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Ecosystem processes performed by unionid mussels in stream mesocosms: species roles and effects of abundance

Caryn C. Vaughn[1,*], Keith B. Gido[1,2] & Daniel E. Spooner[1]
[1]*Oklahoma Biological Survey and Department of Zoology, University of Oklahoma, Norman, OK 73019, USA*
[2]*Present address: Kansas State University, Division of Biology, Ackert Hall Manhatten, KS 66506, USA*
*(*Author for correspondence: Tel.: +1-405-325-4034, Fax: +1-405-325-7702, E-mail:cvaughn@ou.edu)*

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Abstract

Unionid mussels are a guild of freshwater, sedentary filter-feeders experiencing a global decline in both species richness and abundance. To predict how these losses may impact stream ecosystems we need to quantify the effects of both overall mussel biomass and individual species on ecosystem processes. In this study we begin addressing these fundamental questions by comparing rates of ecosystem processes for two common mussel species, *Amblema plicata* and *Actinonaias ligamentina*, across a range of abundance levels and at two trophic states (low and high productivity) in stream mesocosms. At both low and high productivity, community respiration, water column ammonia, nitrate, and phosphorus concentrations, and algal clearance rates were all linearly related to overall mussel biomass. After removing the effects of biomass with ANCOVA, we found few differences between species. In a separate series of experiments, nutrient excretion (phosphorus, ammonia, and molar N:P) and biodeposition rates were only marginally different between species. For the species studied here, functional effects of unionids in streams were similar between species and linearly related to biomass, indicating the potential for strong effects when overall mussel biomass is high and hydrologic residence times are long.

Introduction

In marine and estuarine systems bivalve mollusks have large influences on ecosystem processes where they dominate benthic biomass and couple benthic and pelagic energy and material cycling (Dame, 1996). In freshwater systems, a large body of recent research has focused on the functional effects of invasive, epifaunal zebra mussels (*Dreissena polymorpha*) that impact lakes and streams via high rates of filter feeding (Mellina et al., 1995; MacIsaac, 1996; Caraco et al., 1997; Strayer et al., 1999). Freshwater mussels (Bivalvia: Unionoida) are a guild of benthic, burrowing, filter-feeding bivalves. The biomass of healthy unionid assemblages can exceed the biomass of all other benthic organisms by an order of magnitude (Negus, 1966; Layzer et al., 1993), and production by mussels (range from 1 to 20 g dry mass $m^{-2}y^{-1}$) can equal that by all other macrobenthos in many streams (Strayer et al., 1994). Thus, in rivers where they are abundant, mussels should play an important role in ecosystem functioning.

Despite the potential importance of unionids to stream ecosystems, we have very little quantitative information on the overall importance of mussels to stream function. Although it may seem intuitive that mussel effects on ecosystem processes should increase with overall mussel abundance/biomass, this has not been demonstrated for unionids

(Vaughn & Hakenkamp, 2001). Historically, unionids dominated the benthic biomass of eastern North American rivers (Parmalee & Bogan, 1998), especially in undisturbed systems. In recent years, many North American mussel populations have undergone a drastic decline (Bogan, 1993; Neves et al., 1997). In most cases it is not only the rare mussel species that are declining, but common species are in decline as well (Vaughn & Taylor, 1999). For example, 42% of North Carolina's historically abundant unionid populations are in poor condition and only 31% may remain viable over the next 30 years (Neves et al., 1997). Such a decline represents a significant loss of benthic, filter-feeding biomass. Thus, it is important to understand the relationship between mussel biomass and ecosystem processes to predict how biomass losses will impact stream function.

It is equally important to document the roles of individual mussel species in streams. Mussels are one of the most imperilled groups globally, with 70% of species considered threatened (Bogan, 1993). If mussel species perform similar roles in ecosystems, the loss of some species may have little impact on stream function. However, if species play distinct roles, multi-species assemblages must be maintained to protect ecosystem health and services (Vaughn & Hakenkamp, 2001).

The potential for redundancy in ecological roles among mussel species should be high for the following reasons: (1) Mussels have similar life histories. Riverine species are very long-lived (usually >25 years) and slow-growing, adults are relatively sedentary, and most larvae are obligate ectoparasites on fishes (Kat, 1984; Vaughn & Taylor, 2000). (2) Mussels are a highly speciose group that typically occur as dense, multi-species assemblages (Vaughn, 1997). For example, in the Kiamichi River, Oklahoma, a typical mussel bed contains 13–17 co-occurring unionid species (Vaughn et al., 1996) at mean densities of 21 individuals m^{-2} (Vaughn et al., 1997). (3) There is little evidence for differences in microhabitat preference between mussel species within stream reaches and within actual mussel beds or patches (Strayer, 1981; Holland-Bartels, 1990; Strayer & Ralley, 1993; Vaughn & Pyron, 1995). (4) Most studies have found that mussels feed non-selectively and have high diet overlap, ingesting phytoplankton, bacteria and organic material in proportion to their availability (Bronmark & Malmqvist, 1982; Paterson, 1984; Nichols & Garling, 2000; Raikow & Hamilton, 2000).

