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Density-dependent predation by blue crabs *Callinectes sapidus* on natural prey populations of infaunal bivalves

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ABSTRACT: We used field and laboratory mesocosm experiments to examine the effects of the functional response of the blue crab *Callinectes sapidus* foraging on Balthic clams *Macoma balthica* in the upper Chesapeake Bay. Field experiments measured the density-dependent effect of blue crabs on clam patches in both mud and sand substrates at multiple sites spanning the natural range of clam densities, allowing us to examine the effects of larger-scale variation in prey abundance on prey mortality patterns. We compared the results of our field experiments to mesocosm experiments with 1 and 2 blue crabs to determine differences in the effects of single and multiple predators on the density-dependence of clam mortality. We observed predator behavior to identify mechanisms responsible for differences in prey mortality patterns. In the field, *M. balthica* mortality was not significantly density dependent, but the natural density of prey surrounding experimental patches had a negative density-dependent effect on clam mortality in mud. In the mesocosms, 1 or 2 blue crabs caused density-dependent mortality. Density dependence was weaker in mesocosms with 2 crabs. Agonistic behaviors were not significantly affected by clam density, but the presence of a conspecific increased a crab's foraging time at the lowest clam density. Changes in behavior when multiple crabs forage together may partly account for the reduction in density dependence of clam mortality. Predator responses such as the effects of conspecifics on foraging and patch choice that were lacking in the laboratory appear to be key in determining prey mortality patterns in the field. Larger-scale patterns of prey density variation were more important in determining prey mortality rates than the small-scale variation represented by the experimentally manipulated patches.

KEY WORDS: Predator–prey interactions · Foraging behavior · Density dependence · Functional response · Experimental scale · Agonism · *Callinectes sapidus* · *Macoma balthica*

INTRODUCTION

Predation is considered to be an important ecological determinant of prey abundance, distribution, and population structure. One of the key elements affecting predator–prey interactions is prey density. A predator's response to prey density can occur in several ways. Over relatively long time scales, a predator population can respond with changes in reproduction (numerical response) or the rate of growth and development (developmental response). Individual predators can respond on shorter time scales with behavioral changes in feeding rate (functional response) or movement pattern (aggregative response) (Murdoch 1971, Murdoch & Oaten 1975).

The forms of these various predator responses to changes in prey density are crucial to the outcome of predator–prey interaction and the persistence and stability of populations (Solomon 1949, Murdoch & Oaten 1975). For example, the form of the predator's functional response, the relationship between the per capita attack or consumption rate and prey density, can influence whether prey populations or patches will be regulated or extinguished by predation (Murdoch & Oaten 1975, Lipcius & Hines 1986, Anderson 2001). In terms of general foraging theory, the functional

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response is a description of an individual predator's behavior while in single prey patches of varying prey density. Functional response curves are usually categorized into 3 groups based on the initial shape of the curve before it levels off as the predator reaches satiation (Solomon 1949, Holling 1959). A Type I response increases linearly; a Type II response is a decelerating curve; and a Type III response is sigmoid, initially accelerating then decelerating. These 3 types of curves result in density-independent (Type I), inversely density-dependent (Type II), or initially density-dependent (Type III) percent mortality rates for the prey. Because density-dependent mortality may impart stability to a predator–prey system (Solomon 1949, Murdoch & Oaten 1975), the identification of a Type III functional response has been suggested to be indicative of a mechanism for promoting prey persistence by creating a low-density refuge for prey (Lipcius & Hines 1986, Eggleston et al. 1992).

Although the different types of functional response can be difficult to distinguish on the basis of the number of prey consumed, they cause divergent patterns in proportional mortality at low prey densities. That is, proportional mortality declines with decreasing prey density for a Type III functional response, increases with decreasing density for a Type II functional response, and does not change with density for a Type I response (Lipcius & Hines 1986, Eggleston et al. 1992, Taylor & Eggleston 2000, Seitz et al. 2001). Thus, the pattern of proportional mortality at low prey density is the distinguishing criterion for Type II vs. Type III functional responses, and, if the crucial prey densities are known, the response form can be determined with relatively few experimental prey densities (Dittel et al. 1995).

