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Consumer Aggregations Drive Nutrient Dynamics and Ecosystem Metabolism in Nutrient-Limited Systems

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Abstract

Differences in animal distributions and metabolic demands can influence energy and nutrient flow in an ecosystem. Through taxa-specific nutrient consumption, storage, and remineralization, animals may influence energy and nutrient pathways in an ecosystem. Here we show these taxa-specific traits can drive biogeochemical cycles of nutrients and alter ecosystem primary production and metabolism, using riverine systems that support heterogeneous freshwater mussel aggregations. Freshwater unionid mussels occur as distinct, spatially heterogeneous, dense aggregations in rivers. They may influence rates of production and respiration because their activities are spatially concentrated within given stream reaches. Previous work indicates that mussels influence nutrient limitation patterns, algal species composition, and producer and primary consumer biomass. Here, we integrate measures of organismal rates, stoichiometry, community-scaled rates, and ecosystem rates, to determine the relative source–sink nutrient dynamics of mussel aggregations and their influence on net ecosystem processes. We studied areas with and without mussel aggregations in three nitrogen-limited rivers in southeastern Oklahoma, USA. We measured respiration and excretion rates of mussels and collected a subset of samples for tissue chemistry and for thin sectioning of the shell to determine growth rates at each site. This allowed us to assess nutrient remineralization and nutrient sequestration by mussels. These rates were scaled to the community. We also measured stream metabolism at three sites

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Author contributions
C. Atkinson designed the study, conducted the research, analyzed the data, and wrote the initial draft of the paper. B. Sansom assisted with data analysis. C. Vaughn assisted with study design. K. Forshay assisted with data analysis. All authors contributed to writing the manuscript and subsequent revisions.

with and without mussels. We demonstrated that mussel species have distinct stoichiometric traits, vary in their respiration rates, and that mussel aggregations influence nutrient cycling and productivity. Across all mussel aggregations, we found that mussels excreted more nitrogen than they sequestered into tissue and excreted more phosphorus than they sequestered except at one site. Furthermore, gross primary productivity was significantly greater at reaches with mussels. Collectively, our results indicate that mussels have ecosystem-level impacts on nutrient availability and production in nutrient-limited rivers. Within these streams, mussels are affecting the movement of nutrients and altering nutrient spiralling.

Introduction

Animals have an important role in the biogeochemical cycles of terrestrial and aquatic ecosystems because they alter producer biomass, primary and secondary production, decomposition rates, and nutrient fluxes (Spooner and Vaughn 2006; Allgeier and others 2013; Atkinson and others 2013; Whiles and others 2013). When animals comprise a large amount of biomass in ecosystems, they can constitute an essential component of nutrient and energy flux (McIntyre and others 2008; Small and others 2009; Rugenski and others 2012). Animals directly consume and store nutrients as well as indirectly facilitate nutrient recycling in and across ecosystems (Polis and others 1997; Vanni 2002; Wesner and others 2012). This recycling can have substantial impacts on ecosystem processes across multiple trophic levels (Flecker and Taylor 2004). Consequently, these processes can strongly regulate productivity within ecosystems.

Ecological stoichiometry (ES) predicts that organisms with high metabolic requirements for an element should retain that element more efficiently relative to other elements that are non-limiting (Elser and Urabe 1999; Elser and others 2000), potentially altering nutrient cycles through selective uptake, retention, and excretion. Several studies have highlighted the effect of animals on nutrient recycling and consequential increases in primary producer and consumer biomass (Spooner and Vaughn 2006; Vaughn and Spooner 2006), alterations in plant or algae community structure (Knapp and others 1999; Allen and others 2012; Atkinson and others 2013), changes in decomposition rates (Rugenski and others 2012), and strong effects on food webs (Atkinson and others 2014b). Aquatic ecosystems are typically limited by nitrogen (N) or phosphorus (P), so the ratio of these nutrients that animals excrete and store can determine production rates and the degree of N versus P limitation (Sterner and Elser 2002; Small and others 2009; Atkinson and others 2013). Furthermore, the role of animal-mediated nutrient transformations can be significant at multiple spatial scales (Doughty and others 2015). Animal excretion returns readily available dissolved nutrients back to the water soon after ingestion, whereas nutrient sequestration is important for nutrient storage within an ecosystem because nutrients used for growth and production are retained in biomass and unavailable to the rest of the ecosystem (until consumers or predators feed on them or decomposers recycle their nutrients). Furthermore, animals can serve as nutrient sinks if the tissue is recalcitrant, they leave the ecosystem, or if the populations are increasing in biomass (Vanni and others 2013). Consequently, animals can act as biological sinks for nutrients depending on spatial and temporal scales, yet few

researchers have quantified nutrient sequestration rates by animals in relation to excretion to test these concepts (but see, Kraft 1992; Vanni and others 2013; Hill and Griffiths 2016).

The impact of consumers on ecosystem processes depends on the density and biomass, and corresponding species traits of the consumers (Moore 2006; McIntyre and others 2008; Small and others 2011). Aggregating animals, in particular, can form biogeochemical hot spots that result in enhanced rates of production and respiration because their activities are spatially concentrated (Taylor and others 2006; McIntyre and others 2008; Rugenski and others 2012; Atkinson and others 2013; Capps and Flecker 2013b). Yet, these aggregations can be composed of multiple species that may have varying stoichiometric requirements and consequently may supply nutrients at various ratios. The creation of hot spots by aggregated animals can arise through herding and schooling behaviors (Knapp and others 1999; McClain and others 2003) or through the creation of stable patches of organisms (e.g., oysters; Porter and others 2004; Waldbusser and others 2013). These hot spots are spatially and temporally variable in their biogeochemical contributions due to changes in the abundance, species composition, distribution and movement of organisms, but the extent to which these animal aggregates can drive ecologically relevant nutrient storage or ecosystem metabolic processing is largely unknown (Atkinson and others 2017).

