

Multiple predator effects in an intertidal food web

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Summary

1. We examined the effects of multiple predators from an intertidal boulder food web to test whether and how three different predator species affected the survival of a small amphipod species.
2. Predators were chosen because they differ in their foraging mode, two feeding at the bottom and in benthic refuges (nemertean and shrimp) and one in the water-column (juveniles of a fish).
3. Mortality of amphipods was not affected by nemerteans, but was high in the presence of shrimp or fish. Highest mortalities were observed in predator-combinations that contained both shrimp and fish. Amphipods responded to shrimp by escaping into the water column, while they avoided fish by remaining in the refuge. We conclude that predator-specific defence causes conflicts for prey when both shrimp and fish are present.
4. Comparing observed effects of multiple predators with expected effects revealed risk enhancement for the shrimp + fish combination. A comparison of different predictive models revealed that the multiplicative model was most appropriate, although additive models may work well under certain conditions.
5. Based on known consumption-ranges of the predators used, we conclude that nemerteans were saturated with prey while fish were far from their saturation point. A predator's functional response curve (prey consumption in relation to prey abundance) determines its impact on prey populations. This knowledge appears essential in order to predict whether prey organisms face risk enhancement, risk reduction or additive effects of multiple predators.

Key-words: amphipods, emergent effects, predation, predator-specific responses, risk enhancement.

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Introduction

A growing body of evidence demonstrates that animals exhibit behavioural plasticity that may reduce their exposure to predators (e.g. Lima & Dill 1990; Lima 1998a). Such behavioural plasticity has the benefit of reducing the risk of predation but it also carries costs (reviewed by Lima 1998b) such as reduced time for feeding (e.g. Kohler & McPeck 1989; Willman, Hill & Lodge 1994) or missed reproductive opportunities (e.g. Forsgren 1992; Sih & Krupa 1992; Arthur, Pech & Dickman 2004).

Although it is well known that most prey live with a suite of functionally different predators, the majority of experimental studies dealing with predator–prey interactions have focused on the effect of single or functionally

similar predator species on prey organisms. However, several recent studies have yielded insight into effects of multiple predators on prey (reviewed by Sih, Englund & Wooster 1998). These authors defined a multiple predator effect (MPE) as one where the combined effects of predators differ from the sum of individual predator effects.

If prey densities are high, multiple predators may have a relatively weak impact on prey populations. Under such conditions their combined effects may converge on an additive model (Soluk 1993). The study of MPEs, however, reveals that in many situations the combined effects of multiple predators are not linear (Nyström *et al.* 2001). Comparing observed impacts of multiple predators to their expected impacts may identify such non-linear MPEs. Discrepancies between expected and observed MPEs are generated mainly by three distinct phenomena: (a) predator–predator interactions such as mutual interference (Hurd & Eisenberg 1990; Wissinger 1992; Siddon & Witman 2004) or intraguild predation (Lucas, Coderre & Brodeur 1998;

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Huhta *et al.* 1999; Finke & Denno 2002); (b) a general increase in antipredator behaviour (i.e. non-specific prey responses) with increasing predator densities (Abrams 1993); and (c) conflicting predator-specific prey behaviour (Losey & Denno 1998; Stapley 2004; Templeton & Shriner 2004), which may result from exposure to functionally different predators. The effects of multiple predators causing the two first phenomena may result in prey experiencing risk reduction, while the latter may result in risk enhancement.

McIntosh & Peckarsky (1999) predicted that prey have a range of different behavioural responses to multiple predators, and that these predictions need to be tested in a wide range of predator–prey systems. So far, few studies of MPEs have been conducted with marine species (but see Martin, Wright & Crowder 1989; Wootton 1994; Crowder, Squires & Rice 1997; Hixon & Carr 1997). Due to the ubiquity and abundance of functionally different predators in marine ecosystems, MPEs can be expected to be a common feature of these systems (e.g. Siddon & Witman 2004). Among the preferred prey organisms in intertidal food webs are amphipods, which are common prey for predators such as shorebirds, fish, crustaceans, polychaetes, nemerteans and sea anemones (e.g. Reise 1985; Emmerson & Raffaelli 2004).