The functional response for a particular predator–prey system is typically determined in the laboratory, where individual predators are presented with a single prey patch of a given density (Holling 1959, Murdoch & Oaten 1975, Lipcius & Hines 1986, Eggleston 1990, Eggleston et al. 1992, Hagen & Mann 1992). This represents the predator–prey system at its simplest. What is usually of interest, however, is the the total effect of a predator population on the whole prey population, where the prey may be distributed in patches of spatially- and temporally-varying density and where other levels of response by the predator are possible. For example, individual predators are able to choose among an array of prey patches of varying prey (and perhaps conspecifics) density (i.e. an aggregative response; Murdoch & Oaten 1975, Anderson 2001). The presence of alternate prey species (Colton 1987, Chesson 1989), competitors (Goss-Custard et al. 1984, Holbrook & Schmitt 1992, Clark et al. 1999b), and other needs of the predator, such as predation avoidance (Lima & Dill 1990, Micheli 1997) and reproduction, may affect an individual's foraging choices. Moreover, the foraging behavior of individual predators may not be independent because of agonism, mating, other social interactions, synergy in prey capture, and physiological constraints.

Hence, the occurrence of a low-density prey refuge predicted from laboratory measures of a predator's functional response will depend on the nature of these other factors that contribute to the total effect of the predator population in nature. One of the goals of this study was to evaluate empirically whether predictions from a simple laboratory system will carry through to the more complicated situation in the field, and if not, to determine why.

In addition to prey density, other characteristics of prey patches can influence predator–prey interactions. For example, patch size can have effects on foraging behavior (Sih & Baltus 1987, Bach 1988, Whitlatch et al. 1997, Fulton & Bellwood 2002, Wellenreuther & Connell 2002). Despite these findings, most field experimental approaches to predator–prey interactions involve manipulations of small patches of prey, which, as a matter of practical logistics, may be much smaller than the scale of predator foraging behavior and movement (Cummings et al. 1997, Hines et al. 1997). When small experimental patches are used, the potential effects of the larger 'background' prey patches into which the experiment is inserted must also be considered. In this study, we explicitly incorporated the effects of larger-scale prey patches into the design of the experiment. We were thus able to examine the effects of larger-scale natural variation in prey patches on the outcome of our experiments and extend the level of inference for our results (Foster 1990, Beck 1997).

We examined the effects of a predator's functional response in a well-studied predator–prey system: blue crabs *Callinectes sapidus* Rathbun (Arthropoda: Crustacea: Portunidae) foraging on Balthic clams *Macoma balthica* (L.) (Mollusca: Bivalvia: Tellinidae) in the Rhode River subestuary of the upper Chesapeake Bay. Previous research has shown that single blue crabs foraging on *M. balthica* in the laboratory show a Type III (density-dependent) functional response in both mud and sand substrates (Eggleston et al. 1992), although sediment type affects functional response for some prey types (Lipcius & Hines 1986). In the field, blue crab predation on *M. balthica* was density dependent in 1 of 2 yr (Seitz et al. 2001).

We use a combination of field and mesocosm experiments to provide an additional test of the predictions from laboratory studies of blue crab functional responses and to begin investigating mechanisms that might explain the population effects of blue crabs for-

aging on clams. First, we conducted field experiments to measure the total effect of blue crabs on clams in patches of varying density in both mud and sand substrates. To examine the effects of the background prey density into which our experimental patches were placed, field experiments were conducted at multiple sites spanning the natural range of clam densities within the study area. Next, we conducted mesocosm experiments to determine if there were differences in the effects of single and multiple predators on the density-dependence of clam mortality. We were also able to determine if variation in predator behavior correlated to findings from the field studies.