The high abundance and filtration rates of bivalves in both marine and freshwater systems suggest that bivalves may exert large effects on ecosystem function (Wotton and others 2003; Porter and others 2004; Vaughn and others 2008). Freshwater mussels (Bivalvia: Unionidae, hereafter “mussels”) are a diverse group of long-lived (6–100 year), burrowing, filter-feeding bivalves that live in river sediments. Mussels are currently experiencing rapid biodiversity declines (Strayer and others 2004), but once dominated the biomass of many riverine ecosystems (Haag 2012). These factors make them a useful model group to explore stoichiometric nutrient hypotheses with practical ecological relevance (Atkinson and others 2014a). Despite mussels belonging to the same guild (filter-feeding bivalves), different species exhibit differential feeding (Galbraith and others 2009), brooding requirements (Haag and Warren 2003; Culp and others 2011), and thermal sensitivity traits (thermally sensitive vs. tolerant; Spooner and Vaughn 2008). Thus, species composition may play a strong role in the effect of mussels on ecosystem structure and function. Ecological functions performed by mussels (for example, filter-feeding, nutrient excretion, biodeposition, bioturbation) affect both primary producers and consumers through direct and indirect pathways (Vaughn and Spooner 2006; Atkinson and others 2013, 2014b). Previous work has shown that mussel aggregations are biogeochemical hot spots in rivers (Atkinson and Vaughn 2015) and can lead to alteration in algal species composition and macroinvertebrate abundance (Howard and Cuffey 2006; Spooner and Vaughn 2006; Atkinson and others 2013). Patches of filter-feeding mussels and algae create a mosaic that controls productivity of stream reaches in ways that are often neglected in models of stream ecosystems.

Here, we integrate measures of mussel growth, tissue and excretion stoichiometry, and organismal and community respiration, to determine the relative nutrient remineralization and biomass sequestration flux of mussel aggregations and their influence on a critical, basal ecosystem function, net ecosystem production. Our prior results in these systems found that

nutrient limitation, macroinvertebrate species richness and abundance, and algae species composition vary between reaches with and without mussels, and that mussel-derived nitrogen provides bottom-up support to stream food webs (Spooner and Vaughn 2006; Allen and others 2012; Atkinson and others 2013, 2014b). We hypothesized that (1) the nutrient remineralization and nutrient sequestration flux of aggregated mussel communities is strongly controlled by species identity and biomass of various species in the communities; (2) mussels with low tissue N:P will lead to high areal excretion N:P that should be essential in alleviating limitation in these N-limited systems; and (3) due to the alleviation of N-limitation in mussel reaches there will be enhanced overall net ecosystem productivity because aggregations will positively influence both net primary productivity and respiration through bottom-up effects on primary producer and microbial communities, resulting in overall higher rates of gross and net ecosystem productivity.

Methods

Study Area and Mussel Sampling

We studied three mid-sized perennially flowing rivers in the southcentral USA (Kiamichi—K, Little—L, and Mountain Fork—MF; Figure 1A), where previous work indicated that mussels play an important role in supporting primary and secondary production (Vaughn and Spooner 2006; Spooner and Vaughn 2009). Rivers in this region tend to be N-limited, and mussel aggregations are known to enhance nutrient cycling and food web provisioning (Allen and others 2012; Spooner and others 2012; Atkinson and others 2013, 2014b). Nine mussel beds were quantitatively sampled during the summer of 2012 (Figure 1A) by excavating 10–15, 0.25-m^2 quadrats randomly placed within each study site. Quadrats were excavated to a depth of 15 cm, and all mussels were removed, identified to species, and measured to the nearest 0.1 mm. Length data were used to estimate tissue biomass based on previously determined length-weight regressions (Atkinson, *unpublished data*). At three of these sites (one site per river), we measured ecosystem metabolism. Additionally, for comparison we chose an additional three sites without mussels (quantitatively surveyed in 2010; Atkinson and others 2013) with similar streambed and flow characteristics across the three rivers to measure ecosystem metabolism (Figure 1).

Tissue Chemistry, Respiration Rates, and Excretion Rates

During the summer of 2010, five individuals of the most common mussel species from each site (7 of 25 species found during survey; *Actinonaias ligamentina*, *Amblema plicata*, *Fusconaia flava*, *Lampsilis spp.*, *Ptychobranchus occidentalis*, *Quadrula pustulosa*, *Quadrula verrucosa*) were retained for tissue chemistry analyses. We assumed that these organisms are homeostatic in their body nutrient tissue content across years within the same season (Christian and others 2008). Mussel soft tissue and shell samples were analyzed on a Finnigan Delta Plus mass spectrophotometer in the University of Georgia's Analytical Laboratory for the determination of %C and %N. For %P, samples were weighed, combusted at 500°C for 2 h, and then digested with 1 N HCl followed by SRP analysis (Solorzano and Sharp 1980).

Excretion rates of multiple mussel species were measured at each of these sites as described in Atkinson and others (2013, 2014a) during the summers of 2010, 2011, and 2012. Mussels were placed in 500 or 1000 ml of filtered stream water for 1 h, and total dissolved organic carbon, total dissolved nitrogen, and total dissolved phosphorus concentrations were compared to stream water controls containing sham mussel shells. Sham shell is clean dead shell from the stream. Samples for total dissolved N (TDN) and P (TDP) were retained, field filtered, acidified, and then analyzed (following persulfate digestion) within 28 days of collection using a Lachat QuikChem FIA +8000 Series flow injection analyzer (Hach Company, Loveland, CO, USA). Total dissolved carbon was determined from filtered (GF/F) samples collected in 40-ml VOA vials using a Phoenix 8000 carbon analyzer (Teledyne Tekmar, Mason, OH, USA). Excretion rates were expressed as the difference between the treatments (chambers with a mussel) and the controls (chambers with a sham shell). The carbon, nitrogen, and phosphorus composition was then converted to molar ratios to express stoichiometric ratios.

Concurrently, respiration rates were measured in the field in 1000–1500-ml sealed plastic containers during the summer of 2010. Containers were filled completely with filtered stream water, and dissolved oxygen was measured with a Hach LDO meter (Hach, Loveland, CO) prior to and following a mussel being placed in the container for 1 h. Containers were placed in the stream during the 1-h incubation period to maintain stream temperatures. Three containers with a sham shell controlled for other sources altering dissolved oxygen concentrations over time. We conducted respiration measurements on the most abundant species (five replicates of each species at each site) with water temperatures varying between 27 and 31°C.

