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AN INTEGRATIVE APPROACH TO UNDERSTANDING MUSSEL COMMUNITY STRUCTURE: LINKING BIODIVERSITY, ENVIRONMENTAL CONTEXT AND PHYSIOLOGY.

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Abstract

As ecosystems become increasingly imperiled due to species loss, habitat alteration, and climate change, understanding the functional significance of communities has become a critical research need. This field has expanded considerably over the past couple of decades, but has primarily been empirically addressed in short-lived terrestrial annual plant communities. These studies have manipulated species richness while keeping densities equal. While this approach has yielded many important insights, it is unrealistic because in nature species typically are log-normally distributed, often as a result of autecological adaptations to particular environmental conditions. This artifact of biodiversity methodology confounds the interpretation of experimental results making it difficult to distinguish whether the observed effects are due to true species interactions (facilitation/competition) or to a result of the expression of novel traits associated with species identity.

The research detailed in my dissertation broadens our understanding of the biodiversity-ecosystem function paradigm using long-lived invertebrates in a freshwater ecosystem. Freshwater mussels (Unionoidea) are a globally threatened fauna with 70% of taxa considered threatened, yet little is known concerning their functional role. In addition to species extinctions, the overall biomass of both abundant and rare unionid species is declining in most rivers, and this loss of filter-feeding biomass is predicted to impact river function.

My first chapter integrated biodiversity partitioning techniques with mussel community data across twenty one mussel beds to determine if mussel community biomass could be explained by patterns of species richness or species dominance. This

partitioning approach tested the null hypothesis that biomass accrual within mussel beds is equal at all sites. The results of this work demonstrated that mussel biomass is largely explained by complementarity, which indicates that either niche partitioning or facilitation between mussel species is occurring. This conclusion was further supported by the fact that complementarity was highest in species rich, thermally variable mussel beds. In addition, numerically rarer species were in better condition (reduced oxygen consumption rates and higher body condition indices) in species-rich, thermally variable mussel beds which suggests that there is an energetic benefit to living in species rich communities.

The research detailed in my second chapter built upon observed patterns of alternating species dominance by asking if different mussel species performed differently under a variety of thermal regimes. To address this question, I acclimated eight mussel species (Lampsilis cardium, Fusconaia flava, Actinonaias ligamentina, Megalonaias nervosa, Amblema plicata, Quadrula pustulosa, Obliquaria reflexa, and Truncilla truncata) to four temperatures (5, 15, 25, and 35^{o}C). I quantified resource acquisition (clearance rate and oxygen consumption), assimilation (glycogen, body condition index, and Q_{10} rates of anabolism and catabolism), and ecosystem services (ammonia and phosphorus excretion rates, and biodeposition rates) using temperature-controlled respirometers. The results of this experiment demonstrate that although mussels are generally categorized as "filter feeders", there are distinct guilds within this functional group associated with their response to temperature. Megalonaias nervosa, Amblema plicata, Obliquaria reflexa, and Fusconaia flava are thermally-tolerant species assimilating energy at 35^{o}C and increasing the magnitude of services (nutrient excretion,

clearance and biodeposition rates) they contribute to ecosystems. Alternatively, A. ligamentina, L. cardium, Q. pustulosa, and Truncilla truncata appear to be thermally-sensitive with increased rates of catabolism at 35°C. However, the functional responses of thermally-sensitive species appeared to differ with some species decreasing filtration activity and increasing rates of nutrient excretion and others increasing both filtration and nutrient excretion rates. Extrapolating these data to real mussel communities highlighted the importance of the relative dominance between thermally-sensitive and tolerant-species under differing environmental contexts. Furthermore, shifts in community structure would be predicted to influence the nature of filtration, biodeposition and nutrient dynamics under current models of climate change.

The focus of my third chapter is an integration of the physiology information collected in chapter two to address how species dominance of two distinct thermal guilds (thermally-tolerant and thermally-sensitive) influences gross primary production. I manipulated temperature (15, 25, and 35°C) and species dominance of five mussel species (A. ligamentina, A. plicata and Q. pustulosa, M. nervosa, and O. reflexa) using 110 l re-circulating stream mesocosms housed in an environmentally-controlled room. I quantified individual-based measures of resource acquisition (oxygen consumption, body condition index) and ecosystem services (ammonia and phosphorus excretion rates) for each species. In addition, I quantified gross primary production in the water column, benthos, and the entire stream mesocosm. Gross primary production was highest at 35°C and was positively related to both A. ligamentina and A. plicata dominance with communities. However, species dominance differentially influenced gross primary production of different compartments within the mesocosms with A. plicata (a thermally-

tolerant species) positively influencing benthic production, and A. ligamentina (a thermally-sensitive species) positively influencing water column production. Species interactions within treatments were context dependent with A. ligamentina positively influencing A. plicata, M. nervosa, and O. reflexa at 25^{o}C and negatively influencing M. nervosa and O. reflexa at 35^{o}C. In addition to influencing resource acquisition, species dominance also influenced species-specific nutrient excretion rates and subsequently water-column nutrient levels.

Species richness influences biomass of freshwater mussel beds via complementarity: A partitioning approach applied to natural communities.

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Abstract

To increase the generality of biodiversity-ecosystem function theory, studies must be expanded to include real communities in a variety of systems. We modified the partitioning approach outlined by Fox (2005) to partition the effect of species richness on standing crop biomass (net biodiversity effect) of 21 native freshwater mussel communities into the following components: Complementarity effect, dominance effect (species with particular traits dominate at the expense of others), and distinctive species effect (species with particular traits dominate without impacting other species). This approach deviates from historical experimental-plot partitioning techniques by comparing species biomass within a local community to the predicted average biomass of communities on a regional basis. Overall, species-rich mussel beds have greater biomass than predicted based on the average biomass of species across the region. This effect is due largely to complementarity with the condition of minor (numerically lower ranked) species living within a community associated with high body condition and reduced metabolic rates, indicating an energetic benefit to living in a speciose community. These measures also relate positively to spatial thermal variation, suggesting that thermal niche partitioning may be an important determinant of mussel species coexistence and ecological services provided to benthic ecosystems. This research emphasizes the importance of species interactions and environmental context in understanding the structure and functioning of ecosystems.

Introduction

Recent interest in the functional role of communities has resulted in numerous theoretical and empirical studies, most involving manipulation of species richness or functional groups in terrestrial plant assemblages followed by quantification of variables attributed to ecosystem function (e.g., productivity, stability and resistence to invasion) (Fridley 2001, Loreau et al. 2001, Naeem and Wright 2003, Hooper et al. 2005). Most patterns that have emerged demonstrate a positive relationship between biodiversity and ecosystem function (Naeem and Wright 2003, Hooper et al. 2005) and were established by comparing the additive contribution of monoculture yields to species mixtures (Loreau 1998, Cardinale et al. 2002, Hector et al. 2002). Overyielding occurs when the performance of species in polyculture is greater than their expected additive performance in monoculture and is considered to be the net result of interspecific interactions (Loreau 1998, Hector et al. 2002, Fox 2005). The underlying mechanisms that drive these patterns have been subject to debate because of the experimental constraints that are associated with building artificial communities from a variety of species pools (Huston 1997, Wardle 1999).

Species interactions that lead to biodiversity effects on ecosystem function can be due to the relative contribution of the whole community (complementarity among species) or the separate effects of dominant species (selection effect), or a combination of both factors. Complementarity can occur: (1) via facilitative interactions between organisms that enhance the efficiency of resource processing and assimilation, or (2) as the result of resource partitioning, where species use different niche components, and thus increase the overall use of resources (Hooper 1998, Loreau and Hector 2001,

Cardinale et al. 2002, Petchey 2003). The selection effect occurs when dominant species outperform others in polyculture and result in more diverse assemblages that exhibit greater ecosystem effects (Loreau 1998, Wardle 1999, Smith et al. 2004). Dominant species arise due to the expression of specific traits under environmental conditions that favor their growth and supremacy over other species (Loreau and Hector 2001, Fox 2005). Environmental conditions in plot-style experiments often tend to be constricted due to low spatial habitat heterogeneity favoring specific traits of dominant species. Conversely, fluctuating environmental conditions may offer sufficient heterogeneity for coexistence and enhanced ecological services of a broad assortment of species.

The black-box nature of most biodiversity experiments makes it difficult to distinguish complementarity from the selection effect. Loreau and Hector (2001) used a modification of Price's Selection equation (Price 1970) to demonstrate that the selection component (i.e. dominant species effect) of the net biodiversity effect was analogous to natural selection of ecological traits associated with high yield monoculture species, thus favoring their dominance over others in polyculture (Sala 2001). Fox (2005) expanded Loreau and Hector's (2001) approach by partitioning the effect of biodiversity into three distinct components: 1) Trait-independent complementarity, a process in which species in polyculture increase in yield independently of their traits, but without negatively impacting co-occurring species within the plots. This is quantitatively and theoretically equivalent to complementarity as defined by Loreau and Hector (2001); 2) the dominance effect, a true analogue of natural selection in which species with particular traits dominate at the expense of other species within a plot; and 3) trait-dependent complementarity, a process in which the yield of species increases in polyculture due to

the expression of particular traits, but not at the expense of other species in the plots. As defined by Fox (2005), trait-dependent complementarity is analogous to one-way complementarity where only species with particular traits benefit. Therefore, trait-dependent complementarity actually has components of both complementarity and the dominance effect. For the sake of clarity, in this paper we consider trait-independent complementarity as "complementarity," the dominance effect as the "dominance effect," and trait-dependent complementarity as the "distinctive species effect."

The additive partition technique has been applied primarily to experimental manipulations, where yields from monocultures and mixtures could be explicitly compared (Petchey 2003). However, communities that are artificially assembled within experimental plots may not represent species that naturally co-occur. Natural communities are the end result of multiple processes (intra and interspecific interactions, biogeographical constraints, recruitment limitations), each of which are relevant to understanding species occurrences, dominance, and subsequent contributions to ecosystem function (Brown 1984, Wilson and Keddy 1986, Grime 1987, Palmer et al. 1996, Stachowicz 2001). To increase our understanding of services provided by communities to ecosystem function, studies must expand beyond experimental plots to real communities (Hector et al. 2001, Srivasta and Vellend 2005).

Freshwater mussel (Bivalvia: Unionidae) communities represent an excellent system to examine questions of biodiversity and ecosystem function because they encompass very different life-history and habitat characteristics from most organisms studied to date, and therefore can potentially expand the generality of existing theories. They also possess characteristics that make them amenable to partitioning approaches.

Freshwater mussels are long-lived, sessile, filter feeders that occur as aggregated, multi-species assemblages in lakes and streams (Vaughn 1997, McMahon and Bogan 2001). Mussels provide important ecological services, coupling energy from the water column to the benthos through filtration, biodeposition of feces and pseudofeces, and mineralization of nutrients (Vaughn and Hakenkamp 2001, Strayer et al. 2004, Spooner and Vaughn 2006). The magnitude of these services increases with overall mussel biomass (Vaughn *et al*. 2004), which can be substantial. For example, biomass of mussel beds in Oklahoma can reach as high as 19 000 kg (wet weight) encompassing up to 30 different species (Vaughn and Taylor 2000). Ecological services provided by mussels contribute to higher biomass and diversity of co-occurring macroinvertebrates and periphyton (Spooner and Vaughn 2006, Vaughn and Spooner 2006). The magnitude of their influence is context dependent with highest impacts associated with low flow (high hydraulic residence time) and warmer temperatures (increased metabolic activities) (Vaughn et al. 2004, Spooner and Vaughn 2006).

Despite being a highly speciose, aggregated fauna, few differences in habitat or dietary preferences among species have been documented. Thus, aquatic ecologicts generally believe that mussel species have high niche overlap, and therefore, high functionally redundancy (Strayer and Ralley 1993, Nichols and Garling 2000, Christian et al. 2004). Most mussel larvae (glochidia) require an obligate ectoparasitic phase on fish hosts (McMahon and Bogan 2001); some mussels are host-fish specialists and others are generalists (Haag and Warren 1998). Watters (1993) hypothesized that host-fish partitioning may be the sole mechanism that allows species coexistence in mussel beds (Watters 1993). However, comparative laboratory studies have shown that different

mussel species have suites of physiological traits and may optimally perform at different temperatures (Spooner unpublished, (Baker and Hornbach 2001)). In addition, we have observed differences in dominance patterns within mussel beds that may be linked to differences in species-specific thermal performance. Southern U.S. streams experience considerable thermal variability; we believe that this variability may act as an additional resource axis that allows mussel species to differentially acquire or assimilate resources and interact with each other. In addition to community assembly, thermal niche partitioning may also have relevant repercussions on the services provided by mussel communities to stream ecosystems.

We modified the tripartite partition technique to address the following questions in freshwater mussel communities: (1) is biomass of local, species-rich communities greater than that predicted based on the average biomass of species across the region? and (2) if speciose communities have higher biomass, what factors (complementarity, distinctive species effect, or dominance effect) may account for this phenomenon? Using the criteria outlined by Fox (2005), we tested the following predictions: (1) if complementarity leads to increased biomass in communities through niche differentiation or facilitation, then its magnitude should correlate positively with the number of thermal niches (coefficient of thermal variation) at a given site. However, if the distinctive species effect and the dominance effect are responsible for increased biomass due to preferential selection and expression of traits associated with dominant species within communities, then the magnitude of both factors should be highest at sites exhibiting temperatures close to the thermal optima of dominant species and, therefore, would be independent of the number of thermal niches; (2) If all species within a community

benefit via niche complementarity and/or facilitation, then the condition of both numerically dominant (major) and subordinate (minor) species within communities should correlate positively to the magnitude of complementarity. However, if the dominance effect is the result of selecting traits associated with major species at the expense of minor species within a community, we would expect the magnitude of the dominance effect to correlate positively with the condition of major species and negatively with the condition of minor species. Likewise, if the distinctive species effect is the result of selecting traits associated with major species without influencing minor species within a community, then we would expect a positive relationship between the magnitude of the dominance effect and major species body condition, and no relationship with minor species body condition.

Methods

Study area and sampling methods

Our study was conducted in the Ouachita Highlands of eastern Oklahoma and western Arkansas. This area of mid-sized streams with gravel-cobble substrates has been minimally disturbed (Mayden 1985) and contains a largely intact mussel fauna (i.e. most rivers have experienced no species extirpations). Most mussel species occur in all rivers across the region (Vaughn *et al.* 1996), indicating that all sites have similar regional species pools. Therefore, we defined local patches as individual mussel beds, and the regional species pool as the set of all local patches combined.

We sampled 21 mussel beds (sites) across three rivers (Little River, Kiamichi River, and Ouachita River). At each site we hand-excavated 15 randomly placed 50 x 50

cm quadrats to a depth of ~20 cm, collecting all mussels encountered (Vaughn *et al.* 1997). Mussels were identified to species and their length was recorded. We used species-specific shell length-wet weight regressions to estimate mussel biomass for all sampled individuals; regression equations were derived from previous measurements taken over multiple sampling sites and dates (Spooner unpublished). Quadrat sampling is a reliable method for determining population density, but underrepresents local species richness (Vaughn *et al.* 1997). We performed a one person/hour snorkel search at each site to ensure an accurate estimate of site specific species richness (S) (Vaughn *et al.* 1997b).

Each mussel bed displayed a log-normal distribution of species biomass, with four species accounting for over 70% the biomass. These four species were subsampled for measurement of wet weight and body condition index. Wet weight was measured for 20 individuals per site of each of the four species with an OHAUS balance following gentle scrubbing to remove biofilm. Body condition index was non-lethally calculated as the entire wet mass of mussel divided by shell length (Crosby and Gale 1990).

We measured respiration rates of five individuals from each of the four dominant species in 1-hr in-situ bioassays individually placed into plastic sealed containers containing 500 ml of GF/F filtered river water. Oxygen concentration was measured using a Thermo Orion 835A oxygen meter and the container sealed and placed into the river. Five control containers filled with 500ml of filtered river water were used as a control for respiration or photosynthesis associated with algae and bacterial fauna passing through the sieve. After an hour, each container was collected and final oxygen concentrations were quantified. Mass-specific respiration rate was calculated for each

individual as the oxygen consumed per hour corrected for water volume, mussel biomass, and change in oxygen in control treatments. Upon the completion of each census, all mussels were returned to the mussel bed unharmed.

For each site, the four dominant species were divided into two groups (major and minor species). The species containing the highest biomass at a given site were considered to be "major" species, while the three other species were averaged and considered "minor" species. Body condition index (BCI) and mass-specific respiration were used as non-lethal surrogate measures of condition at a given site. These measures lend insight into relative species fitness at two scales of inference; BCI characterizes the integration of energy throughout the lifespan of the mussel, while mass-specific respiration represents a more proximate measure of energy assimilation. Condition indices (BCI, mass-specific respiration) were calculated for both groups.

We used the spatial coefficient of thermal variation as an index for the number of thermal niches. At each site, we used a digital thermometer to quantify water temperature ($\pm 0.1^{o}C$) in each of the fifteen quadrats. Fifteen measurements were taken at the sediment water interface at each quadrat to account for relevant temperatures experienced by mussels. Thermal coefficient of variation was calculated as the standard deviation divided by mean temperature (n=15) for each site. We used thermal coefficient of variation as a surrogate index for the number of thermal niches. Sites that experienced higher coefficients of thermal variation were assumed to have a larger number of thermal niches available to mussels.

Quantification of biodiversity effect

In a departure from typical plot-style diversity experiments, Cardinale *et al*. (2005) used species–specific regional production estimates in an additive fashion to predict local community biomass, in essence comparing site-specific production against what one would expect from a "typical" community. This approach, along with diversity partitioning approaches, are readily amenable to systems of fast growing, short-lived organisms due to the ease of quantifying rates of primary and secondary productivity. However, estimating primary or secondary productivity of long-lived organisms becomes problematic due to constraints associated with estimating growth rates or fitness within a relevant time frame.

We modified the partitioning approach outlined by Fox (2005) to partition the effect of biodiversity on mussel bed biomass. However, instead of building additive models based on monoculture, we estimated expected yields using pooled regional data for each species. Thus, our null hypothesis was that regional factors influencing the colonization and growth of mussels are identical to local factors. If the null hypothesis is falsified, then we might infer that either local processes, including species interactions and identity, are important to the growth of mussels within an assemblage, or that the distribution of propagules to local patches (mussel beds) is asymmetrical from the regional species pool.

We quantified the magnitude of the effect of species richness on species biomass using two common measures of biodiversity effect: the deviation between expected vs. observed yield and the net biodiversity effect.

We defined for each site (modified from Fox 2005):

$$\Delta Y = Y_O - Y_E$$

$$= \underbrace{N(\overline{\Delta RY})(\bar{M})}_{\text{Complementarity}} + \underbrace{N\text{cov}(M, RY_O - \frac{RY_O}{RYT_O})}_{\text{Distinctive species effect}} + \underbrace{N\text{cov}(M, \frac{RY_O}{RYT_O} - RY_E)}_{\text{Dominance effect}}$$

Where, Y_O is the observed total yield (total community biomass), and Y_E is the expected total yield (total expected community biomass) of all mussel species at a given site. The expected total yield Y_E was calculated as the sum of the regional average biomass across all sites for each species. The net biodiversity effect ΔY was calculated as the sum of complementarity effects, distinctive species effects, and dominance effects. The deviation in relative yield (ΔRY) was calculated as the difference in relative observed (RY_O) and relative expected yield (RY_E). RY_O for a given species was quantified as the observed biomass of that species at a given site divided by its mean regional biomass (M)(see Figure 1). RY_E for a given species was calculated as the relative contribution of that species to regional biomass. Previous estimates of RY_E in terrestrial systems have been quantified historically as the initial planted abundance divided by the total planted abundance of the mixture (Loreau 1998). Our RY_E relationship is based on the null hypothesis that the relative expected biomass at a given site is a function of its regional distribution.

There are several measures of regional biomass that can be used to estimate "typical" species-specific biomass, each with their own advantages and disadvantages. Cardinale *et al*. (2005) used median estimates of biomass in an effort to minimize the skew associated with sites containing species with particularly high biomass. The disadvantage of using the median is that it may locally inflate the influence of regionally

rarer species, biasing results towards finding complementarity. We used the average regional biomass for each species to estimate local biomass. The average is advantageous because, unlike the median that locally assumes zero biomass for regionally rare species and it includes all species found within a site minimizing the potential for an inflated effect of rare species. However, this measure is susceptible to skew at sites with high major species biomass and overcompensates for common species, biasing our results in the direction of finding the dominance or distinct species effects.

Data analyses

We used linear regression to test the effect of site species richness (S) on: ΔY, net biodiversity effect, dominance effect, complementarity, and distinctive species effect. We used total site species richness (S) using both quadrat and time search data as our predictor variable for the analysis. We used linear regression to examine the relationship of coefficient of thermal variation on the dominance effect, complementarity, and distinctive species effect. Linear regression also was used to examine the effect of complementarity, distinctive species effect, and the dominance effect on the body condition index and mass specific respiration of major and minor species. Values of complementarity, distinctive species effect, and dominance effect were square-root transformed, and their sign preserved, to meet parametric assumptions of homogeneity Statistical analyses were performed using SPSS software (Version 13.0)

Results

Comparison of mussel biomass across sites suggests that, both regionally and locally, species are log-normally distributed. Three species, *Actinonaias ligamentina* (Lamarck 1819), *Amblema plicata* (Say1817), and *Quadrula pustulosa* (Lea 1831) respectively, contributed the first, second and third largest proportions of biomass to the mussel assemblages (Figure 1). Overall, both ΔY ($F_{1,20}$ = 4,852, r^2 = 0.203, p = 0.040), and the net biodiversity effect ($F_{1,20}$ = 19.87, r^2 = 0.513, $p < 0.001$) increased with species richness, suggesting that mussel biomass accumulates in a non-additive fashion with increasing species richness (Figure 2). The ΔY approach appeared to have two distinct data clusters; one set in which communities had overall biomass standing crops below predicted, and another set in which biomass exceeded predictions. Both clusters appear to increase in a linear fashion with species richness suggesting some community-level benefit to increased diversity. Despite the fact that ΔY and the net biodiversity effect were calculated differently, both estimates were highly correlated ($F_{1,20}$ = 11.725, R^2 = 0.682, $p < 0.001$), bolstering our confidence in the approach.

