

# Inhibition between invasives: a newly introduced predator moderates the impacts of a previously established invasive predator

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## Summary

1. With continued globalization, species are being transported and introduced into novel habitats at an accelerating rate. Interactions between invasive species may provide important mechanisms that moderate their impacts on native species.
2. The European green crab *Carcinus maenas* is an aggressive predator that was introduced to the east coast of North America in the mid-1800s and is capable of rapid consumption of bivalve prey. A newer invasive predator, the Asian shore crab *Hemigrapsus sanguineus*, was first discovered on the Atlantic coast in the 1980s, and now inhabits many of the same regions as *C. maenas* within the Gulf of Maine. Using a series of field and laboratory investigations, we examined the consequences of interactions between these predators.
3. Density patterns of these two species at different spatial scales are consistent with negative interactions. As a result of these interactions, *C. maenas* alters its diet to consume fewer mussels, its preferred prey, in the presence of *H. sanguineus*. Decreased mussel consumption in turn leads to lower growth rates for *C. maenas*, with potential detrimental effects on *C. maenas* populations.
4. Rather than an invasional meltdown, this study demonstrates that, within the Gulf of Maine, this new invasive predator can moderate the impacts of the older invasive predator.

**Key-words:** amensalism, interference competition, predator density, spatial scale.

## Introduction

Invasion of marine habitats by non-indigenous species is of increasing global concern (Ruiz *et al.* 1997), with significant ecological and evolutionary implications for native populations (Groszholz *et al.* 2000; Cox 2004). Interactions between native and invasive species are common, and influence not only native communities, but also the success and impact of invasive species (e.g. Herbold & Moyle 1986; Robinson & Wellborn 1988; Baltz & Moyle 1993; Reusch 1998; Crawley *et al.* 1999; Byers 2002; deRivera *et al.* 2005). Because of high rates of species introductions, many systems harbour multiple invasive species that also interact with each other, potentially moderating or exacerbating their impacts on native communities. Recent work has focused largely on synergism among invaders and the possibility of invasion meltdown (where previous invaders facilitate the success of subsequent invaders,

Simberloff & Von Holle 1999; see references in the review by Simberloff 2006). However, negative interactions may be just as important in determining the impacts of an invader.

In a review of interactions among invaders, Simberloff & Von Holle (1999) concluded that interactions with positive (+) effects on one species and negative (–) effects on the other are by far the most extensively documented. Mutualism (+/+), competition (–/–) and commensalisms (+/0) have been reported less frequently, and no instances of amensalism (–/0) have been reported. Thus, more studies are needed to assess the threat of invasional meltdown with multiple invasions (Simberloff 2006).

The types of interactions (both positive and negative) that occur between species depend in part on their ecological roles within the community (i.e. predator, herbivore, primary producer, etc.). Based on the competitive exclusion principle (Hardin 1960), negative interactions (either competition or amensalism) may be expected when species use similar resources or perform similar ecological roles (i.e. when they are functionally redundant; Lawton & Brown 1993; Rosenfeld 2002). In this study we demonstrate an amensal

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interaction in the trophic functions of two invasive predatory crabs, *Carcinus maenas* (Linnaeus 1758) and *Hemigrapsus sanguineus* (De Haan 1835), by which resource use by the first invader is moderated through negative interactions with the subsequent invader.

*C. maenas*' many invasions have resulted in a cosmopolitan range that includes the east and west coasts of North America, South Africa and Australia (Grosholz & Ruiz 1996). *C. maenas* was first noted on the Atlantic coast of North America in New York and New Jersey in 1817 (Say 1817), and spread into the Gulf of Maine by the early 1900s (Rathburn 1905). Because of its aggressive nature, *C. maenas* can have detrimental impacts on invaded communities (Grosholz & Ruiz 1996; Grosholz *et al.* 2000). Its frequent predation on mollusks (Ropes 1968) makes bivalve populations particularly vulnerable (e.g. soft-shelled clams; Glude 1955). The native blue mussel *Mytilus edulis*, an important species ecologically on open coast shores of New England (Menge 1976), is a major component of *C. maenas*' diet (Elner 1981). *C. maenas* can consume mussels at very high rates, with destructive consequences for mussel populations (Ebling *et al.* 1964).

Recently, the Asian shore crab *H. sanguineus*, has invaded much of the same region along the east coast of North America. First documented in New Jersey in 1988 (Williams & McDermott 1990), *H. sanguineus* spread rapidly into the Gulf of Maine within less than a decade (McDermott 1998a). Similarly to *C. maenas*, *H. sanguineus* also consumes large quantities of mussel prey (Ledesma & O'Connor 2001; Bourdeau & O'Connor 2003; DeGraaf & Tyrrell 2004; Brousseau & Baglivo 2005) and has been implicated in significant reductions in mussel populations within Long Island Sound (Lohrer & Whitlatch 2002b).

