Intraguild predation reduces redundancy of predator species in multiple predator assemblage

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Summary

1. Interference between predator species frequently decreases predation rates, lowering the risk of predation for shared prey. However, such interference can also occur between conspecific predators.

2. Therefore, to understand the importance of predator biodiversity and the degree that predator species can be considered functionally interchangeable, we determined the degree of additivity and redundancy of predators in multiple- and single-species combinations.

3. We show that interference between two invasive species of predatory crabs, *Carcinus maenas* and *Hemigrapsus sanguineus*, reduced the risk of predation for shared amphipod prey, and had redundant per capita effects in most multiple- and single-species predator combinations.

4. However, when predator combinations with the potential for intraguild predation were examined, predator interference increased and predator redundancy decreased.

5. Our study indicates that trophic structure is important in determining how the effects of predator species combine and demonstrates the utility of determining the redundancy, as well as the additivity, of multiple predator species.

Key-words: functional equivalency, multiple predator effects, predator interference, risk reduction, substitutable effects.

Introduction

Species that perform similar functions within a community are sometimes grouped together into functional guilds that are followed as single units without regards to individual species within the guild (e.g. aquatic invertebrates: Cummins 1973; marine fish: Greenstreet 1996; amphibians and reptiles: Inger & Colwell 1977; stream fish: Winemiller & Pianka 1990). This approach is often taken as a step to simplify community dynamics. For example, many ecosystem simulation models lump species together into functional groups (e.g. Ecopath). This approach may most appropriately be applied when the impacts of different species are functionally equivalent, or redundant, meaning they can be readily substituted without changing ecological or community processes (Lawton & Brown 1993).

The utility of the guild approach has been questioned due to potential oversimplification of complex systems (Polis & Strong 1996). As an example of this complexity, interactions between members of predator guilds often do not result in additive combined predation (Sih, Englund & Wooster 1998). Rather, interactions between predator species that share a common prey often yield less than additive predation (risk reduction, e.g. Eklöv 2000; Eklöv & Werner 2000; Finke & Denno 2002; Crumrine & Crowley 2003; Lang 2003; Warfe & Barmuta 2004), or sometimes, greater than additive predation (risk enhancement, e.g. Losey & Denno 1998; White & Eigenbrode 2000; Eklov & VanKooten 2001; Cardinale *et al.* 2003; DeWitt & Langerhans 2003; Meyer & Byers 2005).

However, the presence of nonadditive impacts of multiple predators need not automatically preclude use of a predator guild approach. While nonadditivity may occur when multiple predator individuals are combined, this may be independent of the identity of the predator species, i.e. whether conspecifics or heterospecifics are combined. For instance, interference between predator species can decrease predation rates of one or

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both species, causing risk reduction (e.g. Eklöv & Werner 2000; Warfe & Barmuta 2004; Griffen & Byers 2006). However, interference between predators of the *same* species can also cause predators to decrease their rates of prey consumption (Mansour & Lipcius 1991; Clark *et al*. 1999). Previous studies have shown that such interference between conspecific and hetero-specific predators may not only be nonadditive, but may also be redundant (Peckarsky 1991), leading to similar levels of risk reduction for shared prey (Vance-Chalcraft, Soluk & Ozburn 2004; Vance-Chalcraft & Soluk 2005a; Griffen 2006). We will refer here to this aspect of redundancy as redundancy in the interference effects of predators.

In addition to redundant interference effects between predators, prey consumption by predator combinations may also be redundant. That is, heterospecific predator combinations often cause similar levels of prey mortality as conspecific predator combinations (White & Eigenbrode 2000; Schmitz & Sokol-Hessner 2002; Sokol-Hessner & Schmitz 2002), indicating that predators are substitutable (*sensu* Sih *et al*. 1998). We will refer here to this aspect of redundancy as redundancy in the trophic effect of predators.