Partitioning

Overall, complementarity contributed the greatest to the net biodiversity effect (60%), followed by distinctive species effect (34%) and dominance effect (6%). Complementarity ($F_{1,20}$ = 23.281, R^2 = 0.551, $p < 0.001$) increased positively with respect to species richness (Figure 3a), suggesting that all species had higher biomass than regionally expected and were performing equally well. The distinctive species effect displayed no relationship with respect to species richness ($F_{1,20}$ = 0.155, R^2 = 0.008, p =

0.698) (Figure 3b). Positive distinctive species effect values suggest that species with high regional biomass also have high local biomass. Negative values suggest that species with low regional biomass display high biomass locally. The dominance effect was negative and decreased with increasing species richness (Figure 3c) suggesting that species with overall low regional biomass have proportionally higher local biomass at the expense of the species with high regional biomass (Figure 3) ($F_{1,20} = 19.167$, $R^2 = 0.502$, $p < 0.001$). However, like the distinctive species effect, nested within this relationship was a positive linear increase up to the nine species mark followed by a strong linear decline.

Complementarity was highest at sites that displayed high coefficients of spatial thermal variation (number of thermal niches) ($F_{1,19} = 10.148$, $R^2 = 0.361$, $p = 0.005$) (Figure 4a). However, the distinctive species effect ($F_{1,19} = 3.972$, $R^2 = 0.181$, $p = 0.062$) and the dominance effect ($F_{1,19} = 2.626$, $R^2 = 0.127$, $p = 0.123$) displayed no relationship with the spatial coefficient of thermal variation (Figure 4).

Condition

There was no significant relationship between condition (BCI, mass-specific respiration) of major species with respect to species richness (BCI: $F_{1,20} = 0.568$, $R^2 = 0.032$, $p = 0.461$, mass-specific respiration: $F_{1,20} = 1.307$, $R^2 = 0.017$, $p = 0.587$), or coefficient of thermal variation (BCI: $F_{1,20} = 0.568$, $R^2 = 0.032$, $p = 0.461$, mass-specific respiration: $F_{1,20} = 1.181$, $r^2 = 0.065$, $p = 0.292$) (Figure 5). However there was a significant positive relationship between the body condition of minor species and both species richness (S) ($F_{1,19} = 8.209$, $R^2 = 0.313$, $p = 0.010$) and the coefficient of thermal

variation ($F_{1,19} = 10.492$, $R^2 = 0.382$, $p = 0.005$ (Figure 5). There also was a significant negative relationship between mass-specific respiration of minor species and both species richness (S) ($F_{1,20} = 25.596$, $R^2 = 0.587$, $p < 0.001$) and the coefficient of thermal variation ($F_{1,19} = 11.813$, $R^2 = 0.410$, $p = 0.006$) (Figure 5).

Complementarity displayed no significant relationship between the body condition of major species ($F_{1,20} = 0.075$, $R^2 = 0.004$, $p = 0.788$) and mass-specific respiration ($F_{1,20} = 0.065$, $R^2 = 0.003$, $p = 0.802$), suggesting that the condition of major species is independent of the degree of complementarity occurring at a given site. However, the body condition of minor species correlated positively ($F_{1,20} = 6.377$, $R^2 = 0.273$, $p = 0.018$) and mass-specific respiration correlated negatively ($F_{1,20} = 6.797$, $R^2 = 0.273$, $p = 0.017$) with complementarity (Table 1).

The distinctive species effect correlated positively with major species body condition index ($F_{1, 20} = 5.445$, $R^2 = 0.232$, $p = 0.031$) and negatively with mass-specific respiration ($F_{1,20} = 5.915$, $R^2 = 0.237$, $p = 0.025$) supporting the prediction that major species should have higher condition at sites displaying higher distinctive species effect. In addition, there was no significant relationship between minor species body condition index ($F_{1,20} = 0.375$, $R^2 = 0.020$, $p = 0.548$) and mass-specific respiration ($F_{1,20} = 0.514$, $R^2 = 0.029$, $p = 0.458$) with respect to the distinctive species effect demonstrating that the added benefit to major species did not negatively influence the condition of minor species (Table 1).

The dominance effect had no significant relationship with major species body condition ($F_{1,20} = 0.007$, $R^2 = 0.000$, $p = 0.935$) and mass-specific respiration ($F_{1,20} = 1.042$, $R^2 = 0.052$, $p = 0.320$) suggesting there is no added benefit to major species as the

dominance effect increases. However, minor species body condition index decreased ($F_{1,20} = 7.504$, $R^2 = 0.294$, $p = 0.013$) and mass-specific respiration increased ($F_{1,20} = 4.030$, $R^2 = 0.175$, $p = 0.059$) with respect to the dominance effect suggesting reduced condition of minor species living at sites that display higher levels of the dominance effect (Table 1).

Discussion

Freshwater mussel communities dominate large fractions of benthic biomass in some rivers, linking pelagic and benthic compartments and serving as effective nutrient and energy pumps. Thus, the nature of interactions between community assembly, environmental context, and mussel biomass accrual within these communities may have important consequences to stream ecosystem function. Our results demonstrate that mussel biomass in species-rich mussel communities is substantially higher than that predicted based on the average biomass of species across the region. In addition, complementarity accounted for the highest fraction of the net biodiversity effect, suggesting that this increased biomass is associated with the growth of the entire mussel community rather than the supremacy of a few dominant species.

That complementarity accounted for the highest fraction of the net biodiversity effect suggests that niche differences or facilitation between species may be important factors governing the growth and potential fitness of mussels. Complementarity effects were positive and linearly increased with respect to species richness, suggesting that communities perform better in a species-rich arena. Positive complementarity effects occur when all species produce higher biomass locally compared to regional predictions of species biomass. Large complementarity effects also indicate that different species

occupy a variety of distinct niches. Current knowledge of unionid ecology suggest that they share broad over-lapping resource requirements, limiting the number of potential ecological traits that may be partitioned along a niche axis. However, empirically-derived mussel performance estimates suggest that the magnitude for which different mussel species perform services (i.e., clearance rate, metabolism, nutrient excretion, biodeposition) and assimilate energy varies along a thermal gradient (Spooner unpublished). We predicted that if mussels partition resources along a thermal gradient, then complementarity should be highest at sites with the highest coefficient of thermal variation (a surrogate for the number of thermal niches). Indeed, complementarity correlated positively with the coefficient of thermal variation, indicating that sites with high spatial thermal variation have more thermal niches available for specialization, potentially relaxing competition and maximizing uptake and assimilation of food resources.

If niche differences were solely the dominant mechanism for which different species acquired and assimilated energy, we would expect to see an additive relationship between the net biodiversity effect and species richness (Hooper 1998, Petchey 2003, Cardinale et al. 2005). For example, if different mussel species occupied different substrate types or used different food resources, the added presence of those species in a community should be a function of locally added habitat heterogeneity (Loreau 2000). Our results demonstrate that the relationship between biomass and species richness was non-additive, suggesting that in addition to niche complementarity, potential facilitative interactions may also be important (Cardinale *et al.* 2002). Although we can only speculate on mechanisms, we suspect higher spatial coefficients of thermal variation may

differentially influence mussel activity and lead to an increase in facilitative interactions (i.e., resuspension and/or coprophagy of food, decrease in metabolic costs associated with resource capture and respiration).

Overall, both the dominance and distinctive species effects increased with respect to species richness up to a point where values declined and the relationship disappeared. Positive distinctive species effects occur when species with high regional biomass locally increase in biomass without impacting other species. Conversely, negative values imply that species with low regional biomass locally increase without impacting other species. At low species richness, we believe one or more traits are being selected that favor the growth of regionally abundant species. However, as species richness continues to increase, the advantage of such traits diminish to the benefit of species with low regional biomass. Overall, the dominance effect was negative, but displayed the same trend as the distinctive species effect with respect to species richness indicating that species with low regional biomass are locally increasing at the expense of regionally high biomass species, especially in species-rich mussel beds.

If the dominance effect and the distinctive species effect behaved in a fashion truly analogous to natural selection, we would expect selection to act upon and favor the traits of major species at sites approaching the optimal growth conditions for those species. Therefore, we would expect the magnitude of the dominance effect and the distinctive species effect to increase as the mean local temperature approaches the optimal temperature of the major species, and not with local thermal variation. Our results support this prediction, as both the dominance effect and the distinctive species

effect were unrelated to the spatial coefficient of thermal variation, implying these effects are independent of the number of available niches.

The partitioning approach has been applied typically to experimental manipulations, in which relative rates of energy transfer and flux can be quantified in a standardized and controlled fashion (Loreau and Hector 2001). For example, the influence of species richness on relative growth rates of terrestrial plants and marine algae has been partitioned under the hypothesis that species interactions drive species growth rates (Fridley 2001). The duration of these experiments typically vary from several months to a year. Our study partitioned the effect of diversity on standing crop biomass (used as a surrogate for secondary productivity) of assemblages of long-lived bivalves. Because our study represents a snapshot in time, it is difficult to discern if the patterns we observed reflect current species interactions or those that occurred in the past. To address this issue, we must observe either: 1) changes in relative fitness, or 2) changes in energy uptake and assimilation. Freshwater mussels are extremely long-lived (25-100 yrs), making direct fitness measures and relative-growth rates difficult to quantify. However, since these mussels are iteroperous, and allocate energy into reproduction when a threshold energy level is met (Bauer 1998), body condition can be used as a surrogate measure of fitness. In addition, we quantified mass-specific respiration to estimate relative rates of energy uptake as a proximate measure of secondary productivity. We predicted that major and minor species living at sites that exhibit higher complementarity should have higher measures of body condition index (BCI), and lower mass-specific respiration. We found a strong positive relationship between minor species body condition index and complementarity implying that minor species living in a

speciose assemblage are in better condition with potentially higher fitness. In addition, there was a strong negative relationship between mass-specific respiration of minor species with respect to complementarity indicating that there is an energetic benefit to living in a speciose assemblage. Despite these strong findings, there was no relationship between condition (body condition index and mass-specific respiration) of major species and complementarity, suggesting that other factors may influence the growth and fitness of major species.

Mussels living within species-rich communities may benefit via two different mechanisms. Species-rich mussel beds may occur in areas of high habitat quality with abundant food resources and minimal disturbance maximizing their growth and overall fitness (Strayer 1999). However, an alternative (but not mutually exclusive) hypothesis is that species-rich mussel communities somehow manipulate resources to favor increased energy acquisition and assimilation, and thus growth. Recent studies have shown that mussel assemblages, through suspension feeding, excretion and biodepositon, transfer energy from the water column to the sediment (Dame 1996, Vaughn et al. 2004). We know these benthic subsidies influence the abundance and biomass of non-bivalve invertebrates in the benthos (Spooner and Vaughn 2006), although more research on actual mechanisms is needed. Further, mussel burrowing behavior and shell architecture may increase flow heterogeneity and resource transfer to other mussels in a fashion similar to other assemblages of filter feeders, such as caddisfly communities (Cardinale et al. 2001, Cardinale et al. 2002).

We predicted that the condition of major species should increase at sites displaying high distinctive species effects, with no change in condition associated with

minor species. Our predictions were supported by increased body condition and reduced respiration rate associated with major species and no change in minor species condition. Sites that contained low species richness typically had positive distinctive species effects favoring regionally abundant species, whereas more speciose sites were variable favoring species with regionally low biomass and high biomass. Whether a regionally rare or an abundant species locally dominated a bed, the major species still increased in condition with higher distinctive species effects. This suggests that one-way complementarity related to other potential niche axes or thermal modes may be important to community dominance. Dominance of mussel bed biomass typically alternated between two coexisting species; *Actinonaias ligamentina*, which performs best at 25^{o}C, and *Amblema plicata* which performs best around 35^{o}C (Spooner unpublished). Recent warming trends in southeastern Oklahoma associated with extended periods of drought may explain an apparent shift in community dominance from *A. ligamentina* to *A. plicata* over the past decade (Galbraith *et al.*, unpublished).

We found no relationship between the body condition index or mass-specific respiration of major species and dominance effects. However we did observe a decline in condition of minor species, with lower body condition index and higher respiration rates associated with sites displaying higher dominance effects. We also observed a pattern similar to the distinctive species effect and species richness relationship with an increase in dominance effect followed by a negative slope implying that regionally abundant species benefit at low species richness and regionally rare biomass species benefit in species rich sites. Although we only detected condition effects on minor species, we think differences in thermal mode may also be important to the expression and selection

of traits associated with species governing the dominance effect. Given that our study determined that the overall importance of the dominance effect was negligible compared to complementarity, we would expect this relationship to be weak. However, not all dominance effects need be at the expense of minor species, positive interactions including facilitation may also occur due to dominant species effects (Bruno et al. 2003). Smith et al. (2004) found significant effects of dominant species on ecosystem function by alleviating stressful conditions, and thereby favoring invasibility.

Recent studies have demonstrated that recruitment limitation and propagule pools operate at different spatial scales and may influence the nature of biodiversity-ecosystem function relationships (Palmer et al. 1996, Bond and Chase 2002, Foster and Dickson 2004). For the purpose of this study, we assumed that local propagule settlement at a given mussel bed directly matched the regional relative abundance for each species and local propagule colonization is an exact lottery function of the regional species pool. Upon arrival, species interactions would dictate the uptake and assimilation of energy, and thus growth, changing the relative distribution of biomass compared to the regional model. However, a similar pattern may occur if mussel beds themselves altered the nature of propagule settlement allowing a higher proportion of propagules to settle at species rich-mussel beds. Larval dispersal is mediated via host fish, and encompasses a broad continuum of host-fish generalists and specialist mussel species. Several studies have documented a strong positive correlation between mussel and fish species richness but stop short at determining any direct mechanism for this relationship (Watters 1993, Vaughn and Taylor 2000). One hypothesis is that mussels alter the substrate conditions (substrate stability, food availability) in a manner that favors fish recruitment and

succession over time, which in turn, facilitates recruitment of new mussel species. Species-rich mussel beds may increase the encounter rate of propagules by attracting novel fish, favoring colonization and growth of more juveniles. Although this mechanism may explain the higher occurrence and biomass of mussels in species-rich beds, it does not explain the higher body condition and subsequent reduced respiration of mussels within those beds, thus other mechanisms, including species interactions, may still play a prominent role.

We demonstrated that species-rich freshwater mussel communities contained biomass above that expected from an additive model of a "typical community." This effect is largely due to complementarity, with the condition of minor species living within a community positively associated with complementarity, indicating a benefit to living in a speciose community. These measures also relate positively to the spatial thermal coefficient of variation, suggesting that thermal niche partitioning may be an important mechanism explaining the coexistence and subsequent performance of mussel communities. In addition, complementarity explained the highest fraction of the net biodiversity effect, and the non-additive nature of this relationship suggests that in addition to niche partitioning, facilitative interactions may also be important. Although the general approach to this study focused primarily on local species interactions, we cannot exclude the possibility that the influence of species richness on propagule settlement may also explain the pattern highlighting a need for explicit studies.

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Table 1. Summary of expected and observed results of the relationship between diversity effect (complementarity, distinctive species effect, and dominance effect) and surrogate fitness measure (body condition index and mass-specific respiration mg O_2 g wet wt.$^{-1}$l^{-1}hr^{-1}). Shaded rows represent statistically significant relationships.

Predictor variable	Group	Dependent variable	Prediction	Result	F-value $df_{1,20}$	R^2	*P*
Complementarity	Major	Condition index (BCI)	+	0	0.08	0.00	0.79
	Minor	Condition index (BCI)	+	+	6.37	0.27	0.02
	Major	Oxygen consumption	-	0	0.07	0.00	0.80
	Minor	Oxygen consumption	-	-	6.80	0.27	0.02
Distinctive species effect	Major	Condition index (BCI)	+	+	5.44	0.23	0.03
	Minor	Condition index (BCI)	0	0	0.38	0.02	0.02
	Major	Oxygen consumption	-	-	0.24	0.23	0.02
	Minor	Oxygen consumption	0	0	0.57	0.02	0.46
Dominance effect	Major	Condition index (BCI)	+	0	0.01	0.00	0.94
	Minor	Condition index (BCI)	-	-	7.50	0.29	0.01
	Major	Oxygen consumption	-	0	1.04	0.05	0.32
	Minor	Oxygen consumption	+	+	4.03	0.17	0.05

Figure legends

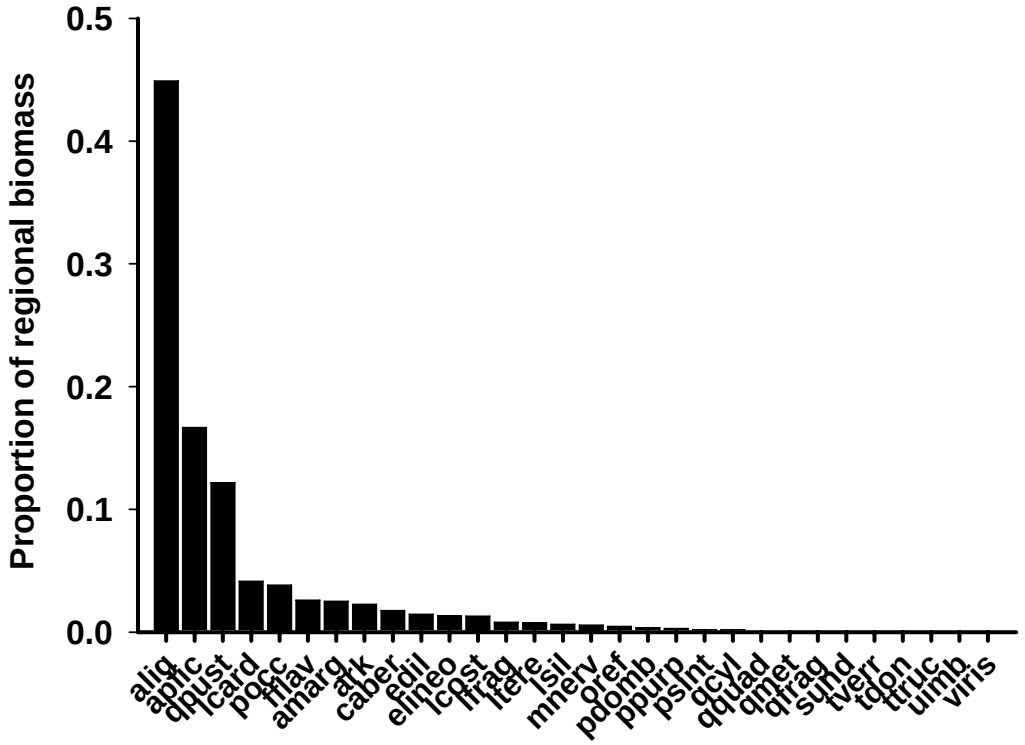
Figure 1. Proportion of biomass across the region. Data represent mean biomass of all pooled local sites.

Figure 2. Relationship between species richness and two measures of ecosystem function. (A) Species richness and Delta Y (Deviation in observed minus expected biomass). (B) Species richness and Net biodiversity effect (sum of trait dependent, trait independent, and dominance effect).

Figure 3. Relationship between species richness (S) and: (A) Complementarity, (B) Distinctive species effect, (C) Dominance effect. All values were square-root transformed and signs preserved.

Figure 4. Relationship between coefficient of spatial thermal variation and: (A) Complementarity, (B) Distinctive species effect, (C) Dominance effect. All values were square-root transformed and signs preserved.

Figure 5. Relationship between mass-specific respiration (mg O_2 g wet $wt.^{-1}l^{-1}hr^{-1}$) and (A) species richness, (B) coefficient of thermal variation. Relationship between body condition index and (C) species richness, coefficient of thermal variation.