However, there is also evidence pointing towards unique ecological roles for mussel species, and that species roles may vary with environmental context. DiDonato (1998) used growth measurements to demonstrate competition between two unionids in a food-limited lake, and linked this to differences in filtering abilities between the two species. Water temperature, particle size and concentration, flow regime, and bivalve size and gill morphology all have been found to influence mussel filtration rate (Vaughn & Hakenkamp, 2001). Both the size of the gill (Payne et al., 1995; Lei et al., 1996) and the number and structural complexity of cirri on the gill (Silverman et al., 1995, 1997) influence filtering abilities. Excretion rate varies between species of bivalves, as well as with individual size, temperature, stage in reproductive cycle and food availability (Dietz, 1985; James, 1987; Lauritsen & Mozley, 1989; Nalepa et al., 1991; Baker & Hornbach, 2001).

To predict how the loss of both mussel species and overall mussel biomass will impact stream ecosystems, we must quantify the effects of both overall mussel abundance and individual species on ecosystem processes. In this study we begin addressing these fundamental questions by comparing rates of ecosystem processes for two common mussel species across a range of abundance levels in stream mesocosms. Because species roles may vary under different environmental conditions, we examine these questions under two sets of environmental conditions (low and high food availability). Finally, we extrapolate our results to the level of a stream reach to postulate mussel effects on stream ecosystems and the potential impact of their decline.

Methods

Study organisms and field site

The Kiamichi River, in the Ouachita Uplands of southeastern Oklahoma, is a comparatively undisturbed, medium-sized river (180 km in length, watershed area is 4800 km^2) that was recently selected by The Nature Conservancy as one

of the most critical watersheds in the US for protecting biodiversity (Master & Flack, 1998) based largely on its healthy mussel populations (Vaughn & Pyron, 1995). The Kiamichi River contains an intact mussel fauna (no species extinctions), with high mussel abundance and richness (~30 species; Vaughn et al., 1996).

We selected two unionid species that occur together in the Kiamichi River and are common throughout the Mississippi River drainage, *Amblema plicata* (Say) (subfamily Ambleminae) and *Actinonaias ligamentina* (Lamarck) (subfamily Lampsilinae) (Parmalee & Bogan, 1998). These two species are the most dominant in the Kiamichi system in terms of overall abundance and incidence (Vaughn & Pyron, 1995). We expected that these species might differ in their ecological roles. In addition to different phylogeny, the species use different reproductive strategies (Parmalee & Bogan, 1998) and have differences in physiology and biochemical composition (Baker & Hornbach, 2001). In the Kiamichi system, *A.ligamentina* tends to be larger and more active than *A. plicata* (Spooner, 2002).

Mesocosm experiment

A mesocosm experiment was conducted in February, 2000. Individuals of *A. plicata* and *A. ligamentina* were collected from the Kiamichi River and held in the laboratory in sediment-free Frigid Units Living Streams at 10 °C for 3 weeks. Individuals were inactive at this cold temperature and were not fed during the holding period. One week before beginning the experiment, water temperature in the Living Streams was gradually brought up to 21 °C, also the temperature of the stream mesocosms (see below). Immediately prior to the experiment, each mussel was scrubbed gently to remove any attached algae and microbial material and its wet weight was recorded.

The experiment was conducted in recirculating stream mesocosms (122 × 48 × 28 cm). The use of recirculating mesocosms is common in ecological studies of stream invertebrates (Lamberti & Steinman, 1993; Cardinale et al., 2002) and allowed us to obtain much more precise estimates of what mussels were putting into and taking out of the water and sediment than would have been possible in a similar experiment in flow-through artificial streams or in a natural stream. Mesocosms were lined with clean, dry sand and filled with 70 l of water from a local reservoir. Water was circulated at a rate of 2527 l h^{-1} with 47 w pumps. Mesocosms were illuminated with 15 w, wide spectrum fluorescent lights on a 12:12 h light-dark cycle. Water temperature was maintained at 21 °C.

We would expect ecosystem effects of mussels to vary with stream trophic state because of differing food availability for mussels and differing nutrient regeneration by algae. To simulate these varied field conditions, the experiment was conducted under both low and high productivity conditions. Prior to the experiment, each mesocosm was filled with water from a local reservoir (Lake Thunderbird, Cleveland Co., OK). In the low productivity treatments beginning mean chlorophyll *a* concentration was 10 μg l^{-1} and mesocosms were not supplemented with algae for the remainder of the experiments. In the high productivity experiment beginning mean chlorophyll *a* concentration was 20 μg l^{-1} and mesocosms were spiked daily with a mixed-culture algal slurry to maintain high algal concentrations in the water column. The dominant form in the slurry was the green alga *Ankistrodesmus* sp. Preliminary observations and gut analyses confirmed that both mussel species readily fed on the algal slurry.