Mussel Thin Sectioning

Using shells from organisms killed for tissue chemistry, we assessed age and growth rates of mussels using growth increment analysis (total shells examined = 105) across our sites as in Sansom and others (2016). We prepared radial thin sections (~350 μm thick) from one valve of each specimen using a saw with a diamond-impregnated blade following standard methods for bivalves (Neves and Moyer 1988; Clark 1980). Each thin section was viewed and interpreted by two individuals using a dissecting microscope. True annuli were differentiated from non-annual rings following criteria in Haag and Commens-Carson (2008). Once the true annuli were identified, we measured the annual growth increments using a linear encoder and digital readout in MeasureJ2X (Project J2X, VoorTech Consulting). Measurements, taken along the dorso-ventral growth increment between the prismatic and nacreous shell layers, began at the most recent complete growth year and proceeded toward the umbone. Growth pattern analysis and quality control measures followed dendrochronological methods described in Rypel and others (2008) and Sansom and others (2013). These measurements allowed us to assess yearly and average growth rates of mussels from our sites.

Areal Excretion, Areal Storage, and Shell Decay Rate

We estimated areal excretion rates for both N (total dissolved nitrogen) and P (total dissolved phosphorus) by scaling the measured excretion rates to the species composition

and biomass of the mussel bed at each reach. Areal storage was calculated as the product of biomass (grams of dry mass per m^2; based on the quadrat sampling mentioned above) and the tissue chemistry (%C, %N, or %P). Areal nutrient biomass accrual rates were estimated by calculating species-weighted storage rates (Table 1) of C, N, and P for each mussel bed community by taking the product of the areal nutrient storage rate of each species and their growth rate as found above or reported in Haag and Rypel (2011). Furthermore, during May 2012, we deployed five shell decomposition bags at our most downstream sites in the Kiamichi and Little Rivers. Six fresh *A. plicata* valves were individually tagged, weighed, and then placed into labeled mesh bags. Each bag was attached to a piece of rebar at the bottom of the stream to maintain its position. Bags were checked, and valves were individually weighed in June 2013 and then again June 2016. Between the June 2013 and 2016 sampling periods, three bags were lost from the Little River site and four from the Kiamichi site. We calculated the rate of shell loss (k, day^{-1}) as:

$$k = (1 / t)[\ln(\text{mass}_{\text{final}} / \text{mass}_{\text{initial}})]$$

where t is the length of time (in days) that the shells were in the river. We calculated k separately for the two sample time periods.

Ecosystem Metabolism

We measured reach-scale ecosystem metabolism in 100-m reaches to determine gross primary production (GPP) and ecosystem respiration using the 2-station method at six sites (two sites in each river; one reach without and one reach with mussels per stream) at baseflow using the diel change in dissolved oxygen in the open stream channel (for example, Marzolf and others 1994; Young and Huryn 1996; Dodds and others 2008). The change in dissolved oxygen concentration ($\Delta [O_2]$) is related to photosynthesis (PS), respiration (R), and exchange with the atmosphere (E) in the stream: $\Delta [O_2] = PS - R \pm E$. Dissolved oxygen, temperature, and conductivity were logged at 5-min intervals for 48 h using two Hydrolab MS5 data-logging sondes. We calibrated the sondes together in the field immediately before deployment. Following calibration, we allowed them to record for 30 min. If sondes were not reading within 3% of each other, we repeated calibration until all sondes were within 3% before deployment. Distance between the upstream and downstream stations was 100 meters allowing for an approximate 40-min travel time. Concurrently, we measured light every 5 min at the sites with a Li-Cor LI-1000 datalogger equipped with a photosynthetically active radiation (PAR) sensor (Li-Cor, Lincoln, Nebraska). We placed the PAR sensor on a level, elevated object in an area with open canopy next to the stream in full sunlight to measure daily variation in light availability for primary producers. The exchange with the atmosphere, the reaeration rate (kO_2), was estimated with SF_6 (sulfur hexafluoride) releases in conjunction with a conservative tracer release (KBr). We modelled GPP and community respiration as in Dodds and others (2013) in which we used the equations from Holtgrieve and others (2010), but fit the models to minimize the sum of squares error (SSE) between observed and modelled dissolved O_2 concentrations. Model fitting was done using the same parameters as described by Riley and Dodds (2012). We used physical stream measurements (channel length, depth, width, average velocity, discharge, barometric pressure, and light) and change in dissolved O_2 over time between stations to parameterize

models. All measurements of ecosystem metabolism were taken between May 25, 2012, and June 20, 2012.

Statistical Analyses

The differences among mussel species in C:N and N:P of both soft tissue composition and excretion stoichiometry were assessed using Kruskal–Wallis one-way analysis of variance (ANOVA) because the data did not meet the assumption of equal variance. Significant ANOVAs were followed by Dunn's pairwise multiple comparisons. We also used a Kruskal–Wallis ANOVA to test differences in weight-corrected respiration rates across species followed by pairwise multiple comparisons to assess differences across species. The relationship between areal respiration rates and areal excretion (both N and P) was determined using linear regression. We used *t* tests to compare the ecosystem respiration, net primary productivity, gross primary productivity, and P/R between sites with and without mussels. We estimated the potential direct contribution mussels can have to stream respiration by scaling their respiration rates to the areal scale (mg m^{-2} h^{-1}) and comparing it to the whole-stream respiration.

Results

Stoichiometry, Growth, Excretion, Sequestration, and Decomposition

Our sites varied in species community composition (Figure 1B), and mussel species within these communities varied in soft tissue C:N ($H = 12.4$, $P < 0.03$), soft tissue N:P ($H = 27.8$, $P < 0.001$), excretion C:N ($H = 39.1$, $P < 0.001$), and excretion N:P ($H = 17.7$, $P < 0.004$). Soft tissue C:N ranged from 4.11 to 4.94 across all the species, and only *A. plicata* and *Q. pustulosa* were significantly different from one another (Figure 2A). Soft tissue N:P was more variable, ranging between 10.2 (*A. ligamentina*) and 43.4 (*A. plicata*), but only *A. ligamentina* was significantly different from all other species (Figure 2B). Excretion C:N varied across species (range: 3.6–12.7), with *A. ligamentina* having significantly lower C:N than all other species except *P. occidentalis* (Figure 2C). *A. ligamentina* also had a significantly lower excretion C:N than *Q. pustulosa* and *Q. verrucosa* (Figure 2C). Excretion N:P also varied across species with *A. ligamentina* having a significantly higher excretion N:P than both *P. occidentalis* and *Q. pustulosa* (Figure 2D).

