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Do mobile consumers homogenize the distribution of resources in stream food webs? A test with overlapping fish and mussel aggregations

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Abstract

1. In streams, unionoid mussels and fish form aggregations that exert bottom-up and top-down effects on food webs, but the magnitude and spatial extent of their effects are controlled by species traits. Sedentary mussels live burrowed in the sediment in patchily distributed dense aggregations (mussel beds) where they filter seston and provide a local, relatively constant nutrient subsidy. In contrast, fish move on and off mussel beds, and thus comprise a transient nutrient subsidy.

2. We asked how overlap between fish and mussels influences nutrient recycling and resource distribution in streams. We conducted an 8-week study in experimental streams where we created mussel beds (comprised of two species, *Actinonaias ligamentina* and *Amblema plicata*), manipulated the occurrence of a grazing minnow (*Campostoma anomalum*), and tracked nutrient (nitrogen and phosphorus) and resource (algae, detritus, and chironomids) abundance up and downstream of the mussel beds.

3. In general, neither consumer had strong effects on the concentration or spatial distribution of nutrients. Water turnover time in our experimental streams may have diluted fish and mussel nutrient excretion effects, making it difficult to detect spatial patterns during a given sampling period.

4. Fish controlled the abundance and productivity of algae. In treatments without fish, large mats of filamentous algae formed early in the experiment. These algae senesced, decomposed, and were not replaced. When fish were present, algae consisted of attached biofilms with consistent biomass and spatial distribution over time.

5. Although previous work has shown that mussels can have strong, seasonal bottom-up effects on both primary and secondary production, our results suggested that adding grazing mobile fishes, led to a more consistent and homogenous supply of algal resources. Because mussels rarely occur in the absence of fish, considering their combined influence on ecosystem dynamics is likely to be important.

1 | INTRODUCTION

Animals simultaneously affect food webs from the top-down by consuming resources and from the bottom-up by providing excreted and egested nutrients. The importance of direct consumption of resources (i.e. herbivory) to food webs is well established (Polis & Strong, 1996). Indirect contributions of animals to food webs, via bottom-up provisioning of nutrients, are increasingly recognised as important (Atkinson et al., 2017; McNaughton, 1984; Vanni, 2002). As freshwater animal consumers such as snails, fish, and mussels metabolise food resources, they transform organic nutrients into inorganic nutrients, which they excrete back into the environment (Hall et al., 2003; Vanni, 2002). The importance of these interactions varies over space and time as environmental factors disperse and concentrate the density of animals (Hopper et al., 2018). When animals occur in dense aggregations, nutrients from their metabolic wastes drive biogeochemical *hotspots* where high inorganic nutrient availability stimulates primary production (McClain et al., 2003; Schmitz et al., 2018). Such hotspots can be especially important in nutrient-limited freshwater and marine systems where they locally concentrate nutrients and biological activity and increase food web productivity (Atkinson et al., 2013; Peterson et al., 2013).

Streams, with their naturally patchy, dendritic networks that expand and contract with hydrologic conditions, provide a good model system for examining interactions between consumer aggregations and ecosystem function (Junk et al., 1989). Stream animal aggregations as diverse as salamanders (Keitzer & Goforth, 2013), crayfishes (Evans-White et al., 2003), and insects (Wotton, 2003) serve as important *nodes of ecological function* embedded within the larger catchment landscape (Winemiller et al., 2010). However, the strongest documented biogeochemical effects of aggregated stream animals have been found in fishes and unionoid mussels (Atkinson & Vaughn, 2015; McIntyre et al., 2008; Taylor et al., 2012).

To date, studies on the ecosystem effects of animal-mediated biogeochemical hotspots have focused on individual groups or guilds. However, most ecosystems contain more than one type of consumer aggregation. Feedbacks between these groups and their cumulative effects are likely to be important for food web and ecosystem function (Agrawal et al., 2007). Fish and unionoid mussels are important in many rivers globally, and frequently co-occur and interact. Both fish and mussels exert bottom-up and top-down effects on stream food webs, but the magnitude and spatial extent of their effects are controlled by their distinct life histories. Mussels live burrowed in the sediment and only move short distances (1–100 m) (Kappes & Haase, 2012). They typically occur as dense (up to 100 individuals/m^2), patchily distributed aggregations called mussel beds (Strayer, 2008). Mussel metabolism of seston filtered from overlying waters and subsequent excretion and biodeposition

of nutrients has strong bottom-up effects, stimulating primary and secondary production (Figure 1a) (Atkinson et al., 2021; Vaughn & Hoellein, 2018). Mussel soft tissue and shells provide long-term nutrient storage, alter nutrient limitation, and decrease movement of nutrients downstream (Atkinson et al., 2013, 2018). Thus, excreted nutrients from mussel beds represent a local, immobile, long-term, and relatively constant nutrient subsidy.

In contrast to mussels, stream fish are shorter-lived (typically 2–5 years), can belong to multiple feeding guilds/trophic levels, and move between habitats in response to hydrology and resources. While fish are frequently found in stream reaches with mussel beds (Sansom et al., 2017), they move in and out of these areas, tending to concentrate over mussel beds during periods of low flow (Figure 1b) (Hopper et al., 2018). Stream fish can have strong top-down and bottom-up effects, but those effects are highly dependent on flows and species functional traits (Gido et al., 2010; Murdock et al., 2010; Power et al., 1985; Vanni, 2002). Thus, mobile, shorter-lived fish comprise a transient *boom-or bust* nutrient subsidy that is dependent on hydrologic conditions (Hopper et al., 2018).

