Community and foodweb ecology of freshwater mussels

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Abstract. Freshwater mussel (Superfamily Unionoidea) communities are important components of food webs, and they link and influence multiple trophic levels. Mussels filter food from both the water column and sediment with ciliated gills. Differences in cilia structure and arrangement might allow mussel species to partition food resources. Mussels are omnivores that feed across trophic levels on bacteria, algae, detritus, zooplankton, and perhaps, dissolved organic matter. Living mussels and their spent shells provide or improve habitat for other organisms by providing physical structure, stabilizing and bioturbating sediments, and influencing food availability directly and indirectly through biodeposition of organic matter and nutrient excretion. Effects of mussel communities on nutrient translocation and cycling depend on mussel abundance, species composition, and environmental conditions. Nutrient-related mussel effects influence multiple trophic levels. Healthy mussel communities occur as multispecies assemblages in which species interactions are probably very important. Food limitation and competition among species have been documented, but so have positive species interactions, and rare species have been shown to benefit energetically from living in species-rich communities. Effects of mussel species on ecosystem services and food webs vary across spatial and temporal scales, and the relative importance of competition and facilitation might change at different scales.

Key words: Unionoidea, feeding behavior, nutrient cycling, species interactions, context-dependent effects.

Freshwater mussels (Superfamily Unionoidea, hereafter mussels) are a guild of sedentary, suspension-feeding bivalves that perform important functions in lakes and streams (Vaughn and Hakenkamp 2001, Strayer et al. 2004). These large, long-lived invertebrates can be considered ecosystem engineers because they modify habitat, making it more suitable for conspecifics and other organisms (Gutierrez et al. 2003, Spooner and Vaughn 2006). Mussels transfer nutrients and energy from the water column to the

sediments through their filtering activity and stimulate production across trophic levels (Howard and Cuffey 2006, Spooner and Vaughn 2006, Vaughn et al. 2007). Other groups of bivalves have similarly strong effects. For example, aggregations of marine bivalves (i.e., mussel beds, oyster reefs) control production, nutrient cycling, and invertebrate species composition and abundance (Dame 1996), and zebra mussels have similar effects in freshwater ecosystems (Strayer et al. 1999, Caraco et al. 2006). However, unlike marine bivalves and zebra mussels, which usually occur as aggregations of one to a few species, unionoid mussels typically occur as diverse, multispecies assemblages (Vaughn 1997). Community structure and underlying species interactions should be important to ecosystem

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function because these mussels have evolved to live in diverse groups.

Historically, mussels dominated the benthic biomass of many eastern North American rivers (Parmalee and Bogan 1998), especially in undisturbed systems. In recent years, many of these mussel populations have declined significantly, primarily because of habitat alteration, particularly impoundment and channelization of rivers (Bogan 1993, Williams et al. 1993, Neves et al. 1997, Vaughn and Taylor 1999). These declines represent a significant reduction in benthic filter-feeding biomass. Rates of ecological processes done by mussels often scale linearly with biomass (Strayer et al. 1999, Vaughn et al. 2004). Thus, decreases in biomass should lead to alterations in ecosystem function. What is less understood is how related changes in species composition and species interactions will affect ecosystem function.

Here, we review what is known about the feeding behavior and diet of unionoid mussels and how feeding behavior and diet at the community level are related to ecosystem services that affect the rest of the food web. We present new data on how ecosystem services provided by mussels are influenced by species interactions, patterns of species abundance, and environmental context. Last, we suggest critical research directions and discuss implications for restoration and conservation.

Mussel Feeding Behavior and Diet

Many of the effects of mussel communities on ecosystem processes are a direct result of mussel feeding behavior. Mussels initially were categorized as suspension feeders, but recent research indicates that mussels can access benthic, as well as planktonic, food supplies (Nichols et al. 2005). Food capture is facilitated by a series of cilia located on the inner surface of the mantle, demibranches, and visceral mass. These cilia are either single stalks or fused. The degree of fusion and the density of cilia vary among genera and species (e.g., Silverman et al. 1997, H. S. Galbraith, S. Smith, CCV, University of Oklahoma, unpublished data). The synchronous movement of the cilia generates water currents inside and outside the shell. The currents bring a continuous supply of fresh water with O_2 and food inside the shell and remove waste products as water exits the shell. Cirri (fused cilia) sweep potential food items from the water toward the mouth.

An individual mussel can pump a substantial amount of water through its shell in a 24-h period. The amount of water an individual can filter varies according to many abiotic and biotic factors, including water temperature, species, animal size, and population density. Estimates of volume filtered also differ among testing procedures. In spite of the potential variability, several studies have produced similar volume estimates. Maximum filtration has been estimated at ~0.5 to 1 L/h for a 61-mm-long mussel (Alimov 1969, Kryger and Riisgard 1988, Pusch et al. 2001, McIvor 2004). Water entry and exit from the shell were thought to occur only through the inhalant and exhalant siphons, which can be expanded or contracted in size and shape to alter hydrodynamic flow patterns. However, recent research indicates that water also can enter the shell anteriorly whenever the shell is open (Nichols et al. 2005).

Mussels can feed on a variety of food particles and are not exclusively phytoplankton suspension feeders. Mussel guts contain a mixture of phytoplankton, zooplankton, rotifers, and detritus, and much of this material survives gut passage alive and undamaged. Furthermore, diet studies based solely on gut-content analyses cannot differentiate between accidental by-catch and material intentionally captured, digested, and assimilated. Studies based on recent improvements in methods for tracking nutrient assimilation, such as stable-isotope analyses and fatty-acid profiles, show that mussels certainly eat and assimilate phytoplankton, but they also rely on other types of food material to meet their nutritional needs. N stable-isotope ratios are used to track trophic position and to determine whether an animal feeds solely as a primary consumer or selects material from multiple trophic levels. N stable-isotope ratios indicate that mussels in some oligotrophic habitats, such as subalpine lakes, are strictly primary consumers (e.g., Vander Zanden and Rasmussen 1999). However, mussels in more enriched habitats feed across multiple trophic levels and eat primary producers and various consumer groups (Nichols and Garling 2000). C stable-isotope ratios can be used to identify individual food resources. C stable-isotope ratios show that mussels feed heavily on bacteria and phytoplankton in small temperate streams (Nichols and Garling 2000, Raikow and Hamilton 2001, Christian et al. 2004), whereas they feed almost exclusively on phytoplankton in large productive rivers such as the Mississippi (Thorp et al. 1998).

