

LETTER

Predator diversity strengthens trophic cascades in kelp forests by modifying herbivore behaviour

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Abstract

Although human-mediated extinctions disproportionately affect higher trophic levels, the ecosystem consequences of declining diversity are best known for plants and herbivores. We combined field surveys and experimental manipulations to examine the consequences of changing predator diversity for trophic cascades in kelp forests. In field surveys we found that predator diversity was negatively correlated with herbivore abundance and positively correlated with kelp abundance. To assess whether this relationship was causal, we manipulated predator richness in kelp mesocosms, and found that decreasing predator richness increased herbivore grazing, leading to a decrease in the biomass of the giant kelp *Macrocystis*. The presence of different predators caused different herbivores to alter their behaviour by reducing grazing, such that total grazing was lowest at highest predator diversity. Our results suggest that declining predator diversity can have cascading effects on community structure by reducing the abundance of key habitat-providing species.

Keywords

Behaviourally modified interaction, biodiversity ecosystem function, kelp forest, multiple predator effects, predator diversity, trait-mediated indirect interactions, trophic cascade.

Ecology Letters (2006) 9: 61–71

INTRODUCTION

Mounting evidence suggests that the diversity of trophically basal species, such as plants and sessile marine invertebrates, can critically affect ecosystem processes (Tilman *et al.* 1997; Loreau & Hector 2001; Stachowicz *et al.* 2002; Hooper *et al.* 2005). The presence or absence of even one or two species at higher trophic levels, however, can cause cascading effects on basal trophic levels and overwhelm this diversity effect (Paine 2002; Schmitz 2003). Human-induced extinctions and local extirpations are often biased towards higher trophic levels (Pauly *et al.* 1998; Jackson *et al.* 2001; Duffy 2002, 2003), as evidenced by recent dramatic declines in predator abundance and diversity in the sea due to fishing (Halpern & Warner 2002; Myers & Worm 2003). Thus, our knowledge of the functional role of diversity is weakest for the groups of species that often have the largest effects and may be at greatest risk of extinction (Duffy 2002; Raffaelli 2004).

Trophic cascades, in which the removal of top predators leads to increases in herbivory and decreases in plant biomass, occur in a wide variety of systems (Shurin *et al.* 2002). Limited evidence characterizes communities display-

ing trophic cascades as simple, linear food chains (Halaj & Wise 2001). In contrast, complex, diverse food webs are thought to be less likely to exhibit major shifts in community states when individual consumers are removed (Polis & Strong 1996). For example, in the relatively simple food webs of Alaskan kelp forests, kelp biomass is maintained by sea otter predation on herbivorous sea urchins (Estes *et al.* 1998). In kelp forests with more complex food webs containing a greater diversity of predatory and herbivorous fish and invertebrates, such as those of southern California (Graham 2004), the extirpation of otters appears to have not had as large an impact on kelp (Steneck *et al.* 2002).

While it is tempting to conclude from this contrast between Alaskan and Californian kelp forests that diversity affects the likelihood of a system to cascade, caution is warranted. The differences between these two regions may be due to other factors, and the relationship between diversity and cascade strength may be more complex. For example, herbivore diversity may decrease the strength of trophic cascades by limiting the ability of predators to control herbivory (Leibold 1996; Polis & Strong 1996;

Steiner 2001; Duffy *et al.* 2005). The effects of changing predator diversity on the strength of trophic cascades are less clear and may depend on diversity at other trophic levels (Cardinale *et al.* 2003; Aquilino *et al.* 2005; Duffy *et al.* 2005; Gamfeldt *et al.* 2005). There are at least three mechanisms that could determine the effect of changing predator diversity on cascade strength. First, predators might be complementary in suppressing herbivores such that increasing predator diversity decreases total herbivory, thereby increasing plant biomass (Duffy 2002; Cardinale *et al.* 2003; Duffy *et al.* 2003; Gamfeldt *et al.* 2005). This effect might be mediated through changes in herbivore density (i.e. different predators consume different herbivores) and/or behaviour (i.e. different predators cause different herbivores to hide or emigrate and thus reduce feeding within a patch) (Sih *et al.* 1998; Peacor & Werner 2001; Dill *et al.* 2003; Trussell *et al.* 2003; Schmitz *et al.* 2004; Preisser *et al.* 2005). Second, interspecific interference among predators, including intra-guild predation, may reduce predator effects on herbivores (Siddon & Witman 2004), leading to a decrease in plant biomass with increasing predator diversity (Finke & Denno 2004). Third, increasing diversity of predators may increase the probability of including a predator with a dominant effect on all prey densities or behaviours, similar to the sampling effect (Huston 1997; Tilman *et al.* 1997). The strength of the trophic cascade would then be driven by the presence of this keystone predator (Paine 1966). Which of these three mechanisms predominate has critical implications for predicting the effects of observed worldwide predator extirpations (Pauly *et al.* 1998; Myers & Worm 2003).

In this study, we address the effects of predator diversity on the strength of trophic cascades in kelp communities in California, USA. Kelps provide critical habitat for a variety of invertebrates, fishes and mammals (Dayton 1985; Graham 2004), and changes in abundance can have major ecosystem level consequences (Simenstad *et al.* 1978; Tegner & Dayton 2000; Graham 2004). To test the idea that predator diversity can affect kelp biomass, we use a combination of field surveys and experimental mesocosm manipulations. First, we use survey data from a 19-year survey of 16 sites around the Channel Islands to assess whether and how predator diversity is correlated with kelp and herbivore abundance in the field. A positive correlation between predator diversity and kelp abundance may be due to a top-down trophic cascade or the provision of more habitat for predators. We therefore used mesocosms stocked with *Macrocystis* sp. and a variety of predators and herbivores from central California kelp forests to explicitly manipulate predator diversity and examine its top-down effect on the strength of trophic cascades. Finally, we use additional mesocosm experiments to assess the contribution of predator-induced behavioural responses to the effect of diversity on cascade strength.

METHODS

Field correlations between predator diversity and kelp abundance

In order to test whether predator diversity is associated with kelp abundance at large scales, we used survey data collected for the National Park Service Channel Islands Kelp Forest Monitoring program (see Supplementary Material and Davis *et al.* 1997 for a full description of the program, and contact the Superintendent of the Channel Islands National Park to obtain these data). Data were collected at 16 sites from 1986 to 2004 and included the abundance of four species of kelp, 13 species of herbivores, and 19 species of predators (Davis *et al.* 1997; Graham 2004; Micheli & Halpern 2005). Two sites are located within a reserve, while other sites are fished for a variety of predatory species (Behrens & Lafferty 2004; Lafferty 2004). We standardized the data for all species to number of individuals per m² for our analyses and calculated the abundance of organisms at each trophic level and the Shannon–Weiner diversity (Mouillot & Lepretre 1999) for predators at each site for each year. We then averaged the data over all years and used site ($n = 16$) as our unit of replication. To examine the effect of predators on community composition, we examined the correlation between both kelp and herbivore abundance against predator diversity, abundance and their interactions. We also examined the correlation between herbivore abundance and kelp abundance. As both response variables could not be negative, we used a log-link regression with a negative binomial error fit using maximum likelihood (SAS proc genmod, SAS Inc, Cary, NC). As there is currently little consensus on the most appropriate way to calculate R^2 for these types of regression, we used the correlation between observed and predicted values (Cameron & Windmeijer 1996), as it provides an intuitive measure of the degree to which the model explains the observed variation in the data.