Both mussel and fish aggregations are individually important hotspots of ecological function in streams, but we do not know how these functions change when they occur together. Thus, we asked how overlap between mobile fish and sedentary mussels in streams influenced nutrient recycling and the distribution of resources—benthic algae, organic matter, and benthic macroinvertebrates (Figure 1), and how those factors changed over time. We conducted an 8-week study in experimental streams with simulated riffle–pool structure, where we created mussel beds, manipulated fish occurrence, and tracked nutrient (ammonia [NH_4^+], soluble reactive phosphorus [SRP], N:P) and resource abundance (gross primary production [GPP], algal biomass as chlorophyll *a*, ash-free dry mass [AFDM]) up and downstream of mussel beds over time (Figure 1). We used a simplified consumer food web of two mussel species (*Actinonaias ligamentina* and *Amblema plicata*) and an algae-grazing fish (stoneroller minnow, *Campostoma anomalum*). Previous studies examining these taxa individually showed that they stimulated benthic algae production via bottom-up fertilisation from nutrient excretion (Figure 1a,b), but that grazing fish also simultaneously decreased algal biomass through top-down consumption (Figure 1b) (Atkinson et al., 2013; Martin et al., 2016; Vaughn et al., 2007). We predicted that mussels would create heterogeneity in resource distribution by generating nutrient subsidies in the middle pool of our experimental streams. We predicted that mobile fish would distribute excreted nutrients throughout an experimental stream, reducing the spatial variability in both nutrients and resources compared to treatments containing mussels (Figure 1b). We also predicted that over time grazing by fish would lead to decreased algal productivity and biomass, and subsequently increased nutrient availability due to lower algal nutrient demand.
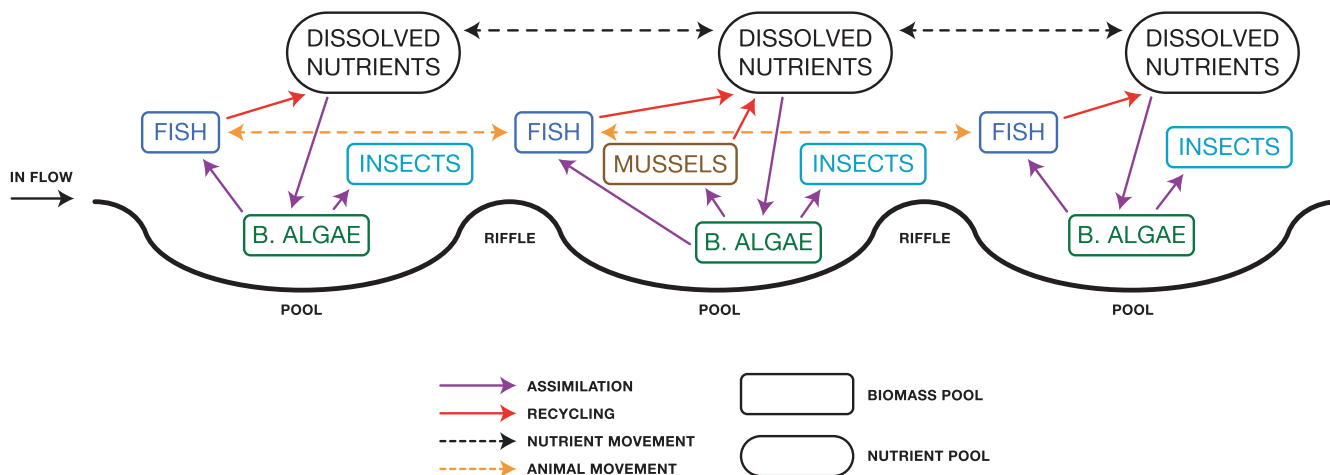
(a) MUSSELS
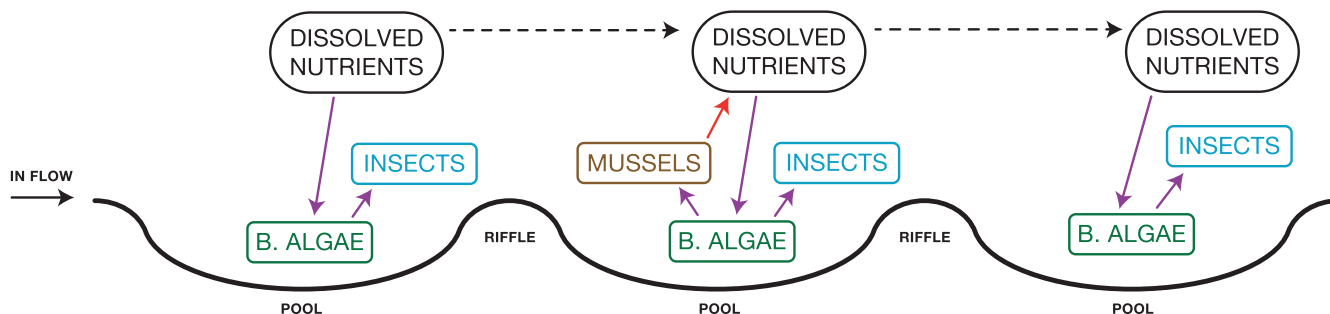
(b) MUSSELS and FISH