When accounting for species-weighted growth rates, many of the mussels in the downstream reaches in each of the respective watersheds had slower growth rates. These growth rates contributed to lower nutrient storage rates. Areal excretion rates varied greatly across sites (1.32–6.16 mg N h^{-1} m^{-2}; 0.23–83 mg P h^{-1} m^{-2}; Figure 3). Areal sequestration also varied greatly across sites (Figure 4) with the majority of nutrients stored in the shell (83–94% of C, 72–88% of N, and 88–96% of P storage). Across all the sites, N areal excretion rates exceeded N sequestration rates (Table 1; Figures 3,4). The site in which N areal excretion exceeded N sequestration the most, K2, was dominated by two of the largest and longer-lived species, *A. plicata* (Figure 1B; 12% of the community; max age = 79 years) and *A. ligamentina* (67% of the community; max age = 52 years). Areal P excretion rates were greater than the P sequestration by mussels across all sites except for one, K3. Our results further suggest that the nutrients stored in these shells can be sequestered for long periods

following the animal's death. Shell decay rates were similar across the two time periods, and based on our measurements, the shells would take approximately 31.6 years to decay (average $k = -0.0001$ day^{-1}) at the benthic–water interface.

Ecosystem Metabolism and Respiration

Mussel weight-corrected respiration varied across species (Figure 5A; $H = 30.02$, $P < 0.001$); *A. ligamentina* had a significantly higher weight-corrected respiration rate than *A. plicata*, *F. flava*, *Q. pustulosa*, and *V. lienosa* (Figure 5A), indicating that community composition and not just biomass have a significant impact on ecosystem function. Using community-weighted respiration values for each site, we found that both mussel biomass and community composition were important determinants of areal respiration rates (Figure 5B). Across the nine sites, areal respiration rates strongly and positively predicted areal excretion of both N and P (Figure 6A, B). Community respiration, net ecosystem productivity, and the P/R were not significantly different between the sites with and without mussels ($t_4 = 2.21$, $P = 0.09$; $t_4 = 1.40$, $P = 0.24$; $t_4 = 0.31$, $P = 0.77$, respectively), but gross primary productivity ($t_4 = -4.55$, $P = 0.01$) was significantly higher at sites with mussels (Table 2). When we compare our mussel community areal respiration rates directly to our whole-stream metabolism measurements, our results suggest freshwater mussels contribute 16–43% of the respiration occurring in these stream reaches during summer base flow conditions.

Discussion

By examining two indicators of organismal metabolic rates (respiration and excretion), organismal growth rates, and rates of ecosystem metabolism, we have demonstrated that mussel species perform differently and that mixed species aggregations have diverse ecosystem-level impacts on nutrient cycling and productivity. Across all mussel aggregations studied, we found that mussels were a net source of dissolved nitrogen when comparing the areal excretion rates to the sequestration rates. Mussels were typically net sources of phosphorus based on comparing their sequestration and excretion rates, but one aggregation of mussels acted as a net sink for phosphorus in the system. The aggregation that acted as a net sink for phosphorus had the highest species richness and a higher proportion of thermally sensitive species (Spooner and Vaughn 2008). These species also tended to have higher tissue phosphorus content (Figure 2B; Atkinson and others 2013). By incorporating both nutrient sequestration rates and excretion rates, we were able to compare the net contribution of mussel communities to nutrient excretion and sequestration. Previous studies have used net remineralization as a metric to understand the importance of organisms to nutrient availability (Capps and Flecker 2013a) and to compare across species and systems (Capps and others 2015). Here we examined both the sequestration and excretion rates to examine the net impact. In contrast to Capps and Flecker (2013a) who studied the role of an invasive fish (*Pterygoplichthys*) with high density at one site, we found that many of our mussel aggregations had higher areal N excretion rates than sequestration rates, and while one of our sites had a higher P sequestration than areal excretion, most communities excreted more P than they sequestered. Overall, these results show that areal excretion and sequestration by mussels varies greatly across communities and is a product of the biomass

and species composition of the community. Differences in species composition, even within this one functional guild (that is, filter-feeding bivalves), can lead to differences in the nutrients remineralized and stored within this ecosystem. These relationships suggest that species-rich aggregations can lead to enhanced ecosystem resiliency of nutrient cycling.

Although we found an overall positive influence of mussels on nutrient availability, our estimates only accounted for soft tissue biomass. Mussel tissue's low N:P can be an important factor in the high N:P of excretion in these mussel communities (Atkinson and others 2013). Mussels store a large quantity of N and P in shell tissue, mainly because shells make up a large proportion of their biomass (Atkinson and Vaughn 2015). Because mussels are often long-lived (Strayer 2008; Haag 2012), the nutrients stored in soft tissue and especially shell are unavailable for long periods of time. Shell tissue is largely recalcitrant, taking a long time to breakdown (Strayer and Malcom 2007), so large quantities (e.g., >100 g C m^{-2} y^{-1}) of nutrients are sequestered even after mussel death (here ~31.6 years). Thus, our study only accounts for the capability of living mussels to store and cycle nutrients in their soft tissue. Following the sequestration of these nutrients, the quantities stored in the shell can be maintained for several years after mortality. Given the nutrient storage capacity of the shells (e.g., a large amount of mass), the age of many mussels (>40 years old), and slow breakdown rates, mussels likely act as long-term nutrient sinks within river ecosystems (Vanni and others 2013).

As anticipated, measured physiological rates (respiration and excretion) were highly correlated (Spooner and Vaughn 2008). Yet, once these rates were scaled to the community, there was some variation. These rates are useful to help understand the effect of species and/or communities on ecosystem processes. As found in other studies of multi-species assemblages (Vanni and others 2002), our results show that different species have varying stoichiometric traits and thus distinct effects on nutrient availability (McIntyre and others 2008; Small and others 2011). Collectively, our results in conjunction with previous findings (Hall and others 2003; Whiles and others 2013) indicate that animal consumers play a large role in determining the structure and function of ecosystems.