Effects of predator diversity manipulations on trophic cascade strength

In order to assess whether there is a causal link between predator diversity and kelp abundance, we assembled a subset of the organisms from the kelp forests of Bodega Bay, California in outdoor mesocosms. Mesocosms varied in predator richness (one to three species) but not herbivore richness or composition. We added two cut fronds (30–50 cm long) of pre-weighed giant kelp (*Macrocystis* sp.) attached to rocks on the bottom of mesocosms. Each mesocosm contained five brown turban snails (*Tegula brunnea*), five black turban snails (*T. funebris*), two purple sea urchins (*Strongylocentrotus purpuratus*), a single red sea urchin (*S. franciscanus*), and a single kelp crab (*Pugettia*

producta). All of these herbivores except *T. funebris* are regularly found within kelp beds around Bodega Bay and vary greatly in density among sites (J. Byrnes, personal observation). We chose densities of herbivores in an attempt to equalize the total grazing impact of each species to the same order of magnitude, while also staying well within natural densities (Foster & Schiel 1985). Mesocosms were then stocked with predators using a replacement design (Huston 1997) with either three individuals of a single predator species ($n = 3$), no predators ($n = 3$), or a polyculture of a single predator from each species ($n = 4$). There was also a treatment with no predators and no herbivores ($n = 3$) to control for change in kelp mass due to factors other than herbivory (e.g. growth, senescence). Predators included the red rock crab (*Cancer productus*), the Dungeness crab (*C. magister*), and the sun star (*Pycnopodia helianthoides*). All predators used were abundant in kelp beds around Bodega Bay and are known to consume at least one species of herbivore in our experiment as well as engage in intraguild predation and aggression (Fig. 1) (Mauzey *et al.* 1968; Gotshall 1977; Hamilton & Heithaus 2001).

Mesocosms were free standing 1 m diameter \times 0.5 m deep (400 L) cylindrical tanks with a central standpipe and had flow-through filtered seawater delivered at an approximate rate of 45 L min⁻¹. Kelp was removed from the mesocosms and weighed after 8 days, as by this time nearly 100% of the kelp had been consumed in some herbivore only mesocosms. Kelp did grow (exhibit positive mass change) in the no herbivore treatments (see Results). In the few cases of herbivore death from causes other than predation, herbivores were replaced within 48 h. This experiment was repeated in August 2003, September 2003 and July 2004, giving a total of nine replicates for each monoculture and control and 11 replicates for each polyculture after excluding one replicate that included a misidentified predator. We measured: (1) change in kelp

mass (growth – herbivory) as a metric of the strength of the trophic cascade and (2) predator-caused mortality of herbivores to help assess the mechanism underlying an effect. Our design manipulated both predator richness (one species vs. three) and Shannon–Weiner diversity (0 vs. 1.09) simultaneously. Analyses were performed only on richness.

To assess the effect of predator richness on change in kelp mass, we used a multiple linear regression, with predator species richness and initial kelp mass as continuous predictor variables. We included trial as an additional block effect in our model. We tested for homogeneity of slope, and when confirmed ($P > 0.05$), eliminated interactions from our statistical model. To test whether polycultures were truly different from monocultures, we performed a separate ANCOVA using predator treatment as a categorical variable. This minimized the total error for an *a priori* contrast in which predator monocultures were grouped together and compared against the predator polyculture. A significant difference here would indicate that the polyculture yields a stronger cascade than would be predicted by the performance of the three monocultures, so called non-transgressive overyielding from some form of complementarity (Loreau 2004). We also used a *post-hoc* Tukey test to compare the predator polycultures to all of the monocultures to see whether the polycultures created a stronger cascade than the best performing monoculture (i.e. transgressive overyielding).

As consumption of one prey species could be correlated with the consumption of another prey species, we used MANOVA to separate the effects of trial, treatment, and their interaction on consumption of herbivores. If complementary predation were the driver of the diversity effect, we would expect different herbivores to be more strongly affected by different predators or total predation to be higher in high diversity treatments. Thus, when MANOVA indicated significant effects, we used ANOVA and accompanying Tukey’s HSD tests to examine the patterns of predation on each herbivore. To test the effects of diversity on total predation, we compared the predation rate on all herbivores for predator monocultures with the predator polyculture using a two-way factorial ANOVA including trial as above.

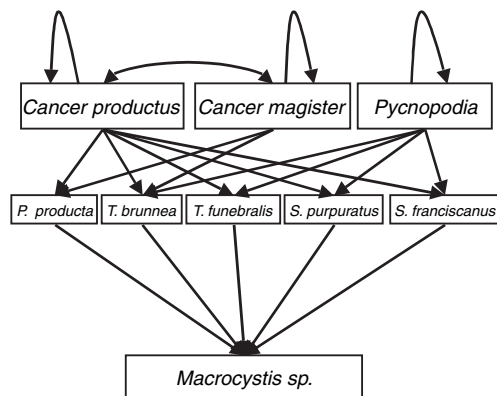


Figure 1 Experimental food web in mesocosms of giant kelp (*Macrocystis* sp.) forests.

Effects of predator diversity on herbivore behaviour

Although we found that predator diversity affected the change in kelp mass, we could not clearly link this pattern to changes in herbivore density in different treatments during the timescale of the experiment (see Results), suggesting a non-density-mediated mechanism. A variety of herbivores, including many marine species, react to the perceived risk of predation by reducing activity level, including food intake (Sih 1980; Peacor & Werner 2001; Dill *et al.* 2003; Trussell *et al.* 2003; Preisser *et al.* 2005). To test the effects of

predator-induced changes in herbivore behaviour on change in kelp mass, an identical mesocosm experiment was run that allowed herbivores to experience predator cues, but protected them from being consumed. In this behavioural cascade experiment, individual herbivores of each species (one individual of each species per tank) were placed in flow-through containers with pre-weighed pieces of kelp. Containers were placed in mesocosms with predator combinations as above (container sizes: 15.5 L for red urchin, 7.7 L for purple urchins, and 1.1 L for snails). We also included three tanks with kelp that contained no predators and no herbivores. The experiment was repeated in July, September, and October of 2004. During the second and third trial, predatory crabs had their claws banded, and *Pugettia* were allowed to roam free in tanks with a loose piece of kelp tethered to the bottom. This was done to include physical and visual cues in addition to chemical cues that can be important for *Pugettia* (Zimmer-Faust & Case 1982). We added similarly sized paired control pieces of kelp from the same stipe enclosed in flow-through containers without herbivores in the same mesocosm to control for autogenic changes in the kelp over the experiment. Kelp mass consumed was calculated by subtracting the change in a treatment kelp piece from the change in a paired control treatment piece after 3 days.