Although *C. maenas* is found more broadly (e.g. subtidally and in soft sediment habitats), both of these species are found abundantly in rocky intertidal areas, where extensive overlap exists in both diet and habitat use (Tyrrell & Harris 1999; Lohrer *et al.* 2000; Jensen, McDonald & Armstrong 2002). Similarity in resource use in turn leads to lower use of refuge habitat by *C. maenas* in areas where both crabs are found (Jensen *et al.* 2002), and aggressive interactions between the species while foraging (Jensen *et al.* 2002) that can reduce the combined impacts of these predators on shared prey (Griffen 2006; Griffen *et al.* 2006a,b). Additionally, negative interactions between these crabs have led to the apparent displacement of *C. maenas* from rocky intertidal habitats in southern New England (Lohrer & Whitlatch 2002a); however, *C. maenas* within the Gulf of Maine have not yet been displaced, and the two species currently coexist within rocky intertidal habitats (Griffen & Byers 2006b).

In this study we examine resource use and interactions between invasive populations of *C. maenas* and *H. sanguineus* in the region where they currently overlap (central Massachusetts to central Maine). We first measure densities of both species at large scales (sites separated by > 1 km), intermediate scales (coves within a single site separated by ~50–100 m) and local scale (within individual 0.5 m<sup>2</sup> sampling quadrats) in

order to determine whether densities and distributions are consistent with previously documented trends in resource use and interactions between the species. We expect that densities of the two species will vary in relationship to each other based on different processes at each spatial scale. Specifically, crab densities at the large scale are determined mainly by patterns of larval settlement (Moksnes 2002; Thresher *et al.* 2003) and subsequent crab mortality (Moksnes 2004), and should display a latitudinal gradient reflecting the expansion of *H. sanguineus*' range and subsequent displacement of *C. maenas* (Lohrer & Whitlatch 2002a). Crabs move tens of metres over a single tidal cycle in response to resources availability (Brousseau *et al.* 2002; Moksnes 2002), and densities at intermediate scales should be correlated positively at this scale due to similar resource requirements of the two species (McDermott 1998a; Tyrrell & Harris 1999; Lohrer *et al.* 2000). Finally, crab densities at the local scale should reflect competitive/aggressive interactions between individual crabs, and a negative correlation is therefore expected (Jensen *et al.* 2002).

In addition to sampling population densities and distributions, we determined how foraging by both species is influenced by interactions between the species using field experiments and an examination of crab diets throughout the region of overlap. We did this to determine whether documented negative interactions influence these species equally or whether impacts are asymmetrical. Finally, we examine how mussel consumption influences growth rates to infer possible implications for negative interactions between the species that reduce mussel consumption.

## Methods

### SPECIES DENSITIES OVER DIFFERENT SPATIAL SCALES

We examined densities of both invasive predator species at three spatial scales in order to examine resource use and interactions between the species in the region of overlap. All sampling was conducted at moderately exposed sites characterized by extensive intertidal boulder fields. We are concerned here with interactions between crabs that potentially share the same food resources. Mussels are a preferred food item for both species (Ropes 1968; Brousseau & Baglivo 2005) and may therefore play an important role in the distribution of these species and in competitive interactions between the species (Jensen *et al.* 2002). We therefore report on sizes of crabs that readily consume mussels (*C. maenas* ≥ 20 mm carapace width (CW), *H. sanguineus* ≥ 18 mm CW) (Ropes 1989).

Sampling at the three different scales was performed specifically to examine the scale-specific hypotheses described above. We therefore did not use a nested sampling design (i.e. sampling differed at each scale) that would have facilitated comparisons across scales, as such comparisons were not our purpose. Sampling at the large scale was conducted during June and July 2006 at 14 sites from central Massachusetts to central Maine (range = 175 km), representing the range over which extensive overlap between *C. maenas* and *H. sanguineus* occurs in rocky intertidal areas. Differences in environmental factors across sites were limited due to the relatively small

geographical scale of our sampling and because we selected sites that had similar topography. At each site we determined crab density and mussel density within 15 randomly placed 1 m<sup>2</sup> quadrats at approximately 0.5 m above mean low water. Sampling within each site was conducted within a 200 m region of coastline. We used separate multiple regressions for each species to examine how mean crab density was influenced across sites by mean density of heterospecific crabs, mean mussel density and latitude. As crab densities and mussel density were each correlated with latitude, we used residuals of crab and mussel densities (after accounting for latitude) as response variables in each analysis to avoid multicollinearity (Graham 2003). With this and all other multiple regression analyses presented here, final models were selected using a stepwise procedure with 0.25 probability to enter the model and 0.15 probability to leave (Sokal & Rohlf 1995). Model assumptions for these and other analyses were tested by visual inspection of residual plots and appropriate transformations were performed when necessary.

Sampling at the intermediate and local scales was conducted at Odiorne Point, NH during July 2005. This site was chosen due to accessibility and because it has a series of coves, each separated by bedrock outcroppings, which facilitated designation of separate intermediate scale sampling areas. Within 15 separate coves we sampled from 15 randomly placed quadrats (0.5 m<sup>2</sup>) at approximately 0.5 m above mean low water. Sampling within each cove was conducted within a 5 × 20 m area. Densities of the two crabs at the intermediate scale were determined from mean densities of each species among coves.