FIGURE 1 Nutrient and resource pools and fluxes measured in a series of connected experimental stream riffles and pools. (a) Mussels alone, (b) mussels and fish. Mussels and fish both excrete nutrients, which should stimulate algal growth and subsequently benthic insect production. When the two consumer groups overlap, fish graze on benthic algae which should decrease algal biomass, and they move up and downstream from mussel beds, redistributing nutrients and resources

2 | METHODS

2.1 | Experimental design

To examine the ecosystem effects of mussel beds alone versus mussel beds harbouring fish, we manipulated fish presence and absence in experimental streams containing mussel beds. We had two treatments with four replicates: mussels alone (M treatment) and mussels and fish together (MF treatment). We conducted the experiment at the University of Oklahoma Aquatic Research Facility (ARF) in eight replicated, flow-through experimental streams like those used in multiple food web experiments with stream fishes (Martin et al., 2016; Matthews et al., 2006; Nelson et al., 2021; Parr et al., 2019). Each stream consisted of three circular tanks (pools) connected by two rectangular troughs (riffles) with a total surface area = 9.6 m² and water volume of *c.* 3840 L (Figure 2). Stream sediments were a 50:50 (v/v) mix of 9.5 and 16.0 mm washed river gravel. Groundwater was continuously supplied at an average rate of 0.10 L/s at the start and 0.65 L/s by the end, resulting in turnover times of approximately 2–12 times per day. Several weeks before the start of the experiment on 5

May 2016, streams were filled with water and seeded with algae from a pond at the ARF. Experimental streams were naturally colonised by macroinvertebrates from an adjacent stream through emergent insects, primarily Chironomidae, laying eggs in the mesocosms that rapidly developed into larvae (Allen et al., 2012). To control temperature, streams were covered by a 70% shade cloth canopy. The experiment ran for 8 weeks ending on 12 July 2016, after which mussels were returned alive to the river and fish were euthanised.

In both M and MF treatments we used a simple mussel assemblage of 2 species, *Actinonaias ligamentina* and *Amblema plicata*, that are numerical and biomass dominants in rivers of the southcentral U.S.A., have strong effects on food web and nutrient fluxes, and have been used successfully in past mesocosm experiments (Allen et al., 2012; Vaughn et al., 2008). Mussels were collected from the Little River, OK, and held in Living Streams (Frigid Units Inc., Toledo, OH, U.S.A.) kept at 15°C and a natural light regime in a greenhouse at the ARF where they were fed an algal mixture cultured from an adjacent pond, as used in previous mesocosm experiments (Allen et al., 2012). Mussel beds were established by placing 10 *A. plicata* and 10 *A. ligamentina* in middle pools of both treatments (Figure 2a; *c.* 8 mussels/m² = a moderate
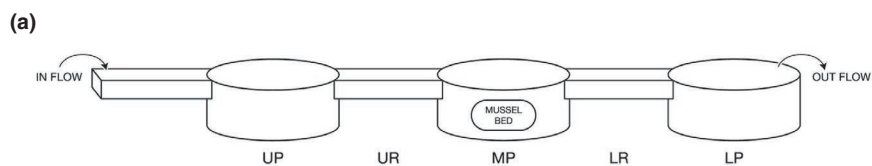
(a)

(b)

FIGURE 2 (a) Diagram of an experimental stream. UP = upper pool, UR = upper riffle, MP = the middle pool containing the mussel bed, LR = lower riffle, and LP = lower pool. (b) Photograph of experimental streams

density for the region). Mussel lengths were measured and converted to soft tissue dry weight (STDW) with species-specific regression equations [dry weight = a × length[b]; Atkinson et al. (2020)]. Mussel mass was measured at the beginning and end of the experiment to assess physiological condition (File S1). Biomass was maintained throughout the experiment by replacing dead mussels (determined by visual inspection) with mussels from a holding colony (File S2). We replaced 29 mussels during the course of the experiment.

The MF treatments were stocked with central stonerollers, *Campostoma anomalum*. These abundant, schooling, algal grazers frequently co-occur with mussels and have strong top-down and bottom-up effects in stream food webs (Martin et al., 2016; Power et al., 1985). Fish were collected from second- to fourth-order streams in the Big Blue River basin, KS, and stocked to a target biomass of *c.* 4 g/m^2 STDW in each stream (3.7–4.3 g/m^2, 51–67 individuals per stream), which is typical for the region (Hopper et al., 2018). At the beginning of the experiment, we photographed fish in a cooler with a ruler on the bottom and used ImageJ software (Version 1.48, Rasband, NIH) to estimate lengths from the photos (Taylor et al., 2012). We used a length to STDW regression equation for *C. anomalum* (Hopper et al., 2018) to determine biomass. Dead fish (19 over the course of the experiment) were immediately replaced throughout the experiment with similarly sized individuals (File S2).

