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Species traits and environmental conditions govern the relationship between biodiversity effects across trophic levels

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Abstract Changing environments can have divergent effects on biodiversity–ecosystem function relationships at alternating trophic levels. Freshwater mussels fertilize stream foodwebs through nutrient excretion, and mussel species-specific excretion rates depend on environmental conditions. We asked how differences in mussel diversity in varying environments influence the dynamics between primary producers and consumers. We conducted field experiments manipulating mussel richness under summer (low flow, high temperature) and fall (moderate flow and temperature) conditions, measured nutrient limitation, algal biomass and grazing chironomid abundance, and analyzed the data with non-transgressive overyielding and tripartite biodiversity partitioning analyses. Algal biomass and chironomid abundance were best explained by trait-independent complementarity among mussel species, but the relationship between biodiversity effects across trophic levels (algae and grazers) depended on seasonal differences in mussel species' trait expression (nutrient excretion and activity level). Both species identity and overall diversity effects were related to the magnitude of nutrient limitation. Our results demonstrate that biodiversity of a resource-provisioning (nutrients and habitat) group of species influences foodweb dynamics and that understanding species traits and environmental context are important for interpreting biodiversity experiments.

Keywords Biodiversity partitioning · Complementarity · Ecosystem function · Environmental context · Freshwater · Mollusk · Nutrient limitation · Species traits · Trophic level

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Introduction

A primary reason for concern over the current accelerated loss of species is the associated loss of ecological function (Naeem et al. 1994; Vitousek et al. 1997; Worm et al. 2006). Ecosystem function is the product of the expression of species' functional traits (Diaz et al. 2001; Ackerly and Cornwell 2007). Increased ecological function with higher species richness can be due to niche diversification (complementarity; Tilman et al. 2001; Kahmen et al. 2006), facilitative interactions among species (Cardinale et al. 2002), or strong effects from a unique species in the mixture (species identity or selection effects; Symstad et al. 1998; Loreau 1998), all of which are ultimately due to species trait expression (Naeem and Wright 2003). Thus, in terms of biodiversity contributions to ecosystem function, it is not species richness per se that is important, but the traits of the species involved (Diaz et al. 2001; Naeem and Wright 2003). Environmental gradients increase the complexity of this concept because they determine which species exist where, how their traits are expressed, as well as the direction and magnitude of how traits affect ecosystem function (Poff 1997; McGill et al. 2006; Hillebrand and Matthiessen 2009).

Biodiversity ecosystem function (BEF) studies need to integrate linkages both across (vertical diversity effects) and within (horizontal diversity effects) trophic levels (Duffy et al. 2007; Griffin et al. 2008). Biodiversity changes at one trophic level can have cascading effects within foodwebs, and these responses can differ at alternating trophic levels (Hillebrand et al. 2004; Duffy et al. 2007). Primary producer biomass is often considered to have a monotonic relationship with species richness; thus, their biomass increases as a function of habitat and nutrient availability, thereby creating novel niche opportunities (Hillebrand et al. 2007; Cardinale 2011). However, consumers confound the concept of "bottom–up" regulation because selective grazing (top–down) coupled with nutrient recycling (bottom–up) can influence both the available pool of primary producer species and their relative abundance within communities (McIntyre et al. 2008; Kominoski et al. 2010). Consequently, most of the research carried out to date on how the relationship between biodiversity and trophic structure regulates ecosystem function has focused on either the "top–down" roles of predator diversity (Duffy 2003) or the "bottom–up" roles of primary producer diversity (Leibold et al. 1997). In most of these cases, the ecology of the species is well known and easily functionally categorized within the foodweb. However, some species are not easily classified within foodwebs, especially species that indirectly provision resources via non-predatory interactions. Although seminal studies have demonstrated the role of biodiversity on nutrient use and efficiency within primary producers (Hooper 1998; Symstad et al. 1998) along gradients of nutrient availability (Tilman 1994), few studies have addressed how the biodiversity of resource-provisioning species (those that indirectly provision habitat and nutrient resources) influence trophic relationships between primary producers and grazers (Gessner et al. 2010).

Freshwater mussels (Bivalvia, Unionoida; hereafter "mussels") are a group of benthic, burrowing, long-lived (10 to >100 years), filter-feeding bivalves. Mussels are primary consumers that can occur as dense, multi-species assemblages (mussel beds) and serve important roles in lakes and rivers by transferring materials and nutrients between benthic and pelagic compartments (Vaughn et al. 2008). Mussels directly impact primary producers via consumption, but also indirectly affect them by providing excreted nutrients (Vaughn et al. 2007). Recent work has demonstrated that algae (periphyton) readily colonize freshwater mussel shells (Spooner and Vaughn 2006), that algal growth is stimulated by nutrients excreted by mussels (Vaughn et al. 2008), and that invertebrate grazers are attracted to this algal food resource (Spooner and Vaughn 2006; Vaughn et al. 2008). Thus, mussels are effectively ecosystem engineers, provisioning resources (habitat, organic matter and nutrients) to both primary producers and grazing consumers.

Mussels are thermo-conformers, thus temperature governs the rates at which they clear material from the water column and excrete ammonium and phosphorus (Spooner and Vaughn 2008). Different species have different optimal temperatures for these functions, and the interaction of temperature regime with species composition has a significant influence on primary production (Spooner and Vaughn 2008; Spooner and Vaughn 2011). In a large, manipulative field experiment we examined the effects of mussel species richness on a suite of ecosystem functions across two sets of seasonal environmental conditions in a small, southern U.S. river (Vaughn et al. 2007). We found strong seasonal effects of species richness on the accrual of algae on the sediment (benthic algae), which we hypothesized was due to the physiological traits of a unique species (*Actinonaias ligamentina*) that excreted more nutrients at warmer temperatures and thus had a greater fertilization effect on algae (Vaughn et al. 2007). Unfortunately, our metric of ecosystem function, benthic algal biomass, was measured at the treatment scale, so we could not assess relative species performance *within* treatments.

In the study reported here, we examined the role of mussel biodiversity in regulating trophic interactions between primary producers and consumers. New, distinct data from the above experiment on algal and invertebrate colonization of the shells of individual mussels within treatments are presented. Using biodiversity partitioning techniques that allow us to evaluate the relative performance of individual species within and among monoculture and polyculture treatments, we addressed the following questions**:** How do biodiversity effects associated with mussel species composition (species identity vs. assemblage level complementarity) influence the abundance of algae and invertebrates on mussel shells? Do these relationships differ for primary producers and consumers? What role does environmental context play between species trait expression (nutrient excretion) and ecosystem response (magnitude of nutrient limitation)? We predicted that because mussels influence the abundance of primary producers through fertilization, they should indirectly influence grazing consumer abundance. In addition, these effects should differ depending on species composition and season, because mussel excretion rates vary with both species and temperature (Spooner and Vaughn 2008).

Methods

The experiment and results described here are a new, previously undocumented component of a large field experiment conducted in the Kiamichi River, Oklahoma, USA, during

Table 1 Traits of mussels used in the experiment

Traits	*Actinonaias ligamentina*	*Amblema plicata*	*Fusconaia flava*	*Obliquaria reflexa*
Dry weight (g) (mean ± SD)	5.99 ± 0.08	3.36 ± 0.11	1.58 ± 0.006	1.49 ± 0.004
Length (mm) (mean ± SD)	108.44 ± 0.71	86.57 ± 0.95	58.51 ± 0.45	54.12 ± 0.418
Thermal guild[a]	Sensitive	Tolerant	Tolerant	Tolerant
Shell architecture	Smooth	Ridged	Smooth	Knobs
Typical summer activity	Active	Sedentary	Sedentary	Active
Typical fall activity	Sedentary	Sedentary	Sedentary	Sedentary
Ammonia excretion at 35°C[a] (μg NH_3 L^{-1} h^{-1} g^{-1})	1.35	0.65	0.84	1.19
Phosphorus excretion at 35°C[a] (μg P L^{-1} h^{-1} g^{-1})	0.36	0.22	0.27	0.26
Ammonia excretion at 15°C[a] (μg NH_3 L^{-1} h^{-1} g^{-1})	0.76	0.42	0.49	0.57
Phosphorus excretion at 15°C[a] (μg P L^{-1} h^{-1} g^{-1})	0.26	0.21	0.21	0.20
Net anabolism and catabolism rates[a] ($Q_{15\text{-}25°C}$)	1.12	0.35	0.51	0.42
Net anabolism and catabolism rates[a] ($Q_{25\text{-}35°C}$)	−0.82	0.25	0.48	0.53