Although initial replication was identical to the trophic cascade experiment, data were excluded from analyses when *Pugettia* were eaten or otherwise missing (two during trial 1 and three during trial 3) or moulted (one during trial 2 and 3), as were data in which *S. franciscanus* were found dead due to disease (one during trial 3). There were therefore seven total no predator replicates, seven *C. productus* replicates, nine *C. magister* replicates, eight *Pycnopodia* replicates, 11 polyculture replicates, and nine no herbivore replicates. When any one herbivore species was excluded within a tank, none of the data from that tank were used to calculate total kelp consumption of all herbivores. We analysed total herbivory in the same manner as previous experiment. We analysed individual species data in the same manner as the previous herbivore mortality data.

Relative importance of behaviour to overall cascade strength

To test the relative strength of behavioural vs. behavioural and consumptive cascade strengths for relevant treatments, we examined the relative strength of the cascade as defined by $(\Delta K - \Delta K_{\max}) / \Delta K_{\max}$, where ΔK is the change in kelp mass for a given replicate and ΔK_{\max} is the maximum change in kelp from any replicate during a given temporal block. Net cascade strength varied among the three temporal blocks of the two experiments, so this approach normalizes the amount consumed in each replicate to the

maximum in each temporal block. To compare effects between the behavioural cascade experiment and the experiment with both behaviour and density effects, we assumed herbivores behaved independently and extrapolated the behavioural cascade strength by doubling kelp consumption values for *S. purpuratus* and quintupling kelp values for both snails. This assumes little to no exploitative competition, which is reasonable given that only the no predator treatment ever showed near-complete kelp consumption. It also assumes no interference competition, which seems reasonable for urchins and snails; crabs might engage in interference competition, but because we only used one individual *Pugettia* per replicate in both experiments, such interference was not an issue. We used ANOVA to compare cascade strength for the *C. productus*, *Pycnopodia* and polyculture treatments, as they were the only treatments with a significant trophic cascade (see Results). We calculated the percentage of the total cascade strength comprised by behaviourally mediated interactions. Given the proportion of the behaviour and density-mediated cascade accounted for by behaviour alone in monocultures, we can use a proportional hazard analysis (Sih *et al.* 1998) to create a prediction of how important behavioural interactions should be in polyculture. We used proportional hazard analysis (1) as it compensates for the non-additivity of combining percentages by using a multiplicative model and (2) as we used a replacement design, if the observed value matched the predicted, this implies that changes in the densities of an individual predator (i.e. reducing the density of a predator reduces the strength and effect of its cue) are not important. Hence, a single predator of a given species would have the same behavioural impact as three individuals of a single species. If cue dilution was important, however, then the percentage of the cascade strength accounted for by behaviour should be the same or less in polyculture when compared with monocultures (i.e. the percentage accounted for by each species would be reduced by 1/3).

RESULTS

Patterns in Channel Islands kelp forests

Patterns from field data were broadly consistent with the idea that predator diversity enhances kelp abundance by increasing trophic cascade strength. Predator diversity but not predator abundance or their interaction was positively correlated with kelp abundance (Table 1a, Fig. 2a,b, $R^2_{\text{COR}} = 0.491$, d.f. = 12, deviance = 13.419). Predator diversity, but not predator abundance, was negatively correlated with herbivore abundance (Table 1b, Fig. 2c,d, $R^2_{\text{COR}} = 0.140$, d.f. = 12, deviance = 16.186). We found no significant correlations between abundances of individual predator species and kelp abundance. Herbivore abundance

Table 1 Values for log link regression functions with negative binomial error terms for the Channel Islands data set. Dispersion parameters are for the negative binomial error term (variance = $\mu + \epsilon\mu^2$ where μ is the estimated value and ϵ is the dispersion parameter). Independent variables that are significant are highlighted in bold. (a) Coefficients for the regression of kelp abundance against predator abundance, diversity, and their interaction. Only predator diversity is significant. (b) Coefficients for the regression of herbivore abundance against predator abundance, diversity, and their interaction. Only predator diversity is significant. (c) Coefficients for the regression between herbivore abundance and kelp abundance. Herbivore abundance is significant

Parameter	Estimate	Standard error	Wald 95% confidence limits		<i>P</i>
(a) Kelp abundance					
Intercept	-2.4859	1.622	-5.6649	0.6931	0.1254
Predator diversity	3.1562	1.304	0.6004	5.7119	0.0155
Predator abundance	0.3522	0.8554	-1.3244	2.0287	0.6805
Interaction	-0.6382	1.0628	-2.7212	1.4448	0.5482
Dispersion	0.0589	0.164	-0.1387	0.3803	
(b) Herbivore abundance					
Intercept	6.6937	1.079	4.5789	8.8085	< 0.0001
Predator diversity	-3.0765	1.017	-5.0699	-1.0832	0.0025
Predator abundance	-0.5692	0.4798	-1.5096	0.3713	0.2356
Interaction	0.5497	0.6888	-0.8003	1.8997	0.4248
Dispersion	0.27	0.1053	0.0636	0.4764	
(c) Kelp abundance					
Intercept	1.7121	0.3267	1.0717	2.3524	< 0.0001
Herbivore abundance	-0.0422	0.0145	-0.0707	-0.0138	0.0037
Dispersion	0.0977	0.1796	-0.1387	0.4498	

