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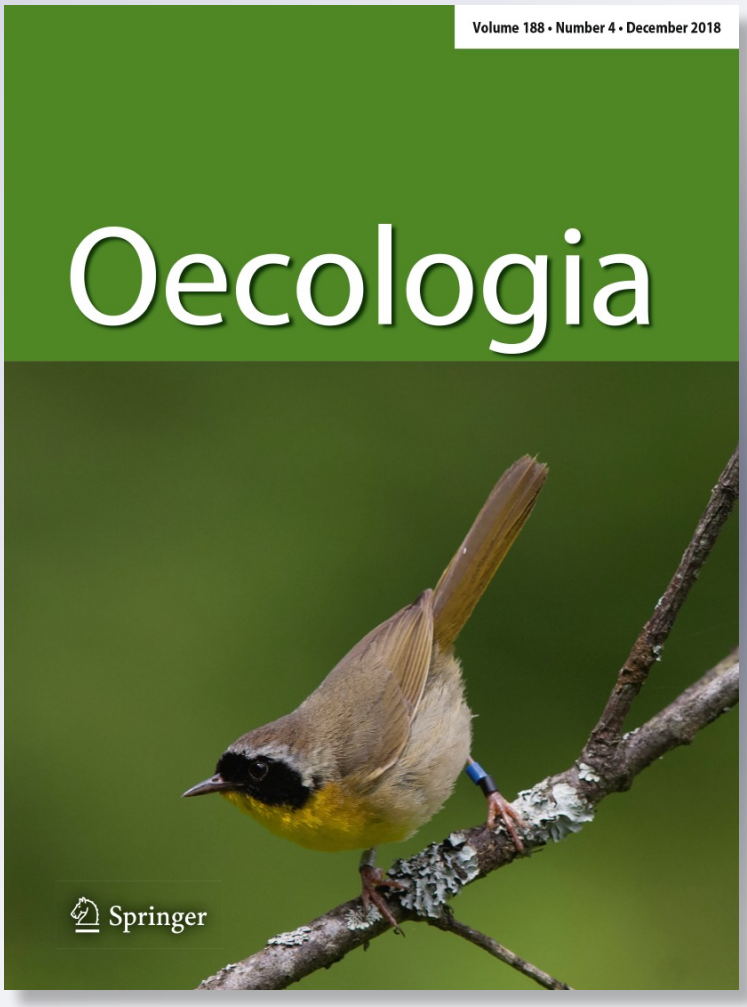

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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Biomass distribution of fishes and mussels mediates spatial and temporal heterogeneity in nutrient cycling in streams

Garrett W. Hopper[1] · Keith B. Gido[1] · Caryn C. Vaughn[2] · Thomas B. Parr[2] · Traci G. Popejoy[2] · Carla L. Atkinson[3] · Kiza K. Gates[2,4]

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Abstract

Animals can play important roles in cycling nutrients [hereafter consumer-driven nutrient dynamics (CND)], but researchers typically simplify animal communities inhabiting dynamic environments into single groups that are tested under relatively static conditions. We propose a conceptual framework and present empirical evidence for CND that considers the potential effects of spatially overlapping animal groups within dynamic ecosystems. Because streams can maintain high biomass of mussels and fish, we were able to evaluate this framework by testing if biogeochemical hotspots generated by stable aggregations of mussels attract fishes. We predicted that spatial overlap between these groups may increase the flux of mineralized nutrients. We quantified how different fish assemblage biomass was between mussel bed reaches and reaches without mussels. We compared fish and mussel biomass at mussel beds to test whether differences in animal biomass mediate their contributions to nutrient cycling through nitrogen and phosphorous excretion. We estimated areal excretion rates for each group by combining biomass estimates with measured excretion rates. Fish biomass was homogeneously distributed, except following a period of low flow when fish were more concentrated at mussel beds. Mussel biomass was consistently an order of magnitude greater than fish biomass and mussel areal excretion rates exceeded fish excretion rates. However, the magnitude of those differences varied spatially and temporally. Mussel excretion stoichiometry varied with changes in assemblage composition, while fish excretion stoichiometry varied little. Biogeochemical hotspots associated with mussels did not generally overlap with fish aggregations, thus, under these conditions, animal processes appear to exert additive ecosystem effects.

Keywords Consumer-driven nutrient dynamics · Unionid mussels · Stream fish · Communities · Excretion

Introduction

Animals across all ecosystems can have strong top-down effects through the consumption of resources (Power et al. 1988; Knapp et al. 1999) and bottom-up effects through excretion and egestion of nutrients (Small et al. 2011; Subalusky et al. 2015). The importance of animals in mediating and maintaining resource heterogeneity through indirect provisioning of nutrients is becoming widely accepted (Atkinson et al. 2017; Sitters et al. 2017). Animals ranging from ungulates to snails maintain resource heterogeneity and provide important nutrient subsidies to primary producers through urine, feces, and frass (McNaughton 1984; Zaady et al. 1996; Meehan and Lindroth 2007). The relative importance of animals in mediating nutrient heterogeneity varies temporally and spatially across species and ecosystems (Vanni 2002; Atkinson et al. 2017) and depends primarily on the interaction of density, biomass, and traits with

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environmental factors such as climate, ambient nutrient concentration, ecosystem size, and season (Benstead et al. 2010; Griffiths and Hill 2014). The effects of these interactions often become apparent at environmental extremes that redistribute the biomass of one or more groups of animals. For example, in stream ecosystems under hydrologic low flow conditions, a larger fraction of ecosystem nutrient demand may be supplied by animal excretion compared to catchment run-off (Grimm 1988; Atkinson et al. 2014; Childress et al. 2014). Animal biomass may be further redistributed if facilitation of one animal group by another, through the production of spatial subsidies, concentrates animal biomass. Though properties of ecosystems produced by animals are often a product of interactions among multiple animal taxonomic and functional groups and environmental factors, most studies have simplified these processes by investigating the role of a single animal group under relatively stable environmental conditions (Hillebrand et al. 2004; Leiss and Hillebrand 2006, but see Evans-White and Lamberti 2005, 2006).

