

Context-dependent effects of freshwater mussels on stream benthic communities

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SUMMARY

1. We asked whether unionid mussels influence the distribution and abundance of co-occurring benthic algae and invertebrates. In a yearlong field enclosure experiment in a south-central U.S. river, we examined the effects of living mussels versus sham mussels (shells filled with sand) on periphyton and invertebrates in both the surrounding sediment and on mussel shells. We also examined differences between two common unionid species, *Actinonaias ligamentina* (Lamarck 1819) and *Amblema plicata* (Say 1817).
2. Organic matter concentrations and invertebrate densities in the sediment surrounding mussels were significantly higher in treatments with live mussels than treatments with sham mussels or sediment alone. Organic matter was significantly higher in the sediment surrounding *Actinonaias* than that surrounding *Amblema*. *Actinonaias* was more active than *Amblema* and may have increased benthic organic matter through bioturbation.
3. Living mussels increased the abundance of periphyton on shells and the abundance and richness of invertebrates on shells, whereas effects of sham mussels were similar to sediment alone. Differences in the amount of periphyton growing on the shells of the two mussel species reflected differences in mussel activity and shell morphology.
4. Differences between living and sham mussel treatments indicate that biological activities of mussels provide ecosystem services to the benthic community beyond the physical habitat provided by shells alone. In treatments containing live mussels we found significant correlations between organic matter and chlorophyll *a* concentrations in the sediment, organic matter concentrations and invertebrate abundance in the sediment and the amount of chlorophyll *a* on the sediment and invertebrate abundance. There were no significant correlations among these response variables in control treatments. Thus, in addition to providing biogenic structure as habitat, mussels likely facilitate benthic invertebrates by altering the availability of resources (algae and organic matter) through nutrient excretion and biodeposition.
5. Effects of mussels on sediment and shell periphyton concentrations, organic matter concentrations and invertebrate abundance, varied seasonally, and were strongest in late summer during periods of low water volume, low flow, and high water temperature.
6. Our study demonstrates that freshwater mussels can strongly influence the co-occurring benthic community, but that effects of mussels are context-dependent and may vary among species.

Keywords: context dependent, ecosystem engineer, ecosystem function, macroinvertebrate, periphyton, Unionidae

Introduction

In many shallow-water marine systems, filter-feeding bivalves dominate the benthic biomass and serve as a link between pelagic and benthic compartments by filtering large quantities of phytoplankton and fine particulate organic matter (FPOM) from the water column and biodepositing organic matter to the sediment (Dame, 1996; Gutierrez *et al.*, 2003). Marine bivalve aggregations increase secondary space and thus habitat for colonising epifauna, and bivalve activities such as nutrient cycling and transformation, biodeposition, and bioturbation enhance infaunal communities (Dame, 1996; Peterson & Heck, 1999). Comparative studies of the ecological roles of freshwater bivalves have been primarily limited to the epifaunal zebra mussel (*Dreissena polymorpha*) and infaunal Asian clam (*Corbicula fluminea*), both invasive species in North America. These species can control both phytoplankton dynamics and benthic invertebrate community structure through a combination of their biological activities (i.e. filter-feeding, nutrient cycling, biodeposition) and the physical habitat provided by their shells (Stewart, Miner & Lowe, 1998; Strayer *et al.*, 1999; Hakenkamp *et al.*, 2001).

Freshwater mussels (Unionacea) are a guild of benthic, burrowing, filter-feeding bivalves. In rivers, the biomass of healthy unionid assemblages can exceed the biomass of all other benthic organisms by an order of magnitude (Negus, 1966; Vaughn & Hakenkamp, 2001) and production by mussels (range from 1 to 20 g dry mass m⁻² year⁻¹) can equal that by all other macrobenthos (Strayer, 1994). Mussels filter phytoplankton and other suspended material from the water column, excrete nutrients back to the water column and biodeposit organic material to the sediment as faeces and pseudofaeces. By burrowing in the sediment they increase sediment water and oxygen content and release nutrients from the sediment to the water column. Finally, the physical presence of both living mussels and their spent shells stabilises sediment and likely creates habitat for other benthic organisms (Vaughn & Hakenkamp, 2001; Strayer *et al.* 2004). Given the processes they perform and their high biomass, unionid mussels have the potential to have strong effects in rivers where they are abundant, by modifying habitat and controlling the availability of resources to other organisms. We would expect them to have particularly strong influences on the organisms

with which they are most closely associated, the co-occurring benthic community; however, the effects of unionids on the rest of the benthic community have not been investigated.