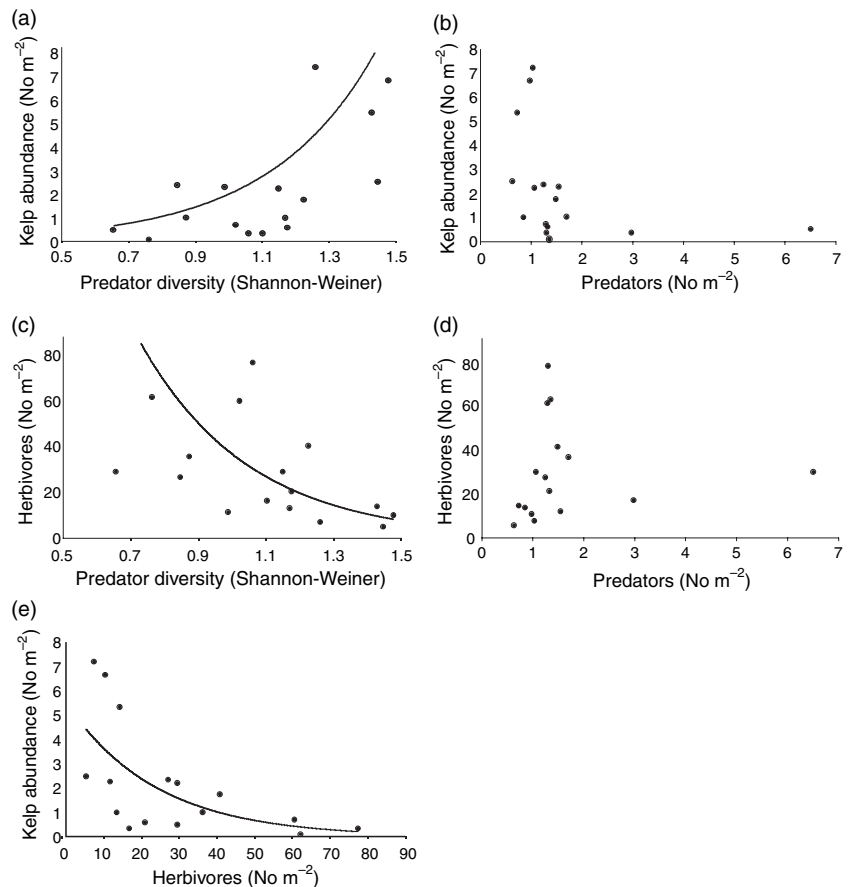


Figure 2 Patterns from the Channel Islands Kelp Forest surveys. (a) Predator diversity (Shannon–Weiner) is positively correlated with kelp abundance ($y = e^{(3.1562x - 2.4859)}$, $P = 0.0155$, $R^2_{COR} = 0.490$). (b) Predator abundance is not correlated with kelp abundance ($P = 0.681$). (c) Predator diversity is negatively correlated with herbivore abundance ($y = e^{(-3.0765x + 6.694)}$, $P = 0.0025$, $R^2_{COR} = 0.140$). (d) Predator abundance is not correlated with herbivore abundance ($P = 0.236$). (e) Herbivore abundance is negatively correlated with kelp abundance ($y = e^{(-0.0422x + 1.7121)}$, $P = 0.0037$, $R^2_{COR} = 0.408$). Taken together, these patterns indicate a trophic cascade that increases in strength in more diverse predator assemblages, and that predator diversity better explains patterns in kelp abundance than predator abundance.

was negatively correlated with kelp abundance (Table 1c, Fig. 2e, $R^2_{\text{COR}} = 0.408$, d.f. = 14, deviance = 13.191), indicating that this may be a full community-level trophic cascade with more diverse assemblages reducing abundances of herbivores, and, in consequence, enhancing kelp abundance.

Effects of predator diversity manipulations on trophic cascade strength

Increasing predator richness positively affected the change in kelp mass, indicating decreased total kelp consumption by the herbivore assemblage in more diverse predator treatments (Fig. 3a, $F_{1,41} = 14.71$, $P = 0.0004$, $R^2 = 0.39$, $y = 42.21x - 126.05$) after accounting for initial kelp mass ($F_{1,41} = 5.23$, $P = 0.027$) and trial ($F_{2,41} = 14.7$, $P = 0.024$). This increase in top-down control occurred despite observations of interspecific agonism among predators (e.g. lost claws), suggesting that any negative effects of intraguild interactions were more than offset by other mechanisms in our experiment. While less kelp was consumed in three species treatments than in single species treatments ($F_{1,47} = 4.352$, $P = 0.042$), this effect was non-additive and greater than would have been predicted from the average monoculture. A *post-hoc* Tukey test reveals, however, that despite reducing the density of the two most effective predators, kelp loss in polycultures did not differ from monocultures of these species. However, as kelp loss was less in the predator polyculture than would have been anticipated based on the per capita reduction by each predator in monoculture we can conclude that non-transgressive overyielding was occurring.

Decreased consumption of kelp by herbivores was not driven by complementary consumption of herbivores by predators. Consumption of herbivores by predators did not differ between one and three predator species treatments (Fig. 3b, $F_{1,32} = 0.029$, $P = 0.866$) nor was it affected by trial ($F_{2,32} = 1.57$, $P = 0.225$) or an interaction between trial and diversity ($F_{2,32} = 1.104$, $P = 0.343$). Different predator treatments did experience varying levels of predation on different herbivores (MANOVA, $F_{15,61} = 4.11$, $P < 0.0001$, Fig. 3c). Predation did not differ across replicate trials (MANOVA: $F_{10,44} = 1.564$, $P = 0.150$) nor did trial and treatment interact ($F_{30,90} = 1.552$, $P = 0.058$). *Cancer productus* was the only predator to consume *Pugettia*, although it did so in only two monoculture replicates; *Pycnopodia* was the largest consumer of all herbivores other than *Pugettia*. This pattern suggests that *C. productus* and *Pycnopodia* may have somewhat complementary patterns of consumption, although the differences were not statistically significant. In addition, predation rates of *C. productus* on *Pugettia* were even lower in predator polycultures than in monoculture, and were not statistically different from 0.

