

Influence of predator density on nonindependent effects of multiple predator species

Blaine D. Griffen · Tucker Williamson

Received: 19 October 2006 / Accepted: 10 October 2007 / Published online: 30 October 2007
© Springer-Verlag 2007

Abstract Interactions between multiple predator species are frequent in natural communities and can have important implications for shared prey survival. Predator density may be an important component of these interactions between predator species, as the frequency of interactions between species is largely determined by species density. Here we experimentally examine the importance of predator density for interactions between predator species and subsequent impacts on prey. We show that aggressive interactions between the predatory shore crabs *Carcinus maenas* and *Hemigrapsus sanguineus* increased with predator density, yet did not increase as fast as negative interactions between conspecifics. At low density, interactions between conspecific and heterospecific predators had similar inhibitory impacts on predator function, whereas conspecific interference was greater than interference from heterospecifics at high predator density. Thus the impact of conspecific interference at high predator density was sufficient in itself that interactions with a second predator species had no additional impact on per capita predation. Spatial and temporal variability in predator density is a ubiquitous characteristic

of natural systems that should be considered in studies of multiple predator species.

Keywords *Carcinus maenas* · *Hemigrapsus sanguineus* · Multiple predator effects · Predator interference · Risk reduction

Introduction

Density is an important factor contributing to the overall function and impact of species within ecological communities. Density is particularly important in interactions between species, and its consideration has been instrumental in understanding fundamental ecological processes that occur between interacting species, including interspecific competition (Connell 1961), consumer–resource interactions (Volterra 1926), predator functional responses (Holling 1959), and resulting trophic cascades (Hairston et al. 1960).

One type of species interaction that has recently received much attention is the combined effects of multiple predator species (Sih et al. 1998). Predator species that share the same prey frequently interact, altering the influence of one or both species on prey so that their impacts are nonindependent. When predator nonindependence occurs, prey mortality as predator species forage together is either less than expected based on prey mortality when each predator species forages separately (risk reduction) or greater than expected (risk enhancement). Experimental examinations of nonindependent effects of multiple predator species have focused mainly on behavior (i.e., trait-mediated interactions), such as prey responses to different predator species that conflict and can therefore not be expressed simultaneously (Soluk 1993; Losey and Denno 1998; Eklöv and

Communicated by Pete Peterson.

B. D. Griffen
Zoology Department, University of New Hampshire,
Durham, NH 03824, USA

B. D. Griffen (✉)
Odum School of Ecology, University of Georgia,
Athens, GA 30602, USA
e-mail: bgriffen@uga.edu

T. Williamson
School of Science and Math, College of Charleston,
Grice Marine Laboratory, 205 Fort Johnson,
Charleston, SC 29412, USA

VanKooten 2001; Harvey et al. 2004) or aggression between predators that alters predator foraging behavior (Peckarsky 1991; Crumrine and Crowley 2003; Warfe and Barmuta 2004; Griffen and Byers 2006b).

These studies have amply demonstrated the importance of individual behavioral traits in systems with multiple predator species; however, species density is also important. This fact has been empirically shown for prey, as the strength of nonindependent effects of multiple predator species (i.e., the strength of risk reduction or risk enhancement) can vary with prey density (Soluk 1993; Losey and Denno 1998; Vance-Chalcraft and Soluk 2005b; Griffen 2006). The importance of predator density has received only cursory attention, with the main focus on changes in the way that additive and substitutive experimental designs manipulate the relative densities of two interacting predator species (Griffen 2006). However, an extensive search of the literature revealed no studies that systematically varied predator density in multiple predator combinations in an effort to examine the influence of predator density in eliciting nonindependent effects of multiple predators.

In contrast to studies of multiple predator species, the importance of predator density when only a single predator species occurs is well-documented. Interference among conspecific predators generally increases with predator density due to higher frequency and intensity of interactions (Mansour and Lipcius 1991; Clark et al. 1999; Mistri 2003; Schenk et al. 2005; Smallegange et al. 2006), resulting in lower per capita effects of predators on prey (Arditi and Ginzburg 1989; Arditi and Akcakaya 1990; Clark et al. 1999; Abrams and Ginzburg 2000; Mistri 2003). Similarly, the behaviors that elicit nonindependent effects of multiple predator species may interact with predator density, potentially resulting in density-dependent strengths of risk reduction or risk enhancement. Thus, the overall implications for prey of interacting predator species may depend on spatially and temporally variable predator densities and the resulting influence on predator interactions.

Here we investigate the combined impacts of two co-occurring predators across a range of densities in an effort to determine how predator density affects the way that consumption by multiple predator species combines. The European green crab *Carcinus maenas* and the Asian shore crab *Hemigrapsus sanguineus* are two invasive predators on the Atlantic coast of the United States and are presently the dominant shore crab species along much of the coast. These species utilize similar habitats and prey resources (Tyrrell and Harris 1999; Lohrer et al. 2000), resulting in interference competition between the two (Jensen et al. 2002). A range of sizes of individuals of these species frequently overlaps in rocky intertidal areas, and intraguild predation and cannibalism are both strong given a sufficient size difference between individuals (Lohrer and Whitlatch

2002a; Griffen and Byers 2006a). Aggressive interference among predatory crabs frequently reduces prey consumption (Mansour and Lipcius 1991; Clark et al. 1999; Taylor and Eggleston 2000; Sietz et al. 2001; Mistri 2003; Smallegange et al. 2006), and previous work with these particular species has demonstrated that the strength of interspecific interference depends on habitat type (Griffen and Byers 2006b), the relative sizes of interacting individuals (Griffen and Byers 2006a), and prey density (Griffen 2006).