Most of the particles identified as potential food items are <20 μm in size for all species tested. Examination of digestive enzymes confirms the ability of mussels to feed on nutrient-poor detrital food resources because they produce appropriate enzymes for digesting this type of material (Christian et al. 2004). Fatty-acid profiles have been examined in a few localities and support the picture of mussels as

omnivores feeding on particles <20 μm in size. In Lake St Clair, mussels of several species contained up to 15% fatty acids that could have been obtained only from bacteria, but mussels also contained fatty acids derived from algae (Metcalfe-Smith et al. 2007).

Field studies have not addressed dissolved organic matter as another potential food source, but molecules such as glucose or NH_3 can be directly absorbed through the gills of all species tested in laboratory studies (Silverman et al. 1997). Such labile compounds are rarely abundant in nature, but research on other bivalves (e.g., Roditi et al. 2000) shows that dissolved organic matter can be a significant source of nutrition for some populations, so its role in mussel nutrition cannot be ignored.

Unionoid mussels tend to be epibenthic, i.e., half-buried in the sediments with their extended foot anchoring them in the sediments and their siphons extended up into the water column. Mussels can access food items in sediments. Marine bivalves capture nonsuspended food items (Dame 1996). Many marine bivalves use their foot to sweep food from the sediments into their shells (pedal feeding), whereas others bend their inhalant siphons down to the sediments and vacuum materials from the sediment surface (deposit feeding). Yeager et al. (1994) demonstrated that juvenile mussels actively pedal feed. In a laboratory study, Nichols et al. (2005) found that adult mussels do not actively pedal feed but are capable of accessing benthic food items through cilia-generated water currents that pull material in through the anterior portion of the shell while the foot is extended. While studying a stream labeled with ^{15}N, Raikow and Hamilton (2001) showed that some benthic feeding by adult mussels might occur under natural conditions because benthic organic material was assimilated by adult mussels. More field research addressing suspension feeding vs deposit feeding is needed because this topic is directly related to understanding benthic and water-column linkages and the role of mussels in food webs.

Effects of Mussel Communities on Ecosystem Services and Food Webs

The feeding activities of mussels link the water-column and benthic compartments in freshwater habitats. These activities provide ecosystem services that influence the rest of the food web (Table 1). Effects of mussel communities vary with mussel abundance, community composition, environmental factors, such as hydrologic residence time and temperature, and spatial and temporal scales.

Mussels as habitat: shells and sediment processes

Mussels as habitat generators.—Living mussels and their spent shells provide or improve habitat for other organisms through: 1) the physical structure of the shells, 2) sediment stabilization and bioturbation, and 3) biodeposition of organic matter and nutrient excretion, which directly and indirectly influence food availability (Vaughn and Hakenkamp 2001, Gutierrez et al. 2003) (Table 1). Spent shells are important as habitat in areas where other hard substrata are unavailable (Gutierrez et al. 2003). However, the importance of mussels as habitat generators extends beyond provision of physical structure and often is consequent to the activities of living mussels. For example, macroinvertebrate densities are higher in mussel beds (aggregations of mussels) than outside beds (Vaughn and Spooner 2006b), and macroinvertebrates aggregate on sediments with mussel biodeposits (Howard and Cuffey 2006, Spooner and Vaughn 2006).

Mesocosm experiment.—Spooner and Vaughn (2006) conducted a 1-y experiment in the Kiamichi River in the south-central USA to test whether mussels influence the distribution and abundance of co-occurring benthic algae and invertebrates on mussel shells and on the sediment. This experiment is described in detail elsewhere (Spooner and Vaughn 2006); here, we report previously unpublished data related to periphyton and invertebrate colonization of shells during the summer portion of the experiment. We buried enclosures (50 cm × 50 cm × 30 cm) constructed of a polyvinyl chloride frame and poultry netting 15 cm deep in the streambed and stocked them with 10 individuals of *Actinonaias ligamentina*, *Amblema plicata*, or sham mussels (empty shells filled sand). After 1 mo (August to September 2000), we randomly selected 5 mussels from each enclosure, placed them in a plastic bag with distilled water, and scrubbed them with a brush to create a water–biofilm slurry. We used the slurry to estimate the abundance of periphyton (measured as chlorophyll *a* concentration) and invertebrates on the shells. We extracted chlorophyll *a* with acetone and measured it spectrophotometrically with a correction for pheophytin (APHA 1995).

We examined the relationships among invertebrate communities, mussel treatments, and periphyton biomass (as chlorophyll *a* concentration) on shells. We did $log_{10}(x)$ transformation of the abundances of invertebrate taxa and periphyton. We analyzed invertebrate abundances with Principal Components Analysis (PCA) and regressed invertebrate PCA axis 1 scores against periphyton biomass. PCA axis 1 explained 39.1% of the variation among invertebrate

TABLE 1. Summary of ecosystem services provided by freshwater mussel (Unionoidea) communities.