Aggregating animals in particular, produce spatially heterogeneous distributions of biomass which can generate biogeochemical hotspots—areas with disproportionately high rates of nutrient recycling and material flux (McIntyre et al. 2008). Such hotspots are dynamic and can be driven by environmental events such as hydrology and temperature (Atkinson and Vaughn 2015; Wetzel et al. 2005). These patches of biogeochemical activity promote resource heterogeneity that maintains biodiversity (Bump et al. 2009) and can provide important nutrient subsidies in otherwise nutrient-limited systems (McIntyre et al. 2008; Atkinson et al. 2013). For example, nutrients and biological activity become locally concentrated and food web productivity increases in grazing ungulate systems (McNaughton 1984), bird roosting trees on the savanna (Dean et al. 1999), coral reefs (Allgeier et al. 2013), Everglade tree islands (Wetzel et al. 2005) and streams (Grimm 1988). While individual groups of animals such as these have been recognized for their ability to generate biogeochemical hotspots (McIntyre et al. 2008; Atkinson and Vaughn 2015), ecosystems comprise taxonomically and functionally diverse groups of animals that differ in their spatial overlap as well as their pathways and potentials for generating biogeochemical hotspots. Thus, understanding how overlapping, aggregated animal groups interact to influence nutrient and resource heterogeneity is a fundamental knowledge gap.

We propose a simple conceptual framework that considers how spatially overlapping aggregations of different animal groups might influence ecosystem properties (Fig. 1). Spatial or temporal overlap by multiple groups of aggregated animals is common in many ecosystems and may be driven by either abiotic or biotic mechanisms, with potentially cumulative or synergistic (non-additive) ecosystem-level

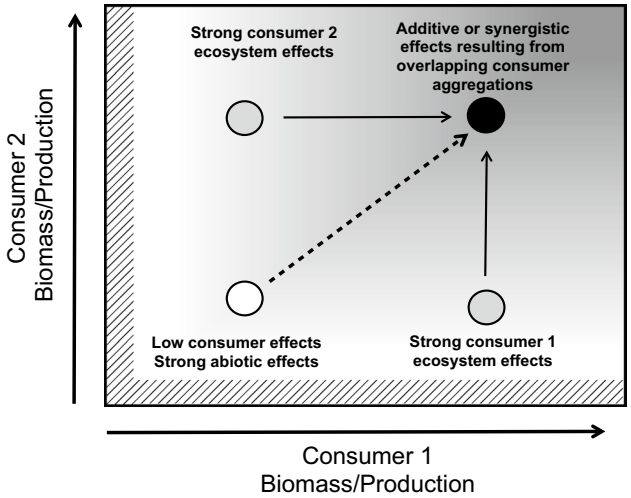

Fig. 1 Conceptual diagram illustrating the importance of spatial overlap in regulating the ecosystem effects of animal consumer groups (hereafter consumers). Axes represent a gradient of either consumer biomass or production that should index their ecosystem effect. Darker shading indicates the strongest predicted effects by consumers. In the upper-left and lower right regions of the figure a single consumer plays a dominant role in ecosystem function. Overlapping aggregations of consumer 1 and consumer 2 in the upper right region create the highest potential for cumulative or synergist effects. The dashed arrow connecting the white and black circles represent the case of one consumer facilitating or attracting the other consumer through a resource subsidy, potentially generating a positive feedback on combined ecosystem effects. The solid arrows connecting gray circles to the black circles represent abiotic conditions (e.g., stream contraction) that force consumer aggregations to overlap. The hatched area along the *X* and *Y* axis represents the context in which most studies investigate the effects of consumers on ecosystem structure and function. For instance, increasing levels of consumer 1 or consumer 2 are only compared with very low levels of consumer 2 and consumer 1, respectively, or increasing levels of consumer 1 and consumer 2 are compared individually with zero presence of consumer 2 and consumer 1, respectively

effects (Fig. 1). Abiotic and biotic mechanisms might drive the overlap of multiple animal aggregations. For example, animal groups might aggregate during particular abiotic conditions, such as around a water source during drought conditions or at low elevation fields during winter (Western 1975; Ferrari and Garrott 2002; Redfern et al. 2003).

Aggregating animals might also overlap if the activities of one animal attracts the other, with the potential of resulting ecosystem changes by those aggregations to lead to a positive feedbacks (Fig. 1). For instance, prairie dogs (*Cynomys ludovicianus*) occur as heterogeneously distributed colonies in prairie ecosystems that attract bison (*Bison bison*) grazing by triggering a broad array of compositional, structural, and nutritional changes in the vegetation through both direct and indirect effects (Coppock et al. 1983). Moreover, grazing and urine and fecal deposits of bison stimulate additional changes to the vegetation assemblage and increases nutrient

cycling (Knapp et al. 1999). Thus, we predict the potential for strong ecosystem effects occurs where abiotic and biotic mechanisms cause the spatial and temporal overlap of dominant animal functional groups.

Stream ecosystems present an ideal opportunity to investigate the ecosystem consequences of overlapping animal aggregations. Streams are spatially heterogeneous, dynamic systems that expand and contract with hydrologic condition. Thus, the presence or absence of water fundamentally constrains the availability of habitat (Junk et al. 1989; Grant et al. 2007). Stream animals have evolved several general adaptations to this constraint—high mobility, desiccation resistance, and/or high fecundity to compensate for the loss of adults through drying. Contrasting adaptations to stream drying are exemplified by mobile fish and sedentary unionid mussels (hereafter mussels), which can elicit some of the strongest documented ecosystem effects by stream animals (McIntyre et al. 2007, 2008; Atkinson and Vaughn 2015; Capps et al. 2015). While fish disperse as stream ecosystems expand, mussel populations are constrained to perennially wetted segments of the stream (Gough et al. 2012). Mussels and fish commonly co-occur in streams of the southern United States as high biomass aggregations and both can form biogeochemical hotspots (McIntyre et al. 2008; Atkinson and Vaughn 2015).