On the regional scale, the densities and distributions of these two species have shifted dramatically over the last decade as the introduction of *H. sanguineus* appears to have decreased the numbers of *C. maenas* in rocky intertidal habitats along its northward range expansion, which has presently reached central Maine (Lohrer and Whitlatch 2002a). As a result, the region of overlap between these species has steadily shifted northward. This region of overlap currently occurs in the central Gulf of Maine, from Massachusetts to mid-coast Maine. Both species are found abundantly at our field site at Odiorne Point, New Hampshire, the midpoint of this region (Griffen and Byers 2006b). This site is delineated into a series of coves, each separated by approximately 50–100 m, and the mutual aggregation of predators in coves with abundant food and refuge habitat results in a positive correlation in the densities of *C. maenas* and *H. sanguineus* across coves (Griffen et al. 2007b). This system thus provides an excellent opportunity to examine the (in)dependence of predation by two predator species whose densities naturally covary across a wide range.

Using field and laboratory experiments, we examined how predator density influences the combined effects of *C. maenas* and *H. sanguineus* on the blue mussel *Mytilus edulis*, an important food source for both species (Ebling et al. 1964; Elnor 1981; Lohrer and Whitlatch 2002b; Bourdeau and O'Connor 2003; DeGraaf and Tyrrell 2004; Griffen et al. 2007b). We also compared the influence of predator density on heterospecific predator interactions to the effect of density on interactions between conspecific predators. Finally, we observed predator behavior to determine whether the effects of predator density can be explained mechanistically by changes in aggressive interactions between predators.

Methods

Field experiment on the impacts of predator density

Field experiments were conducted on a semi-exposed beach at South Odiorne Point, New Hampshire. This site is characterized by a series of coves separated by bedrock

outcroppings. The dominant substrate is boulders overlying a substrate of sand and shell. Sampling at low tide revealed densities of large *C. maenas* (>30 mm carapace width, CW) ranging from 0 to 28 m⁻², while densities of large *H. sanguineus* (>20 mm CW) ranged from 0 to 16 m⁻² between coves (Griffen et al. 2007b). We conducted experiments in a cove with relatively low densities of both crabs (*C. maenas*, 2.8 ± 2.8 m⁻²; *H. sanguineus*, 1.5 ± 1.8 m⁻²; mean ± SD) in order to minimize the influence of ambient crabs.

Experiments were conducted in enclosures (0.6 × 0.5 × 0.3 m) deployed at approximately 0.5 m above the mean low water level. Enclosures were constructed of 2.5-cm galvanized PVC-coated wire mesh and were lined with 0.5-cm plastic mesh. Small boulders that had been cleared from the substrate to allow for placement of the experimental enclosures were placed inside the enclosures to mimic ambient habitat. Naturally occurring flora and fauna were left on these boulders so that a naturally occurring array of prey species was available inside the enclosures. These included urchins, limpets, snails, amphipods, polychaetes, small sea stars (<2 cm diameter), brittle stars, small fish, juvenile crabs, and macroalgae. Thus, although we focused our experiments on the consumption of mussel prey, predators were not artificially limited in their food choices. While this may have diluted the impacts on focal prey, it was desirable in order to provide a more realistic picture of predation in the natural habitat where these omnivorous predators have a variety of prey to choose from.

After all naturally occurring mussels had been removed from the enclosures, 50 experimental mussels that had been collected from the surrounding area were scattered haphazardly into each enclosure 24 h before the inclusion of predators to allow time for byssal thread attachment. This mussel density (167 m⁻²) is similar to the natural densities of mussels in the lower intertidal regions of Odiorne Point (198 ± 197 m⁻²) where the experiment was conducted (Tyrrell and Harris 1999). We used mussels with a shell length of 15–20 mm, which is the preferred size of mussel prey for adult *C. maenas* (Elner and Hughes 1978). Using this size of mussel likely decreased mussel consumption rates by *H. sanguineus*, given that this size of mussel is larger than their preferred size of <10 mm (Bourdeau and O'Connor 2003). However, while not the preferred size, *H. sanguineus* can and does consume this size of mussel prey (McDermott 1998; DeGraaf and Tyrrell 2004; BD Griffen, personal observation).

To examine the impact of predator density on multiple predator effects, we experimentally increased the density of *C. maenas* and *H. sanguineus* simultaneously (rather than orthogonally), mimicking the positive correlation between the two species observed between coves at our field site

(Griffen et al. 2007b). We used an experimental design that combined components of the additive and substitutive experimental designs commonly in use (see review in Griffen 2006). This allowed us to examine the influence of predator density on interspecific interference and its importance relative to intraspecific interference.

Experimental treatments included each species foraging alone at densities of one, two, three, four, six, and eight individuals per enclosure (equivalent to approximately 0–26 crabs m⁻²), and both species foraging together at densities of one, two, three, and four individuals of each species per enclosure. This range of densities is similar to the range observed at our field site for large *C. maenas*, is greater than that observed at our field site for large *H. sanguineus*, but is well within the range of densities observed for *H. sanguineus* at sites in its invaded range (Brousseau et al. 2003). Each of these 16 treatments and the no predator control were replicated five times by including a single replicate of each treatment within each of five blocked trials during June and July 2004. Adult males (*C. maenas*, 49.5 ± 7.2 CW; *H. sanguineus*, 23.9 ± 2.5 mm CW) that had been starved for 24 h to standardize hunger were allowed to forage in each trial for 6 days, following which we removed the contents of each enclosure and assessed the number of surviving mussel prey. No other predators that potentially consume mussels were included in experimental cages (e.g., no whelks or large sea stars), thus while a small amount of non-predatory mortality occurred (see Results), prey mortality was attributable largely to crab predation.

