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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 square meter in sandy areas. However, the effect of this species on 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/m²), and sand with live clams (1000/m²). After 2 mo 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 increased after mass mortality of *C. fluminea* populations. Our results indicate that shells can provide valuable hard surfaces for species that prefer 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.

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 and Hakenkamp 2001). Among the most invasive species are clams of the genus *Corbicula* (Morton 1979). Originating from Southeast Asia, *Corbicula fluminea* has been introduced into North and South America (Ituarte 1981, McMahon 1982, Darrigran 2002) and Europe (Mouthon 1981, den Hartog et al. 1992). In Germany, it quickly replaced the zebra mussel as the dominant mollusc in large rivers (Bachmann et al. 2001). Within 15 y, 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 and Mörtl 2003), where it reaches local densities of up to 3520 individuals >5

mm in length per square meter and can constitute up to 90% of the biomass of the littoral community (SW and KOR, unpublished data). Temperatures <2°C (French and Schloesser 1991) and low water levels (White and White 1977) can kill *Corbicula*; thus, severe conditions during winter have caused periodic mass mortalities, after which only 1% of the littoral *C. fluminea* population may remain in Lake Constance (SW and KOR, unpublished data). 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 molluscs 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 feces and pseudofeces, which produces organic matter (Vaughn and Hakenkamp 2001). Therefore, effects of empty shells and living clams might influence populations of other

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species. However, interactions between *Corbicula* and benthic invertebrates have rarely been studied (Vaughn and 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 that prefer 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 on the border of 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, which covers 63 km², and 2) the larger, deeper, nutrient-poor Upper Lake Constance (maximum depth: 254 m, mean depth: ~100 m), which covers 473 km² (Internationale Gewässerschutzkommission für den Bodensee 1999).

We conducted our study in the southeastern part of Upper Lake Constance near the city of Bregenz. The study site (lat 47°30'00.3"N, long 9°37'00.4"E) 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 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 (ind.) at a naturally occurring density of 2000 single shells/m² (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./m² (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./m². According 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 held the clams in a lake-water flow-trough system with a natural water temperature range until use. The lake water contained algae for filtration. We also 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 mollusc 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 using a global positioning system (GPS) unit.

Sampling methods and laboratory analyses

We terminated the experiment after 2 mo 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 has shown 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 sieves of various mesh sizes (20, 5, 2, and 0.2 mm). As soon as possible, we fixed samples in 95% ethanol.

TABLE 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	1.0
<i>Bithynia tentaculata</i> (Gastropoda)	2077	209	11.1
<i>Potamopyrgus antipodarum</i> (Gastropoda)	357	41	1.9
<i>Dreissena polymorpha</i> juvenile (Bivalvia)	7184	906	38.3
<i>Corbicula fluminea</i> juvenile (Bivalvia)	5486	1051	29.3
<i>Pisidium</i> spp. (Bivalvia)	727	113	3.9
<i>Caenis</i> spp. (Ephemeroptera)	283	27	1.5
Chironomidae	9972	933	53.2
Total (excluding postveliger <i>C. fluminea</i> and <i>D. polymorpha</i>)	18,737	1687	100
Total	29,871	2179	

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 cm² (foil area = $0.3247 \times \text{foil mass} - 0.1362$; $R^2 = 0.999$).

We used this equation to calculate the area provided by 2000 shells/m², a regularly occurring density 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./m² in December to 53 ± 9 living ind./m² 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./m² 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 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), *Potamopyrgus 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 we reran every algorithm 50 times for each plot (Clarke and 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/m²) nearly doubled the surface area of soft substrata. The shells (mean shell length: 12.27 ± 0.31 mm) expanded a 1-m² area of sand by 0.95 ± 0.05 m². The bearing surface of the shells lying with the inner side up in the sediment was $13.98 \pm 0.5\%$ of the total area of the outer sides of the shells.

After 2 mo of exposure, the overall density of benthic invertebrates inside the boxes ($29,871 \pm 2179$ ind./m²; Table 1) was similar to their in situ density

TABLE 2. Analysis of variance results for benthic taxa (>1% of total density). (*) = not significant after sequential Bonferroni adjustment; * = significant with $0.05 > \alpha > 0.01$, *** = $\alpha < 0.001$.