Mussels and fish have different life histories that influence how their distribution varies with hydrology, their degree of spatial overlap, and in turn their effects on ecosystem function. Mussels are long-lived (6 to > 100 years), sedentary, filter feeders that spend their adult life in dense, multi-species aggregations (up to 100 individuals m^{-2}) called mussel beds (Strayer 2008). Mussel beds are patchily distributed in streams because mussels are constrained to perennial stream reaches where sediments are stable with low shear stress (Allen and Vaughn 2010). Mussels have strong bottom-up effects through nitrogen excretion where they are abundant, which reduces nutrient limitation to primary producers leading to increased benthic algae (Vaughn et al. 2008), macroinvertebrates (Spooner and Vaughn 2006) and riparian spiders (Allen et al. 2012). In contrast, stream fish are typically shorter-lived (2–5 years), mobile animals, and their distribution and abundance are largely controlled by hydrology (Fausch et al. 2001; Grossman 2010). Stream fishes can have strong top-down (Power et al. 1985) and bottom-up effects (Gido and Matthews 2001), but those effects can be mediated by hydrology (Gido et al. 2010). Thus, the distribution of fish aggregations shifts seasonally and with stream discharge (Lobón-Cerviá 2009), while mussel beds remain stable (Strayer 2008). Therefore, mussels represent localized, stable hotspots that supply spatially predictable nutrient subsidies, while fishes are widespread, mobile hotspots that provide nutrient subsidies more dependent upon hydrological conditions. Consequently, there is great potential for co-occurring fish and mussel hotspots to overlap spatially or temporally, presenting an opportunity to investigate the potential for cumulative effects resulting from overlapping biogeochemical hotspots. Overlapping hotspots may also be generated independently of abiotic factors such as hydrology. Fish and mussel hotspots may overlap through positive feedback mechanisms where basal trophic resources stimulated by aggregations of mussels or habitat created by their shells facilitates habitat selection by fishes (Spooner and Vaughn 2006). Synergies may result when fishes, feeding on algal or insect prey, also excrete additional limiting nutrients thereby promoting more algal production (Gido and Matthews 2001). Thus, overlap of dominant animal functional groups may fundamentally alter ecosystem properties during periods of spatial overlap.

To understand the potential for spatial overlap to occur between fish and mussels, in the context of our conceptual model, we examined how aggregations of these two animal groups were distributed relative to each other and estimated their potential contributions to nutrient cycling through excretion, especially with regards to hydrologic condition. We hypothesized that fish assemblage biomass would be greater in stream reaches with mussel aggregations compared to reaches with few mussels, because basal trophic resources stimulated by aggregations of mussels or habitat created by their shells may facilitate habitat selection by fishes (Spooner and Vaughn 2006). However, we expect aggregations of fish at mussel bed reaches to be greatest under low flow conditions because they will be more dispersed when habitat volume increases (Ross et al. 1985; Schlosser 1991; Stanley et al. 1997). Finally, we hypothesized that spatial and temporal differences in the distribution of animal group biomass would lead to different contributions of fish and mussel assemblages to nutrient cycling, a fundamental component of biogeochemical hotspots. We tested these hypotheses through field experiments conducted across 2 years. The objectives of these experiments were to (1) compare fish biomass at mussel bed reaches and non-mussel bed reaches, (2) test how mussel and fish biomass differ when they co-occur at mussel beds and if differences in animal biomass and coarse taxonomic composition result in different flux and stoichiometric contributions to nutrient cycling through differential excretion of nitrogen (N) and phosphorus (P) and (3) evaluate spatial and temporal changes in flux and stoichiometric contributions to nutrient cycling of fish and mussel populations associated with assemblage composition and hydrology.

Materials and methods

Study location

The Kiamichi River and Little River are adjacent tributaries to the Red River in the south-central USA. The Kiamichi

River (KR) drains 4500 km^2 and is typically susceptible to extremely low water levels in the summer (Allen et al. 2013, Vaughn et al. 2015). The Little River (LR) drainage is 10,720 km^2 and is less hydrologically variable than the KR but experiences lower flows during the summer relative to the fall. The Glover River (GR) is an unimpounded tributary to the Little River that drains 828 km^2 and can experience almost complete desiccation to rapid flash flooding within a relatively short time period (Dauwalter and Fisher 2008). These well-studied rivers are recognized for their high fish (KR 86 species, LR 110 species, GR 33 species) and mussel (KR 31 species, LR 35 species, GR 22 species) diversity (Vaughn 2003; Matthews et al. 2005). In addition, animals are known to influence nutrient cycling in these rivers. For example, sites without mussels in the Kiamichi River and Little River, are N-limited while sites with high mussel biomass are co-limited by N and P (Atkinson et al. 2013; Vaughn et al. 2007), which should strengthen the role of animal aggregations in nutrient cycling. The locations and spatial extent of most mussel beds in these rivers have been mapped and their species compositions are well known (Spooner and Vaughn 2009; Atkinson et al. 2012; Atkinson and Vaughn 2015).

We selected paired reaches at seven locations within these rivers to understand the influence of mussel beds on fish biomass distribution and how mussel and fish aggregations influence nutrient cycling. Reaches were sampled for fish during the fall and summer to understand the influence of seasonal hydrological variation on fish biomass distribution and consumer-driven nutrient cycling. Each location contained a 100 m stream reach with a large mussel bed (mussel bed reach) and a 100 m reach without mussels or with very low densities of mussels (range 0–15.7 mussels m^{-2}, non-mussel bed reach). Mussel and non-mussel reaches were separated by an average distance of 346 m (range of 112–686 m). Non-mussel bed reaches served as references to test the effects of mussel beds on fish biomass distribution.

Overlapping fish and mussel biomass

To test our hypothesis that fish biomass would be higher in mussel bed reaches compared to non-mussel bed reaches, we sampled fish assemblages in each stream reach using a combination of backpack electrofishing and seining. Fish collection was accomplished through a two-pass closed population mark–recapture approach using two to six channel units per reach. Channel units were defined as relatively homogeneous areas of the channel that differ in depth, velocity, and substrate characteristics from adjacent areas (Bisson and Montgomery 2017). Individual fish collected during the first pass were identified to species, measured (total length, mm) and given a noticeable clip on the caudal fin prior to being returned to their respective channel unit. Individuals less than 40 mm were not marked to avoid high mortality related to handling stress (G. Hopper personal observation). Fish greater than 200 mm were also excluded because of their sparse distribution, high mobility and ability to avoid our sampling gear. Each reach was resampled 4–12 h later using identical methods. Length–mass regressions from a subset of individuals collected on-site or previously collected individuals of the same species or genus were used to estimate wet mass (K. Gido unpublished data) of all captured individuals (Online Resource 1). The Chapman mark–recapture population estimator was used to calculate population sizes. Areal biomass was estimated for each channel unit separately as the product of the population estimate and the mean predicted mass of individuals collected from each channel unit, respectively (Seber 1982; Hayes et al. 2007). Within reach-level estimates used for comparisons were calculated from area-weighted averages of channel units. Reach estimates were calculated during August and October of 2015 and 2016; three paired reaches were not sampled during 2015 due to extreme flooding that prevented access to the stream. Finally, fish assemblage biomass was converted to dry mass, using measured wet–dry mass conversion ratios (dry mass = 22.9% of wet mass, G. Hopper unpublished data). It was necessary to convert fish biomass to dry mass to compare with previously reported estimates of mussel dry soft tissue mass (shell excluded).