To examine the overall impact of the two crab species on prey survival in single-species treatments, we conducted separate two-way ANOVAs for each species, with predator density (seven levels including the no predator control) as a fixed factor and trial block (five levels) as a random factor. We further examined differences in per capita predation rates by the two crabs in single species treatments of our experiment (calculated as the number of mussels consumed × the number of crabs in cage⁻¹ × trial length in days⁻¹) using an ANCOVA on log-transformed per capita predation rates, with species as a fixed factor and predator density as a covariate.

The experimental treatments listed above allowed us to compare observed prey survival when one, two, three, and four predators of each species foraged together to expected survival. At each of these predator densities, we calculated two different values for expected prey survival for each replicate blocked trial. We calculated expected prey survival when predators are combined ($E_{C,H}$) in an additive fashion (based on multiplicative risk of predators): $E_{C,H} = N_C \times N_H / N_{\text{control}}$, where N_C , N_H , and N_{control} are the number of prey that survive each trial with *C. maenas*, *H. sanguineus*, and no predator (control). Prey survival that is different from the expected based on this model would indicate that

interactions between the two predator species alter their combined predation on shared prey (Billick and Case 1994; Vonesh and Osenberg 2003; Vance-Chalcraft and Soluk 2005a; Griffen 2006).

We also calculated prey survival when predators are combined in a substitutive fashion: $E_{C,H} = (N_{C,C} \times N_{H,H})^{0.5}$, where $N_{C,C}$ and $N_{H,H}$ are the numbers of prey surviving when foraged on by conspecific combinations of *C. maenas* and *H. sanguineus*, respectively (Griffen 2006). This model compares predator interference in treatments with multiple predator species to interference among predators of the same species at the same total density. Prey survival that is different from expected based on this substitutive model would thus indicate that heterospecific predator interference has a different effect on prey consumption than conspecific predator interference (Griffen 2006).

We compared observed prey survival to both of these estimates of expected prey survival using separate three-way ANOVAs on prey survival with observed and expected as two levels of a fixed factor, predator density as a fixed factor (four levels), and trial as a random blocking factor (five levels). Interaction terms including the blocking factor were nonsignificant ($P < 0.25$) and so were not included in the analysis. This was followed by planned linear contrasts of observed and expected survival at each predator density. We chose this analysis rather than the standard technique (Sih et al. 1998) for detecting nonadditive predation using ANOVA on log-transformed prey mortality with each species treated as a separate factor because of the additional complexity of nonorthogonal increases in predator density in our experiment. Given our experimental design, our analysis accomplished our primary goal of explicitly examining how predator density influenced additivity and substitutability of predation by *C. maenas* and *H. sanguineus*.

Laboratory examination of predator aggression at different densities

We examined aggression by *C. maenas* and *H. sanguineus* in a laboratory experiment in which each species foraged alone or together, respectively, at different predator densities. Experiments were conducted during July and August 2004 in 0.5×0.4 -m polypropylene tanks with flowing seawater at the Shoals Marine Laboratory, Isles of Shoals, Maine. To facilitate visual observations, the refuge habitat inside the tanks was simple (compared to the field refuge) and consisted of a single 20-cm-diameter rock placed in the center of each tank, resting on 2 cm of sediment. Sediment was added to facilitate mobility for crabs after it was observed during preliminary experiments that crabs tended to slip while attempting to walk within experimental tanks without sand. However, adding sand had the additional benefit of allowing crabs to burrow (although shallowly),

thus avoiding confrontations with aggressors. Fifty *M. edulis* (shell length 15–20 mm) were scattered inside each experimental tank 12 h before the start of the experiment. We used single and multiple predator species combinations at three different predator densities, resulting in nine different predator treatments (single species treatments two, four, or eight *C. maenas* or *H. sanguineus*; multiple species treatments one *C. maenas* + one *H. sanguineus*, two *C. maenas* + two *H. sanguineus*, or four *C. maenas* + four *H. sanguineus*).

Crabs, with identifying numbers painted on their carapaces, were placed in tanks 2 h before data collection started (*C. maenas* 46.5 ± 8.2 mm CW; *H. sanguineus* 23.4 ± 2.8 mm CW). Experiments were conducted at night, as this is when crabs forage most actively (Saigusa and Kawagoye 1997). Under red lights (to minimize disturbance to crabs), we recorded the behavior of each crab in a tank at 6-min intervals for 2 h (yielding a total of 20 observations per crab). We were particularly interested in aggressive behaviors, which we defined as fighting, display of threat behavior (extending chelipeds), or displacement of one crab by another (see Smallegange et al. 2006 for a full explanation of identically defined aggressive behaviors).

This type of instantaneous scan sampling requires that behaviors from one scan to the next be independent. If behavior differs more between successive samples as inter-sample duration increases, then behaviors sampled at shorter time intervals can be inferred to be nonindependent. We verified that a 6-min interval between observations was sufficiently long to ensure independence of behaviors by determining the proportion of 6-, 12-, or 18-min intervals over which the behavior of a given crab changed (between aggression, foraging/walking, or inactive). We did this for each crab within the mixed species treatment with eight crabs (as this treatment provided the most data within a single treatment to make the comparison for both species). We used separate ANOVAs for each species to compare the proportion of the 6-, 12-, or 18-min time intervals over which behavior changed.