Here we describe the results of a year-long field experiment that examined the effects of unionid mussels on other benthic invertebrates and periphyton occurring in both the sediment and on mussel shells. Our experiment addresses three fundamental questions: (i) do mussels influence the composition and abundance of the benthic community and if so, are effects the results of processes performed by living mussels or merely the results of habitat provided by shells?, (ii) do different mussel species have different effects on the benthic community? and (iii) do effects of mussels on the benthic community vary with environmental context (season)?

Methods

Study site

We performed the experiment in the Kiamichi River, a medium-sized tributary (watershed area 4560 km²) of the Red River in the Ouachita Mountains of southeastern Oklahoma, U.S. The Kiamichi is a relatively pristine river known for its high aquatic biodiversity (Master, Flack & Stein, 1998). The river harbours approximately 30 species of mussels and there are no documented extirpations of mussel species within the last century (Vaughn & Pyron, 1995). Mussel beds typically occur in reaches several hundred metres long with densities as high as 64 individuals m⁻². Seasonal discharge variation is high, ranging from an average 200 cm³ s⁻¹ in August to 6000 cm³ s⁻¹ in February (Fig. 1). Our study site, a shallow, 200 m stream reach with a gravel/cobble streambed and homogenous depth and flow, was chosen to minimise any effects of habitat heterogeneity. The site was located between a large upstream pool and a downstream riffle sequence and could only be conveniently accessed from private land, protecting the experiment from tampering.

Experimental design

We were interested in differentiating effects on the benthic community of processes performed by live mussels versus the mere physical presence of mussel shells and in determining differences between unionid

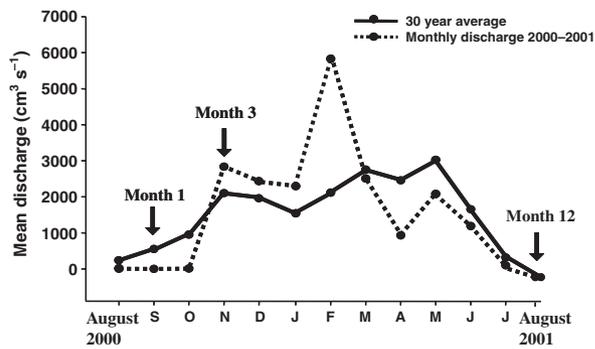


Fig. 1 Mean monthly discharge (2000–2001 and 30 year average; USGS data) near the study site. Arrows indicate sampling periods.

species. Our design consisted of four mussel treatments [live *Actinonaias ligamentina* (Lamarck 1819), live *Amblyma plicata* (Say 1817), 'sham' mussels (see below) and a mussel-free control (sediment alone)] and three time treatments (1, 3 and 12 months), with each mussel by time treatment combination replicated five times. This design allowed us to use planned orthogonal contrasts, to compare effects of live mussels (*Actinonaias* + *Amblyma*) to sham mussels as well as examine differences between species.

Actinonaias ligamentina and *Amblyma plicata* are typical of the Interior Basin mussel fauna (Parmalee & Bogan, 1998), and together represent over 70% of mussel biomass in the Kiamichi River (Vaughn & Pyron, 1995). The species differ in phylogeny, morphology and behaviour, characteristics that might influence their ecological role. *Actinonaias* (subfamily Lamprosilinae) has a smooth shell and is more active than *Amblyma* (subfamily Amblyminae), which has a ridged shell and tends to be sedentary (Vaughn, Gido & Spooner, 2004). Sham mussels were created by filling clean, relict *Actinonaias* and *Amblyma* shells with sand, then gluing the shells together with non-toxic epoxy.

The experiment was performed using 60 enclosures (50 cm × 50 cm × 30 cm deep) constructed with a polyvinyl chloride (PVC; 3.3 cm schedule 40) pipe frame and the sides and bottom encased in 2.5 cm diameter wire poultry netting. To control for depth, current velocity and substrate type, enclosures were placed within one stream reach (200 m). Enclosures were placed in the stream reach within three blocks, with one block of 20 enclosures for each time treatment. Within each block, enclosures were located

2 m from shore and approximately 1.5 m apart (to minimise downstream cage-effects). The 1-month block was furthest downstream and the 12-month block was furthest upstream. This design allowed us to sample from and remove enclosures at the end of a time period, without disturbing enclosures for subsequent time treatments.