We quantified mussel densities in August 2015, 2016 and 2018 during low flow conditions when mussel abundance is most accurately estimated (Vaughn et al. 1997). Because they are sessile, it was not necessary to estimate abundance during higher flows. Mussels were sampled by excavating 15–20 (depending on the size of the mussel bed) haphazardly placed, 0.25 m^2 quadrats to a depth of 15 cm at each mussel reach (Vaughn et al. 1997, 2015; Galbraith et al. 2010; Atkinson et al. 2014). Mussels were identified, counted, their longest axis measured and then returned to the stream alive. We used species-specific length-mass regressions to estimate individual mussel dry soft tissue masses (DW) (Atkinson and Vaughn 2015). A global length–mass regression was generated when length–mass data were insufficient using a bootstrapping procedure that subsampled (10,000 times) the existing data set so that no one taxon was represented by more than 10 individuals (Online Resource 2). Areal mussel biomass (g DW m^{-2}) was based on the sum of estimated dry soft tissue mass of all species within each quadrat. Reach-level estimates were calculated from averages of the quadrats.

Fish and mussel nutrient excretion rates

Individual excretion rates were measured for four fish species that made up more than 80% of total biomass across reaches to estimate excretion for fish assemblages. Fish

species included a grazing minnow (*Campostoma spadiceum*), benthic insectivore (*Etheostoma radiosum*), mesopredator (*Lepomis megalotis*) and water column insectivore (*Notropis boops*). Fish were collected from the Glover River using a seine and occasionally a backpack electrofishing unit to corral fish into the seine. Fish excretion rates were measured during 2016 in the spring (March) when temperatures ranged from 18.9 to 21.9 °C, summer (August) when temperatures ranged from 29.7 to 32.4 °C and fall (October) when temperature ranged from 20.0 to 22.9 °C. Individual excretion rates were measured for at least seven individuals of each species during each season, except for *N. boops*, which was not included in the October sample because we were unable to collect enough individuals > 40 mm. Captured fish were placed into a cooler of fresh stream water and allowed to recover for 15 min. Individual fish were taken from the cooler and placed in a 1000 mL Nalgene bottle with a known volume of filtered stream water (GF/F; 0.7 µm pore size; Whatman Buckinghamshire, UK) and incubated for 1 h. Total length and wet mass were recorded for individual fish and wet mass was converted to dry mass as described above.

Water samples were collected at the end of each trial, placed on ice and transported back to the laboratory for analysis. Nutrient analysis focused on NH_4^+ and soluble reactive phosphorus (SRP). Analyses were performed using the indophenol blue and ascorbic acid methods for NH_4^+ and SRP, respectively, using an O-I Analytical Flow Solution IV autoanalyzer (APHA 2005). Excretion calculations were based on the difference between nutrient concentrations of identical containers incubated simultaneously with and without fish. We applied a conversion factor of 1.37 (SE ± 0.04, $n = 7$) to fish excretion values (TP = 1.37•SRP) to compare mussel excretion measured as TP to fish excretion measured as SRP. This conversion was based on a subsample of fish excretion samples where we measured both SRP and TP (G. Hopper unpublished data).

Size scaling of NH_4^+ and TP (hereafter N and P, respectively) excretion and molar N: P for all fish species was visualized using least-squares regression of $\log_{10}$-transformed excretion rates against $\log_{10}$-transformed dry mass. We removed measurements if they exceeded expected excretion rates of conspecifics by > tenfold to avoid the influence of outliers. A total of eight outliers were removed from the N excretion data set (4% of the data set) and only a single individual was removed from the P data set (< 1% of the data set) using this criterion. When slopes for individual species were equal (overlapping confidence intervals), we used ANCOVA to test for interspecific differences of $\log_{10}$ transformed excretion rates and molar N:P ratios, using $\log_{10}$ transformed dry mass as a covariate. We used ANOVA to test for interspecific differences in excretion if no relationship was found between excretion rates and the covariate. We found no differences in N or P excretion rates among fish species (see "Results" and Table 1; $P > 0.74$) and were able to use a simple biomass model ($\log(E) = 0.84 + 0.67 \times \log(M)$) to predict fish N excretion rates and ($\log(E) = -0.11 + 0.49 \times \log(M)$) P excretion rates.

We used previously published, field-measured excretion data to derive areal excretion rates for mussel assemblages. These data were collected during the summer at 30 °C by Atkinson et al. (2013) for four species of mussels that are common in mussel beds in these rivers: *Actinonaias ligamentina, Amblema plicata, Ptychobranchus occidentalis,* and *Cyclonaias pustulosa*, (Online Resource 2). Excretion rates were corrected for nutrient reuptake using a control with empty shells. Values were measured and calculated as µmol TN or TP g DW^{-1} h^{-1} (Online Resource 2. Full methods in Atkinson et al. 2013). First, because excretion rates increase with increasing body size (Vanni and McIntyre 2016) we calculated the body size-dependent mass-specific excretion rate for each individual of these four species (excretion = $b \times DW^a$). For species not measured, we used the overall scaling relationship derived from all

Table 1 Fish species for which ammonium and phosphorus excretion were directly measured

Measured taxa	*N*	Dry mass (g)	NH_4^+		R^2	*N*	TP		R^2
			a (SE)	*b* (SE)			*a* (SE)	*b* (SE)	
Campostoma spadiceum	30	0.14–0.76	**0.87 (0.07)**	**0.53 (0.15)**	**0.27**	33	**−0.01 (0.17)**	**0.78 (0.36)**	**0.13**
Etheostoma radiosum	36	0.11–0.48	**0.71 (0.07)**	**0.57 (0.10)**	**0.49**	33	**0.17 (0.21)**	**1.03 (0.33)**	**0.24**
Lepomis megalotis[a]	29	0.68–1.93	**0.83 (0.03)**	**0.50 (0.27)**	**0.50**	32	−0.37 (0.08)	0.55 (0.64)	0.02
Notropis boops	24	0.14–0.70	**0.86 (0.08)**	**0.74 (0.15)**	**0.51**	25	**1.07 (0.13)**	**1.07 (0.25)**	**0.44**
All species[b]	119	0.11–1.93	**0.84 (0.02)**	**0.67 (0.05)**	**0.64**	123	**−0.11 (0.06)**	**0.49 (0.11)**	**0.13**