Because more crabs were present in high-density treatments, we initially conducted more replicates of the lower density treatments. However, to avoid problems associated with an unbalanced design, we randomly removed replicates from the lower density treatments, resulting in three replicates per treatment (Shaw and Mitchell-Olds 1993). The proportion of the 20 observations in which aggressive behaviors were displayed by individual crabs was averaged among all crabs of a single species within each individual replicate. This value (arcsine square root transformed to achieve homogeneity of variance) was compared using a three-way ANOVA, with species (two levels), mixed species combinations (two levels: yes/no), and density (three levels) as fixed factors.

Results

Field experiment on impacts of predator density

Carcinus maenas and *H. sanguineus* both decreased prey survival in single-species treatments, although their effects were quite different. Prey survival in *C. maenas* treatments varied across trials (these differences across trial followed no apparent pattern, such as systematic increases or decreases over time; ANOVA, $F_{4,24} = 8.20$, $P = 0.0003$), and decreased relative to the no-predator controls (ANOVA, $F_{6,24} = 13.53$, $P < 0.0001$). However, prey survival did not differ with *C. maenas* density (Tukey’s post hoc comparison). In contrast, prey survival in the *H. sanguineus* treatments was similar across trials (ANOVA, $F_{4,24} = 0.78$, $P = 0.55$) and only decreased (relative to that in no-predator controls) in treatments with four or six *H. sanguineus* (ANOVA, $F_{6,24} = 4.95$, $P = 0.002$, followed by Tukey’s post hoc comparison).

Overall, *C. maenas* had much higher predation rates than *H. sanguineus* in single-species treatments (main factor in ANCOVA, $F_{1,56} = 93.86$, $P < 0.0001$; Fig. 1). Per capita predation rates of both species decreased with predator density (covariate in ANCOVA, $F_{1,56} = 44.87$, $P < 0.0001$; species \times predator density effect $F_{1,56} = 0.07$, $P = 0.79$; Fig. 1). Effects of predator density were not simply an artifact of prey depletion, given that more than 30% of mussels survived in all predator treatments (Fig. 2a). Predators also consumed non-focal prey species, as forensic evidence of this predation (e.g., crushed snail and urchin shells, etc.) were at times observed within experimental enclosures.

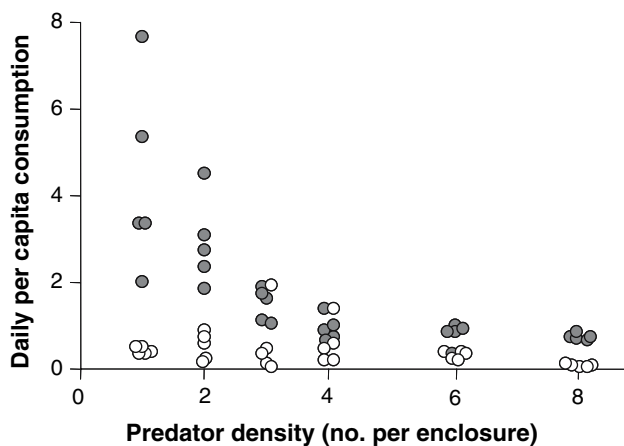


Fig. 1 Daily per capita mussel consumption by *Carcinus maenas* (filled circle) and *Hemigrapsus sanguineus* (open circle) when present in single-species treatments at different densities in a field experiment at South Odiome Point, New Hampshire in June/July 2004. Dots represent mean prey consumption by all crabs within a single 0.3-m² experimental enclosure ($n = 5$)

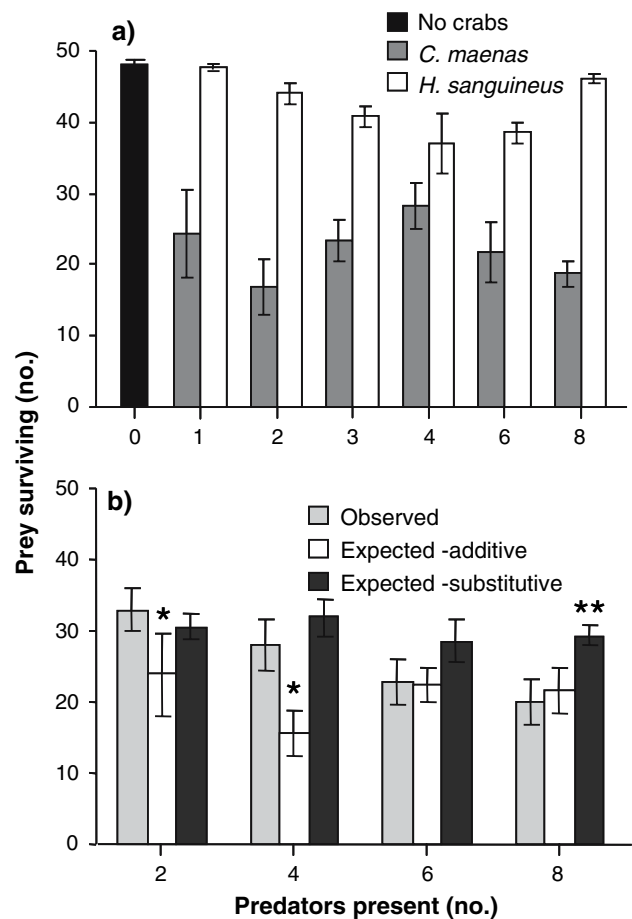


Fig. 2 **a** Prey survival in 0.3-m² field enclosures with zero to eight predators present in single-species treatments and in predator-free controls (means \pm SE, $n = 5$). **b** Comparison of observed and expected prey survival when predator species are combined with equal numbers of each species (means \pm SE, $n = 5$). Expected values were calculated using both an additive and a substitutive model (Griffen 2006) and assume that predators have independent effects. Asterisks indicate observed values that differed significantly from expected, where $*P < 0.05$ and $**P < 0.001$

Cannibalism and/or intraguild predation caused crab mortality in 25 of the 80 total replicates with crab predators in our field experiment. Further, the incidence of crab mortality increased with overall crab density (logistic regression, $\chi^2 = 3.87$, $P = 0.049$). However, in the majority of cases (15), this resulted in only a single crab loss per replicate.