Within each cove we also quantified the abundance of important resources. *C. maenas* and *H. sanguineus* utilize several resources for food and shelter, including mussels (Ropes 1968; McDermott 1998b; Lohrer *et al.* 2000; Ledesma & O'Connor 2001; Lohrer & Whitlatch 2002b), barnacles (Rangeley & Thomas 1987; McDermott 1998b; Lohrer *et al.* 2000), macroalgae (Lohrer *et al.* 2000; Tyrrell & Harris 1999) and rocks (Ledesma & O'Connor 2001; Jensen *et al.* 2002). We determined the percentage cover of macroalgae (*Ascophyllum nodosum* and *Fucus* spp.) and rocks using a 100-point, 5 × 20 m grid running parallel lengthwise to the water. We determined the density of mussels and barnacles within six separate, randomly placed 0.5 m<sup>2</sup> quadrats within each cove. While both of these species have specific size preferences for mussel prey (Elner & Hughes 1978; DeGraaf & Tyrrell 2004), both are capable of consuming mussels over a wide size range (McDermott 1998b; B.D. Griffen, personal observation). We therefore determined total mussel density rather than simply the density of mussels within the preferred size ranges. To assess potential aggregation of crabs across coves (i.e. at intermediate scales) to each of the resources listed above, we used separate multiple regression analyses for each species. Rocks were correlated positively across sites with mussels and macroalgae. We therefore avoided problems of multicollinearity using residuals of the less important variables as recommended by Graham (2003), and by considering rocks to be ecologically most important for *H. sanguineus* (Ledesma & O'Connor 2001), and mussels to be most important for *C. maenas* (based on individual correlation coefficients of *C. maenas* to each of these variables).

Crab densities at the local scale were determined using the same data from Odiorne Point as were used for examining intermediate scales, but focusing on individual sampling quadrats rather than means from all sampling quadrates within a cove. We regressed *C. maenas* density against *H. sanguineus* density (both log-transformed) after removing quadrats where no crabs of either species were found.

## INFLUENCE OF CRAB DENSITY ON MUSSEL CONSUMPTION

We examined how the density of both conspecific and heterospecific crabs influenced mussel consumption by *C. maenas* and *H. sanguineus*. To do this, we examined gut contents of several crabs of each species ( $14 \pm 6$ , mean  $\pm$  SD) from each of the 14 sites used in our large scale sampling described above. Crabs were collected haphazardly from the mid to lower intertidal on the same mornings that we sampled crab density, and were then placed in 95% ethanol for later analysis. Both males and females from a range of sizes (*C. maenas* 22–65 mm CW,  $n = 142$ ; *H. sanguineus* 18–35 mm CW,  $n = 171$ ) were sampled, and only intermoult crabs (i.e. those with hard carapaces) were used. Because crabs forage most actively during night-time high tides (Lindberg 1980; Willason 1981; Batie 1983; Depledge 1984; Saigusa & Kawagoye 1997) we collected crabs during ebb tides at dawn. All sites were sampled within a 3-week period of time to minimize seasonal differences.

Gut contents of each crab were analysed by spreading the contents evenly over a premarked grid and identifying food items overlying each grid point using a dissecting microscope (Tyrrell & Harris 1999). Unidentifiable particles were counted as detritus. Percentage contribution of mussels to the diet was determined by dividing the number of grid points with mussels by the sum of grid points that had any food items for each crab. This was then averaged across all crabs for each species within each site. Only crabs with guts full enough to cover 10% of the grid points were used (*C. maenas*  $n = 88$ , *H. sanguineus*  $n = 117$ ).

We determined the importance of crab density and mussel availability for mussel consumption by both crabs using separate multiple regression analyses for each species. We used percentage contribution of mussels to the diet at each site as the response variable with mussel density, *H. sanguineus* density (square root-transformed to equalize spacing of values along the  $x$ -axis and avoid giving undue weight to values with very high crab densities), *C. maenas* density (square root transformed) and latitude for each site as potential explanatory variables. We also explored the possibility that any decreased mussel consumption was compensated by increasing consumption of other animal prey (barnacles, snails, amphipods, urchins). To do this we examined the correlation between mussels and each of these other prey species found in the guts. Increasing presence of these other food items with decreasing presence of mussels would indicate compensative feeding.

## EXPERIMENTAL EXAMINATION OF HETEROSPECIFIC EFFECTS ON FORAGING

We examined experimentally changes in foraging by *C. maenas* and *H. sanguineus* as a result of interactions in the field by examining the amount consumed and the diet of each species when foraging separately and together. We deployed 18 cages (0.21 m<sup>2</sup>, constructed of 1.27 cm wire mesh) at approximately 0.5–1.0 m above mean low water at Broad Cove, Isle of Shoals, located approximately 10 km off the coast of New Hampshire. Small boulders from the surrounding habitat with attached algal and faunal prey were placed haphazardly in the cages. We further supplemented each cage with 40 mussels and 10 g wet weight each of *Fucus* spp., *Ulva intestinalis*, *Chondrus crispus* and *Mastocarpus stellata*. An abundance of food was thus available in the cages and remained at the end of each trial. Food limitation was therefore not a factor. Crabs were starved for approximately 1 week before being assigned randomly to three treatments: one *H. sanguineus* only, one *C. maenas* only, and one *H.*

*sanguineus* and one *C. maenas* together (*C. maenas*:  $42.3 \pm 8.8$  and *H. sanguineus*:  $25.9 \pm 2.6$  mm CW, mean  $\pm$  SD). Crabs were placed inside cages and were allowed to forage for 48 h. Three trials were conducted during late July and early August 2005, yielding 18 replicates of each treatment.

