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Predator richness has no effect in a diverse marine food web

Mary I. O'Connor[1,2]* **and John F. Bruno**[2]

[1]*Curriculum in Ecology, The University of North Carolina, Chapel Hill, NC 27599-3275, USA; and* [2]*Department of Marine Sciences, The University of North Carolina, Chapel Hill, NC 27599-3300, USA*

Summary

1. In many ecosystems, predator abundance, composition and diversity vary naturally among seasons and habitats. In addition, predator assemblages are changing due to overharvesting, habitat destruction and species invasions.
2. Predator species composition and richness can influence prey community structure and these effects can cascade to influence plant abundance and composition.
3. To test the effects of predator presence, composition and species richness on prey abundance, species richness and composition, we conducted three experiments in a subtidal marine food web. Experimental food webs were drawn from species pools of 5–7 predator species, 19–52 prey species, benthic micro-algae and 5 macro-algae.
4. Predators reduced prey abundance in the mesocosm experiment, but this effect was diminished or absent in field experiments. Predator species differed in their effects on prey, but we found no effect of predator richness (via complementarity or selection) on any aspect of prey community structure.
5. The absence of a predator richness effect could be due to several factors including potentially opposing effects of individual predator species, intraguild predation, or greater importance of colonization relative to competition in structuring prey assemblages. Although predators can have strong top-down effects in this system, selection or resource-use complementarity among predators do not affect prey community structure.

Key-words: amphipod, composition, diversity, food web, herbivore, immigration, isopod, marine, predator, richness, prey

Introduction

Predators strongly influence community structure and ecosystem function in many communities (Sih *et al.* 1985). Typically, predator effects are considered either as the aggregate effects of a predator assemblage (Morin 1995; Chalcraft & Resetarits 2003) or the effects of a single species, such as a keystone species, that strongly interacts with an important prey (e.g., Paine 1966; Estes & Palmisano 1974). Such approaches to studying community-level effects of predators do not distinguish among three aspects of multi-predator assemblages that can distinctly influence prey abundance and diversity: predator abundance, species composition and species richness (Rosenheim 1998; Sih, Englund & Wooster 1998; Cardinale *et al.* 2003; Chalcraft & Resetarits 2003; Byrnes *et al.* 2006). In nature, predator abundance, composition and richness vary seasonally, spatially, and as a result of human activities (Woodroffe 2000; Myers & Worm 2003; Ovadia & Schmitz 2004; Akin & Winemiller 2006). The relative importance of variation in these three structural aspects of predator assemblages for prey abundance and diversity are largely unknown.

Predators influence prey assemblages directly through effects of consumption on prey abundance and diversity, and indirectly through cascading effects of predator–prey interactions or by altering prey behaviour (Sih *et al.* 1985; Polis, Myers & Holt 1989; Holt & Lawton 1994; Peacor & Werner 2001). Consequently, predators can cause increases or decreases prey abundance and diversity, depending on the mechanism of effect (Paine 1966; Sih *et al.* 1985; Hixon & Carr 1997). In addition to the aggregate effects of individual predator species (*composition* effects), there may be emergent effects of predator assemblages due to species richness such as the sampling effect or resource use complementarity (*richness* effects) (Tilman, Lehman & Thomson 1997; Loreau & Hector

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*Correspondence author. Mary I. O'Connor, National Center for Ecological Analysis and Synthesis, 735 State Street, Suite 300, Santa Barbara, CA 93101, USA. E-mail: oconnor@nceas.ucsb.edu

2001; Fox 2005). For example, in grassland plant assemblages, experimental increases in plant species richness increased productivity through the inclusion of functionally unique species with regard to their use of nitrogen and the inclusion of a greater complement of species traits in the assemblage (Hooper & Vitousek 1997; Tilman *et al.* 2001).