This study complements and extends earlier research by: (1) expanding the field studies to incorporate the full range of natural prey density variation found in a well-studied ecosystem so that the results can be extrapolated to the larger natural prey population (Beck 1997), and (2) specifically seeking behavioral mechanisms that might be responsible for differences between single-predator laboratory functional response studies and field experiments.

Based on previous studies (Eggleston et al. 1992, Seitz et al. 2001), we expected that blue crab predation on *Macoma balthica* would be density dependent in both sand and mud substrates in the field. Blue crabs are highly agonistic, and aggressive interactions appear to decrease foraging efficiency (Mansour & Lipcius 1991, Clark et al. 1999b, 2000). Because aggressive interactions may compete with and be more likely during foraging (Clark et al. 1999a), we expected that foraging activity for multiple predators would be reduced relative to single foragers. Agonistic interactions should be most intense at low prey densities, where competition is heightened (Clark et al. 1999b, Triplet et al. 1999). If prey are in excess, a simple increase in predator numbers might be expected to eliminate density dependence by increasing mortality more at low prey densities than at high prey densities (where satiation may occur). However, in blue crabs, higher rates of agonism at high predator densities should at least partly counteract that. As a result, we predicted that an increase in the number of blue crabs in laboratory tanks would decrease but not eliminate density dependence in clam mortality.

MATERIALS AND METHODS

Study area. This study was conducted during the summer of 1998 at the Smithsonian Environmental Research Center, Edgewater, Maryland, USA, and the adjacent Rhode River (38° 51′ N, 76° 32′ W), a small (485 ha), shallow (≤4 m depth) subestuary of the lower mesohaline zone of Chesapeake Bay (Fig. 1). The bottom sediment is mostly fine, silty mud (~80%), with some regions of fine sand near shore (~20%) (Hines & Comtois 1985, Hines et al. 1990). During the study period, surface water temperature ranged from 20.5 to 27.5°C and salinity ranged from 6 to 9 ppt.

Study organisms. The blue crab *Callinectes sapidus* is a commercially important, seasonally abundant, epibenthic omnivore in the Chesapeake Bay (Hines et al. 1987). Although blue crabs consume a wide variety of species, including vegetation, fish, and other blue crabs, infaunal clams make up the majority of the diet of adult and subadult crabs in Chesapeake Bay (Laughlin 1982, Hines et al. 1990). Consistent with the blue crab's catholic diet, laboratory studies have found that individual foraging behavior is quite flexible and responds to a variety of factors. For example, the functional response of individual blue crabs can be affected by sediment type (Lipcius & Hines 1986), and previous feeding experience influences both feeding rate (Terwin 1999) and prey size selection (Micheli 1995).

Tracking studies in the Rhode River reveal that blue crabs tend to aggregate and concentrate feeding activ-