SD Standard deviation

* Data from Spooner and Vaughn (2008)

the summer and fall of 2003. The Kiamichi River, a tributary of the Red River in the Mississippi drainage, is a small (drainage area 4,650 m^2), relatively pristine river known for its high fish and mussel biodiversity (Matthews et al. 2005). The river is typically shallow, with warm water temperatures in the summer and more moderate temperatures and flow during the remainder of the year (Galbraith et al. 2010). The overall experimental design, described in detail in Vaughn et al. (2007), was a factorial design with 12 species treatments and two environment treatments, with each combination replicated five times. We used four mussel species that co-occur in mussel beds in the river and vary in adult size, shell morphology, phylogeny, and temperature-dependent filtration and excretion rates (Table 1; Spooner and Vaughn 2008) and which comprise 84% of the mussel biomass in the river (Galbraith et al. 2008): *Actinonaias ligamentina* (Lamarck 1819) (hereafter *Actinonaias*), *Amblema plicata* (Say 1817) (hereafter *Amblema*), *Fusconaia flava* (Rafinesque 1820) (hereafter *Fusconaia*), and *Obliquaria reflexa* (Rafinesque 1820) (hereafter *Obliquaria*). Species treatments included monocultures of each species, all possible two-species mixtures, a four-species mixture, an eight-species mixture (the 4-species above plus 4 rarer species), and a no-mussel control (Vaughn et al. 2007). The eight-species mixture is not included in the analyses here because we did not have monocultures for all eight species. We used a replacement-series design, stocked mussels at the average density for mussel beds in the Kiamichi River (8 individuals per enclosure, 32 individuals m^{-2}), and combined species in treatments at equal densities (e.g. in the 4-species treatments, 2 individuals of each species for a total of 8 individuals). The environmental treatments were the two 6-week periods in which the experiment was performed: 18 July–30 August 2003 [summer; mean water depth 57 (±0.79) cm, mean water temperature 31 (±0.18)°C, mean discharge 0.48 (±0.12) m^3 s^{-1}] and 26 September–6 November 2003 [fall; mean depth 61 (±1.68) cm, mean temperature 17 (±0.38)°C, mean discharge 5.69 (±1.47) m^3 s^{-1}] (Vaughn et al. 2007).

We used sixty 0.25-m^2 (50 × 50 × 15 cm) enclosures made from 2.33-cm-diameter PVC pipe with 2.5-cm-diameter wire poultry netting covering the bottom and sides (Spooner and Vaughn 2006; Vaughn et al. 2007). The enclosures were staggered 2 m apart within one stream reach (50 m × 15 m) to minimize any variation in depth and current velocity between enclosures. Prior to setting up the experiment, we extracted sediment from the riverbed (cobble, gravel, and sand) and mixed it in 246-L plastic trashcans to homogenize the distribution of invertebrates and algae among treatments. All mussels were removed prior to homogenization, and no mussels except for treatment mussels were included in the experiment. While experimental mussels varied in size among species, we intentionally selected individuals within species of the same size to avoid confounding effects of ontogeny. The enclosures were buried 15 cm deep in the sediment and filled with the homogenized sediment. All enclosures were numbered, and treatments were randomly assigned to enclosures (Vaughn et al. 2007).

At the end of each 6-week experiment, individual mussels were removed from enclosures and placed in Ziploc (S.C. Johnson & Son, Racine, WI) bags with river water, where their shells were scrubbed to create a biofilm slurry (Spooner and Vaughn 2006). The slurry samples were divided into subsamples for chlorophyll *a* (frozen) and invertebrate (preserved with buffered formalin) analysis. Chlorophyll *a* samples (125 ml) were filtered through 47-mm, 0.45-μm glass fiber filters, and the chlorophyll was extracted with acetone and measured spectrophotometrically

with a correction for pheophyton (ASTM 1995). Invertebrates were identified to the family level and counted. As the majority of invertebrates were larval chironomids, we restricted our analyses to this group.

To examine the relationship between background nutrient context and mussel effects, we measured algal growth (biomass) on nutrient-diffusing substrates (Pringle and Triska 1996) consisting of 20-ml glass scintillation vials filled with nitrogen- (N; 0.1 M L^{-1}), phosphorus- (P; 0.01 M L^{-1}), and N + P-enriched agar (0.1 and 0.01 M L^{-1}, respectively) and a non-enriched control. The vials were covered with a porous silica disc affixed with silicone and buried in the sediment with only the silica disc exposed. Each enclosure received all four nutrient treatments with the control always upstream of the other treatments. For both the summer and fall experiments, the vials were placed in the stream in week 2 and removed at the end of week 6. Chlorophyll *a* was extracted from the discs with acetone and measured as described above (Vaughn et al. 2007). The magnitude of nutrient limitation was calculated as the net difference in chlorophyll *a* concentration between treatments (N, P, N + P) and agar controls. Treatments with stronger algal growth relative to the controls were assumed to be limited for that particular nutrient or combination of nutrients.

To evaluate how biodiversity influenced our measured response variables, we first assessed how algae biomass and chironomid abundance on the shells (hereafter referred to as algal or chironomid yield) differed among treatments (Fig. 2). We then calculated an index of overyielding of algal biomass and chironomid abundance for each species to assess how mussel species in polyculture performed relative to those in monoculture. Overyielding was calculated as the weighted average proportional deviation of algae or chironomids on the shells of mussels in monoculture compared to polyculture (D_{mean}), otherwise known as non-transgressive overyielding (Loreau 1998; Schmid et al. 2002). We then used Fox's (2005) tripartite equations to partition species treatment effects on the relative yield of algal biomass and chironomid densities into: trait-independent complementarity (TIC), trait-dependent complementarity (TDC), dominance, and the net biodiversity effect (NBE). The tripartite equations are a modification of the additive partitioning technique (Loreau and Hector 2001) and compare the relative yield of species mixtures to expected functioning based on species monocultures. TIC is analogous to complementarity, as defined by Loreau and Hector (2001). When TIC is positive, performance in polycultures is greater than expected based on that in monocultures, performance of a species in polyculture does not depend on its monoculture performance, and increased performance of a species does not come at the expense of other species. The underlying mechanism for this effect is assumed to be either niche partitioning or facilitation. The tripartite equation further splits Loreau and Hector's (2001) "selection effect" into two components: TDC and dominance. Like TIC, TDC also is positive when species perform better in polyculture, and this increased performance does not come at the expense of other species. However, here species with increased performance in mixtures also have increased performance in monocultures, indicating that the underlying mechanism depends on that species' traits. The dominance effect is positive when species with the greatest performance in monocultures also have the greatest performance in polycultures, and at the expense of other species. Here the assumed mechanism is interspecific competition (Loreau et al. 2001; Fox 2005). Both TDC and dominance effects can be negative when species with the greatest monoculture performance perform poorer in species mixtures. NBE represent the combined (net sum) impact of TIC, TDC, and dominance effects.

Data analysis

Accurately quantifying the area on freshwater mussel shells available for colonization by algae and chironomids is difficult because burrowing mussels move up and down in the sediment (Allen and Vaughn 2009). Thus, the "patch size" of a mussel shell protruding above the sediment can vary considerably over time. In addition, mussel species vary in shell sculpture and shape, which can also affect settlement area. However, mussel dry weight is an accurate and standard metric of overall mussel shell size (Spooner and Vaughn 2008). Therefore, we standardized algal biomass and chironomid abundance by log-transformed mussel dry weight to correct for differences in body size among treatments. Diversity metrics were square root transformed (with signs retained) (Loreau and Hector 2001).

For each species, we used a two-way analysis of variance (ANOVA) to assess whether biodiversity (hereafter referred to as species combination) or season influenced the yield of algae or chironomids and/or overyielding of algae and chironomids, on the shells of mussels in monoculture versus polyculture. We defined species treatment as monocultures, all species pairs, and four-species polycultures. We then used the same two-way ANOVA design to examine the effects of species combination and season on biodiversity effects (TIC, TDC, dominance, and NBE) and nutrient limitation responses (N, P, and N + P). For the latter analysis, we examined measurements for an entire enclosure (species combinations) rather than individual species. For all analyses except yield, monocultures were omitted because overyielding and partitioning calculations were standardized to monoculture yields. Multiple comparisons among treatments were performed using the Sidak MCP procedure.