Linearized power functions were used to describe the scaling of excretion rates (*E*, µmol/h) relative to body dry mass (M, g): log (*E*) = *a* + *b* log (M). Bold font indicates statistically significant equations ($P < 0.05$)

[a]The relationship between N excretion rate and body mass for *L. megalotis* was marginally significant ($P = 0.07$)

[b]Indicates the equation used to predict fish assemblage N and P areal excretion rates

observations in Atkinson et al. (2013). Second, we adjusted excretion rates for seasonal temperature differences. Mussel species have strong differences in thermal tolerances, which affect their excretion rates, particularly *A. ligamentina* and *A. plicata* which comprise the majority of mussel biomass in rivers in this region (Spooner and Vaughn 2008). To derive excretion rates for our mussel assemblages at 20 °C (fall temperature), we used published laboratory data on the temperature dependence of excretion for six common mussel species: *A. ligamentina*, *A. plicata*, *Lampsilis cardium*, *Obliquaria reflexa*, *C. pustulosa*, *Truncilla truncata* (Spooner and Vaughn 2008). For these data, we fit 2nd order polynomials for each species and calculated the ratio of excretion at 20 °C to excretion at 30 °C. We then multiplied each species' field-measured excretion rates at 30 °C by this ratio to estimate excretion rates at 20 °C. It is important to note that our excretion estimates for fish and mussel assemblages are based on NH_4^+ and TN, respectively. This corresponds to a conservative estimate for fish N excretion while providing a maximum estimate for N excreted by mussels. Although this discrepancy exists, it is likely that fish excretion rates measured as TN would result in a similar pattern presented here since NH_4^+ is a majority of excretion measured as TN (Vanni 2002; Ramamonjisoa and Natuhara 2018).

Comparing mussel and fish contributions to nutrient cycling

We used spatially explicit mussel and fish species composition and biomass data to estimate the variation in aggregate nutrient excretion between mussel beds and associated fish assemblages. Mussel assemblage excretion estimates were calculated by multiplying species-specific excretion rates (μmol P h^{-1} g DW^{-1}, μmols NH_4^+ h^{-1} g DW^{-1}) by the total biomass estimate for a quadrat (g DW m^{-2}) or the mean excretion rates for all species if species-specific rates were unavailable. We estimated assemblage excretion rates for fish by multiplying the measured excretion scaling equations by dry mass estimates for individuals in the assemblage data set. Species-level nutrient excretion was then calculated as the product of population estimates for fish and the per capita excretion rates. Assemblage excretion rates were estimated separately for each sampling unit (channel units for fish and quadrats for mussels), with reach-level estimates calculated from area-weighted averages. Averaging across sampling units within a reach yielded N and P areal excretion rates (μmol m^{-2} h^{-1}) for each assemblage. The estimated areal excretion rates of N and P for each assemblage were used to calculate assemblage excretion N:P ratios. We used the variation among reaches in aggregate excretion rates and N:P to compare the contributions of fish and mussels to nutrient recycling in these reaches.

Data analysis

Paired *t* tests were used to test for differences in fish assemblage biomass at mussel bed reaches and non-mussel bed reaches for each sampling period and log response ratios (lnR) were used to visualize proportional differences in areal biomass of fish assemblages at mussel bed reaches and non-mussel bed reaches. In addition to *t* tests, we calculated 95% confidence intervals of lnR to determine if effects of mussel beds on fish biomass distribution were significant (not overlapping zero). We used linear models to compare fish and mussel biomass at reaches where they co-occur. "Consumer" (i.e., mussel or fish), "season", "reach", "year" and their interactions were included as factors. Finally, fish and mussel assemblage areal excretion rates for N and P were compared using linear models with "consumer, "season", "reach" and "year" and their interactions. Statistical analyses were performed in R version 3.4.4 (R Development Core Team 2016). We used the function *aov ()* to carry out linear models in the package car (Fox and Weisberg 2018). All biomass (g m^{-2}) and excretion (μmol m^{-2} h^{-1}) data were $\log_{10}+1$ transformed prior to analyses to conform to assumptions of normality and homogeneity of variances.

Results

Fish assemblage biomass

Fish and mussel species richness and biomass were highly variable within and among reaches. Areal fish biomass estimates within reaches exhibited high spatial variation among channel units sampled, often varying an order of magnitude or more (Online Resource 3). Contrary to our prediction, there was no difference ($P > 0.05$) in fish assemblage biomass among mussel bed and non-mussel bed reaches during the summer and fall of 2015 (Figs. 2, 3). However, areal fish biomass was greater at mussel bed reaches during the summer of 2016 ($t_{0.05} = -3.41$, $df = 6$, $P = 0.007$, Fig. 3) compared to non-mussel bed reaches, but returned to the previous year's pattern during the fall of 2016. In support of our expectations, this result was driven by relatively higher fish biomass at six mussel bed reaches during the summer 2016 sampling period, which followed a period of lower flow (Online Resource 3, 4, 5, 6).

Fish and mussel excretion rates

Three fish species (*C. spadiceum*, *E. radiosum*, and *N. boops*) showed a significant positive relationship between body mass and measured N excretion rates ($P < 0.05$), while *L. megalotis* showed only a marginally significant relation between body mass and N excretion rates ($P = 0.07$).