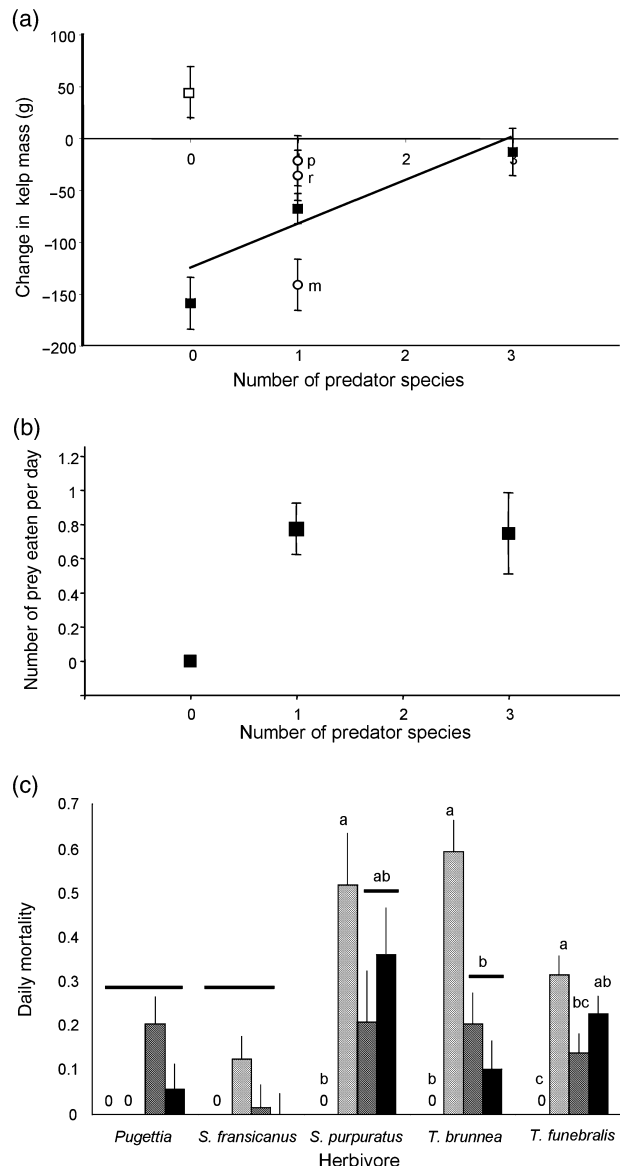


Figure 3 Predator diversity increases the strength of trophic cascades. Error bars represent 1 standard error. (a) Predator diversity plotted against change in kelp mass (growth – consumption) adjusted for initial mass. The correlation is positive ($y = 42.21x - 126.05$) and $R^2 = 0.39$ and significant ($P = 0.0004$). Closed squares are mean values for each level of predator diversity. Open circles are values for single predator treatments broken down by species (p = *Pycnopodia*, r = *C. productus*, m = *C. magister*). The open square is the no herbivore treatment (not included in statistical analysis). (b) Number of individuals consumed daily as a function of predator diversity excluding the no predator treatment. The 0 number of herbivores consumed from the no predator treatment is plotted for reference. Diversity had no effect on number of herbivores consumed. (c) Rate of mortality due to predation for individual herbivore species separated by treatment. Bars and letters indicate groupings that are not significantly different by Tukey's HSD drawn from univariate ANOVAs.

Thus, evidence for consumptive complementarity remained uncertain (Fig. 3c).

Effects of predator diversity on herbivore behaviour

Complementary effects of predators on herbivore feeding rates appear to explain the impact of predator diversity on cascade strength in our mesocosms. Total kelp consumption, summed over all herbivores, decreased with increasing predator richness in the behavioural cascade experiment ($F_{1,38} = 5.5318$, $P = 0.024$, $R^2 = 0.36$, Fig. 4a), with a clear difference between predator monocultures and the polyculture ($P = 0.03$). Predator polyculture treatments had, on average, about one-third less kelp consumed than even the best performing monoculture, indicating transgressive overyielding. This result indicates that predator diversity can enhance control of herbivory, and increase the strength of a trophic cascade, at least in the short-term, simply through behavioural reductions in herbivore feeding rates.

The effect of predator diversity on kelp biomass was driven by behavioural complementarity: while predators caused grazers to reduce feeding rates, no single predator species reduced grazing by all herbivore species. When all herbivore species are considered together, predators strongly reduce herbivore consumption of kelp (MANOVA: $F_{25,113} = 4.8729$, $P < 0.0001$). *Post-hoc* ANOVAS demonstrated that the diversity effect is driven by differential responses of *Strongylocentrotus purpuratus* and *Pugettia*, the two herbivores that consumed the most kelp in our experiments (Fig. 4b and Table S2). When *Pugettia* are confronted with chemical and physical cues from *C. productus*, either in monoculture or polyculture, they reduce their kelp consumption by 48% relative to no predator controls (Fig. 4b, Table 1). *Pycnopodia*, however, do not affect *Pugettia* grazing rates. In contrast, *S. purpuratus* reduce their kelp consumption by 78% in the presence of *Pycnopodia* (Fig. 4c), but their feeding rates are unaffected by the presence of predatory crabs. Only in the multi-predator treatments is feeding of both *Pugettia* and *S. purpuratus* simultaneously minimized.

Comparing the strength of cascades

Behavioural cascade strength was significantly less than that of the cascade due to both density and behaviour effects together, indicating that direct consumption of herbivores does play a role in the total trophic cascade, even though it did not contribute significantly to the diversity effect in our experiment (Fig. 5, *Pycnopodia*: $F_{1,16} = 12.2$, $P \leq 0.0003$; *C. productus*: $F_{1,14} = 23.3$, $P \leq 0.0003$; polyculture: $F_{1,20} = 10.9$, $P \leq 0.004$). In *Pycnopodia* treatments, behaviour accounted for 43.2% of the cascade. In *C. productus* treatments, it accounted for only 30.1% of the cascade. In