Enclosures were buried 15 cm into the streambed and filled with homogenised sediment (see below), so that the sediment in the enclosures was level with the streambed and the upper 15 cm of the cage extended into the water column. This design allowed movement of invertebrates in and out of enclosures through both the sediment and water column, but prevented immigration/emigration of mussels so that we could maintain constant mussel densities over time.

Prior to the experiment, sediment was extracted from the riverbed and mixed in 246 L plastic trash cans to homogenise the distribution of invertebrates, organic matter and algae among treatments. Mussels were removed prior to homogenisation. We define sediment to encompass both the organic (invertebrate and other organic matter) and inorganic fractions typically found in the benthic substrate. Live *Actinonaias* [mean wet weight (mg) 7.79 ± 0.39 SE] and *Amblyma* [mean wet weight (mg) 4.02 ± 0.16 SE] were collected at the site. Prior to placing mussels in enclosures, periphyton and other biofilm were removed from their shells by scrubbing with a plastic brush. Each mussel-treatment enclosure (*Actinonaias*, *Amblyma* and sham) was stocked with 10 individuals, a density representative of the local assemblage (Vaughn & Pyron, 1995). Four glass microscope slides were placed on the streambed surface in each enclosure to allow measurement of benthic organic matter and periphyton.

Response variables

Enclosures were placed in the river and stocked with mussels in August 2000. Twenty enclosures were removed and response variables measured after one (September 2000), three (November 2000) and 12 (August 2001) months. The experiment was monitored frequently to ensure that leaf packs and other debris did not significantly influence water velocities in the cages. The following procedures were followed for each time-period. For each enclosure except

controls, five mussels were randomly selected, removed and individually placed in a plastic bag with 500 mL of distilled water. Each mussel was scrubbed with a plastic brush for 2 min, creating a water-biofilm slurry that was subsampled (50 mL) and stored on ice for chlorophyll *a* determination. Two sediment cores (10 cm wide by 8 cm deep) were taken from each enclosure and preserved in 5% formalin. Glass slides were placed in a jar with 125 mL distilled water and stored on ice.

In the laboratory, core samples were elutriated, passed through a 210 µm sieve, and invertebrates identified and counted. Glass slides were scraped with a razor blade into 125 mL of water and two 50 mL aliquots were removed. To determine organic content, one of these aliquots was filtered through a 47 mm, 0.45 µm glass fibre filter, dried at 105 °C for 12 h, and ashed at 550 °C for 1 h. The other aliquot was analysed for chlorophyll *a*. Chlorophyll *a* samples of both the mussel shell slurry and glass slide slurry were filtered as above. Chlorophyll *a* was extracted with acetone and measured spectrophotometrically with a correction for pheophytin.

We recorded the shell length of all mussels used in the experiment, and the tissue dry weight of a subsample of these mussels. We used a dry weight-shell length regression ($y = 1.06 - 14.14x$, $R = 0.88$) to estimate biomass of non-sacrificed mussels and sham mussels. Response variables were standardised to tissue dry mass to factor out potential confounding effects of mussel size differences among treatments.

Data analyses

Sediment response variables (invertebrate abundance in the core samples, chlorophyll *a* and organic matter on the glass slides) were compared among treatments using planned orthogonal contrasts for each time-period (Toothaker 1993). Our *a priori* hypothesis was that living mussels should have stronger effects than shells or sediment alone. We tested this hypothesis by comparing 'biologically active treatments' (*Actinonaias* + *A. plicata*) to 'non-biologically active treatments' (sham mussels + sediment). To examine differences in sediment response variables between the two live mussel species treatments we used ANCOVA with biomass as a covariate and time as a separate factor.

Shell response variables (invertebrate abundance, chlorophyll *a* and organic matter) across treatments (*Actinonaias*, *Amblema*, sham mussels and time-period) were compared using an ANCOVA with biomass as a covariate. Bonferroni multiple comparison procedures were performed to control for type I error.

We used Pearson product-moment correlation to examine associations between response variables that might otherwise go unnoticed in an ANOVA design. We examined associations between organic matter, chlorophyll *a* and invertebrate abundance in both the sediment and on shells.