Because we were interested in effects of both mussel abundance and individual species on ecosystem processes, we designed the experiment using a 'regression approach' (e.g., Scheiner & Gurevitch, 1993; Gido & Matthews, 2000), whereby mussel densities were manipulated across their natural range rather than at just two or three values. Our design consisted of two productivity treatments (low and high) × two species (*A. plicata* and *A. ligamentina*), with each species stocked at eight densities (3, 7, 10, 14, 20, 27, and 34 mussels m^2 and a no mussel control), resulting in a total of 32 mesocosm experimental units, with each mesocosm containing only a single species of mussel. The selected mussel densities represent a range of natural densities within mussel beds in the Kiamichi River (mean density is 21 m^{-2}; Vaughn et al., 1997). Within a species we attempted to use equivalent sized individuals, but any size differences were corrected later by presenting data on a per biomass basis. The experiment ran for 6 days.

This time span was long enough to allow us to examine nutrient contributions by the mussels, but short enough that we avoided potential negative effects of nutrient accumulations.

Mussels should 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 feces and pseudofeces (Vaughn & Hakenkamp, 2001). The ecosystem variables we examined were chosen to encompass these fundamental processes. All of these variables were measured for whole mesocosms, not individual mussels. Response variables included phosphate, ammonia, and nitrate measured on days 0, 1, 2, 4, and 6 and whole-stream respiration rates on days 1, 2, 4, and 6. We measured chlorophyll *a* concentrations after 0, 6 and 24 h, and 2 and 4 days in the high productivity treatments to allow estimation of clearance rates. Chlorophyll *a* concentrations in the low productivity treatments, which were not supplemented, were too low for accurate estimation of clearance rates.

Water samples for soluble reactive phosphorus (SRP), ammonia (NH_3–N), and nitrate (NO_3–N) were filtered through Gelman A/E filters and immediately placed on ice and analyzed within 12 h of collection. Nutrient concentrations were determined colorimetrically using a Beckman DU 520 spectrophotometer. A detailed description of nutrient and chlorophyll *a* analysis is given in APHA (1995). In short, phosphate was determined with the Ascorbic Acid method, ammonia with the Phenate method, and nitrate was estimated using cadmium reduction. Water samples for chlorophyll *a* (from 0.5 to 2 l) were filtered through a Gelman A/E filter and filters were frozen to lyse cells. Chlorophyll *a* was extracted with acetone and samples were analyzed spectrophotometrically with a correction for pheophytin (APHA, 1995).

Community respiration was measured on days 1, 2, 4 and 6 during mid-day. Here we define 'community' as everything living in the mesocosms. The pumps were turned off and each mesocosm was covered with a tarp. Initial oxygen concentrations were measured, the mesocosms were left for 1 h, and a final oxygen reading was taken. Community respiration was then estimated as oxygen consumption of each stream mesocosm in the dark over a 1 h period (Wetzel & Likens, 1991).

We used a repeated measures analysis of covariance (Sokal & Rohlf, 1995) to test for the effects of mussel biomass (the covariate), species and time on various ecosystem properties in the stream mesocosms. Each mesocosm unit was considered a single variate. Measurements from all response variables were examined for normality prior to analyses; no transformations were necessary.

Individual excretion rates

Individual nutrient excretion rates were estimated using methodology similar to that used for fishes (Schaus et al., 1997). At the completion of the mesocosm experiment, a subsample of mussels was removed from the sediment and all biofilm was gently scrubbed from the shells. Individual mussels were placed in a ZipLock® bag with 0.5 l pre-filtered water from the mesocosm. An initial water sample was taken from the pre-filtered water and immediately placed on ice. The bag was then placed in the mesocosm for one hour after which a second water sample was removed and placed on ice. Water samples were analyzed for ammonia and SRP as described above. Water temperature was 21 °C in each mesocosm during the excretion measurements.

At the end of the excretion experiment wet weight was recorded for all individuals. Mussels used to measure excretion rates were dissected from their shell and dried at 60 °C for 2 days; other individuals were returned to the river. Total wet weight (including shell) – tissue dry weight regression models were used to estimate dry weight for individuals that were not sacrificed (*A. ligamentina* tissue dry weight = 0.039 (total wet weight) − 2.943, $r^2 = 0.569$, $p = 0.001$; *A. plicata* tissue dry weight = 0.016 (total wet weight) + 0.168, $r^2 = 0.525$, $p = 0.005$). Using these models, all rates are presented on a dry weight basis. Individual excretion rates were examined with linear regression and species were compared using analysis of covariance with biomass as the covariate (Sokal & Rohlf, 1995).