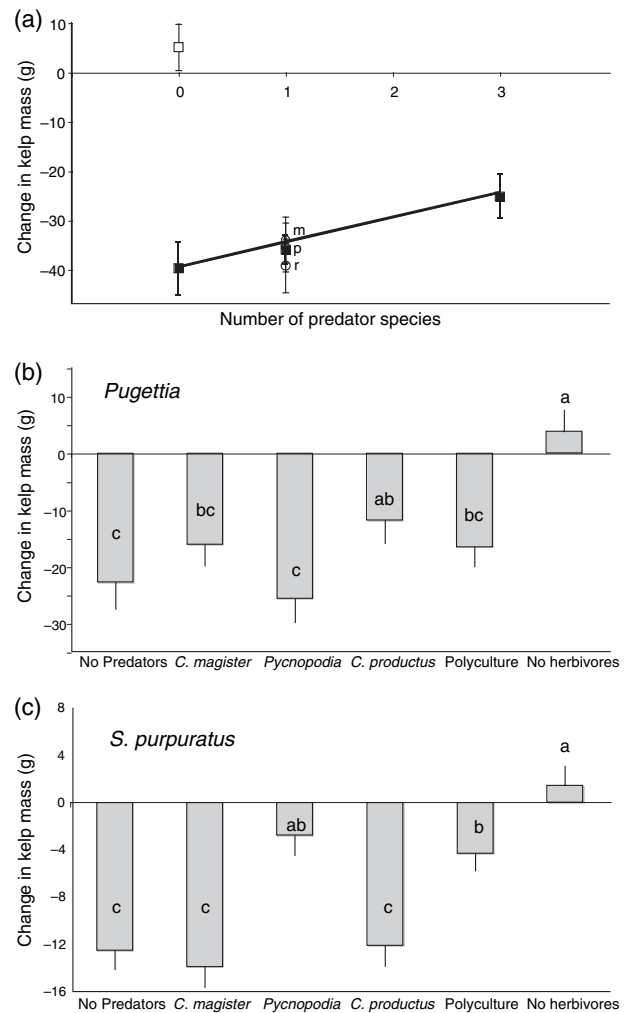


Figure 4 Predator diversity effects are largely due to differential behavioural responses of each herbivore to each predator. Error bars represent 1 standard error. (a) Predator diversity plotted against change in kelp mass (change in herbivore box – change in paired no herbivore control box) with consumption summed across all herbivores. Closed squares are values for the predator diversity treatments. Open circles are values for single predator treatments broken down by species (p = *Pycnopodia*, r = *C. productus*, m = *C. magister*). The open square is the no herbivore treatment. (b) Kelp consumption by the kelp crab *Pugettia producta* when exposed to physical and chemical cues from different predator treatments. Letters denote groups that are not significantly different by Tukey’s HSD. (c) Kelp consumption by the purple urchin *Strongylocentrotus purpuratus* when exposed to physical and chemical cues from different predator treatments. Letters denote groups that are not significantly different by Tukey’s HSD. Note that these two herbivores respond differently to cues from *Pycnopodia* and *Cancer productus*, indicating behavioural complementarity.

polycultures, however, behaviour accounted for 60.1% of the total cascade indicating that the contribution of behaviour to the mesocosm trophic cascade increases along

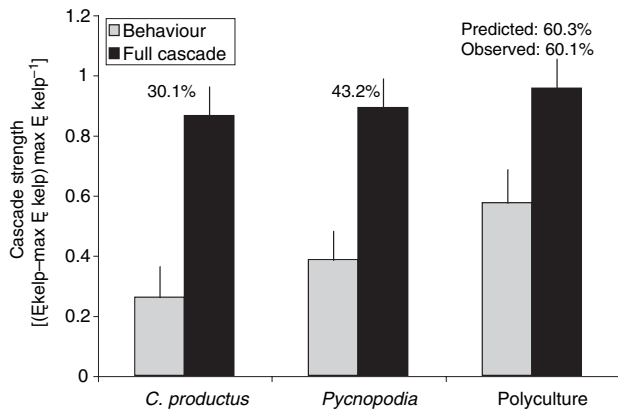


Figure 5 Strength of trophic cascade and behavioural cascade only plotted for treatments that expressed a strong trophic cascade. Each pair of values is significantly different by ANOVA indicating that behaviour accounts for only a fraction of the total effect of the trophic cascade. Values above data bars indicate the percentage of the trophic cascade that can be accounted for by the behavioural cascade. Note that the percentage of the cascade explainable by behaviour is greater in the high predator diversity treatments.

with diversity. This percentage is no different than the predicted combined value (see Methods) of 60.3%, indicating that predator density did not alter this behavioural effect. These results suggest that as diversity increases, the relative importance of the behavioural component of trophic cascades may also increase, potentially compensating for reduced consumption of herbivores by any single predator species.

DISCUSSION

Both patterns from the field and data from manipulative experiments in mesocosms suggest that predator diversity enhances the strength of trophic cascades in kelp forest food webs, leading to greater kelp biomass when predator diversity is high. The lack of a correlation between predator abundance and herbivore or kelp abundance (Fig. 2b,c) suggests that this trend is not simply driven by enhanced consumption of herbivores (and release of kelp from herbivory) at high predator abundances. Data from mesocosm experiments provide a potential mechanism consistent with this trend, as predators in our experiments had complementary effects on feeding rates of herbivores, although we cannot rule out complementary consumption over larger temporal and spatial scales. As kelps both serve as important habitat-providing foundation species and provide a significant energy source for much of the food web (Dayton 1985; Graham 2004), declining predator diversity may have significant consequences for kelp forest ecosystem structure and function.

The positive correlation between predator diversity and kelp density in the field could have either top-down or bottom-up explanations. While predator diversity may lead to a stronger trophic cascade, increasing kelp density may also provide habitat that increases predator diversity. Previous analyses of these data have suggested that differences among sites in the predator community are associated with fishing pressure as are differences in whether a site is characterized as a kelp forest or a barren (Behrens & Lafferty 2004; Lafferty 2004). These analyses suggest that extrinsic forces may affect predator diversity. Additionally, the lack of a correlation between predator abundance and kelp density weakens support for the bottom-up hypothesis. Top-down and bottom-up explanations of the field data are not mutually exclusive, however, and there may be a positive feedback between predator diversity and kelp abundance that may increase the stability of the system.

Mesocosms such as the ones used here allow rigorous manipulation of predator diversity, but do require some compromises, such as increased predator densities, and necessarily simplify nature. For logistical reasons, we could not include several potentially important predators (e.g. fishes), in our mesocosms. The field surveys, however, include these predators, suggesting that the mechanisms identified in mesocosms may operate for additional species in the field. Few diversity-ecosystem functioning studies combine both manipulative and observational approaches, and those that have are limited to basal trophic levels and decomposers (Tilman *et al.* 1996; Levine 2000; Stachowicz *et al.* 2002; Dangles & Malmqvist 2004). This combined approach may prove particularly useful when attempting to understand the ecosystem consequences of changing predator diversity, which is notoriously difficult to manipulate in the field.

Our mesocosm experiments, combined with previous studies, highlight several ways in which predator diversity may enhance the control of herbivore in kelp beds, maintaining a kelp-dominated ecosystem. First, diversity may provide redundancy to buffer the system from the loss of component species. The guild of invertebrate predators we used is likely redundant to keystone predators like sea otters (Estes *et al.* 1998). Our results suggest that this guild may become important for herbivore suppression in areas of California where otters are rare or locally extinct. Secondly, species within a guild can have complementary effects on herbivores such that the loss of any single predator species has an incremental, but significant, effect on maintaining kelp biomass. In our experiments, such effects occurred via complementary behavioural responses of herbivores to different predators (Fig. 4b,c). Additional behavioural mechanisms may operate in the field, such as refuge and alternate habitat use (Fortin *et al.* 2005; Grabowski &

Kimbrow 2005), emigration (Vadas *et al.* 1986), or synergistic effects of predators (Hixon & Carr 1997; Losey & Denno 1998). For example, we observed kelp crabs and snails escaping benthic predators by climbing kelp fronds, potentially making them more susceptible to fish predation in the field. Given the importance of behavioural cascades in a variety of systems and at multiple spatial and temporal scales (Trussell 2000; Peacor & Werner 2004; Schmitz *et al.* 2004; Preisser *et al.* 2005), behavioural mechanisms deserve serious consideration in any attempt to understand the functional consequences of predator diversity.