Results

Sediment

Mean discharge at the study site was minimal in late summer when we began and ended the experiment, but increased considerably in late autumn and peaked in the winter (Fig. 1). Some glass slides and sham mussels were lost to high flow during the winter, thus these data were unavailable for sediment chlorophyll *a* and organic matter estimates in August 2001. Therefore, sediment organic matter for month 12 was estimated from a 125 mL sub-sample of the sediment cores collected for invertebrate enumeration. Although these different sampling methods (glass slides versus cores) hindered temporal comparisons in sediment organic matter, we were able to test for differences between mussel treatments.

Sediment organic matter was significantly higher in treatments with live mussels (biologically active) than treatments with sham mussels or sediment alone (non-biologically active). This effect varied seasonally, with organic matter significantly higher in late summer (September 2000 $F_{1,16} = 6.637$, $P < 0.05$ and August 2001 $F_{1,14} = 5.897$, $P < 0.05$), but not in autumn (November 2000 $F_{1,13} = 1.256$, $P > 0.05$; Fig. 2a). Organic matter was significantly higher in the sediment surrounding *Actinonaias* than *Amblema*, even after correcting for biomass differences ($F_{1,28} = 11.019$, $P = 0.003$; Fig. 2b). Sediment chlorophyll *a* did not differ significantly in treatments with live mussels versus sham mussels or sediment (September 2000 $F_{1,16} = 3.444$, $P > 0.05$, November 2000 $F_{1,13} = 0.281$, $P > 0.05$; Fig. 2c) or between mussel species ($F_{1,18} = 0.145$, $P > 0.05$; Fig. 2d).

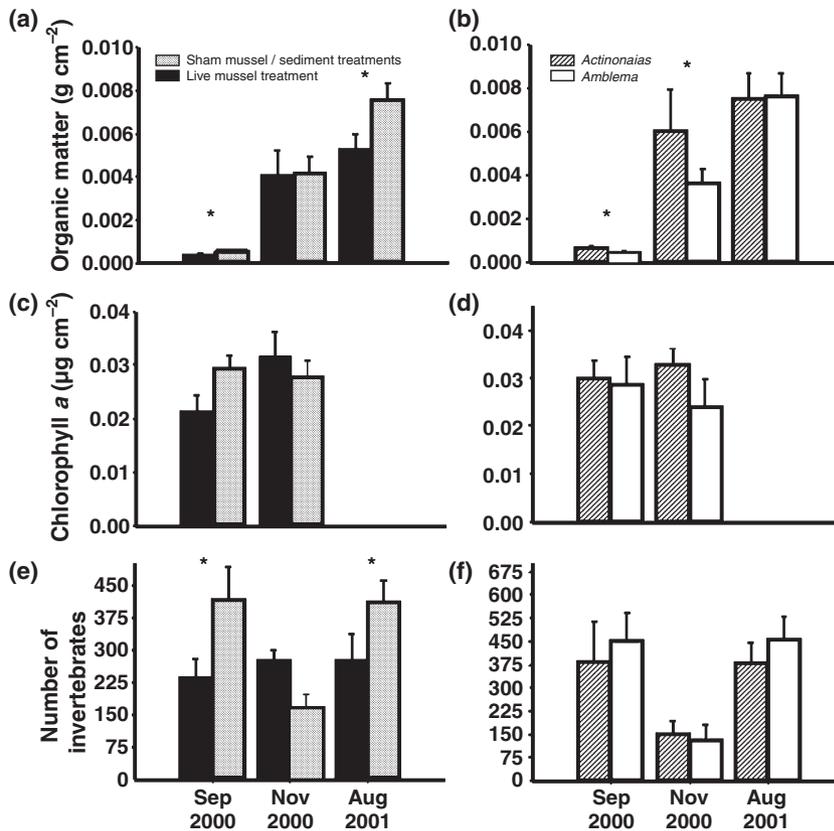


Fig. 2 Mean + 1 SE for sediment response variables. (a), (c) and (e) are ANOVA comparisons of live mussel versus sham mussel/sediment treatments. (b), (d) and (f) are ANCOVA comparisons of the two species. Asterisks represent significant differences from multiple comparison procedures.