2.2 | Response variables

2.2.1 | Nutrient fluxes

We measured nitrate (NO_3^-), NH_4^+, and SRP at weeks 4 and 8 from each riffle and pool in each stream. Two replicate 20 ml samples

were collected from the middle of the water column and filtered through pre-combusted (500°C) 0.7-µm glass-fibre filters. Nutrients were analysed with colorimetric methods on an OI Analytical nutrient analyser. Nitrate was analysed using the cadmium reduction method (EPA Method 353.2), NH_4^+ with the alkaline phenol method (EPA Method 350.1), and SRP with the molybdate blue method (EPA Method 365.1). We estimated N:P as molar DIN:SRP.

2.2.2 | Gross primary production

We estimated benthic metabolism in sealed recirculating chambers (Ruegg et al., 2015). Before the experiment, strawberry baskets (10 × 10 × 6 cm) were buried flush with the sediment and allowed to be colonised by algae. At weeks 4 and 8, three baskets from each riffle and pool in each stream were removed and placed in rectangular 10-L propeller-driven recirculating chambers to measure net ecosystem production (NEP) of dissolved oxygen (DO; mg/L) during natural light incubations and community respiration (CR) or consumption of DO during dark incubations. DO was logged every 30 s with a YSI ProODO luminescent DO meter. Light was measured with Fisherbrand Traceable Dual-Display Light Meter. Metabolism (g O$_2$ m^{-2} hr^{-1}) was calculated as GPP = NEP + |CR| (Ruegg et al., 2015). All calculations account for specific basket areas, chamber volumes and light differences (Parr et al., 2019; Ruegg et al., 2015). To correct for light differences, we developed a light correction curve for one high and one low algal biomass chamber. The curve used a series of irradiance levels produced by placing layers of 1.5 mm window screen over the chambers while measuring LUX and change in DO concentration (Parr et al., 2019).

To determine if mesocosms were autotrophic or heterotrophic, production to respiration ratios were calculated as GPP÷|CR|.

2.2.3 | Food web pools

The same baskets used to measure GPP were subsequently processed for benthic chlorophyll *a*, organic matter, and macroinvertebrates. Baskets were placed in a bucket with 20 L of clean well water and the contents were scrubbed and manually homogenised to create a slurry. Two 100-ml subsamples of slurry were filtered (GF/C–1.2 μm pore size; Whatman, Buckinghamshire, U.K.) and filters were frozen. Chlorophyll *a* was extracted with acetone and concentration was measured spectrophotometrically using the acid addition method (APHA, 2017). Organic matter was measured as AFDM—the dry mass (organic matter) lost after combustion at 500°C for 4 hr. The remaining slurry was washed through a 246-μm sieve and macroinvertebrates were removed and preserved in 10% buffered formalin. Macroinvertebrates were identified to family following Merritt and Cummins (1996) and Voshell (2002), photographed, and their lengths measured using ImageJ (Schneider et al., 2012). We converted lengths to dry mass using published regressions (Benke et al., 1999).

2.3 | Data analyses

We tested whether the distribution of nutrients and other resources differed when mussels were alone versus when they overlapped with fish, and how these distributions changed over time. We used linear mixed-effects models to examine fixed effects of consumer treatment (M and MF), stream location (upper pool, upper riffle, middle pool [where the mussel bed was located], lower riffle, lower pool), time (weeks 4 and 8), and their interactions. If there were significant interactions with time, we ran a reduced model to identify specific treatment and/or location effects for each week. We included mesocosm number (1–8) as a random effect to account for variation across units attributable to initial conditions, solar inputs, or other factors we were unable to control. The *lmer* function in the lme4 package (Bates et al., 2015) in Program R was used to develop models and the lmerTest package (Kuznetsova et al., 2017) was used to estimate *p*-values for fixed effects and their interaction. Model residuals versus fitted values were examined to evaluate assumptions of the linear model and as a result, all response variables except N:P ratios were log10 transformed to meet assumptions.

3 | RESULTS

3.1 | Fish impacts on the distribution of nutrients

Ammonium concentrations were slightly higher, on average, in treatments with fish, but the dependence of those differences varied by location and week, as indicated by a marginally significant 3-way interaction (Figure 3a,b, Table 1). Post hoc tests indicated a marginally significant location by treatment effect in week 4 ($p = 0.06$) and week 8 ($p = 0.09$), but limit our interpretation of spatial patterns because they were obscured by several outlier points. Phosphorus concentrations were on average twice as high in week 8, and declined from upstream to downstream, resulting in a significant location, week, and week by location effect (Figure 3c,d, Table 1)—post hoc tests suggest that the location effect was only present in week 8 ($p = 0.003$) and not related to consumer treatment. N:P patterns also included a significant location by week interaction (Figure 3e,f, Table 1). Post hoc tests indicated a significant location effect in week 4 ($p = 0.019$) due to the highest concentrations in the upstream pool in contrast to higher N:P ratios in downstream locations in week 8 ($p = 0.003$).

3.2 | Fish controlled the abundance and distribution of resources

Algal dynamics varied across treatments and time, as indicated by a significant interaction between those variables (Table 1). Algal biomass changed dramatically over time in M treatments, but remained constant where fish were present. Midway through the experiment (week 4) we observed large blooms of filamentous algae in M treatments, whereas MF treatments had grazed lawns of algae (Figure 4). There was a 92% decline in chlorophyll *a* concentrations in M treatments between weeks 4 and 8 as filamentous algae formed senescent mats, decomposed, and were not replaced (Figure 5a,b). In contrast, chlorophyll *a* concentrations in MF treatments only declined 31% over time (Figure 5a,b). Post hoc analysis by week suggested lower chlorophyll *a* in MF treatments (*p*-value = 0.008) and a general decline in chlorophyll *a* from up to downstream in week 4 for both treatments (*p*-value = 0.001). In week 8, there was higher chlorophyll *a* in MF treatments (*p*-value < 0.001), but no differences among locations.