Ecosystem service	References
Energy transfer	
Mussels remove algae and other seston from the water column or sediment; filtering rates vary with size, particle concentration, and environmental conditions	Pusch et al. 2001, Raikow and Hamilton 2001, Thorp and Casper 2002, Beck and Neves 2003, Christian et al. 2004, Vaughn et al. 2004, Nichols et al. 2005, Ostroumov 2005, Howard and Cuffey 2006; pre-2000 literature summarized in Vaughn and Hakencamp 2001
Mussels compete for limited food resources	Brönmark and Malmqvist 1982, Kat 1982, Jokela and Mutikainen 1995, Jokela 1996, Strayer 1999a, DiDonato and Stiven 2001, Kesler et al. 2007, Vaughn et al. 2007
Mussels enhance resource acquisition by other mussels	DiDonato and Stiven 2001
Mussels convert food into fine particulate organic matter used by other organisms	Nichols and Garling 2000, Raikow and Hamilton 2001, Howard and Cuffey 2006
Nutrient cycling	
Excretion rates of mussels vary with species, size, stage in reproductive cycle, food availability, or other environmental conditions	Potts 1954, Dietz 1985, James 1985, Davis et al. 2000, Baker and Hornbach 2001, Spooner 2007
Nutrient quality (i.e., N:P) of mussel excretions varies with species or environmental conditions	Vaughn et al. 2004, Spooner 2007
Mussels control nutrient concentrations in the water column	Nalepa et al. 1991, Welker and Walz 1998, Soto and Mena 1999, Vaughn et al. 2004
Mussels transfer nutrients from the water column to the riverbed	Lewandowski and Stanczykowska 1975, Stanczykowska et al. 1976, Sephton et al. 1980, Matisoff et al. 1985, Nalepa et al. 1991, Vaughn et al. 2004, Howard and Cuffey 2006, Spooner and Vaughn 2006, Spooner 2007
Mussels act as capacitors, storing nutrients in body tissue for long time periods; nutrients are released and made available to other organisms when mussels die	Raikow and Hamilton 2001, Spooner 2007
Nutrients excreted by mussels stimulate primary production	Spooner and Vaughn 2006, Spooner 2007, Vaughn et al. 2007, CCV, DES, and H. S. Galbraith, University of Oklahoma, unpublished data
Nutrients excreted by mussels stimulate secondary production	Howard and Cuffey 2006, Spooner and Vaughn 2006, CCV, DES, and H. S. Galbraith, unpublished data
Habitat availability and quality	
Shells of living mussels provide habitat for other benthic organisms	Beckett et al. 1996, Francoeur et al. 2002, Spooner and Vaughn 2006, Vaughn and Spooner 2006b, CCV, DES, and H. S. Galbraith, unpublished data
Mussels provide habitat for other benthic organisms indirectly through biodeposition, bioturbation, or sediment stabilization	McCall et al. 1979, 1995, Sephton et al. 1980, Howard and Cuffey 2006, Spooner and Vaughn 2006

taxa on mussel shells and was significantly and positively related to periphyton biomass on mussel shells (standardized by mussel wet mass) ($R^2 = 0.678$, $F_{1,14} = 27.393$, $p < 0.0001$; Fig. 1). The abundance of both periphyton and invertebrates was much higher on shells of living mussels than on sham shells (Fig. 1). Taxa that increased with increasing periphyton biomass included larval caddisflies, mayflies, and chironomids, and mites and tardigrades.

Mussel shells are readily colonized by periphyton (Table 1) and, sometimes, by vascular plants (Vaughn et al. 2002). However, our study was the first to demonstrate that periphyton biomass is higher on the shells of living mussels than on empty shells and that taxa of grazing invertebrates appear to respond to the higher periphyton biomass on shells of living mussels (Fig. 1; Spooner and Vaughn 2006). In a separate experiment examining mixed assemblages of 8 mussel species (described in *Mixed-assemblage experiment* below), Vaughn et al. (2007) demonstrated that chironomid grazers tracked periphyton biomass on mussel shells.

Substrate stabilization and bioturbation.—Several recent studies indicate that dense mussel beds occur in stream areas that remain stable during peak flood events (Strayer 1999b, Hardison and Layzer 2001, Morales et al. 2006, Gangloff and Feminella 2007). Strayer et al. (2004) hypothesized that this distribution is not coincidence but that the presence of buried mussels might stabilize streambed sediments. If mussels stabilize sediments, they might provide refugia for macroinvertebrates and their food resources during floods. However, mussels do not always remain stationary and buried. Bioturbation of sediments during mussel burrowing activities increases sediment water, nutrient, and O_2 content, thereby improving invertebrate habitat (Table 1). Bioturbation in marine systems stimulates microbial metabolism (Dame 1996). If bioturbation also stimulates microbial metabolism in freshwater sediments, then it might increase bacterial food resources for mussels and co-occurring invertebrates.

Differences in shell morphology, rates of biodeposition, and behavior among mussel species lead to different influences on biogenic structure and sediment processes. For example, colonization of periphyton and invertebrates on the shells of 2 species, *A. ligamentina* and *A. plicata*, differed and reflected differences in shell morphology, biodeposition, and behavior between these species (Spooner and Vaughn 2006). Mussel species vary enormously in size and shell sculpture, which could, in turn, influence their abilities to stabilize sediments. Species also vary in how much they typically move (some species are quite
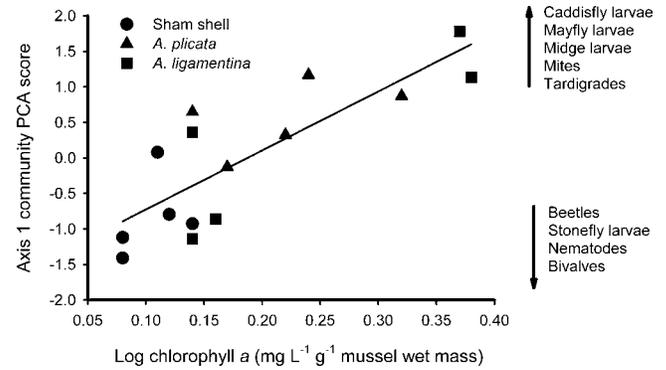

FIG. 1. Relationship between chlorophyll *a* and the invertebrate community on mussel shells, represented as Principal Components Analysis (PCA) axis 1 scores.

active and others are more sedentary; Saarinen and Taskinen 2003), and movements should influence bioturbation. Thus, distinctive morphologies and behavior patterns of different mussel species probably structure the subsurface ecosystem and create a biogenic habitat matrix (Meysman et al. 2006). These issues have not been addressed in freshwater mussel communities, but they might be factors that lead to the development and survival of mussel beds.

Effects of mussels on nutrient storage, translocation, and cycling

Mussels provide nutrients to other organisms and to the mussel community through excretion of NH_3 and P, through biodeposition of feces and pseudofeces, and by release of stored nutrients as dead mussels decay (Vaughn and Hakenkamp 2001). Mussels are particularly important in transferring nutrients from the water column to the sediment (Lewandowski and Stanczykowska 1975, Stanczykowska et al. 1976, Welker and Walz 1998). Excretion rates vary with species, size, reproductive stage, food availability, and environmental conditions (Table 1).