One of the most important prerequisites in order to reveal MPEs is keeping the total predator density constant throughout the experiment (Sih *et al.* 1998). An increase in predator density may lead to increased consumption of prey, not necessarily as a result of an emergent MPE (i.e. risk enhancement) but rather as a result of more predators consuming more prey in total. Here we tested whether and how three different predators affected survival of an intertidal amphipod while keeping the total predator density constant. A fish, a shrimp and a nemertean were chosen for their differences in foraging mode and tested if combined MPEs were additive or non-additive. We predicted expected MPEs using both the additive model (e.g. Hixon & Carr 1997) and the multiplicative model (e.g. Soluk 1993; Eklöv & VanKooten 2001), and their adjusted versions (adjusting for densities of each predator species) since the conclusion of the existence of emergent MPEs may depend on which model is applied to predict combined predator effects.

Materials and methods

STUDY ORGANISMS

Four species, three predators and one prey species, were used in the experiment. All organisms were collected from the intertidal zone of La Pampilla (29°57' S; 71°21' W), Coquimbo, Northern Chile, during the austral spring (November 2001). Predators consisted of the nemertean *Amphiporus nelsoni*, the shrimp *Betaeus truncatus* and juveniles of the fish *Girella laevis*, and they were chosen because they differ in foraging

mode; two of them feeding at the bottom and in benthic refuges (nemertean and shrimp) and one of them in the water-column (juvenile fish). Nemerteans live in the mid intertidal zone and are often found highly aggregated (Thiel, Ullrich & Vásquez 2001), reaching densities of > 25 individuals per 100 cm² (personal observations). Shrimp are found in the mid- to lower intertidal zone and often live in dense aggregations (50 individuals per m²) under boulders cohabiting with porcellanids and juveniles of brachyuran crabs (personal observations). Juvenile fish *G. laevis* inhabit the shallow subtidal–mid-intertidal zone, mainly in tide pools (Varas & Ojeda 1990; Pulgar, Bozinovic & Ojeda 1999; Berrios & Vargas 2000). Being among the most abundant intertidal fish species they can reach very high densities of 20–25 individuals per m² (personal observations). The size of the fish individuals used in the experiment measured between 3 and 4 cm. The distribution of predator species is overlapping and they are potentially able to encounter the prey simultaneously. The amphipod *Hyale maroubrae*, which was used as prey in the experiment, lives in close association with red algae growing on boulder substrata (Lancellotti & Trucco 1993). They exhibit a patchy distribution, and reach densities of > 100 individuals per 100 cm² in the intertidal zone (Lancellotti & Trucco 1993). Due to their small size (approx. 5 mm body length) the risk of crowding around the experimental refuge (see below) was low.

Animals were kept in the laboratory for a minimum of 3 days and a maximum of 5 days before being used in the experiment. Amphipods and shrimp were maintained in aquaria with a continuous air-supply, and filtered seawater was changed daily. Fish were kept in a tank with constant flow of seawater, while nemerteans were kept in containers and had the water changed daily. All predators were food deprived for 3 days before being used in the experiment.

EXPERIMENTAL DESIGN

The experiments were conducted during the austral summer (November and December 2001) in containers with constant water flow pumped and filtered from Bahía La Herradura, Coquimbo. The containers had a bottom area of 17 cm × 27 cm (= 459 cm²) and a water level of 8 cm. The water exit consisted of a plastic tube allowing prey but not shrimp or fish to emigrate. Outside, and next to the container, a trap was placed to catch emigrants. The trap consisted of a plastic cup with a slit covered by fine mesh, which let water pass but trapped emigrating amphipods. Traps were checked once every hour because nemerteans could potentially emigrate through the plastic tube. An empty gastropod shell of *Calyptreaa radians* (diameter of 7–8 cm) was placed in the containers to serve as refuge for the amphipods. Only complete shells were used, that allowed nemerteans and shrimp but not fish to enter.