Predictions about the effects of predator richness on prey populations in diverse and open prey assemblages must be drawn from theory and inferred from results of related experiments. Predator richness effects on closed, single-species prey assemblages seem to depend on the presence, strength and direction of predator–predator interactions or resource-use complementarity. For example, predator richness had no effect on populations of a single prey species when net predator effects were simply the sum of species-specific effects on prey abundance and diversity (Schmitz & Sokol-Hessner 2002; Straub & Snyder 2006). In systems with stronger predator–predator interactions, predominantly positive interactions led to a positive effect of predator richness and stronger predator effects (Cardinale *et al.* 2003), while negative interactions decreased topdown effects on prey populations (Finke & Denno 2005). However, in more complex food webs, prey species interactions and diversity may modify the total effect of a predator assemblage and predator richness effects in particular (Hillebrand & Cardinale 2004). For example, in closed, multispecies prey assemblages, stronger effects of higher predator species richness have been attributed to complementary effects of specialized predators on the density (Cardinale *et al.* 2003; Snyder *et al.* 2006) or behaviour (Byrnes *et al.* 2006) of different prey species. Such effects may depend on prey species traits, such as the existence of a competition – consumer avoidance trade-off (Fox 2004). Dispersal also has been found to modify effects of species richness in multitrophic assemblages (France & Duffy 2006; Matthiessen & Hillebrand 2006), and prey dispersal may modify effects of predator richness. Shurin (2001) found that prey richness declined in the presence of predators in closed experimental lake systems, but increased with systems where open to prey colonization. In this case, as in many other studies of predator effects, system openness reversed predator effects on prey richness by allowing immigration to compensate for predator-induced changes in prey abundance and richness.

Despite much work on food web dynamics, multiple predator effects and the relationship between diversity and ecosystem function (Rosenheim 1998; Cardinale *et al.* 2006; Stachowicz, Bruno & Duffy 2007), there are no published field experiments testing the effects of changing predator richness on prey community assembly in a diverse food web open to natural prey dispersal. We conducted two field experiments open to natural prey dispersal and one closed mesocosm experiment to test three hypotheses about the effects of predator presence, composition and richness on prey community structure in a diverse marine food web: (1) predators alter total prey abundance (hereafter called the *predator presence* hypothesis), (2) predator species have distinct effects on prey abundance and species composition (the *predator composition* hypothesis), and (3) predator species richness (via selection or complementarity) alters prey abundance and composition (the *predator richness* hypothesis). Predictions for the direction and mechanism of predator richness effects on prey communities are numerous and varied (Snyder, Chang & Prasad 2005). We tested the null prediction that the effect of a multispecies predator assemblage is the average of the effect of each species in monoculture (an additive model of multiple predator effects).

Study system

Predator composition and richness were experimentally manipulated in a shallow, subtidal estuarine food web in Bogue Sound, North Carolina, USA, near the University of North Carolina's Institute of Marine Sciences. This food web provides an ideal system for community-level experiments because its dynamics are fairly well understood and important individual- and population-level interactions occur on tractable spatial and temporal scales (Nelson 1979a; Jernakoff, Brearley & Nielsen 1996; Duffy & Hay 2000).

Benthic macro-algae attached to hard substrates are a principal habitat-forming guild, and together with epiphytic micro-algae are important primary producers. Patchily distributed macro-algal beds provide food and habitat for a rich assemblage of small, mobile invertebrate grazers (Hay & Sutherland 1988; Duffy 1989). These 'mesograzers', specifically amphipods, isopods and gastropods, can strongly control epiphytic and macro-algal biomass (Jernakoff *et al.* 1996; Duffy & Hay 2000). High rates of dispersal among plants and habitat patches (e.g., Edgar 1992) and generation times on the order of weeks (Virnstein & Curran 1986) allow rapid demographic responses to changes in predation or habitat quality. Mesograzer composition and abundance is therefore highly dynamic over spatial scales on the order of metres and time-scales of days to weeks (Nelson 1979a; Jernakoff *et al.* 1996).

The abundance of small, mobile predators on rocky substrates and seagrass beds is also dynamic and fluctuates seasonally (Hay & Sutherland 1988). We focused our work on small, primary predators known to consume amphipod and isopod mesograzers (Nelson 1979b; Martin, Wright & Crowder 1989; Duffy & Hay 2000; Bruno & O'Connor 2005). This functionally diverse predator guild includes several highly mobile crabs and fish (Table 1) that actively forage in the water column and along the edges of plants. Other predators are benthic, such as blennies and shrimp that forage on the substrate or in physically complex macro-algal habitat. These predators have different degrees of specialization and different preferences of species and sizes of invertebrate prey (Nelson 1979b; Bruno & O'Connor 2005).