Our results indicated that mussels had a strong influence on ecosystem metabolism with gross primary productivity being significantly higher at reaches with mussels. This conclusion suggests that the bottom-up influence of mussel excretion can stimulate primary productivity. This finding corroborates with previous studies that have found higher periphyton biomass in the presence of mussels (Howard and Cuffey 2006; Spooner and Vaughn 2006) and that mussels alleviate strict N-limitation in these systems (Atkinson and others 2013). Furthermore, our results indicate that mussel community areal respiration could account for approximately 16–43% of the total respiration occurring at these sites. However, we did not find significant differences in community respiration or net ecosystem production between the non-mussel and mussel sites. Holtgrieve and Schindler (2011) noted a decline in GPP:ER in streams with the system shifting from a net autotrophic to a net heterotrophic state in response to bioturbation of the benthos by salmon. The metabolism by live salmon in that study could not account for the observed increase in ER during the salmon run, suggesting salmon nutrients enhanced in situ heterotrophic respiration. We noted differences in gross primary productivity at sites with mussels as

opposed to respiration, indicating that mussels were stimulating primary producers via nutrient recycling. Although we observed differences in gross primary productivity between sites with and without mussels, our replication was low. Yet, these data corroborate with previous work in the system that found higher algal biomass (controlling for light and substrate) and invertebrate biomass in stream reaches with mussels (Spooner and Vaughn 2006; Vaughn and Spooner 2006; Atkinson and others 2013). Further measurements of ecosystem metabolism are needed at locations varying in the densities, species composition, and size of consumer aggregations to understand the role of aggregating consumers on ecosystem rates.

Our study provides evidence that mussel aggregations strongly regulate nutrient cycling having a bottom-up impact on ecosystem metabolism. Whiles and others (2013) found that nitrogen uptake and heterotrophy were reduced following extirpation of a major consumer, amphibians, from streams, and that fluxes of N from basal resources to animals were also reduced. Similarly, Allgeier and others (2013) showed in a marine setting that reef-dwelling fish enhance primary production of both micro-algae and seagrass. Our results in conjunction with the previous findings across ecosystems suggest that consumers can have large effects on overall ecosystem function through both bottom-up and consumptive affects (Schmitz and others 1997; Schmitz and others 2010; Allgeier and others 2013). Yet, mussels are anticipated to continue to decline across stream systems due to increased severity and intensity of droughts (Golladay and others 2004; Haag and Warren 2008; Galbraith and others 2010; Atkinson and others 2014a; Vaughn and others 2015), which are predicted to intensify due to climate change (Palmer and others 2008; Stocker and others 2013). These predicted losses will further reduce the direct and indirect contributions of mussels to stream ecosystem function and potential ecosystem services (Vaughn and others 2015; Castro and others 2016).

The streams studied here have low nutrient concentrations and are generally N-limited (Vaughn and others 2007; Electronic supplementary material; Atkinson and others 2013). Our results show that mussel aggregations alter the availability of nutrients and strongly influence the availability of the limiting nutrient, in this case nitrogen. These aggregations can enhance productivity in these rivers through stoichiometric coupling as stream metabolism and nutrient uptake rates are often highly coupled (Hoellein and others 2007). Previous work in these systems indicates that nitrogen is taken up rapidly and incorporated into both the stream and terrestrial food web (Allen and others 2012; Atkinson and others 2014b). Thus, remineralization by mussels is an important regulator of productivity and heterogeneity of biogeochemical activity within stream and terrestrial ecosystems (Atkinson and Vaughn 2015). Although examining both areal nutrient excretion and sequestration rates was useful to determine the importance of mussel aggregations control of nutrient availability and storage, these measurements do not include egestion. Further work needs to be conducted to assess egestion rates as well as the effect of aggregations on stream systems shifting between N and P limitation (Atkinson and others 2017). Furthermore, our shell decay rates were only conducted with one species, *A. plicata,* which is one of the most common species in the systems. Although this gives us a good estimate for a common species, undoubtedly, decay rates vary as a function of species-specific shell characteristics

(Strayer and Malcom 2007). Future studies incorporating more species will be useful to inform these decomposition rates.

Community composition has been proposed as an important determinant of stream ecosystem structure and function (Flecker 1996; Vanni and others 2002; McIntyre and others 2007), and our results show that mussels play an essential role through nutrient cycling and creation of functionally diverse patches. In the context of the importance of species loss on ecosystems, the loss of freshwater mussels across a multitude of freshwater systems worldwide (Bogan 1996, 2008) has been a detriment to overall ecosystem function through the loss of storage and recycling (Strayer 2013; Vaughn and others 2015). Mussels are long-lived organisms and can impart a large influence on both nutrient recycling and overall ecosystem productivity. Previous results have indicated that the provisioning of nutrients by mussels enhances primary and secondary productivity (Vaughn and Spooner 2006; Vaughn and others 2007), strongly influences the food web (Atkinson and others 2014b), and leads to biogeochemical hot spots in rivers (Atkinson and others 2013; Atkinson and Vaughn 2015). Here we show that mussels are provisioning more nutrients than they store. Benthic algae, aquatic plants, and the microbial community respond to this supplement though enhanced production. They do this largely through the reduction in the length of dissolved and particulate nutrient uptake length, thus reducing nutrient spiralling length in streams (Newbold and others 1982; Small and others 2009; Schade and others 2011). Collectively, these results indicate that mussels have ecosystem-level impacts on nutrient availability and production in nutrient-limited rivers. Thus, previous and ongoing losses in mussel biomass and biodiversity (Golladay and others 2004; Galbraith and others 2010; Atkinson and others 2014a), particularly in rivers in the southeastern USA, could have far-reaching consequences on ecosystem function in many streams. Future work should help disentangle the direct and indirect impacts mussels have on ecosystem function.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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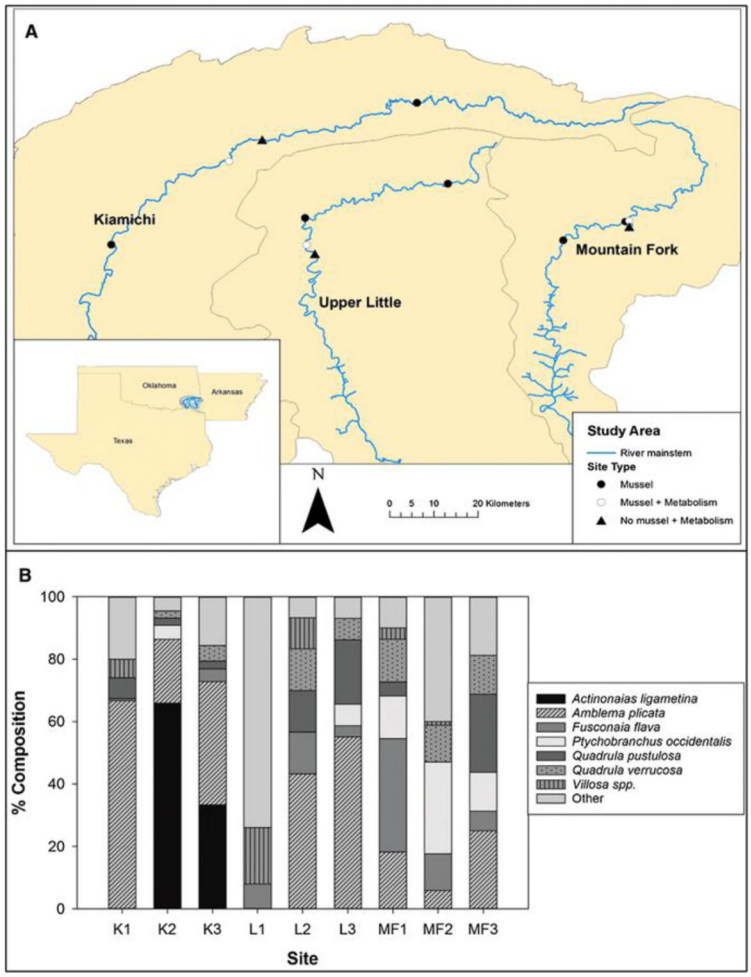