GPP followed a similar trend to chlorophyll *a*. It was higher in fish treatments in week 8, resulting in significant week by treatment effects (Figure 5c,d, Table 1); however, the post hoc test did not indicate a treatment effect in either week (*p*-values > 0.18). GPP in MF treatments increased 71% between week 4 and 8 indicating rapid turnover of algal cells, but only increased 11% in treatments without fish. Mussel treatments were always autotrophic with mean P/R ratios of 1.5 (± 0.19) in week 4 and 2.9 (± 0.98) in week 8. P/R ratios indicate that MF treatments were heterotrophic in week 4 (mean P/R 0.74 ± 0.14), but autotrophic in week 8 (mean P/R 4.04 ± 0.98).

Fish did not notably impact the quantity and distribution of benthic organic matter (Figure 5e,f). Over time, AFDM declined in both M (68%) and MF treatments (30%), resulting in a significant week effect (Table 1). AFDM to chlorophyll *a* ratios indicated that a large proportion of benthic organic matter was benthic algae.

Most macroinvertebrates in the basket samples were Chironomidae larvae in the genus *Chironomus*. Chironomid biomass
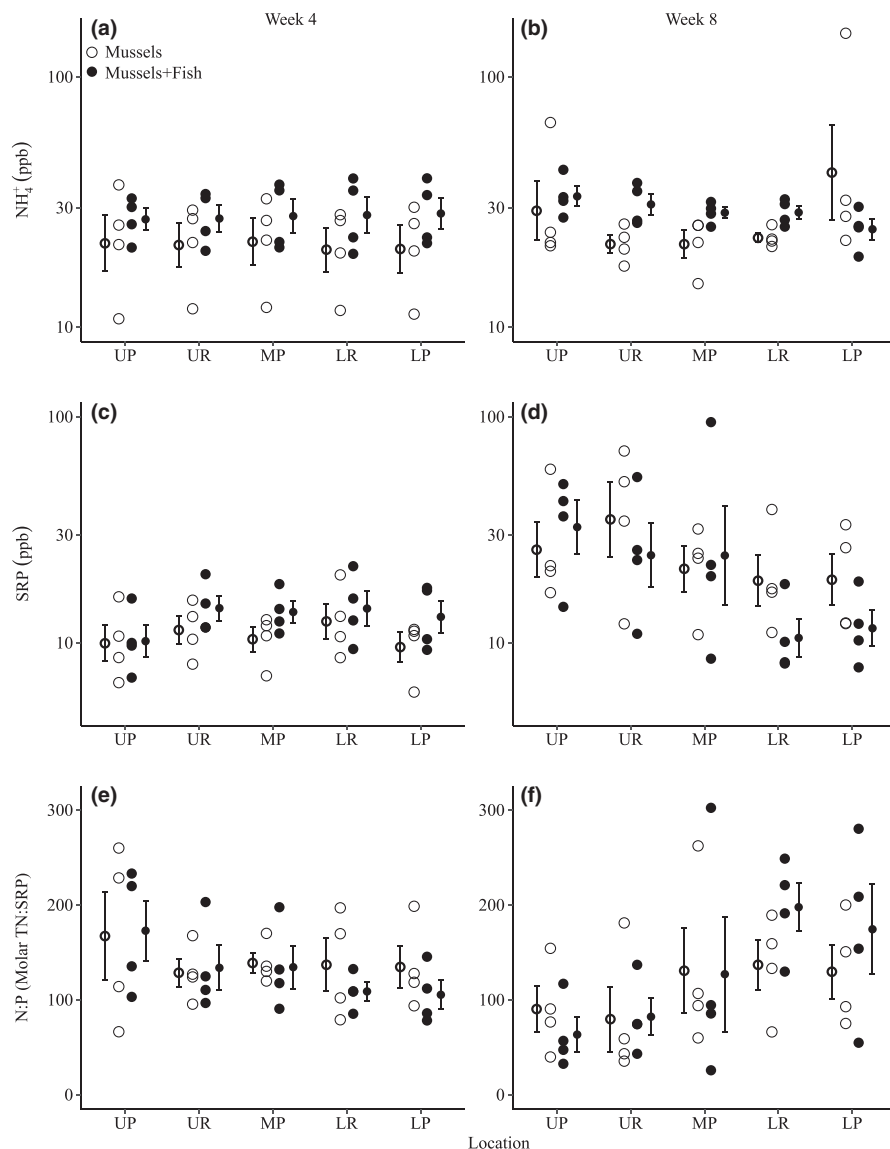
FIGURE 3 Nutrient responses to treatments and stream location at weeks 4 and 8. Raw data and means $\pm$ *SE*. Open circles are mussel treatments and black circles are mussel + fish treatments. (a) NH_4^+ week 4, (b) NH_4^+ week 8, (c) soluble reactive phosphorus (SRP) week 4, (d) SRP week 8, (e) N:P week 4, (f) N:P week 8

declined over time in both treatments resulting in a significant week effect (Table 1), but there were no significant treatment or location effects on chironomid biomass (Figure 6a,b, Table 1).