While previous studies have examined either the interference or the trophic effect, we believe that examining both effects of predators together may provide a more complete assessment of the redundancy of predators than examining only one or the other. Understanding these different facets of multispecies predator–prey interactions will provide insight into the dynamics of natural communities, will inform the extent to which predator biodiversity is important for ecosystem functioning in the face of rapid changes in biodiversity resulting from species/habitat loss and biological invasion (Ruesink & Srivastava 2001; Kinzig, Pacala & Tilman 2002; Ives, Cardinale & Snyder 2005), and will more comprehensively inform the extent to which a predator guild approach may be applied in determining the impacts of predators on prey populations.

Determining whether multiple predator species are additive and/or redundant may, however, be complicated by processes and interactions that occur other than consumption of a shared prey. One interaction that often influences the effects of multiple predators is intraguild predation (IGP) (Polis, Myers & Holt 1989; Rosenheim 1998; Finke & Denno 2002; Crumrine & Crowley 2003; Lang 2003; Rosenheim & Corbett 2003; Warfe & Barmuta 2004; Griffen & Byers 2006). IGP occurs when competing predators also consume each other (Polis *et al*. 1989), and can result in both density indirect effects and trait mediated indirect effects on prey (Werner & Peacor 2003). (We use the term IGP here to include cannibalism.) IGP often occurs only between certain life history stages, such as adults preying on juveniles (reviewed in Polis *et al*. 1989). Interactions between predator species in the field may thus be highly variable when multiple sizes of individuals of the two species overlap, leading to the potential for IGP in

some interactions and not in others. Thus it may be necessary to determine the additivity and redundancy of many pair-wise interactions of different sized predators to understand fully how multiple predator species combine to affect shared prey. To examine these issues of redundancy, we examined predation by two invasive species of intertidal crab predators that share the same prey resources.

Natural history

Two invasive predatory crabs are predominant on New England shores, the European green crab *Carcinus maenas* (Linnaeus, 1758) and the Asian shore crab *Hemigrapsus sanguineus* (De Haan, 1835). *C. maenas* invaded the east coast of North America in the mid-1800s and subsequently spread from Maryland to Nova Scotia. *H. sanguineus* was introduced around New Jersey in 1988 and has quickly spread over much of the same region from North Carolina to central Maine. In the Gulf of Maine, multiple sizes of these predators share the same intertidal distribution and are often found under the same rocks (Griffen & Byers 2006). IGP occurs among these species, with larger individuals of each species consuming smaller heterospecific and conspecific individuals (Lohrer & Whitlatch 2002). We could thus control whether IGP was possible by manipulating the sizes of predators in experimental treatments. Encounters between different sized individuals of the two species are frequent due to their overlapping distribution. Thus, operationally we must understand whether combinations of different sizes of the two predators are additive and/or redundant to understand better the combined impacts of these predators on prey resources.

Previous work has shown that these generalist predators have similar diets (Griffen unpubl. data; Tyrrell & Harris 1999; Lohrer *et al*. 2000) and that they interfere with each other while competing for the same food resources (Jensen, McDonald & Armstrong 2002; Griffen & Byers 2006). Gammarid amphipods are an abundant prey source in areas where these predators are found together. For example, at Odiorne Point, NH, a semiexposed site where both crabs are found abundantly (Griffen & Byers 2006), amphipods are present in the mid intertidal in patchily high densities (368 ± 390 m^{-2}, mean $\pm$ SD, $n = 21$; Griffen unpubl. data). Further, amphipods are a common prey for both crab species. McDermott (1998) found amphipods in the guts of 22% of *H. sanguineus*, and our own analyses indicate that 10–20% of the diet of *C. maenas* is composed of amphipods (Griffen, unpubl. data). Thus, using *C. maenas* and *H. sanguineus* as predators of shared amphipod prey provided a realistic, experimentally tractable predator–prey system that allowed us to assess redundancy of multiple predators with and without IGP.