Methods

Predator presence, composition and richness were manipulated to determine the effects on prey community structure in three separate experiments in 2004. In two field experiments (1 and 2), predator inclusion treatments allowed continuous prey dispersal (immigration and emigration). In the third experiment (3), predator treatments

Table 1. Predator size and density. Wet weights of typical animals used in experiments (mean (±SD)). Densities are minimum–maximum observed field density over 0·25 m^2 for 60 s visual surveys at benthic macro-algal habitats where species normally co-exist (e.g., rock jetties, floating docks, oyster reefs) in summer

Species	Common name	Experiment	Mass (g)	Density
Portunus spinimanus	Swimming crab	2, 3	2·2 (±1·2)	0–8
Callinectes sapidus	Blue crab	1	1·0 (±0·4)	0–4
		2	4·3 (±0·8)	
Panaeus aztecus, *Panaeus setiferus*	Brown shrimp, White shrimp	2, 3	0·2 (±0·1)	0–3
Palaemonetes vulgaris	Grass shrimp	1	0·3 (±0·1)	0–24
Lagodon rhomboides	Pinfish	1, 2	0·8 (±0·2)	3–40
		3	1·2 (±0·4)	
Hypleurochilus geminatus,	Blenny	1, 2	3·3 (±1·6)	0–5
Hypsoblennius hentzi, *Starksia ocellata*		3	2·7 (±0·6)	
Fundulus heteroclitus	Mummichog	3		0–21
Fundulus majalis	Striped killifish	1,2	11·8 (±4·7)	0–17
Sygnathus fuscus	Pipefish	2	1·6 (±0·5)	
All predators				0–49

Table 2. Experimental design. Location, treatments, replication (*n*) and duration of three experiments manipulating predator presence, richness and composition. Average net minimum prey immigration to no-predator control treatments is presented for comparison among experiments

	E1	E2	E3[1]
Location	Field	Field	Meso
n	4	8	12
Duration	6/18–6/28	7/12–7/29	9/25–10/20
Prey immigration	Open: 660 (±250)	Open: 725 (±171)	Closed
Pred. density	5/50 L	12/50 L	5/30 L

[1] Bruno and O'Connor (2005).

were maintained in outdoor mesocosms and with limited prey dispersal. In addition to prey dispersal, predator species composition and richness, replication, and physical conditions such as flow and turbidity varied among the three experiments (Table 2).

In the field, predator inclusion treatments were maintained in subtidal cages at Radio Island Jetty. Cylindrical (50-L) cages made of 5 mm polyethylene mesh enclosed predators while allowing flow of water, influx of light and immigration and emigration of small invertebrates (Figure S1). Each cage included an artificial habitat made of frayed nylon rope to provide refuge for invertebrates and substrate for epiphytic algae (Virnstein & Curran 1986; Edgar 1991). Frayed rope habitats mimic seagrass or branching macro-algae (e.g., *Gracillaria verrucosa*) (Virnstein & Howard 1987; Parker, Duffy & Orth 2001). Identical rope habitats were soaked outdoors in flowing seawater for 3 days before the experiment to facilitate the colonization of micro-algae. Cages were anchored to cinder blocks placed on a sandflat at 1–2 m depth at low tide, and randomly arranged approximately 2 m from an extensive macro-algal community associated with a rock jetty. Light levels at this location typically range from 500–1000 μM m^{-2} s^{-1} at low tide, and summertime temperatures are typically between 25 °C and 28 °C. This macro-algal bed provided source populations of invertebrate grazers that naturally colonized the experimental treatments. Each enclosure was checked at least twice during the experiments and missing predators were replaced.

The duration of each experiment was sufficient to allow initial community assembly (>300 individuals per habitat patch), consistent with previous predation experiments in this system (Nelson 1979a). Before removing the cages from the field, we collected the assembled invertebrates by placing a 1-gallon Ziploc bag over the rope habitats, sealing the invertebrates and habitat inside the bag. In the laboratory, we rinsed the patches and preserved invertebrates in 70% ethanol, and sorted each sample by size class (>2 mm, >1·4 mm, >1 mm). All organisms retained on a 1-mm sieve were identified to lowest taxonomic level possible, usually species.

