affect macrophyte growth. For example, reduced organic content of sediments due to the feeding activity of *C. fluminea* seems to affect shoot lengths of macrophytes (unpublished data). Anyhow, the interactions between burrowing *C. fluminea* and macrophytes should be subject to further studies.

Dispersal and prevention

C. fluminea might have arrived to Lake Constance by overland transport of recreational boats or by release from aquaria (Werner & Mörtl 2004). Compared to the expansion of the zebra mussels in Lake Constance in the 1960s (Siessegger 1969), the distribution of *C. fluminea* is rather slow. However, a planktonic stage – such as the veligers of *D. polymorpha* – is lacking in the life cycle of *C. fluminea* (Britton & Morton 1979, Karatayev *et al.* 2005). Independently from boats as vectors, natural upstream mobility of *C. fluminea* is about of 1.2 km per year (Voelz *et al.* 1998). Compared to this expansion rates, the spread within Lake Constance is faster. Within 5 years the clams spread about 30 km to the northwestern shore (Chapter 1), perhaps this dispersal was mediated by the mucus dragline of juveniles (Prezant & Chalermwat 1984). After floods, currents of the alpine Rhine – that pass by close to the study site – often carry huge amounts of driftwood to the northern shore of Lake Constance (IGKB 2004b). Some juvenile clams might have attached to the driftwood, before it was transported further north. However, boats could have dispersed the juveniles as well. Interestingly, despite the mucus draglines allow dispersal with water currents and entanglement on feet of shore birds (Prezant & Chalermwat 1984), *C. fluminea* did not spread into the shallow water depths. The mucus dragline may only allow suspension of small clams in unidirectional water currents.
The invasion of *C. fluminea* to Lake Constance is not reversible, and established invaders cannot be removed from an ecosystem. However, Lake Constance has the golden opportunity to be isolated from downstream merchant shipping routes by natural barriers. The falls of the River Rhine and a long reach with intact indigenous benthic communities in the Hochrhein seem to build a buffer against upstream mobility of most invading species such as *D. polymorpha, Chelicorophium* spp., *C. fluminea*, and *Dikerogammarus villosus* (Rey & Ortlepp, personal communication). Unfortunately, this part of the River Rhine was colonized from

Lake Constance downstream by *D. polymorpha* and *D. villosus*; *L. benedeni* and *C. fluminea* will follow. Due to the largely isolation of Lake Constance, prevention from further biological invasions would be possible.

If recreational boating and water sports were restricted by legislation like in the United States (see www.protectyourwaters.net and www.icais.org), chance of future invasions could be reduced to a minimum. The examples from North America as well as results of my thesis contributed to the development of preventive actions against further invasions to Lake Constance. In the project 'Aquatische Neozoen Bodensee (ANEBO)', coordinated by the Institut für Seenforschung in Langenargen, we developed strategies to reduce the chances of biological invasion to Lake Constance. Legal policies are hard to achieve at Lake Constance, as it is bordering three different states. By this, so far, the proposed remedial actions are on a voluntary base. However, the environmental program 'Blauer Anker' of the Internationale Wassersportgemeinschaft Bodensee e. V. joined our recommendations: Recreational boats that leave any body of water should be cleaned carefully; all visible mud, plants and animals (e.g. *D. polymorpha*) must be removed. Water must be eliminated from motor, bilge, boat hull and other equipment. Afterwards, boats and equipment should be dried for at least 7 days before entering Lake Constance. Boats that leave Lake Constance should also be processed in the same manner. Hopefully, these arrangements are put into action to prevent our sensitive ecosystem from further invaders that could be less harmless as the invasion of *C. fluminea* seems to be.

8 Summary

The burrowing bivalve *Corbicula fluminea*, originating from Southeast Asia, impacts organic matter dynamics in sediments and water column processes. It invaded a wide range of freshwater ecosystems all over the globe. *C. fluminea* was first recorded in Lake Constance in 2003. In the soft sediments of this large oligotrophic lake it developed local mass occurrences with up to 3520 individuals > 5 mm in length per m^2 (1580 g dry mass m^{-2}). The population of *C. fluminea* and associated macroinvertebrates was monitored at our study site (Rohrspitz) for three years along a depth gradient. The population of *C. fluminea* in Lake Constance is slow growing, has a maximum life span of 4 years and builds one generation per year, except for an additional cohort of juveniles in heat summers and in very shallow depths. Low water temperatures (around 2 °C for longer than 3 months) associated with a centennial low water in winter 2005/2006 produced a size-class and depth dependent mass mortality of the *C. fluminea* population. At the greatest depth more clams > 5 mm survived than at the three shallower depths, where populations nearly vanished completely. Only about 1% of the density and 3% of the dry mass of the overall population of *C. fluminea* survived until spring 2006. The population recovered slowly, but ecosystem engineering of *C. fluminea* via shell production increased substrate diversity and settlement surface for benthic macroinvertebrates considerably. The benthic soft bottom community of pre-alpine Lake Constance differed depending on depth and showed high seasonal dynamics. The community pattern indicated that the benthic assemblage is also influenced by physical disturbances, such as water level fluctuations and the impact of wave action, as number of taxa, density and biomass increased with depth and therewith linked habitat stability. The biomass of the community was dominated by the invasive species *C. fluminea* and *D. polymorpha* that contributed more than 95 % to the total biomass.