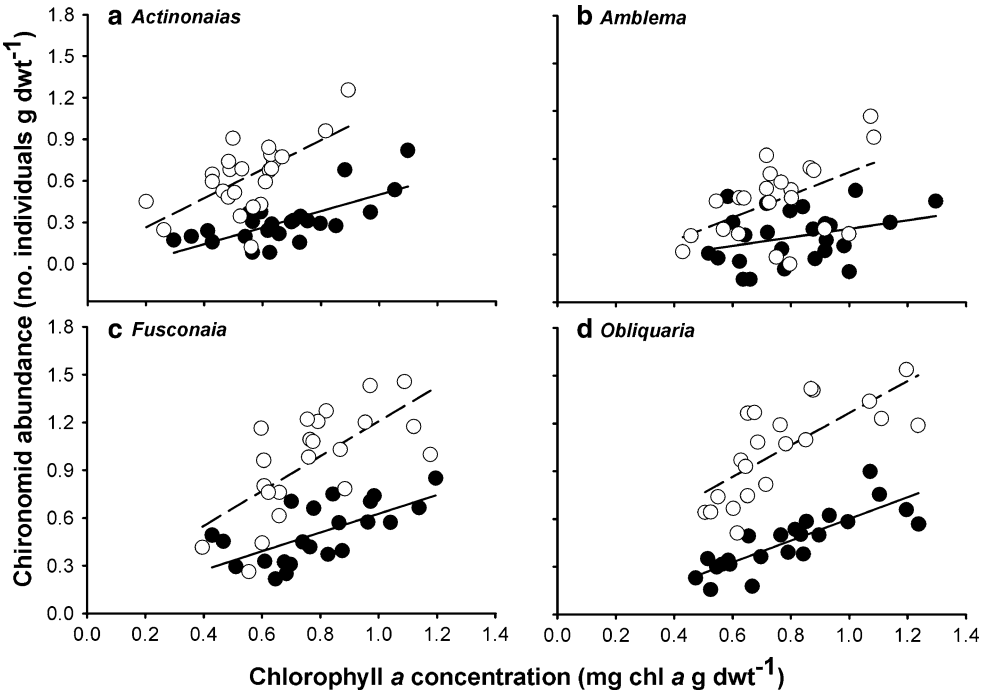

Fig. 1 Chironomid abundance as a function of algal biomass on four species of mussel shells during the fall (*white circles*) and spring (*black circles*) in 2003 in the Kiamichi River, Oklahoma, USA. **a** *Actinonaias* (fall $F_{1,23} = 38.7$, $r = 0.80$, $P < 0.001$; summer $F_{1,23} = 32.9$, $r = 0.77$, $P < 0.001$), **b** *Amblema* (fall $F_{1,23} = 14.7$, $r = 0.650$, $P = 0.001$; summer $F_{1,23} = 3.06$, $r = 0.33$, $P = 0.09$), **c** *Fusconaia* (fall $F_{1,23} = 9.5$, $r = 0.323$, $P = 0.006$; summer $F_{1,23} = 19.7$, $r = 0.496$, $P < 0.001$), **d** *Obliquaria* (fall $F_{1,23} = 14.4$, $r = 0.432$, $P = 0.001$; summer $F_{1,23} = 22.9$, $r = 0.522$, $P < 0.001$). Each *point* represents the mean of an enclosure, $n = 5$. Note that the scales for both axes are log + 1 and are reported per gram of mussel dry weight (g dwt^{-1})

To determine if biodiversity effects were equal across trophic levels, we used the linear least squares analysis to examine the strength of the relationship between the calculated biodiversity effects (TIC, TDC, dominance, and NBE) of mussels associated with primary producers (algal biomass) and consumers (chironomid abundance). Since we also suspected that nutrients provided through mussel excretion indirectly influenced biodiversity effects, we performed a correlation analysis between the nutrient addition responses and biodiversity effects (TIC, TDC, dominance, and NBE) on algae. We hypothesized that algal nutrient limitation would be dampened in the presence of increased nutrient provisioning from mussels. For each enclosure, we calculated the expected mussel nutrient provisioning rate (ammonia and P) based on species-specific mussel excretion rates collected by Spooner and Vaughn (2008).

Results

Average mass-specific algal biomass (chlorophyll *a* g^{-1} dry weight of mussel) and chironomid abundance were positively correlated on shells of all mussel species for both seasons, suggesting that chironomids were tracking algal food resources (Fig. 1). Patterns of over- and underyielding varied with season, species, and response variable. In general, algae and chironomids overyielded in the summer in all polyculture treatments, with effects greatest in the four-species treatments (Table 2; Figs. 2, 3). In the fall, each species generally had the greatest overyielding algal biomass in the four-species polycultures, and algae on *Obliquaria* and *Fusconaia* shells underyielded in the two-species polycultures (Table 2; Fig. 3j, n). Chironomid overyielding was also generally higher in the four-species polycultures during both seasons (Table 2; Fig. 3). However in the fall, chironomids on *Amblema* shells only overyielded in the presence of *Actinonaias* (2-species polycultures) (Fig. 3h) and on *Obliquaria* shells in the four-species polycultures (Fig. 3l).

Partitioned effects of mussel biodiversity on algal biomass

Trait-independent complementarity was the main diversity effect associated with algal biomass and was greater in the four-species treatments, especially in the summer (Table 3; see magnitude of *y*-axis in Fig. 4a–d). Summer TDC effects on algae ranged from marginally positive in the two-species polycultures lacking *Actinonaias* to strongly negative in two-species and four-species polycultures with *Actinonaias* (Fig. 4e). Similarly, fall TDC effects on algae ranged from positive to negative; although these values were marginally larger in the four-species treatments in the fall, the two-species polycultures did not consistently differ with regard to *Actinonaias* presence (Fig. 4f). Dominance effects on algae were negligible in the summer and more pronounced in the fall (Fig. 4i, j), ranging from negative to positive in both seasons. Moreover, there was a significant season × treatment interaction, with fall enclosures containing *Actinonaias* (2 and 4-species polycultures) having greater positive dominance effects than those without this species (Table 3), a pattern that was not apparent in the summer (Fig. 4i, j). Net biodiversity effects represent the combined influence of

Table 2 Results of two-way ANOVAs for effects of mussel species combination and season on yield (algal biomass and chironomid abundance) and overyielding (algae and chironomid) on mussel shells

Factor	Variables	*Actinonaias*			*Amblema*		*Obliquaria*		*Fusconaia*	
		df	*F*	*P*	*F*	*P*	*F*	P	*F*	*P*
Algae yield (biomass)	Species combination	1	7.75	<0.001*	5.35	<0.001*	11.9	<0.001*	10.1	<0.001*
	Season	1	7.41	0.01*	1.47	0.23	2.95	0.09	0.64	0.43
	Species combination × season	1	1.54	0.21	0.8	0.53	3.82	0.01*	2.16	0.09
	Error	34								
Chironomid yield (abundance)	Species combination	6	2.54	0.055	1.38	0.26	4.57	<0.001*	5.49	<0.001*
	Season	1	31.9	<0.001*	15	<0.001*	34.7	<0.001*	75.3	<0.001*
	Species combination × season	6	0.13	0.969	1.53	0.21	0.9	0.48	0.37	0.83
	Error	4								
Algae overyielding	Species combination	3	4.89	0.006*	2.71	0.05*	13.2	<0.001*	11.4	<0.001*
	Season	1	10.6	0.003*	6.07	0.02*	47.6	<0.001*	34.2	<0.001*
	Species combination × season	3	1.73	0.18	0.66	0.056	2.4	0.09	2.18	0.10
	Error	30								
Chironomid overyielding	Species combination	3	3.36	0.03*	2.31	0.09	9.22	<0.001*	10.5	<0.001*
	Season	1	2.08	0.16	11.0	0.002*	79.9	<0.001*	12.5	<0.001*
	Species combination × season	3	1.25	0.30	2.67	0.07	2.72	0.06	3.71	0.02*
	Error	30								

ANOVA Analysis of variance

* Significant at $P < 0.05$

all partitioned biodiversity effects. As such, in both seasons, four-species polycultures had the greatest magnitude of NBE effects. In addition, there were significant differences in NBE effects among two-species treatments (with and without *Actinonaias*) in the fall, but not the summer (Table 3; Fig. 4m, n).

Partitioned effects of mussel biodiversity on chironomid abundance

Trait-independent complementarity was the main mussel biodiversity effect associated with chironomid abundance and was greatest in the four-species polycultures, especially in the fall (Table 3; Fig. 4c, d). The TDC effect on chironomids was only positive in two-species *Actinonaias* polycultures, and overall its magnitude was negligible in the summer (Fig. 4g). In the fall, TDC was considerably more variable, with the highest values in the four-species polycultures (Table 3; Fig. 4h). The error associated with these values was substantial, however, and thus the mean was indistinguishable from zero and displayed no discernable pattern with respect to *Actinonaias* treatment identity (Fig. 4h). Summer dominance effects on chironomids were positive in treatments containing *Actinonaias* and negative in treatments without *Actinonaias* (Fig. 4k). In addition, the magnitude of dominance effects on chironomids was greater in the fall, with a similar overall pattern to those of summer with the exception of the (Amb + ob) treatment, which was positive (Fig. 4l). The NBE of mussels on chironomid abundance were largest in the four-species treatments in both summer and fall (Table 3; Fig. 4o, p); they followed a similar overall pattern to those of algae but were greater and more variable in fall (Table 3; Fig. 4o, p).