The field experiments were designed to explore two aspects of the potential species richness – ecosystem function relationship. Experiment 1, conducted in June, 2004, included four predator treatments: (i) no predators, (ii) predator monocultures, and diverse polycultures of (iii) intermediate, and (iv) higher richness that varied in species composition among replicates. This design tested the effects of predator presence, composition and species richness. In contrast, experiment 2, conducted in July 2004, included only two treatment types, no predators and different levels of predator species richness (2, 4 and 6) drawn randomly from a pool of seven species. Using this design, the relationship between richness and function could be quantified across a greater range of richness levels while varying species composition among replicates, even at the highest richness levels, but could not cleanly partition the effects of predator species composition from effects of predator richness (Huston 1997). Experimental richness levels ranged from zero to six species and are within the natural range of richness of foraging predators over a similar area (Table 1).

We conducted a third experiment in 30-L outdoor mesocosms (experiment 3) in September and October of 2004 (Table 2). Mesocosms were stocked with a random sample of about 100 grazers added from a pool of grazers collected from the field, and with equal biomass of five species of macro-algae (see Bruno & O'Connor 2005, for detailed methods and algal results). Prey immigration was limited to the initial conditions plus possible contamination of a few individuals during the experiment. Mesocosms were shaded to reduce natural light levels to match those of field experimental conditions (approximately 500 μM m^{-2} s^{-1}), and nutrients and temperature conditions are very similar to concurrent conditions at the field site (Bruno *et al.* 2005). Gravel filtered seawater passed through 200-μm mesh filter bags to minimize immigration and fouling before reaching dump buckets above each mesocosm.

In all experiments, predator density was held constant across treatments in a replacement-series design (Jolliffe 2000, Table 2). For example, in experiments 1 and 3, predator monocultures contained five individuals per cage or mesocosm, and one individual of each species in the five-species polycultures. An alternative (additive) design increases overall predator density with predator richness so that intraspecific density does not change with diversity. Although there are advantages to the additive design (Cardinale *et al.* 2003), it would require predator densities in the high diversity treatments to be six times the monoculture densities. Such densities are far higher than observed in the field for most species (Table 1).

These experiments were designed to test for effects of species richness through the theoretical mechanisms of complementarity and sampling (Loreau & Hector 2001; Fox 2005). Intraguild predation is an important interaction that influences net predator effects through consumption of predators by predators and altered predator foraging behaviour (Finke & Denno 2004). To test for effects of species richness without the confounding effect of local absences, we maintained predator richness treatments through the replacement of missing or dead predators (Bruno & O'Connor 2005; O'Connor & Bruno 2007), and consequently reduced any effects of altered species composition due to lethal intraguild predation.

Statistical analyses

In all three experiments, we measured the effects of predator presence, composition and richness on three aspects of prey community structure: density, richness, and composition. To more specifically characterize prey diversity, we calculated Fisher's α (Fisher, Corbet & Williams 1943), which is robust to sample size and therefore provides a metric insensitive to variation in prey abundance. We also calculated prey evenness (Simpson's index, Simpson 1949).

One-factor ANOVA (performed in the Fit Model platform of JMP) was used to test treatment effects on final invertebrate abundance, richness and the calculated indices of diversity and evenness. Least squared means (LSM) planned contrasts were then used to test for effects of predator presence, composition and richness (as described in Bruno *et al.* 2005; Bruno & O'Connor 2005; Duffy, Richardson & France 2005). Contrasts between predator treatments were used to test for a predator presence effect by comparing the no-predator treatments to the predator treatments. Similarly, we tested for a richness effect by comparing the mean of the predator monocultures to the performance of the predator polyculture (Bruno *et al.* 2005). To test for an effect of predator composition, the remaining sum of squares (SS) was used after subtracting the richness SS from the overall model SS (Duffy *et al.* 2005). In experiment 2, which did not include monocultures, planned contrasts in a one-factor ANOVA were used to test for a predator presence effect, and the residual SS were used to test for an effect of richness. The magnitude of effects for predator presence, richness and composition were calculated as ω^2, the variance component of each factor in the ANOVA relative to the total variance (Graham & Edwards 2001).