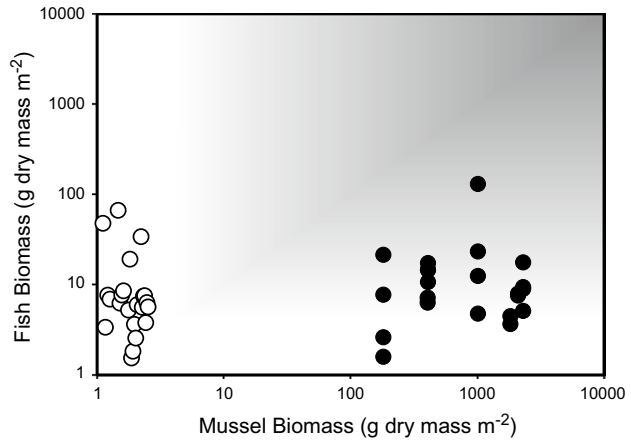

Fig. 2 Empirical data of fish and mussel assemblage biomass estimated at seven paired mussel and non-mussel bed reaches across 2 years. Non-mussel fish biomass is staggered between 1 and 2.5 on the *X* axis to prevent overlap at zero. Figure shading corresponds to predicted ecosystem response of animal biomass or production, where the darkest shading indicates the strongest predicted effects by consumers

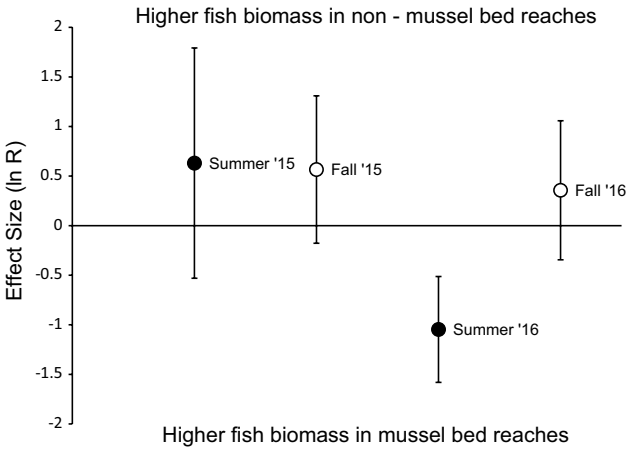

Fig. 3 Effect sizes and 95% confidence intervals illustrating the proportional response of fish biomass to the presence of mussel beds during fall and summer over a 2 year study period. The season and year are listed to the right of their respective symbols

Similarly, *C. spadiceum*, *E. radiosum*, and *N. boops* P excretion rates were positively related to body mass ($P < 0.05$, Table 1). However, P excretion rates for *L. megalotis* were not significantly related to body mass. ANCOVA testing for interspecific differences among species with body mass as a covariate revealed no difference for rates of N excretion ($F_{3,114} = 0.42$, $P = 0.73$) or P excretion ($F_{3,115} = 0.28$, $P = 0.8$). Estimated individual mussel N and P excretion rates (mean ± SD) used to estimate mussel assemblage areal excretion were much higher at 30 °C (263.4 µmol N h^{-1} ± 135.2 and 42.9 ± 7.6 µmol P h^{-1}) compared to rates measured at 20 °C (10.1 ± 5.33 µmol N h^{-1} and 0.7 ± 0.4 µmol P h^{-1}; Online Resource 2).

Fish and mussel contributions to nutrient cycling

Major differences in fish and mussel life history traits (i.e., mobility) resulted in an order of magnitude difference between mussel areal biomass and fish areal biomass during both fall and summer ($F_{6,274} = 10.97$, $P < 0.05$; Fig. 4a). This pattern generally increased with stream size (Fig. 5). We predicted biomass differences among mussel and fish assemblages would lead to considerable spatial and temporal differences among co-occurring fish and mussel areal excretion rates. Both mussel and fish areal excretion rates closely paralleled differences in animal biomass among reaches, with mussel areal N excretion rates being consistently an order of magnitude greater than fish areal excretion rates (Online Resource 3). Areal excretion rates for N differed among co-occurring mussel and fish assemblages (Fig. 4b) and showed substantial variation across sites and both seasons sampled ($F_{6,274} = 6.21$, $P < 0.05$). Mussel assemblage N areal excretion rates decreased from summer to fall as water temperature fell, while fish assemblage N areal excretion rates were similar although fish biomass distribution fluctuated with stream discharge across seasons ($F_{1,274} = 7.12$, $P < 0.05$, Fig. 4a, b). Similarly, mussel P areal excretion rates were an order of magnitude greater than fish assemblage P excretion rates and both groups varied among reaches ($F_{6,274} = 6.8$, $P < 0.05$, Fig. 4c). In contrast to N areal excretion rates, fish or mussel P areal excretion rates did not differ significantly among seasons ($P > 0.05$).

The ratio of N:P excreted by mussel and fish assemblages varied considerably across seasons ($F_{1,274} = 15.04$, $P < 0.05$) as mussel assemblages responded to decreasing temperatures (Fig. 4d) by excreting at a lower N:P. Differences in mussel bed composition among reaches also led to distinct differences in mussel assemblage N:P compared to fish assemblage excretion N:P ($F_{6,274} = 10.76$, $P < 0.05$, Fig. 4d). In mussel beds with greater densities (mean ± SD = 1719.1 g m^{-2} 106.5) of the thermally sensitive mussel species, *A. ligamentina*, assemblage excretion N:P (summer mean ± 95% CI = 15.4, 1.6; fall mean ± 95% CI = 9.9, 1.2) was consistently higher than fish excretion N:P (summer mean ± 95% CI = 10.8, 1.8, fall mean ± 95% CI = 7.2, 2.0), but the magnitude of difference between co-occurring fish and mussel assemblages exhibited a strong decline at lower water temperatures during the fall (Vaughn et al. 2007; Atkinson et al. 2013). At three mussel beds where *A. ligamentina* was present at low densities (mean ± SD = 220.3 g m^{-2} ± 48.9), lower fall water temperatures reduced mussel assemblage excretion N:P (summer mean N:P ± 95% CI = 11.1, 1.2; fall N:P mean ± 95% CI = 6.7, 0.8) below the excretion stoichiometry of the fish assemblage (summer mean N:P ± 95% CI = 9.8, 1.2; fall mean N:P ± 95%