Biodeposition experiment

We conducted a separate experiment to estimate biodeposition rates. Here we define biodeposition

as feces and pseudofeces produced by mussels and deposited onto the sediment (Dame, 1996; Iglesias et al., 1998). We conducted this experiment under no-flow conditions to obtain a baseline estimate of biodeposition not confounded by potential downstream transport in the current. There were three mussel treatments (*A. ligamentina, A. plicata* and a shell control) and three food concentrations (3, 6 and 10 mg AFDM l^{-1}), each replicated eight times. Mussels were collected from the Kiamichi River as in the previous experiment, held at 21 °C, and starved for 1 week prior to initiating the experiment. Individual mussels were then placed in plastic beakers that were filled with 500 ml of clean sand. Beakers were enclosed within 4, 48 l glass aquaria filled with filtered water from a local reservoir. Each aquarium contained two beakers with *A. ligamentina*, two beakers with *A. plicata,* and two beakers with either an *A. ligamentina* or *A. plicata* shell. Each aquarium was aerated with an airstone suspended in the water column so that biodeposits within the beakers were not disturbed. Mussels were fed the same algal slurry used in the previous experiment. Experiments ran for 48 h, after which all biodeposits were carefully pipetted from the sediments. Biodeposits were dried at 60 °C for 24 h and then combusted at 550 °C for 1 h to determine ash free dry mass (APHA, 1995). Water temperature was maintained at 21 °C throughout the experiments. We used a one-way ANOVA to test for differences in biodeposits (mg AFDM g mussel dry $mass^{-1}$ h^{-1}) among the three treatments (*A. plicata*, *A. ligamentina*, and control). We then compared biodeposition rates for the two species across three food concentrations using a repeated measures ANOVA with food concentration as the repeated factor.

Field extrapolation

The rate at which mussels filter food from the water column is often measured as clearance of chlorophyll from the water column (Coughlan, 1969; Kryger & Riisgård, 1988). Clearance rates were determined by comparing chlorophyll *a* concentrations in treatment mesocosms with control (i.e., no mussels added) mesocosms in the high productivity treatments. We then extrapolated our laboratory-measured clearance rates to estimate clearance time in days for a stream reach in the Kiamichi River under three known hydrologic states and three natural mussel densities (following Strayer et al., 1999). Our model was based on an actual reach in the Kiamichi River that is 1300 m^2 with an average mussel density of 21 individuals m^{-2} (Vaughn et al., 1997, unpublished data). Although this particular stream reach contains 17 species of mussels, over 80% of individuals are either *A. ligamentina* or *A. plicata* (Vaughn, unpublished data), thus by examining the effect of these species we should get a good indication of the potential effects of the entire mussel assemblage. We used the mean 12 h clearance rate for both species combined. Hydrologic residence times in days were estimated from field measurements of depth and discharge collected from this site in August (low flow), May, and January (peak flow) 2000.

Results

Mesocosm experiment

Strong biomass effects, and no significant species effects, were observed for most response variables in the mesocosm experiment, in both low and high productivity treatments (Table 1). Water column chlorophyll *a* concentrations in the high productivity treatments illustrate this trend. The amount of chlorophyll in the water column decreases with increasing mussel biomass, reflecting increased clearance of chlorophyll from the water column by mussels. This trend holds for both species and across days (food was added daily to the high productivity treatments) (Fig. 1). While *A. ligamentina* remove more chlorophyll from the water than *A. plicata*, this difference is non-significant once data are standardized for biomass (Table 1). The only variable not significantly affected by biomass was phosphate in the high productivity treatment.

In general, biomass effects increased over the duration of the experiment, resulting in significant interactions between time and biomass for most variables (Table 1). This trend is nicely illustrated by water column nitrate concentrations. Nitrate concentrations increase over time regardless of species or productivity treatment, and increases are greater in treatments with higher mussel biomass (Fig. 2).

Table 1. *F*-statistics and associated *p*-values (in parentheses) derived from repeated measures ANCOVAs that tested for the effects of biomass (covariate) and species on the various ecosystem properties of experimental mesocosms

	Respiration	NH_3-N	NO_3-N	PO_4-P	Chlorophyll *a*
Effect – low productivity					
Biomass	**59.83 (<0.001)**	**181.42 (<0.001)**	**100.14 (<0.001)**	**17.60 (0.001)**	
Species	0.54 (0.480)	1.42 (0.259)	0.27 (0.613)	0.32 (0.581)	
Time	0.23 (0.798)	1.32 (0.289)	**7.61 (0.003)**	**7.56 (0.001)**	
Time × biomass	**9.81 (0.001)**	**9.86 (0.001)**	**75.72 (<0.001)**	**4.31 (0.026)**	
Time × species	0.73 (0.494)	0.13 (0.879)	0.20 (0.818)	0.07 (0.930)	
Effect – high productivity					
Biomass	**9.11 (0.012)**	**58.52 (<0.001)**	**37.47 (<0.001)**	0.44 (0.520)	**12.93 (0.004)**
Species	0.09 (0.773)	0.05 (0.828)	0.23 (0.642)	0.65 (0.435)	1.72 (0.216)
Time	**3.68 (0.022)**	0.64 (0.595)	**6.97 (0.001)**	0.46 (0.713)	**9.83 (<0.001)**
Time × biomass	2.77 (0.057)	**11.79 (<0.001)**	**43.83 (<0.001)**	**3.57 (0.024)**	**2.58 (0.019)**
Time × species	0.77 (0.515)	0.37 (0.775)	0.32 (0.810)	0.91 (0.449)	0.26 (0.966)

Bold-face font highlights significant relationships.