When *C. maenas* and *H. sanguineus* foraged together, the independence of their predation effects varied with predator density. Specifically, prey survival was greater than expected based on the additive model (i.e., risk reduction occurred) for the two lowest predator densities (three-way ANOVA with planned linear contrasts; one predator of each species: $F_{1,32} = 4.53$, $P = 0.04$; two predators of each species: $F_{1,32} = 8.24$, $P = 0.008$; Fig. 2b). In contrast, at the two highest predator densities, prey survival was not

different from expected based on the additive model, indicating that at high densities the two species had independent effects (three-way ANOVA with planned linear contrasts; three predators of each species: $F_{1,32} < 0.001$, $P = 0.99$; four predators of each species: $F_{1,32} = 1.50$, $P = 0.23$; Fig. 2b).

Predator density also influenced the strength of conspecific predator interference relative to heterospecific interference. Conspecific and heterospecific interference were similar in strength at the two lowest predator densities, resulting in no difference between observed prey survival and expected based on the substitutive model (three-way ANOVA with planned linear contrasts; one predator of each species: $F_{1,32} = 0.60$, $P = 0.45$; two predators of each species: $F_{1,32} = 1.45$, $P = 0.24$; Fig. 2b). In contrast, at the two highest predator densities, observed prey survival was greater than expected based on the substitutive model (although this trend was only marginally significant when three predators of each species were present), indicating that conspecific predator interference was stronger than heterospecific interference (three-way ANOVA with planned linear contrasts; three predators of each species: $F_{1,32} = 3.12$, $P = 0.09$; four predators of each species: $F_{1,32} = 19.53$, $P < 0.001$; Fig. 2b).

Laboratory examination of predator aggression at different densities

The behavior of *C. maenas* changed (between aggression, foraging/walking, or inactive) from one observation to the next 38 ± 10 , 47 ± 17 , $50 \pm 20\%$ of the time for the 6-, 12-, and 18-min intervals, respectively. The behavior of *H. sanguineus* changed 51 ± 11 , 58 ± 13 , $55 \pm 14\%$ between each time interval, respectively. These differences were not significant for either species (*C. maenas*: one-way ANOVA, $F_{2,33} = 0.81$, $P = 0.45$; *H. sanguineus*: one-way ANOVA, $F_{2,33} = 60$, $P = 0.56$). Thus, crab behaviors were similarly independent at the short and long time intervals. We therefore used shorter time intervals to maximize replication and thus the resolution provided by the data.

Carcinus maenas displayed more aggressive behavior than *H. sanguineus* in our laboratory experiment ($F_{1,24} = 4.16$, $P = 0.05$; Fig. 3). Aggression by both species increased with predator density ($F_{2,24} = 21.46$, $P < 0.0001$; species \times density interaction $F_{2,24} = 0.47$, $P = 0.63$; Fig. 3). In general, predators were more aggressive when combined only with conspecifics than when combined with heterospecifics ($F_{1,24} = 5.24$, $P = 0.03$; Fig. 3), although this trend was only significant for *C. maenas* (post hoc linear contrasts of mixed vs. unmixed for *C. maenas*: $F_{1,24} = 5.16$, $P = 0.03$; for *H. sanguineus*: $F_{1,24} = 0.93$, $P = 0.34$).

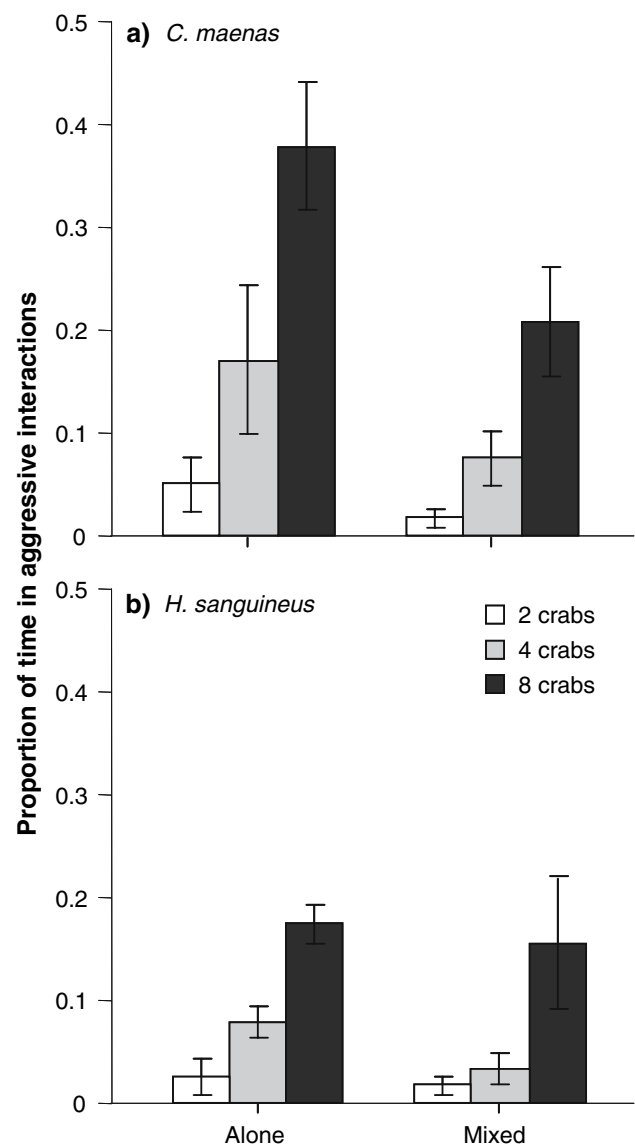


Fig. 3 Proportion of time spent in aggressive interactions by *C. maenas* (a) and *H. sanguineus* (b) (mean \pm SE, $n = 3$) when paired with conspecifics only (alone) or in mixed species assemblages (mixed) at two, four, or eight crabs per 0.2-m² chamber. Mixed species assemblages contained a 1:1 ratio of *C. maenas* and *H. sanguineus*