The experiment consisted of eight different treatments including the control, monospecific and multispecific

predator treatments. All treatments had an initial predator density of six and an initial prey density of 50. Total predator density (i.e. the sum of predator individuals) was constant throughout the treatments as required to verify if emergent MPEs exist. The assignment of treatments to a container was randomized, and each treatment was replicated six times.

In all treatments, in order to allow prey to acclimatize, amphipods were introduced 30 min before the predators. In multispecific predator treatments, the predators were introduced in the following order: first nemerteans, then 5 min later the shrimp, and subsequently the fish. All organisms were used only once, and predators were released immediately after being used. Each replicate lasted 8 h and at the end, emigrants, survivors in the refuge and survivors outside the refuge were preserved in 4% formalin for later quantification. Missing amphipods were considered consumed prey and their numbers used to estimate mortality. Because mortality in the controls was close to zero (mean mortality: 0.013), no adjustments of mortality for experimental artefacts were necessary.

All predators survived the experiment. Occasionally a nemertean was missing, which is most probably a result of emigration from the container. Nemerteans were found in the trap (one case) or crawling on the upper edge of the containers (several cases). We made no observations suggestive of intraguild predation between predators, and it is well known that most other predators do not prey on nemerteans (McDermott 2001).

PREDICTION OF COMBINED EFFECTS

We used two different models and their adjusted versions to predict the combined effects of multiple predators on prey mortality based on the results from monospecific predator treatments (see, e.g. Sih *et al.* 1998). Because our experimental design was randomized, we calculated the expected values using the respective replicates from the monospecific treatments.

The additive model

The additive model assumes linear, independent effects of multiple predators on prey mortality: $p_a + p_b$

The multiplicative model

The multiplicative model assumes dependent effects between predators (i.e. prey cannot be consumed twice):

$$p_a + p_b - p_a p_b$$

Prey mortality when exposed to predator *a* alone is p_a , and when exposed to predator *b* alone, p_b .

The adjusted models

The adjusted models assume linear predator-density effect on prey mortality (i.e. six fish consume twice as

much prey as three fish). As predator density is always constant ($n = 6$), prey mortality due to predator *a* when adjusted would be: $p_{a(adj)} = 1/x p_a$, where x is the number of combined predator species in the treatment. The adjusted additive and multiplicative model can be calculated by substituting p_a with $p_{a(adj)}$ and p_b with $p_{b(adj)}$ in the respective models. Single species effects are averaged.

STATISTICAL ANALYSIS

Data were arcsine-transformed to meet the assumptions of parametric tests. The effects of monospecific and multispecific predators on amphipod mortality and survival were analysed using a one-way ANOVA. Subsequently, Tukey's test was applied for multiple comparisons. For each treatment with multiple predators, a one-way ANOVA was applied to test for differences between observed combined effects and expected combined effects of all four models. Using observed effects as the control, a two-sided Dunnett test was used for each multiple predator treatment. This allowed us to analyse whether observed effects differed significantly from expected effects for each model.