Experiments were terminated during ebbing tides at dawn, and gut contents were then analysed as described previously. We determined percent gut fullness by counting the proportion of the grid points that were covered by food. Full guts of large crabs will cover more grid points than full guts of small crabs. We therefore corrected for differences in crab size by standardizing to the largest size crab for each species within the experiment (no. of grid points covered by gut content of crab Y  $\times$  largest crab size/crab Y size). Gut fullness for each species foraging independently was compared to gut fullness in the presence of a competitor using analyses of variance (ANOVAS) with presence and absence of a competitor as a fixed factor, and trial treated as a random factor (three levels). We also determined whether each species changed the proportion of foods in their diet in the presence of a competitor by comparing the gut contents of each predator species foraging independently and in the presence of a competitor using separate multiple analyses of variance (MANOVAS) for each species on arcsine square root-transformed proportion of diet composed of the major food items (mussels, barnacles, snails, amphipods, macroalgae and detritus).

#### EFFECT OF MUSSELS ON CRAB GROWTH

We examined experimentally whether changes in mussel consumption affect growth rates of *C. maenas* or *H. sanguineus*. We placed individual *C. maenas* (initial CW:  $20.7 \pm 1.6$ , mean  $\pm$  SD) and *H. sanguineus* (initial CW:  $16.8 \pm 3.7$ ) into enclosed 500 mL plastic containers with mesh sides, suspended in a flow-through aquarium at the University of New Hampshire coastal marine laboratory in Newcastle, NH.

We provided each crab with 5 g of the alga *Chondrus crispus* and one of 11 mussel abundances (< 5 mm shell length): 0, 4, 8, 12, 16, 20, 24, 32, 40, 50 or 60. Each of these treatments was repeated with one male and one female of each crab species. *C. crispus* was chosen because it is found abundantly throughout the Gulf of Maine, was frequently found in guts of field captured crabs and was favoured by both crab species over other species of macroalgae in preliminary trials. Crabs ate < 0.5 g day<sup>-1</sup> in preliminary feeding trials (T. Guy & B.D. Griffen, unpublished data), thus the 5 g we used provided excess food to sustain the crabs for 1 week (at which time it was replenished), allowing us to examine the effects of mussel consumption on crab growth without limiting food (i.e. growth was a function of proportion of diet composed of mussels rather than total amount of food eaten). Initial carapace width was measured after 1 week in the laboratory (rather than at the start of the experiment) to ensure that any growth was due to experimental treatments rather than to food consumption in the field prior to the start of the experiment.

The experiment ran for 14 weeks from June to September 2006. Each week we assessed the number of mussels consumed and the mass of remaining algae. We then provided each crab with fresh algae and the appropriate number of mussels. We included three controls that contained only algae to assess consumption-free changes in algal mass. At the end of the 14 weeks we measured the carapace width of each crab to assess growth. Crabs grow incrementally by moulting rather than continuously. With the size of crabs used, the experimental duration chosen was sufficient to allow zero, one or two moults over the course of the experiment, with the expectation that moulting would occur more frequently when more mussels were included in the diet. Total growth was compared between

the species using paired *t*-tests (grouped by mussel treatment within each sex). We compared the total number of mussels consumed over the duration of the experiment and the mass of algae consumed using separate analyses of covariance (ANCOVAs), with species and sex as fixed factors and mussel treatment as a covariate. We used multiple regression to compare percentage change in carapace width for each species separately based on sex, initial carapace width, total algal consumption over the duration of the experiment (corrected for changes in algal mass as observed in no-crab controls) and total number of mussels consumed over the duration of the experiment.