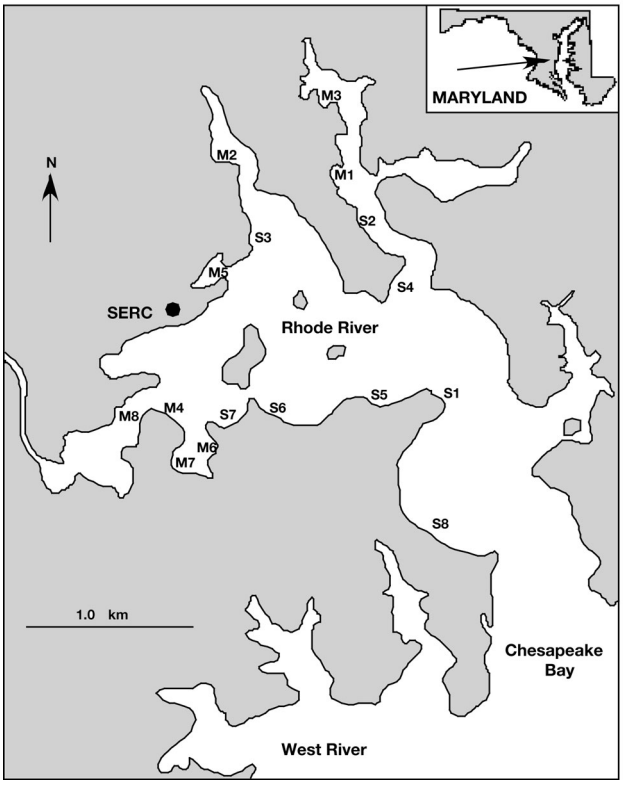

Fig. 1. Rhode River subestuary showing the location of the field experiment sites (sand substrate sites: S1 – S8; mud substrate sites: M1 – M8). The site labels correspond to Table 1. SERC = Smithsonian Environmental Research Center. The location of the study area in Maryland is shown in the inset

ity in areas of high clam density (Wolcott & Hines 1989, Clark et al. 1999a). Claw spreading, a characteristic blue crab threat display (Jachowski 1974), also increases in preferred prey patches because of increased agonistic encounters with other individuals (Clark et al. 1999a, 1999b). In the laboratory (Mansour & Lipicus 1991) and field enclosures (Clark et al. 1999b) individual crab feeding rates decline at higher predator densities as a result of agonism.

These studies show that blue crab distribution is a function of clam density (i.e. an aggregative response), and that behavioral changes (e.g. agonism) caused by predator aggregation also affect individual feeding rate (i.e. the functional response). The overall effect of blue crabs on clam populations is therefore a result of complex interactions between the functional response, aggregation, and agonism, but the relative contribution of, or interactions among, each of these factors has not been measured.

The Balthic clam *Macoma balthica* is a thin-shelled, infaunal deposit feeder and facultative suspension feeder that grows to about 40 mm shell length (SL). In Chesapeake Bay, *M. balthica* is widely distributed in both sand and mud substrates of meso- and polyhaline regions (Blundon & Kennedy 1982, Holland et al. 1987, Hines et al. 1990). While *M. balthica* is generally common and can reach high densities (>1000 m^{-2} during spring recruitment peaks), its abundance is also highly heterogeneous on many scales: seasonally (Blundon & Kennedy 1982), annually (Holland et al. 1987, Hines et al. 1990), between sediment types (Hines & Comtois 1985, Seitz et al. 2001), and spatially within sediment types (Table 1).

Juvenile clams are vulnerable to a variety of predators, but deep-buried adult clams attain a partial refuge from predators (Blundon & Kennedy 1982). Adult clams are subjected to sublethal siphon nipping by epibenthic fish, but the blue crab is the only common predator of adult *Macoma balthica* in the Rhode River (Hines et al. 1990).

Field experiments: total predator response. To measure the effect of clam density on mortality in the field, we conducted separate experiments at sites with sand and mud substrate. For each experiment, we haphazardly selected 8 sites from among areas with the proper substrate along undeveloped, gradually sloping shorelines, not likely to be disturbed by boaters (Fig. 1). To ensure we incorporated as wide a range of natural prey densities as possible, we sampled *Macoma balthica* density prior to the experiment. At each site, we took 4 0.166 m^2 × 30 cm-deep suction samples at 5 m intervals along a transect parallel to shore at a depth of 1 to 1.5 m below MLLW. We counted and measured the shell length (SL) of all *M. balthica* larger than 15 mm SL. The sites with muddy sand (hereafter, sand) substrate were sampled from 1 to 10 July 1998. Nine sites with mud substrate were sampled from 28 to 31 July, 1998; 1 site (*M. balthica* density = 0 clams m^{-2}) was dropped because large amounts of detritus in the mud interfered with suction sampling. Densities of large (>15 mm SL) clams were 1.51 to 43.67 clams m^{-2} in sand and 1.51 to 271.08 clams m^{-2} in mud (Table 1).