Discussion

Nonindependent effects of multiple predator species do not occur uniformly wherever species overlap; rather, they are often spatially and temporally variable due to changes in various factors, including habitat complexity (Finke and Denno 2002; Warfe and Barmuta 2004), habitat type (Griffen and Byers 2006b), and prey density (Soluk 1993; Losey and Denno 1998; Vance-Chalcraft and Soluk 2005b; Griffen 2006). Our study demonstrates that effects of multiple predator species can also differ with predator density.

We determined that multiple predator effects can influence the survival of primary prey species, even in the presence of a diverse prey community. Evidence of consumption of alternative prey types was present in our experiment, and, although not quantified, predation probably reduced the availability of these alternative prey through successive trials (because the same plots were used for each successive trial). However, we found no evidence of increasing predation pressure on focal mussel prey during successive trials that may have resulted from depletion of alternative prey. Furthermore, comparisons of observed and expected predation did not differ across trials (nonsignificant interaction term with block, $P > 0.25$). Thus, while the presence of naturally occurring alternative prey probably diluted the multiple predator effects detected here, this dilution did not occur in a systematic manner that would have influenced our results.

Carcinus maenas eats less and broadens its diet as a result of interference from both conspecifics and from heterospecifics (Fig. 2; Griffen 2006; Smallegange et al. 2006; Griffen et al. 2007b). *Hemigrapsus sanguineus* predation also decreases at high conspecific densities (Fig. 2a; Griffen and Delaney 2007a), but is not influenced by the presence of *C. maenas* (Griffen et al. 2007b). Thus, the risk reduction observed at the two lowest predator densities (Fig. 2b) was likely due to reductions in *C. maenas* mussel consumption because of interactions with both *H. sanguineus* and with conspecifics, explaining why effects were substitutable at low densities (Fig. 2b). Based on this assertion that *H. sanguineus* did not eat fewer mussels in the presence of *C. maenas*, more than 80% and more than 60% of the mussels mortality was due to *C. maenas* consumption when one and two predators of each species foraged together, respectively.

In contrast, at high predator densities the two species had similar influences on mussel mortality because of drastic reductions in *C. maenas* predation at high predator densities (Figs. 1, 2a). Additionally, because *H. sanguineus* also reduces mussel consumption at high conspecific densities (Fig. 2a; Brousseau and Baglivo 2005), conspecific interference that influences both species was stronger than heterospecific interference that influences only *C. maenas*, resulting in low per capita predation by both species that combined additively.

This pattern of increasing the relative importance of conspecific interference as predator density rises may be general across systems. Based on ecological theory, intraspecific competition must be greater than interspecific competition in order for competitors to coexist. Also, predator interactions that result in interference competition generally become stronger or more frequent with greater predator density (Fig. 3, and see references cited in Introduction). Putting these two factors together, we may expect

conspecific interference to become progressively more important relative to heterospecific interference if densities of multiple predator species increase together.

In addition to reduced foraging, other mechanisms may have contributed to prey survival in our field experiment. Both *C. maenas* and *H. sanguineus* broaden their diets with increasing competitor density (Brousseau and Baglivo 2005; Griffen et al. 2007b). Additionally, similar levels of prey survival across all predator densities (Fig. 2a) suggests that prey may have experienced some degree of refuge at low density. Thus, reduced foraging, diet shifts, crab mortality due to cannibalism and/or intraguild predation, and low density refuge for prey may have combined to reduce prey mortality.

Over much of the region where these two species overlap (central to southern Gulf of Maine), *H. sanguineus* is much more dense than *C. maenas* (Griffen and Delaney 2007a). Thus, while our experiment demonstrates that conspecific interference for *C. maenas* can be as strong as or stronger than interference from *H. sanguineus* on a per capita basis, interference from *H. sanguineus* may be functionally more important due to its higher densities. Consistent with this, the contribution of mussels to the diet of *C. maenas* is negatively correlated with *H. sanguineus* densities across sites within the Gulf of Maine, but is uncorrelated with the much lower conspecific densities (Griffen et al. 2007b). In contrast to the importance of predator interference for *C. maenas* foraging, both conspecific and heterospecific interference appear to be relatively unimportant for *H. sanguineus* foraging (Griffen et al. 2007b), likely facilitating its high population densities (Griffen and Delaney 2007a).