## Results

#### SPECIES DENSITIES OVER DIFFERENT SPATIAL SCALES

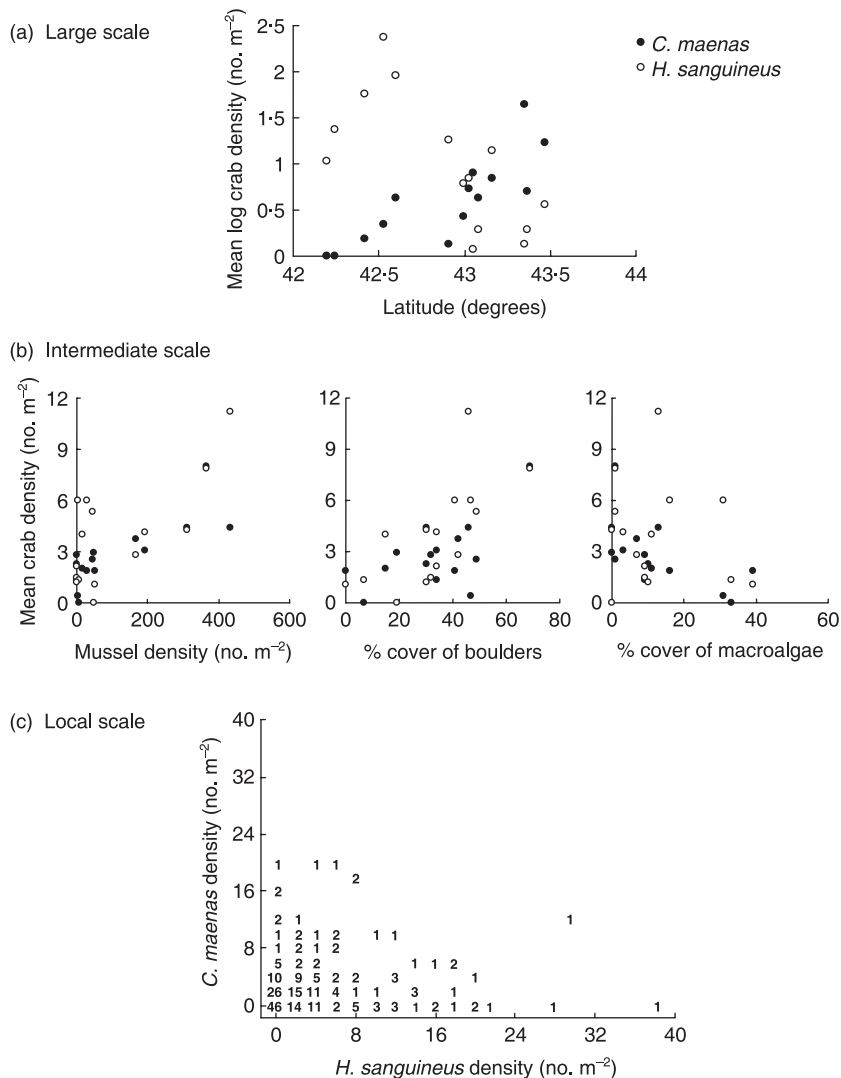
The correlation between the two invasive species was scale dependent. At the large scale, *C. maenas* and *H. sanguineus* showed an overall negative correlation in abundance across latitude. Specifically, *C. maenas* densities decreased from north to south ( $F_{1,12} = 23.66$ ,  $P = 0.0004$ ,  $R^2 = 0.66$ , Fig. 1a), while *H. sanguineus* densities increased from north to south ( $F_{1,11} = 15.57$ ,  $P = 0.002$ , Fig. 1a) and were also higher at sites with higher mussel densities ( $F_{1,11} = 5.67$ ,  $P = 0.037$  for mussel density; whole model  $F_{2,11} = 10.62$ ,  $P = 0.003$ , model  $R^2 = 0.66$ ). However, while densities of the two species were correlated negatively across sites ( $R^2 = 0.34$ ), after accounting for effects of latitude, the density of heterospecific crabs did not explain a significant amount of the variation in density for either species (not included in selected models at  $\alpha = 0.15$ ).

In contrast, at intermediate scales (within a single site), there was a weak positive correlation in the densities of the two species ( $F_{1,13} = 3.61$ ,  $P = 0.08$ ,  $R^2 = 0.22$ ). Multiple regression analyses indicated that densities of the two species showed similar positive correlations to food and habitat resources across covers at Odiorne Point. Specifically, at intermediate scales *C. maenas* density increased with mussel density ( $F_{1,12} = 20.96$ ,  $P = 0.0006$ , Fig. 1b) and decreased with percentage cover of macroalgae ( $F_{1,12} = 6.02$ ,  $P = 0.03$ , Fig. 1b) (77% of total variance in *C. maenas* density explained by these two factors,  $F_{2,12} = 20.51$ ,  $P < 0.0001$  for full model), while *H. sanguineus* densities were correlated positively with mussel densities ( $F_{1,10} = 11.11$ ,  $P = 0.008$ , Fig. 1b), percentage boulder coverage ( $F_{1,10} = 20.90$ ,  $P = 0.001$ , Fig. 1b) and correlated negatively with percentage cover of macroalgae ( $F_{1,10} = 4.93$ ,  $P = 0.05$ , Fig. 1b) (78% of total variance in *H. sanguineus* density explained by these three factors,  $F_{4,10} = 9.07$ ,  $P = 0.002$  for full model).

At the local scale at which crabs interact (within individual 0.5 m<sup>2</sup> sampling quadrats), although variance was high, a negative relationship was found between the two species ( $F_{1,187} = 10.06$ ,  $P = 0.002$ ,  $R^2 = 0.051$ , Fig. 1c).

#### INFLUENCE OF CRAB DENSITY ON MUSSEL CONSUMPTION

Percentage contribution of mussels to *C. maenas*' diet was highly variable, increasing with higher mussel density