Relationship among biodiversity effects across trophic levels

For the most part, the extent to which biodiversity effects of mussels on algae and chironomids were 1:1 across trophic levels depended on environmental (i.e., seasonal) conditions. These significant isometric relationships occurred primarily in the fall (Fig. 5b, d, f, h), indicating that the magnitude of diversity effects across trophic levels were equal in effect size (Fig. 5). Notable disparities (i.e., a non-1:1 relationship) across trophic levels, however, were most pronounced in the summer and were largely associated with polyculture treatments that included *Actinonaias*. For example, summer polycultures with *Actinonaias* were consistently below the 1:1 isocline for TIC effects (Fig. 5a) and were above the 1:1 isocline for TDC and dominance effects (Fig. 5c, e).

As a consequence, negative *Actinonaias* TDC and dominance effects on algae dampened the strong influence of TIC in the summer, resulting in a dampened relationship between NBE effects among algae and chironomids in the summer and a strong 1:1 relationship in the fall.

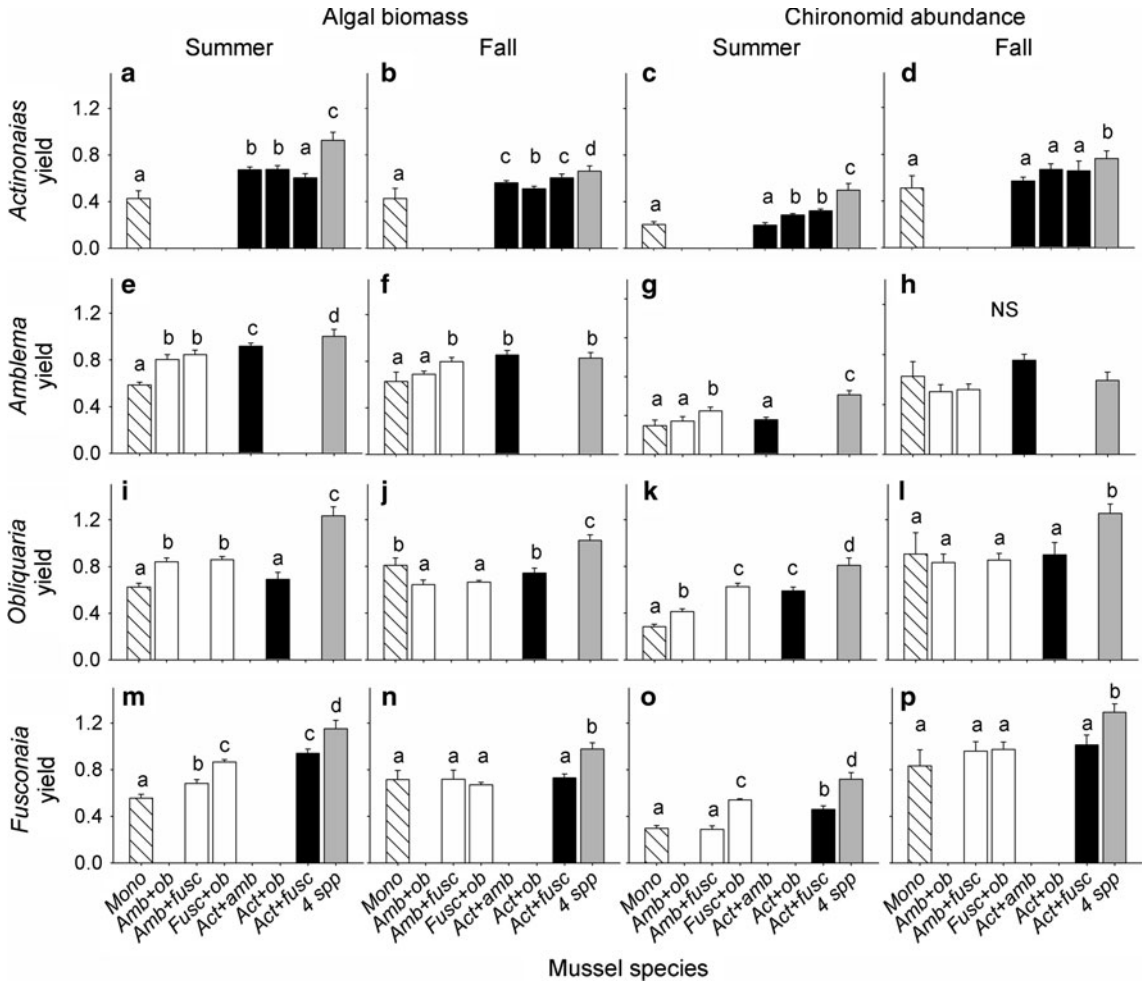

Fig. 2 Algal biomass (log mg chl *a* g mussel dry weight^{-1}) and chironomid abundance (log no. of individuals g mussel dry weight^{-1}) yield for each mussel species in monoculture, two-species polyculture (with and without *Actinonaias*), and four-species polyculture (*4 spp*) treatments. *Hatched bars* Monoculture treatments, *white bars* two-species polycultures without *Actinonaias*, *black bars* two-species polyculture treatments with *Actinonaias*, *gray bars* four-species polycultures. *Different letters above bars* represent significant differences among treatments at alpha = 0.05 based on the Sidak comparison procedure

Response to nutrient additions

Responses to nutrient additions varied among species combinations and across seasons (Table 4; Fig. 6). For example, algae responded most strongly to N additions in the summer and N + P additions in the fall (Fig. 6). For the most part, however, P additions during both seasons resulted in a reduction of algal biomass relative to the controls. The only significant main effect was an interaction between season and species composition in the summer (Table 4). Algal biomass only differed predictably with respect to mussel species composition treatments in the summer in response to N + P additions (Fig. 6e). As such, algal responses were greatest in the four-species treatments, followed by the two-species treatments with *Actinonaias*, and lowest in the two-species treatments without *Actinonaias* (Fig. 6e). Furthermore, the magnitude of algal responses to nutrient additions only correlated to biodiversity effects in two situations (Fig. 7). First, TIC effects on algae were positively correlated to N additions in the fall, and this pattern appeared strongest in treatments containing *Actinonaias* (both 2- and 4-species treatments; Fig. 7b). Second, both TIC and NBE effects on algae were strongly correlated to N + P addition responses in the summer, and both were strongest in the presence of *Actinonaias* treatments that had higher mussel-provided ammonia (Fig. 7e). That TIC and NBE were both so strongly related to N + P is unsurprising as these parameters are highly correlated due to the strong contribution of TIC to the NBE. Therefore, we present only the TIC–nutrient addition response relationships in Fig. 7.

Discussion

In this study mussel biodiversity effects extended across trophic levels, impacting both primary producers and