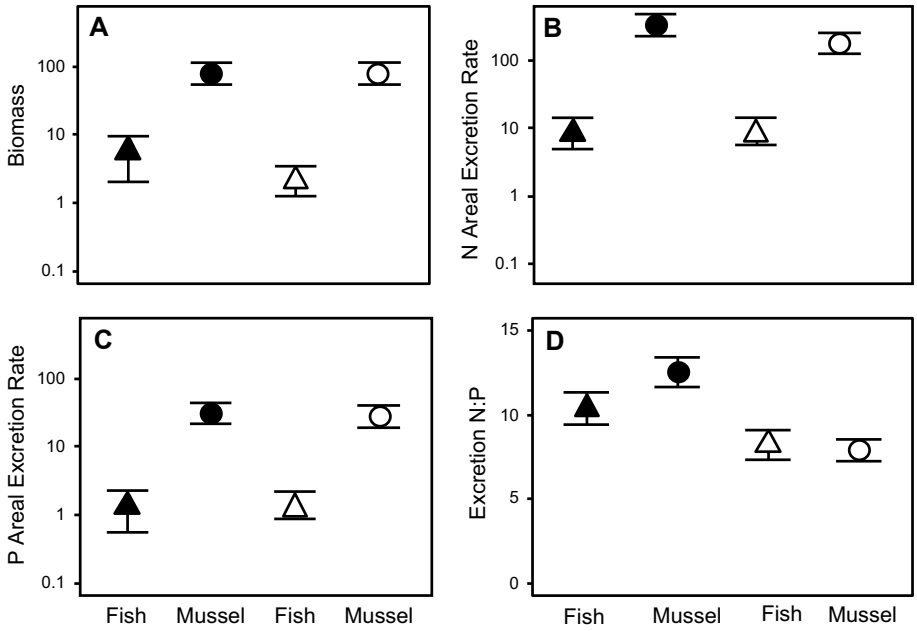

Fig. 4 Summary of the seasonal comparison of fish (triangles) and mussel (circles; **a**) biomass (g DW m^{-2}), **b** areal nitrogen excretion rates (μmol N m^{-2} h^{-1}), **c** areal phosphorus excretion rates (μmol P m^{-2} h^{-1}), and **d** molar N:P of mussel and fish assemblage excretion averaged across seven mussel bed reaches (±95% confidence intervals, $N=310$). Summer sampling is represented by closed symbols and fall by open symbols

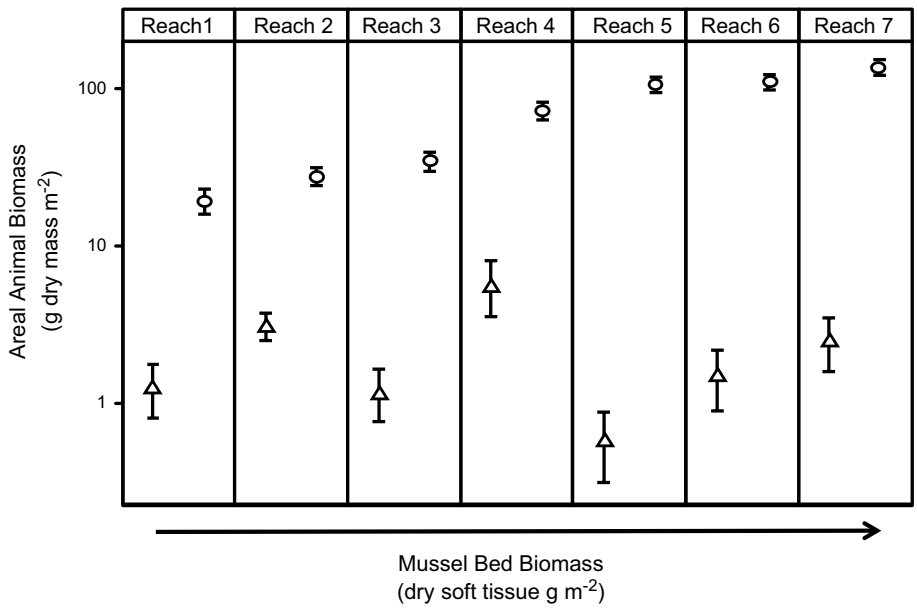

Fig. 5 Comparison of fish (triangles) and mussel (circles) biomass (g DW m^{-2}) along the stream size gradient represented by each of the seven mussel bed reaches sampled (±95% confidence intervals, $N=310$). Reaches are arranged in order of increasing mussel bed biomass

CI=8.8, 1.0). When *A. ligamentina* was absent, mussel assemblage excretion N:P (summer mean±95% CI=7.2, 2.2; fall mean±95% CI=5.0, 1.4) was lower compared to fish assemblages during summer (mean N:P±95% CI=11.0±2.8) and fall (mean N:P=8.7, 1.8).

Discussion

Aggregated animals can form biogeochemical hotspots that influence ecosystem function. The strongest effects should occur where abiotic and biotic mechanisms result in the highest spatial and temporal overlap of dominant animal groups (Fig. 1). We tested this prediction by examining the biomass overlap and ecosystem effects (nutrient recycling) of two dominant groups of stream animals, mussels and fish. We found that biomass of mussel aggregations was often an order of magnitude greater than fish biomass and was spatially concentrated and temporally stable. In contrast, fish biomass was temporally variable and was only aggregated in mussel beds during one relatively low flow period. Thus, using biomass as a metric to estimate the potential contributions of animals to nutrient cycling, we found strong ecosystem effects of mussels, but only weak effects from

fishes (Figs. 1, 2). Although standing stock or biomass might reflect production, such as when production to biomass ratios are stable (Gido and Hargrave 2009), shifting the axes of the conceptual framework to biomass production or element specific production might offer a more accurate representation of animal effects on nutrient dynamics, such as altering rates and supplies of key nutrients like N and P.

In our study, abiotic factors (i.e., hydrology) seemed to influence the distribution of fish aggregations relative to stable mussel beds, with fish aggregating on mussel beds during low flow conditions in summer 2016. However, mussel aggregations themselves did not generally appear to attract fish aggregations, as fish biomass was similar on and off mussel beds during all other sampling periods. We note that the conditions that we sampled were atypical of these rivers, which in most recent years have been prone to extremely low summer flows (Allen et al. 2013; Vaughn et al. 2015). Summer 2015 was a 100-year flood event for the Kiamichi River and we were unable to sample three sites there in 2015 because they were not accessible (Online Resource 5). Although hydrologic conditions did not reach typical low flow extremes during the summer of 2016, we found that during periods of relatively low flow fish biomass can become concentrated on mussel beds, but that more extreme conditions may be required to aggregate fish and mussels, thus eliciting strong ecosystem-level effects.