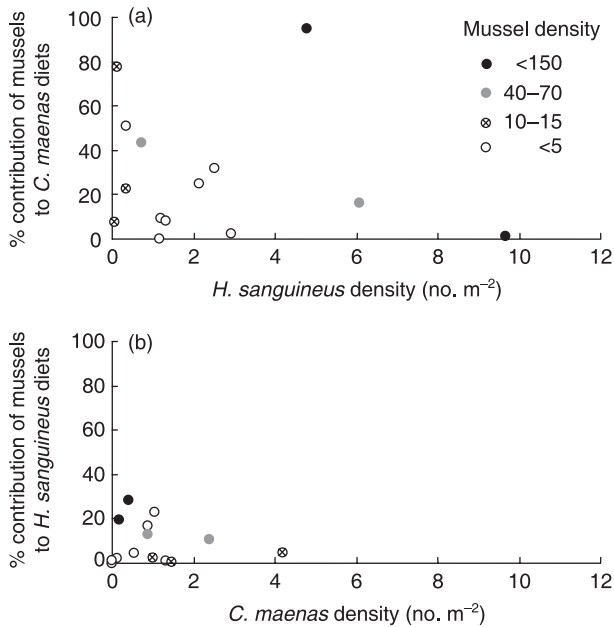


**Fig. 1.** Density of large *C. maenas* and large *H. sanguineus* at different spatial scales. (a) Large scale of species distributions across sites within the southern Gulf of Maine. Values are averages from 15 quadrats at each site. (b) Intermediate scale indicating crab density in relation to mussel density, percentage cover of boulders and percentage cover of macroalgae between coves separated by 50–100 m at Odiorne Point, NH. Values are averages from 15 quadrats from each cove. (c) Local scale on which individual crabs interact. Values represent the number of individual sampling quadrats [from sampling in (b)] with a specific density of each crab species. For example, 46 quadrats had no individuals of either species.

( $F_{1,11} = 11.15$ ,  $P = 0.006$ , Fig. 2a and decreasing with higher *H. sanguineus* densities ( $F_{1,11} = 7.85$ ,  $P = 0.017$ , Fig. 2a). Decreased mussel consumption by *C. maenas* was not compensated by increasing consumption of any other animal prey, as there was no correlation between the relative abundance of mussels and other animal prey in *C. maenas* guts ( $R^2 < 0.001$  each for barnacles, snails, amphipods and urchins). In contrast, percentage contribution of mussels to *H. sanguineus*' diet increased with higher mussel density ( $F_{1,12} = 8.33$ ,  $P = 0.014$ , Fig. 2b), but was not influenced by *C. maenas* density (not included in selected regression model at  $\alpha = 0.15$ ). Similarly, conspecific density did not influence mussel consumption by either species. Across all sites, a greater proportion of *C. maenas* diet was composed of mussels ( $30 \pm 8\%$ , mean  $\pm$  SE) than for *H. sanguineus* ( $9\% \pm 3\%$ ), and we found no influence of crab size on percentage contribution of mussels to the diet within the ranges of crab sizes examined here for either species ( $P > 0.20$ ; size ranges: *C. maenas* 22–65 mm CW, *H. sanguineus* 18–35 mm CW).

#### EXPERIMENTAL EXAMINATION OF HETEROSPECIFIC EFFECTS ON FORAGING

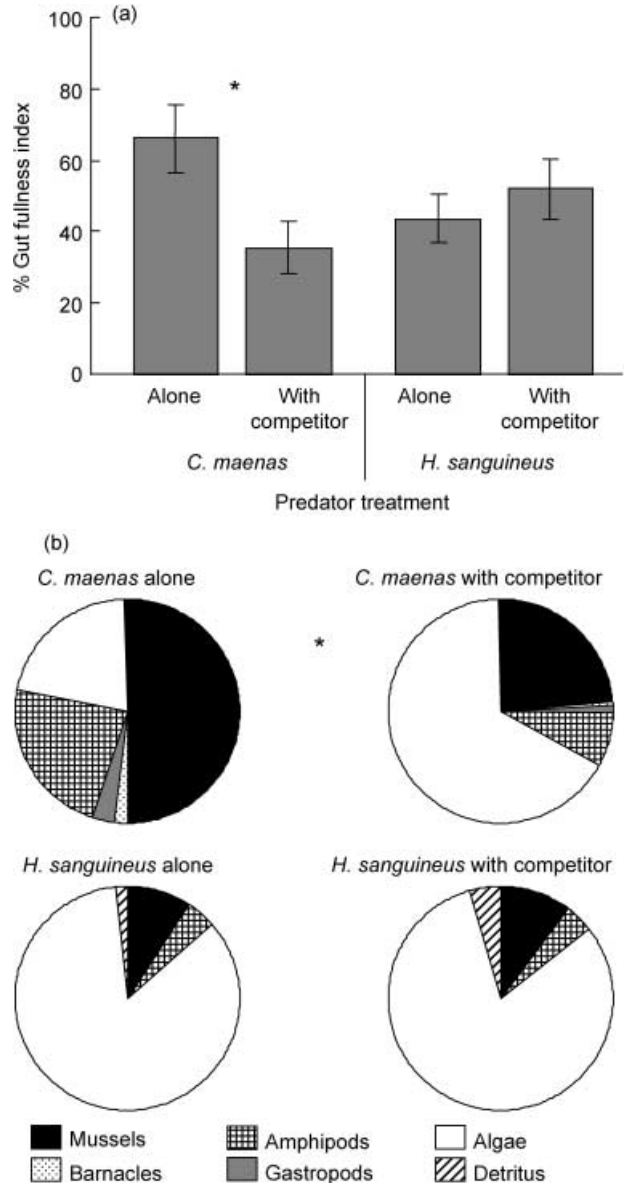
The presence of *H. sanguineus* strongly influenced prey consumption by *C. maenas* in our field caging experiment as evidenced by gut content analyses. *C. maenas* consumed less food when *H. sanguineus* was present ( $F_{1,32} = 7.72$ ,  $P = 0.009$ ; Fig. 3a), although the strength of *H. sanguineus*' influence varied across trials (its influence was stronger during the second trial than during the first or third trials, although the reason for this difference is unclear; trial  $F_{2,32} = 3.80$ ,  $P = 0.03$ , trial  $\times$  *H. sanguineus* presence  $F_{2,32} = 4.28$ ,  $P = 0.02$ ). Additionally, *C. maenas* consumed fewer mussels and amphipods and consumed more red algae when *H. sanguineus* was present (Wilks' lambda = 0.56,  $P = 0.006$ ; Fig. 3b). In contrast, *H. sanguineus* did not alter the amount of food that it consumed ( $F_{1,32} = 0.71$ ,  $P = 0.41$ ; Fig. 3a) or the content of its diet (Wilks' lambda = 0.75,  $P = 0.19$ ; Fig. 3b) when *C. maenas* was present.