Individual excretion rates

Within a species, there were no significant associations between individual excretion rates and individual biomass for either log phosphorus (*A. ligamentina*, $r^2 = 0.01$, $p = 0.77$; *A. plicata*, $r^2 = 0.05$, $p = 0.57$), log ammonia (*A. ligamentina*, $r^2 = 0.11$, $p = 0.32$; *A. plicata*, $r^2 = 0.005$, $p = 0.85$), or N:P molar ratios (*A. ligamentina*, $r^2 = 0.012$, $p = 0.746$; *A. plicata*, $r^2 = 0.008$, $p = 0.817$) (Fig. 3). ANCOVA using body mass as the covariate revealed no significant differences

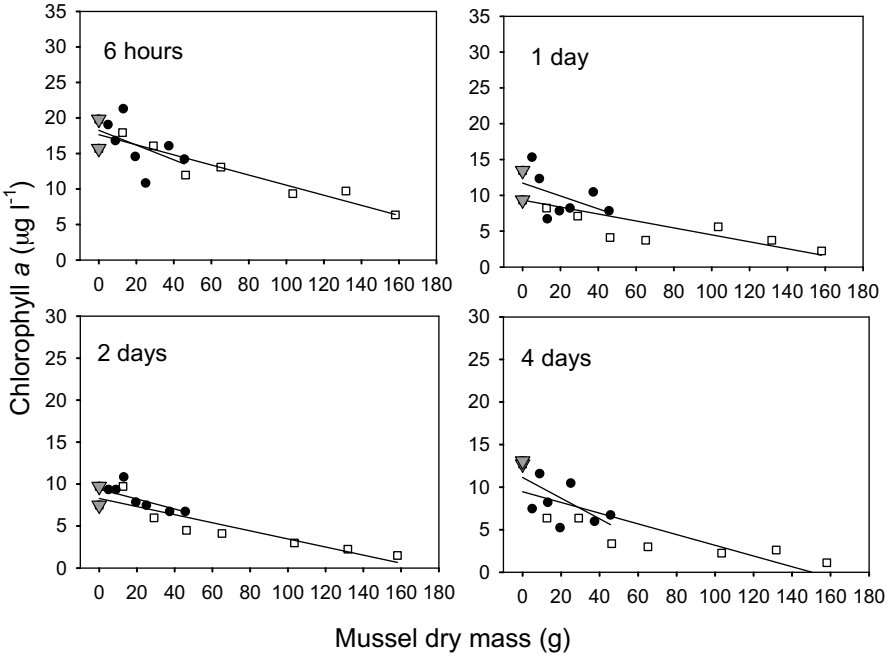

Figure 1. Chlorophyll concentrations in the high productivity experiment at 6 h, 1 , 2, and 4 days. Squares represent *A. ligamentina*, circles represent *A. plicata*, and the controls are shown as triangles.

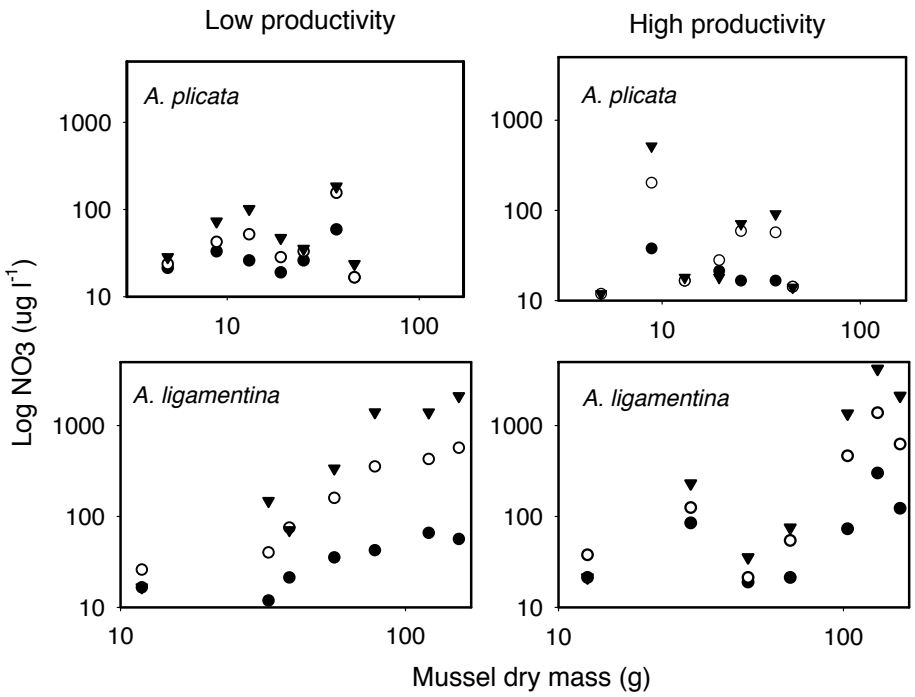

Figure 2. Relationship between log mussel dry mass and log water column nitrate concentration on days 2, 4 and 6. Points represent day 2 (●), Day 4 (○), and Day 6 (▼).

between the two species for either log ammonia excretion ($F = 1.357$, $p = 0.26$) or for molar N:P ratio ($F = 1.2$, $p = 0.289$). However, there was a marginally significant difference between species in log phosphorus excretion ($F = 4.015$, $p = 0.06$). With both species combined log excretion rates for phosphorus ($r^2 = 0.46$, $p < 0.001$) and ammonia ($r^2 = 0.39$, $p = 0.004$) significantly increased with biomass (Fig. 3). The slope of the relationship between log phosphate excretion rate and log dry mass is <1, suggesting a declining per capita excretion rate in larger individuals.