Mixed-assemblage experiment.—Effects of mussels on nutrient cycling and translocation vary with hydrologic and trophic conditions, but conversion of suspended material to dissolved nutrients by mussels stimulates primary production where nutrients are limiting (Vaughn et al. 2007). We manipulated mussel species abundance and composition in replicated recirculating laboratory mesocosms to examine the relationships among mussel feeding behavior (measured as clearance rates), the significance of nutrient recycling by mussel excretion, and primary production (Vaughn et al. 2004). Species treatments ($n = 34$) included a no-mussel control, and *A. ligamentina, A. plicata, Fusconaia flava,* and *Obliquaria reflexa* in mono-
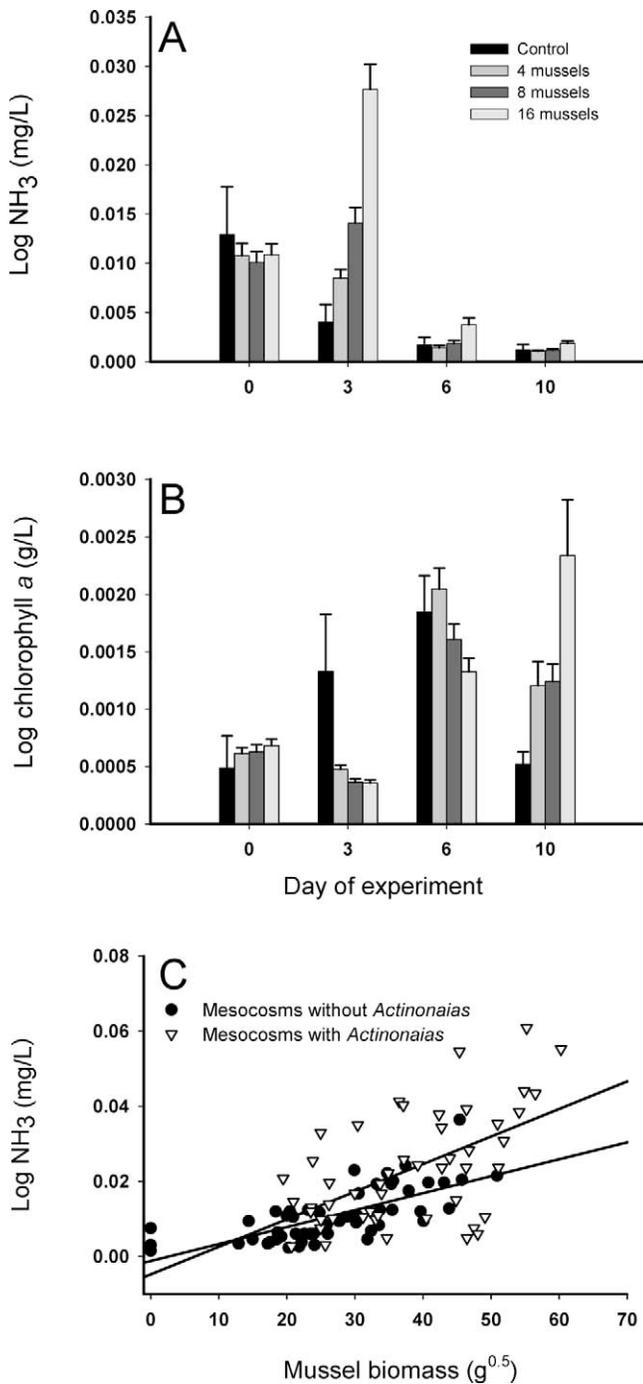
FIG. 2. Excretion and clearance rates of mussels in the mesocosm experiment. A.—Mean (+1 SE) water-column NH_3 concentration (representing excretion rate) at different mussel densities over days of the experiment. B.—Mean (+1 SE) water-column chlorophyll a concentration (representing clearance of algae from the water column) at different mussel densities over days of the experiment. C.—Regression of water-column NH_3 concentration on mussel biomass (tissue dry mass) on day 3 of the mesocosm experiment. Regressions were done for mesocosms with and without *Actinonaias*.

culture, all possible species pairs, and all 4 species, at densities of 4, 8, and 16 mussels per mesocosm. We collected mussels from the Kiamichi River, cleaned the shells of all biofilm, and held them in living streams at 10°C without food for 2 wk prior to beginning the experiment. Each experimental run lasted 10 d, and we replicated the experiment over time for a total of 5 runs from July to September 2005.

We collected initial NH_3 and chlorophyll a samples from each mesocosm before adding mussels on day 0. We added 500 mL of a multispecies algal slurry (Vaughn et al. 2004) to each mesocosm every evening for 10 d. We collected water samples for NH_3 (20 mL) and chlorophyll a (250 mL) analysis from all 34 mesocosms on days 3, 6, and 10. We quantified chlorophyll a and NH_3 concentrations as described already. We used water-column chlorophyll a concentration to estimate the amount of algae mussels had filtered from the water column. We compared chlorophyll a and NH_3 concentrations across mussel-density treatments using a repeated measures analysis of variance. We used linear regression to examine the relationship between the biomass of mussels in a mesocosm and water-column NH_3 concentration.

NH_3 contributed to the water column by mussels was greatest on day 3 and was highest in treatments with the greatest mussel densities (density: $F_{3,95} = 17.86$, $p < 0.001$; day: $F_{3,285} = 38.16$, $p < 0.001$; day × density: $F_{9,285} = 12.826$, $p < 0.001$; Fig. 2A). Chlorophyll a in the water column was higher in higher-density treatments and increased over time (density: $F_{3,126} = 3.3$, $p < 0.022$; day: $F_{3,384} = 10.79$, $p < 0.001$; day × density: $F_{9,384} = 5.025$, $p < 0.001$; Fig. 2B) because of an NH_3 fertilization effect. Higher NH_3 and chlorophyll a levels were caused primarily by the presence of 1 species, *A. ligamentina*, which is larger and has a higher NH_3 excretion rate under summer conditions than the other species (Fig. 2C; Spooner 2007, Vaughn et al. 2007).