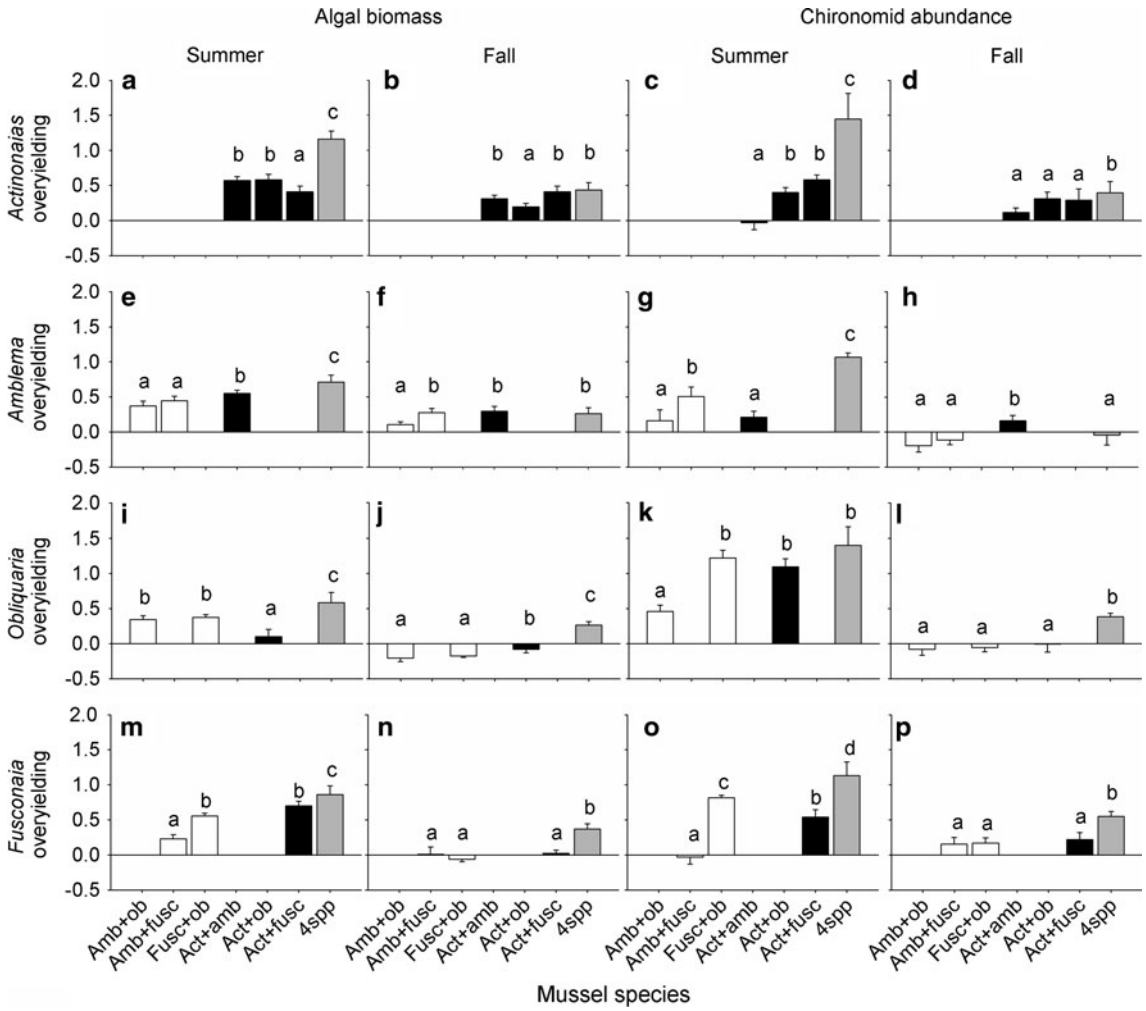

Fig. 3 Magnitude of species-specific overyielding [net polyculture yield relative to average monoculture yield, mean ± 1 standard error (SE)] for two-species polyculture treatments without *Actinonaias* (*white bars*), two-species polyculture treatments with *Actinonaias* (*black bars*), and four-species polyculture (*4spp*) treatments (*gray bars*). *Different letters above bars* represent significant differences among treatments at alpha = 0.05 based on the Sidak comparison procedure

consumers, but varied seasonally with a strong linear relationship between net effects of mussel biodiversity on algae and chironomid grazers in the fall but not in summer. Fall relationships were 1:1, with an equal effect of mussel diversity on chironomid abundance for every unit of effect on algal biomass, indicating that similar mechanisms may underlie diversity effects among these trophic levels. In contrast, NBE on algal biomass and chironomids were not 1:1 in the summer, suggesting that different mechanisms are likely driving the importance of mussel species composition among trophic levels during this season.

We attribute these seasonally divergent patterns to the influence of one key species, *Actinonaias ligamentina*, which impacts both algal biomass accrual and chironomid abundance on the shells of all mussel species in polyculture. In summer, polycultures with *Actinonaias* tended to display a higher magnitude of biodiversity effects relative to non-*Actinonaias* treatments (Fig. 4) and were the only treatments that did not follow a 1:1 relationship among trophic levels (Fig. 5). Summer treatments with *Actinonaias* had the greatest TIC effects on algae (Fig. 4a), indicating that mussels in polyculture with *Actinonaias* had proportionally more algae on their shells (*Fusconaia*, *Amblema*, *Actinonaias*; Fig. 3). However, these same treatments also had greater negative TDC effects, i.e., a species in polyculture with proportionally less algae on their shells compared to others in polyculture. These negative effects consequently counteracted the positive effect of TIC and dampened the overall NBE (Fig. 4). In this case, *Obliquaria* shells in the *Actinonaias* two-species polycultures (Fig. 3i) had proportionally less algae relative to the monoculture compared to the other species.

Strong effects associated with *Actinonaias* were also observed in the fall, but these diversity effects differed in magnitude and direction. For example, TIC effects on algae were still larger than other biodiversity effects (TDC or

Table 3 Results of two-way ANOVAs for effects of species combination and season on mussel biodiversity effects on algal biomass and chironomid abundance

	TIC			TDC		Dominance		NBE	
	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Algae									
Species combination	6	19.358	<0.001*	2.628	0.026*	3.402	0.006*	5.307	<0.001*
Season	1	17.866	0.007*	1.422	0.13	11.679	0.001*	0.104	0.749
Species combination × season	6	0.56	0.18	0.87	0.52	6.05	<0.001*	3.227	0.009*
Error	55								
Chironomidae									
Species combination	6	7.647	<0.001*	0.327	<0.001*	7.454	<0.001*	5.651	<0.001*
Season	1	16.257	<0.001*	0.005	0.947	6.688	0.012*	11.799	0.001*
Species combination × season	6	0.928	0.482	0.727	0.63	3.95	0.002*	2.965	0.014*
Error	53								

TIC trait-independent complementarity, *TDC* trait-dependent complementarity, *NBE* net biodiversity effect

* Significant at $P < 0.05$

dominance)—but to a lesser extent compared to the summer (Fig. 4). TDC effects on algae were negligible although variable (Fig. 4f), yet fall dominance effects were mainly positive and substantially larger in the *Actinonaias* polycultures (Fig. 4j). This pattern suggests that some species had more algae on their shells in the presence of *Actinonaias*, as evidenced by the overyielding of algal biomass on *Actinonaias*, *Amblema*, and *Fusconaia* shells compared to underyielding on *Obliquaria* shells (Fig. 3).

We believe the seasonally disproportionate influence of *Actinonaias* on algae growing on the shells of other mussel species stems from an interaction between local nutrient conditions and mussel species' trait expression. Temperature governs the rates at which mussels filter feed and excrete nutrients, and species have different optimal temperatures for these functions (Spooner and Vaughn 2008). The species in our study can be placed in two thermal guilds based on resource assimilation and nutrient excretion rates at 15 and 35°C (Spooner and Vaughn 2008), temperatures within the normal annual range experienced by mussels in the southern USA (Matthews et al. 2005) and directly comparable to the two seasonal treatments of our experiment (Vaughn et al. 2007). "Tolerant" species have increased assimilation and nutrient excretion rates at 35°C, whereas "sensitive" species have decreased assimilation and variable nutrient excretion rates at this temperature. Our experiment included three tolerant species (*Amblema*, *Fusconaia*, *Obliquaria*) and one sensitive species (*Actinonaias*) (Table 1). While *Actinonaias* was the largest species in the study, it also had the highest mass-specific N and P excretion rates at both temperatures (Table 1; Spooner and Vaughn 2008). In both seasons, treatments responding most strongly to nutrient additions contained *Actinonaias* (Fig. 6). These results suggest that *Actinonaias* effects are linked to nutrient excretion. Further, these results corroborate findings from the sediment compartment component of our study. In that study, we examined the effects of mussel diversity on sediment algae and found that benthic algal biomass was greatest in *Actinonaias* monocultures, declined as a function of decreased dominance of *Actinonaias* in higher richness treatments, and varied seasonally (Vaughn et al. 2007).