Results

OBSERVED PREDATOR EFFECTS

Predators (with the exception of the nemerteans) caused significant mortality and increased emigration rates of amphipods (Fig. 1). There were highly significant differences in mortality between treatments ($F = 77.57$, d.f. = 7, $P < 0.001$). Both shrimp alone and fish alone had significant negative effects on amphipod survival rate (Tukey, $P < 0.001$), while nemerteans alone had no significant impact on amphipod survival rate (Tukey, $P = 0.995$, Fig. 1a). The combination of shrimp + fish (sf) left significantly fewer surviving amphipods than any single predator treatment (Tukey, $P < 0.001$). The emigration rate was significantly different among treatments ($F = 43.40$, d.f. = 7, $P < 0.001$). In the presence of shrimp, but in the absence of fish, amphipods exhibited a significantly higher rate of emigration than in the rest of the treatments (Tukey, $P < 0.001$, Fig. 1b). There were significantly more prey individuals surviving in the refuge in the presence of fish alone than in the presence of shrimp alone (Tukey, $P < 0.05$, Fig. 1c). Amphipod survival in the refuge when exposed to nemerteans was identical to the control (Tukey, $P = 1.000$). In general, few survivors were found in the container outside of the refuge (Fig. 1d).

EXPECTED VS. OBSERVED PREDATOR EFFECTS

The differences between the observed effects and expected effects (predicted by the four models) were highly significant for all treatments [$F = 17.84$ (ns), $F = 14.57$ (nf), $F = 41.86$ (sf), $F = 31.79$ (nsf), d.f. = 3, $P < 0.001$]. Observed values were always smaller than those

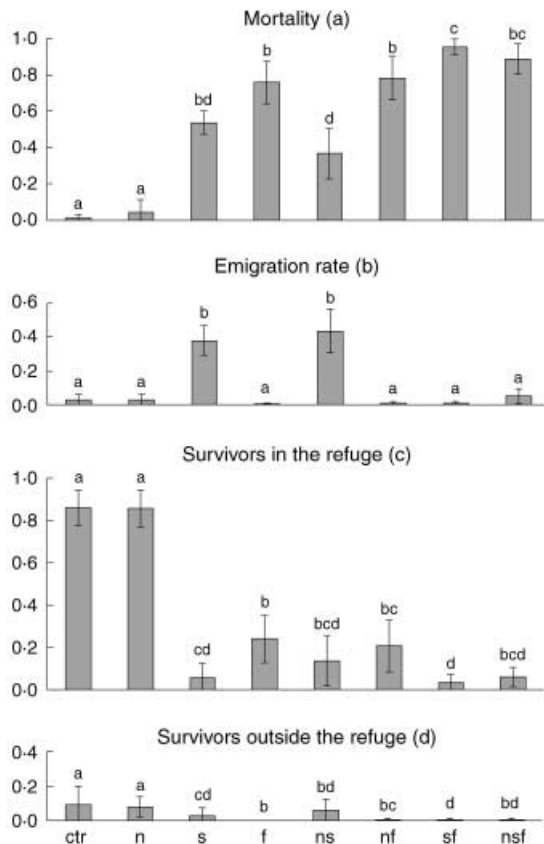


Fig. 1. (a) Amphipod mortality; (b) emigration rate; (c) survival rate in refuge; and (d) survival rate outside the refuge (mean proportions \pm SD); same letters indicate no significant differences among treatments; treatments were controls (ctr) without predators, single-predator treatments with nemerteans (n), shrimp (s), fish (f) and the respective combined predator treatments; $n = 6$ replicates of each treatment; see text for further explanations.

predicted by the additive model, while they were often substantially higher than those predicted by the adjusted versions of the models (Table 1). When compared to values predicted by the multiplicative model, the observed values were smaller in one treatment, larger in another treatment, and in two treatments did not differ from the predicted values.

Observed effects of nemerteans + shrimp (ns) were not significantly different from expected effects as predicted by the adjusted versions of the models (Dunnett, $P = 0.35$ for adjusted additive model, $P = 0.29$ for adjusted multiplicative model). However, in this treatment observed values were significantly smaller than those predicted by the multiplicative and the additive model (Dunnett, $P < 0.005$). When nemerteans and fish were together (nf), observed values did not differ from those predicted by the multiplicative and the additive model (Dunnett, $P = 0.999$ and $P = 0.881$, respectively), but were significantly larger than those predicted by the adjusted versions (Dunnett, $P < 0.001$). In the shrimp + fish (sf) treatment, the additive model overestimated the expected effects to impossible proportions (i.e. mortality rate higher than 1.0). For all three remaining models the observed mortalities were significantly higher than the expected values (Dunnett, $P < 0.05$). Similar results were found for the three-predator treatment, nemerteans + shrimp + fish (nsf), with the exception that there was no significant difference between observed and expected effects according to the multiplicative model (Dunnett, $P = 0.969$).