Effects of *C. fluminea* on benthic invertebrates depended on the structural complexity of the respective habitats. On bare sand, densities of *D. polymorpha* and other epifaunal taxa increased with biomass of *C. fluminea*, whereas at a macrophyte-dominated depth, *C. fluminea* had no effect. Densities of infaunal taxa were independent from *C. fluminea* biomass.

The patterns found *in situ* were analyzed in experiments at our study site using boxes containing bare sand, sand with *C. fluminea* shells (2000 m^{-2}; arising from 1000 individuals), and sand with live clams (1000 m^{-2}). After 2 month of exposure, the overall benthic community did not differ among treatments. Only density of the mayfly *Caenis* spp. increased

in boxes containing shells compared to the boxes containing sand or sand with living clams. Our results approve the important role of mollusk shells that provide valuable hard surfaces for species preferring structured habitats, especially in unstructured soft-bottomed habitats. In addition, density of juvenile *C. fluminea* was lower in boxes containing live adult clams than in boxes containing sand or sand and shells, possibly because of a chemical cue that might hinder settlement of juveniles in areas with high intraspecific concurrence. *In situ* density of juveniles did not correlate with the biomass of *C. fluminea*.

In laboratory habitat choice experiments, we surveyed the response of ten different macroinvertebratetaxa to *C. fluminea* (1012 ind. m^{-2}). We distinguished between biotic effects of living infaunal *C. fluminea* that were either starved (only bioturbation) or fed with algae (biodeposition, bioturbation and nutrient reallocation), and we tested the importance of their structural role using *C. fluminea* valves lying on sand. Each treatment was tested pairwise against sand. We evaluated the habitat choice of taxa typical for the littoral zone of Lake Constance: two species of Hirudinae, three species of Crustacea, three gastropod species, and two taxa of insect larvae. No taxon avoided areas with live *C. fluminea* or their valves. But living clams had less impact on the habitat choice of benthic taxa than their valves, since only three taxa preferred living clams over sand: The detritivorous gastropod *Lymnaea stagnalis* and the amphipod *Gammarus roeselii* favoured fed *C. fluminea* and the amphipod *Dikerogammarus villosus* preferred starved clams over sand. Six epifaunal taxa preferred areas with *C. fluminea* valves to areas with sand, whereas gastropods and chironomids did not select for valves of *C. fluminea*.

In the last study, we focused on the impact of intraspecific and interspecific interactions on the growth of *C. fluminea* and *D. polymorpha* in laboratory experiments. After 30 days with limiting food, the growth of five individuals of *C. fluminea* and *D. polymorpha* each was lower than that of controls containing one individual. When food was not limiting, the growth of *D. polymorpha* and *C. fluminea* was unaffected by the density of conspecifics, providing evidence for intraspecific competition. However, when the two species were kept together (one *C. fluminea* and four attached *D. polymorpha*), the growth rate of *C. fluminea* on sand was higher than under all other conditions, even when food was not limiting, which indicated that *C. fluminea* facilitated from biodeposits produced by the associated zebra mussels. This effect did not occur when *C. fluminea* grew on pebbles, even with the same unlimited amount of food, because the *D. polymorpha* biodeposits fell into the substrate interstices and were unavailable to *C. fluminea*. In the dynamic interactions between individuals of the two species facilitation and competition varied with changing conditions. Our results indicate that biodeposition and

the sediments play a major role in the outcome of the interactions. Biodepostion of *D. polymorpha* facilitates the growth of *C. fluminea* on sand and *D. polymorpha* is only able to settle permanently on soft bottoms due to *C. fluminea,* which builds biogenous hard substrate. The successful co-existence of the two species in freshwaters may therefore be a reflection, at least in part, of facilitative interactions between them. We conclude that *C. fluminea* increases the surface area and substrate diversity on poorly structured sediments, what can lead to an increase of most epifaunal benthic invertebrates. This positive effect does not occur in more structured habitats and may partly due to the indirect effect, that *C. fluminea* facilitates the settlement of *D. polymorpha*, which is an important ecosystem engineer that facilitates most macroinvertebrates. So far, *C. fluminea* had no detectable negative consequences for ecosystem function or benthic soft bottom communities in Lake Constance.