We hypothesized that treatments contributing more nutrients would dampen nutrient limitation and therefore expected a negative relationship between the TIC effect of mussel diversity on algal biomass and nutrient addition responses. If this were the case, we would expect to see (1) a negative relationship between TIC and nutrient addition responses and (2) the magnitude of nutrients provided by mussel excretion decrease with increased nutrient addition response. Instead, we found the opposite pattern, namely, a positive relationship between TIC, mussel-provided ammonia excretion, and N + P nutrient addition response, suggesting that nutrient limitation may increase in the presence of complementary nutrient excretion associated with *Actinonaias* (Fig. 7). This paradoxically strong response to nutrient subsidies (N + P) related to a species that contributes more nutrients can be interpreted several ways. First, mussel-contributed nutrients in treatments with *Actinonaias* may be quickly sequestered by local algae on mussel shells, resulting in decreased nutrient dispersion within an enclosure. Consequently, algae on mussel shells further away from an excreting *Actinonaias*, but within the same species combination enclosure, would receive fewer nutrients and would have the strongest response to nutrient subsidies, exacerbating the degree of N + P co-limitation in the summer and N limitation in the fall. However, algal biomass on mussels in *Actinonaias* treatments was only slightly greater

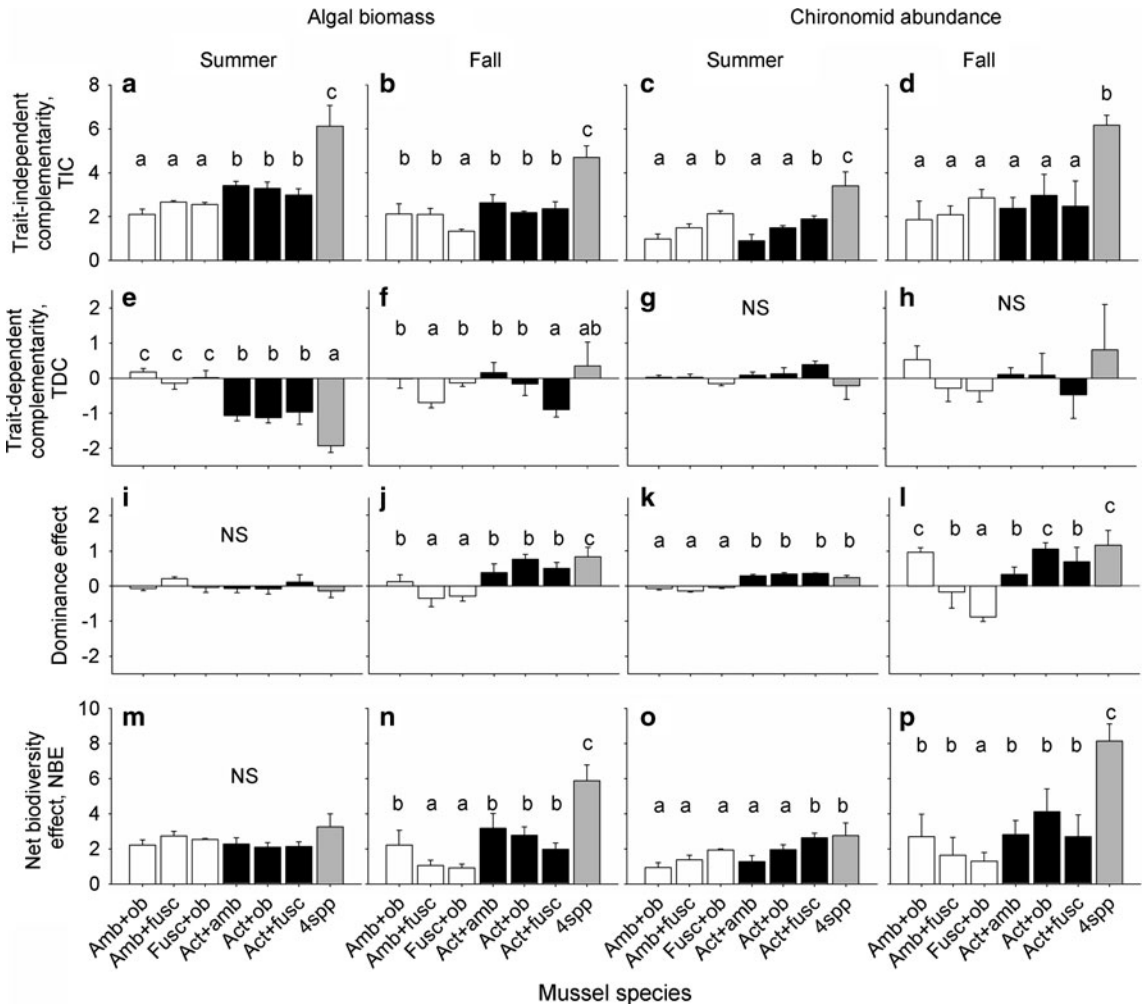

Fig. 4 Magnitude of mussel biodiversity effects (mean ± 1 SE) on algae and chironomids for trait-independent complementarity (*TIC*; **a**–**d**),trait-dependent complementarity (*TDC*; **e**–**h**), dominance effect (**i**–**l**), and net biodiversity effect (*NBE*; **m**–**p**). *White bars* Two-species polyculture treatments without *Actinonaias*, *black bars* two-species polyculture treatments with *Actinonaias*, *gray bars* four-species (*4spp*) polyculture treatments. *NS* Non-significant effects. *Different letters above bars* represent significant differences among treatments at alpha = 0.05 based on the Sidak comparison procedure. Note different scales on the *y*-axes

than that in non-*Actinonaias* polycultures (Fig. 2). Alternatively, *Actinonaias* may have contributed so many nutrients that effects in *Actinonaias* polycultures were swamped. If this were to be true, we should have observed increased algal biomass in all nutrient-addition treatments with *Actinonaias* across seasons, which was not the case (Fig. 6). Finally, nutrient limitation patterns in *Actinonaias* treatments might not be related to algal productivity, but could be due to increased microbial activity from a combination of *Actinonaias* organic matter production and nutrient excretion. Interestingly, there was seasonal variation in nutrient amendment responses, indicating that N was the predominant limiting factor in the summer and that both N and P were the most predominant limiting factors in the fall. This finding is somewhat in contrast with current meta-analyses that indicate co-limitation to be dominant in freshwater streams (Elser et al. 2007). These analyses, however, do not necessarily account for temporal variation in nutrient amendment responses, nor do they account for heterotrophic microbial responses, both of which could potentially influence the availability of P and N in the summer when temperatures are warmer. Whatever the mechanism, diversity effects and nutrient responses were both greatest in *Actinonaias* polycultures, suggesting that this species somehow provisions resources (nutrients and energy) in a way that contributes to both the availability and demand for nutrients on the shells of other mussel species. More studies are required to evaluate the mechanisms underlying this pattern.

We also observed diversity effects associated with *Actinonaias* on grazing chironomids, although these patterns were more variable in the fall compared to the summer. In