All diversity and similarity statistics were calculated in PRIMER version 5 (Clarke & Gorley 2001). Data were untransformed, to examine the effects driven by the most abundant species, and fourth-root transformed data to amplify the responses of rare species (Clarke & Warwick 2001). ANOSIM analyses were used to test for significant differences in prey species composition. ANOSIM compares the similarity in species presence and abundance within and among samples, and generates an R statistic for every pair of treatments (Clarke & Warwick 2001).

Results

Predator manipulations resulted in distinct predator richness and composition treatments (Table 2). Final invertebrate densities in the experimental assemblages ranged from 0 to 1402 individuals representing 66 taxa, including 18 species of amphipod and 16 species of bivalve (Table S1). Invertebrate richness was significantly greater in the second experiment (Fig. 1d vs. E, $P < 0{\cdot}0001$) due to the natural recruitment of juvenile bivalves later in the summer (Table S1). In the mesocosm experiment, amphipod and isopod populations grew nearly 10-fold over 3 weeks in the absence of predators, yet reached final densities much lower than in the field experiments that were open to colonization (Fig. 1a–c). Amphipod and isopod grazers comprised 99% of total invertebrates in experiment 3, and an average of 97% (95% CI 96–99%) and 49% (95% CI 35–63%) in experiments 1 and 2, respectively.

Missing or dead predators were replaced in each experiment. We detected evidence of antagonistic predator–predator interactions in the replacement rates of certain predator species (for example, shrimp were replaced twice as often as other predators). Overall, predators were present in more than 75% of censuses, so replacement rates were relatively low but suggest some intraguild predator antagonism.

Predators significantly decreased invertebrate abundance in field experiment 2 and in the mesocosm experiment (Table 3, Fig. 1a–c). Reduced abundance was accompanied by reduced prey richness and altered invertebrate composition in both experiments (Tables 3, S2, Fig. 1d–f, Fig. 2b–c). However, there was no effect on prey richness after richness was normalized to sample abundance (Fisher's α; Table 3).

Predator species composition altered invertebrate density and richness (Table 3). Even in field experiment 1, in which predator treatments taken together had no effect relative to the no-predator control, invertebrate density differed significantly among predator monocultures (Fig. 1a). Invertebrate abundance increased in Portunid crab monocultures (*Callinectes sapidus* and *Portunus spinimanus*) relative to other predator treatments (Fig. 1a and c). This increase corresponded with an increase in richness and altered species composition in experiment 3, but not in experiment 1 (Tukey's HSD, Fig. 1c,

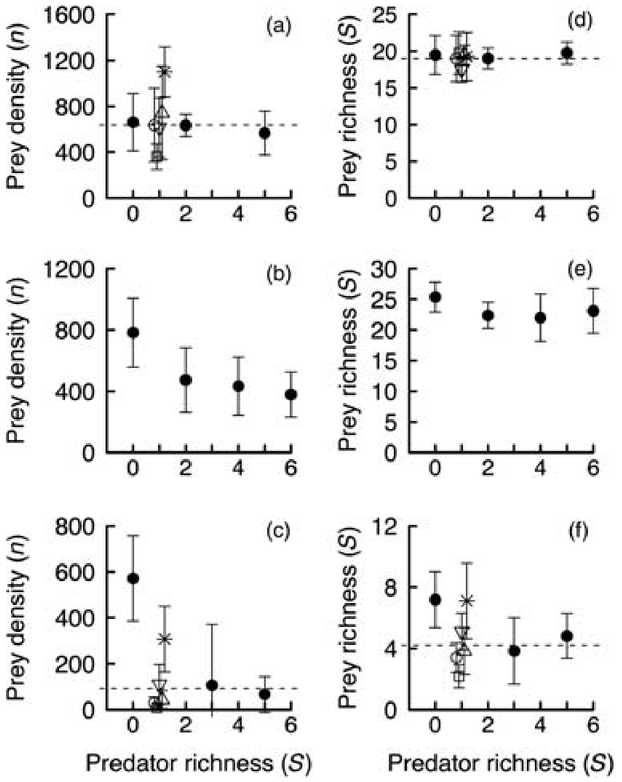

Fig. 1. Invertebrate prey richness and density responses to manipulations of predator presence, composition and species richness. Field experiments are shown in panels a and d (experiment 1) and in panels b and e (experiment 2), and the mesocosm experiment is shown in panels c and f. Dashed lines indicate the mean of predator monoculture treatments. Symbols: ● 0 or multiple predator species, open symbols for predator monocultures: ○ pinfish, □ shrimp, ▽ killifish/mummichogs, △ blennies, * crabs.