Overall, there were more invertebrates in the sediment of live mussel treatments than in sham mussel and sediment treatments. These differences were significant for summer months (September 2000 $F_{1,16} = 6.12$, $P < 0.05$; August 2001 $F_{1,12} = 10.119$, $P < 0.05$), but not in November ($F_{1,14} = 0.587$, $P > 0.05$; Fig. 2e). We found no significant differences in sediment invertebrate abundance between *Actinonaias* and *Amblema* treatments ($F_{1,27} = 1.761$; Fig. 2f).

In live mussel treatments we found significant correlations between the amount of organic matter and chlorophyll *a* in the sediment ($r = -0.649$, $P = 0.003$), organic matter and invertebrate abundance in the sediment ($r = 0.491$, $P = 0.008$), and the amount of chlorophyll *a* on the sediment and invertebrate abundance ($r = -0.452$, $P = 0.052$). There were no significant correlations among sediment response variables in the sham mussel or sediment treatments.

Shells

Chlorophyll *a* was significantly higher on the shells of living than sham mussels ($F_{2,31} = 3.684$, $P = 0.037$) in

September 2000 but not November 2000 (Fig. 3a; sham mussels were not available for August 2001). When standardised for biomass, *Amblema* had higher chlorophyll *a* concentrations on their shells than *Actinonaias* (Fig. 3a).

Overall, total invertebrate abundance was not significantly different on the shells of live and sham mussels ($F_{2,31} = 1.319$, $P > 0.05$). There were seasonal differences, with higher invertebrate abundance on both live and sham mussel shells in September 2000 ($F_{2,31} = 32.740$, $P < 0.001$; Fig. 3b). At a finer taxonomic scale, there were significantly more tardigrades ($F_{2,31} = 4.081$, $P = 0.031$) and mites ($F_{2,31} = 4.712$, $P = 0.02$) on the shells of *Amblema* and *Actinonaias* than on sham mussel shells.

Mussel biomass (size) was correlated with invertebrate abundance in the live mussel treatments ($r = 0.51$, $P = 0.026$), but not in the sham mussel treatments. Despite a marginally significant correlation between shell invertebrate abundance and chlorophyll *a* ($r = 0.49$, $P = 0.067$), there were no other significant correlations among shell response variables in either the living or sham mussel treatments.

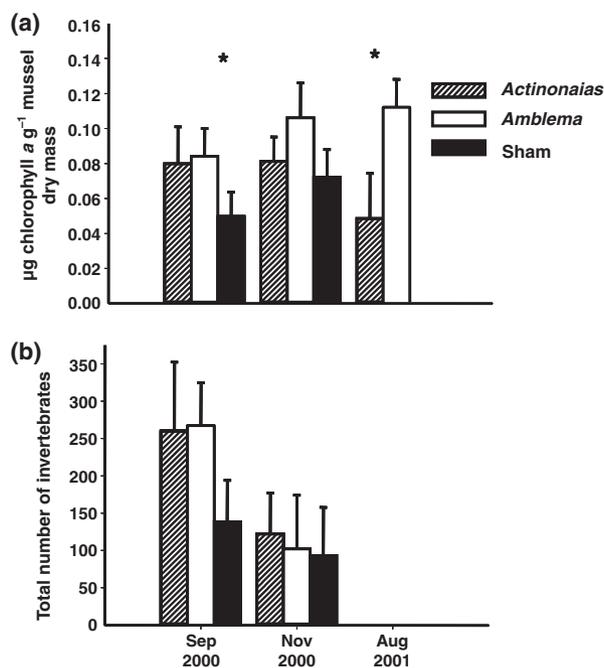


Fig. 3 Mean + 1 SE for shell response variables. Results shown are for ANCOVA comparisons of *Actinonaias ligamentina* and *Amblema plicata* with sham mussels. Asterisks represent significant differences from multiple comparison procedures.

Discussion

We found that live unionid mussels influenced the distribution and abundance of other benthic organisms, periphyton and invertebrates, in both the surrounding sediment and on mussel shells. Differences between living and sham mussel treatments indicate that biological activities of mussels provide ecosystem services to the benthic community beyond the physical habitat provided by shells alone. Mechanisms by which mussels likely provide these ecosystem services include biodeposition of faeces and pseudofaeces, excretion of nutrients, and bioturbation of sediments (Vaughn & Hakenkamp, 2001; Vaughn *et al.*, 2004).