The experimental design incorporated 4 densities of marked, planted *Macoma balthica* (10, 20, 40, and 80 clams m^{-2}) replicated across each of the 8 sites. We used a wide range of densities because we could not predict where density-dependence would occur in the field. The logistics of planting and recovering clams limited us to relatively small (0.5 m^2) patches, yet we needed to have enough clams per patch to reasonably calculate proportional mortality, our main response variable of interest. Therefore, we restricted the lower limit of our density treatment to 10 clams m^{-2} (5 clams $patch^{-1}$).

Clams for the experiments were collected by suction dredging in mud and held in the laboratory in flow-through tanks until used. Only clams > 20 mm SL with a strong siphon-withdrawal response were used. Prior to an experiment, we marked all clams with paint on one valve, measured SL of a subset (10) with calipers, and randomly assigned the clams to treatment (density) groups.

We conducted the sand substrate experiment from 13 to 24 July 1998, and the mud substrate experiment from 11 to 21 August 1998. At each site, 4 0.5 m^2 patches were created at 10 m intervals along a transect

Table 1. *Macoma balthica.* Density of large (≥15 mm shell length) clams at experimental sites in the Rhode River during July, 1998. N = 4 suction samples per site (0.166 m^2 × 30 cm). Site labels as in Fig. 1

Substrate	Label	Site name	Density (no. m^{-2})
Sand	S1	Locust Point Tip	1.51
	S2	Bear Neck Creek 2	3.01
	S3	Selman Creek	6.02
	S4	Bear Neck Creek	7.53
	S5	Locust Point	7.53
	S6	East Murray Wharf	7.53
	S7	West Murray Wharf	13.55
	S8	Canning House Bay	43.67
Mud	M1	Bear Neck Creek Cove 2	1.51
	M2	Selman Creek Cove 1	15.06
	M3	Bear Neck Creek Island	16.57
	M4	Bagman's Wharf	54.22
	M5	Sheephead Cove	57.23
	M6	Boathouse Creek	97.89
	M7	Corn Island	198.80
	M8	Muddy Creek	271.08

parallel to shore at a depth of about 1 m below MLLW. Each square patch was assigned randomly to one of the experimental clam densities and marked with steel rods at the corners pushed flush with the substrate. Clams were gently pushed, siphon-end up, finger-deep into the sediment in a regularly spaced pattern within the patch. Existing clams were not removed from patches in order to replicate the setup of previous experiments (Seitz et al. 2001) and because of the large amount of potentially predator-attracting disturbance it would involve. Each patch was covered with a hardware cloth cage (7 mm mesh) for 3 d to allow sediment disturbance to subside and the clams to bury to their preferred depth (Eggleston et al. 1992) before the cages were removed to expose the clams to predators.

Seven days after cage removal, surviving marked clams were recovered by suction dredging to a depth of ~30 cm inside a 1 m diameter (0.79 m^2 area) sheet-metal cylinder placed around each patch. All living, marked clams as well as marked shell fragments were counted, and unmarked *Macoma balthica* were counted and measured. Because we recovered numerous marked shell fragments with damage characteristic of blue crab predation and no marked dead, whole clams, we assume that non-predatory mortality was negligible. The planted clams were not restrained from moving, and small *M. balthica* are known to move by creeping on the surface (Brafield & Newell 1961) or by drifting in the presence of a current (Sörlin 1988, Beukema & de Vlass 1989). However, our experimental clams were much larger than those reported to creep or drift, and numerous caged control plots in the field conducted for earlier studies as well as preliminary laboratory observations found no evidence that *M. balthica* >10 mm SL move laterally in either muddy or sandy sediments (A. H. Hines unpubl. data). Therefore, for analysis, we assumed that all marked clams not recovered alive had been eaten.