Taxon	F	df	p
Nematoda	0.7902	2	0.4829
Oligochaeta	0.0286	2	0.9719
Hirudinea	4.7570	2	0.0395(*)
<i>Bithynia tentaculata</i>	0.7832	2	0.4857
<i>Potamopyrgus antipodarum</i>	0.0648	2	0.9377
<i>Dreissena polymorpha</i> juvenile	0.1282	2	0.8813
<i>Corbicula fluminea</i> juvenile	10.2688	2	0.0048*
<i>Pisidium</i> spp.	0.3237	2	0.7316
<i>Caenis</i> spp.	39.0393	2	<0.0001***
Chironomidae	1.1919	2	0.3474

(54,412 $\pm$ 3455 ind./m²). 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) $\geq 1\%$ of the mean total density, excluding newly settled postveliger larvae of bivalves (Table 1). Seven of these taxa (Nematoda, Oligochaeta, *B. tentaculata*, *P. antipodarum*, juvenile *D. polymorpha*, *Pisidium* spp., and Chironomidae; Table 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 2, Fig. 1A). Density of the mayfly, *Caenis* spp., was significantly higher in boxes containing shells than in the other treatments (Table 2, Fig. 1B). Density of juvenile *C. fluminea* was significantly lower in boxes with live adult clams than in the other treatments (Fig. 1C).

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. 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. 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 ($p = 0.057$).

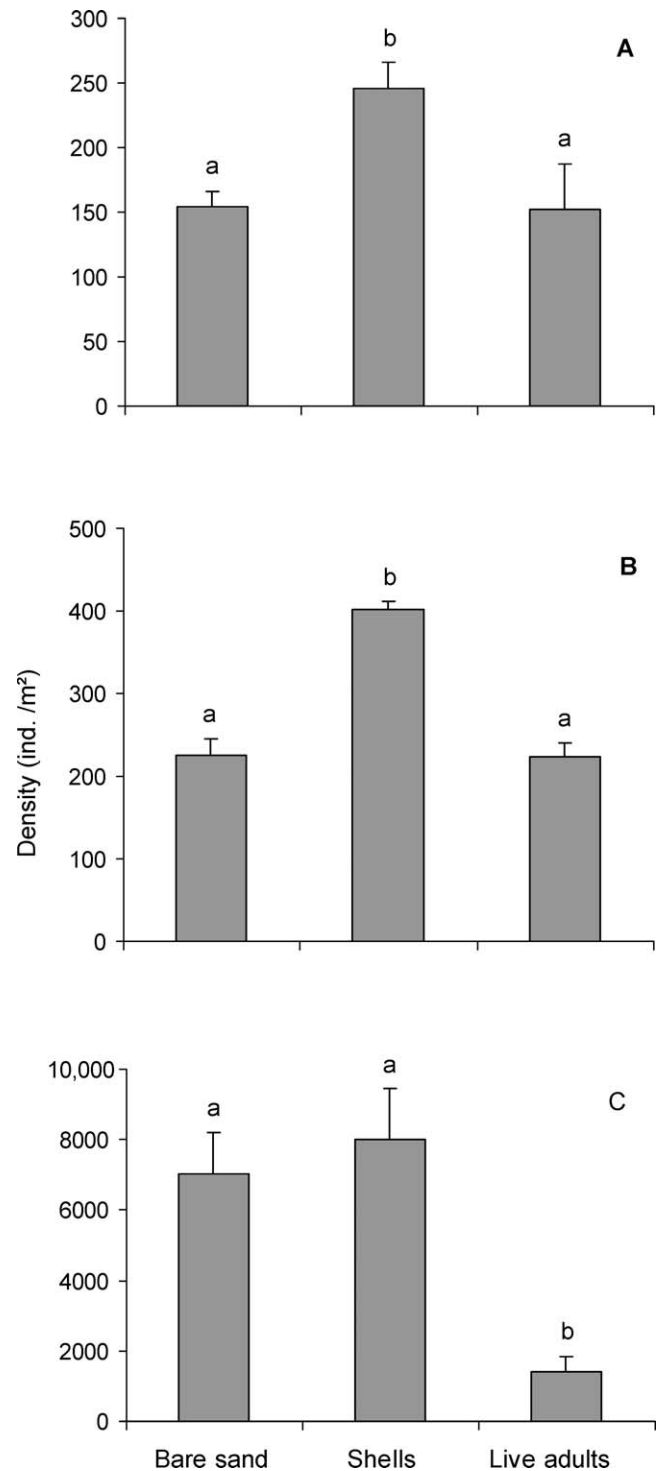


FIG. 1. Effects of treatments on Hirudinea (A), *Caenis* spp. (B), and *Corbicula fluminea* juveniles (C). Differences for Hirudinea were not significant after sequential Bonferroni adjustment.