4 | DISCUSSION

We predicted that mussels would create heterogeneity in resource distribution by generating nutrient subsidies in the middle pool of our mesocosms and that fish would distribute nutrients up and downstream of mussel beds. Thus, fish would reduce spatial variability in nutrients, and subsequently in food web compartments using the nutrients such as algae and insects. However, overall the water turnover time in our experimental streams (between two and 12 times per day) may have diluted fish and mussel nutrient excretion effects, making it difficult to detect spatial patterns during a given sampling period. Mussels did not influence the spatial distribution of nutrients, which were relatively evenly distributed among stream compartments. Ammonium was generally higher in

fish treatments, but interactions between treatments and location were obscured by several outlier points. Phosphorus concentrations increased over time in both treatments. This could have been caused by a decrease in phosphorus uptake due to a decrease in algal biomass late in the experiment. High $N(NH_4^+ + NO_3^-)$:P ratios (>100) suggest that phosphorus is more likely to be limiting, thus changes in algal biomass are likely to be reflected in soluble phosphorus concentrations. Phosphorus attenuated downstream in both treatments in week 8. This pattern is consistent with phosphorus limitation and microbial uptake as water flowed through the mesocosms. Although we did observe lower mean phosphorus concentrations in the downstream pools of MF treatments, which had overall higher algal biomass in week 8, highly variable concentrations within treatments limited our statistical power to support a treatment by location interaction. An alternative explanation for the patterns in phosphorus could have been changes in concentration in the input water.

We predicted that fish grazing would decrease algal productivity and biomass, which would lead to decreases in other

TABLE 1 Estimates and standard error (SE) for fixed effects in linear mixed effects model testing treatments (M, MF), location (UP, UR, MP, LR, LP), time (weeks 4 and 8), and their interactions on ecosystem properties in the mesocosm experiment

	Intercept	Treatment (T)	Location (L)	Week (W)	T*L	T*W	L*W	T*L*W
Ammonium								
Estimate	3.04	0.53	0.07	0.05	−0.14	−0.35	−0.09	0.17
SE	0.18	0.27	0.05	0.23	0.07	0.32	0.07	0.10
p		0.102	0.939	0.457	0.242	0.286	0.927	0.082
Soluble reactive phosphorus								
Estimate	3.52	0.28	−0.12	−1.15	−0.17	−0.24	0.12	0.21
SE	0.24	0.34	0.07	0.34	0.10	0.49	0.10	0.15
p		0.496	**0.015***	**<0.001***	0.422	0.628	**0.002***	0.147
Nirogen:phosphorous								
Estimate	72.56	−44.93	13.59	85.60	20.14	65.68	−19.27	−30.45
SE	30.23	42.75	9.11	42.75	12.89	60.46	12.89	18.23
p		0.690	0.163	**<0.001***	0.591	0.281	**<0.001***	0.099
Gross primary productivity								
Estimate	−1.13	0.92	0.03	0.28	−0.10	−1.81	−0.07	0.13
SE	0.48	0.66	0.10	0.49	0.13	0.63	0.13	0.19
p		0.981	0.685	**0.049***	0.733	**0.006****	0.995	0.482
Chlorophyll a								
Estimate	1.53	1.47	0.40	3.42	−0.11	−3.13	−0.35	0.31
SE	0.35	0.47	0.10	0.46	0.14	0.64	0.14	0.19
p		0.772	**0.018***	**<0.001***	0.631	**<0.001***	**0.045***	0.116
Ash-free dry mass								
Estimate	0.54	0.30	0.01	1.35	−0.05	−0.93	−0.12	0.07
SE	0.26	0.37	0.089	0.37	0.11	0.53	0.11	0.16
p		0.549	0.161	**0.001****	0.898	0.084	0.327	0.643
Chironomid biomass								
Estimate	5.43	0.36	0.03	0.82	−0.03	−0.39	−0.03	0.01
SE	0.21	0.29	0.05	0.25	0.07	0.33	0.07	0.10
p		0.466	0.947	**<0.001***	0.616	0.244	0.604	0.903

Significant tests are bolded with *p < 0.05, **p < 0.01, and ***p < 0.001.

FIGURE 4 Photograph showing the contrast in benthic algal abundance between mussel (M) and mussel + fish (MF) treatments in middle pools in week 4