For analysis, we calculated proportional prey mortality rates (no. of clams missing/no. of clams planted) for each patch. The 2 substrate types were analyzed as separate experiments rather than treatments because the trials were not done concurrently, confounding sediment type and time. For each substrate type, we used an analysis of covariance model (ANCOVA) to examine the effects of planted clam density (fixed factor) and background clam density (covariate) on proportional clam mortality after confirming that the assumptions of equal slopes was met for the covariate (Underwood 1997). For background clam density, we used the average clam density at each site from the pre-experiment sampling. Proportional mortalities were log transformed to reduce heteroscedasticity based on examination of residual plots (Underwood 1997).

Because clam density was not measured at each patch and sites were sampled up to 2 wk prior to the density manipulation, background clam density represents a relative index of average *Macoma balthica* density in the area surrounding the patches at a given site, rather than a quantitative measure of wild clam density at each patch. Although we also measured the density of unmarked clams at each patch at the end of the experiment (when surviving marked clams were recovered), this estimate of clam density could be biased by the experimental treatments. The number of unmarked clams recovered from each patch at the end of the experiment was highly correlated to background density (sand: $r = 0.623$, $p < 0.001$; mud: $r = 0.754$, $p < 0.001$), and results of ANCOVAs using the density of recovered unmarked clams as the covariate are qualitatively similar to the results we report here.

Mesocosm experiment: functional response and behavior. We conducted a mesocosm experiment to examine the effects of blue crab density on predator functional response and behavior. The experiment was conducted in 8 outdoor, fiberglass tanks, each 1 m wide × 2 m long × 0.6 m deep. Each tank contained muddy sand from the Rhode River to a depth of 20 cm, 25 cm (depth from top of sand) of flow-through Rhode River water, and air stones for aeration. Two air-driven sponge filters provided additional aeration and helped improve water clarity for behavioral observations. We used 2 blue crab densities (1 or 2 crabs $tank^{-1}$) and 3 *Macoma balthica* densities (20, 40, or 80 clams m^{-2}) in a fully factorial design. We did not include the 10 clams m^{-2} treatment level used in the field experiment in order to reduce the number of treatment combinations and to reduce the likelihood of all the clams being consumed in the 2 crab treatments. Experimental crab densities are higher than those found naturally over large areas but are similar to those at prey patches where crabs aggregate (Clark et al. 1999b, 2000). Experimental clam densities fall within the lower end of natural clam densities in the Rhode River (Eggleston et al. 1992, Seitz et al. 2001) (Table 1).

Trials were run simultaneously in groups of 4 tanks. We rotated through the 6 treatment combinations systematically to keep approximately balanced numbers of replicates. Treatments were assigned randomly to the 4 tanks within a set of trials. Instances of trials in which a crab died or where no clam mortality occurred were dropped from the analysis. Final sample size for each treatment ranged from 6 to 10 replicates.

Macoma balthica were collected and held as described above. Large (≥130 mm carapace width [CW]) male intermolt blue crabs were collected from seines and baited crab pots and held in wire cages in the Rhode River or in an outdoor holding tank for up to 5 d until use. Prior to use, crabs were fed ad libitum clams,

mussels, and frozen fish. Crabs were not fed for 48 h prior to use in an experiment to standardize their hunger level.

Prior to the start of a trial, we marked all *Macoma balthica* with a dot of paint on the shell of a color unique to that set of trials. We also measured the size (SL) of a subset of 10 haphazardly selected clams. Clams were planted in a 1 m^2 patch at one end of the tank by gently pushing them about 10 cm into the sand in a regular pattern within the patch area. After a 24 h acclimation period, 1 or 2 large male crabs, individually marked with white paint on the carapace, were placed in the tank and allowed to forage for 48 h.