Proportion of regional biomass
0.5
0.4
0.3
0.2
0.1
0.0
aliq
apfic
qpust
lcard
pocc
fmav
amarg
atk
caber
edil
elineo
lcost
hrag
lterre
lsil
mnerv
oref
pdomb
ppurp
pslnt
qcyl
qquad
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qfrag
sumd
tverr
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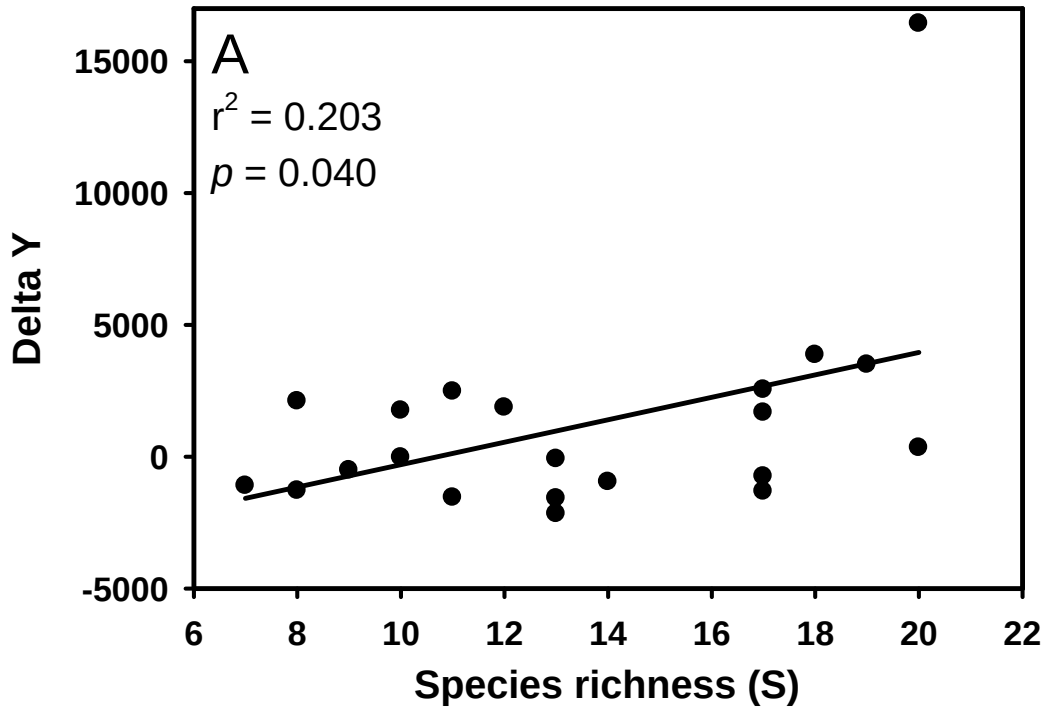
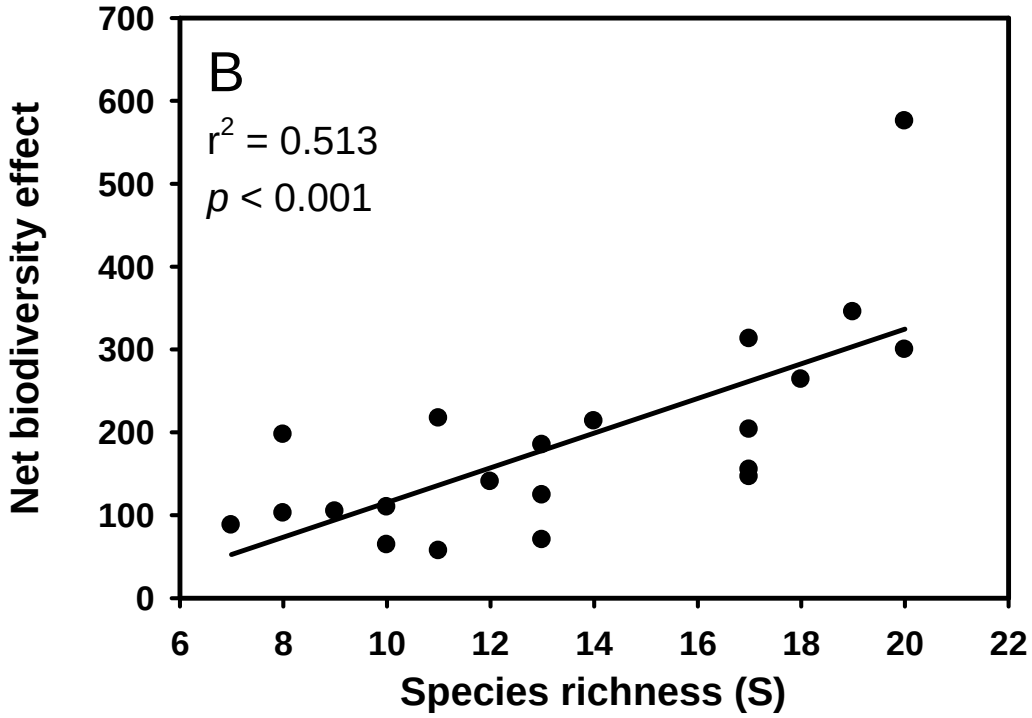
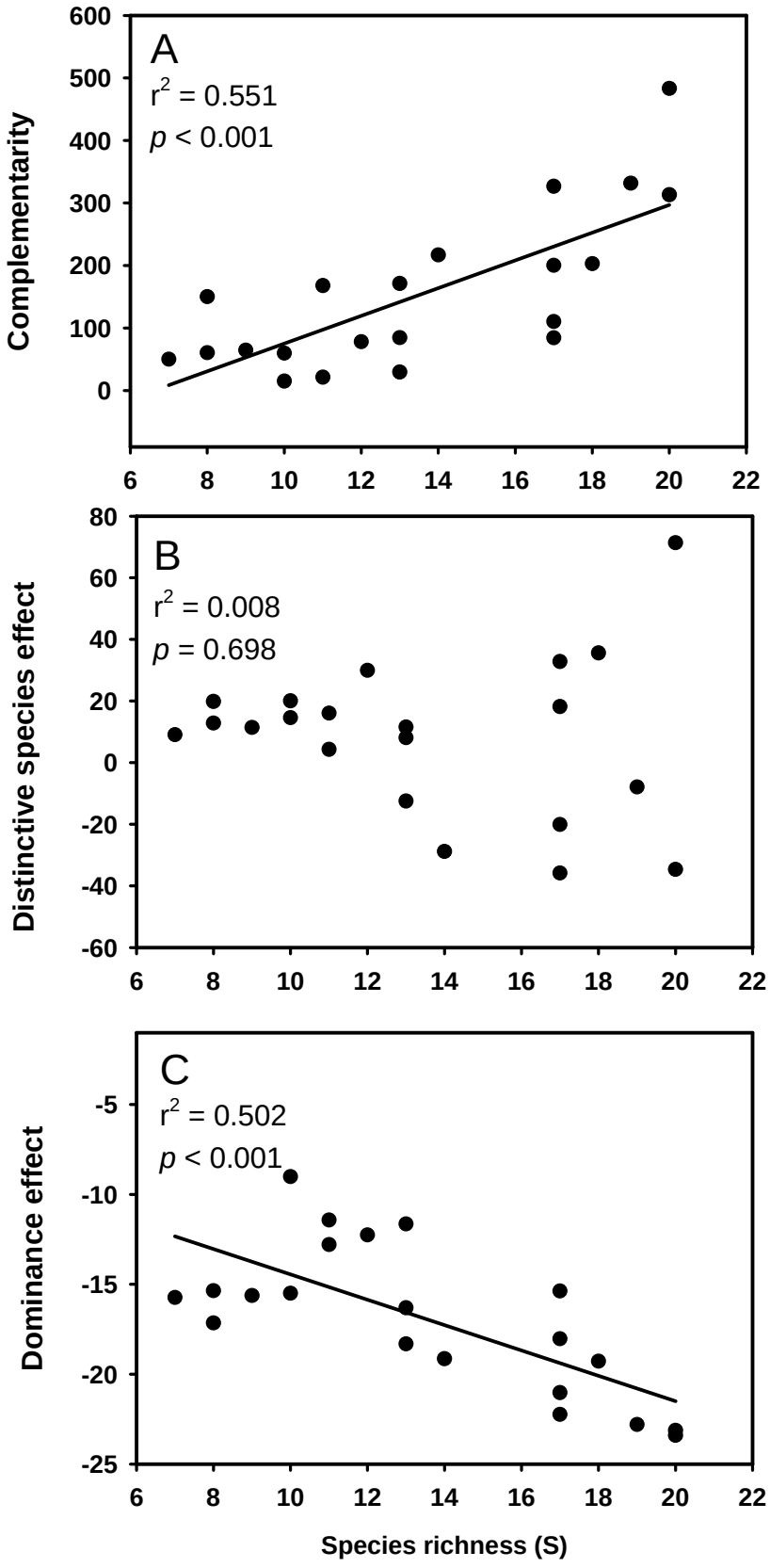
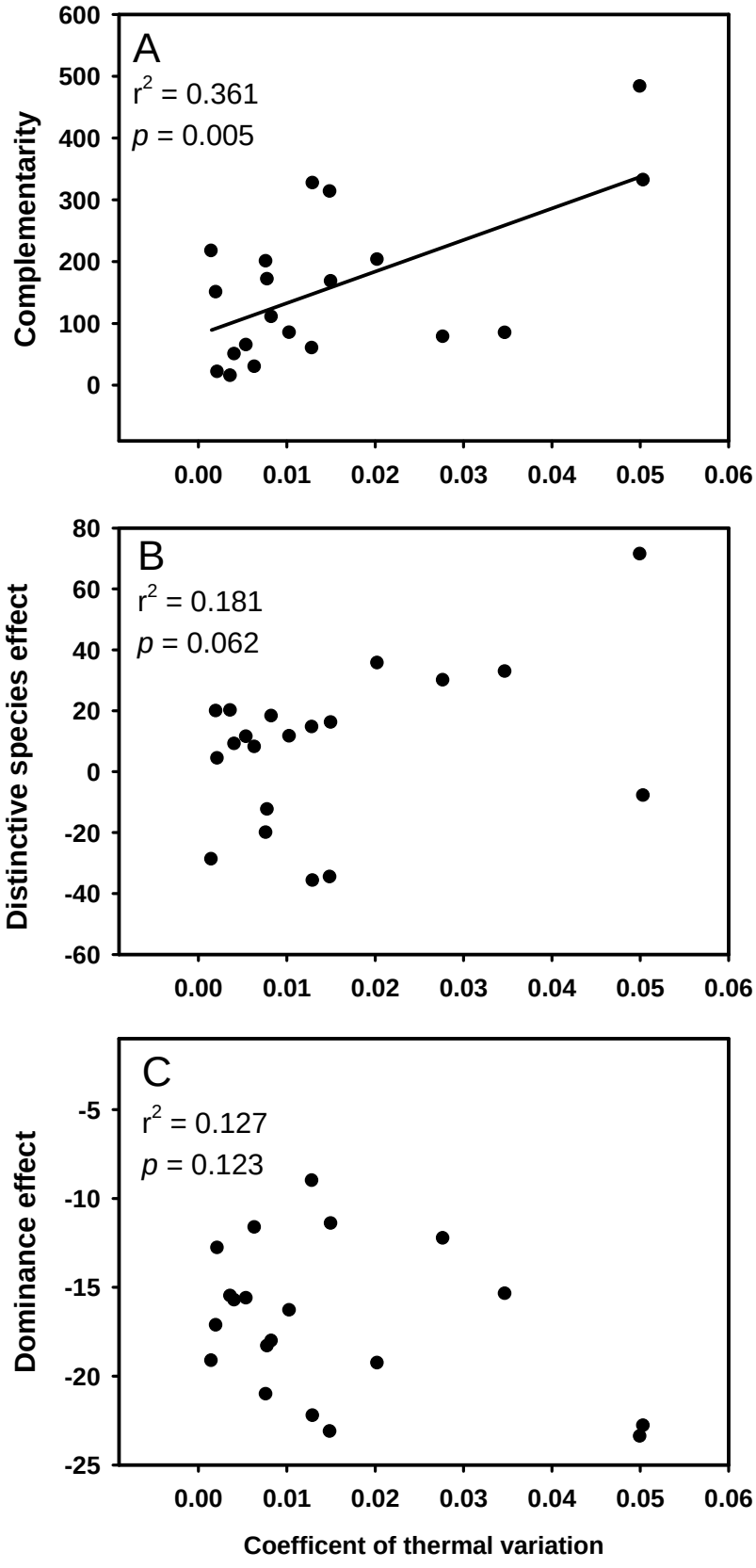
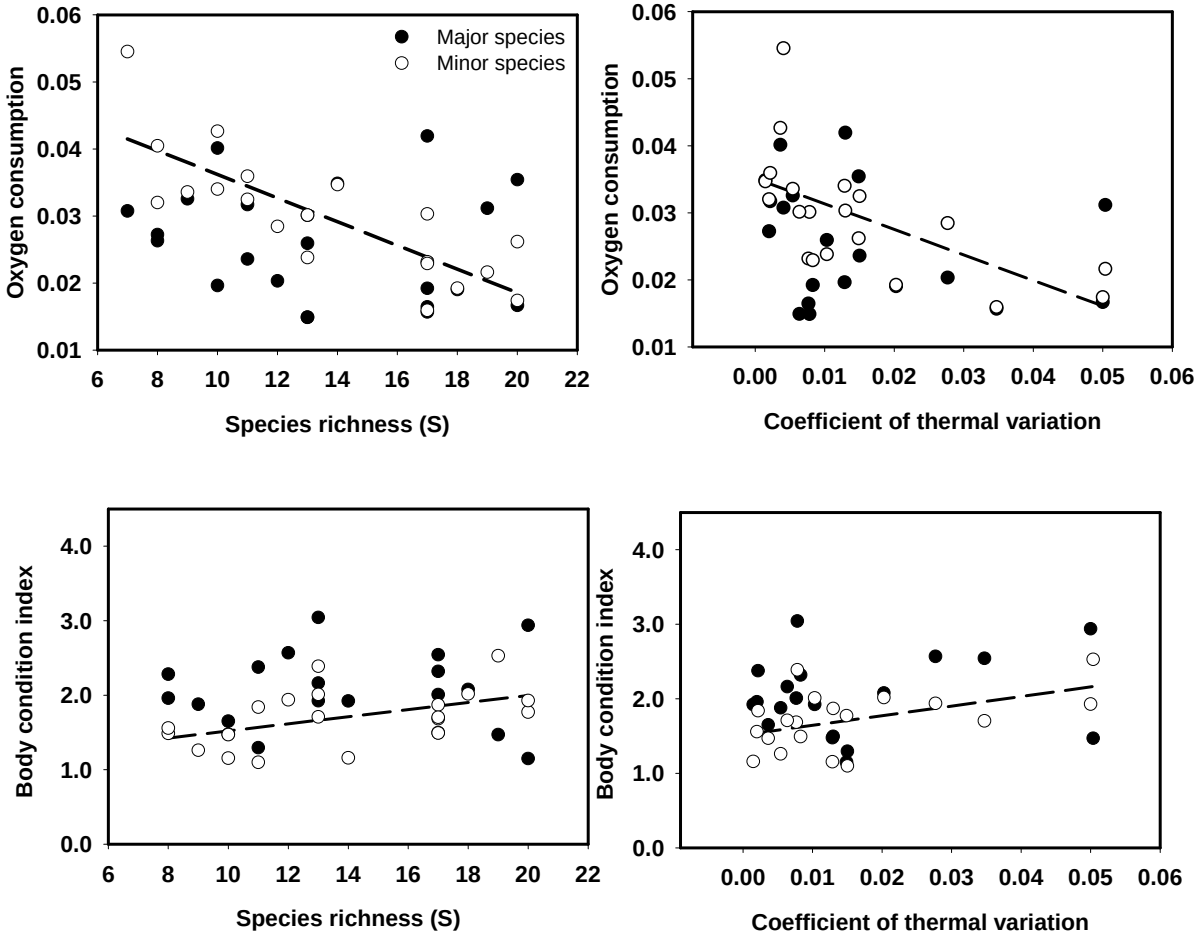

A
r^2 = 0.203
p = 0.040
Delta Y
15000
10000
5000
0
-5000
6
8
10
12
14
16
18
20
22
Species richness (S)


B
r^2 = 0.513
p < 0.001
Net biodiversity effect
700
600
500
400
300
200
100
0
6
8
10
12
14
16
18
20
22
Species richness (S)


A
r2 = 0.551
p < 0.001
Complementarity
600
500
400
300
200
100
0
6
8
10
12
14
16
18
20
22
B
r2 = 0.008
p = 0.698
Distinctive species effect
80
60
40
20
0
-20
-40
-60
C
r2 = 0.502
p < 0.001
Dominance effect
-5
-10
-15
-20
-25
Species richness (S)


A
r2 = 0.361
p = 0.005
Complementarity
600
500
400
300
200
100
0
0.00
0.01
0.02
0.03
0.04
0.05
0.06
B
r2 = 0.181
p = 0.062
Distinctive species effect
80
60
40
20
0
-20
-40
-60
C
r2 = 0.127
p = 0.123
Dominance effect
-5
-10
-15
-20
-25
Coefficent of thermal variation


Major species
Minor species
Oxygen consumption
Species richness (S)
Coefficient of thermal variation
Body condition index

A trait-based approach to evaluating species' roles in stream ecosystems: Implications for the effects of climate change on community structure and material cycling.

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Unionidae, ecosystem services, climate change, biodiversity, mussel

Abstract

The sustained decline in habitat quality and community integrity highlights the importance of understanding how communities and environmental variation interactively contribute to ecosystem services. We performed a laboratory experiment manipulating effects of acclimation temperature (5, 15, 25, 35^{o}C) on resource acquisition, assimilation and subsequent ecosystem services provided by eight freshwater mussel species. Our results suggest that although freshwater mussels are broadly categorized as filter feeders, there are distinct nested functional guilds (thermally-tolerant and sensitive) associated with their thermal performance. At 35^{o}C, thermally-tolerant species have increased resource assimilation and higher rates of contributed ecosystem services (nutrient excretion, benthic-pelagic coupling). Conversely thermally sensitive species have decreased assimilation rates and display an array of functional responses including increased/decreased benthic-pelagic coupling and nutrient excretion. Although thermally sensitive species may be in poorer physiological condition at warmer temperatures, their physiological responses can have positive effects on ecosystem services. We extrapolated these results to real mussel beds varying in species composition to address how shifts in community composition coupled with climate change may shift their contributed ecological services. Comparative field data indicate that two co-existing, abundant species with opposing thermal performance (Actinonaias ligamentina, Amblema plicata) differentially dominate community biomass. Additionally, communities differing in the relative proportion of these species differentially influence the magnitude (benthic-pelagic coupling) and quality (N:P excretion) of ecosystem services. As species are increasingly threatened by climate change, greater emphasis

should be placed on understanding the contribution of physiological stress to the integrity and functioning of ecosystems.

Introduction

The sustained decline in habitat quality and community integrity highlights the importance of understanding how communities and environmental variation interactively contribute to ecosystem services (Brown et al. 2001, Bond and Chase 2002, Cardinale et al. 2005). Most studies addressing this issue have identified parameters that promote or limit patterns of species distributions and diversity, including biogeography, physiological tolerances, and resource requirements (Petchey et al. 2002), such that species in a community exist as a net result of overcoming various stressors to acquire, assimilate, and convert resources into biomass and offspring (Tilman 1986). Recent studies have examined the functional significance of community structure by asking how species interactions influence ecosystem services such as productivity, invasibility and stability (Naeem et al. 1994, Wardle and Peltzer 2003). These studies assume that competitive and facilitative interactions occur between species, and that their functional traits enhance or inhibit ecosystem services (Loreau and Hector 2001, Turnbull et al. 2005).

Performance-based species traits vary along ecological gradients (Cottenie 2005), Thus the degree to which species' traits match the environment should dictate both where species can live and how they contribute services to the ecosystem (Ackerly 2003). Positive species richness effects on productivity have been perceived to result from increased species performance, and species in good condition contribute a greater

magnitude of services (Hooper 1998, Fridley 2001). However, communities include species with distinct functional traits that perform differently under different environmental conditions (Symstad et al. 1998, Petchey and Gaston 2002). It is important to also understand how community structure influences the functional contributions of species in sub-optimal environments (Petchey et al. 2002). For example, biochemical catabolism, a common response to stress,results in higher nutrient excretion, and thus increased ecosystem services, although the organism may have reduced physiological condition.

Climate change threatens to create a disjunction between species' traits and the environmental landscape they inhabit by pushing organisms beyond their biologically stable limits. These shifts influence not only species distributions, and ultimately local and regional species pools, but the services they provide to ecosystems. Thus, there is a need to understand how species' functional performances change along environmental gradients. This is particularly important in systems that contain large proportions of ectothermic organisms such as benthic stream ecosystems, which are highly constrained by regional climate and prone to shifts in precipitation and temperature regimes (e.g. drought).

This study examines how species' traits influence their contribution to important ecosystem services under different thermal regimes and with varying community composition, using freshwater mussels as a model system. Freshwater mussels (Bivalvia: Unionidae) are a guild of filter-feeding, sessile, burrowing bivalves that occur in speciose aggregations (mussel beds) that dominate the benthic biomass of many eastern North American lakes and streams (Strayer et al. 1981). Because of their large biomass and

filtering abilities, they link benthic and pelagic compartments by removing particulate matter from the water column and transferring it to the sediment and in turn subsidizing benthic algae and invertebrates via nutrient mineralization and organic matter biodeposition (Spooner and Vaughn 2006, Vaughn and Spooner 2006). Freshwater mussels living in streams experience considerable extremes in both water temperature and flow (Spooner 2002). For example, in rivers in southern Oklahoma summer water temperatures can exceed 40^{o}C and flow can become negligible. The magnitude of ecological services performed by mussels is greatest under these extreme physical conditions (Spooner and Vaughn 2006, Vaughn et al. 2007) and is likely related to increased metabolic costs at these high temperatures (Portner 2002).

To determine how differences in functional traits between freshwater mussel species contribute to differences in ecosystem function under different thermal regimes we quantified various measures of resource acquisition, resource assimilation, and resulting ecosystem services for a subset of a natural assemblage of mussels from the southern U.S.. We then extrapolated our results to real mussel beds varying in species composition to address how shifts in community composition coupled with climate change may change ecological function in these rivers.

Methods

We measured rates of resource acquisition, resource assimilation and ecosystem services for eight species of mussels at four different temperatures. Mussels were collected from the Little River in southeastern Oklahoma, U.S. Over 35 mussel species are known from this river, but most are relatively rare (Vaughn and Taylor 1999). We

chose species that (1) were common and thus could be important to river ecosystem processes and (2) encompassed the natural range of sizes, life histories and phylogenetic histories, and thus represent the range of mussel functional traits in the river. We collected 40 individuals each of Actinonaias ligamentina (Lamarck, 1819) (244.94 mm mean shell length ± 9.21 g dry wt), Amblema plicata (Say, 1817) (202.503 ± 9.90), Megalonaias nervosa (Rafinesque, 1820) (406.203 ± 30.85), Lampsilis cardium (Rafinesque, 1820) (139.76 ± 8.40), Fusconaia flava (Rafinesque, 1820) (75.87 ± 4.42), Truncilla truncata (Rafinesque, 1820) (43.35 ± 1.99), Obliquaria reflexa (Rafinesque, 1820) (45.48± 2.53), and Quadrula pustulosa (Lea, 1831) (57.26 ± 3.98). Biofilm was gently removed from mussel shells (Spooner and Vaughn 2006) and mussels were maintained in the laboratory at typical river temperature (15^{o}C) prior to the experiment.

Although we initially suspected that functional differences may present themselves at warmer temperatures, we had no a priori directional prediction and therefore thermal treatments (5, 15, 25, and 35^{o}C) were chosen to represent the natural range and extremes of temperatures experienced by mussels in the southcentral United States. Mussels were acclimated to experimental temperatures over a period of two weeks in separate 500 l Frigid Units re-circulating streams. Experiments were performed on individual mussels in four, 1.8 m^3 environmental chambers which allowed us to precisely control water temperature. Over a period of 20 days, each chamber held four, randomly selected mussels (without replacement) and a non-mussel control (10 replicates for each species at a given temperature).