Figure 1.

A Map depicting the study area. We quantitatively sampled mussels at nine sites in three watersheds. At three of the sites with mussels, we measured ecosystem metabolism. The sites without mussel sites had no mussels or very low densities of mussels (<0.8 mussels m^{-2}), and we also measured ecosystem metabolism. **B** Proportion of the community represented by various mussel species at the mussel sites.

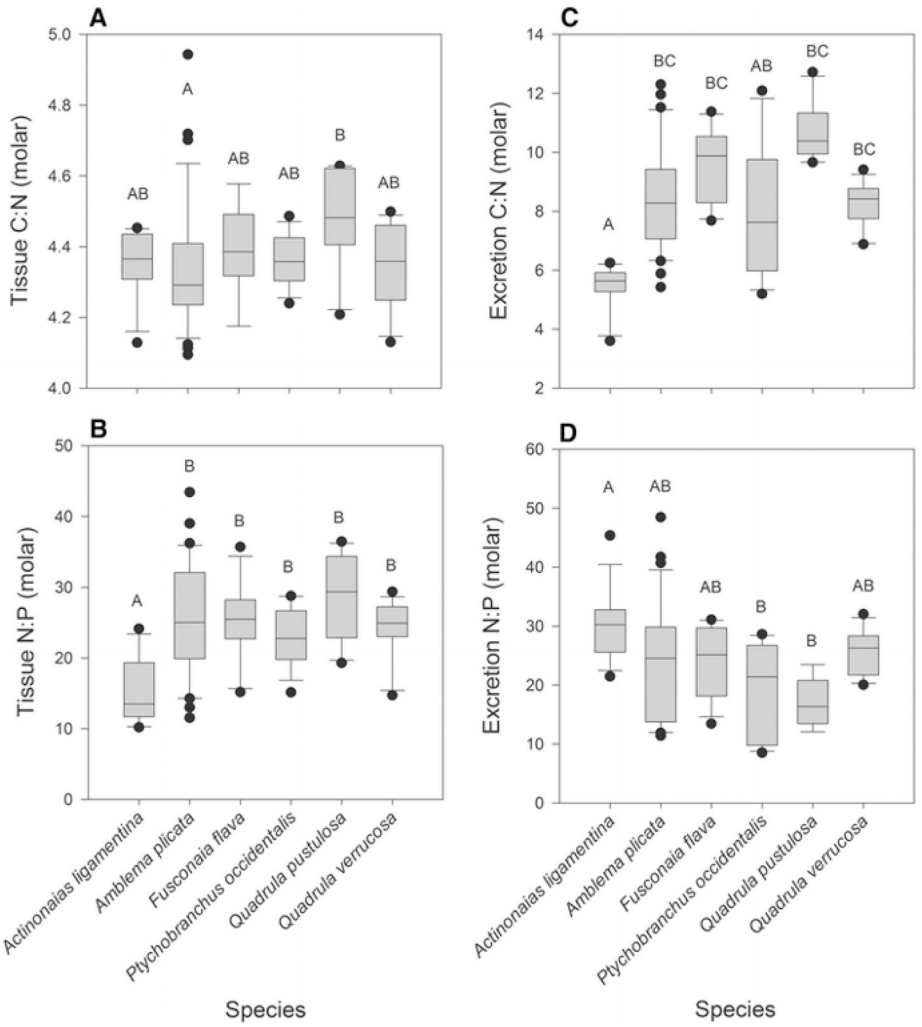

Figure 2.

Common mussel species found in the three study rivers and their **A** soft tissue C:N **B** soft tissue N:P **C** excretion C:N, and **D** excretion N:P. Significant differences ($P < 0.05$) among species are denoted with different letters as indicated by a ranked ANOVA followed by a Dunn's test.