Table 2. *Callinectes sapidus*. Description of recorded crab behavior categories

Behavior	Description
Buried	Crab fully or partly beneath sediment surface
Sitting	Crab motionless on sediment surface
Locomotion	Directional walking, usually sideways, or swimming
Searching	Slow forward movement accompanied by probing with legs and chelae, frequent changes in direction
Digging	Excavating sediment, either with tips of both chelae or by dragging sediment in the crook of 1 bent cheliped
Feeding	Prey capture, handling, and consumption
Threat	Meral spread (extended chelipeds) (Jachowski 1974)
Fight	Contact with other crab, usually chela-to-chela

During the first 24 h of a trial, each tank was videotaped for 30 min during each of the following periods: dawn, day, dusk, and night. At the end of the trial, crabs were removed, checked for damage (lost limbs or carapace wounds), and released. Each tank was searched by hand to recover surviving clams and marked shell fragments.

We observed behavior by reviewing video-tapes and recording the duration of pre-defined activities (Table 2). Behaviors (mostly digging and fighting) that were very short in duration (less than 5 s) were simply noted as events. We also recorded the location (on or off the clam patch) of all activities. For analysis, we summarized the individual behaviors into 4 key general and foraging behavior variables and 3 agonistic behavior variables (Table 3). Duration variables were converted to proportions of total time observed. In trials with 2 crabs, we recorded behavioral data for both crabs but only used one (randomly chosen) for analysis.

We examined the effects of the experimental treatments (clam density and number of crabs) on several measures of clam mortality and crab behavior using fully factorial multivariate analysis of variance (MANOVA). We used one MANOVA to examine clam mortality and crab activity and foraging behavior. Because there was no agonism in treatments with 1 crab, we analyzed the effects of clam density on crab agonistic behavior in the 2 crab treatment only with a separate MANOVA. Variables were transformed when necessary (based on examination of residual plots) to minimize heteroscedasticity. When significant multivariate treatment effects were found, we conducted univariate tests of individual variables followed by post-hoc means comparisons (Student-Newman-Keuls [SNK] tests) where appropriate (Underwood 1997, Zar 1999). Summary data are reported as means ± 1 SE throughout, except where noted.

Table 3. *Callinectes sapidus*. Description of behavioral variables used in analyses

Category	Description
Activity and foraging	
Feeding frequency	Total number of feeding events
Foraging time (proportion)	Proportion of total time foraging = (search time + digging time + feeding time)/ total time observed
Active time (proportion)	Proportion of total time active = (foraging time + locomotion time + threat time + fight time)/total time observed
Active time on clam patch (proportion)	Proportion of total time active on clam patch = (active time on patch side of tank)/total time observed
Agonistic behaviors	
Agonism frequency	Total frequency of agonistic behaviors = number of fights + number of threats
Agonism time (proportion)	Proportion of total time spent in agonistic behavior = (fight time + threat time)/ total time observed
Agonism on patch (proportion)	Proportion of agonistic events on clam patch = number of agonistic events on patch/total frequency of agonism

Table 4. *Macoma balthica.* Analyses of covariance of log transformed proportional mortality of planted clams in field clam-density experiments. Background clam density is the covariate

Experiment	Source of variation	df	MS	*F*	p
Sand	Planted clam density	3	0.00756	2.242	0.106
	Background clam density	1	0.00143	0.425	0.520
	Error	27	0.00342		
Mud	Planted clam density	3	0.00143	0.359	0.783
	Background clam density	1	0.02898	7.283	0.012
	Error	27	0.00398		

RESULTS

Field experiments: total predator response

Planted clam size ranged from 23.8 to 38.4 mm SL (mean = 28.69 ± 0.20 mm, n = 180 measured) and did not differ significantly between experiments (*t*-test, p = 0.63).

In the sand substrate experiment, proportional mortality differed among the planted clam densities only at the p = 0.106 level (Table 4). However, mean clam mortality increased about 1.6-fold from the 10 clams m^{-2} to the 20 clams m^{-2} treatments (Fig. 2). These data suggest that mortality was weakly density dependent in this experiment. Background clam density, the covariate, did not have a significant effect on planted clam mortality (Table 4, Fig. 3a).