For each mussel and control, the following was performed: Individuals were placed in a glass beaker (500 ml for small mussels, 1500 ml for large mussels) with a stir

bar, fed an initial aliquot of algae (89.7mg C l^{-1}), a 50 ml water sample was collected for chlorophyll a analysis, and beakers were placed on stir plates in the environmental chambers. Beakers were stirred and mussels were allowed to filter feed for 1.5 hrs, after which beakers were removed from the chambers and feces and pseudofeces (particles rejected during feeding) were collected with a pipette and filtered (glass fiber filter GF/F). We recorded water volume, then filtered the water from each beaker (glass fiber filter GF/F) and froze the filter. Each mussel was gently washed and placed in a covered glass respirometer (500 ml for small mussels, 1500 ml for large mussels) with a stir bar and filtered water. We collected water samples from each respirometer for nutrient analysis and measured oxygen concentration with an Orion oxygen meter. Respirometers were placed in environmental chambers, stirred for 1.5 hours, then were removed, oxygen was measured, two additional 10 ml water samples were collected, and water volume was recorded. We recorded the shell length and wet weight (tissue + shell) of each mussel and took a 20-40 mg mantle tissue sample for glycogen analysis (Berg et al. 1995). We then dried mussels and determined dry weight (tissue + shell).

Resource acquisition

We used biomass-corrected clearance rates (the volume of water from which a mussel has filtered all algal particles) as our measure of resource acquisition. Clearance rates were calculated following (Horgan and Mills 1997) as:

$$CR = V \ln(conc_i / conc_f) (M t)^{-1}$$

Where CR is clearance rate (volume of water filtered per g dry $weight^{-1}hour^{-1}$), V is water volume (l) $conc_i$ is initial algal concentration (mg chl a L^{-1}), $conc_f$ is final algal

concentration (mg chl a L^{-1}), M is dry mass (g), and t is time (h). Chlorophyll a was extracted and quantified from frozen glass fiber filters using the acetone method (ASDM 1996).

Resource assimilation

We used respiration rates, Q_{10}, and tissue glycogen concentration as measures of resource assimilation. Mass-specific oxygen consumption was calculated as the change in oxygen concentration over time corrected for respirometer volume and mussel dry mass. Preliminary studies showed that rates of oxygen uptake recorded at 15 min intervals for all eight species were linear, and work with other mussel species has shown that uptake rates with respect to declining $p0_2$ are linear until extreme hypoxia occurs (Chen Li-Yen et al. 2001). Our final oxygen concentrations were above 50% saturation for most trials, and we assumed that oxygen consumption rates were linear. All respiration measurements were corrected for oxygen changes associated with control treatments.

We compared the rates of net catabolic processes to anabolic processes to determine the overall condition of mussels relative to their thermal treatment. We used Q_{10} values (25-35^{o}C) of oxygen consumption as a surrogate index of rates of anabolism, and Q_{10} values (25-35^{o}C) of ammonia excretion as a surrogate index of rates of catabolism. Q_{10} values quantify the relative change in reaction rate between two temperatures differing by 10^{o}C. Since different individuals were used for each treatment, it was not possible to calculate Q_{10} values on the same individuals, therefore, mean oxygen and ammonia excretion values for each treatment for each species were used to

calculate Q_{10} rates. Mantle tissue glycogen concentration was quantified with the Phenol-Sulfate method (Naimo et al. 1998).

Ecosystem services

We used ammonia, phosphorus, molar N: P excretion and organic biodeposition rates as measures of ecosystem services. Ammonia was measured spectrophotometrically with the Phenate method (ASTM 1996), and corrected for mussel biomass ammonia evolution in control treatments. Phosphorus was digested with persulfate, analyzed with the ascorbic acid method (ASDM 1996), and corrected for mussel biomass and phosphorus evolution in control treatments. Molar N:P is the ratio of ammonia excreted (assuming minimal urea production) to phosphorus excreted. Biodeposition rates were determined as the ash-free dry weight of feces and pseudofeces, corrected for mussel biomass (ASDM 1996).

Extrapolation of results to natural mussel beds:

We extrapolated our data to nine mussel beds in three rivers (Kiamichi River, Little River and Ouachita River) in the Ouachita Uplands biogeographic province of southeastern Oklahoma and western Arkansas. We chose these rivers, because they are relatively undisturbed (Matthews *et al.* 2005), are very well known to us through decades of work by the Vaughn lab, and contain diverse, healthy mussel assemblages (Vaughn and Spooner 2006). Our eight experimental species accounted for over 75% of the total mussel biomass in the nine mussel beds. For each bed, we measured mussel densities in randomly placed 0.25 m^2 excavated quadrats (Vaughn et al. 1997). We recorded the shell

length of all sampled individuals and returned them alive to the mussel bed. We determined the areal extent of mussel beds, and multiplied this by mussel density to estimate the number of mussels in each bed. Species-specific length-dry weight regressions were used to estimate mussel biomass.

Data analyses

We used ANOVA with Sidak posthoc procedures to compare effects of independent variables: species, temperature, and species * temperature on dependent variables: acquisition (clearance rate), assimilation (oxygen consumption and glycogen concentration), and ecosystem services (biodeposition rate, ammonia and phosphorus excretion rates). Dependent variables were log transformed to meet assumptions of variance homogeneity. We used linear regression to determine the relative influence of species composition on mussel bed nutrient dynamics and water column turnover. All statistical analyses were performed using SPSS software (SPSS 2006).

Results

Resource acquisition

Mass-specific clearance rates increased with temperature (Fig 1a). Highest rates were at 35^{o}C for all species except A. ligamentina, L. cardium and T. truncata, which had greatest clearance rates at 25^{o}C and declined at 35^{o}C (Fig. 1a). Differences between species were largely due to higher mass-specific clearance rates in smaller-bodied mussel species.

Resource assimilation

Mass-specific oxygen consumption rates increased with temperature and were highest at 35°C for all species except A. ligamentina, L. cardium, and T. truncata (Table 1). These species had highest mass-specific oxygen consumption at 25°C and declined at 35°C, suggesting that thermal stress may cause these species to become partially anaerobic (Fig.1b).

Anabolism rates (Q_{10} oxygen) exceeded catabolism rates (Q_{10} ammonia) for A. plicata, F. flava, M. nervosa, and O. reflexa, indicating that investment into growth or maintenance may still be occurring at 35°C (Fig. 2). However, anabolism rates were considerably lower than catabolism rates for A. ligamentina, L. cardium, T. truncata, and Q. pustulosa, indicating that catabolic functions such as protein breakdown and/or glycogen catabolism may be occurring, resulting in a decline in condition (Fig. 2).

Mantle glycogen concentrations were highly variable and differed significantly between species (Table 1). Temperature alone did not have a significant influence on glycogen concentration. This may indicate that a longer time period or higher magnitude of stress is required before glycogen is mobilized. However, there was a significant interaction between temperature and species with both A. ligamentina and L. cardium, with having lowest glycogen concentrations at 35°C (Table 1), which indicates that these two species may use carbohydrate catabolism as an energetic supplement.

Ecosystem services

Ammonia production increased steadily with increasing temperature for all species and was highest at 35°C with the exception of T. truncata and M. nervosa which

tapered off (Fig. 3) (Table 1). Despite having larger body sizes, A. ligamentina and L. cardium, along with Q. pustulosa had highest mass-specific ammonia excretion rates at 35°C relative to other species (Fig. 3). Phosphorus excretion also increased with temperature with highest rates at 35°C for A. ligamentina, L. cardium, T. truncata, and M. nervosa (Fig. 3) (Table 1). Fusconaia flava had highest excretion rates at 25°C, while A. plicata and O. reflexa had negligible differences in excretion rates (Table 1).

Temperature and species-specific excretion rates led to considerable variability in N:P excretion rates (Fig. 3). At cooler temperatures (5-15°C), molar N:P ratios were similar for all species varying from 6-16. At 25°C, N:P excretion rates increased with the exception of L. cardium which decreased (Fig. 3).

Extrapolation

N:P excretion rates for whole mussel beds increased as a function of the biomass of one species, A. ligamentina, in the mussel bed at 15 °C ($F_{1,8} = 7.294$,$R^2 = 0.510$, $P = 0.031$), 25 °C ($F_{1,8} = 7.369$,$R^2 = 0.513$, $P = 0.030$), and 35°C ($F_{1,8} = 5.315$, $R^2 = 0.432$, $P = 0.055$) (Fig. 4). Relative biomass of A. plicata in the bed had no significant effect on overall N:P excretion at.15 °C ($F_{1,8} = 3.711$, $R^2 = 0.346$, $P = 0.095$), 25 °C ($F_{1,8} = 3.840$,$R^2 = 0.354$, $P = 0.091$), or 35°C ($F_{1,8} = 3.442$, $R^2 = 0.330$, $P = 0.106$). Mussel bed N:P excretion rates also increased as a function of overall community biomass at 15 °C ($F_{1,8} = 6.274$, $R^2 = 0.473$, $P = 0.041$), 25 °C ($F_{1,8} = 12.408$, $R^2 = 0.693$, $P = 0.010$), or 35°C ($F_{1,8} = 7.294$, $R^2 = 0.510$, $P = 0.031$) (Figure 4).

Mussel bed water column clearance rates decreased as a function of A. ligamentina relative biomass in the mussel bed at 15 °C ($F_{1,8} = 6.023$, $R^2 = 0.462$, $P =$

0.044), 25 °C ($F_{1,8}$ = 7.380 , R^2 = 0.513, P = 0.030), and 35°C ($F_{1,8}$ = 2.758 , R^2 = 0.283, P = 0.141) (Fig. 5). Although not statistically significant, increased relative biomass of A. plicata in the bed increased water column clearance rates at 15 °C ($F_{1,8}$ = 0.250, R^2 = .001, P = 0.626), 25 °C ($F_{1,8}$ = .008 ,R^2 = 0.001, P = 0.930), or 35°C ($F_{1,8}$ = 0.149 , R^2 = 0.021, P = 0.711). Mussel bed water column turnover rates increased as a function of total biomass at all temperatures 15°C ($F_{1,8}$ = 17.621 , R^2 = 0.716, P = 0.004), 25°C ($F_{1,8}$ = 11.957 , R^2 = 0.631, P = 0.011), and 35°C ($F_{1,8}$ = 15.519 , R^2 = 0.689, P = 0.006) (Fig. 5).

Discussion

Freshwater mussels are ectothermic filter feeders that occur in dense, highly speciose assemblages. Their reliance on host fish for their larval stages, and trophic subsidies via benthic pelagic coupling, make them important in stream ecosystems and a good model of overall stream ecosystem health. Our results demonstrate that mussel species have distinct physiological responses to stress that result in different contributions to ecosystem processes under varying environmental conditions. We found that mussel species had different filtration, biodeposition, and nutrient excretion rates under different levels of thermal stress, and that these differences in ecosystem services were the direct result of different functional (i.e. physiological) traits. These trait-based responses indicate possible habitat limitations for mussel species as well as the potential magnitude and type of services they provide to the ecosystem (Table 2). In addition, we detected at least two distinct thermal guilds. In our experiments, four species (A. plicata, F. flava, M. nervosa, and O. reflexa) were “thermally-tolerant”; these species had their highest

clearance and oxygen consumption rates at 35°C and were still assimilating energy at this temperature (anabolism > catabolism, Fig. 2). In contrast, the other 4 species (A. ligamentina, L. cardium, T. truncata, and Q. pustulosa) were "thermally-sensitive"; these species decreased their clearance and oxygen consumption rates at 35°C and depleted energetic stories via anaerobic mechanisms (anabolism < catabolism, Table 2). All of the species used in our experiments (and indeed the entire 297 species in the family Unionidae) are considered to belong to the same "functional group" of filter-feeding bivalves (Vaughn and Hakenkamp 2001). Our results illustrate that although all these species are considered "filter feeders", their optimal performance differs along a thermal continuum creating functional groups nested within the broader "filter feeder" guild.

The thermal guilds had different influences on ecosystem processes. Ectotherms are expected to increase performance with increasing temperature, and the thermally-tolerant guild did this. With increasing temperature, A. plicata, M. nervosa, F. flava. and O. reflexa increased their clearance, biodeposition, and nutrient excretion rates, and had a greater impact on the surrounding ecosystem by increasing the rate and magnitude of energy and nutrient transfer from the water column to the sediment (Fig. 7, Table 2). In contrast, species in the thermally-sensitive guild varied in their response to warmer temperatures and contributions to ecosystem services. A. ligamentina and L. cardium experienced thermal stress somewhere between 25 and 35°C as demonstrated by decreased assimilation rates. Their decreased filtration and biodeposition rates resulted in reduced carbon transfer from the water column to the sediment. To compensate for reduced energy, these mussels catabolyzed biochemical reserves. This degradation of biomolecules affected the quantity (more ammonia) and quality (higher N:P ratio) of

excreted nutrients. Such stress-mediated differences in nutrient excretion could have stoichiometric implications for the composition of benthic periphyton and macroinvertebrate communities. Truncilla truncata decreased both clearance and biodeposition rates to a lesser extant than A. ligamentina or L. cardium, and may represent an intermediate functional type between the thermally sensitive and thermally tolerant species. Quadrula pustulosa had its highest clearance, biodeposition, and nutrient excretion rates at 35^{o}C, but assimilation was low, resulting in higher biodeposition rates and greater benthic-pelagic coupling.

Our results also highlight the potential importance of species functional traits in structuring communities. Niche differentiation by using different types and/or magnitudes of resources is an important mechanism of species co-existence (Tilman 1994, Wardle and Peltzer 2003). In terrestrial systems, spatial differences in habitat use (plant root depth, canopy height) and differences in resource requirements (shading, nutrients) dictate the competitive outcome of ecologically similar species, and ultimately community structure (Hooper 1998). Our comparative field data of 21 mussel beds within the same biogeographic region reveal that while thermally tolerant and sensitive species co-occur, their dominance alternates within mussel beds. Specifically, two co-occurring species with opposing thermal performance, A. ligamentina (thermally sensitive) and A. plicata (thermally tolerant), constitute the greatest fraction of mussel biomass across the region, and differentially dominate community biomass (Fig. 6). In addition, we have field- derived physiology data showing that mussels in thermally variable, species-rich mussel beds have lower mass-specific respiration rates and higher body composition (weight/length) indices) (Spooner, unpublished data), indicating an

energetic benefit to living in a speciose, thermally variable environment. These findings, coupled with our new knowledge that mussels differentially assimilate energy under a variety of temperatures, supports the hypothesis that mussel community structure is influenced by thermal niche partitioning (Magnuson et al. 1979). Given that studies have demonstrated only a few other mechanisms of niche partitioning in speciose mussel communities (Haag and Warren 1998, Rashleigh and DeAngelis 2007), this is an hypothesis worth testing. Our experiments were performed at a limited set of temperatures intended to encompass the end and mid-points of temperatures experienced by mussels in our target rivers. Future work should include experiments conducted at a narrower range of temperatures to establish more precisely how mussels differentially assimilate energy along thermal gradients, field measurements of the range of temperatures within mussel beds, and studies identifying alternative niche axes that structure mussel communities.

We integrated our lab-derived physiology information with field-collected community data to evaluate the importance of thermal regime, mussel community composition, and mussel functional traits on services provided to stream ecosystems. Stream temperatures in the south-central U.S. are highly variable, with summer extremes as high 40^{o}C during periods of extended drought (personal observation). Our extrapolation indicates that temperature significantly influences the N:P ratio of nutrients excreted by mussel communities with highest N:P ratios at 35^{o}C and lowest at 15^{o}C (Fig. 4). Species composition also influences the quality of nutrients excreted by mussel communities. Thermally sensitive species excrete higher rates of ammonia than tolerant species, and therefore contribute higher community N:P ratios. Conversely, mussel beds

with greater relative abundance of thermally tolerant species excrete at lower N:P ratios (Fig. 4). McIntyre et al. (2007) compared random versus non-random extirpations in Lake Malawi cichlids and found significant differences in community excretion rates associated with shifts in community structure. Our results suggest that losses of thermally sensitive mussel species will have similar effects on mussel community excretion.

Interactive effects of temperature and nutrient regime have both stoichiometric and trophic implications in benthic foodwebs (Cross et al. 2006, Gafner and Robinson 2007). In our system, the magnitude of temperature and species composition influences on community nutrient excretion should be governed by local nutrient limitation. For example, mussel communities excreting above Redfield ratios (>16:1) should facilitate periphyton with high N demand, while communities excreting below Redfield (<16:1) should benefit periphyton with high P demands (Hall et al. 2005). In a field experiment in the Kiamichi River, OK, with the same suite of species used in this study, Vaughn et al. (2007) found that A. ligamentina had strong effects on periphyton and macroinvertebrate assemblages in summer when it excreted high levels of ammonia in this N-limited system (Vaughn and Spooner 2006, Vaughn et al. 2007), but no significant effects in fall when ammonia excretion rates were reduced.

Shifts in temperature regimes and species dominance also influenced the nature of benthic-pelagic coupling (Fig. 5). Water column clearance rate extrapolations demonstrated that benthic-pelagic coupling declined with increased dominance of thermally-sensitive species (A. ligamentina), but increased with greater dominance of thermally-tolerant species (A. plicata). In general, mussel beds have lower clearance

rates at 15°C resulting in decreased benthic-pelagic coupling. However, unlike nutrient excretion, mussel beds have equal water column turnover rates at 25°C and 35°C resulting in similar benthic pelagic coupling across temperatures.

Density/biomass compensation proposes that reductions of one species will be offset by increases of functionally-similar species, such that the magnitude of ecosystem services is maintained (Yachi and Loreau 1999, McGrady-Steed and Morin 2000). This concept is likely not applicable to long-lived (5-100 yrs), slow-growing and late maturing organisms (~4-5 yrs) such as unionid mussels (McMahon and Bogan 2001). Rather, our results suggest that unionids, and perhaps other organisms with similar life history traits, may use physiological compensation (shifts in species activity level) to account for species losses and/or declines in order to maintain ecosystem services. However, like density compensation, physiological compensation is highly dependent on the pool of species traits within a community and the nature of environmental heterogeneity.

The magnitude, periodicity and duration of droughts are increasing in the southern U.S and mean summer temperatures are predicted to increase by as much as 4°C over the next 50 y (Mulholland et al. 1997). Many mussel species are already experiencing temperatures in the upper end of their thermal tolerance zone in this region, thus these increased temperatures (and associated decreased precipitation) will likely profoundly influence mussel community structure and the resulting ecosystem services in rivers in this region. For example, we detected significant effects of temperature on the physiology and ecological services provided by mussels at 35°C, and we observed mortality of 3 of the thermally–sensitive species at 37-38°C, indicating that these temperatures are their upper limits for survival and reproduction. We have already

observed changes in mussel community structure that are linked to stream warming. Monitoring data for 10 sites in the Kiamichi River shows that overall mussel abundance and species richness have declined over the past 17 years as water temperatures have increased, and that mussel beds once dominated by thermally-sensitive species are now dominated by thermally-tolerant species (Galbraith et al, unpublished).

Studies linking species traits to biodiversity and ecosystem function have typically been performed in systems where there is significant variation in modes of resource acquisition. Our study demonstrates that physiological trait differences within a functional feeding group can lead to differences in community composition and provided ecosystem services. In addition, we show that both positive and negative physiological performance can have positive effects on the surrounding ecosystem. As species are increasingly threatened by climate change, greater emphasis should be placed on understanding the contribution of physiological stress to the integrity and functioning of ecosystems.

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Table 1. Two way ANOVA results of the effect of species, temperature and their interaction on resource acquisition, resource assimilation and ecosystem services.

Variable	Source	Df	F	P
Resource acquisition				
Clearance rate	Species	7	9.219	<0.001
	Temperature	3	75.936	<0.001
	Interaction	21	4.151	<0.001
Resource assimilation				
Oxygen consumption	Species	7	17.171	<0.001
	Temperature	3	51.909	<0.001
	Interaction	21	3.781	<0.001
Glycogen	Species	7	9.711	<0.001
	Temperature	3	0.777	ns
	Interaction	15	2.486	0.003
Ecosystem services				
Ammonia	Species	7	5.949	<0.001
	Temperature	3	61.432	<0.001
	Interaction	21	2.021	0.006
Phosphorous	Species	7	3.533	0.007
	Temperature	3	4.111	0.001
	Interaction	21	1.073	ns
Molar N : P	Species	3	6.166	<0.001
	Temperature	7	20.754	<0.001
	Interaction	21	1.476	0.006
Biodeposition	Species	7	11.662	<0.001
	Temperature	3	8.7	<0.001
	Interaction	21	0	ns

Table 2. Species-specific functional responses to experimental temperatures.

Species	Acquisition	Assimilation		Rendered ecological services				Functional group
	Clearance rate	O2 consumption	Q10	Biodeposition	NH3 excretion	P excretion	Molar N:P	
A. ligamentina	-	-	A < C	-	+	+	+	2a
L. cardium	-	=/-	A < C	-	+	+	+	2a
Q. pustulosa	+	+	A < C	+	+	+	-	2b
T. truncata	=/-	-	A < C	+	-	+	-	2c
A. plicata	+	+	A > C	+	+	-	+	1
F. flava	+	+	A > C	+	+	=	+	1
M. nervosa	+	+	A > C	+	+	+	=	1
O. reflexa	+	+	A > C	+	+	=	+	1

Figure Legends

Figure 1. Mean (± 1 SD) (A) resource acquisition measured as clearance rate and (B) resource assimilation measured as oxygen consumption for the 8 mussel species at the 4 experimental temperatures. Filled bars represent thermally sensitive species and hatched bars represent thermally tolerant species.

Figure 2. Mean (± 1 SD) Q_{10} anabolism (dark bars) and catabolism (light bars) rates between 25 and 35^{o}C for the 8 mussel species. Thermally sensitive species have lower rates of anabolism compared to catabolism.

Figure 3. Effect of acclimation temperature onMean (± 1 SD) ammonia excretion rate, phosphorus excretion rate, molar N:P excretion rate, and biodeposition rate for the 8 mussel species across the 4 experimental temperatures. Filled bars represent thermally sensitive species and hatched bars represent thermally tolerant species.

Figure 4. Extrapolation of nutrient excretion data to mussel beds. Relationship between mussel bed N:P ratio and (A) the percentage of A. ligamentina in a bed (B) the percentage of A. plicata in a bed, and (C) total mussel bed biomass. Each point represents a mussel bed experiencing a different temperature regime (filled circle = 15^{o}C, open circle = 25^{o}C, and filled triangle = 35^{o}C). The hatched line represents the Redfield ratio.