Predator density may be particularly important to multiple predator effects in systems with intraguild predation (predation among predators). Intraguild predation can cause nonindependent effects of these and other predator species through prey switching by top predators (from consuming shared prey to consuming intermediate predators) and reduced foraging by intermediate predators in the presence of top predators (Crumrine and Crowley 2003; Griffen and Byers 2006b). These mechanisms may each become stronger with increased densities of intermediate predators (Stephens and Krebs 1986) and top predators (Lima and Dill 1990; Lima 1998), respectively. Intraguild predation and cannibalism that increased with predator density were observed in our field experiment and may have contributed to reduced mussel consumption. In general, multiple predator effects caused by intraguild predation between these crabs are negatively correlated with the quality of refuge habitat that limits intraguild predation (Griffen and Byers 2006b), and the densities of both species increase with the density of boulders that provide refuge habitat (Griffen et al. 2007b). By

extrapolation then, multiple predator effects may potentially become less important as boulder coverage increases (Griffen and Byers 2006b), both because of the mitigating influence of refuge habitat and because of the overriding importance of conspecific interference at high predator densities (Fig. 2b). The interaction between factors that influence multiple predator effects, such as habitat type and species density, merits further study.

Previous studies have highlighted the importance of prey density in determining the outcome of combined predation by multiple species (Soluk 1993; Losey and Denno 1998; Vance-Chalcraft and Soluk 2005b; Griffen 2006). As with systems with a single predator species (Abrams and Ginzburg 2000), prey density and predator density may interact to influence the combined effects of multiple predator species. Because predators often aggregate to areas of high resource abundance (Fretwell and Lucas 1970), there is often a positive correlation between prey density and predator density. Predator and prey density have simultaneous, but independent impacts on predation rates of *C. maenas* and *H. sanguineus* when each forages independently – per capita predation rates increase with prey density and decrease with predator density (Griffen and Delaney 2007a). However, to the best of our knowledge, there is no study to date that has simultaneously co-varied prey density and predator density to examine their combined impacts on multiple predator effects in this or any other system.

In conclusion, predator density is likely to have a large influence on multiple predator effects across most systems, just as it does in other ecological processes. Incorporating the range of natural predator densities into multiple predator studies and further investigating how predator density interacts with other important factors, such as prey abundance and refuge use, to influence multiple predator effects should therefore improve the applicability of experimental results and increase our understanding of natural systems.

Acknowledgments Thanks to D. Niemaszyk for assistance in conducting the field experiments. We thank I. Altman, A. Blakeslee, J. Buck, J. Byers, A. Freeman, T. Guy, W.J. Lee, L. Page, C.H.P. Peterson, O. Schmitz, G. Trussell, and anonymous reviewers for comments on the manuscript. We also thank Shoals Marine Laboratory for use of their facilities. This work was supported in part by an NSF grant to the Shoals Marine Laboratory in support of the Research for Undergraduates program, and by a University of New Hampshire Dissertation Fellowship.

References

- Abrams PA, Ginzburg LR (2000) The nature of predation: prey dependent, ratio dependent or neither? *Trends Ecol Evol* 15:337–341
- Arditi R, Akcakaya HR (1990) Underestimation of mutual interference of predators. *Oecologia* 83:358–361
- Arditi R, Ginzburg LR (1989) Coupling in predator–prey dynamics: ratio dependence. *J Theor Biol* 139:311–326
- Billick I, Case TJ (1994) Higher order interactions in ecological communities: what are they and how can they be detected? *Ecology* 75:1529–1543
- Bourdeau PE, O'Connor JN (2003) Predation by the nonindigenous Asian shore crab *Hemigrapsus sanguineus* on macroalgae and molluscs. *Northeast Nat* 10:319–334
- Brousseau DJ, Baglivo JA (2005) Laboratory investigations of food selection by the Asian shore crab *Hemigrapsus sanguineus*: algal versus animal preference. *J Crustac Biol* 25:130–134
- Brousseau DJ, Kriksciun K, Bagliva JA (2003) Fiddler crab burrow usage by the Asian crab, *Hemigrapsus sanguineus*, in a Long Island Sound salt marsh. *Northeast Nat* 10:415–420
- Clark ME, Wolcott TG, Wolcott DL, Hines AH (1999) Intraspecific interference among foraging blue crabs *Callinectes sapidus*: interactive effects of predator density and prey patch distribution. *Mar Ecol Progr Ser* 178:69–78
- Connell JH (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Cthamalus stellatus*. *Ecology* 42:836–849
- Crumrine PW, Crowley PH (2003) Partitioning components of risk reduction in a dragonfly–fish intraguild predation system. *Ecology* 84:1588–1597
- DeGraaf JD, Tyrrell MC (2004) Comparison of the feeding rates of two introduced crab species, *Carcinus maenas* and *Hemigrapsus sanguineus*, on blue mussel, *Mytilus edulis*. *Northeast Nat* 11:163–167
- Ebling FJ, Kitching JA, Muntz L, Taylor CM (1964) The ecology of Lough Ine. XIII. Experimental observations of destruction of *Mytilus edulis* and *Nucella lapillus* by crabs. *J Anim Ecol* 33:73–82
- Eklöv P, VanKooten T (2001) Facilitation among piscivorous predators: effects of prey habitat use. *Ecology* 82:2486–2494
- Elnor RW (1981) Diet of green crab *Carcinus maenas* (L.) from Port Herbert, southwestern Nova Scotia. *J Shellfish Res* 1:89–94
- Elnor RW, Hughes RN (1978) Energy maximization in the diet of the Shore Crab, *Carcinus maenas*. *J Anim Ecol* 47:103–116
- Finke DL, Denno RF (2002) Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. *Ecology* 83:643–652
- Fretwell SD, Lucas HL (1970) On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:16–19
- Griffen BD (2006) Detecting emergent effects of multiple predator species. *Oecologia* 148:702–709
- Griffen BD, Byers JE (2006a) Intraguild predation reduces redundancy of predator species in multiple predator assemblage. *J Anim Ecol* 75:959–966
- Griffen BD, Byers JE (2006b) Partitioning mechanisms of predator interference in different habitats. *Oecologia* 146:608–614
- Griffen BD, Delaney DG (2007a) Species invasion shifts the strength of predator dependence. *Ecology* (in press)
- Griffen BD, Guy T, Buck J (2007b) Inhibition between invasives: a newly introduced predator moderates the impacts of a previously established invasive predator. *J Anim Ecol* (in press). doi: 10.1111/j.1365-2656.2007.01304.x
- Hairston NG, Smith FE, Slobodkin LB (1960) Community structure, population control, and competition. *Am Nat* 94:421–425
- Harvey BC, White JL, Nakamoto RJ (2004) An emergent multiple predator effect may enhance biotic resistance in a stream fish assemblage. *Ecology* 85:127–133
- Holling CS (1959) The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Can J Entomol* 91:293–320
- Jensen GC, McDonald PS, Armstrong DA (2002) East meets west: competitive interactions between green crab *Carcinus maenas*, and native and introduced shore crab *Hemigrapsus* spp. *Mar Ecol Progr Ser* 225:251–262