Table S2, Fig. 2a and c). In contrast to the crab effect, shrimp reduced prey density relative to all other predators in both experiments (Fig. 1a,c). Shrimp also reduced invertebrate richness (Table 3, Fig. 1d and f) and evenness (Table 3, Fig. 2 c), and altered composition relative to some, but not all, predator monocultures in experiment 3 (Tukey's HSD). Although not significant, a similar trend is apparent in response to shrimp monocultures in experiment 1 (Fig. 2a).

Predator species richness did not influence any measured aspect of prey communities (Tables 3, S2). The highest level of predator richness tested caused a minor but significant shift in prey composition in experiment 2 relative to the no-predator controls (Fig. 2b). Visual comparison of relative abundances of prey species (Fig. 2b) suggests the significant difference is likely driven by changes in the abundance of rare taxa, such as shrimp, crab megalopae, brittle stars and several gastropods. There were no trends in invertebrate size class distribution in response to predator treatment (See Results in Supporting Information).

Discussion

Three independent experiments indicate that predator presence and composition can affect prey community structure. Contrary to our prediction, predator richness had no effect on prey assemblages in these food webs. These results therefore do not support the predator richness hypothesis or the idea that resource use complementarity or the sampling effect are important aspects of diverse predator assemblages with regard to prey suppression (Cardinale *et al.* 2003; Byrnes *et al.* 2006). The absence of a predator richness effect might be attributable to weakened or contrasting effects of different predator species in diverse assemblages, to the minimization of intraguild predation or to the complexity of diverse food webs. Variation in the strength of effects of predator presence among experiments raises interesting questions about the possible role of prey migration in the context of understanding overall predator effects.

Several aspects of the predator assemblage could explain the absence of an effect of predator richness in our experiments. These include a combination of antagonistic effects of different predator species, predator density, restricted predator mobility or the complement of specialist and generalist predators (Thebault & Loreau 2003). Although predator replacements minimized effects of lethal intraguild predation, behavioural effects of predator–predator antagonism may have occurred. These intraguild behavioural effects would counteract negative effects of complementarity on overall predation, and may explain the absence of an overall richness effect. Comparisons between monocultures and diverse predator assemblages provide some evidence that predator species also may have had non-interactive and opposing effects on prey. Specifically, crabs and shrimp caused opposite trends in prey abundance and richness in monoculture (Fig. 1), and these opposing predator effects could have contributed to an absence of a net predator richness effect in mixtures (e.g., Martin *et al.* 1989). In addition, intraguild predation by blue crabs on shrimp may have further reduced top-down effects of predators in mixtures by reducing predator density and activity before replacements could be made (Denno, Finke & Langellotto 2005). The reduced strength of predator effects in diverse predator assemblages relative to monocultures could also be a consequence of reduced intraspecific density inherent in the replacement experimental design. The net effects of strong interactors (e.g. crabs and shrimp) may be density dependent, and these predators may not be as effective when only one or two individuals (vs. five in monoculture) are foraging, as would be the case in experimental polycultures. In addition, limited predator mobility and dispersal in our experimental treatments might have reduced top-down effects, as has been shown for grazers (France & Duffy 2006; Matthiessen *et al.* 2007). Although there are differences in the preferred size and species of prey among predators in this system, predator diets include multiple species of prey, and thus should be considered moderately generalist predators. Theoretical work by Thebault and Loreau (2003) suggests that increasing generalist predator richness would be expected to have a greater effect on prey abundance than increasing richness of specialist predators, but our results do not support this specialist–generalist hypothesis.