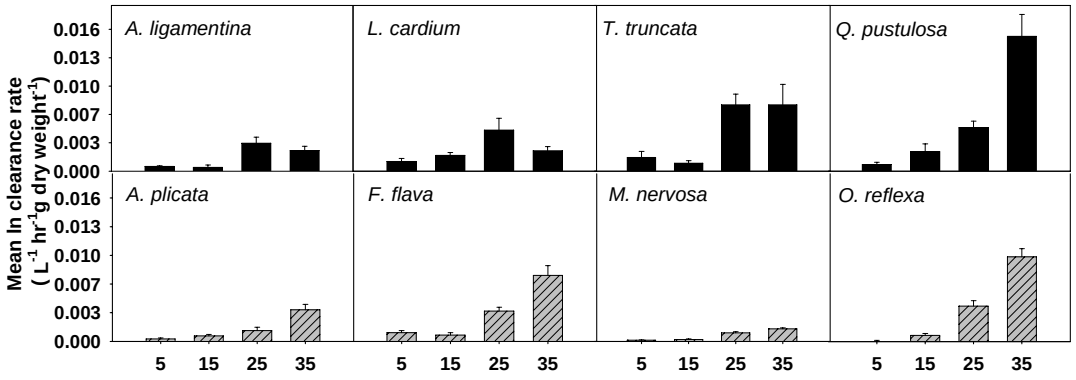
Figure 5. Extrapolation of water column clearance rate data to mussel beds. Relationship water column turnover and (A) the percentage of A. ligamentina in a bed (B) the percentage of A. plicata in a bed, and (C) total mussel bed biomass. Each

point represents a mussel bed experiencing a different temperature regime (filled circle = 15^{o}C, open circle = 25^{o}C, and filled triangle = 35^{o}C).

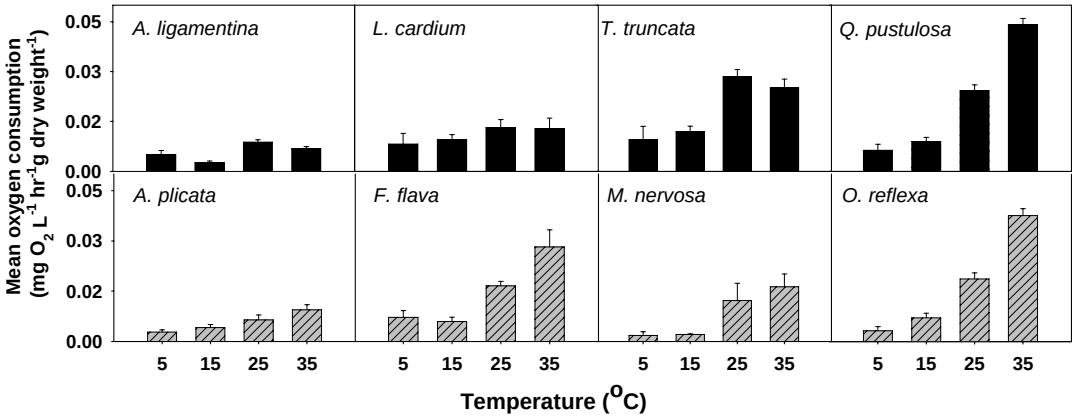
Figure 6. Relative biomass dominance of mussel species in 21 mussel beds in three rivers of the Ouachita Highlands. Black sections are A. ligamentina, grey sections are A. plicata, and white sections are other species.

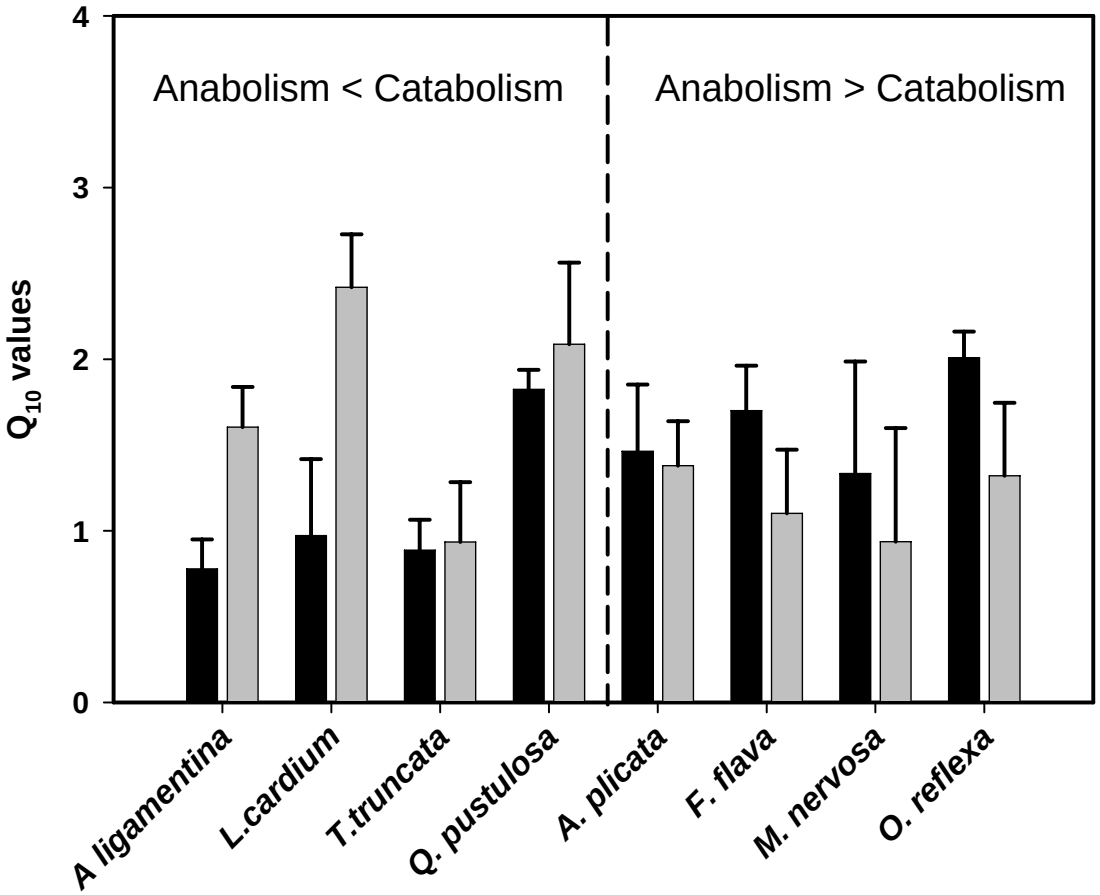
Figure 7. Conceptual model of (1) physiological response to water temperature and (2) different functional responses of mussel species upon the onset of thermal stress. Mussels increase activity level up to the onset of thermal stress (1), at which point their functional contribution depends upon their physiological response (2). These functional responses can result in: (a) reduced, (b) stable, and (c) increased benthic-pelagic coupling.

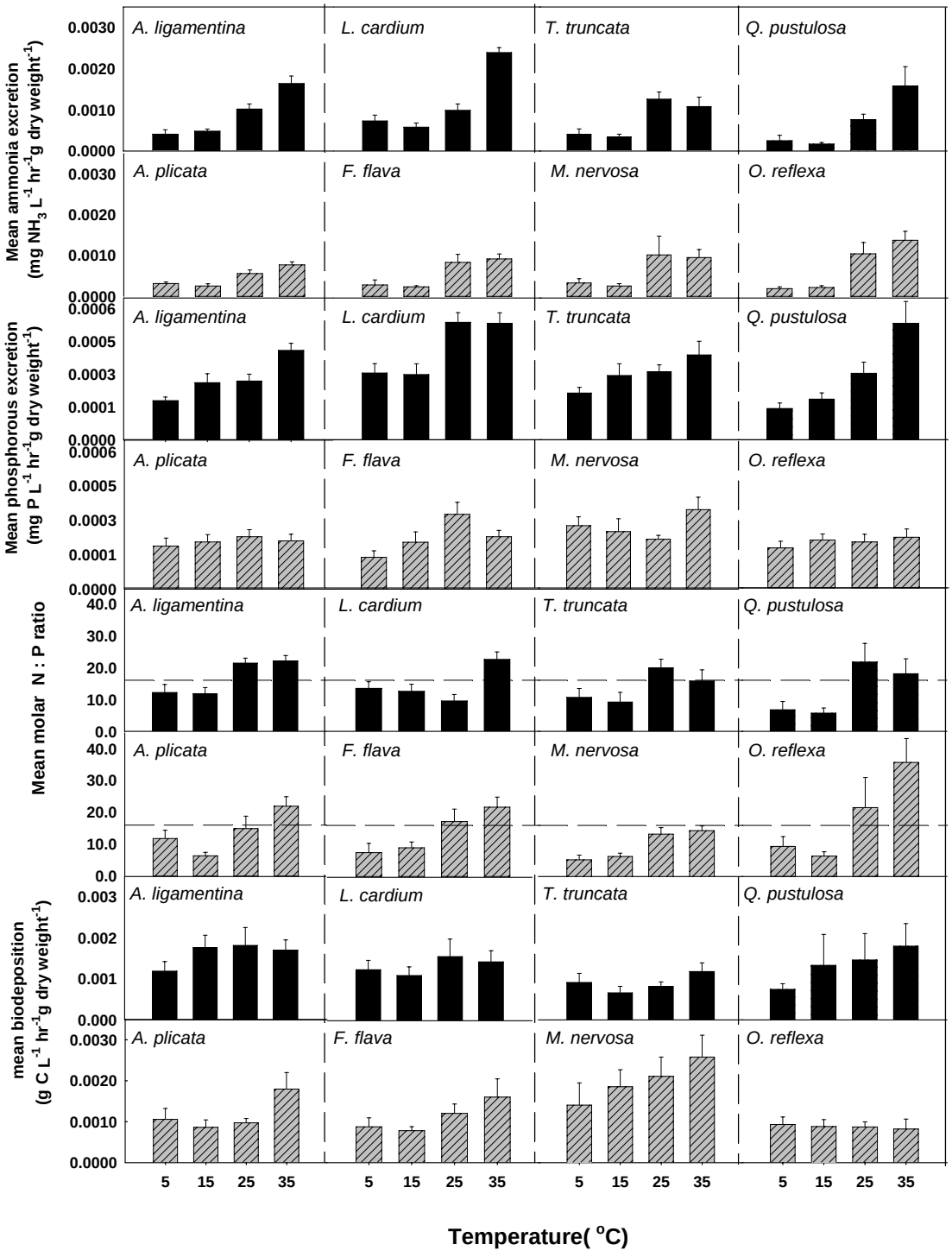
A.

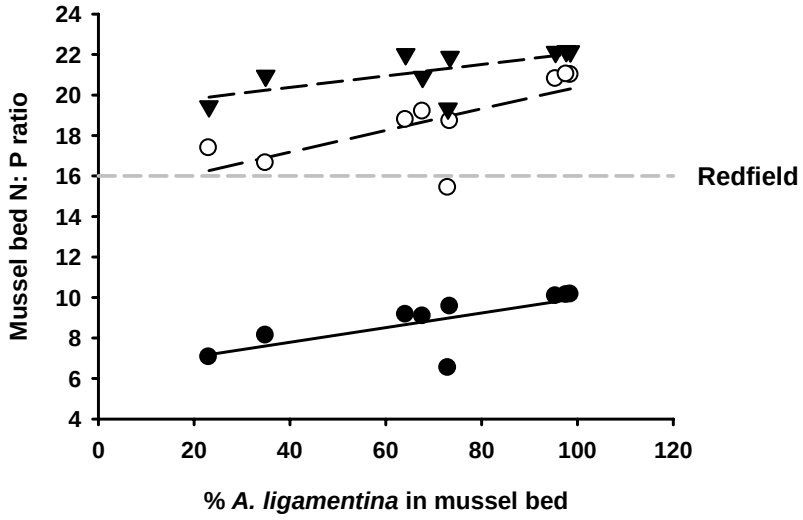

A. ligamentina
L. cardium
T. truncata
Q. pustulosa
A. plicata
F. flava
M. nervosa
O. reflexa
Mean In clearance rate
(L-1 hr-1g dry weight-1)
0.016
0.013
0.010
0.007
0.003
0.000
5
15
25
35

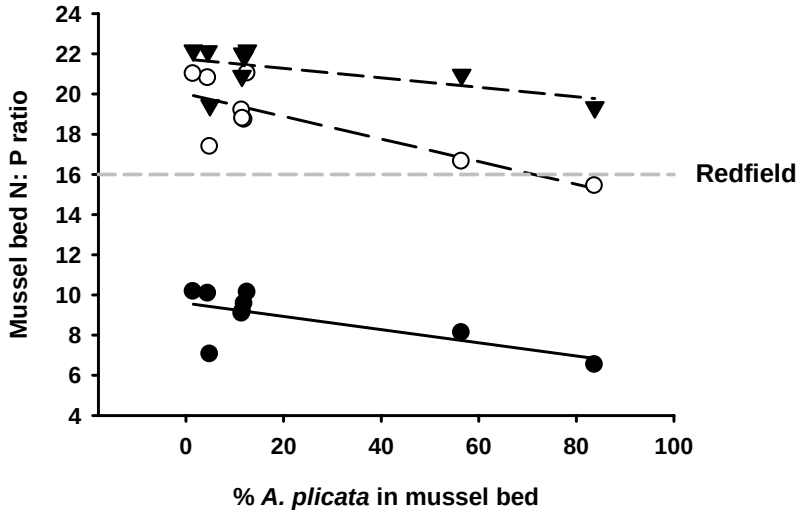
B.

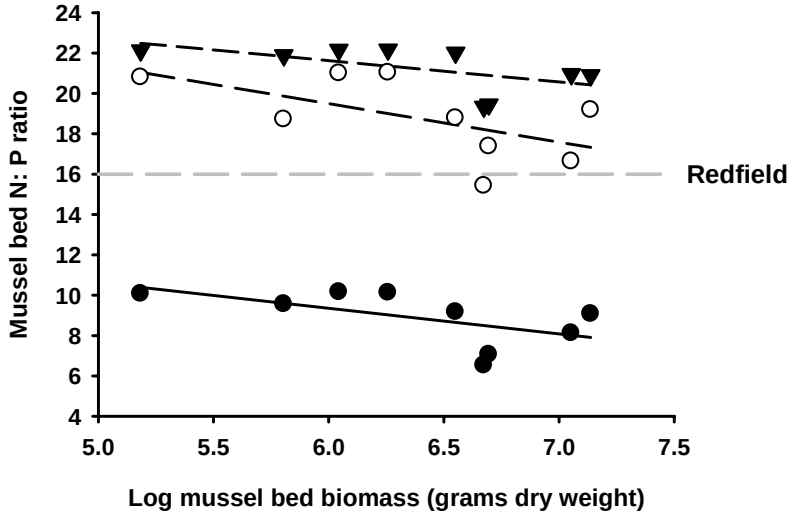

A. ligamentina
L. cardium
T. truncata
Q. pustulosa
A. plicata
F. flava
M. nervosa
O. reflexa
Mean oxygen consumption
(mg O2 L-1 hr-1g dry weight-1)
0.05
0.03
0.02
0.00
5
15
25
35
Temperature (OC)

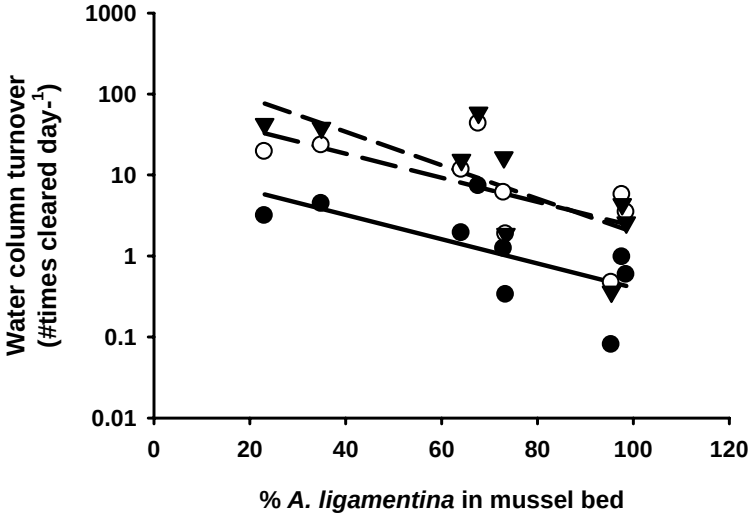

Anabolism < Catabolism
Anabolism > Catabolism
Q_{10} values
4
3
2
1
0
A ligamentina
L.cardium
T.truncata
Q. pustulosa
A. plicata
F. flava
M. nervosa
O. reflexa

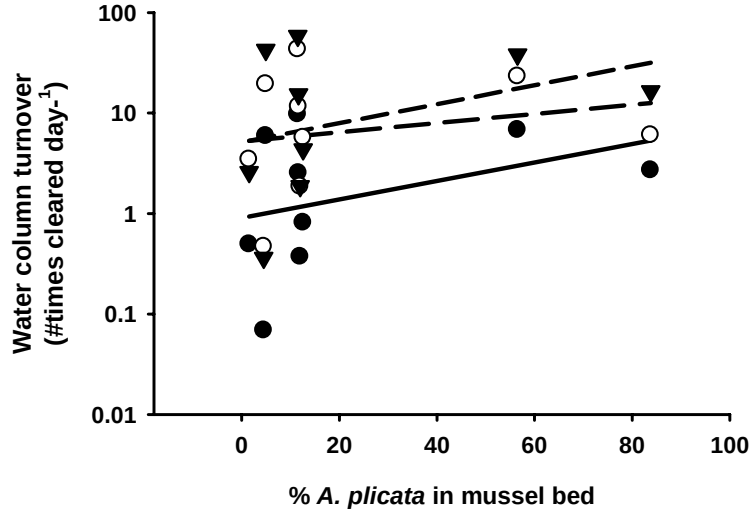

Mean ammonia excretion (mg NH_3 L^{-1} hr^{-1}g dry weight^{-1})
Mean phosphorous excretion (mg P L^{-1} hr^{-1}g dry weight^{-1})
Mean molar N : P ratio
mean biodeposition (g C L^{-1} hr^{-1}g dry weight^{-1})
A. ligamentina
L. cardium
T. truncata
Q. pustulosa
A. plicata
F. flava
M. nervosa
O. reflexa
0.0030
0.0020
0.0010
0.0000
0.0006
0.0005
0.0003
0.0001
40.0
30.0
20.0
10.0
0.0
0.003
0.002
0.001
0.000
5
15
25
35
Temperature(°C)

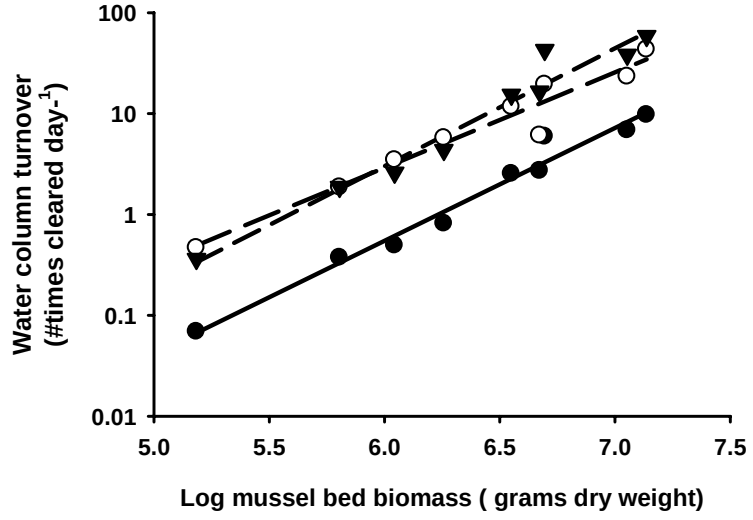

Mussel bed N: P ratio
24
22
20
18
16
14
12
10
8
6
4
0
20
40
60
80
100
120
Redfield
% A. ligamentina in mussel bed

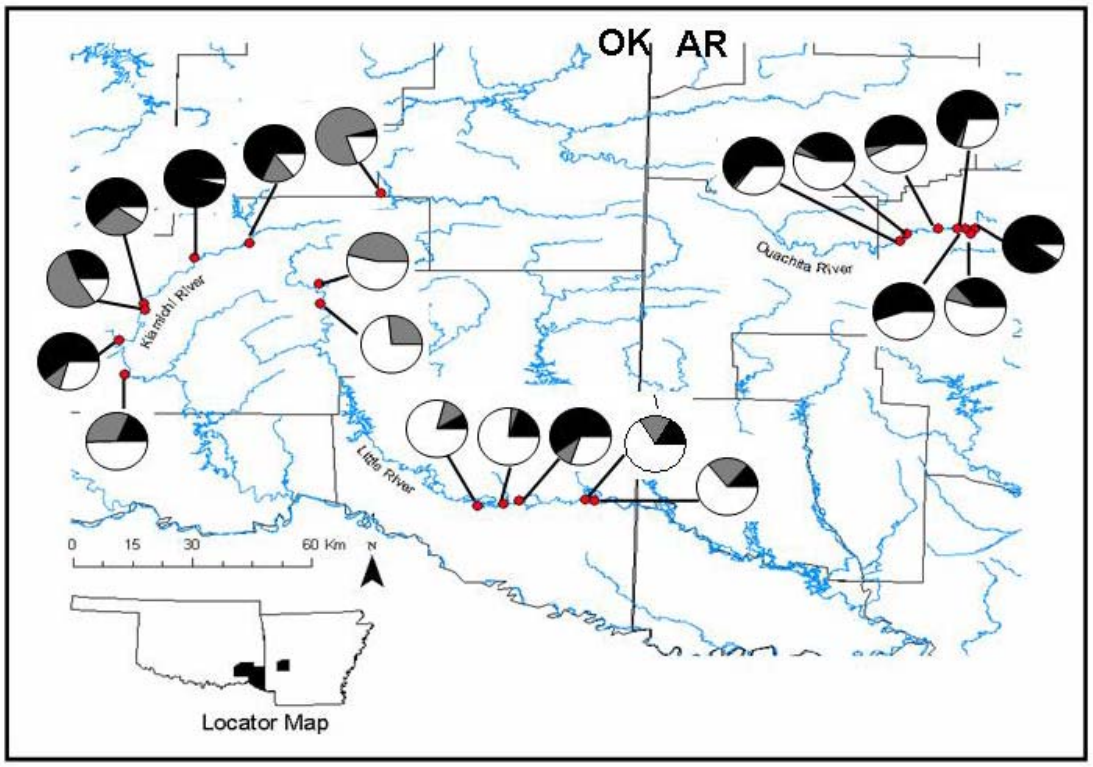

Mussel bed N: P ratio
24
22
20
18
16
14
12
10
8
6
4
0
20
40
60
80
100
Redfield
% A. plicata in mussel bed

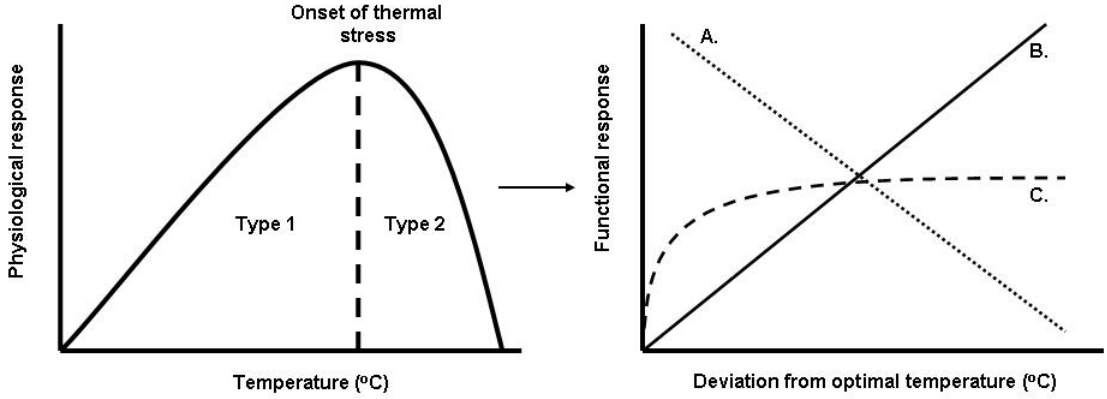

Mussel bed N: P ratio
24
22
20
18
16
14
12
10
8
6
4
5.0
5.5
6.0
6.5
7.0
7.5
Redfield
Log mussel bed biomass (grams dry weight)


Water column turnover
(#times cleared day-1)
1000
100
10
1
0.1
0.01
0
20
40
60
80
100
120
% A. ligamentina in mussel bed


Water column turnover
(#times cleared day-1)
100
10
1
0.1
0.01
0
20
40
60
80
100
% A. plicata in mussel bed


Water column turnover
(#times cleared day-1)
100
10
1
0.1
0.01
5.0
5.5
6.0
6.5
7.0
7.5
Log mussel bed biomass (grams dry weight)


OK
AR
Kiamichi River
Ouachita River
Little River
0 15 30 60 Km
N
Locator Map


Onset of thermal stress
Physiological response
Type 1
Type 2
Temperature (ºC)
Functional response
A.
B.
C.
Deviation from optimal temperature (ºC)

Species' dominance and environmental gradients interact to govern primary productivity in freshwater mussel communities.