M treatment   MF treatment
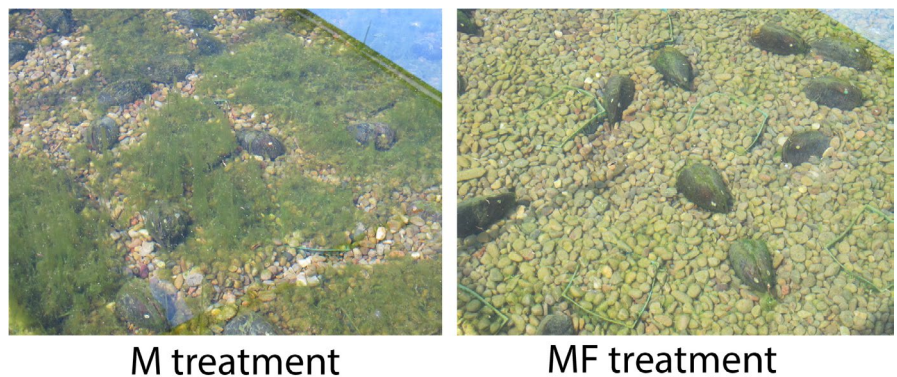
resources—AFDM and insects. We also predicted that the distribution of resources would be less spatially variable in treatments where fish were grazing and moving between riffles and pools. Fish indeed had strong impacts on algal dynamics. In the absence of grazing fish, large mats of filamentous algae developed early in the experiment. These algae later floated to the surface, senesced, and decomposed leaving these treatments less productive later in the experiment. Most responses in fishless treatments were more variable than in treatments with fish, reflecting this boom-and-bust cycle of filamentous algae. In contrast, in fish treatments, algae primarily consisted
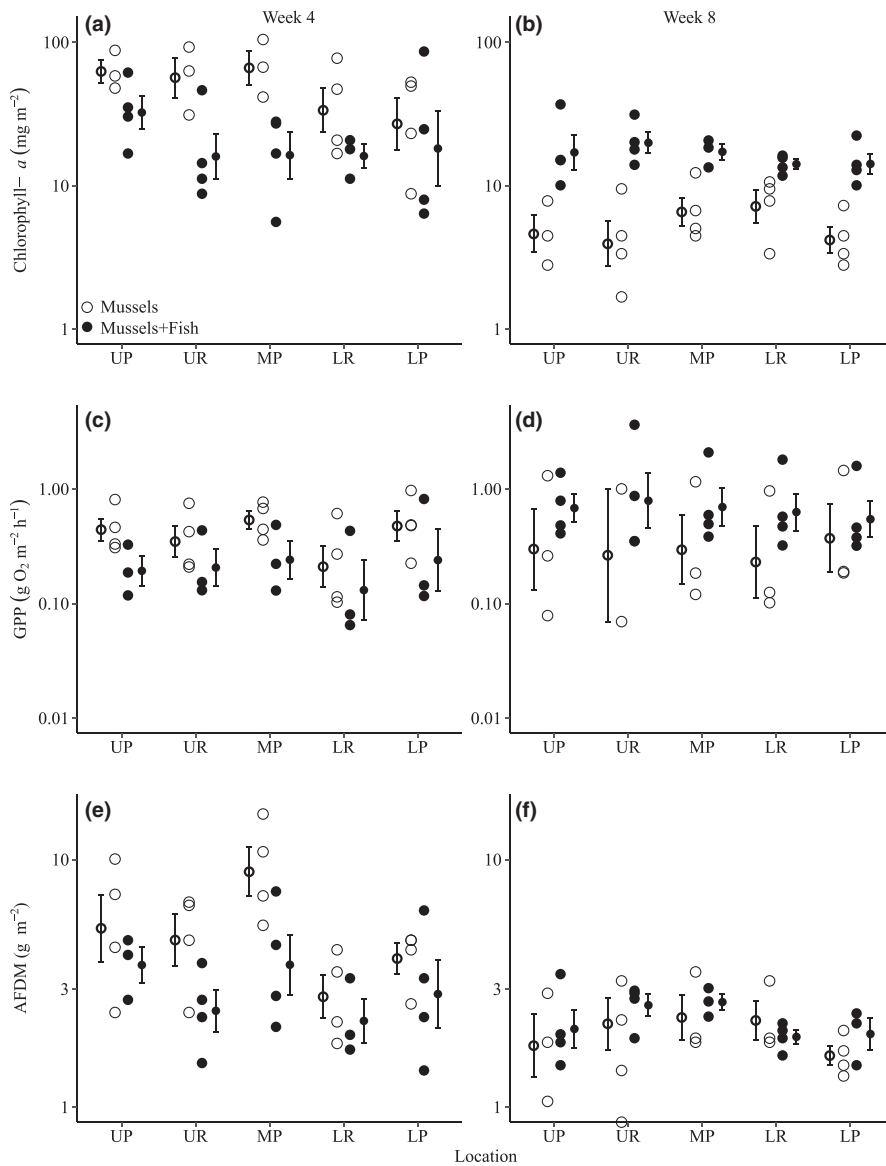
FIGURE 5 Algal dynamics and organic matter responses to treatments and stream location at weeks 4 and 8. Raw data and means ± *SE*. Open circles are M treatments and black circles are MF treatments. (a) chlorophyll-*a* week 4, (b) chlorophyll-*a* week 8, (c) gross primary productivity (GPP) week 4, (d) GPP week 8, (e) ash-free dry mass (AFDM) week 4, (f) AFDM week 8
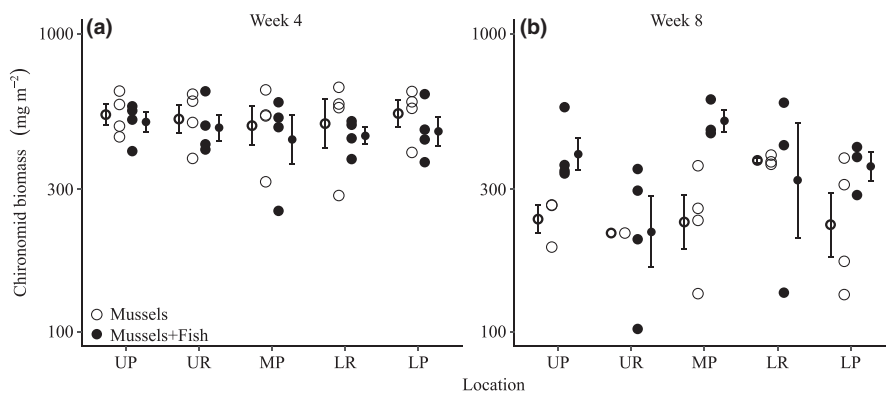