- Lima SL (1998) Stress and decision-making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Adv Study Behav* 27:215–290
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640
- Lohrer AM, Whitlatch RB (2002a) Interactions among aliens: apparent replacement of one exotic species by another. *Ecology* 83:710–732
- Lohrer AM, Whitlatch RB (2002b) Relative impacts of two exotic brachyuran species on blue mussel populations in Long Island Sound. *Mar Ecol Progr Ser* 227:135–144
- Lohrer AM, Whitlatch RB, Wada K, Yasuo F (2000) Home and away: comparison of resource utilization by a marine species in native and invaded habitats. *Biol Invas* 2:41–57
- Losey JE, Denno RF (1998) Positive predator–predator interactions: Enhanced predation rates and synergistic suppression of aphid populations. *Ecology* 79:2143–2152
- Mansour RA, Lipcius RN (1991) Density-dependent foraging and mutual interference in blue crabs preying upon infaunal clams. *Mar Ecol Progr Ser* 72:239–246
- McDermott JJ (1998) The western Pacific brachyuran *Hemigrapsus sanguineus* (Grapsidae) in its new habitat along the Atlantic coast of the United States: feeding, cheliped morphology and growth. In: von Vaupel Klein JC (eds) *Crustaceans and the biodiversity crisis*. Brill, Leiden, pp 425–444
- Mistri M (2003) Foraging behaviour and mutual interference in the Mediterranean shore crab, *Carcinus aestuarii*, preying upon the immigrant mussel *Musculista senhousia*. *Estuar Coast Shelf Sci* 56:155–159
- Peckarsky BL (1991) Mechanisms of intraspecific and interspecific interference between larval Stoneflies. *Oecologia* 85:521–529
- Saigusa M, Kawagoye O (1997) Circatidal rhythm of an intertidal crab, *Hemigrapsus sanguineus*: synchrony with unequal tide height and involvement of a light response mechanism. *Mar Biol* 129:87–96
- Schenk D, Bersier L, Bacher S (2005) An experimental test of the nature of predation: neither prey-nor ratio-dependent. *J Anim Ecol* 74:86–91
- Shaw RG, Mitchell-Olds T (1993) ANOVA for unbalanced data: an overview. *Ecology* 74:1638–1645
- Sietz RD, Lipcius RN, Hines AH, Eggleston DB (2001) Density-dependent predation, habitat variation, and the persistence of marine bivalve prey. *Ecology* 82:2435–2451
- Sih A, Englund G, Wooster D (1998) Emergent impacts of multiple predators on prey. *Trends Ecol Evol* 13:350–355
- Smallegange IM, van der Meer J, Kurvers RHJM (2006) Disentangling interference competition from exploitative competition in a crab-bivalve system using a novel experimental approach. *Oikos* 113:157–167
- Soluk DA (1993) Multiple predator effects – predicting combined functional-response of stream fish and invertebrate predators. *Ecology* 74:219–225
- Stephens DW, Krebs JR (1986) *Foraging theory*. Princeton University Press, New Jersey
- Taylor DL, Eggleston DB (2000) Effects of hypoxia on an estuarine predator–prey interaction: foraging behavior and mutual interference in the blue crab *Callinectes sapidus* and the infaunal clam prey *Mya arenaria*. *Mar Ecol Progr Ser* 196:221–237
- Tyrrell MC, Harris LG (1999) Potential impact of the introduced Asian shore crab *Hemigrapsus sanguineus*, in northern New England: diet, feeding preferences, and overlap with the green crab, *Carcinus maenas*. In: Pederson J (ed) *Proc Natl Conf Mar Bioinvas*. M.I.T Press, Cambridge, pp 208–220
- Vance-Chalcraft HD, Soluk DA (2005a) Estimating the prevalence and strength of non-independent predator effects. *Oecologia* 146:452–460
- Vance-Chalcraft HD, Soluk DA (2005b) Multiple predator effects result in risk reduction for prey across multiple prey densities. *Oecologia* 144:472–480
- Volterra V (1926) Variations and fluctuations in the numbers of individuals in animal species living together. Reprinted in 1931. In: Chapman RN (ed) *Animal ecology*. McGraw-Hill, New York
- Vonesh JR, Osenberg CW (2003) Multi-predator effects across life-history stages: non-additivity of egg- and larval-stage predation in an African treefrog. *Ecol Lett* 6:503–508
- Warfe DM, Barmuta LA (2004) Habitat structural complexity mediates the foraging success of multiple predator species. *Oecologia* 141:171–178

Copyright of *Oecologia* is the property of Springer Science & Business Media B.V. and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.