Excretion rates of mussels vary with temperature and species (Spooner 2007). Mussels coexist in multispecies aggregations, but different species can have differing thermal performances, and these differences might lead to novel species-dependent effects. For example, at extreme temperatures (~34–40°C), oxidative stress associated with high temperatures differentially influences the activity level of mussel species within a bed, and some species use anaerobic strategies (Spooner 2007). Catabolism of energy reserves through protein or other biomolecular breakdown processes changes the relative amount of N excreted and, ultimately, the N:P ratio excreted to the environment (Spooner 2007).

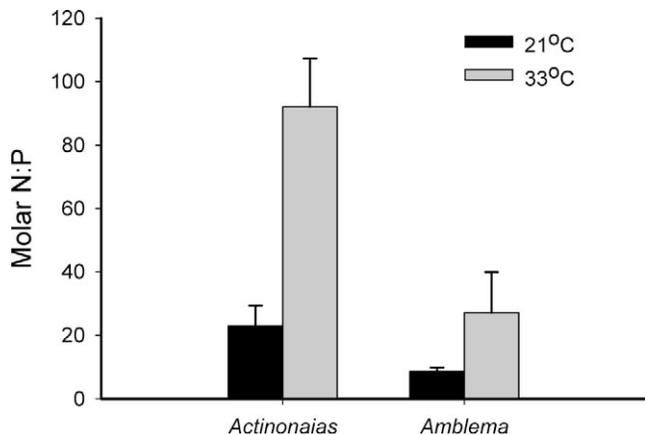*Two-species excretion experiment.*—We measured ex-

FIG. 3. Mean (+1 SE) water-column molar N:P in mesocosms with *Actinonaias ligamentina* or *Amblema plicata* at 21 and 33°C.

FIG. 4. NH$_3$ contributed to the water column under summer low-flow conditions by 4 species in 8 river mussel beds of different areas. NH$_3$ excretion rates were estimated from the mesocosm experiment. Species composition and biomass data are from 8 mussel beds in the Ouachita Highlands described by Vaughn and Spooner (2006a, b).

cretion rates of 2 species (*A. ligamentina* and *A. plicata*) for 2 thermal regimes (21°C [April], 33°C [July]) in the Kiamichi River. For each regime, we collected 10 individuals of each species and gently scrubbed them clean of all biofilm. We placed mussels individually in small plastic containers containing 1 L of filtered river water. We used 5 containers containing only filtered water as controls for residual algal and microbial activity in the water. We collected two 10-mL initial water samples (1 NH$_3$ and 1 P) from the containers and placed them back in the river. After 90 min, we removed the containers from the river and collected final water samples. We measured mussel wet mass and length and returned them to the bed. We froze the water samples and took them to the laboratory for analysis. We converted the P in samples to total reactive P (orthophosphate) by acid persulfate digestion, and quantified total reactive P on a spectrophotometer using the ascorbic acid method (APHA 1995). We quantified NH$_3$ on a spectrophotometer using the phenate method.

Temperature significantly influenced the excretion rates of both species of mussels, and the highest molar N:P ratios were associated with the 33°C thermal regime. However, the difference in N:P ratios between *A. ligamentina* and *A. plicata* was much greater at 33°C than at 21°C (Fig. 3). This result has potential consequences for algal community structure—and subsequently the rest of the food web—depending on which nutrients are limiting the algal community.

Species effects on nutrient cycling.—Effects of mussels on nutrient processing are stronger where mussels are more abundant, but effects also should vary with species composition because of the differences in species traits. We combined NH$_3$ excretion rates from the mesocosm experiment with information on the
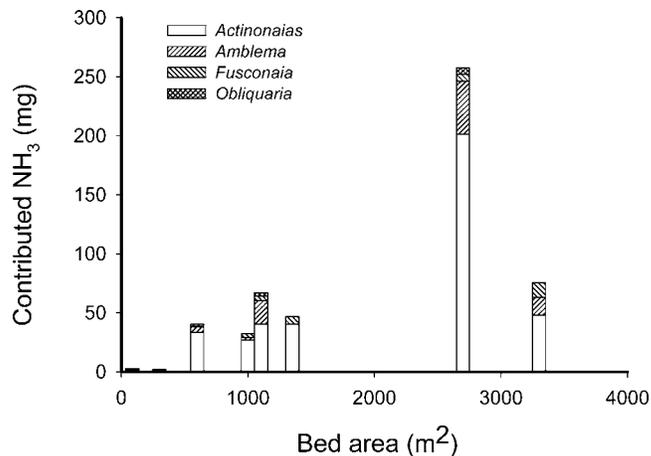
species composition and biomass in actual mussel beds to estimate the amount of NH$_3$ contributed to the water column by *A. ligamentina*, *A. plicata*, *F. flava*, and *O. reflexa* in different mussel beds under summer low-flow conditions. We used data from 8 mussel beds in 5 rivers (Saline, Ouachita, Little, Kiamichi, and Glover) in the Ouachita Uplands of Oklahoma and Arkansas. Beds varied in size, mussel density, and species composition. Sampling methods and mussel communities in these rivers are described elsewhere (Vaughn and Spooner 2006a, b). We determined the NH$_3$ excretion rate in mg L^{-1} g^{-1} mussel dry mass from the mesocosm experiment (described above) on day 3. We used density estimates and length–dry mass regressions (Vaughn and Spooner 2006a, b) to estimate mean biomass/m^2 of each species in the mussel beds.

Mussel biomass tended to be dominated by *A. ligamentina* in these beds, and this species also had a higher NH$_3$ excretion rate than other species in the summer. Therefore, in this example, most of the NH$_3$ was contributed by *A. ligamentina* (Fig. 4) at a high N:P ratio (Fig. 3). Other work has shown that N tends to be limiting during summer conditions in these rivers (Vaughn et al. 2007). Therefore, under these conditions, *A. ligamentina* should have a large effect on primary production and algal community structure. Under a different temperature regime, in which N is not limiting or *A. ligamentina* is not a dominant species, potential effects would be different.

Effects of mussels on primary production can cascade across trophic levels. For example, N is limiting in the summer in the Kiamichi River. The

densities of 8 species were manipulated in a field experiment in this river, and accrual of periphyton biomass on the sediment was higher in enclosures with species known to excrete more NH_3 (Vaughn et al. 2007). In this same experiment, higher periphyton densities resulted in higher densities of grazing chironomid larvae on mussel shells (Vaughn et al. 2007).