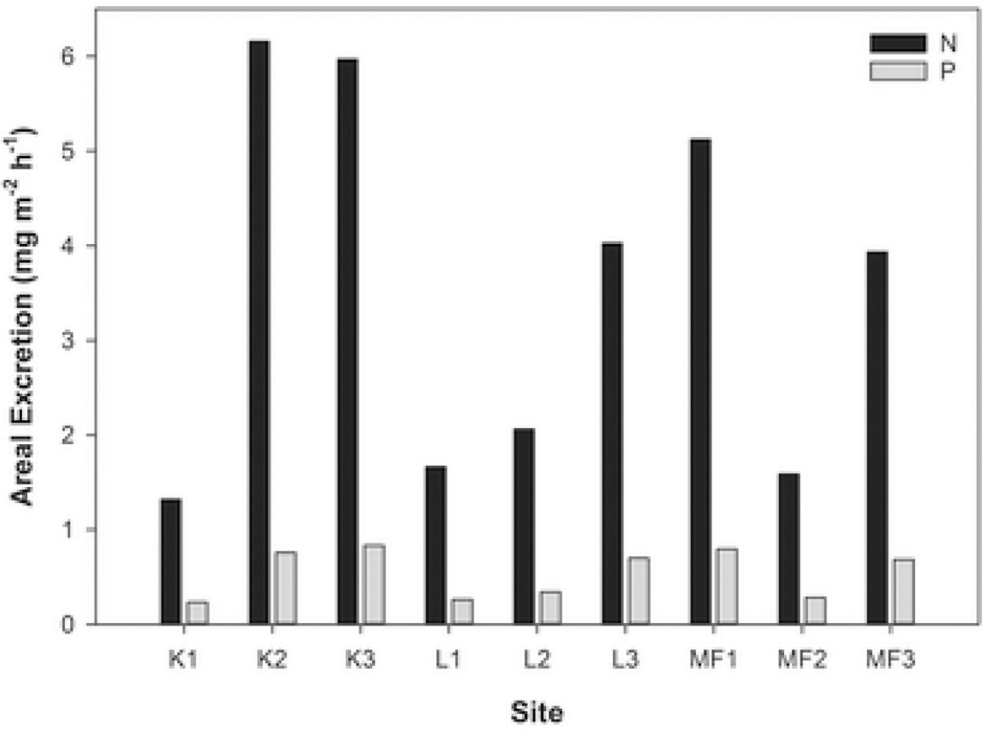

Figure 3.

Mean areal community N and P excretion rates (±SE) across nine aggregations sampled for community composition, biomass, and density in southeastern Oklahoma streams (K = Kiamichi, L = Little, MF = Mountain Fork).

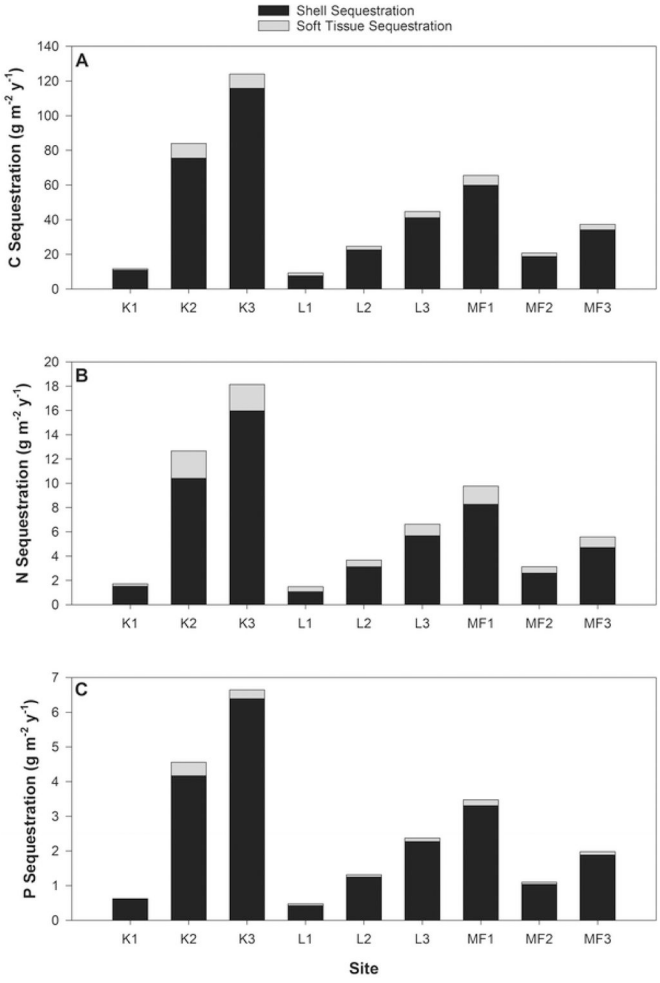

Figure 4.

Estimated sequestration rates of nutrients based on annual growth rates into both mussel soft and shell tissue biomass of **A** N and **B** P across nine aggregations sampled for community composition, biomass, and density in southeastern Oklahoma streams (K = Kiamichi, L = Little, MF = Mountain Fork).

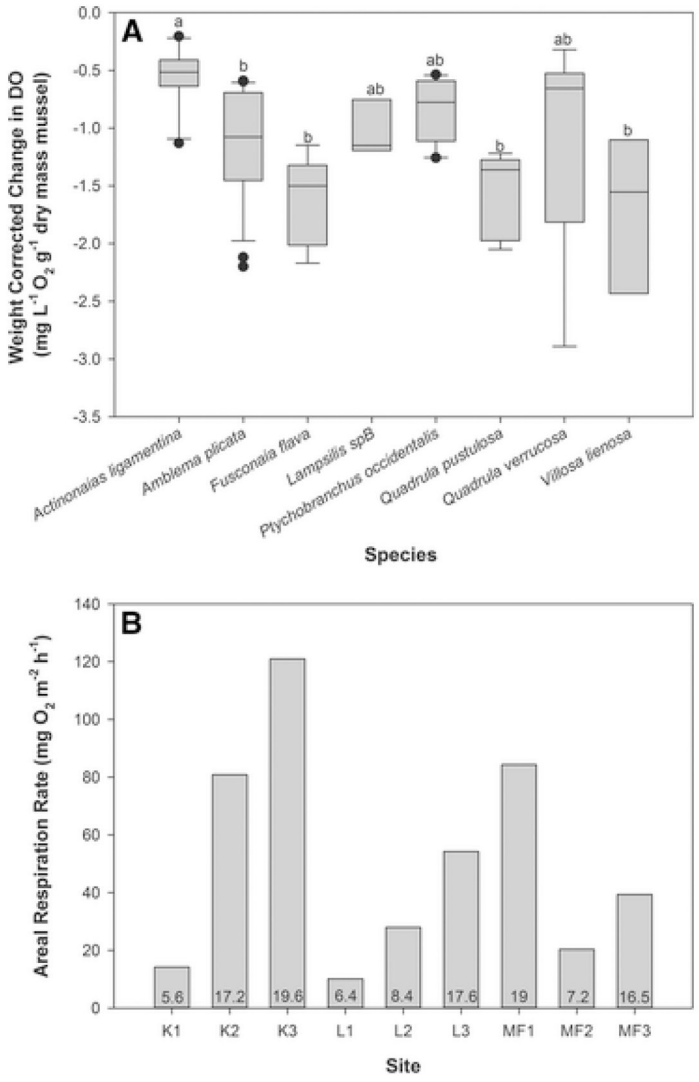

Figure 5.