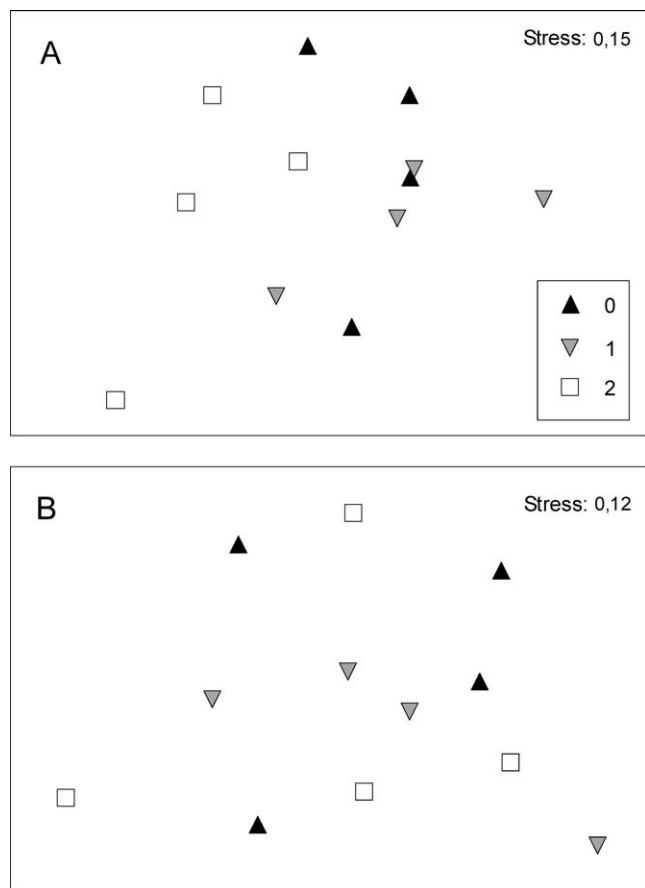


FIG. 2. Nonmetric multidimensional scaling ordination plot of invertebrate densities including juvenile *Corbicula* (A) and excluding juvenile *Corbicula* (B). Treatment codes are: 0 = bare sand, 1 = shells, and 2 = live adults.

than in boxes with bare sand and with shells (Table 3). Communities were more similar when juvenile *C. fluminea* were excluded from the analysis (Table 3).

Discussion

Interspecific effects

Molluscs act as ecosystem engineers (Jones et al. 1994, 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 and Hakenkamp 2001, Mörtl and Rothhaupt 2003). Most populations of benthic invertebrates benefit from these bivalve effects (Stewart et al. 1998, Karatayev et al. 1997, 2005, Nalepa et al. 2003). 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 *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 have shown that the density of *Caenis* spp. larvae increases with structural diversity (Mörtl and 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 freshwater with relatively unstructured sandy areas. Our study could not provide support for this hypothesis, probably because *Corbicula* had 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.

TABLE 3. Results of analysis of similarity (ANOSIM) for differences in community composition between treatments.

Comparison	Juvenile <i>Corbicula</i> included		Juvenile <i>Corbicula</i> excluded	
	<i>R</i>	<i>p</i>	<i>R</i>	<i>p</i>
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

In addition to their ecosystem engineering effects, bivalves such as *Corbicula* deposit feces and pseudofeces, which enrich the organic content of benthic sediments (Vaughn and Hakenkamp 2001) and provide an additional food resource for benthic invertebrates (Roditi et al. 1997, R. Gergs, Limnological Institute, University of Konstanz, and KOR, unpublished data). However, no effects of live clams on other benthic invertebrates were observed in our study or previous studies (Hakenkamp and 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 and 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 have seemed to play only a minor role in other studies (Hakenkamp and Palmer 1999, Karatayev et al. 2005). By comparison, the nonburrowing zebra mussel *D. polymorpha* changes benthic communities considerably (Karatayev et al. 1997, Nalepa et al. 2001, 2003), possibly because live zebra mussels simultaneously provide substrate structure, bioturbation, and biodeposition, 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 (MacIsaac et al. 1991), but it is unlikely for *C. fluminea* because the released postveligers have a shell length of 250 μm (Meister 1997, SW, 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 and 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 freshwater 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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