9 Zusammenfassung

Die aus Südostasien stammende Muschel *Corbicula fluminea* gräbt sich im Substrat ein, wo sie die Dynamik von organischen Stoffen im Sediment und im Freiwasser beeinflussen kann. Sie ist eine invasive Art, die weltweit in diversen Süßwassersystemen etabliert ist. *C. fluminea* wurde 2003 erstmals im oligotrophen Bodensee nachgewiesen, wo sie in den Weichsubstraten lokale Massenvorkommen mit bis zu 3520 Individuen > 5 mm pro m² (1580 g Trockenmasse m^{-2}) entwickelte. Die Populationen von *C. fluminea* und assoziierten Makroinvertebraten wurden an unserer Untersuchungsstelle (Rohrspitz) entlang eines Tiefengradienten über drei Jahre hinweg untersucht. Die Population von *C. fluminea* im Bodensee wächst langsam, hat eine maximale Lebenserwartung von 4 Jahren und pflanzt sich – abgesehen von einer zusätzlichen Kohorte von Jungmuscheln in Hitzesommern und in sehr flachen Tiefen – einmal im Jahr fort.

Niedere Wassertemperaturen (über 3 Monate um 2 °C) und ein gleichzeitiges Jahrhundertniederwasser im Winter 2005/2006 führten zu einem tiefen- und größenklassenspezifischen Massensterben der *C. fluminea*-Population. In der größten Tiefe überlebten mehr Muscheln >5 mm als in den drei flacheren Tiefen, in denen die Populationen fast vollständig erloschen. Nur etwa 1% der Abundanz und 3 % der Biomasse der gesamten *C. fluminea*-Population verblieb im Frühjahr 2006. Die Muschelpopulation erholte sich danach nur langsam, aber das Habitat, das von den verbleibenden Schalen gebildet wurde, erhöhte die Substratdiversität und die für Makroinvertebraten besiedelbare Oberfläche beträchtlich.

Die benthische Lebensgemeinschaft der Weichsubstrate unterschied sich tiefenabhängig und zeigte eine hohe saisonale Dynamik. Die Muster innerhalb der Lebensgemeinschaften zeigen, dass physikalische Störungen wie Wasserstandsschwankungen und Wellenschlag die Biozönose beeinflussen, da Artenzahl, Dichte und Biomasse mit der Tiefe und der damit verbundenen Habitatstabilität zunahmen. Die Biomasse der Lebensgemeinschaft wurde von den Neozoen *C. fluminea* und *Dreissena polymorpha* dominiert; zusammen machten sie über 95% der Gesamtbiomasse aus.

Ob *C. fluminea* Auswirkungen auf die benthischen Invertebraten hatte, war von der Strukturkomplexität des jeweiligen Habitats abhängig. Auf reinem Sand stiegen die Dichten von *D. polymorpha* und von anderen epifaunischen Taxa mit der Biomasse von *C. fluminea*; in makrophyten-dominierten Tiefen hingegen hatte *C. fluminea* keinen Effekt. Die Dichte von im Substrat lebenden Taxa war von der Biomasse von *C. fluminea* unabhängig.

Die Muster, die im Freiland gefunden wurden, sollten in Experimenten in den sandigen Bereichen an unserer Untersuchungsstelle mithilfe von Boxen genauer untersucht werden. Die nach oben offenen Kunststoffbehältnisse enthielten entweder nur Sand, Sand mit 2000 Schalen von *C. fluminea* m^{-2} (die von 1000 Individuen stammten) oder Sand mit lebenden *C. fluminea* (1000 m^{-2}). Nach zweimonatiger Expositionszeit unterschieden sich die benthischen Lebensgemeinschaften zwischen den drei Ansätzen nicht. Nur die Dichte der Eintagsfliegenlarven *Caenis* spp. war in den Boxen mit den Schalen im Vergleich zu den Boxen mit Sand oder lebenden Muscheln erhöht. Unsere Ergebnisse bestätigen die wichtige Funktion der Muschelschalen, die insbesondere auf strukturarmen Weichsubstraten wertvolles Hartsubstrat für strukturliebende Arten bilden. Zusätzlich zeigten juvenile *C. fluminea* in den Boxen mit lebenden adulten Muscheln geringere Dichten als in den Boxen, die nur Sand oder Sand mit Schalen enthielten. Möglicherweise ist das auf ein chemisches Signal zurückzuführen, das die Ansiedlung juveniler Muscheln in Gebieten mit hoher interspezifischer Konkurrenz verhindern soll. *In situ* korrelierte die Dichte der Juvenilen jedenfalls auch nicht mit der Biomasse von *C. fluminea*.