Prey dynamics could also explain the absence of a predator richness effect. In a diverse prey community with high prey

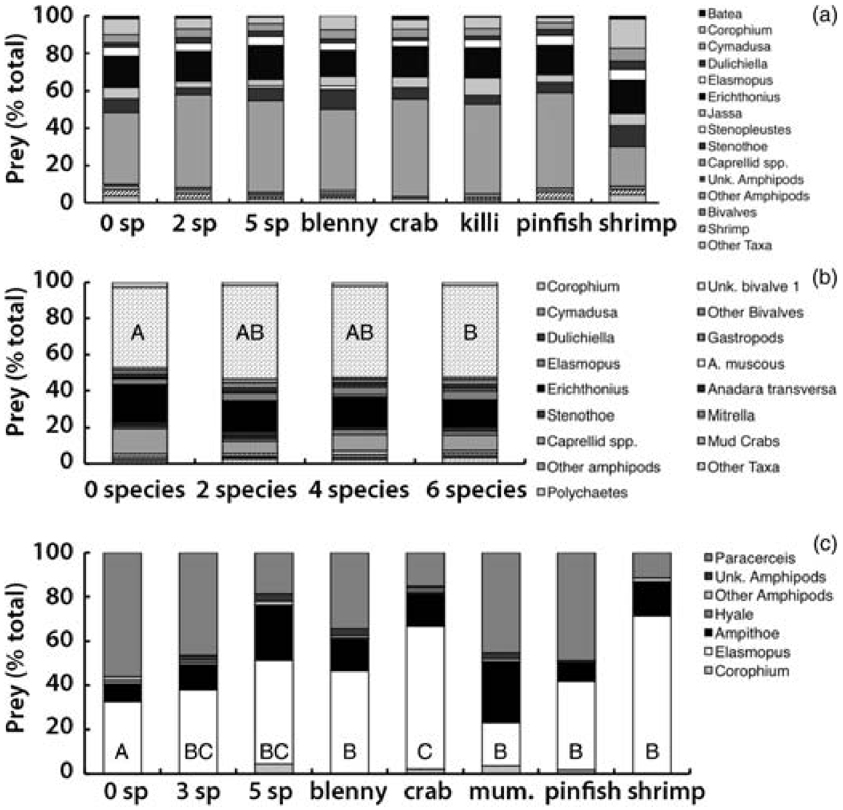

Fig. 2. Prey species composition. Relative mean abundance of invertebrate prey in (a) field experiment 1, (b) field experiment 2 and (c) the mesocosm experiment (3). Taxa comprising <1% of the mean total for each treatment were pooled. Genus names listed here, see Table S1 for full species names. Letters indicate significant differences according to ANOSIM (see Table S1). In experiment 3, in addition to the differences noted in C, shrimp monocultures differed significantly from mummichog monocultures (mum.) and five-species polycultures.

Table 3. ANOVA results for tests of the effect of predator presence, richness and composition on invertebrate community metrics. Density data and Fisher's α values for experiment 3 were log transformed to meet the ANOVA assumption of normality

	SS	d.f.	F	ω^2	SS	d.f.	F	ω^2
	Prey density				Prey richness			
Experiment 1								
Presence	301·3	1	0·00		0·5	1	0·08	
Richness	52291·9	1	0·74		1·9	1	0·30	
Composition	1149348·5	4	4·07*	0·38	12·5	4	0·51	
Experiment 2								
Presence	758881·6	1	19·78***	0·54	52·5	1	5·37*	0·21
Richness	35852·4	2	0·4686		1·9	2	0·10	
Experiment 3								
Presence	12·9	1	62·66***	0·72	72·8	1	30·47***	0·55
Richness	<0·0	1	0·02		2·4	1	0·99	
Composition	12·4	4	15·12***	0·48	147·4	4	15·43***	0·49
	Prey evenness (Simpson's I)				Prey diversity (Fisher's α)			
Experiment 1								
Presence	<0·0	1	0·55		<0·0	1	0·02	
Richness	<0·0	1	0·42		0·2	1	0·53	
Composition	<0·0	4	1·04		4·2	4	2·43	
Experiment 2								
Presence	<0·0	1	0·07		<0·0	1	0·08	
Richness	<0·0	2	0·03		0·5	2	0·44	
Experiment 3								
Presence	<0·0	1	0·75		<0·0	1	0·65	
Richness	<0·0	1	0·86		0·1	1	2·10	
Composition	0·3	4	3·46*	0·14	0·1	4	0·47	