Discussion

Due to the ubiquity of intraguild predation in complex food webs, prey risk reduction is the most commonly reported consequence of MPEs (Sih *et al.* 1998). However, in our study there was no indication of intraguild predation and we found strong indication for prey risk enhancement in treatments where shrimp and fish predators preyed simultaneously upon the amphipods. Together with other studies, our study confirms that amphipods exhibit complex antipredator behaviour (Wudkevich *et al.* 1997; Wisenden, Cline & Sparkes 1999; Åbjörnsson *et al.* 2000).

PREY RESPONSES TO SINGLE PREDATORS

In the present study, amphipods showed predator-specific responses, as has also been demonstrated in other studies with single predators (Thiel 1999; Åbjörnsson

Table 1. Comparisons of observed to expected effects according to different models. Data are expressed as proportions of consumed amphipods (mean \pm means in brackets demonstrate how the additive model overestimates expected combined effects to impossible proportions; bold numbers represent significant differences between observed and model values; treatments were controls (ctr) without predators, single-predator treatments with nemerteans (n), shrimp (s), fish (f) and the respective combined predator treatments; $n = 6$ replicates of each treatment; see text for further explanations

Treatments	Observed mean \pm SD	Multiplicative model mean \pm SD	Adjusted multiple model mean \pm SD	Additive model mean \pm SD	Adjusted additive model mean \pm SD
ctr	0.01 \pm 0.02				
n	0.04 \pm 0.07				
s	0.54 \pm 0.06				
f	0.76 \pm 0.12				
ns	0.37 \pm 0.14	< 0.56 \pm 0.07	0.28 \pm 0.04	< 0.58 \pm 0.08	0.29 \pm 0.04
nf	0.78 \pm 0.12	0.77 \pm 0.12	> 0.39 \pm 0.07	0.80 \pm 0.15	> 0.40 \pm 0.08
sf	0.95 \pm 0.04	> 0.88 \pm 0.07	> 0.54 \pm 0.06	(1.29 \pm 0.17)	> 0.65 \pm 0.09
nsf	0.89 \pm 0.09	0.89 \pm 0.07	> 0.39 \pm 0.05	(1.34 \pm 0.20)	> 0.45 \pm 0.07

et al. 2000). Amphipods exhibited a strong escape response to nearby shrimp, contrasting strongly with their behaviour towards fish feeding on nearby conspecifics, which elicited no escape response (personal observations). In the presence of fish, most amphipods survived in the shell refuge, suggesting that amphipods showed increased hiding behaviour. Amphipod behaviour towards fish in our study is similar to that found in the amphipod *Gammarus lacustris*, which responds to chemical stimuli from pike (*Esox lucius*) by reducing activity in the water column and assuming a more demersal lifestyle (Wudkevich *et al.* 1997).

Our study confirms that amphipods are able to escape from benthic predators, as has been shown in previous studies (Ambrose 1984a; Thiel 1999). However, in our experiments, nemerteans did not elicit any specific escape response or any other avoidance behaviour in the amphipods. Possibly, in the wave-exposed environment inhabited by the amphipod *Hyale maroubrae*, nemerteans prefer to forage at low tide (Thiel *et al.* 2001). Because our experiment was conducted under continuous water coverage, nemerteans may not have represented a real threat to the amphipods.