Previous studies have found that cascade strength is largely driven by the consumptive ability of only one of the predator species (Finke & Denno 2004; Aquilino *et al.* 2005). Importantly, both of these studies used a single species of herbivore, precluding the sort of complementarity (i.e. *Pycnopodia* affecting urchins and *C. productus* affecting kelp crabs) we describe here. As more herbivores are included, the dominant effects of individual predator species on particular herbivores can combine to create a complementary effect on the community-wide trophic cascade. Similarly, predator synergisms can depend on the presence of multiple herbivore species (Cardinale *et al.* 2003). Thus, we expect the consequences of predator diversity will be greatest when herbivore diversity is high, and that single predator effects will dominate when herbivore diversity is low. Clearly, a full understanding of the effects of changes in biodiversity must therefore consider diversity at multiple trophic levels (Gamfeldt *et al.* 2005; Ives *et al.* 2005).

Human activities have already reduced predator densities by an order of magnitude in some places, causing a variety of changes to marine ecosystems (Pauly *et al.* 1998; Jackson *et al.* 2001; Myers & Worm 2003). Our results argue that significant changes in community states may also result from changes in the diversity of the predator community, even if total predator abundance remains constant. In kelp forests, the loss of predator diversity can lead to reductions in kelp abundance, thereby reducing benefits derived from kelp forests such as fisheries, tourism, and reduced shoreline erosion (Leet *et al.* 2001). Given that declines in predator diversity and the presence of trophic cascades are common features of marine systems (Shurin *et al.* 2002; Stibor *et al.* 2004; Worm *et al.* 2005), such effects of declining predator diversity may be widespread.

ACKNOWLEDGEMENTS

Thanks to Ransom Myers, Oswald Schmitz, and three anonymous referees for providing helpful feedback. Amy Larson, Marie Nydam and Cameron Coates helped maintain the experiments. Adam Baukus, Michael O'Farrell, David Kimbro, and Jay Tustin aided in organism collection. We are indebted to Channel Islands National

Park's kelp forest monitoring program and David Kushner for their continued support in collecting long-term kelp forest monitoring data. Funding and/or space was provided by the National Science Foundation (Grant No. OCE 03-51778 and the IGERT program NSF-DGE No. 0114432), Bodega Marine Laboratory, and the UC Davis Center for Population Biology. C.S.T. was supported by an NIGMS MORE Institutional Research and Academic Career Development Award to UC Davis and San Francisco State University (see <http://prof.ucdavis.edu>), Grant No. K12GM00679.

REFERENCES

- Aquilino, K.M., Cardinale, B.J. & Ives, A.R. (2005). Reciprocal effects of host plant and natural enemy diversity on herbivore suppression: an empirical study of a model tritrophic system. *Oikos*, 108, 275–282.
- Behrens, M.D. & Lafferty, K.D. (2004). Effects of marine reserves and urchin disease on southern Californian rocky reef communities. *Mar. Ecol. Prog. Ser.*, 279, 129–139.
- Cameron, A.C. & Windmeijer, F.A.G. (1996). R-Squared measures for count data regression models with applications to health-care utilization. *J. Bus. Econ. Stat.*, 14, 209–220.
- Cardinale, B.J., Harvey, C.T., Gross, K. & Ives, A.R. (2003). Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. *Ecol. Lett.*, 6, 857–865.
- Dangles, O. & Malmqvist, B. (2004). Species richness-decomposition relationships depend on species dominance. *Ecol. Lett.*, 7, 395–402.
- Davis, G.E., Kushner, D.J., Mondragon, J.M., Mondragon, J.E., Lema, D. & Richards, D.V. (1997). *Kelp Forest Monitoring Handbook. Volume 1: Sampling Protocol*. National Park Service, Channel Islands National Park, Ventura, CA.
- Dayton, P.K. (1985). Ecology of kelp communities. In: *Annual Review of Ecology and Systematics*, Vol. 16 (ed. Johnston, R.F.). Annual Reviews Inc., Palo Alto, CA, USA, pp. 215–245.
- Dill, L.M., Heithaus, M.R. & Walters, C.J. (2003). Behaviorally mediated indirect interactions in marine communities and their conservation implications. *Ecology*, 84, 1151–1157.
- Duffy, J.E. (2002). Biodiversity and ecosystem function: the consumer connection. *Oikos*, 99, 201–219.
- Duffy, J.E. (2003). Biodiversity loss, trophic skew and ecosystem functioning. *Ecol. Lett.*, 6, 680–687.
- Duffy, J.E., Richardson, J.P. & Canuel, E.A. (2003). Grazer diversity effects on ecosystem functioning in seagrass beds. *Ecol. Lett.*, 6, 637–645.
- Duffy, J.E., Richardson, J.P. & France, K.E. (2005). Ecosystem consequences of diversity depend on food chain length in estuarine vegetation. *Ecol. Lett.*, 8, 301–309.
- Estes, J.A., Tinker, M.T., Williams, T.M. & Doak, D.F. (1998). Killer whale predation on sea otters linking oceanic and near-shore ecosystems. *Science*, 282, 473–476.
- Finke, D.L. & Denno, R.F. (2004). Predator diversity dampens trophic cascades. *Nature*, 429, 407–410.
- Fortin D., Beyer H.L., Boyce M.S., Smith D.W., Duchesne T. & Mao J.S. (2005). Wolves influence elk movements: behavior