Biodeposition experiment

The amount of organic material deposited on the sediment in the biodeposition experiment was significantly higher in the mussel treatments than the control ($F = 38.65$, $p < 0.001$; mean AFDM for *A. plicata* treatments = 2.15 mg, *A. ligamentina* treatments = 6.81 mg, and control = 0.35 mg). Biomass-corrected biodeposition significantly increased with increasing food concentration ($F = 50.01$, $p < 0.001$), but was only marginally different between species ($F = 3.38$, $p = 0.087$) (Fig. 4).

Discussion

Both mussel species had strong effects on ecosystem processes in our experiments. We were able to quantify rates of algal removal, nutrient excretion, and biodeposition of organic material. Mussel effects on these processes usually were linearly related to biomass, regardless of species, and mussels influenced these processes even at low biomass. These effects were observed in both low and high productivity treatments, suggesting that mussels have the potential to influence ecosystem processes across a range of stream trophic states. Our results corroborate and expand on other studies that report substantial effects of high bivalve abundance on ecosystem processes (Cohen et al., 1984; Phelps, 1994; Welker & Walz, 1998; Strayer et al., 1999). For example, Welker & Walz (1998) reported that a very dense bed of unionid mussels caused 'biological oligotrophication' of the River Spree,

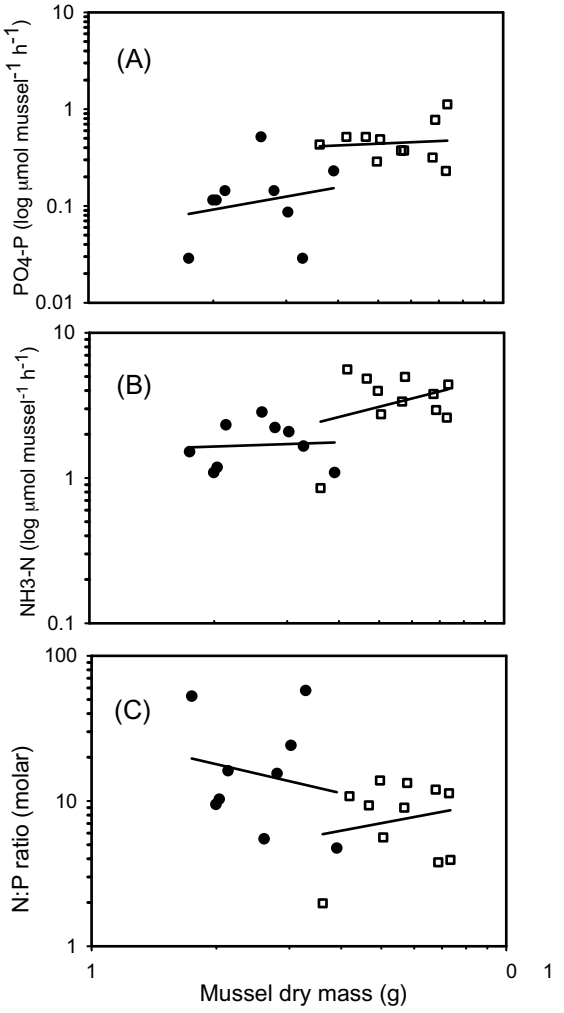

Figure 3. Nutrient excretion by individual mussels. (A) phosphate, (B) nitrate, (C) N:P ratios. Squares represent *A. ligamentina* and circles represent *A. plicata*.

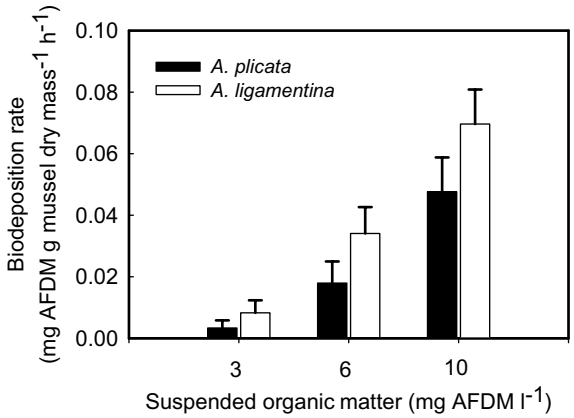

Figure 4. Mean biodeposition by *A. ligamentina* and *A. plicata* at three food concentrations.