The potential importance of species interactions

The potential for species interactions in mussel beds should be high because mussels typically occur as aggregated, multispecies, and multi-age assemblages. Interactions might include competition for space, food, fish hosts, and other resources, as well as positive interactions, such as facilitation. There is little evidence of spatial competition between adult mussel species within stream reaches, mussel beds, or patches (Strayer 1981, Holland-Bartels 1990, Strayer and Ralley 1993, Vaughn and Pyron 1995). However, mussel distributions are dependent on the distribution and abundance of their fish hosts (Watters 1992, Haag and Warren 1998, Vaughn and Taylor 2000), and the evolution of diverse and sophisticated fish-host attraction strategies among mussels species is probably the result of competition for fish hosts (Watters 2001, Zanatta and Murphy 2006).

Competition for algae and bacteria from the water column and benthic sediments has been the subject of much debate (Strayer 1999a, Vaughn and Hakenkamp 2001) (Table 1). Studies to date have not shown substantial interspecific or intergenerational differences in diet. Stable-isotope ratios or fatty-acid profiles can differ slightly among locations, but essentially, all mussels tested, regardless of age, size, or species, tend to feed on the same types of food items. Howard et al. (2005) found that the N stable-isotope ratio changed between young and old *Margeritifera*, but they were unable to determine whether this change was the result of a dietary shift or of different fractionation patterns as the animal aged. Metcalfe-Smith et al. (2007) found differences in fatty-acid profiles based on location within Lake St Clair, but these differences were caused more by differences in location rather than differences among species. Silverman et al. (1997) found differences among species in the number and type of gill cilia used to remove food particles from the water column. Species from streams had thicker and denser cirri (per cm^2 of gill surface) than did lake species. Species from streams were ~10× more efficient than species from ponds and lakes at capturing bacteria under laboratory conditions. However, field studies using the same species were unable to show differences in bacterial nutrient concentrations in the tissues of each species (Nichols and Garling 2000).

Competition for food resources should occur where food is limiting. The winner in a competitive interaction is the species that can survive and reproduce at the lowest food concentration and is not necessarily the species feeding the most or fastest (Strayer 1999a). Food limitation is difficult to measure using traditional methods because of the slow growth and reproductive rates of mussels and the long timescales required for experiments and comparative studies. New techniques for determining nutritional status and body condition, such as glycogen and lipid content and RNA/DNA ratios, will help to resolve this issue (Naimo et al. 1998, Nichols and Garling 2000, Baker and Hornbach 2001, Gao et al. 2006, Norkko et al. 2006).

Food limitation has been documented within and among mussel species. At high population densities, mussel growth declined and migration behavior increased with young animals leaving the area (Kat 1982). *Elliptio complanata* growth rates were directly related to lake food levels in a long-term (1991–2005) reciprocal transplant experiment in 3 Rhode Island lakes (Kesler et al. 2007). In a similar transplant study, food became limiting to *Anodonta piscinalis* as densities increased, and this limitation caused individuals to adjust their energy allocation to reproduction over somatic growth (Jokela and Mutikainen 1995, Jokela 1996). In a study of Bavarian trout streams, *Margaritifera margaritifera* was able to grow in rivers with low food availability, whereas 2 mussels, *Unio crassus* and *Anodonta piscinalis,* were unable to grow because their higher metabolic rates required higher food levels (Bauer et al. 1991). DiDonato and Stiven (2001) used growth measurements to demonstrate competition between 2 mussels in a food-limited lake and linked differences in growth to differences in filtering abilities. *Actinonaias ligamentina* caused decreases in body condition of several other species in our mixed-assemblage experiment (Vaughn et al. 2007). Vaughn et al. (2007) attributed this result to exploitative and interference competition. Competition among mussel species for food resources should, in turn, influence the rest of the food web. For example, mass-specific biodeposition rates were higher when conditions favored higher productivity, which would, in turn, lead to production of more aggregates of organic material for invertebrates to consume or colonize.

Most studies of species interactions in mussels have focused on competition, but positive species interactions should be both common and important. Recent studies with sedentary, aggregated assemblages in marine systems indicate that positive species interac-

tions are widespread (Bertness and Callaway 1994, Bruno et al. 2003, Altieri et al. 2007), and positive interactions have been documented frequently in freshwater systems (Jonsson and Malmqvist 2000, Crowl et al. 2001, Jonsson and Malmqvist 2003, McCabe and Gotelli 2003, Hooper et al. 2005).

Mussels living in multispecies assemblages might benefit from enhanced resource acquisition, resource quality, habitat stability, juvenile survival, and host-fish attraction, among other possibilities. For example, increasing species richness and evenness in assemblages of suspension-feeding caddisflies increased the topographical complexity of the streambed, which altered near-bed flow and increased feeding success of individuals (Cardinale et al. 2002). This type of scenario might be common in mussel beds. Different sizes, shell morphologies, and behaviors of mussel species often cause species to reside at different depths and angles above or below the sediment–water interface. Such diversity might decrease current shading (deceleration of flow from upstream to downstream neighbors; Cardinale et al. 2002) and increase delivery of suspended particles to mussel siphons. In addition, burrowing activities of different mussel species might resuspend deposited material, making it available to other mussels.

Competition and facilitation can occur concurrently (Bertness 1989), but these 2 processes often have opposite outcomes that lead to null or weak net effects. Thus, species interactions among mussels might be difficult to detect if both processes are operating. Concurrence of competition and facilitation (positive density dependence) was observed in a community of mussels in a pond (DiDonato and Stiven 2001). In their mixed-assemblage experiment, Vaughn et al. (2007) found a strong species-identity effect—*A. ligamentina* decreased the condition of co-occurring mussel species. However, facilitation also occurred in that experiment because algal growth and invertebrate abundance on shells were greater in mixed-species treatments than in single-species treatments (CCV, DES, and H. S. Galbraith, University of Oklahoma, unpublished data).