*0·05 > P > 0·01, **0·01 > P > 0·001, ***0·001 > P. Sum of squares (SS), degrees of freedom (d.f.), F-statistic (F), and effect size (ω^2)

immigration rates, prey diversity could dampen cascading effects of consumers by increasing resistance through associational defences or the increased probability of including inedible species (Hillebrand & Cardinale 2004). In such a case, complementary effects of selective predation in diverse predator treatments could alter prey species composition but not overall richness (e.g., Shurin 2001; O'Connor & Crowe 2005). The absence of variation in prey composition with increasing predator richness (Fig. 2, Table S2) suggests, however, that compensation by other prey species did not occur and that prey dispersal did not mask an effect of predator richness on prey richness or composition. Furthermore, there was no effect of predator richness when prey migration was limited in the mesocosm experiment (Table 2). In herbivore – plant systems, a strong trade-off between competitive ability and consumer avoidance has been considered a requisite condition for consumer diversity to affect prey abundance and composition (Thebault & Loreau 2003; Fox 2004). Such trade-offs have not been documented for the invertebrate prey community in our experiments, and indeed the absence of a response in prey composition (Fig. 2) suggests that competition is not an important factor structuring the prey assemblages. In summary, we suggest that additive and antagonistic predator effects may have been weakened in a prey assemblage structured predominantly by propagule supply rather than competition.

Studies that report significant effects of increasing predator richness have used low-diversity food webs (two to five prey species) that are closed to prey dispersal (Cardinale *et al.* 2003; Gamfeldt, Hillebrand & Jonsson 2005; Finke & Denno 2005; Byrnes *et al.* 2006). Closed systems can greatly strengthen predator effects because prey species pool size and richness are limited, preventing colonization to replace lost individuals or species. The results of our experiments suggest that significant effects of species richness based on experiments in simplified food webs may be less important under conditions of high prey diversity or systems open to propagule replenishment through immigration. The relevance of simplified food webs has been questioned in the interpretations of the importance of other ecological processes such as trophic cascades (Polis & Strong 1996), and a similar limitation may afflict studies of predator diversity.

While there was no effect of predator richness under any conditions, predator presence and composition did influence prey assemblages. Predator effects on prey abundance and richness were absent or weakest in experiment 1, present in experiment 2 and strongest in experiment 3 (the mesocosm experiment) (Fig. 1, Table 3). Among several factors that vary among experiments, we consider increasing prey dispersal and prey diversity to be likely mechanisms weakening predator effects. Prey immigration and prey diversity can weaken top-down effects of predators by replenishing depleted prey populations and effectively increasing population size and growth rate (Underwood, Denley & Moran 1983; Cooper, Walde & Peckarsky 1990; Sih & Wooster 1994; Hillebrand & Cardinale 2004), thus maintaining prey abundance and diversity within a habitat patch even in the presence of intense predation (Shurin 2001; Holt & Loreau 2002). Predator effects were strongest in the mesocosm experiment with the lowest prey diversity and immigration rates (Table 2, Fig. 1), and were progressively weaker in the two field experiments as prey diversity and immigration levels increased (Table 2). However, it is important to note that we did not directly manipulate prey diversity or immigration rates and factors other than immigration, including greater replication, presence of macro-algae and the prey species pool, varied among experiments and could also explain these differences. Whatever the explanation for the variation in the strength of predator effects among experiments, the strength of predator effects is not linked to the presence or strength of richness effects, demonstrating that predators can be important even if species richness is not.

These findings show that in a system in which predation by multiple, functionally diverse predators is known to strongly influence the local macro-algal and grazer summertime community (Nelson 1979b; Nelson 1981; Martin *et al.* 1989; Duffy & Hay 2000), two widely studied mechanisms of diversity effect (sampling and complementarity) are not important determinants of predator effects on prey. Consistent with previous experiments, the present study shows that predation reduces grazer abundance and richness even under conditions of high prey immigration and diversity. If predator richness has any emergent effects in this system, they may be operating at larger spatial and temporal scales that take into account movement, intraguild predation and interactions among predators and prey.

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Supporting information

Additional supporting information may be found in the online version of this article:

Table S1. Post-hoc contrasts for ANOVA comparing predator treatments.

Table S2. Species abundance in each experiment

Fig. S1. Cages used for field experiments.