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Formatted for Ecology.

Keywords

Biodiversity, species identity, ecosystem function, species interactions, Unionidae

Abstract

To extrapolate the effects of climate change to ecosystems we need to understand how the functional contributions of communities may change along environmental gradients. We examined the effect of species dominance on ecosystem function across an environmental gradient by manipulating the relative dominance of freshwater mussel species in mesocosms across a temperature gradient (15, 25, 35^{o}C) and measuring a suite of ecosystem services (community gross primary productivity, water column primary productivity and nutrient concentrations, and benthic gross primary productivity). Our results demonstrate that environmental context (temperature) combined with the functional traits of numerically dominant species interactively influence the performance and services provided by other species, and that these shifts can have heightened effects on multiple compartments within an ecosystem. Community gross primary production was highest at 35^{o}C, and increased with dominance of each of two species, Actinonaias ligamentina and Amblema plicata. However, at 35^{o}C, benthic gross primary production was highest in communities dominated by A. plicata, a thermally-tolerant species, while water-column gross primary production was highest in communities dominated by A. ligamentina, a thermally-sensitive species. Our results suggest that species interactions within communities depend on species dominance and environmental heterogeneity. Therefore, in addition to declines in species richness, shifts in community dominance also should be considered when interpreting the effects of climate change on the structure and functioning of ecosystems.

Introduction

Experiments manipulating the effects of biodiversity (typically defined as species richness) on ecosystem function have led to proposed explanatory mechanisms including complementarity (niche complementarity and facilitation), functional redundancy, and species identity (Tilman 1999, Naeem and Wright 2003). Niche complementarity occurs when resources are partitioned, leads to more complete use of resources (Hooper 1998, Fridley 2001), and has been largely associated with the diversity of functional groups rather than species (Hooper and Vitousek 1997, Hooper 1998). Facilitation occurs when individuals benefit in the presence of neighbors via enhanced availability of a resource (Stachowicz 2001, Cardinale et al. 2002). The role of species identity confounds the interpretation of biodiversity experiments due to the "sampling effect", i.e. the greater probability of selecting a species with disproportional traits that match the environmental landscape (i.e. a "unique" or "driver" species) in higher richness treatments (Huston 1997). An important question with respect to species identity is whether the unique species contribute more to ecological processes or increase the output of other species in the community through facilitation or competition; answering this question requires concurrent examination of both individual-species and whole-community effects on ecosystem services.

Understanding how the functional contributions of communities may change along environmental gradients is a critical research need if we are to extrapolate the effects of climate change to ecosystems. However, which mechanisms (i.e. complementarity or species identity) are operating depends on variation in species traits within a community, and the degree to which they match the local environment. Within

communities, species vary in abundance, evenness and dominance. Species with optimal physiological performance under particular environmental conditions acquire and assimilate resources most efficiently, resulting in numerical or biomass-based dominance (Wilson and Keddy 1986). This link between performance, dominance and community structure has been associated with species distributions (Root 1988), grassland successional patterns (Grime 1987), and competitive interactions along resource gradients (Bestelmeyer 2000). In addition to elevated performance, dominant species may influence others through facilitation and competition (Jonsson and Malmqvist 2003, Smith et al. 2004). Although understanding the loss of function associated with species extinctions is important, shifts in species dominance within communities may have equal or even more severe ecological consequences (Ogutu-Ohwayo 1990, Symstad et al. 1998)

Freshwater mussel communities are a good system for examining hypotheses linking physiology, species interactions, and species dominance effects on ecosystem function. Mussels (Bivalvia: Unionoida) are a guild of long-lived (6 – 100 yr), benthic, burrowing, filter-feeders that occur as speciose aggregations called mussel beds that can dominate benthic biomass in eastern North American rivers (Strayer et al. 1981, Vaughn and Spooner 2006). Because mussels occur as multi-species assemblages, the potential for species interactions is high. Nutrient mineralization via mussel excretion facilitates benthic algal growth, an important subsidy in nutrient-limited streams (Davis et al. 2000, Vanni 2002, Vaughn et al. 2007). This subsidized periphyton provides biogenic structure and food resources for macroinvertebrates and leads to their increased abundance (Spooner and Vaughn 2006). The magnitude of mussel effects on benthic communities

varies with environmental conditions; strongest effects occur during conditions of low flow and high water temperature (Spooner and Vaughn 2006, Vaughn et al. 2007).

Freshwater mussels are thermo-conformers that passively adjust their metabolism to ambient water temperatures (McMahon and Bogan 2001). We have found distinct nested thermal guilds (thermally tolerant and sensitive) associated with their functional performance (Spooner 2007). At 35^{o}C, thermally-tolerant species have increased resource assimilation and higher ecosystem process rates (e.g. nutrient excretion, filtration, and biodeposition). Conversely, thermally-sensitive species have decreased assimilation rates and display an array of functional responses including increased/decreased filtration, biodeposition and nutrient excretion rates. In addition, studies of mussel beds within the same biogeographic region reveal that while thermally-tolerant and sensitive species co-occur, they alternate in dominance within mussel beds (Spooner 2007). Specifically, two co-occurring species with opposing thermal-performance traits, Actinonaias ligamentina (thermally sensitive) and Amblema plicata (thermally tolerant), comprise the greatest fraction of mussel biomass across the region, and differentially dominate community biomass.

In this study we examined how species' dominance within a community, their thermal traits, and subsequent species interactions interact to determine ecosystem services. Most studies that have investigated the combined role of species interactions, community composition, and ecosystem services have used terrestrial annual plant communities and compared relative yields of species biomass in monoculture to additive models in polyculture (Hooper et al. 2005). In addition, these studies have generally been restricted to primary producers. In these studies, measures of ecosystem services

and species interactions are not independent because the ecosystem response variable (treatment biomass) is autocorrelated with the species interactions variable (species-specific change in biomass within treatments). This makes it difficult to assess how species interactions truly influence ecosystem properties at higher trophic levels. Because mussels can influence multiple trophic levels through their filtering, burrowing, and excretion activities, we can make estimates of ecosystem services (algal accrual and primary production) that are independent of measures of species interactions (body condition index, mass-specific and oxygen consumption).

We performed mesocosm experiments manipulating the relative abundance of mussel species to test two overlapping hypotheses:

H_1: Physiology governs performance and thus ecosystem services.

The relative contributions of species within communities to ecological processes are constrained by physiological responses to environmental temperature.

H_2: Species interactions govern performance and thus ecosystem services.

Dominant species influence the activity and condition of other component mussel species in the community by increasing (facilitation) or decreasing (competition) performance.

Materials and Methods

Experimental Design

We manipulated species dominance of a subset of a natural mussel assemblage. from the Little River, OK. We held species richness and total density constant to allow us to evaluate the relative contribution of species to ecosystem services when all known species traits were present in the community. We mimicked actual abundance patterns

observed in our study rivers (Spooner 2007), thus observed species interactions should be representative of what is occurring in the natural environment. We selected five species that co-occur in this river and are common, but that have different physiological responses to thermal stress resulting in potentially different contributions to ecosystem services (Spooner 2007). Actinonaias ligamentina (Lamarck, 1819) (244.94 mm mean shell length ± 9.21 g dry wt) and Quadrula pustulosa (Lea, 1831) (57.26 ± 3.98) are thermally-sensitive species that catabolyze energy reserves at warm temperatures. Amblema plicata (Say, 1817) (202.503 ± 9.90), (Megalonaias nervosa (Rafinesque, 1820) (406.203 ± 30.85) and Obliquaria reflexa (Rafinesque, 1820) (45.48± 2.53) are thermally-tolerant species that continue to assimilate energy at warm temperatures (Spooner 2007). For A. ligamentina, A. plicata and Q. pustulosa we created relative abundances of 41, 23, 18, 12 and 6%. We placed the two remaining species in treatments to maintain an orthogonal design (Table 1). Correlation of species biomass across mesocosms revealed that assigned dominance treatments were independent of one another (Table 2). We used a replicated (n = 3) ANCOVA design under three, natural temperature regimes (15, 25, 35^{o}C) in re-circulating mesocosms (Vaughn et al. 2004). Each mesocosm contained 17 mussels (23 individuals m^{-2}).

Experiments were performed as three separate runs (1 for each temperature) in 14 (12 treatment and 2 control) re-circulating stream mesocosms (1.5 m height x 0.5 m width x 0.5 m depth) held in an environmentally-controlled (temperature, light) room. Mesocosms consisted of a molded plastic liner suspended inside a fiberglass basin. The liner was positioned 10 cm off the bottom to allow water circulation below. Liners were filled to a depth of 15 cm with clean, pea-sized gravel. We maintained a constant 110 l

volume of conditioned well water in mesocosms, photoperiod was 12 hr light/dark (using Lightgrow® bulbs), and maintained constant flow with a 1/32 horsepower pump (Vaughn et al. 2004). Twelve porous silica disks (Leico Inc., 2.5 cm diameter) were placed in each mesocosm for periphyton colonization.

Mussels were collected from the Little River and held at ambient river water temperature (15°C) in 500 l re-circulating streams (Frigid Units Living Streams). Mussels were acclimated to experimental temperatures for a period of 2 weeks and fed a cultured algal assemblage ad libitum. Prior to each experimental run, we gently removed biofilm from mussel shells, measured, individually marked each mussel with a pre-numbered Floy shellfish tag glued to the shell, and measured their length and wet weight. Mussels were randomly selected from acclimation streams and assigned to treatments. Dry-mass of mussel individuals was calculated using species-specific wet mass-dry mass regressions. This allowed us to account for differences in mussel size, internal cavity water volume, and mesocosm biomass without sacrificing mussels. Each mesocosm was fed a cultured algal assemblage on a daily basis (500 ml, 0.2 mg chl a l^{-1}). Each experimental run lasted two weeks. Following the experiment, mussels were returned alive to the river.

Ecosystem response variables

Community GPP: On 4 sampling dates (Days 1, 4, 9, and 14) mesocosm pumps were turned off and replaced with low-velocity aquarium pumps to allow water circulation with minimal turbulent flow. Dissolved oxygen (DO) concentrations were measured with a Hach LDO meter (±0.1 mg l^{-1}), mesocosms were left in the dark for an

hour and DO re-measured, mesocosms were left in the light for one hour, a final DO measurement was taken, and mesocosm pumps were turned back on. Community gross primary production was calculated as the sum of oxygen production during light incubation oxygen consumed during the dark incubation and corrected for time and mussel community biomass (dry weight).

Water column GPP and nutrients: On the 4 sampling dates (Days 1, 4, 9, and 14), we collected 125 ml of water from each mesocosm for nutrient analysis (total phosphorous, total nitrate, and ammonia). Nutrient concentrations were determined colorimetrically using the ascorbic acid method with persulfate digestion for total phosphorous (TP), and cadmium reduction with alkaline persulfate digestion for total nitrogen (TN) (ASDM 1996), and corrected for mesocosm mussel biomass (dry weight). To measure water column GPP, we collected one l of water in an air-tight glass container from each mescosm, measured DO with a Hach LDO meter, incubated each container in the dark in an enclosed water bath at experimental temperatures for one hr, re-measured DO, incubated containers in the light in the enclosed water bath at experimental temperatures for an additional hour, and recorded final DO. The contents of each container were filtered with a GF/F filter, wrapped in foil, and frozen for subsequent chlorophyll a determination via acetone extraction (ASDM 1996). Water column gross primary production was calculated as the sum of oxygen production during light incubation plus respiration during the dark incubation, corrected for incubation time, water volume, chlorophyll a concentration and mussel community biomass (dry weight).

Benthic GPP: On day 14 of each experimental run, 2 silica disks were removed from each mesocosm and placed in air-tight 125 ml glass containers with filtered well-

water at experimental temperatures. Benthic gross primary production estimates were calculated using the same water bath procedure described above, after which silica disks were wrapped in foil and frozen for chlorophyll a determination. Benthic gross primary production was calculated using the same method as water column gross primary production correcting for incubation time, chlorophyll a concentration, disk surface area, and mesocosm mussel biomass (dry weight).

Mussel response variables

Ecological services (nutrient excretion) and condition (oxygen consumption) of individual mussels were quantified on the last day of each experimental run. For each mesocosm, 3 individuals of the most abundant species in that treatment plus the remaining 2 and single individuals of the least common species (Table 1), were placed in one l plastic containers with filtered well water at experimental temperatures. Two 10 ml water samples were collected and initial DO was measured. Containers were incubated in a 15 m x 1m water bath at experimental temperatures for 1 hour, then two final 10 ml water samples were collected and final DO was recorded. Final mussel wet weight was measured.

Total phosphorus was quantified using the ascorbic acid method with persulphate digestion, and ammonia quantified using the phenate method (ASDM 1996). Excretion rates were calculated as the net difference in initial and final nutrient concentrations corrected for nutrient evolution in control treatments, and standardized for container volume, incubation time and mussel biomass. Molar N : P ratios were calculated as the number of moles of total nitrogen divided by the number of moles of phosphorus.

Oxygen consumption was calculated as the net difference in oxygen depletion between initial and final measurements corrected for oxygen evolution in control treatments, and standardized for container volume, incubation time and mussel dry weight. We compared the difference in body condition index (wet mass / length) for each individual from the beginning to the end of the experiment. Mean values for each species were calculated for all response variables within a mesocosm and treated as an individual replicate, therefore, each species had a sample size of 12.

Data Analyses

All community (GPP), water column (GPP, chl a, TN, and TP), benthic (GPP and chl a), and mussel (body condition index, oxygen consumption, TP and NH_3) response variables were $\log_{10}+1$ transformed to meet assumptions of variance homogeneity. For each mesocosm, the relative proportion of each species was determined by dividing the total dry mass of each species by the total mesocosm dry mass. Species proportion data were square-root +0.5 transformed to meet the assumptions of homogeneity.

We examined our data with a repeated measures ANCOVA with community GPP, water-column GPP, chlorophyll a, TP, TN, NH_3, and N:P as dependent variables, and temperature as an independent variable. We used the relative proportion of each species (A. ligamentina, A. plicata, M. nervosa, O. reflexa, and Q. pustulosa) as covariates to test for the effect of species dominance on response variables. However, to account for unequal slopes and make proper comparisons between species, we performed a Wilcox procedure with a Dunnett multiple comparison procedure to determine the significance of covariates and minimize experiment-wise type 1 errors (Wilcox 1987).

Benthic response variables (GPP, chl a) and individual mussel response variables (oxygen consumption, delta oxygen consumption, phosphorus excretion, ammonia excretion, and BCI) were analyzed using ANCOVA with the Wilcox procedure performed on all covariates. All analyses were performed using SPSS and Wilcox procedure version 3.2 (Constable 1987) software.

Results

Ecosystem response variables

Community GPP: Community gross primary production was highest at 35°C ($F_{2, 26} = 404.295$, $P < 0.001$), decreased as a function of sampling date ($F_{1, 33} = 41.066$, $P < 0.001$), and had a significant sampling date x temperature interaction ($F_{1, 33} = 36.007$, $P < 0.001$) (Fig. 1a). Gross primary production increased as a function of A. ligamentina biomass at 35°C on days 1, 4, and 9 and at 25°C on days 4 and 14 (Fig. 2a). Amblema plicata increased community GPP at 15°C on Day 1, 25°C on days 1, 4, and 9 and at 35°C on days 14 (Fig. 2b). Community GPP was not related to Q. pustulosa relative biomass (Fig. 2c) (Table 4).

Benthic GPP: Benthic gross primary production increased with temperature, and was highest at 35°C ($F_{2, 31} = 69.21$, $P < 0.001$) (Fig. 1b), increasing as a function of A. plicata biomass at 15 and 35°C, but not 25°C (Fig. 2d, Table 3). However, benthic chlorophyll a was highest at 25°C, ($F_{2, 31} = 14.391$, $P < 0.001$) (Table 3), and non-significantly increased with A. plicata biomass at 25°C (Table 3). There was no relationship between benthic gross primary production and A. ligamentina (Fig. 2e) or Q. pustulosa (Fig. 2f) relative biomass.

Water column GPP and nutrients: Water column gross primary production was highest at 15°C but did not differ between 25 and 35°C ($F_{2, 24} = 13.949$, $P < 0.001$) (Fig. 1c). Additionally, there were no significant effects of sampling date ($F_{1, 24} = 0.016$, $P = 0.901$) or temperature x sampling date interactions ($F_{2, 24} = 0.960$, $P = 0.397$). Primary production increased with A. ligamentina biomass on day 9 at 25°C, and Day 14 at 35°C (Fig. 2g) (Table 4). Water column chlorophyll a was variable and did not differ significantly between temperature treatments ($F_{2, 24} = 2.092$, $P = 0.139$), sampling date ($F_{1, 33} = 1.801$, $P = 0.189$) or interaction of the two ($F_{2, 33} = 1.425$, $P = 0.255$). However, chlorophyll a did increase with A. ligamentina biomass at 35°C on Day 4 and 14, Q. pustulosa, at 25°C on Day 4, and A. plicata at 25°C on Day 9 (Table 4).

Water column total nitrogen increased with temperature and was highest at 35°C ($F_{2, 33} = 8.755$, $P = 0.001$), significantly differed among sampling dates ($F_{1, 33} = 8.834$, $P = 0.005$), and had a significant sampling date x temperature interaction ($F_{2, 33} = 47.191$, $P < 0.001$) with TN concentrations highest on day 14 (Supplementary data A). TN increased as a function of A. ligamentina relative biomass at 25°C on days 4 and 9 and at 35°C on day 14. TN increased as a function of A. plicata at 25°C on day 9 (Table 4).

Water column total phosphorus was highest at 35°C ($F_{2, 33} = 10.903$, $P < 0.001$), differed according to sampling date ($F_{1, 33} = 156.505$, $p < 0.001$), and was highest on day 14 at 35°C ($F_{2, 33)} = 20.456$, $p < 0.001$). TP increased as a function of A. ligamentina biomass at 25 and 35°C on day 4, and increased as a function of A. plicata biomass on day 1 at 15 and 25°C, and day 9 at 25°C. Water column N:P ratios increased with temperature ($F_{2, 26} = 8.057$, $p = 0.002$), and sampling date ($F_{1, 26} = 275.668$, $p < 0.001$) but were lowest on day 14, and had a significant sampling date x temperature interaction ($F_{2,}$

$_{26}$ = 12.876, P < 0.001). However, water column N:P ratios were not influenced by dominant species biomass (Table 4).

Individual response variables

Mass-specific oxygen consumption was highest at 25°C for A. ligamentina ($F_{2, 33}$ = 1.667, P = 0.204) (Fig. 3a), and A. plicata ($F_{2, 33}$ = 1.658, P = 0.204). However, oxygen consumption increased with temperature and was highest at 35°C for M. nervosa ($F_{2, 33}$ = 6.232, P = 0.005), O. reflexa ($F_{2, 33}$ = 7.163, P = 0.003), and Q. pustulosa ($F_{2, 33}$ = 17.380, P < 0.001) (Fig. 3m). Actinonaias ligamentina was the only species to influence oxygen consumption rates of other species; this effect was strongest at 35°C where consumption rates of A. plicata (Fig. 3d), M. nervosa (Fig. 3g), and O reflexa (Fig. 3j, Table 5) were increased. Conversely, A. ligamentina decreased oxygen consumption rates of M. nervosa and O. reflexa at 25°C, which suggests that the nature of species interactions between A. ligamentina and other species may depend on thermal context.