Spooner (2007) used an approach that compared the regional biomass of species to local community biomass across 21 mussel beds and demonstrated that individuals living in speciose communities had proportionally higher biomass than did individuals living in species-poor communities. In addition, rarer mussels had higher body condition and lower mass-specific metabolic rates in speciose than in species-poor communities, a result that suggests an energetic and potential fitness benefit to living within speciose aggregations (Spooner 2007). Paterson (1983) hypoth-

esized an energetic benefit associated with living in aggregations after finding that respiration rates of individual mussels were higher than rates of mussels in monoculture populations of northern *Elliptio complanata*. Energetic benefits might occur if aggregations provide nutritive or other energy subsidies to other mussels within the community by recycling deposited fecal material, increasing access to food by altering boundary-layer flow, or increasing local food quality/quantity in the surrounding mussel bed.

Effects of mussel communities are context-dependent

Effects of mussel species on ecosystem services and food webs vary with spatial and temporal scales, and the relative importance of different types of species interactions might change at different scales. For example, if competition and facilitation are important influences on resource use, patterns should be apparent first and strongest at the small spatial scales at which mussels actually interact (Cornell and Lawton 1992). Studies might have failed to document competition and other species interactions simply because they were done at inappropriate scales (Vaughn and Spooner 2006a). In contrast, if complementarity in resource use occurs because different species traits are favored in different environmental conditions, patterns should be most apparent along environmental gradients at large spatial scales (Zedler et al. 2001, Rosenfeld 2002).

Thermal regime.—The differences among mussel species in their responses to temperature should cause species effects on the ecosystem to change depending on thermal regime. For example, species that close their valves and undergo anaerobic metabolism might excrete at high N:P ratios and contribute a large mass of nutrients that benefit surrounding periphyton. However, this response also would decrease filtering activity, which would reduce benthic–pelagic coupling, water-column clearance, and biodeposition of organic material to the sediment. Under the same conditions, species on the cusp of thermal stress might have extremely high filtration rates with low assimilation efficiencies, and this response would increase benthic–pelagic coupling and quantities of organic material distributed to the sediment. Thus, mussel beds that include species with different thermal traits might strongly influence the surrounding ecosystem. Spooner (2007) found that mussel beds with the highest coefficients of spatial thermal variation had proportionally more species-specific biomass. These results might be explained by thermal-niche partitioning (species with different thermal optima avoid competition through specialization) or by enhanced community productivity associated with positive
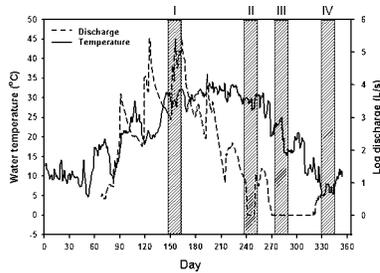
FIG. 5. Water temperature and discharge in the Kiamichi River during 2003.

effects of material cycling associated with a speciose assemblage (Spooner 2007).

Thus, we expect the effects of mussel assemblages on stream ecosystems to change along seasonal environmental gradients, particularly temperature and discharge. In a 1-y mesocosm experiment, Spooner and Vaughn (2006) found strong effects of living mussels on periphyton and invertebrate abundance during summer months with low flow and warm temperatures but no effects during winter months with higher flow and cooler temperatures. Biodeposition by *Margaritifera falcata* increased organic and inorganic fine benthic matter in a California stream, but only during late summer and early autumn (Howard and Cuffey 2006). At other times of the year, passive deposits were greater than deposits provided by mussels because of the seasonal hydrologic regime in the stream (Howard and Cuffey 2006). In the Kiamichi River, the strong effects of a driver species, *A. ligamentina*, were apparent only in summer. *Actinonaias ligamentina* had high filtration, metabolic, and excretion rates at warm summer temperatures and, therefore, was able to reduce food for other mussel species and increase N subsidies to benthic algae. At cooler autumn temperatures, *A. ligamentina* did not have these effects (Vaughn et al. 2007).

Effects of mussel communities on ecosystem services are dependent on mussel biomass and on species composition, but the strength of the effects varies with environmental conditions. The amount of material that mussels can remove from and contribute back to the water column and sediments depends on the abundance of feeding mussels and on the volume and residence time of the water overlying them (Strayer et al. 1999). For example, Vaughn et al. (2004) demonstrated that mussels in a dense, diverse mussel bed in the Kiamichi River could process the entire volume of water above them during August when flows were very low and hydrologic residence time was ~1 d. During spring and winter, water volume and flow were higher than in August, and mussels processed only a small percentage of the water column.

Modeling study.—We used laboratory-derived algal clearance and NH_3 excretion rates from the mixed-assemblage experiment and field-measured temperature and discharge over a 1-y period (Fig. 5A) to predict how ecosystem services provided by mussel communities might change with environmental context and species composition. We modeled communities composed of 2 common species, *A. ligamentina* and *A. plicata*, that vary in abundance across the region and in their physiological responses to environmental stressors, particularly temperature (Spooner 2007). We held biomass constant and modeled mussel beds with biomass composed of 75% *Actinonaias* and 25% *Amblema* (*Actinonaias*-dominated), 50% of each species, or 25% *Actinonaias* and 75% *Amblema* (*Amblema*-dominated). We assumed that the biomass (tissue dry mass) of a mussel bed was 5000 kg, which is typical for the region (Vaughn and Spooner 2006b). We used the laboratory-derived algal clearance and NH_3 excretion rates to predict the proportion of the water column that mussel beds could process in a 24-h period and the amount of NH_3 (in mg) that would be contributed to the water column in a 24-h period.

Species composition and environmental gradients interacted to determine the magnitude of ecosystem services provided by the mussel communities. Effects of mussels were strongest at high water temperatures and low discharge (Fig. 5 [II]). When water temperature was high, *Amblema* had the higher filtration rate, but *Actinonaias* had the higher NH_3 excretion rate (Fig. 6 [II]). Thus, *Actinonaias*-dominated communities contributed more NH_3 but turned the water column over slower than *Amblema*-dominated communities (Fig. 6 [II]). When water temperature was cooler (Fig. 5 [III]), *Actinonaias*-dominated communities turned the water column over faster but contributed less NH_3 than *Amblema*-dominated communities (Fig. 6 [III]). As flow increased (Fig. 5 [IV]), mussels were no longer able to process enough of the water column to influence nutrient levels significantly (Fig. 6 [IV]). At very high discharge (Fig. 5 [I]), the effects of mussels on nutrients were miniscule, even when temperature was high (Fig. 6 [I]).