In Habitatwahlversuchen untersuchten wir im Labor, wie zehn verschiedene Makroinvertebratentaxa auf verschiedene Effekte von *C. fluminea* (1012 Ind. m^{-2}) reagieren. Wir unterschieden zwischen biotischen und strukturellen Effekten der Muschel. Lebende *C. fluminea*, die sich im Sand eingegraben hatten, wurden entweder mit Algen gefüttert (Biodeposition, Bioturbation und Nährstoffumverteilung) oder mussten hungern (nur Bioturbation). Die strukturellen Effekte von *C. fluminea* wurden anhand von Muschelschalen untersucht, die auf dem Sand lagen. Jeder Ansatz wurde jeweils paarweise gegen Sand getestet. Wir untersuchten die Habitatwahl von Taxa, die charakteristisch für das Litoral des Bodensees sind: 2 Egelarten (Hirudinae), 3 Arten Crustacea, 3 Gastropodenarten und 2 Taxa Insektenlarven. Kein Taxon vermied die Bereiche mit lebenden *C. fluminea* oder ihren Schalen. Jedoch hatten lebende Muscheln weniger Auswirkungen auf die Habitatwahl benthischer Taxa als die Muschelschalen, da nur 3 Taxa die lebenden Muscheln gegenüber Sand bevorzugten: die detritivore Schnecke *L. stagnalis* und der Flohkrebs *G. roeselii* bevorzugten gefütterte *C. fluminea* und der Flohkrebs *Dikerogammarus villosus* hungernde Muscheln. Sechs epifaunische Taxa bevorzugten Bereiche mit Schalen von *C. fluminea.* Demgegenüber selektierten Gastropoda und Chironominae die Schalen der Muscheln nicht.

In der letzten Studie betrachteten wir den Einfluss von intra- und interspezifischen Wechselwirkungen auf das Wachstum von *C. fluminea* und *D. polymorpha* in Laborexperimenten. Nach 30 Tagen mit limitierenden Nahrungsbedingungen verzeichneten jeweils fünf Exemplare von *C. fluminea* oder *D. polymorpha* geringere Zuwachsraten als einzelne Individuen. Bei unlimitierter Nahrungszugabe hingegen war das Wachstum von *C. fluminea* und *D. polymorpha* nicht von der Dichte ihrer Artgenossen abhängig, was intraspezifische Konkurrenz beweist. Wenn beide Arten zusammen gehältert wurden (eine *C. fluminea* und vier angeheftete *D. polymorpha*), konnte *C. fluminea* die Wachstumsrate auf Sand im Vergleich zu allen anderen Bedingungen trotz unlimitierten Futterbedingungen noch steigern. Das Wachstum von *C. fluminea* wurde vermutlich durch das Biodepositionsmaterial der assoziierten *D. polymorpha* gefördert. Dieser positive Effekt trat nicht auf, wenn *C. fluminea* mit der gleichen unlimitierten Nahrungsmenge auf Kies wuchs, da das Biodepositionsmaterial von *D. polymorpha* ins Substratinterstitial fiel und dadurch für *C. fluminea* unerreichbar war. In den dynamischen Interaktionen zwischen den Individuen beider Arten wechselten sich fördernde Effekte und Konkurrenz mit den Umweltbedingungen ab. Unsere Ergebnisse zeigen, dass Biodeposition und das Sediment eine wichtige Rolle im Ausgang der Interaktionen zwischen beiden invasiven Muschelarten spielt. Die Biodeposition von *D. polymorpha* fördert das Wachstum von *C. fluminea* auf Sand und *D. polymorpha* kann sandige Bereiche nur dank *C. fluminea*, die biogenes Hartsubstrat bildet, dauerhaft besiedeln. Die erfolgreiche Koexistenz der beiden Arten in zahlreichen Süßwassersystemen könnte zumindest teilweise auf diese positiven Interaktionen zurückzuführen sein.

Zusammenfassend kann *C. fluminea* auf strukturarmen Sedimenten die besiedelbare Oberfläche vergrößern und die Substratdiversität erhöhen, was zu einem Anstieg der meisten auf der Oberfläche lebenden Organismen führt. Der positive Effekt wirkt sich in strukturreichen Habitaten nicht aus und könnte indirekt sein, da *C. fluminea* einen Ansiedlungspunkt für *D. polymorpha* bildet. *D. polymorpha* ist ein bekannter Ökosystembildner, der die meisten Makroinvertebraten fördert. *C. fluminea* hatte bislang weder nachweisbare negative Auswirkungen auf die Funktion des Ökosystems noch auf die Lebensgemeinschaften der Weichsubstrate im Bodensee.

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Record of achievement / Abgrenzung der Eigenleistung

Chapter 2, 3, 4, 5

Results, design, and sample processing described in these chapters were exclusively performed by myself or under my direct supervision.

Chapter 6

I designed the study, and analyzed the data. Katja Lamm, which I was supervising during her Diploma thesis, conducted the laboratory growth experiments and cultivated the algae. Further I wrote the elaboration.

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Publications

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