Germany, but did not test this experimentally or examine effects at lower unionid densities.

Marine bivalves (Dame, 1996) and zebra mussels (Strayer et al., 1999) significantly affect primary production when filtration rates are large compared to food supply. In streams, the amount of food that bivalves filter from the water column is greatly influenced by hydrologic residence time (Strayer et al., 1999). Thus, unionid mussels should be most likely to influence production and other ecosystem processes when biomass is high relative to water volume and current velocity. The extrapolation of our data to a stream reach in the Kiamichi River supports this prediction. In August, water volume in this reach is reduced and flows are very low, thus it takes almost a day for water to move through the reach and across the mussel bed (Fig. 5). Under these conditions, mussels can turn over a substantial proportion of the water column at even relatively low densities. Consequently, at low flows mussels should affect most ecosystem processes in the reach, and the magnitude of these effects will increase with increased biomass. At higher flows and water volumes during May and January, only a small fraction of the water column is filtered by mussels before it flows through the reach (Fig. 5). Under these conditions, small-scale effects of mussel activity are likely overridden by advective forces (Strayer et al., 1999).

There are obvious limitations in extrapolating laboratory data based on a short-term, closed-system study of two species to a natural stream with vagaries in flow and other processes (Hart & Finelli, 1999). A recirculating stream mesocosm design allowed us to examine the contributions of mussels uncoupled from downstream transport effects. This closed-system design closely parallels conditions in the Kiamichi River in late summer and fall, where mussel beds are contained in shallow, isolated reaches with long hydrologic residence times. Thus, our data should be a good approximation of contributions by mussels to the stream at low flows. In addition, our extrapolation is for a mussel bed contained in one stream reach. The degree to which mussels may impact ecosys-

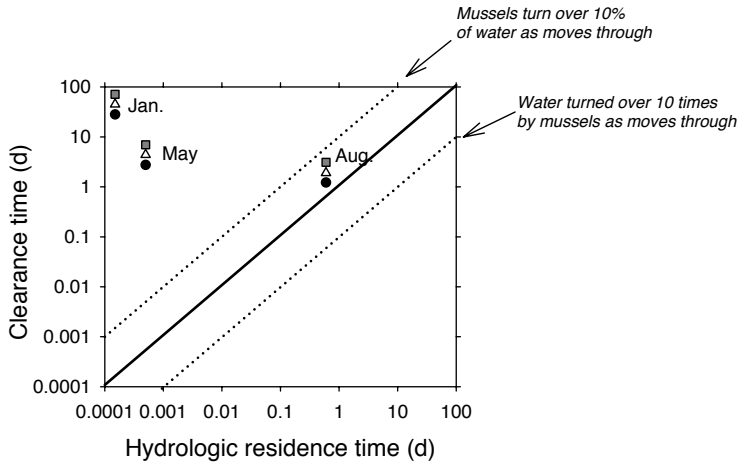

Figure 5. Relationship between hydrologic residence time (time in days required for all water to move through a stream reach) and clearance time (time in days required for the mussel community to filter a volume of water equal to the entire volume of water in the stream reach) for a mussel bed in the Kiamichi River, Oklahoma, during January, May, and August. Points represent mussel densities of 54 m^{-2} (□), 20 m^{-2} (△) and 7 m^{-2} (○). Below the solid diagonal line mussels theoretically filter the entire water volume before it flows across the mussel bed. Above the solid diagonal line water flows across the bed before being completely turned over by mussel filtration.

tem processes in an entire stream will depend on the number and spatial distribution of mussel beds, the biomass of mussels in those beds, overall stream hydrologic state, and interactions with the rest of the stream community.

Excretion of ammonia and dissolved organic nitrogen by bivalves controls primary production in nitrogen-limited marine systems (Dame, 1996). Following the invasion of epifaunal zebra mussels (*Dreissena polymorpha*) in the Hudson River, SRP nearly doubled (Strayer et al., 1999). Excretion by zebra mussels also has been linked to blooms of nitrogen-limited cyanobacteria in several lakes (Arnott & Vanni, 1996; MacIsaac, 1996; Vanderploeg et al., 2001). Our data indicate that unionid mussels can play an important role in nutrient processing in stream ecosystems by removing algae and particulate organic matter from the water column and converting it to dissolved nutrients that can be taken up directly by the algae.

The two species differed in nutrient excretion rates. *A. ligamentina* were about twice as big on average than *A. plicata* and their excretion of ammonia was about twice as much (3.64 ± 0.4 compared to 1.78 ± 0.21 μmol $mussel^{-1}$ h^{-1}). However, phosphorus excretion rates were three times higher for *A. ligamentina* than *A. plicata* (0.49 ± 0.08 compared to 0.16 ± 0.05 μmol - $mussel^{-1}$ h^{-1}). Other studies also have found that nutrient excretion varies between species of mussels, as well as with individual size, temperature, stage in the reproductive cycle and food availability (Potts, 1954; Dietz, 1985; James, 1987; Williams & McMahon, 1989; Davis et al., 2000; Baker & Hornbach, 2001). Such species-specific differences in nutrient excretion may influence the composition of the algal community. For example, based on our results, *A. ligamentina* and *A. plicata* would have equivalent mass-specific effects in a nitrogen-limited system, so mussel species composition would not be predicted to change the algal community. However, in a phosphorus-limited system the dominance of one species or the other could have large effects on the algal community, depending on mussel biomass and hydrologic conditions.