In a laboratory experiment, we addressed the following questions. First, do isolated *C. maenas* and *H. sanguineus*

Table 1. Predator treatments included in laboratory experiment to examine interference between *Carcinus maenas* and *Hemigrapsus sanguineus*. Numbers given are individuals per chamber. Fifty amphipods were used as prey in each of the 15 treatments. Each treatment was replicated eight times

| | Predator(s) | | | |
Treatment no.	CM	HS	cm	hs
1	1	–	–	–
2	–	1	–	–
3	–	–	1	–
4	–	–	–	1
5	2	–	–	–
6	–	2	–	–
7	–	–	2	–
8	–	–	–	2
9	1	1	–	–
10	1	–	1	–
11	1	–	–	1
12	–	1	1	–
13	–	1	–	1
14	–	–	1	1
15	Control: no predators, only amphipod prey			

CM, large *C. maenas*; cm, small *C. maenas*; HS, large *H. sanguineus*; hs, small *H. sanguineus*.

have similar per capita predation rates when foraging on amphipods (i.e. are they redundant in their effects on prey)? Second, do isolated measurements of predation by each crab predator combine additively to predict prey consumption when both forage together? Or does interference between these species reduce predation risk for shared prey? Third, do interactions between heterospecific predators influence predation differently than interactions between conspecifics? Finally, how are these comparisons influenced by IGP?

Methods

EXPERIMENTAL DESIGN

We examined predation by *C. maenas* and *H. sanguineus* on amphipod prey in a laboratory experiment to isolate and quantify predator effects. We included 15 experimental treatments that combined all possible single and multiple species combinations of large and small predators (Table 1). Eight replicates of each treatment were used, with a single replicate of each treatment used during each of eight blocked, 24-h trials. Individual predators were only used in a single replicate.

We conducted the experiment in August 2004 in a controlled temperature/light room (temp = 20 °C; light was a constant 16 : 8 h light/dark cycle, lux = 957). We filled 15 polypropylene containers ($78 \times 31 \cdot 5 \times 30$ cm deep) with 1 cm of beach sand and 18 L (approximately 8 cm depth) of unfiltered seawater. Twelve denuded stones (7–10 cm diameter) placed on top of the sediment created refuge habitat in each chamber. Sand, rocks, and seawater came from the New Hampshire

coast. We changed seawater between trials and aerated continuously. Predators were starved for 24 h prior to experiments.

Large crabs of these species often prey on smaller individuals (Lohrer & Whitlatch 2002). Therefore, we created appropriate size differentials of individuals in our experiments to manipulate the potential for IGP and to control which of the two species was the top and intermediate predator [*H. sanguineus* – large: $2 \cdot 11 \pm 0 \cdot 17$ cm carapace width (CW) (mean ± 1 SD), small: $1 \cdot 35 \pm 0 \cdot 13$ cm CW; *C. maenas* – large: $2 \cdot 63 \pm 0 \cdot 18$ cm CW, small: $1 \cdot 33 \pm 0 \cdot 09$ cm CW]. We collected *C. maenas*, *H. sanguineus* and amphipods (*Gammarus* spp.) by hand from Odiorne Point, NH. We conducted short experimental trials (24 h) using sufficient amphipod prey so that they were never limiting (50 in each treatment). This resulted in, at most, consumption of 50–60% of the prey available during each trial. Amphipod mortality was assessed at the end of each trial.

Combined prey consumption by multiple predator species may be altered by both IGP-related predator mortality (a density indirect effect), and by the threat of IGP that alters foraging behaviour (a trait-mediated indirect effect, Crumrine & Crowley 2003; Griffen & Byers 2006). By using short-term trials and an abundance of prey, we eliminated lethal IGP during our experiment. This was desirable because lethal IGP would have changed the overall density of predators and the presence/absence of intermediate predators, potentially confounding interpretation of our results. We previously showed that behavioural components of IGP are an order of magnitude more influential to amphipod survival in this system than are direct losses of intermediate predators from IGP (Griffen & Byers 2006). Although short-term experiments can heighten behavioural effects (Lima & Bednekoff 1999), the overriding influence of nonlethal (vs. lethal) IGP provided an ideal situation for examining the majority of the influence of IGP without its confounding influence on density.