Mussel areal biomass was consistently an order of magnitude higher than fish areal biomass, although substantial spatial variation existed for both groups. The most apparent pattern was a longitudinal increase in biomass in more downstream reaches for mussels but not for fish (Fig. 4). In reaches where mussel densities were highest, the more than 100-fold difference between mussel and fish biomass resulted in a large difference in assemblage excretion rates during both summer and fall (Fig. 5b, c, Online Resource 3). This longitudinal pattern in mussel biomass distribution means that mussel bed effects intensify as mussel density in beds increases downstream (Atkinson et al. 2012; Atkinson and Vaughn 2015).

Although fish biomass was not spatially heterogeneous across a stream size gradient, spatial heterogeneity was present across channel units within reaches (Fig. 5). For example, mussel bed Reach 1 comprises four unique channel units and fish areal dry mass within this reach ranged from 0.04 to 6.70 g m^{-2} during fall and 0.01–12.73 g m^{-2} during summer, suggesting that species-specific habitat preferences result in locally concentrated fish biomass heterogeneously within reaches (Angermeier and Karr 1983). The mussel beds we sampled occurred in shallow, slow-moving runs, which were dominated by sunfish (Centrarchidae) comprising 80% of fish biomass in our study reaches. In studies of tropical rivers, fish densities increased in riffle habitats (Taylor et al. 2006; McIntyre et al. 2008) that were rarely present at the reaches we sampled and associations between fishes and habitat type might offer a better explanation of fish biomass distribution at the scale we examined. Within the context of our conceptual framework, the combined excretion of mussels and fish at the scale of our stream reaches would likely fall within the lower right region (Figs. 1, 2). Large differences in biomass between co-occurring mussel and fish assemblages in mussel reaches means that mussels govern nutrient availability and overlapping fish assemblages perform a relatively minor role or their influence is concentrated at finer habitat scales. Although fish contributions to nutrient cycling were low compared to mussels within mussel bed reaches, the homogeneous distribution of fish likely means they contribute more broadly to nutrient dynamics compared to sedentary mussel hotspots.

Shifting distributions of fish assemblage biomass altered fish assemblage excretion rates among sampling periods (Online Resource 3) with fish assemblage excretion rates generally paralleling increases or decreases in fish biomass (Fig. 4a–c). However, the Reach 4 fish assemblage was an exception, and excretion rates increased from summer to fall although fish assemblage biomass declined (Online Resource 3).This increase in fish excretion rates was driven by a transition from many small bodied fishes with higher per capita excretion rates that were in high densities during fall sampling of 2015 and 2016 to larger fishes at other sampling periods, leading to a reduction in the assemblage excretion rate. Although our conceptual framework does not incorporate temperature or assemblage composition, it should still prove useful across systems given that biomass often determines the influence of animals on ecosystems (Atkinson et al. 2017; Hall et al. 2007).

We found that where fish and mussel communities overlap, the excretion stoichiometry of fish assemblages was more spatially and temporally stable relative to the excretion stoichiometry of mussels, which varied seasonally and with assemblage composition. In combination with earlier work, our data indicate that two co-existing, abundant species with opposing thermal optima (*A. ligamentina, A. plicata*) differentially dominated mussel assemblage biomass resulting in differences in excretion N:P. Previous work has demonstrated how mussels mediated water column N:P that altered assemblage composition and dominance patterns among algal functional groups (Atkinson et al. 2013). Thus, variation in animal assemblage composition may cause differences in the competitive interactions among primary producers with varying tissue C:N and N:P (Atkinson et al. 2013). By feeding selectively on primary producer tissues with low C:N or high N:P, overlapping grazing fishes may exert top-down effects that help to maintain the balance among algal functional groups within mussel beds. In terrestrial ecosystems, herbivores increase the biomass and abundance of rapidly growing primary

producers with low C:N ratios, because grazing stimulates nutritious regrowth of such plants which increases localized N mineralization rates and N availability (Sitters and Venterink 2015). In summary, variation in animal community composition (i.e., mussels and fish) and associated physiological traits might mediate multiple aspects of consumer-driven nutrient dynamics including excretion N:P, recycling rates, and total excretion volume (Atkinson et al. 2017).

Although mussels did not facilitate fish habitat selection at the scale of our study, we acknowledge that most of the fishes sampled in our study (i.e., sunfish) might not rely on the benthic resources stimulated by aggregations of filter feeding mussels. Our conceptual model, however, is applicable at finer spatial scales where biotic interactions are more likely to occur. For example, growth of juvenile Pacific lamprey aggregated in mussel beds is enhanced through the consumption of mussel derived spatial subsidies (Limm and Power 2011). Thus, it is possible that juvenile fishes that were excluded from our analyses and benthic fishes may benefit by seeking cover or resources in aggregations of mussels that occur at the patch scale (Downing et al. 1993; Strayer and Ralley 1993). Indeed, fish biomass was spatially heterogeneous within mussel bed reaches and a more focused survey within mussel bed reaches may result in fine scale spatial overlap of mussels and fishes that feed in or inhabit the benthos such as the grazing minnow (*Campostoma spadiceum*) or benthic invertivores (darters).

The composition and structure of communities has been presented as one key factor influencing stream ecosystem structure and function (Flecker 1996; Vanni et al. 2002; McIntyre et al. 2007). Within this context, the effects of major functional groups on ecosystems have been largely investigated in isolation and under relatively static conditions. Yet, groups of animals with broadly different life histories often coexist in temporally dynamic ecosystems. Consequently, their effects on ecosystem structure and function operate simultaneously but can shift both spatially and temporally, generating the potential for biogeochemical hotspots to overlap periodically. The scales at which aggregations of fish and mussels occur within rivers is variable between groups. While fish might be aggregated at micro- or meso-habitats, their biomass is widely distributed among stream reaches and might exceed that of mussels within the entire river system. Conversely, mussels are heterogeneously distributed among reaches, and within mussel bed reaches fish assemblages likely provide locally concentrated, transient nutrient subsidies while aggregations of mussels provide stable, long-term nutrient subsidies that vary in importance with stream discharge and temperature (Vaughn et al. 2004; Atkinson and Vaughn 2015). By investigating two co-occurring groups of animal we were able to show differences in the distribution of animal biomass and the potential for ecosystem-level effects by freshwater mussel and fish communities in two river systems in the southern USA.

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Author contribution statement GWH, KBG, and CCV conceived the study. All authors were involved in field work. GWH, TBP, and TGP carried out the fish excretion experiments and CLA provided the mussel excretion data. GWH wrote the manuscript and performed analyses with input from all authors.

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