Critical Research Directions and Lessons for Conservation and Restoration

We have learned a tremendous amount about mussel communities during the past 10 y (Vaughn and Hakenkamp 2001, Strayer et al. 2004), but we require a much better understanding of many aspects of their biology to make informed conservation and restoration decisions. Propagation efforts are proceeding for some species and have been largely successful.
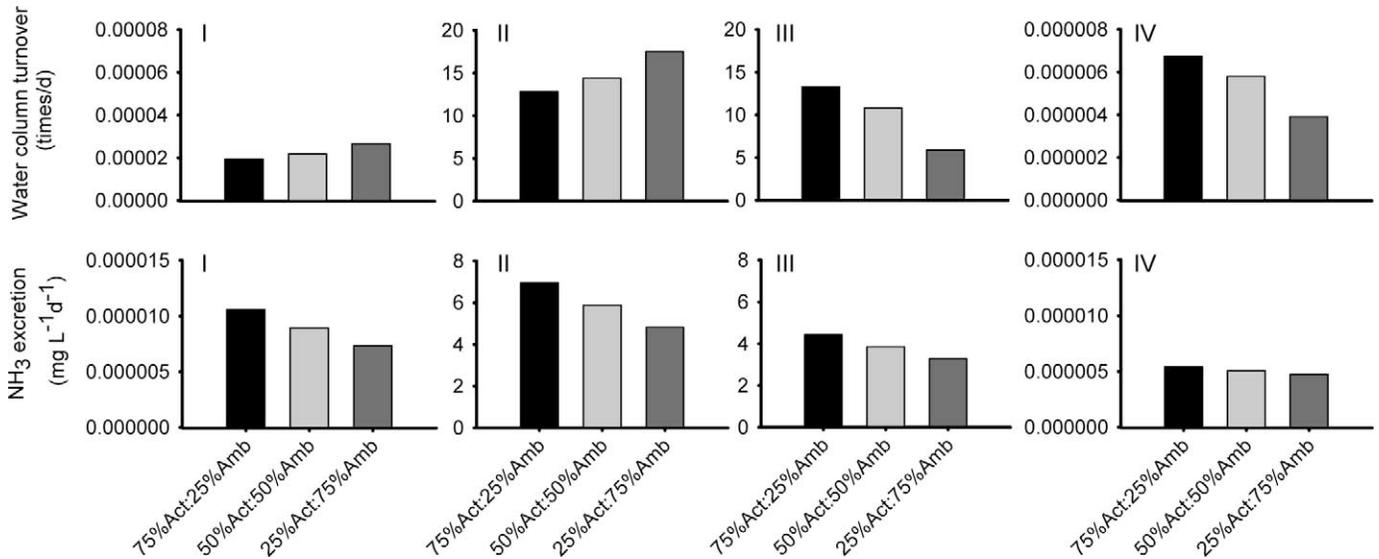
FIG. 6.   Predicted ecosystem services (water-column turnover and NH_3 excretion) provided by 3 simulated mussel communities consisting of different proportions of *Actinonaias* (Act) and *Amblema* (Amb) in 4 different environmental contexts. Environmental contexts correspond to the numbered shaded periods in Fig. 5: I = high discharge, high water temperature, II = low discharge, high water temperature, III = low discharge, intermediate water temperature, IV = intermediate discharge, cool water temperature. Note order-of-magnitude differences in the *y*-axis scales among panels.

Whether these planted juveniles can successfully establish reproducing populations will depend, in large part, on whether the long-term environmental conditions provided are appropriate. Our paper demonstrates that those appropriate environmental conditions begin with suitable food sources for mussels and extend to interactions between species that influence habitat and other resources for mussels and other organisms.

Our understanding of mussel dietary requirements and feeding behavior is improving rapidly because of new techniques. Of particular importance are the discoveries that unionids can suspension-feed within the sediment and that bacterial and detrital resources might be as, if not more, important than algae in many habitats. Alterations in the watershed, which might be caused by changes in land use, water quality, or climate, often cause radical changes in the availability of bacterial and detrital resources that support mussel populations or species. The presence of certain species encourages the development of mussel beds. Thus, restoration and conservation efforts might be more successful if undertaken at the community, rather than at the species, level. This approach will require more in-depth information on food-resource linkages among mussel species and between the mussel community and its surrounding ecosystem.

We will have to examine multiple resource axes and the interactions among these axes as we investigate the resource requirements of mussels and how mussel communities influence each other and the rest of the food web. Traditionally, mussel biologists have been concerned with physical habitat descriptors (especially sediment characteristics), dietary needs, and host-fish requirements, and we have tended to address these factors in isolation. However, mussels live in complex lacustrine and riverine habitats where these environmental variables interact across temporal and spatial scales. For example, the amount of N provided to the stream by mussel communities depends on: 1) the physiological traits of mussel individuals, 2) the species composition and biomass of the mussel community, and 3) the temperature and hydrological regimes of the stream. All of these factors interact to determine how much recycled N is provided by mussels, and this recycled N, in turn, influences the rest of the food web through periphyton, macroinvertebrate, and (probably) fish abundance.

Healthy mussel communities typically occur as multispecies assemblages composed of species that have different traits. Our paper has demonstrated that interactions among species in mussel communities can be quite important. Restoration of already-endangered species is good but probably will do little toward maintaining community and ecosystem function. Thus, when possible, restoration efforts should attempt to restore whole communities rather than individual species alone; this approach is the best way to ensure that species interactions and ecological function are restored—even if we are not completely

sure how these interactions and functions are defined. However, much more work is needed in this area. Few studies have examined species interactions in mussel communities. In particular, positive interactions, which are very important in other ecosystems, have been virtually ignored.

Overall mussel abundance is declining, species composition is changing, and the environment is changing. These alterations are occurring simultaneously. What do these changes this mean for mussel communities, the organisms with which they coexist, and the ecosystem services mussels provide to the rest of the food web? We need to approach restoration and conservation from a larger community scale, but we still are constrained by limitations in our knowledge of how mussel species interact with each other.

Acknowledgements

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