Both organic matter and invertebrate abundance were higher in live than sham mussel or sediment treatments. These results suggest that colonising invertebrates are responding to higher levels of biodeposited organic matter and excreted nutrients in live mussel treatments. Our field observations of both *Actinonaias* and *Amblema* support this conclusion; discrete piles of faeces/pseudofaeces are often observed beside mussel exhalant siphons in the streambed. Peterson & Heck (1999) showed that biodeposits from marine mussels increased pore water

nutrient content and was a function of increased mussel density, with pore water ammonia and phosphate concentration four times higher in the densest mussel beds. Radziejewska (1986) documented a distinct meiofauna community of higher abundance in the sediments of marine mussel beds compared with adjacent areas of sediment. Meiofauna appeared to be responding to higher levels of organic material from biodeposits. Mussels and other invertebrates may interact synergistically to increase organic matter in the sediment (Hakenkamp & Morin, 2000). In addition, mussels stabilise the substrate (Strayer, 1999), which would increase the retention time of organic matter in the sediment (Hakenkamp & Morin, 2000).

Oligochaetes are benthic worms that feed on sediment organic matter (Brinkhurst & Gelder, 2000). Oligochaete abundance in the sediment was higher in live than sham mussel or sediment treatments. Living mussels may facilitate oligochaetes by biodepositing food in the form of faeces and pseudofaeces and by bioturbating the sediment, which decreases compaction and provides higher quality habitat. Ephemeropterans in the sediment were significantly higher in live than sham mussel or sediment treatments and likely responding to increases in organic matter in the sediment (Merritt & Cummins, 1996).

Periphyton abundance, as represented by chlorophyll *a* concentration, was higher on live than sham mussel shells. Previous work at the study site suggests that the Kiamichi River may undergo periods of both phosphorous and nitrogen limitation (C.C. Vaughn and D.E. Spooner, unpubl. data). Thus, higher periphyton abundance on living mussels likely represents a response of nutrient-limited algae to local nutrient excretion by mussels. Algal abundance on glass slides placed on the sediment did not differ among treatments. However, we think the glass slide methodology underestimated local effects of mussel excretion. Slides were placed near the corners of each enclosure, but mussels were rarely in enclosure corners. Assuming excretion of nutrients causes local increases in periphyton, slides may have been located too far from mussels for periphyton on the slides to respond to nutrient excretion. Nutrients directly excreted from the exhalant siphon of mussels may be taken up by periphyton on mussel shells, whereas nutrients would likely be sequestered before reaching glass slides (Blumenshine *et al.*, 1997). Water flow likely magnified this effect by diluting nutrients

excreted by mussels or by transporting nutrients downstream, away from the enclosures.

Invertebrate and periphyton abundance were positively correlated on the shells of live but not sham mussels, indicating that invertebrates are responding to increased algal abundance on living mussel shells as food and/or shelter. Invertebrate abundance and mussel size were positively correlated for shells of live but not sham mussels, and invertebrate richness was higher on larger mussels. Higher abundance and richness of invertebrates on larger mussels might be a reflection of both increased habitat availability (Beckett, Green & Thomas, 1996), as well as increased local ecosystem services. For example, larger mussels excrete more nutrients than smaller mussels (Vaughn *et al.*, 2004).

Total invertebrate abundance on shells did not differ between treatments, but there were some differences among taxonomic groups. Significantly more mites and tardigrades were found on the shells of live mussels than sham mussels. Tardigrades typically live on plants or the sediment and feed on algae (Nelson & Marley, 2000), thus they may be responding to local increases in algae on live mussel shells as both food and habitat, whereas adult mites are likely responding to increased habitat availability (Di Sabatino, Gerecke & Martin, 2000).

After correcting for biomass, *Amblema* had more algae on their shells than *Actinonaias*. We believe this reflects both morphological and behavioural differences between the species. Throughout the experiment *Actinonaias* was more active; individuals moved about enclosures and burrowed up and down in the sediment. These activities would tend to inhibit algal colonisation and slough off attached algae. In contrast, *Amblema* individuals were sedentary and generally stayed in one location, with part of the shell always exposed to the water column and thus sunlight, encouraging algal growth. In addition, shells of *Amblema* are composed of multiple ridges while *Actinonaias* shells are smooth (McMahon & Bogan, 2001). Ridges are thought to help mussels maintain position during high flow events (Watters, 1994) and might present algae a refuge from grazing and/or flow providing increased habitat heterogeneity and area. *Amblema* had more mites and tardigrades on their shells than *Actinonaias*, which probably is a result of the increased algal food and habitat resources on *Amblema* shells.