Ammonia excretion rates increased with temperature for all species ((A. ligamentina, ($F_{2, 33}$ = 2.761, P = 0.054)), (A. plicata, ($F_{2, 33}$ = 4.155, P = 0.026)), M. nervosa, ($F_{2, 33}$ = 1.327, P = 0.279)), (O. reflexa ($F_{2, 33}$ = 1.121, P = 0.338)), (Q. pustulosa ($F_{2, 33}$ = 1.340, P = 0.274)). In addition, A. ligamentina significantly influenced ammonia excretion rates at 25°C for A. ligamentina (decreased), A. plicata, (increased), and O. reflexa at 35°C (Table 5). Phosphorus excretion rates were greatest at 25°C for all species: A. ligamentina, ($F_{2, 33}$ = 20.226, P < 0.001); A. plicata, ($F_{2, 33}$ = 18.021, P < 0.001); M. nervosa, ($F_{2, 33}$ = 14.343, P < 0.001); O. reflexa ($F_{2, 33)}$ = 11.769, P < 0.001); and Q. pustulosa ($F_{2, 33}$ = 30.773, P < 0.001). Actinonaias ligamentina increased

phosphorus excretion rates of Q. pustulosa and O. reflexa at 35°C, whereas A. plicata increased phosphorus excretion of A. ligamentina at 25°C (Table 5).

Molar N:P excretion rates were variable and were highest for all species at 35°C. Amblema plicata N:P ratios increased as a function of A. ligamentina relative biomass at 25°C (Table 5). In addition, A. ligamentina excretion ratios increased at 25 and 35°C, and A. plicata ratios increased at 25°C with increased A. plicata relative biomass (Table 4). Obliquaria reflexa excretion increased with increased Q. pustulosa biomass at 15°C (Table 5).

Discussion

Freshwater mussels occur as large, species-rich aggregations that can account for a large portion of the benthic biomass in lakes and streams (Vaughn and Hakenkamp 2001). Because they are aggregated, sedentary, and forage in a similar manner (i.e. filter feeders), the potential for species interactions is high. Because they are ectotherms, environmental temperature should constrain their activity level and thus the magnitude of their contributions to ecosystems. Our results demonstrate that environmental context (temperature) and the functional traits of numerically dominant species interactively influence resource acquisition and ecosystem services provided by less dominant species, and that this can lead to effects across multiple ecosystem compartments.

The importance of functional trait diversity within communities highlights not only the significance of different functional modes in resource use and material cycling, but also the relative strength of species interactions. Within a community, functionally similar species may exhibit a higher magnitude of interactions (competition or

facilitation) than less similar species due to the increased use of shared resources (Tilman 1994). Although all mussels are filter feeders, filtration rates are strongly influenced by temperature, with different species having different temperature-filtration optima (Spooner 2007). Thus, the importance of different species in cycling and transferring materials should differ with thermal context. Our results highlight the importance of thermal context to species interactions, with positive effects of A. ligamentina dominance on the condition (oxygen consumption) of M. nervosa, O. reflexa, and body condition index of A. plicata at 25°C. Conversely, the condition (oxygen consumption and body condition index) of M. nervosa, O. reflexa, and body condition index of A. plicata at 35°C decreased with A. ligamentina dominance. With the exception of Q. pustulosa increasing the body condition of M. nervosa at 15°C and negatively at 35°C, no other species influenced the condition of others within treatments. In addition to interspecific competition, there appeared to be intraspecific competition between A. ligamentina individuals at 25°C as evidenced by increased oxygen consumption rates with increasing A. ligamentina dominance. Interestingly, the majority of species interactions appear to be the result of increased presence of A. ligamentina within treatments, which was also documented in a field experiment by (Vaughn et al. 2007).

Shifts in the magnitude and direction of species interactions with changing environments are well-documented, but mostly in plant communities (Wardle and Peltzer 2003). However, unlike our findings, most studies have documented facilitative interactions under harsh conditions and competitive interactions under more favorable, stable conditions (Stachowicz 2001, Bruno et al. 2003). For example, Pugnaire and Luque (2001) observed shifts in the net balance of species interactions between legume

shrubs along a soil gradient with positive interactions occurring in water-stressed soil and neutral or negative interactions in fertile, more productive soil. These patterns have also been observed in intertidal invertebrate-plant communities (Bertness and Leonard 1997). Although we found the reverse pattern, the definition of a "stressful environment" is likely different for different mussel species. For example, 35^{o}C may be a stressful environment for A. ligamentina and Q. pustulosa, but a potentially favorable one for other species (A. plicata, M. nervosa, and O. reflexa) that are more tolerant of warmer environments (Spooner 2007). In a field study comparing mussel body condition across 21 mussel beds, we found lower oxygen consumption rates and higher body condition indices in more species-rich mussel beds (Spooner 2007). Mussel condition also was greatest at sites that were more thermally variable, which may imply use of temporal or spatially discrete thermal niches by different mussel species within a bed (Magnuson et al. 1979). However, these patterns may also be explained by greater variation in interactions (facilitation, competition) between species at more environmentally variable sites (Hartley and Jones 2003).

We found that in addition to affecting resource acquisition species interactions associated with dominance also influenced the nutrient excretion rates of other species within communities. For example, A. plicata ammonia excretion increased at 25 and 35^{o}C, and O. reflexa at 35^{o}C as a function of A. ligamentina mesocosm biomass. Additionally, M. nervosa and O. reflexa ammonia excretion increased with A. plicata biomass, and Q. pustulosa and O. reflexa phosphorus excretion rates increased at 35^{o}C with increasing A. ligamentina biomass. Few other studies have addressed the role of competitive interactions between consumers to nutrient excretion ratios; those that have

demonstrated that shifts in dominance or population dynamics within communities can result in changes in nutrients contributed by the entire community because of novel species excreting at different ratios (Vanni et al. 2002). For example, McIntyre et al. (2007) found that shifts in cichlid community composition altered the nature of nutrient cycling in African lakes. Although we have predicted similar effects from altering species composition of mussel communities (Vaughn et al. 2008), our results from this study demonstrate that species interactions can cause changes in excretion rates within species. Further, these effects have the potential to influence both the quantity and quality (N:P ratios) of nutrient subsidies and therefore may have lasting stoichiometric implications at higher trophic levels (Hessen et al. 2004, Diehl et al. 2005).

Primary production differed between compartments within mesocosms, and these differences were related to species composition. For example, benthic gross primary production increased as a function of A. plicata biomass at 35^{o}C (Fig. 2), yet water column gross primary production increased as a function A. ligamentina at 15 and 35^{o}C. Although benthic gross primary production increased as a function of A. plicata relative abundance, there was no relationship between the amount of benthic chlorophyll a and species abundance at any of the experimental temperatures. However, elevated benthic primary production in A. plicata dominated communities may be a result of differences in benthic algal species composition or novel microbial interactions resulting from A. plicata activities. Previous laboratory studies have demonstrated that at 35^{o}C Amblema is somewhat unencumbered and continues to filter materials out of the water column, whereas A. ligamentina slows down and shifts from aerobic activities to tissue catabolism (Spooner and Vaughn 2008). These subtle differences in thermal traits may explain

greater movement of energy and nutrients from the water column to the sediment in A. plicata-dominated communities, resulting in different benthic algal and/or microbial communities.

Both water column gross primary production and chlorophyll a were strongly related to A. ligamentina relative biomass. However, the mechanism for these effects may be due to different species responses to temperature. Primary production increased at 25 and 35°C, and chlorophyll a decreased at 25°C and increased at 35°C with respect to A. ligamentina relative abundance. These changes in chlorophyll a can be explained by increased filtration rates at 25°C and decreased filtration rates at 35°C that are related to A. ligamentina thermal optima. Other species (A. plicata, M. nervosa, and O. reflexa) may have contributed to increased removal of algae through their positive associations with A. ligamentina at 25°C, and decreased algal removal associated with negative associations occurring at 35°C. Moreover, in addition to filtration activities, fertilization effects associated with nutrient excretion may also explain the disparity in chlorophyll a abundance between 25 and 35°C. Water column nitrogen and phosphorus concentrations were highest at 35°C, and for the most part related to the presence A. ligamentina at both 25 and 35°C. Excretion rates of M. nervosa and O. reflexa increased at 35°C; and A. plicata at 25°C, with A. ligamentina relative abundance which may be due to stress associated with competitive interactions. Furthermore, these differences in contributed nutrients may have resulted in differences in water column algal and microbial composition which could explain increased gross primary production at both 25 and 35°C.

Understanding how species traits and species interactions map onto a changing environmental landscape is critical to predicting the consequences of shifts in community structure with climate change. Many mussel species in our study region are already experiencing temperatures in the upper end of their thermal tolerance zone, and we have observed changes in mussel community structure that are linked to stream warming, with thermally-tolerant species increasing and thermally sensitive species decreasing in relative abundance (Galbraith et al., unpublished). The magnitude, periodicity and duration of droughts are increasing in the southern U.S., and mean summer temperatures are predicted to increase by as much as 4^{o}C over the next 50 years (Mulholland et al. 1997). These projected temperature increases (and associated decreased precipitation) will likely profoundly influence mussel community structure and the services that they provide to ecosystems.

Most studies investigating the ecosystem services provided by communities have focused on the role of species richness by comparing the relative yield of species monocultures to those of multiple species (polycultures) (Petchey 2003). The underlying premise of this approach assumes that the resulting effects of species richness are due to either: (1) greater response resulting from interspecific competition/facilitation resulting in enhanced ecosystem services (productivity, stability) (Loreau et al. 2001); or (2) the inclusion of species with novel traits that are better adapted to the experimental conditions, resulting in overall greater ecosystem effects (productivity, stability, etc) (Loreau and Hector 2001). This approach is widely accepted and has demonstrated singular or combined effects of species richness and species identity on ecosystem services (Cardinale et al. 2002, Fox 2005). However, for logistic and statistical purposes,

most of these studies have manipulated species richness by holding species dominance constant across treatments. Our study, which held species richness constant and manipulated the relative dominance of species, allowed us to demonstrate that species traits, species dominance and environmental context interactively contribute to the ecosystem services provided by communities (in this case gross primary production of mussel beds). Our results suggest that the direction and magnitude of species interactions (facilitation/competition) are related to both community composition and environmental context, and suggest that caution should be used in interpreting the results of additive monoculture/polyculture experiments.

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Table 1. Experimental design illustrating the manipulation (number of individuals) of species dominance within each stream. Stream assignment was randomly selected for each experimental run (temperature).

Stream	A.ligamentina	A. plicata	Q. pustulosa	M. nervosa	O. reflexa
1	4	1	7	3	2
2	7	2	1	3	4
3	1	4	7	3	2
4	2	7	4	2	2
5	2	4	1	7	3
6	0	0	0	0	0
7	7	2	4	3	1
8	2	1	7	4	3
9	4	1	2	3	7
10	7	4	2	1	3
11	1	2	4	3	7
12	2	7	1	3	4
13	0	0	0	0	0
14	4	7	2	1	3

Table 2. Pearson correlation coefficients for species biomass demonstrating that dominance treatment assignments were independent of each other (r-value , p-value in parenthesis).

	A. lig.	A. plic.	Q. pust.	M. nerv.	O. refl.
A. ligamentina	1	0.08 (0.77)	0.01 (0.97)	0.08 (0.79)	0.16 (0.58)
A. plicata		1	0.04 (0.90)	0.10 (0.73	0.11 (0.70)
Q. pustulosa			1	0.29 (0.32)	0.04 (0.88)
M. nervosa				1	0.38 (0.19)
O. reflexa					1

Table 3. Regression results demonstrating the relationship between species dominance and benthic gross primary production and chlorophyll a at experimental temperatures. Letters in the slope column denote significantly different slopes using the Wilcox Dunnett multiple comparison procedure evaluated at $\alpha = 0.05$

Variable	Species	Temp	F	R^2	P-value	slope
Benthic GPP	***A. ligamentina***	**15**	0.42	0.045	0.533	a
		25	0.041	0.004	0.844	a
		35	0.65	0.067	0.441	a
	A. plicata	**15**	**4.298**	**0.323**	**0.052**	**b**
		25	2.292	0.186	0.161	a
		35	**12.748**	**0.586**	**0.006**	**b**
	Q. pustulosa	**15**	0.003	0	0.954	a
		25	0.167	0.016	0.692	a
		35	0.084	0.009	0.778	a
Benthic chl a	***A. ligamentina***	**15**	0.08	0.009	0.74	a
		25	3.076	0.235	0.11	a
		35	2.98	0.249	0.118	a
	A. plicata	**15**	1.484	0.142	0.254	a
		25	3.338	0.25	0.098	a
		35	1.352	0.131	0.275	a
	Q. pustulosa	**15**	0.019	0.002	0.894	a
		25	0.731	0.068	0.412	a
		35	0.323	0.035	0.584	a

Table 4. Regression analysis of the effect of species dominance on ecosystem response variables.

Values in the slope column represent significantly different slopes based on Wilcox procedure (Wilcox 1987).

	Water column		GPP				chl a				TN				TP				N:P				Community GPP			
Day	Species	Temp	F	R^2	P	slope	F	R^2	P	slope	F	R^2	P	slope	F	R^2	P	slope	F	R^2	P	slope	F	R^2	P	slope
		15	0.00	0.00	0.97	a	1.83	0.16	0.21	a	3.01	0.23	0.11	a	0.69	0.08	0.43	a	0.19	0.02	0.67	a	0.31	0.03	0.59	a
	A. ligamentina	**25**	1.90	0.21	0.21	a	0.01	0.00	0.93	a	0.62	0.06	0.45	a	1.50	0.16	0.26	a	0.46	0.05	0.52	a	0.64	0.06	0.44	a
		35	0.10	0.01	0.76	a	1.83	0.16	0.21	a	1.54	0.13	0.24	a	3.15	0.28	0.11	a	2.16	0.30	0.20	a	***22.77***	***0.70***	***0.00***	***b***
1		**15**	0.51	0.07	0.50	a	0.11	0.01	0.75	a	1.10	0.10	0.32	a	***18.64***	***0.70***	***0.00***	***b***	0.80	0.07	0.39	a	***8.35***	***0.46***	***0.02***	***b***
	A. plicata	**25**	2.29	0.19	0.16	a	0.13	0.01	0.73	a	2.36	0.19	0.16	a	***5.60***	***0.41***	***0.05***	***b***	0.74	0.09	0.42	a	***26.43***	***0.73***	***0.00***	***b***
		35	0.87	0.11	0.38	a	1.69	0.16	0.23	a	0.60	0.06	0.46	a	1.44	0.15	0.27	b	0.03	0.01	0.86	a	3.67	0.29	0.08	a
		15	0.23	0.03	0.64	a	0.11	0.01	0.75	a	2.30	0.19	0.16	a	0.02	0.00	0.90	b	0.37	0.04	0.56	a	0.03	0.00	0.86	a
	Q. pustulosa	**25**	0.04	0.00	0.84	a	0.13	0.01	0.73	a	0.47	0.04	0.51	a	0.03	0.00	0.87	b	3.18	0.28	0.11	a	0.06	0.01	0.82	a
		35	0.35	0.05	0.57	a	1.69	0.16	0.23	a	0.21	0.02	0.66	a	1.80	0.18	0.22	b	0.03	0.01	0.86	a	0.67	0.06	0.43	a
		15	0.01	0.00	0.93	a	3.06	0.25	0.11	a	0.24	0.02	0.64	a	0.07	0.01	0.80	a	0.21	0..021	0.07	a	3.17	0.24	0.11	a
	A. ligamentina	**25**	0.16	0.02	0.70	a	***3.63***	***0.27***	***0.09***	***b***	***14.62***	***0.59***	***0.00***	***b***	***7.02***	***0.47***	***0.03***	***b***	0.00	0.00	0.96	a	***7.42***	***0.43***	***0.02***	***b***
		35	0.25	0.04	0.63	a	***6.81***	***0.43***	***0.03***	***b***	2.80	0.22	0.13	a	***17.96***	***0.69***	***0.00***	***b***	0.02	0.00	0.90	a	***18.15***	***0.65***	***0.00***	***b***
4		**15**	***4.30***	***0.32***	***0.07***	***b***	0.35	0.04	0.57	a	1.01	0.09	0.34	a	0.03	0.00	0.88	a	1.52	0.13	0.25	a	3.12	0.24	0.11	a
	A. plicata	**25**	0.06	0.01	0.82	a	4.75	0.32	0.54	a	3.70	0.27	0.08	a	1.19	0.13	0.31	a	0.28	0.03	0.61	a	**6.39**	**0.39**	**0.03**	**b**
		35	0.00	0.00	0.99	a	0.84	0.09	0.38	a	0.01	0.00	0.93	a	1.95	0.20	0.20	a	0.08	0.02	0.78	a	3.67	0.27	0.09	a
		15	0.27	0.04	0.62	a	0.35	0.04	0.57	a	0.28	0.03	0.61	a	1.22	0.13	0.30	a	0.55	0.05	0.48	a	0.06	0.01	0.82	a
	Q. pustulosa	**25**	0.53	0.07	0.49	a	***4.75***	***0.32***	***0.05***	***b***	0.48	0.05	0.50	a	0.00	0.00	0.96	a	0.04	0.01	0.84	a	0.02	0.00	0.89	a
		35	0.28	0.04	0.61	a	0.84	0.09	0.38	a	0.48	0.05	0.50	a	0.19	0.02	0.68	a	1.77	0.26	0.24	a	0.37	0.04	0.56	a
		15	0.21	0.03	0.66	a	1.36	0.13	0.27	a	0.11	0.01	0.75	a	0.63	0.07	0.45	a	0.01	0.00	0.94	a	1.94	0.16	0.19	a
	A. ligamentina	**25**	***15.18***	***0.68***	***0.01***	***b***	0.53	0.05	0.48	a	***7.17***	***0.42***	***0.02***	***a***	2.43	0.23	0.16	a	1.41	0.15	0.27	a	1.82	0.15	0.21	a
		35	0.02	0.00	0.89	a	0.57	0.06	0.49	a	0.98	0.09	0.35	a	2.92	0.27	0.13	a	0.23	0.04	0.65	a	***4.57***	***0.31***	***0.06***	***b***
9		**15**	**4.30**	**0.32**	**0.07**	b	3.06	0.25	0.11	a	0.09	0.01	0.77	a	0.00	0.00	0.96	a	0.02	0.00	0.89	a	3.37	0.25	0.10	a
	A. plicata	**25**	0.08	0.01	0.78	a	***8.34***	***0.46***	***0.02***	***b***	***9.72***	***0.49***	***0.01***	***b***	***4.69***	***0.37***	***0.06***	***b***	1.06	0.12	0.33	a	***6.27***	***0.39***	***0.03***	***b***
		35	0.08	0.01	0.78	a	3.21	0.26	0.11	a	0.36	0.03	0.56	a	0.88	0.10	0.38	a	0.30	0.06	0.61	a	3.40	0.25	0.10	a
		15	0.42	0.06	0.54	a	3.06	0.25	0.11	a	0.60	0.06	0.46	a	0.00	0.00	0.98	a	0.18	0.02	0.69	a	0.00	0.00	0.96	a
	Q. pustulosa	**25**	0.02	0.00	0.90	a	***8.34***	***0.46***	***0.02***	***b***	0.06	0.01	0.82	a	0.88	0.10	0.38	a	2.08	0.21	0.19	a	0.91	0.08	0.36	a
		35	0.79	0.10	0.40	a	3.21	0.26	0.11	a	0.79	0.07	0.40	a	0.48	0.05	0.53	a	1.23	0.20	0.32	a	0.51	0.05	0.49	a
		15	0.01	0.00	0.95	a	1.76	0.16	0.22	a	0.35	0.03	0.57	a	0.63	0.07	0.45	a	0.15	0.02	0.71	a	2.02	0.17	0.19	a
	A. ligamentina	**25**	1.28	0.15	0.30	a	1.05	0.10	0.33	a	0.22	0.02	0.65	a	0.00	0.00	0.99	a	1.41	0.15	0.27	a	***5.02***	***0.33***	***0.05***	***b***
		35	***12.25***	***0.64***	***0.01***	***b***	***4.03***	***0.31***	***0.08***	***b***	***3.93***	***0.28***	***0.08***	***b***	1.44	0.15	0.27	a	0.01	0.00	0.94	a	3.47	0.26	0.09	a
14		**15**	1.41	0.17	0.27	a	0.77	0.08	0.41	a	0.90	0.08	0.36	a	1.23	0.13	0.30	a	1.56	0.14	0.24	a	0.91	0.36	0.08	a
	A. plicata	**25**	0.24	0.03	0.64	a	0.00	0.00	0.98	a	1.46	0.13	0.26	a	0.34	0.04	0.57	a	0.54	0.06	0.48	a	3.14	0.24	0.11	a
		35	0.01	0.00	0.94	a	0.08	0.01	0.79	a	0.52	0.05	0.49	a	0.72	0.08	0.42	a	***4.60***	***0.48***	***0.09***	***b***	***11.13***	***0.53***	***0.01***	***b***
		15	0.42	0.05	0.53	a	0.77	0.08	0.41	a	1.78	0.15	0.21	a	1.52	0.16	0.25	a	0.42	0.04	0.53	a	0.53	0.05	0.49	a
	Q. pustulosa	**25**	0.17	1.38	0.28	a	0.00	0.00	0.98	a	0.07	0.01	0.79	a	2.55	0.24	0.15	a	0.00	0.00	1.00	a	0.26	0.03	0.62	a
		35	0.35	0.05	0.57	a	1.23	0.12	0.30	a	1.33	0.12	0.28	a	0.28	0.03	0.61	a	0.92	0.16	0.38	a	0.00	0.00	0.95	a

Table 5. Regression results of the effect of species dominance on resource assimilation and ecosystem services. Values in the slope column represent significantly different slopes (Wilcox 1987).