DATA ANALYSIS

Individual predation rates

We first compared predation rates between the four types of predators (large and small individuals of each species) to determine whether they had redundant (i.e. equal) predation rates when foraging alone. We used a two-way ANOVA with each of the four predator types and the no predator control (treatments 1–4 and 15, Table 1) treated as separate levels of one factor and trial block as the second factor. This was followed by pairwise comparisons at each of the levels of predator treatment (Tukey's, $\alpha = 0 \cdot 05$). For all subsequent analyses described below, prey mortality in the no predator (control) treatment was subtracted from prey mortality in all other predator treatments within each trial before analyses to account for nonpredatory mortality.

Predator additivity

We determined whether predation by *C. maenas* and *H. sanguineus* foraging on amphipods was additive when the two species foraged together by comparing the proportion of prey consumed in each predator combination to values expected if the predators had additive effects. We determined expected (additive) consumption of amphipod prey when both crab species foraged together using a multiplicative risk model (Soluk 1993) and prey consumption by single individuals of each predator type (i.e. treatments 1–4, Table 1). Expected values were calculated independently for each multiple species predator combination and for each trial. We then determined whether the effects of the two predator species were additive using a three-way ANOVA on prey mortality with observed and expected predation as two levels of one factor (Vance-Chalcraft & Soluk 2005b), each heterospecific predator combination as different levels of a second factor (treatments 9, 11, 12 and 14 in Table 1), and trial treated as a blocking factor. This was followed by planned linear contrasts ($\alpha = 0.05$) in which we directly compared observed and expected predation for each predator combination. A significant difference in a linear contrast indicates that predation by that predator combination is nonadditive. We chose this statistical approach because it has higher statistical power (degrees of freedom) than *t*-tests and individual two-way ANOVAs (with species as a factor) performed on each predator combination – the methods typically used to detect nonadditive effects of multiple predators. We confirmed that this analysis yields qualitatively similar results to these other techniques.

Interference and trophic redundancy

We compared two aspects of the redundancy of *C. maenas* and *H. sanguineus* when multiple individuals foraged together: redundancy in the interference effects and in the trophic effects of these predators. We statistically examined each of these separately. We first examined redundancy in the interference effects of large individuals of each species. The magnitude of nonadditivity (observed minus expected prey consumption, see previous section) indicates the degree of interference or facilitation between conspecific or heterospecific predators. We therefore used the multiplicative risk model (Soluk 1993) to calculate expected predation by conspecific predator pairs of each species (Vance-Chalcraft *et al.* 2004), and subtracted this from observed predation (treatments 5–6, Table 1) to determine the magnitude of risk reduction. We then compared risk reduction when conspecific and heterospecific predators were paired to determine whether predator species identity was important in determining effects on other predators. We used two-way ANOVA on the magnitude of risk reduction with the three predator combinations (two large *C. maenas*, two large *H. sanguineus*, or one of each) as levels of one fixed factor, and

trial block as the second factor. This was followed by Tukey's test for multiple comparisons between the three predator combinations. If no difference was found, this indicated that these predators were redundant in their interference effects on each other's predation. Identical analyses were conducted for combinations of small individuals to examine the interference redundancy of these predators.

We then examined the redundancy in the trophic effects of conspecific and heterospecific predator pairs using identical statistical analyses, but with prey mortality rather than risk reduction as the response variable.

When IGP was allowed by combining different sized predators, we analysed each of the four conspecific and heterospecific predator combinations together (treatments 10–13, Table 1). We again used a two-way ANOVA with the four predator combinations treated as separate levels of a fixed factor and trial block as a second factor, followed by Tukey's test for multiple comparisons. and we again conducted two analyses, one with risk reduction as the response variable (to assess the redundancy of the interference effects of these predators) and one with prey mortality as the response variable (to assess the redundancy of the trophic effects of these predators).