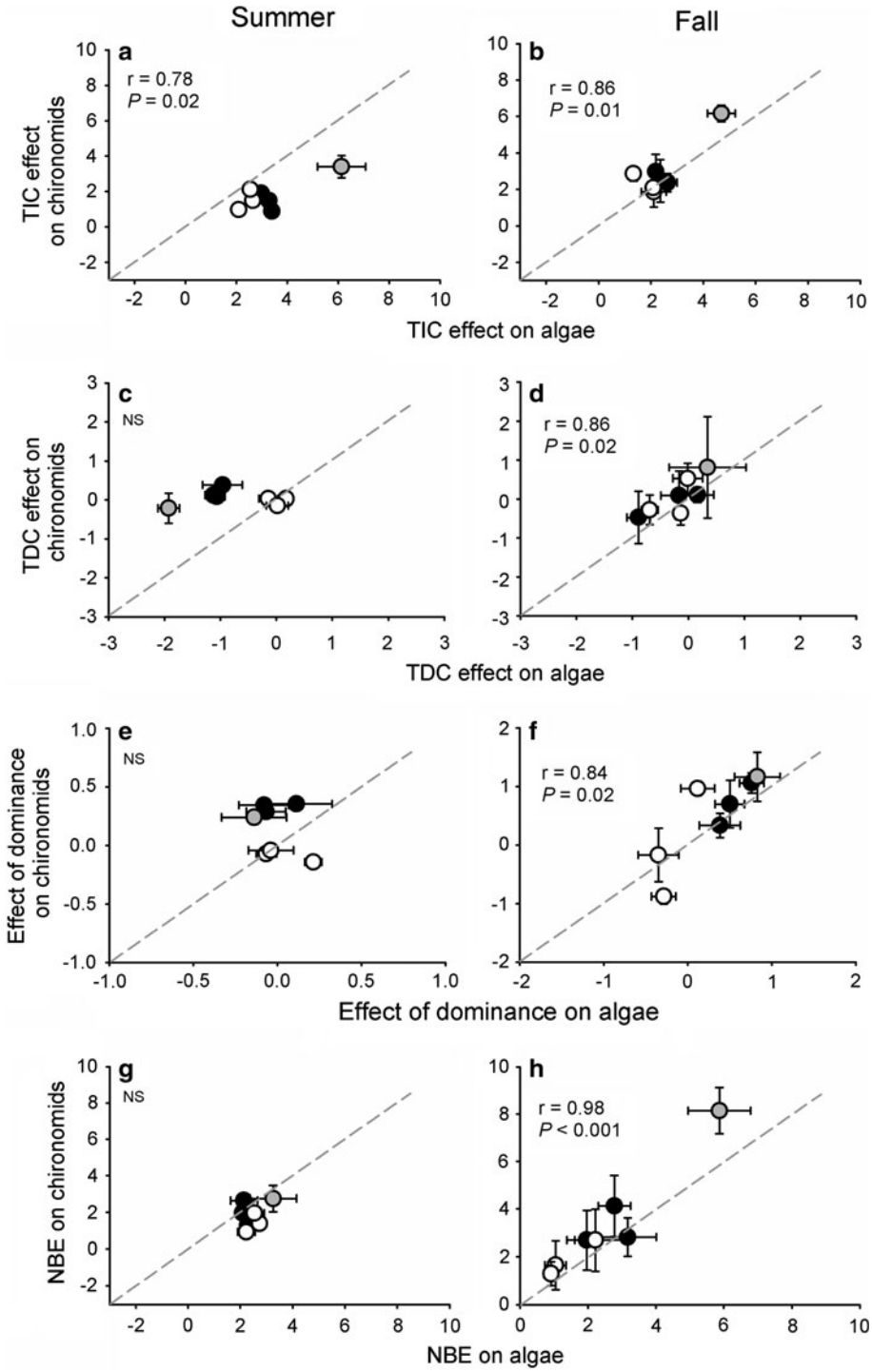

Fig. 5 Correlation between chironomid (mean ± 1 SE) and algal TIC (**a**, **b**), TDC (**c**, **d**), dominance (**e**, **f**), and NBE (**g**, **h**) of mussel diversity in the summer (*left column*) and fall (*right column*).*White circles* Two-species polycultures without *Actinonaias*, *black circles* two-species polycultures with *Actinonaias, gray circles* four-species polycultures. *Gray broken line* represents a 1:1 relationship. Note differences in scale for both axes

both seasons, TIC was the primary effect explaining chironomid abundance, while TDC effects were negligible and centered around zero (Fig. 4). Dominance effects on chironomids, however, were more consistent in the summer than the fall and were positive for all treatments with *Actinonaias*, including the four-species treatments. Even though there was higher overall chironomid abundance on shells in the fall, mussels in the summer polyculture treatments with *Actinonaias* had a higher proportion of chironomids relative to algae on their shells than mussels in non-*Actinonaias* polycultures. This is evidenced in the summer by greater positive TDC (Fig. 4g) and dominance effects (Fig. 4k) on chironomids in *Actinoniais* polycultures and considerably lower TDC effects (Fig. 4e) on algae in *Actinonaias* polycultures in the summer. The net consequence of these effects in the summer is that NBE on mussels associated

Table 4 Results of two-way ANOVAs for effects of species combination on algal response from nutrient additions

Nutrient addition interaction effects	*df*	*F*	*P*
Nitrogen addition			
Species combination	6	0.648	0.692
Season	1	11.362	0.002*
Species combination × season	6	0.365	0.896
Error	55		
Phosphorus addition			
Species combination	6	1.278	0.290
Season	1	1.868	0.098
Species combination × season	6	1.267	0.295
Error	55		
N + P addition			
Species combination	6	1.820	0.177
Season	1	0.005	0.947
Species combination × season	6	3.470	0.042*
Error	55		

* Significant at $P < 0.05$

with *Actinonaias* were heightened on chironomids and dampened on algae (Fig. 5a, c, e, g). These strong species identity effects were not apparent in the fall when there was an equal effect of mussel biodiversity on both shell algal biomass and chironomid densities (Fig. 5b, d, f, h).

Our results suggest that there is an interaction between environmental context (limiting nutrients and water temperature) and expression of species traits (mussel nutrient excretion and burrowing activity) that results in seasonally different bottom–up effects on this stream foodweb. These seasonal effects appear to be driven by one species, *Actinonaias ligamentina*. We propose three non-exclusive hypotheses to explain the strong *Actinonaias* effects on algae and chironomid grazers in polyculture. The first of these is the *palatability hypothesis*, which proposes that increased nutrient excretion by *Actinonaias* in the summer facilitates local algal growth and increases the range of nutritional resources for grazers. In marine systems, enhanced nutrient resources can result in more palatable algae that are then controlled by grazers (Duffy et al. 2007). This hypothesis depends on the identity and magnitude of nutrients contributed by consumers relative to local nutrient limitation (Rosemond et al. 2001; Evans-White and Lamberti 2005). To evaluate this hypothesis, we need data on the species and elemental composition of algae colonizing the mussels, information that was not available in this study. The second is the *disturbance hypothesis*, which proposes that increased burrowing in summer by *Actinonaias* results in algal sloughing and decreased algal biomass on the shells of other mussel species in the mixture. For example, in mesocosm experiments, Allen and Vaughn (2009) observed greater variation in activity and burrowing position among mussels in polyculture than in monoculture. Consequently, the apparent increase in grazer abundance on *Actinonaias* shells may represent spatial variation in the distribution of mobile grazers actively searching for quality resource patches. While this hypothesis provides a physical explanation for decreased algae on mussel shells in *Actinonaias* treatments, it does not explain the strong seasonal relationship between *Actinonaias* treatments, diversity effects, and apparent nutrient limitation (Fig. 7). The third of our hypothesis is the *interactions hypothesis*, which proposes that *Actinonaias* activities via excretion and/or burrowing in the summer influence the performance of other mussel species, including shifts in the quality and quantity of nutrients excreted by other mussels in *Actinonaias* treatments. This hypothesis is supported by results of a mesocosm experiment that manipulated mussel species relative dominance across a temperature gradient. In this experiment, the presence of *Actinonaias* had positive effects on the nutrient excretion rates of other mussels in polyculture at moderate temperatures (25°C) and negative effects at warm (35°C) temperatures (similar to the summer temperatures in this experiment; Spooner and Vaughn 2011). Our excretion estimates outlined in Fig. 7 were experimentally derived from individuals in isolation, based on Spooner and Vaughn (2011). In our study, it is likely that excretion rates in the presence of *Actinonaias* could be even higher as a result of species interactions. These species-specific shifts in nutrient excretion may have influenced species composition, palatability, and/or grazing resistance of algae (Hillebrand and Cardinale 2004; Hillebrand and Shurin 2005).

Disproportionate BEF effects associated with species identity are common in nature, but they have generally been demonstrated in systems where species functional designations are discrete and easily classified (e.g., legumes vs. non-nitrogen fixers, shredders vs. grazers) (Walker 1992). In contrast, we found strong species identity effects *within* a functional group, namely, filter-feeding freshwater mussels. We also found that the combined influence of dominant species and species richness on both primary producer and consumer abundance is dynamic and governed by multiple, interacting environmental factors. The results of our study demonstrate the importance of environmental context in interpreting biodiversity effects (Cardinale et al. 2000) and corroborate recent meta-analyses that suggest novel species traits are important predictors of ecosystem function across trophic levels (Cardinale et al. 2006; Duffy et al. 2007; Kominoski et al. 2010).

Integrating trophic complexity into biodiversity experiments is a daunting task that requires balancing adequately replicated studies with capturing appropriate variation in horizontal and vertical diversity of species traits (Polis and Strong 1996; Worm and Duffy 2003). Studies manipulating