Effects of mussels on the benthic community varied greatly with season. Overall, mussels had strong

effects in late summer (September 2000 and August 2001) and minimal to no detectable effects in mid autumn (November 2000). These differences can be attributed to seasonal differences in depth, discharge, and temperature in the river. At the beginning and end of the experiment water levels were quite low (30 cm depth), flow was minimal (Fig. 1), and water temperatures were high (as high as 41 °C). Under these shallow, low-flow conditions, materials excreted and biodeposited by mussels would remain in the mussel bed where they could be used by the rest of the benthic community (Vaughn *et al.*, 2004), as our data demonstrate. Higher temperatures would increase mussel metabolic rates, which would increase nutrient excretion and biodeposition rates (Aldridge, Payne & Miller, 1995; McMahon & Bogan, 2001). In contrast in October and November our study site experienced high flows (Fig. 1), with large increases in both current velocity and water volume. High flows likely scoured organic matter, algae, and invertebrates from both sediment and shells. Flow remained relatively high throughout the winter and spring, decreasing in June (Fig. 1) and allowing mussel effects to again predominate. These results are corroborated by other studies demonstrating that organic matter dynamics in streams are governed by seasonal flow conditions (Brennan, McLachlan & Wotton, 1978; Palmer *et al.*, 1997) and that the ability of freshwater bivalves to influence ecosystem processes decreases with increases in flow and water volume (Strayer *et al.*, 1999; Vaughn *et al.*, 2004).

This study demonstrates that riverine, unionid mussels influence the co-occurring benthic community, but that effects of mussels are context-dependent and stronger during periods of low water volume, low flow and higher water temperatures. Our results are based on standing crop estimates of production (chl *a* and organic matter) and community structure (benthic invertebrates in the sediment and on shells). While these data provide an important first step, our understanding of how unionids influence the rest of the benthic community will be greatly strengthened by studies that track processing rates of energy and nutrients. While some comparative, field estimates of unionid processing rates have been made (Nichols and Garling 2000, Raikow and Hamilton 2001, Christian *et al.* 2004), it is now imperative to examine these rates experimentally and under different environmental contexts.

Species whose abundance and/or biomass dominates an ecosystem often have corresponding strong effects on ecosystem function by causing physical state changes in biotic or abiotic materials and controlling the availability of resources to other organisms (Levinton, 1995; Gutierrez *et al.*, 2003; Lill & Marquis, 2003; Statzner, Peltret & Tomanova, 2003). Examples of such 'ecosystem engineers' include detrital feeding fish (Flecker, 1996), beavers (Wright, Jones & Flecker, 2002), suspension-feeding blackfly larvae (Wotton *et al.*, 1998), marine bivalves (Dame, 1996) and zebra mussels (Strayer *et al.*, 1999; Ackerman, Loewen & Hamblin, 2001). Based on our results and other recent studies (Vaughn *et al.*, 2004) we think that unionid mussels potentially act as 'ecosystem engineers' in rivers where they are abundant because they both modify the habitat and control availability of resources to other organisms. Further research in this area is needed.

Given the recent body of research on the ecological role of invasive freshwater bivalves (i.e. zebra mussels and Asian clams), it is tempting to make comparisons between the effects of the invasive and native fauna. However, inferences drawn from studies of invasive species that downplay the role of native mussels should be regarded with skepticism. Native mussels occupy different niches (e.g. zebra mussels are epifaunal), are longer lived and thus provide ecosystem services on a much longer temporal scale, and are an integral component of many freshwater systems. This study represents the first empirical test and confirmation of ecological benefits provided by native freshwater mussels.

Freshwater mussels are threatened and declining globally (Bogan, 1993). Historically, mussels dominated the biomass of rivers in eastern North America (Parmalee & Bogan, 1998), but in recent years populations of both rare and common species have undergone catastrophic declines (Vaughn & Taylor, 1999). Our results, and results of other recent studies of ecosystem services performed by riverine bivalves (Strayer *et al.*, 1999; Vaughn *et al.*, 2004), indicate that this catastrophic loss of mussel biomass may lead to changes in the functioning of river ecosystems.

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