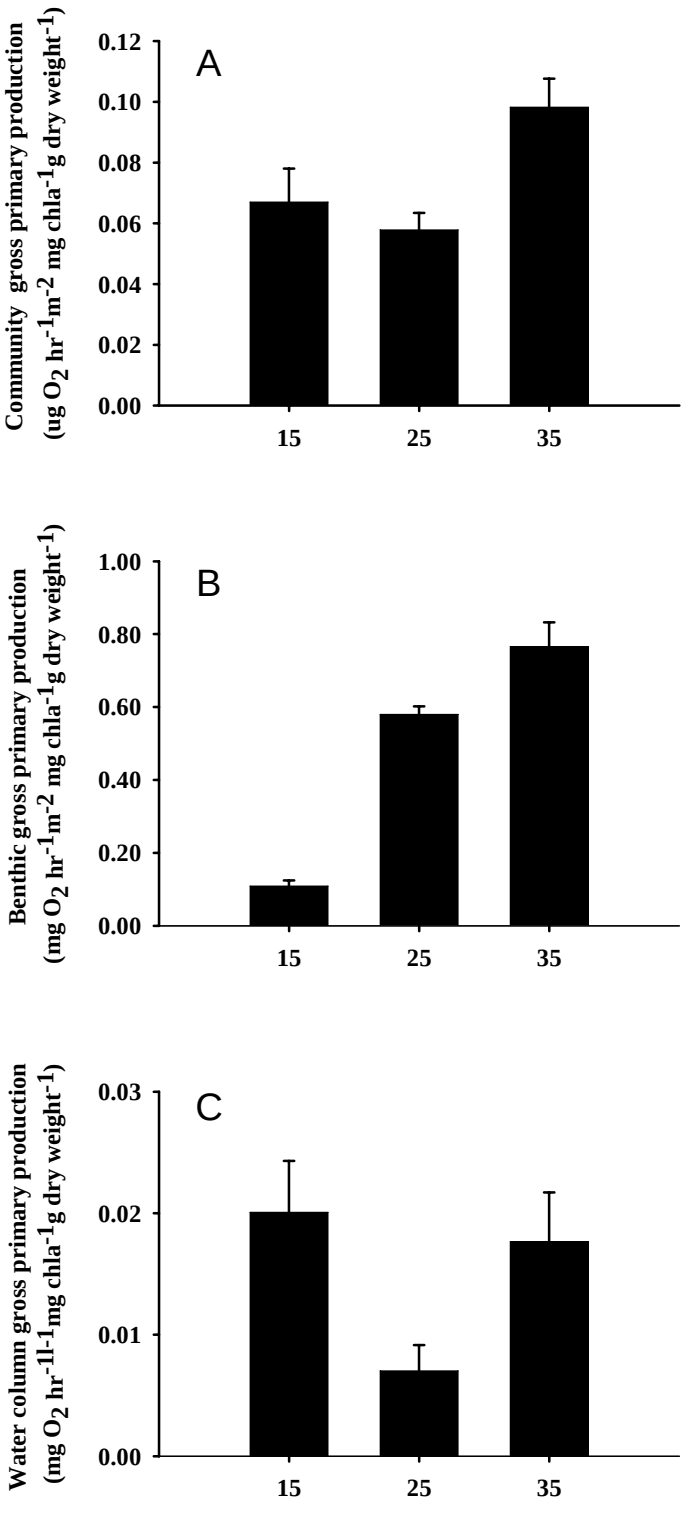
	Individual		Oxygen consumption				Delta BCI				Phosphorus excretion				Ammonia excretion				N:P excretion			
Effect	Species	Temp	F	R^2	P	slope	F	R^2	P	slope	F	R^2	P	slope	F	R^2	P	slope	F	R^2	P	slope
	A. ligamentina	15	0.36	0.04	0.56	a	0.03	0.00	0.88	a	0.08	0.01	0.78	a	0.17	0.02	0.69	a	0.07	0.01	0.79	a
		25	***0.04***	***0.45***	***0.00***	***b***	0.06	0.01	0.81	a	0.35	0.04	0.57	a	***4.81***	***0.40***	***0.03***	***b***	0.00	0.00	0.98	a
		35	1.55	0.15	0.25	a	0.03	0.00	0.87	a	1.26	0.12	0.29	a	0.66	0.07	0.44	a	0.91	0.09	0.37	a
	A. plicata	15	0.13	0.01	0.73	a	0.25	0.02	0.63	a	0.09	0.01	0.77	a	0.82	0.08	0.39	a	0.87	0.08	0.37	a
		25	0.01	0.00	0.94	a	***6.83***	***0.41***	***0.03***	***b***	0.01	0.00	0.92	a	***4.35***	***0.30***	***0.05***	***c***	***8.74***	***0.49***	***0.02***	***b***
		35	***3.98***	***0.36***	***0.09***	***b***	***6.03***	***0.38***	***0.03***	***c***	0.34	0.05	0.58	a	0.04	0.00	0.85	a	0.06	0.01	0.82	a
		15	0.94	0.09	0.36	a	0.93	0.09	0.36	a	0.71	0.07	0.42	a	0.00	0.00	0.99	a	0.10	0.01	0.76	a
A. ligamentina	Q. pustulosa	25	0.17	0.02	0.69	a	0.88	0.08	0.37	a	0.81	0.08	0.39	a	0.62	0.06	0.45	a	0.16	0.02	0.70	a
	-	35	0.05	0.01	0.83	a	0.00	0.00	0.95	a	***3.73***	***0.29***	***0.09***	***b***	1.35	0.13	0.28	a	0.40	0.04	0.55	a
	M. nervosa	15	0.21	0.02	0.66	a	0.01	0.00	0.92	a	0.44	0.04	0.52	a	1.92	0.16	0.20	a	0.34	0.03	0.57	a
		25	***16.4***	***0.62***	***0.00***	***b***	0.88	0.08	0.37	a	0.24	0.02	0.65	a	0.72	0.07	0.41	a	1.89	0.16	0.20	a
		35	***9.02***	***0.50***	***0.02***	***c***	1.76	0.15	0.22	a	0.02	0.00	0.88	a	0.14	0.02	0.72	a	0.04	0.00	0.86	a
	O. reflexa	15	0.40	0.03	0.54	a	***10.8***	***0.52***	***0.01***	***b***	0.01	0.00	0.91	a	0.48	0.05	0.51	a	0.07	0.79	0.40	a
		25	***5.45***	***0.35***	***0.04***	***b***	0.07	0.01	0.79	a	0.01	0.00	0.92	a	0.01	0.00	0.93	a	0.21	0.02	0.65	a
		35	***7.41***	***0.45***	***0.02***	***c***	0.20	0.02	0.66	a	***7.70***	***0.47***	***0.02***	***b***	***7.80***	***0.46***	***0.02***	***b***	1.00	0.10	0.35	a
	A. ligamentina	15	1.30	0.12	0.28	a	1.84	0.16	0.21	a	2.61	0.21	0.14	a	0.00	0.00	0.97	a	***3.51***	***0.26***	***0.09***	***b***
		25	0.57	0.06	0.47	a	0.20	0.02	0.67	a	***13.4***	***0.60***	***0.01***	***b***	0.39	0.04	0.55	a	***9.23***	***0.51***	***0.01***	***b***
		35	0.01	0.00	0.92	a	1.83	0.16	0.21	a	0.36	0.04	0.57	a	0.69	0.07	0.43	a	0.50	0.05	0.50	a
	A. plicata	15	0.04	0.00	0.84	a	0.05	0.01	0.82	a	1.48	0.13	0.25	a	0.86	0.08	0.38	a	***3.68***	***0.27***	***0.08***	***b***
		25	1.50	0.14	0.25	a	0.01	0.00	0.92	a	0.18	0.02	0.68	a	0.00	0.00	0.98	a	1.39	0.13	0.27	a
		35	0.70	0.09	0.43	a	0.23	0.02	0.64	a	1.09	0.13	0.33	a	0.33	0.04	0.58	a	0.13	0.02	0.73	a
	Q. pustulosa	15	1.46	0.13	0.25	a	0.45	0.04	0.52	a	0.70	0.07	0.42	a	0.52	0.05	0.49	a	1.59	0.14	0.24	a
A. plicata		25	2.45	0.20	0.15	a	0.76	0.07	0.40	a	0.35	0.03	0.57	a	2.77	0.22	0.13	a	1.97	0.16	0.19	a
	-	35	0.58	0.06	0.46	a	0.02	0.00	0.90	a	0.00	0.00	0.99	a	0.00	0.00	0.97	a	0.23	0.03	0.64	a
	M. nervosa	15	0.00	0.00	0.99	a	2.32	0.21	0.16	a	3.66	0.27	0.09	a	4.13	0.29	0.07	a	0.14	0.01	0.72	a
		25	1.79	0.15	0.21	a	2.82	0.22	0.12	a	0.81	0.08	0.39	a	1.34	0.12	0.27	a	0.00	0.00	0.99	a
		35	0.24	0.03	0.64	a	0.02	0.00	0.90	a	0.51	0.23	0.50	a	0.68	0.07	0.43	a	0.69	0.07	0.43	a
	O. reflexa	15	0.06	0.00	0.94	a	0.24	0.02	0.64	a	0.02	0.00	0.91	a	***7.6***	***0.4***	***0.0***	***b***	***9.6***	***0.5***	***0.0***	***b***
		25	0.84	0.08	0.38	a	1.19	0.11	0.30	a	0.27	0.03	0.62	a	0.34	0.03	0.57	a	0.00	0.00	0.98	a
		35	0.01	0.00	0.91	a	3.22	0.24	0.10	a	1.08	0.11	0.33	a	1.95	0.20	0.18	a	0.74	0.08	0.41	a
	A. ligamentina	15	1.30	0.12	0.28	a	0.44	0.04	0.52	a	0.02	0.00	0.89	a	1.06	0.10	0.33	a	1.92	0.16	0.20	a
		25	0.63	0.07	0.45	a	1.35	0.13	0.28	a	0.68	0.07	0.43	a	2.78	0.22	0.13	a	0.87	0.09	0.38	a
		35	0.04	0.01	0.84	a	2.74	0.23	0.13	a	1.75	0.16	0.22	a	0.08	0.01	0.79	a	0.12	0.01	0.74	a
	A. plicata	15	2.07	0.17	0.18	a	0.05	0.01	0.83	a	0.01	0.00	0.94	a	1.47	0.13	0.25	a	1.10	0.10	0.32	a
		25	0.09	0.01	0.77	a	2.44	0.21	0.15	a	***7.32***	***0.45***	***0.02***	***b***	4.60	0.32	0.06	a	0.02	0.00	0.90	a
		35	0.30	0.04	0.60	a	0.02	0.00	0.88	a	1.15	0.14	0.32	a	0.48	0.05	0.51	a	0.38	0.05	0.56	a
	Q. pustulosa	15	1.58	0.14	0.24	a	0.17	0.02	0.69	a	2.70	0.21	0.13	a	3.03	0.23	0.11	a	0.84	0.08	0.38	a
Q. pustulosa		25	0.84	0.08	0.38	a	0.10	0.01	0.76	a	0.09	0.01	0.77	a	0.74	0.07	0.41	a	0.10	0.01	0.75	a
	-	35	1.93	0.18	0.20	a	0.05	0.01	0.83	a	0.87	0.09	0.38	a	2.32	0.21	0.16	a	1.31	0.13	0.28	a
	M. nervosa	15	0.43	0.04	0.53	a	***4.67***	***0.32***	***0.06***	***c***	0.12	0.01	0.74	a	0.27	0.03	0.62	a	0.06	0.01	0.82	a
		25	1.37	0.12	0.27	a	1.49	0.13	0.25	a	1.98	0.17	0.19	a	0.50	0.05	0.49	a	0.59	0.06	0.46	a
		35	1.31	0.13	0.28	a	***14.7***	***0.62***	***0.00***	***b***	2.55	0.22	0.15	a	0.06	0.01	0.82	a	0.16	0.02	0.70	a
	O. reflexa	15	3.03	0.23	0.11	a	1.86	0.16	0.20	a	0.40	0.04	0.54	a	1.89	0.16	0.20	a	***4.46***	***0.31***	***0.06***	***b***
		25	0.16	0.02	0.70	a	3.45	0.26	0.09	a	2.07	0.17	0.18	a	1.69	0.14	0.22	a	0.36	0.04	0.56	a
		35	0.37	0.04	0.56	a	1.51	0.14	0.25	a	0.09	0.01	0.77	a	0.19	0.02	0.68	a	0.49	0.05	0.50	a

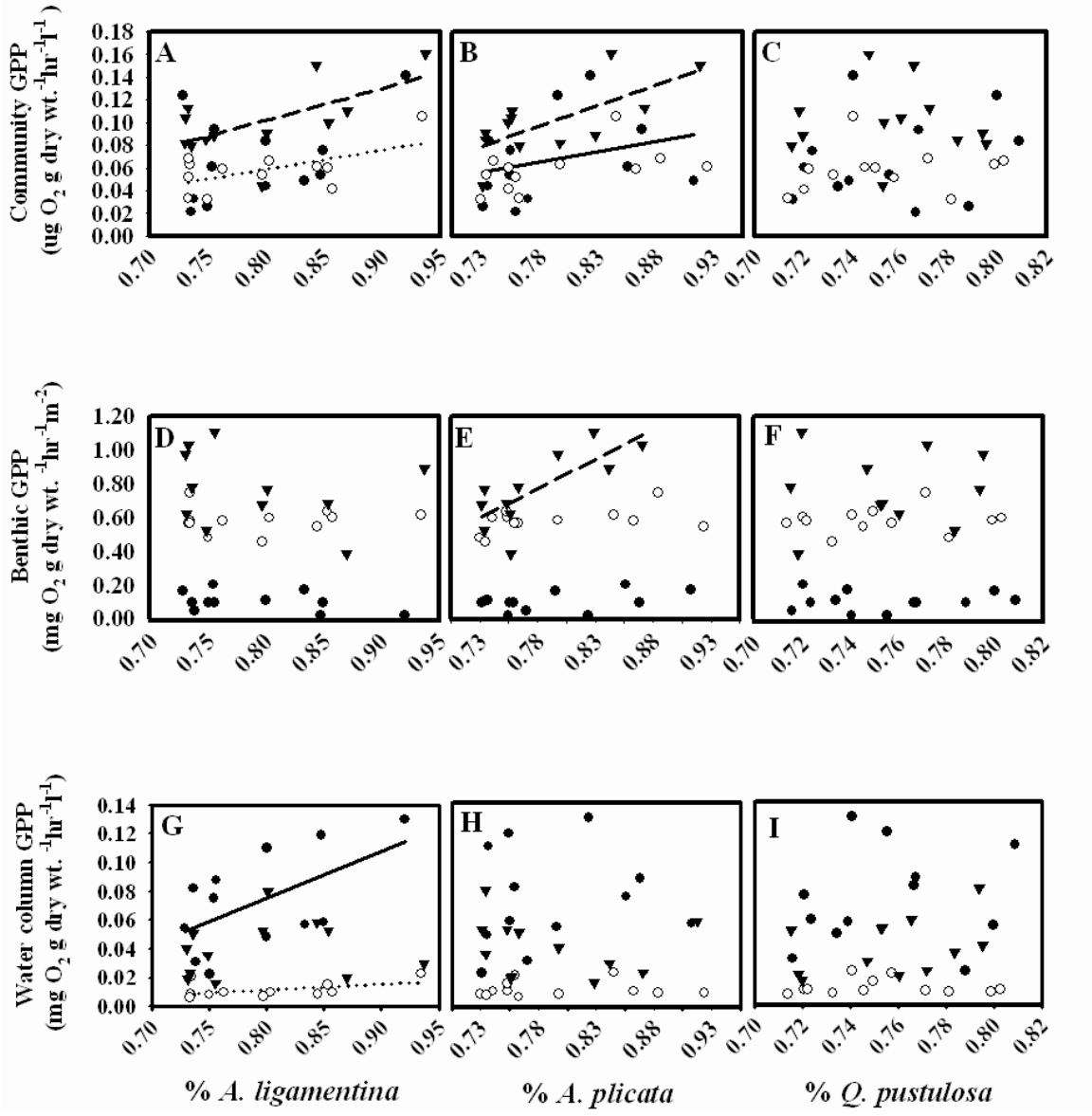
Figure Legend

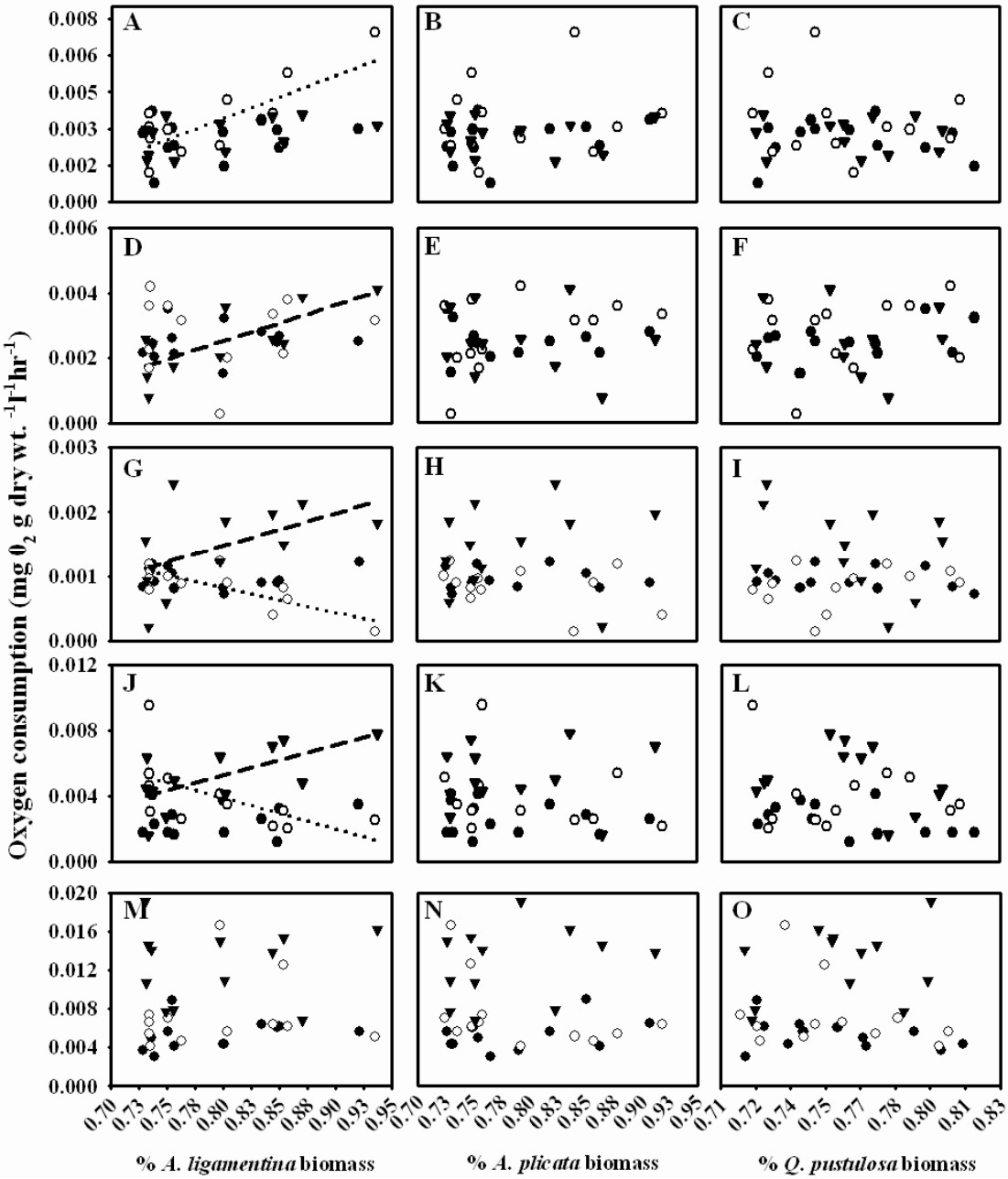
Figure 1. Effect of water temperature on (A) Mean community gross primary production, (B) Mean benthic gross primary production, and (C) Mean water-column gross primary production. Error bars represent ±S.E.

Figure 2. Relationship between community gross primary production and (A) percent A. ligamentina biomass, (B) percent A. plicata biomass, (C) percent Q. pustulosa biomass. Relationship between benthic gross primary production and (D) percent A. ligamentina biomass, (E) percent A. plicata biomass, (F) percent Q. pustulosa biomass.; and the relationship between water-column gross primary production and (G) percent A. ligamentina biomass, (H) percent A. plicata biomass, (I) percent Q. pustulosa biomass. Filled circles with closed lines represent GPP at 15^{o}C, open circles and dotted lines represent GPP and 25^{o}C, and filled triangles and dashed lines represent GPP at 35^{o}C.

Figure 3. Effect of relative species dominance (A. ligamentina, A. plicata, and Q. pustulosa) on the mean oxygen consumption rates of (A-C, A. ligamentina), (D-F, A. plicata), (G-I, M. nervosa), (J-L, O. reflexa), and (M-O, Q. pustulosa). Filled circles with closed lines represent GPP at 15^{o}C, open circles and dotted lines represent GPP and 25^{o}C, and filled triangles and dashed lines represent GPP at 35^{o}C.


A
Community gross primary production
(ug O2 hr-1m-2 mg chla-1g dry weight-1)
0.12
0.10
0.08
0.06
0.04
0.02
0.00
15
25
35
B
Benthic gross primary production
(mg O2 hr-1m-2 mg chla-1g dry weight-1)
1.00
0.80
0.60
0.40
0.20
0.00
15
25
35
C
Water column gross primary production
(mg O2 hr-1l-1mg chla-1g dry weight-1)
0.03
0.02
0.01
0.00
15
25
35


Community GPP
(ug O2 g dry wt.-1hr-1l-1)
Benthic GPP
(mg O2 g dry wt.-1hr-1m-2)
Water column GPP
(mg O2 g dry wt.-1hr-1l-1)
A
B
C
D
E
F
G
H
I
% A. ligamentina
% A. plicata
% Q. pustulosa


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
Oxygen consumption (mg 0_2 g dry wt. $^{-1}$ l^{-1} hr^{-1})
% A. ligamentina biomass
% A. plicata biomass
% Q. pustulosa biomass