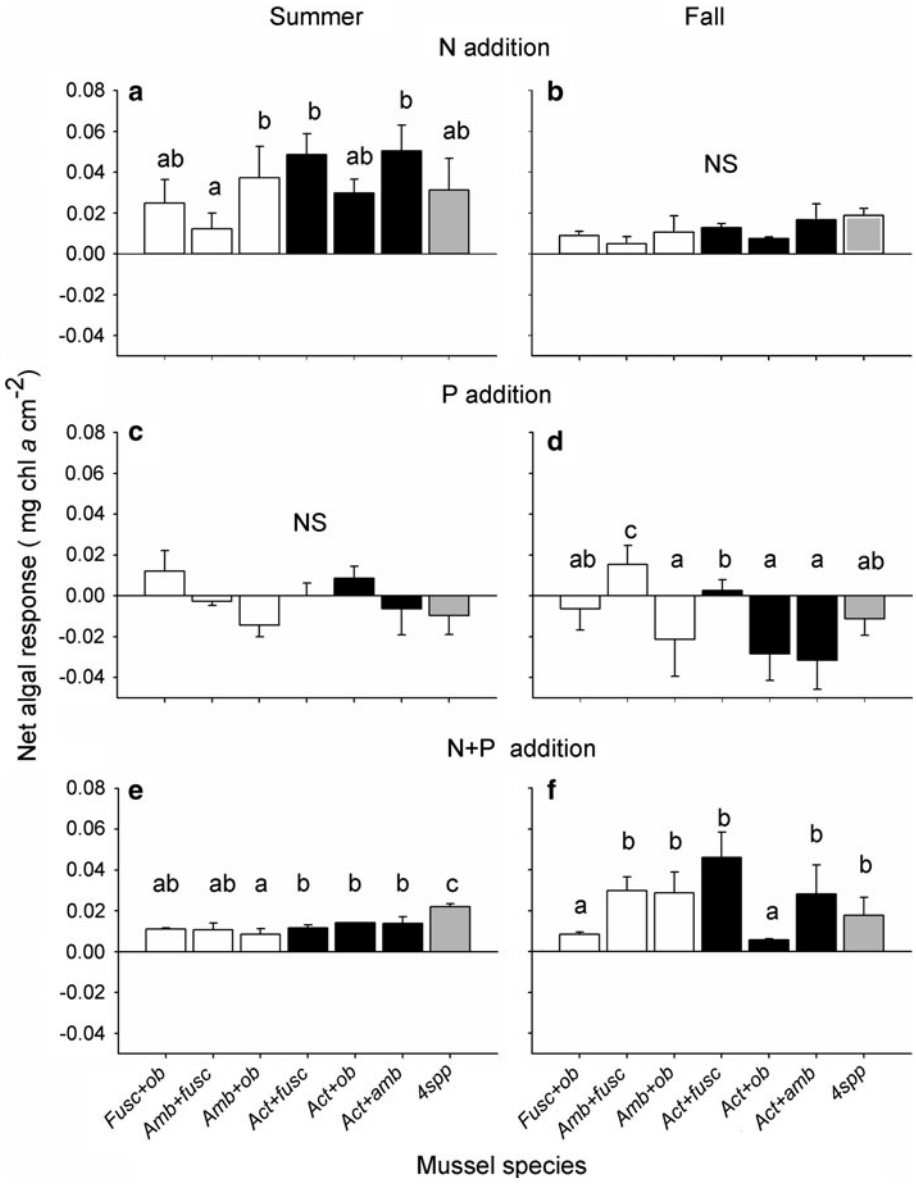

Fig. 6 Magnitude of algae response in summer and fall (mean ± 1 SE) for nutrient addition treatments: **a**, **b** nitrogen (*N*) addition, **c**, **d** phosphorus (*P*) addition, **e**, **f** N + P addition. *White bars* Two-species polyculture treatments without *Actinonaias*, *black bars* two-species polyculture treatments with *Actinonaias*, *gray bars* four-species (*4spp*) polycultures. Algal response values represent differences in chlorophyll *a* (*chl a*) relative to controls (no nutrient addition). *NS* Not significant. *Different letters above bars* represent significant differences among treatments (alpha = 0.05) based on the Sidak comparison procedure

vertical and horizontal diversity in aquatic systems have produced mixed results, demonstrating strong top–down effects of predator identity on grazers (Douglass et al. 2008; Srivastava and Bell 2009), strong within-guild effects of predators (Finke and Denno 2005) and grazers (Gresens 1995; Duffy et al. 2003), and subsequent trophic cascades (Spivak et al. 2007; Srivastava et al. 2009). While most of these studies corroborate the traditional view of top–down trophic cascades (Hairston et al. 1960; Borer et al. 2005), others demonstrate weak direct effects on primary producers, suggesting that bottom–up mechanisms, including nutrient and light availability, are also important. Such bottom–up effects are especially pervasive when the metric of ecosystem function is material transfer (nutrients and organic matter) rather than the strict numerical responses of individuals (Canuel et al. 2007). In our study we found strong, indirect effects of one group of primary consumers (freshwater mussels) on another group of primary consumers (grazing chironomids) via mussel-mediated effects on primary production. Our findings are similar to patterns produced by diversity cascades, where changes in diversity at one trophic level have cascading, indirect effects on non-adjacent trophic levels (Hunter and Price 1992; Dyer and Letourneau 2003; Schmitz et al. 2004), but our study is unique in that changes in horizontal diversity of a resource-provisioning consumer group had indirect effects on a group of consumers essentially occupying a similar trophic level (both are considered herbivores). As such, our results reinforce the importance of incorporating both vertical and horizontal diversity in BEF studies (Duffy et al. 2007).

Our study was limited to two 6-week periods within 1 year; further studies are needed to evaluate the extent to

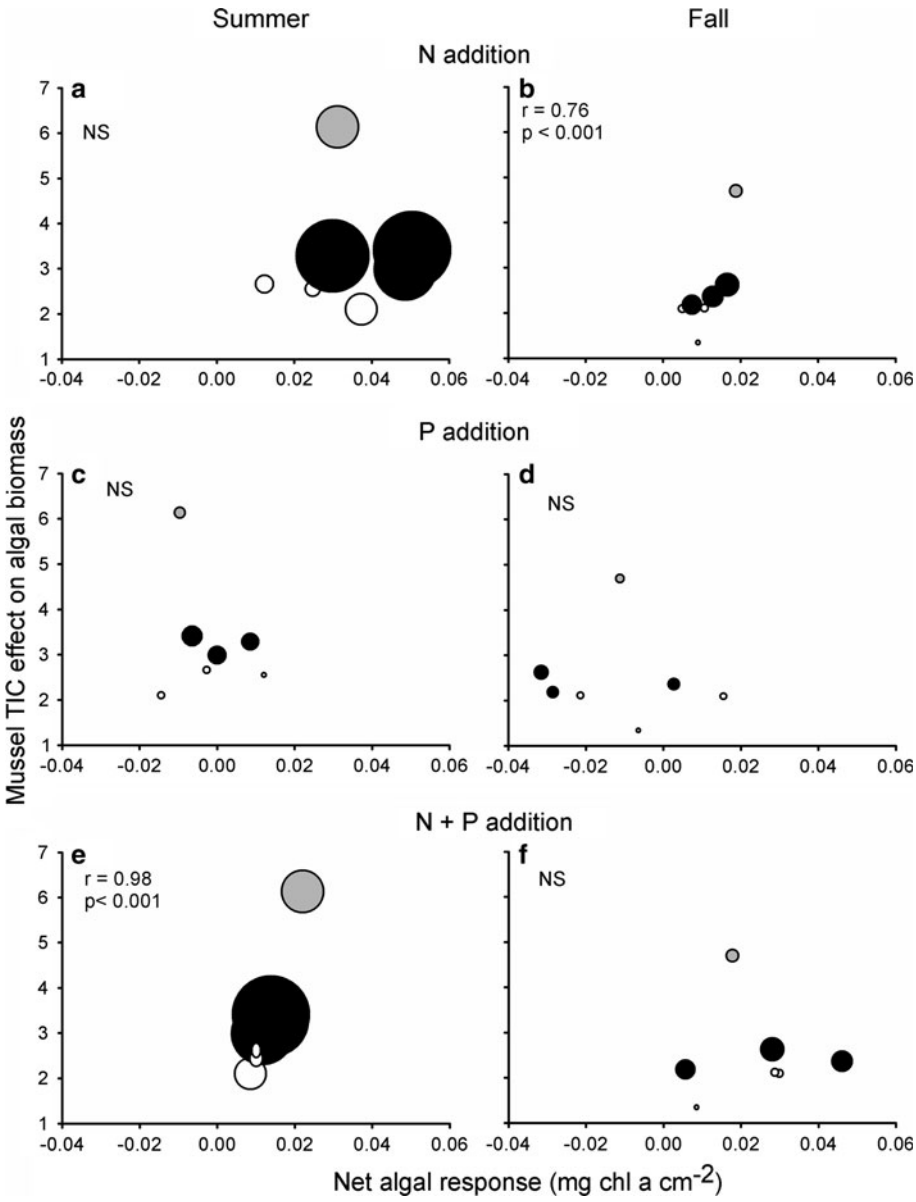

Fig. 7 Seasonal relationships between TIC effects of mussel diversity and N addition responses (**a**, **b**), P addition responses (**c**, **d**), and N + P addition responses (**e**, **f**). *White circles* Non-*Actinonaias* two-species polycultures, *black circles* two-species polycultures with *Actinonaias*, *gray circles* four-species treatments. The *size* of each *bubble* reflects the estimated magnitude of nutrients provided through mussel excretion (**a**, **b**, **e**, **f** ammonia excretion, **c**, **d** P excretion) in the treatment based on species-specific excretion rates (Spooner and Vaughn 2008)

which thermal and nutrient variability change over longer time scales and how this affects mussel trait expression. However, that species trait expression and environmental context (nutrient and thermal) can disproportionately impact trophic provisioning highlights the need for considering environmental context in BEF research, especially in systems that are subject to both natural and human-related environmental variability. Addressing this issue is of particular importance because changing environments will not only determine which species' traits will be expressed, and thus which species will persist, but also their relative contribution to the functioning of ecosystems.

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