Unionid effects on nutrient processing should vary for different nutrients and with stream trophic and hydrologic conditions. Under high productivity conditions we would predict that increased algal densities would lead to more food for unionids which would lead to more nutrient excretion. This is the pattern we observed for nitrogen. Nitrogen concentrations increased with unionid biomass in both the low and high productivity treatments, but were much greater in the

high productivity treatments. However, higher algal densities also might result in faster nutrient uptake and thus a lower water column nutrient concentration. We think this phenomenon explains why phosphorus concentrations increased with mussel biomass in the low productivity treatment but not in the high productivity treatment, where phosphorus likely was immediately taken up by the algae. Unionid effects should be strongest in streams with long hydrologic residence times, particularly in nutrient-limited reaches below dense mussel beds. For example, both nitrogen and phosphorus were limiting in the Kiamichi River in late summer (Spooner & Vaughn, unpublished data), thus mussels have the potential to substantially impact algal growth in this system.

Mussels can sequester nutrients in their tissues and shell (Vaughn & Hakenkamp, 2001), making nutrients less available to algae. However, burrowing activities of mussels have been shown to enhance the rate of nutrient release from the sediments (Matisoff et al., 1985). Thus, mussels should have both negative (through consumption and sequestration) and positive (through direct nutrient excretion and release from the sediments) effects on algae. Spooner (2002) measured algal growth on live mussels compared to empty shells in field enclosures in the Kiamichi River. Algal growth was significantly higher on live mussels, most likely as a direct result of increased nutrient availability to algae through mussel excretion. The direction and magnitude of mussel effects on the algae and nutrient cycling will depend on the ratio of algal abundance to mussel biomass (Strayer et al., 1999), nutrient limitation, physical conditions in the stream, and characteristics of mussel species. For example, in our experiment *A. ligamentina* individuals were much more active than *A. plicata*, moving around in the mesocosms and bioturbating the sediment, whereas *A. plicata* tended to stay in one location for the duration of experiment. These behavior patterns have also been observed in the field (Spooner, 2002). Thus, *A. ligamentina* should be more likely than *A. plicata* to facilitate nutrient release from the sediments.

In marine and estuarine systems, biodeposition of feces and pseudofeces conveys high-quality pelagic resources to the sediment and influences benthic microbial, algal, and invertebrate community structure (Carlton et al., 1990; Nichols et al., 1990; Jaramillo et al., 1992; Navarro & Thompson, 1997). Similar effects have been demonstrated for zebra mussels (Roditi et al., 1997; Stewart et al., 1998) and Asian clams (Hakenkamp & Palmer, 1999; Hakenkamp et al., 2001) in freshwater. In this study, mussels biodeposited a large amount of organic material, and the amount increased with food concentration. For example, at the high food concentration of 10 mg AFDM l^{-1}, an average *A. ligamentina* individual (7.7 g tissue dry mass) biodeposited 0.6 mg or 6% of the seston in the water column within an hour. Thus, an entire assemblage of mussels should have the potential to remove substantial amounts of organic material from the water column and deposit it to the sediment where it can be used by other benthic organisms.

We found few differences in ecosystem processes performed by *A. ligamentina* and *A. plicata*. There were no significant differences between species in whole-stream respiration rates or ammonia concentrations after accounting for biomass. Other studies have reported few mass-specific differences in Q_{10} values between bivalve species (McMahon & Bogan, 2001), although metabolic rate generally decreases with increasing body mass (Alimov, 1975; Heubner, 1982; McMahon & Bogan, 2001). There also were no differences in algal clearance rates between the two mussel species. Few other studies have demonstrated differences in filtering abilities or particle selection among mussel species (Vaughn & Hakenkamp, 2001), and where differences have been found they have been for species from very different habitats (i.e. pond species vs. riverine species; Silverman et al., 1997). Mussels in our experiment were exposed to the same environmental conditions and fed the same algal food source. Thus, any differences in filtering rates should have been a result of inherent species differences.

While we found only a few, relatively subtle differences in the ecological roles of the two mussel species we examined, it is important to remember that these two species, although dominant both numerically and in terms of biomass (Vaughn et al., 1997), are part of a large, multi-species assemblage. The functional roles of other species in the assemblage may be more variable. In addition, our experimental design used single-species

treatments, but the function of multi-species assemblages may not be additive (Jonsson & Malmqvist, 2000; Cardinale et al., 2002). Finally, species roles often change with environmental context (Cardinale et al., 2000; Wellnitz & Poff, 2001). Future studies need to examine the functional role of both additional mussel species and entire, multi-species mussel assemblages under various, realistic environmental scenarios.

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