**Fig. 2.** Percentage contribution of mussels to diets of *C. maenas* (a) and *H. sanguineus* (b) at several sites within the southern Gulf of Maine as a function of heterospecific crab density and mussel density. For presentation purposes the density of mussels is divided into four categories (shown in legend as ranges of density  $m^{-2}$ ), but was continuous for statistical analyses. Heterospecific crab densities were square root-transformed prior to analyses (see text).

#### EFFECTS OF MUSSELS ON CRAB GROWTH

*C. maenas* consumed more mussels in our laboratory growth experiment than *H. sanguineus* (ANCOVA,  $F_{1,40} = 8.09$ ,  $P = 0.007$ ), while *H. sanguineus* consumed more algae (ANCOVA,  $F_{1,40} = 30.26$ ,  $P < 0.0001$ ). Neither consumption of mussels or algae was influenced by crab sex (ANCOVAs,  $F_{1,40} < 1.48$ ,  $P > 0.2$ ). Overall, *C. maenas* grew more (0–40% growth) than *H. sanguineus* (0–30% growth) during the 14-week experiment (two-sided paired  $t$ -test,  $P < 0.0001$ ). Multiple regression indicated that growth for *C. maenas* increased with the number of mussels consumed ( $F_{1,18} = 9.61$ ,  $P = 0.006$ ), and with the total amount of algae consumed ( $F_{1,18} = 3.59$ ,  $P = 0.07$ ), with greater percentage change in carapace width for smaller crabs ( $F_{1,18} = 8.63$ ,  $P = 0.009$ ) (whole model  $F_{3,18} = 8.24$ ,  $P = 0.001$ ,  $R^2 = 0.58$ ). For *H. sanguineus*, growth also increased with the number of mussels consumed (regression,  $F_{1,19} = 15.68$ ,  $P = 0.0008$ ), with greater percentage change in carapace width for smaller crabs (regression,  $F_{1,19} = 38.31$ ,  $P < 0.0001$ ) (whole model  $F_{2,19} = 20.74$ ,  $P < 0.0001$ ,  $R^2 = 0.69$ ). However, if the lowest two abundances of mussels are removed from the analyses (zero and four mussels offered per week), the positive relationship between mussel consumption and growth disappears for *H. sanguineus* (regression,  $P = 0.18$ ), but persists for *C. maenas* (regression,  $P = 0.02$ ).



**Fig. 3.** (a) Percentage gut fullness (mean  $\pm$  SE,  $n = 18$ ) and (b) mean proportion of food items found in guts of *C. maenas* and *H. sanguineus* after foraging in field cages on standardized prey community for 48 h either alone or in the presence of a heterospecific competitor. Asterisk (\*) indicates difference in the absence and presence of competitor ( $P < 0.01$ ).

#### Discussion

Results of our sampling studies were consistent with previously documented interactions between *C. maenas* and *H. sanguineus* and resource utilization by each species at all three spatial scales. Specifically, we found that *H. sanguineus* abundance on the New Hampshire coast has increased relative to abundances seen in the late 1990s and early parts of this decade (Tyrrell, Guarino & Harris 2006). This fact, together with inverse densities of these species across latitudes in the southern Gulf of Maine (Fig. 1a), is consistent with the

advancing invasion of *H. sanguineus* and could potentially indicate displacement of *C. maenas* from Gulf of Maine rocky intertidal areas, similar to displacement from sites in Long Island Sound (Lohrer & Whitlatch 2002a). However, while there was an overall negative correlation between the two crabs across sites when all sites were considered, there appears to be a positive correlation in density of the two species across some adjacent sites (e.g. see the five southernmost sites, Fig. 1a). This may be due potentially to differences in the abundance of biotic and abiotic resources across these sites that are important to the density of both species, such as differences in boulder coverage (although we chose sites with similar boulder coverage to the extent possible).

The positive correlation between these species at the intermediate scale resulted from aggregation to areas with abundant food and refuge (Fig. 1b, Ledesma & O'Connor 2001; Moksnes 2002) and this similarity in resource use by these species (Fig. 1b, Tyrrell & Harris 1999; Lohrer *et al.* 2000) results in aggressive/competitive interactions between the species (Jensen *et al.* 2002), consistent with the negative correlation between these species on a local scale (Fig. 1c). The shift from a positive to a negative correlation in the density of *C. maenas* and *H. sanguineus* between intermediate and local scales is consistent with theoretical predictions of species that interact negatively yet respond similarly to underlying environmental factors (Byers & Noonburg 2003). Density patterns observed here were not influenced by our choice to report only densities of large crabs, as observed trends were strengthened when small crabs were included in analyses. However, densities of large *C. maenas* in intertidal habitats may increase at high tide relative to what we observed in our low tide sampling, as large subtidal crabs may move up with the tide to forage (Hunter & Naylor 1993).