We ensured that variances in the data for all ANOVAs were homoscedastic by examination of residual plots. Block effects were not significant in any of the analyses ($P > 0.15$). Although pooling the data by removing block from the analyses did not change the results, block was retained in all analyses for completeness (Hines 1996).

Results

INDIVIDUAL PREDATION RATES

Large and small crab predators of both species consumed amphipods in our experiments, but at different rates (ANOVA, $F_{4,39} = 60.49$, $P < 0.0001$). Thus the proportion of amphipod prey consumed per trial (i.e. per day) differed between three of the four predators: Large *C. maenas* (0.41 ± 0.03) > large *H. sanguineus* (0.31 ± 0.03) > small *C. maenas* (0.16 ± 0.02) = small *H. sanguineus* (0.12 ± 0.02) > no predator control (0.04 ± 0.01).

PREDATOR ADDITIVITY

Amphipod prey benefited from less than additive predation risk in the presence of some combinations of the two species, but predation by other combinations was additive (Fig. 1). Specifically, predation by large individuals of each species was less than additive (ANOVA with planned linear contrasts between observed and expected predation, $F_{1,49} = 8.44$, $P = 0.005$), as was predation when small *C. maenas* and large *H. sanguineus* were combined ($F_{1,49} = 18.52$, $P < 0.0001$). There was a marginally significant trend towards risk
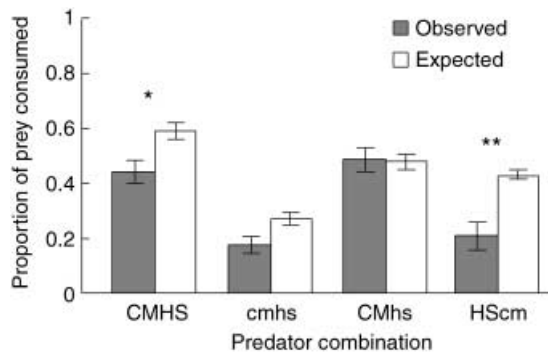
Fig. 1. Observed and expected consumption of amphipods (mean ± 1 SE, $n = 8$) by *C. maenas* and *H. sanguineus* combined. Letters on the *x*-axis represent predators as indicated in Table 1 legend. Expected values indicate predation expected in the absence of interference and were derived from the multiplicative risk model (Soluk 1993). *$*P < 0.01$, *$**P < 0.0001$, from ANOVA with paired linear contrasts.

Fig. 2. Functional niche of *C. maenas* and *H. sanguineus* illustrating both their interference effects on predation by conspecific and heterospecific predators and their trophic effects on shared prey (mean ± 1 SE, $n = 8$). Negative values represent stronger interference effects. Abbreviations next to each point are as given in Table 1. ▲, for combinations of large individuals; ■, for combinations of small individuals; ● (both closed and open) for combinations of large and small individuals. All combinations of large individuals (▲) were similar in both their interference and trophic effects, as were all combinations of small individuals (■). Open and closed circles depict combinations of large and small predators that were different in their trophic effects (an identical pattern was observed in the interference effects, except that HShs treatment was not different from the CMcm and CMhs treatments; Tukey's, $\alpha = 0.05$).

reduction when small individuals of both species were combined ($F_{1,49} = 2.99$, $P = 0.09$). However, when large *C. maenas* and small *H. sanguineus* were combined predation was consistent with the prediction of the multiplicative risk model ($F_{1,49} = 0.03$, $P = 0.86$).

INTERFERENCE AND TROPHIC REDUNDANCY

We plotted predator interference effects and trophic effects together to facilitate comparison of the redundancy of the various predator combinations (Fig. 2). Redundant predator combinations in Fig. 2 cluster closely together. Large individuals interacting with other large conspecific and heterospecific predators were redundant in both their interference (ANOVA on risk reduction in heterospecific and conspecific predator combinations, $F_{2,23} = 0.57$, $P = 0.58$; Fig. 2) and trophic effects (ANOVA on prey mortality caused by conspecific and heterospecific predator combinations, $F_{2,23} = 0.84$, $P = 0.45$; Fig. 2). Similarly, small individuals of each species were redundant both in their interference effects on other predators ($F_{2,23} = 0.25$, $P = 0.78$; Fig. 2) and in their trophic effects on prey mortality ($F_{2,23} = 0.56$, $P = 0.58$; Fig. 2).