- shapes a trophic cascade in Yellowstone National Park. *Ecology*, 86, 1320–1330.
- Foster, M.S. & Schiel, D.R. (1985). *The Ecology of Giant Kelp Forests in California: a Community Profile*. U.S. Fish Wildl. Serv. Biol. Rep. 85(7.2).
- Gamfeldt, L., Hillebrand, H. & Jonsson, P.R. (2005). Species richness changes across two trophic levels simultaneously affect prey and consumer biomass. *Ecol. Lett.*, 8, 696–703.
- Gotshall, D.W. (1977). Stomach contents of northern California Dungeness crabs *Cancer magister*. *Calif. Fish Game*, 63, 43–51.
- Grabowski, J.H. & Kimbro, D.L. (2005). Predator-avoidance behavior extends trophic cascades to refuge habitats. *Ecology*, 86, 1312–1319.
- Graham, M.H. (2004). Effects of local deforestation on the diversity and structure of Southern California giant kelp forest food webs. *Ecosystems*, 7, 341–357.
- Halaj, J. & Wise, D.H. (2001). Terrestrial trophic cascades: how much do they trickle? *Am. Nat.*, 157, 262–281.
- Halpern, B.S. & Warner, R.R. (2002). Marine reserves have rapid and lasting effects. *Ecol. Lett.*, 5, 361–366.
- Hamilton, I.M. & Heithaus, M.R. (2001). The effects of temporal variation in predation risk on anti-predator behaviour: an empirical test using marine snails. *Proc. R. Soc. Lond. B Biol. Sci.*, 268, 2585–2588.
- Hixon, M.A. & Carr, M.H. (1997). Synergistic predation, density dependence, and population regulation in marine fish. *Science*, 277, 946–949.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S. et al. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.*, 75, 3–35.
- Huston, M.A. (1997). Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, 110, 449–460.
- Ives, A.R., Cardinale, B.J. & Snyder, W.E. (2005). A synthesis of subdisciplines: predator-prey interactions, and biodiversity and ecosystem functioning. *Ecol. Lett.*, 8, 102–116.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J. et al. (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293, 629–638.
- Lafferty, K.D. (2004). Fishing for lobsters indirectly increases epidemics in sea urchins. *Ecol. Appl.*, 14, 1566–1573.
- Leet, W.S., Dewees, C.M., Klingbeil, R. & Johnson, E.J. (2001). *California's Living Marine Resources: a Status Report*. State of California Resources Agency and Fish and Game, Sacramento.
- Leibold, M.A. (1996). A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *Am. Nat.*, 147, 784–812.
- Levine, J.M. (2000). Species diversity and biological invasions: relating local process to community pattern. *Science*, 288, 852–854.
- Loreau, M. (2004). Does functional redundancy exist? *Oikos*, 104, 606–611.
- Loreau, M. & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412, 72–76.
- Loosey, J.E. & Denno, R.F. (1998). Positive predator–predator interactions: enhanced predation rates and synergistic suppression of aphid populations. *Ecology*, 79, 2143–2152.
- Mauzey, K.P., Birkeland, C. & Dayton, P.K. (1968). Feeding behavior of asteroids and escape responses of their prey in the puget sound region sea-pen holothurians clams anemones nudibranchs prey sea-urchins. *Ecology*, 49, 603–619.
- Micheli, F. & Halpern, B.S. (2005). Low functional redundancy in coastal marine assemblages. *Ecol. Lett.*, 8, 391–400.
- Mouillot, D. & Lepretre, A. (1999). A comparison of species diversity estimators. *Res. Popul. Ecol.*, 41, 203–215.
- Myers, R.A. & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature*, 423, 280–283.
- Paine, R.T. (1966). Food web complexity and species diversity. *Am. Nat.*, 100, 65–76.
- Paine, R.T. (2002). Trophic control of production in a rocky intertidal community. *Science*, 296, 736–739.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, F. (1998). Fishing down marine food webs. *Science*, 279, 860–863.
- Peacor, S.D. & Werner, E.E. (2001). The contribution of trait-mediated indirect effects to the net effects of a predator. *Proc. Natl. Acad. Sci. U. S. A.*, 98, 3904–3908.
- Peacor, S.D. & Werner, E.E. (2004). How dependent are species-pair interaction strengths on other species in the food web? *Ecology*, 85, 2754–2763.
- Polis, G.A. & Strong, D.R. (1996). Food web complexity and community dynamics. *Am. Nat.*, 147, 813–846.
- Preisser, E.L., Bolnick, D.I. & Benard, M.F. (2005). Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology*, 85, 501–509.
- Raffaelli, D. (2004). How extinction patterns affect ecosystems. *Science*, 306, 1141–1142.
- Schmitz, O.J. (2003). Top predator control of plant biodiversity and productivity in an old-field ecosystem. *Ecol. Lett.*, 6, 156–163.
- Schmitz, O.J., Krivan, V. & Ovadia, O. (2004). Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol. Lett.*, 7, 153–163.
- Shurin, J.B., Borer, E.T., Seabloom, E.W., Anderson, K., Blanchette, C.A., Broitman, B. et al. (2002). A cross-ecosystem comparison of the strength of trophic cascades. *Ecol. Lett.*, 5, 785–791.
- Siddon, C.E. & Witman, J.D. (2004). Behavioral indirect interactions: multiple predator effects and prey switching in the rocky subtidal. *Ecology*, 85, 2938–2945.
- Sih, A. (1980). Optimal behavior can foragers balance 2 conflicting demands. *Science (Washington DC)*, 210, 1041–1043.
- Sih, A., Englund, G. & Wooster, D. (1998). Emergent impacts of multiple predators on prey. *Trends Ecol. Evol.*, 13, 350–355.
- Simenstad, C.A., Estes, J.A. & Kenyon, K.W. (1978). Aleuts, sea otters, and alternate stable-state communities. *Science*, 200, 403–411.
- Stachowicz, J.J., Fried, H., Osman, R.W. & Whitlatch, R.B. (2002). Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. *Ecology*, 83, 2575–2590.
- Steiner, C.F. (2001). The effects of prey heterogeneity and consumer identity on the limitation of trophic-level biomass. *Ecology*, 82, 2495–2506.
- Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A. et al. (2002). Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ. Conserv.*, 29, 436–459.
- Stibor, H., Vadstein, O., Diehl, S., Gelzleichter, A., Hansen, T., Hantzsche, F. et al. (2004). Copepods act as a switch between

- alternative trophic cascades in marine pelagic food webs. *Ecol. Lett.*, 7, 321–328.
- Tegner, M.J. & Dayton, P.K. (2000). Ecosystem effects of fishing in kelp forest communities. *ICES J. Mar. Sci.*, 57, 579–589.
- Tilman, D., Wedin, D. & Knops, J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, 379, 718–720.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science*, 277, 1300–1302.
- Trussell, G.C. (2000). Predator-induced plasticity and morphological trade-offs in latitudinally separated populations of *Littorina obtusata*. *Evol. Ecol. Res.*, 2, 803–822.
- Trussell, G.C., Ewanchuk, P.J. & Bertness, M.D. (2003). Trait-mediated effects in rocky intertidal food chains: predator risk cues alter prey feeding rates.
- Vadas, R.L., Elner, R.W., Garwood, P.E. & Babb, I.G. (1986). Experimental evaluation of aggregation behavior in the sea urchin *Strongylocentrotus-Droebachiensis* – a reinterpretation. *Mar. Biol.*, 90, 433–448.
- Worm, B., Sandow, M., Oschlies, A., Lotze, H.K. & Myers, R.A. (2005). Global patterns of predator diversity in the open oceans. *Science*, 309, 1365–1369.
- Zimmer-Faust, R.K. & Case, J.F. (1982). Organization of food search in the kelp crab, *Pugettia producta* (Randall). *J. Exp. Mar. Biol. Ecol.*, 57, 237.

SUPPLEMENTARY MATERIAL

The following supplementary material is available online for this article from <http://www.Blackwell-Synergy.com>:

Appendix S1 National Park Service Channel Islands Kelp Forest Monitoring Survey Methods.

Table S1 Species list from NPS Channel Islands Kelp Forest Monitoring Survey.

Table S2 ANCOVA table from behavioural experiment.

Editor, Ransom Myers

Manuscript received 11 July 2005

First decision made 22 August 2005

Manuscript accepted 9 September 2005