CONFLICTING RESPONSES OF PREY TO MULTIPLE PREDATORS

The predator-specific responses shown by amphipods in our experiments caused conflicts when amphipods were exposed to multiple predators. For example, the specific response towards benthic predators (escape into the water column) made amphipods much more susceptible to water-column predators. Conflicting predator-specific prey responses have also been reported in other predator-prey systems. Soluk (1993) reported that mayfly larvae faced conflicting predator-specific responses when exposed to both fish (sculpin) and invertebrate predators (stonefly larvae). The presence of the stonefly larvae caused the mayfly larvae to move from the underside of the stones, making it more conspicuous to sculpins. Eklöv & VanKooten (2001) also observed conflicting responses in roach, which prefer open waters when exposed to pike but switch preference to more vegetated habitats in the presence of perch. In the presence of both predators, roach were not able to balance their habitat preference optimally.

EXPECTED VS. OBSERVED MULTIPLE PREDATOR EFFECTS

The impact of multiple predators cannot, in most situations, be predicted from simple assumptions of additive effects (Sih *et al.* 1998; Eklöv & VanKooten 2001; but see Hixon & Carr 1997; Schmitz & Sokol-Hessner 2002). Both predator-predator interactions and antipredator behaviour of prey will contribute to non-additive effects of multiple predators. However, substitutable effects (i.e. different predators exerting equal predation risk alone and together) between predators may overrule factors

that would normally result in non-linear MPEs (e.g. Sokol-Hessner & Schmitz 2002).

Comparing observed with predicted effects reveals the possible existence of emergent MPEs. Interpretation of the observed effects of multiple predators depends upon the model used to calculate expected effects. In general, using predictive models, one may commit two types of error: (a) predicting an MPE when there is none, and (b) not detecting an MPE when there is one. In the following we will briefly evaluate the four different models in the context of emerging MPEs.

Risk enhancement

According to the multiplicative model, the adjusted multiplicative model and the adjusted additive model, amphipods experienced risk enhancement when facing shrimp + fish (sf). This seems highly likely, given the observations on conflicting predator-specific prey responses. Large differences between observed and expected values suggest that the adjusted versions underestimated combined effects, which is probably a result of shrimp and fish not being saturated at prey densities used to estimate combined effects.

Risk reduction

The multiplicative and the additive models suggested the existence of prey risk reduction when exposed to nemerteans and shrimp. This also suggests the existence of mutual interference between the two predators, but we neither observed intraguild predation nor indirect effects between predators. Thus, we consider it most likely that the numerical reduction of shrimp in the combined-predator treatment (half the single-predator treatment) could not be compensated by higher predation rates of either predator thereby leading to overestimates of prey mortality in both models.

In general, it can be concluded that all models have advantages and drawbacks. Given that the additive model often leads to unrealistic values and that the adjusted models may seriously underestimate prey mortality, it can be concluded that the multiplicative model is most appropriate under the conditions of the system studied. It is likely that an increasing number of predator species (especially if differing in foraging mode) may converge on a multiplicative model because predation rates may become increasingly dependent on each other. Nevertheless, the multiplicative model may also have defects, as it appears to overestimate the expected combined effects of predators occasionally. The risk of committing errors in predicting or failing to predict MPEs may also depend on the particular situation and on the prey-predator ratios employed in experiments or encountered in a natural situation. In nature, the prey-predator ratio may be highly variable, both seasonally and spatially. For this reason a wide range of prey-predator ratios should be included in experiments to improve accuracy in prediction of MPEs and ensure further that

the results have relevance with respect to the natural environment.

PREDATION RATES AND MULTIPLE PREDATOR EFFECTS

Since Solomon (1949) introduced functional response curves (i.e. how individual predator consumption rate is related to prey densities), a wealth of studies has been conducted to test and confirm the applicability and theory behind them (e.g. Holling 1959, 1965; Abrams, Hill & Elmgren 1990; Seitz *et al.* 2001). Predators differ in their saturation points and consequently in their impact on prey, depending on both predator-prey size ratios (Aljetlawi, Sparrevik & Leonardsson 2004) and abundance ratios (Schenk, Bersier & Bacher 2005).