When IGP was allowed by combining different sized individuals of each species, there was a large, significant difference in interference effects, but only between treatments with different top predators (ANOVA on risk reduction with all four predator combinations where IGP was possible, $F_{3,31} = 6.07$, $P = 0.004$, Fig. 2). When the identity of the top predator did not change, risk reduction was similar in strength, whether large predators were paired with small conspecifics or with small heterospecifics (closed circles in Fig. 2 are similar to each other, and open circles in Fig. 2 are similar to each other). A similar pattern was observed when comparing the trophic redundancy of these predator combinations (Fig. 2). Specifically, there were no differences in amphipod consumption between treatments with the same top predator regardless of identity of intermediate
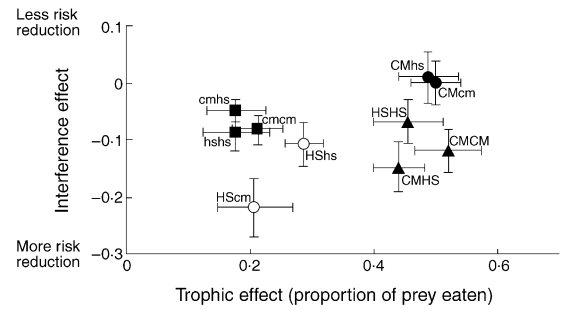
predator, though amphipod consumption was significantly higher when *C. meanas* was the top predator (ANOVA followed by Tukey's test on prey mortality, $F_{3,31} = 9.90$, $P < 0.001$, Fig. 2). No IGP-related predator mortality occurred during our experiment. Thus all effects were due to the threat of IGP rather than changes in predator density resulting from predator on predator mortality.

Discussion

Our study shows that when the threat of IGP is absent (i.e. when predators only interact competitively), *C. maenas* and *H. sanguineus* of a given size have redundant interference and trophic effects. Interference competition between these species has previously been observed. For example, *H. sanguineus* may frequently displace similar sized *C. maenas* when the two species directly compete for the same prey item, causing *C. maenas* to abandon captured prey (Jensen *et al.* 2002). Antagonistic interactions are also common among *C. maenas* (Griffen, pers. obs.), and can decrease predation rates (Griffen 2006). This conspecific interference is capable of altering foraging behaviour to a similar extent as interactions with *H. sanguineus*, leading to redundant interference effects of these predators in the absence of IGP (Fig. 2).

However, the threat of IGP was high when large *H. sanguineus* were combined with small *C. maenas* (see below). In this case, combining the two species resulted in strong risk reduction for amphipods that was not redundant with *C. maenas* as the top predator (Fig. 2). Because the same species were used when IGP was and

was not possible, differences in results could be definitively attributed to changes in trophic structure, and were not confounded by a change in species. Thus, IGP may be an important factor in determining when interference between predator species causes reductions in predation risk for shared prey that cannot be predicted from single-species trials (Fig. 2). This is consistent with a previous examination of several different species combinations of stream predators that found risk reduction to be strongest when predators with the potential for IGP were combined (Vance-Chalcraft & Soluk 2005a), and with a previous study where we demonstrated that habitat-specific increases in consumption of *C. maenas* by *H. sanguineus* resulted in increased risk reduction for shared prey (Griffen & Byers 2006).