FIGURE 6 (A) Chironomid biomass response to treatments and stream location at weeks 4 and 8. Raw data and means ± *SE*. Open circles are mussel treatments and black circles are mussel + fish treatments. (a) chironomid biomass week 4, (b) chironomid biomass week 8

of attached biofilms with consistent biomass over time as fish grazing prevented the development of algal mats. This is consistent with other studies showing that grazing by *Campostoma* reduces algal biomass, encourages adnate forms or turfs of algae, and prevents the development of filamentous mats, thus preventing successional changes (Martin et al., 2016; Taylor et al., 2012; Vadeboncoeur &

Power, 2017). The development of algal filaments in fishless treatments early in the experiment was probably due to a lack of fish grazing.

Most algae that developed in our small experimental streams were attached benthic algae rather than phytoplankton. While the fish in our experiment—grazing minnows—are voracious grazers on

benthic algae as described above, mussels cannot filter long algal filaments. However, they can filter benthic algae and fragments of filaments that have become locally suspended, and open patches in algae around mussel individuals in week 4 indicate that this probably occurred early in the experiment (Vaughn et al., 2008; Yates, 2012). Changes in mussel condition over the course of the experiment indicate that they became food limited (File S1). Although it was surprising that we did not observe higher mean organic matter (AFDM) concentrations over the mussel beds (middle pool) associated with biodeposits, this might have been due to limited feeding.

We predicted that fish grazing would depress algal productivity, but fish actually stimulated GPP. Over time, GPP increased 71% in fish treatments compared to only 11% in fishless treatments, even as algal biomass declined slightly. This pattern was also observed in mesocosm experiments with another grazing minnow (Bertrand & Gido, 2007) and in a whole stream experiment with grazing guppies (Collins et al., 2016). Thus, while grazing fish kept algal biomass at low, consistent levels, the turnover of this biomass was accelerated, ensuring a constant food supply for fish and perhaps insects. This result is consistent with findings that grazing usually increases biomass-specific primary productivity (Vadeboncoeur & Power, 2017). Liess and Hillebrand (2004) found that algivores reduced attached algal biomass more than productivity, and that this is especially true when grazers could move freely from patch to patch. Biomass removal accelerated nutrient turnover in algal biofilms as residual, ungrazed algae rapidly sequester nutrients from excreta and compensates for losses due to grazing (Vadeboncoeur & Power, 2017).

We predicted that fish effects on algae would cascade up the food web and influence the distribution and abundance of insects. Most macroinvertebrates that colonised the experimental streams were Chironomidae larvae in the genus *Chironomu*s, a generalist collector–gatherer feeding on material deposited on the sediment (Pery et al., 2002). As with algae, fish did not affect the spatial distribution of chironomids. Chironomid biomass declined over time in both treatments, probably due to seasonal emergence of adults during this summer experiment. Beyond that, chironomid biomass was likely to be controlled by food availability, specifically algae growing or deposited on the sediment.

Animals have long been known to shape food webs from the top-down through consumption, and a large body of recent work demonstrates equally strong effects of bottom-up nutrient provision (Allgeier et al., 2017; Atkinson et al., 2017; Subalusky & Post, 2019). However, the retention and redistribution of those nutrients depend on the feeding and life history traits of the consumers. Multiple studies have found that aggregations of sedentary, filter-feeding mussels are important nutrient recyclers and consumers of suspended algae in streams (Atkinson et al., 2013, 2018). However, in this study, mussel aggregations were unable to exert top-down grazing controls on algal filaments. Without fish or other mobile macrograzers to suppress filamentous algae (Vadeboncoeur & Power, 2017) this resource senesced, was exported from the local environment, and was thus unavailable to support the rest of the food web. Although previous work has shown that mussels can have strong, seasonal bottom-up

effects on both primary and secondary production (summarised in Vaughn and Hoellein (2018)), our results suggest that adding grazing mobile fishes, led to a more consistent and homogenous supply of algal resources. Thus, our results suggest that mussel benefits to stream ecosystems may depend on interactions with other species and the diversity of traits of those other species. When a larger diversity of traits is present (grazing and filtering), a greater benefit to the local ecosystem may be realised.

CONFLICT OF INTEREST

The authors declare no conflicting interests.

AUTHOR CONTRIBUTIONS

C.C.V. and K.B.G. designed the experiment. All authors conducted the experiment. T.B.P., T.P.D., and K.K.G. processed samples. K.B.G. conducted statistical analyses. C.C.V. wrote the first draft of the manuscript and all authors revised the manuscript.

DATA AVAILABILITY STATEMENT

Data are available through Open Science Framework, https://doi.org/10.17605/OSF.IO/FWJH9.

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