Results of our gut content analysis on freely foraging crabs in the field and on crabs within our field experiment support that *H. sanguineus* is directly responsible for eliciting a diet shift in *C. maenas* from consuming mussels (a preferred food item in laboratory prey choice experiments, T. Guy & B.D. Griffen, unpublished data) to consuming more red algae (the less preferred prey item) (Fig. 3bB). Reduced mussel consumption by *C. maenas* in the presence of *H. sanguineus* may not reflect exploitative competition for a limited resource, as mussel density was high at multiple sites where *C. maenas* mussel consumption was low (Fig. 2a). Rather, it may reflect kleptoparasitism or displacement of *C. maenas* from prey by *H. sanguineus* (Jensen *et al.* 2002), or may potentially reflect a 'hardwired' behavioural response to high densities of any competing individuals (Connell 1980). A 'hardwired' response may further explain our counterintuitive finding that *C. maenas* consumed more algae in the presence of *H. sanguineus* (Fig. 3b). This shift would increase competition between these species, as algae comprised the bulk of *H. sanguineus*' diet. However, *C. maenas* may switch to algae in the presence of a competitor because algae requires less handling time than mussels.

*C. maenas* may reduce its foraging in similar ways because of interference from *H. sanguineus* or from conspecifics, despite our finding that mussel consumption in field-captured

*C. maenas* did not depend on *C. maenas* density (conspecific density was not included in regression model at  $\alpha = 0.15$ ). Combined prey mortality is equally reduced because of predator interference when these two species are combined in conspecific and heterospecific pairs (Griffen & Byers 2006a; Griffen 2006). Further, conspecific interference among experimentally high *C. maenas* densities greatly reduces mussel consumption (Smallegange, van der Meer & Kurvers 2006) and decreases predation in general (Griffen & Delaney, in press). Thus, the impact of *H. sanguineus* on *C. maenas* foraging detected in our field sampling and the absence of an impact of conspecifics may simply reflect frequent interactions of *C. maenas* with *H. sanguineus* because of their high density, and simultaneously infrequent interactions with other *C. maenas* because of their low density.

Maximum *H. sanguineus* densities across our sampling sites were more than twice as high as the maximum *C. maenas* densities (Fig. 1a), and mussel consumption by *C. maenas* was particularly low at some sites where *H. sanguineus* was very abundant (Fig. 2a), despite high mussel densities at these sites indicating that the effect of *H. sanguineus* on *C. maenas* was driven largely by these sites. However, given that *H. sanguineus* densities are frequently much higher than *C. maenas* densities within the invaded region (Fig. 1a, and Griffen & Delaney, in press), the impacts of *H. sanguineus* on *C. maenas* predation may frequently be larger than impacts of conspecifics. If this is the case, then diet changes by *C. maenas* resulting from interactions with *H. sanguineus* could potentially contribute to the replacement of *C. maenas* by *H. sanguineus* in rocky intertidal habitats. Reduced mussel consumption led to lower growth rates in *C. maenas*, due probably to a lack of protein (Poniat & Adelung 1980). Large differences in overall growth between crabs resulted from different numbers of moults (i.e. different intermoult frequency), with most crabs moulting once, crabs with many mussels in their diets moulting twice and crabs with few mussels in their diet moulting not at all. Reduced growth rates may potentially increase mortality by increasing the time necessary to achieve a size refuge from predation/cannibalism (deRivera *et al.* 2005), and could also potentially decrease population growth rates by increasing time to maturity, or by decreasing size at maturity (Twombly & Burns 1996).

In addition to the negative influence of *H. sanguineus* on *C. maenas* mussel consumption and resulting growth rates, *H. sanguineus* also consumes settling *C. maenas* post-larvae (Lohrer & Whitlatch 2002a) and displaces juvenile *C. maenas* from refuge habitat under rocks (Jensen *et al.* 2002). The impacts of *H. sanguineus* on *C. maenas* through these combined mechanisms appear to be significant and are probably responsible for the elimination of *C. maenas* from rocky intertidal habitat that it once inhabited in Long Island Sound (Lohrer & Whitlatch 2002a), and may also be contributing to the low *C. maenas* densities at sites with high *H. sanguineus* densities observed in our large scale sampling (southern most sites in Fig. 1a).

In contrast, no negative impacts of *C. maenas* on *H. sanguineus* have been detected in this or previous studies. Thus,

at least for several important processes (recruitment of new individuals to the population, use of refuge habitat to avoid predation threats and energy acquisition), interactions between these species are severely lopsided, representing amensal (−/0) interactions. The extent to which these individual amensal interactions result in a population level amensal interaction between these species depends on the extent to which *H. sanguineus* benefits energetically from consumption of *C. maenas* juveniles. However, regardless of whether absolute interactions between these species are amensal, this study highlights that, rather than facilitation and an invasional meltdown, interactions between multiple invasive species that fill similar niches may be inhibitory, moderating their impacts on native communities.

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