A The weight-corrected respiration rate at 29.8 ± 1.9° C of eight common mussel species found in the Kiamichi, Little, and Mountain Fork Rivers. The *upper* and *lower* portions of the bar are the upper and lower quartiles, the line in the middle of the box represents the median, the dots are outliers, and the *lower* and *upper lines* represent the lowest and greatest values excluding outliers. Letters above the bars represent level of significance between species. **B** The areal respiration rate of the nine sampled mussel communities in the Kiamichi (K), Little (L), and Mountain Fork Rivers (MF). The numbers on each bar represent the average mussel density (individuals m^{-2}) at each site.

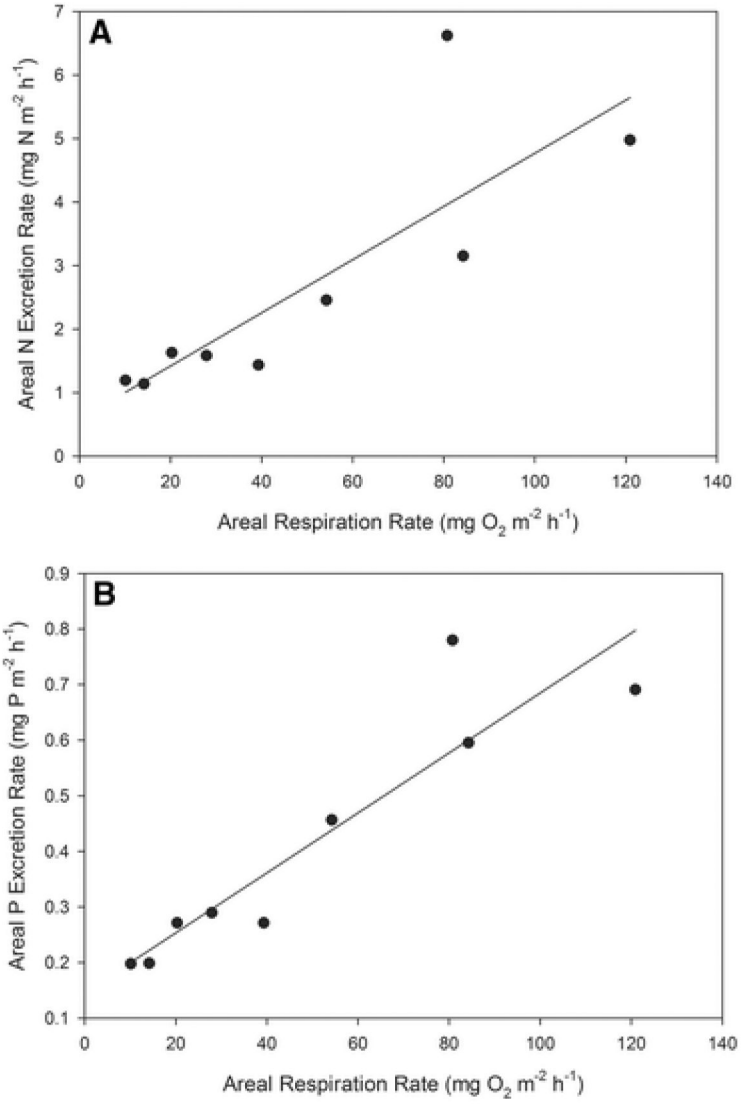

Figure 6.

The relationship between areal respiration and areal N excretion rate across communities was significant (**A**; $y = 0.0042x + 0.058$, $r^2 = 0.68$, $P < 0.001$). Respiration and P excretion rates within mussel communities were also significantly related (**B**; $y = 0.0054x + 0.15$, $r^2 = 0.85$, $P < 0.001$).

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Table 1

Information on Mussel Densities, Species-weighted Community Growth Rates, Nutrient Sequestration, and Shell Decay Rates for Each Site From: Consumer Aggregations Drive Nutrient Dynamics and Ecosystem Metabolism in Nutrient-Limited Systems

Site	Mussel density (ind. m^{-2})	Community-corrected growth rate (day^{-1})	Total C sequestration (g C y^{-1})	Total N sequestration (g N y^{-1})	Total P sequestration (g P y^{-1})	Shell decay rate (day^{-1})
K1	5.6	3.09E−04	1.76E+04	2574.99	940.79	na
K2	17.2	4.07E−04	2.52E+05	38015.98	13665.30	na
K3	19.6	5.29E−04	8.68E+05	126,987.14	46,507.10	−1.00E−04
L1	6.4	1.09E−03	4.62E+03	737.50	238.24	na
L2	8.4	4.34E−04	1.86E+04	2759.12	983.98	na
L3	17.6	3.60E−04	1.41E+05	20,868.69	7468.53	−1.20E−04
MF1	19.0	3.91E−04	6.88E+04	10,249.05	3647.98	na
MF2	7.2	5.85E−04	1.56E+04	2342.71	824.08	na
MF3	16.5	4.69E−04	3.74E+04	5577.99	1977.34	na

1. We calculated the nutrient sequestration rates based on the product of the community-weighted growth rates, species-specific biomass, and species-specific soft tissue and shell stoichiometry for each site (K = Kiamichi River, L = Little River, MF = Mountain Fork River).

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Table 2

Results from the Ecosystem Metabolism Measurements Conducted at a Subset of Sites With and Without Mussels in the Three Rivers From: Consumer Aggregations Drive Nutrient Dynamics and Ecosystem Metabolism in Nutrient-Limited Systems

Site	Average temperature (Range) (°C)	Community respiration (g O_2 m^{-2} day^{-1})	Gross primary productivity (g O_2 m^{-2} day^{-1})	Net ecosystem production (g O_2 m^{-2} day^{-1})	Net primary productivity (g C m^{-2} day^{-1})	P/R
Kiamichi—with	32.6 (29.4-36.5)	−3.74	1.69	−2.05	0.264	0.45
Kiamichi—none	31.9 (28.9-35.2)	−3.61	1.33	−2.28	0.209	0.37
Little—with	31.1 (28.2-35.7)	−4.46	1.57	−2.89	0.245	0.35
Little—none	25.8 (23.9-29.8)	−2.96	1.33	−1.63	0.207	0.45
Mt. Fork—with	31.6 (29.9-33.4)	−4.37	1.53	−2.84	0.239	0.35
Mt. Fork—none	31.8 (29.8-33.6)	−3.77	1.40	−2.37	0.219	0.37

1. Our results indicate that gross primary productivity was significantly higher in sites with mussels (as indicated by t tests), while mean community respiration, net ecosystem production, and P/R were not significantly different in sites with and without mussels.