Keeping the total number of predators constant may facilitate calculation of expected values, but because different predators consume prey at different rates this may do little to improve accuracy of estimated prey consumption. We introduce a conceptual model (Fig. 2) in an attempt to address these problems and highlight important pitfalls in predicting MPEs. The comparison of functional response curves of the respective predators illustrates how potential consumption rate per predator is a function of both prey and predator densities and, thus, dependent on the prey-predator ratio (PPR).

In the present experiment we used three predators that differ not only in the way they pursue prey but also in their potential predation rates. The nemertean *Amphiporus nelsoni*, as indicated in Fig. 2 is likely to be well saturated in our experiment (Thiel *et al.* 2001). In contrast, juvenile *Girella laevis* (Varas & Ojeda

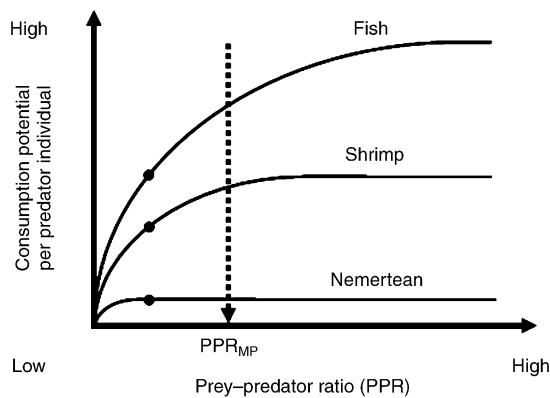


Fig. 2. The prey-predator ratio (PPR) is an important component of a predator's functional response curve. As indicated by their respective curves, our predators differ in their functional response to the amphipod, and thus have different saturation levels. The dashed line indicates where the predators in our study may be located on their respective functional response curve when combined all together (PPR_{MP}) while the single dots indicate where they would be in single-predator treatments, illustrating that predators may be at different points of their functional response curve in multispecific and monospecific predator treatments, respectively; the shift of a predator species on its functional response curve corresponds to the numerical reduction of the respective predator species in the combined treatments.

1990) or other juvenile fish (Gonzalez & Downing 1999) can easily consume several amphipods per hour, indicating that in our experiments the fish are far from saturated. Also shrimp can reach consumption rates of several amphipods day^{-1} (Thiel 1999), but their saturation point is most probably lower than that of fish (see also Corona, Soto & Sánchez 2000). Hence, the three predator species in our experiments were at different parts of their functional response curves, which may have influenced the accuracy in predicting MPEs. Combining different predator species in treatments (while keeping total number of predators constant) results in a reduction of the number of individuals per predator species, and thereby a shift on the functional response curves of the respective predator species (see also Chalcraft & Resetarits 2004). Knowledge of the position of each predator on its specific functional response curve is important in order to choose the most appropriate model to predict effects of multiple predators. Alternative ways of estimating expected effects of multiple predators and subsequent comparisons of their impact on prey include measures of predator biomass or respiration rates.

In nature, few predators may be able to reach their saturation point, as prey consumption rates may be suppressed by other factors such as habitat complexity (Dahl & Greenberg 1997; Swisher, Soluk & Wahl 1998; Corona *et al.* 2000; Arthur *et al.* 2004; Warfe & Barmuta 2004) or strong intraguild interference among predators (e.g. Ambrose 1984b; Van Buskirk 1988; Siddon & Witman 2004; Schenk *et al.* 2005). Because our experimental design was far from the complexity found in nature, observed predation rates may have been higher than would be normal in nature. Future experiments should strive to incorporate more complex habitats when studying MPEs. The results of our study also suggest strongly that incorporation of functional response curves of the involved predators may improve predictions of MPEs.

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