The degree of redundancy in the interference effect of these predators depended on the asymmetry of IGP. In a preliminary experiment, large *H. sanguineus* were much more likely to consume smaller heterospecifics than were *C. maenas*, and both species were more likely to consume heterospecifics than conspecifics (Griffen, unpubl. data). The threat of IGP can cause decreased predation by both top and intermediate predators as a result of changes in foraging behaviour when the two forage together (Crumrine & Crowley 2003), and these behavioural changes are responsible for nearly 90% of the total risk reduction in this system (Griffen & Byers 2006). Changes in foraging behaviour are often greatest when IGP is strong (Lima 1998), and thus were likely much stronger when *H. sanguineus* was the top predator than when *C. maenas* was the top predator and in heterospecific than conspecific predator combinations. Thus, strong IGP led to high risk reduction for shared prey (e.g. when large *H. sanguineus* was combined with small *C. maenas*, Fig. 2), and asymmetry in IGP led to low redundancy (e.g. separation along both axes of Fig. 2 when *H. sanguineus* vs. when *C. maenas* was the top predator).

Our results have implications for determining the effects of *C. maenas* and *H. sanguineus* on amphipod prey populations. Interference between conspecifics and heterospecifics that decreases predation implies that multiple predator individuals should be included when determining the impacts of these predators on prey in order to avoid overestimation of population-level impacts. Further, redundancy in both the trophic and interference effects of these predators when individuals are the same size implies that these species can be combined to some extent into a single trophic guild when determining their impacts on some prey sources. This conclusion may also apply to other important prey for these predators, such as the mussel *Mytilus edulis* (Linnaeus, 1758). For example, similar sized *C. maenas* and *H. sanguineus* consume small mussels at similar rates (DeGraaf & Tyrrell 2004), and conspecific and heterospecific interference between these predators while foraging on mussels can reduce prey mortality by similar amounts (Griffen 2006). However, situations also likely occur where these two predators

are not redundant because of diet shifts or different food preferences.

Some studies have reported only the trophic or only the interference effect of predator combinations (e.g. Sokol-Hessner & Schmitz 2002; Lang 2003; Vance-Chalcraft & Soluk 2005a). While these effects are not independent (trophic effects are observed prey mortality and interference effects are calculated using observed prey mortality), they do provide different information, and it therefore remains beneficial to examine both when determining the combined effects of multiple predators. For example, had we examined only the interference effect in our system, we may have concluded that similar levels of interference provide equal safety for amphipods under different predator combinations. Similarly, had we examined only the trophic effect, we may have concluded only that predation by various predator combinations caused either high or low prey mortality (Fig. 2). However, by examining both effects together it became apparent that some predator combinations with similar levels of interference differed in amphipod consumption by a factor of 2, and that IGP is important in establishing levels of risk presented by different predator combinations (Fig. 2). Examining both of these effects together should lead to greater predictability of the effects of multiple predators.

We have demonstrated that the impacts of *C. maenas* and *H. sanguineus* vary in their additivity and redundancy. This variability became apparent by including two different factors in our study. First, examining both the interference and trophic effects allowed us to utilize these different components of the functional redundancy of these predators to understand more fully their interactions and combined effects (Fig. 2). Understanding the functional redundancy of species along multiple niche dimensions will be crucial to understanding the consequences of continuing changes in biodiversity in natural systems (Rosenfeld 2002). Second, we included different size combinations that incorporated the variable trophic complexity (presence or absence of IGP) that occurs between these species. The simultaneous presence of multiple sizes or life-history stages of predators often results in top and intermediate predators in natural systems (Polis *et al.* 1989) and, though not examined, occurs among many of the species for which the effects of multiple predators have been reported (e.g. McIntosh & Peckarsky 1999; Eklov & Werner 2000; Vance-Chalcraft *et al.* 2004). Our study implies that unique nonadditive impacts of multiple predator species may be stage- or size-specific. The shifting redundancy of these species with trophic structure highlights the importance of IGP as a causative factor in nonredundant, nonadditive effects of multiple predators. The population-level importance of predator species richness may therefore depend on IGP and the degree of interaction (e.g. encounter rates between different size classes), both of which are strongly dependent on population demographics.

Acknowledgements

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