In the mud substrate experiment, planted clam density did not have a significant effect on proportional clam mortality (Table 4), which differed only slightly between treatment levels (Fig. 2). Background clam density, however, did have a significant effect (Table 4), with proportional mortality increasing with decreasing background clam density (Fig. 3b).

Mesocosm experiment: functional response and behavior

The *Macoma balthica* clams used in the functional response experiment ranged in size from 23.3 to 39.2 mm SL (mean = 28.4 ± 0.1 mm, n = 680 measured). Clams did not differ in mean, maximum, minimum, or variance of size (SL) among treatments (2-factor ANOVAs, all p > 0.2). The blue crabs used in the experiment ranged in size from 129 to 176 mm carapace width (mean = 145.06 ± 1.22 mm, n = 67) and did not differ in size between treatments (ANOVA, all p > 0.1). In the 2 crab treatments, crabs differed in size by less than 10% in all trials (mean = 2.93 ± 0.49%, n = 21).

Functional response

The multivariate main effects of clam density and crab density on the clam mortality and crab activity and foraging behavior variables were significant, although the interaction term was not (Table 5a). Univariate tests (2-way ANOVAs) were then conducted on the individual variables.

Proportional clam mortality was significantly affected by both clam density and crab density (Table 5b, Fig. 4). Clam mortality was higher in the 2-crab treatments and was density dependent across the lower range of the experimental clam densities (SNK test, p < 0.05). The interaction term was not significant according to ANOVA, suggesting that density dependence did not differ between crab densities. However, mean clam mortality was almost 3 times greater at 40 clams m^{-2} than at 20 clams m^{-2} in the 1 crab treatments, while in the 2 crab treatments, the highest mean mortality was only 1.2 times the lowest. Thus, while the overall ANOVA indicates that clam mortality is overall density dependent, trends in the means suggest that this density dependence may be stronger with 1 crab than with 2 crabs.

The number of clams eaten per crab tended to increase with clam density (Fig. 5), but the interaction

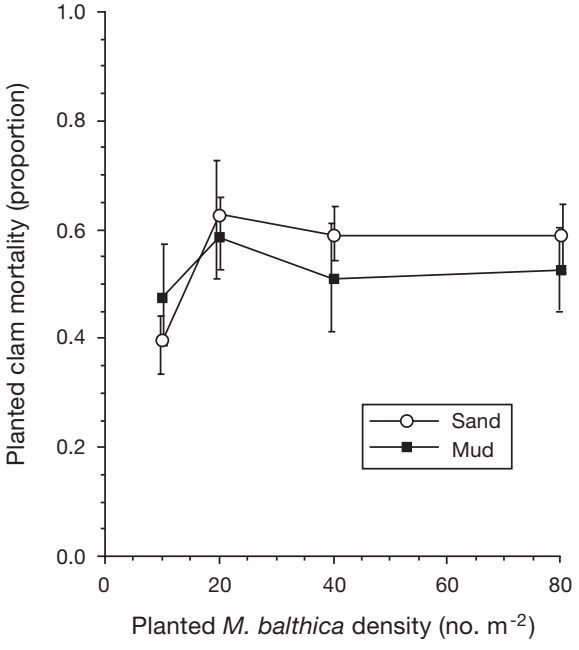

Fig. 2. *Macoma balthica*. Mean (±1 SE) proportional mortality of planted clams in relationship to experimental clam density in the sand and mud field experiments. Means and standard errors are backtransformed from $Y' = \mathrm{Log}_{10}(Y+1)$. N = 8

term was also significant (Table 5b). Means comparisons (SNK tests) found that, with 1 crab, the number of clams eaten per crab increased significantly between 20 and 40 clams m^{-2} but then leveled off, probably a result of satiation. With 2 crabs, the number of clams eaten per crab rose steadily across all clam densities. Crab density only had a significant effect at 40 clams m^{-2}, where the number of clams eaten per crab was higher in the 1 crab treatment.

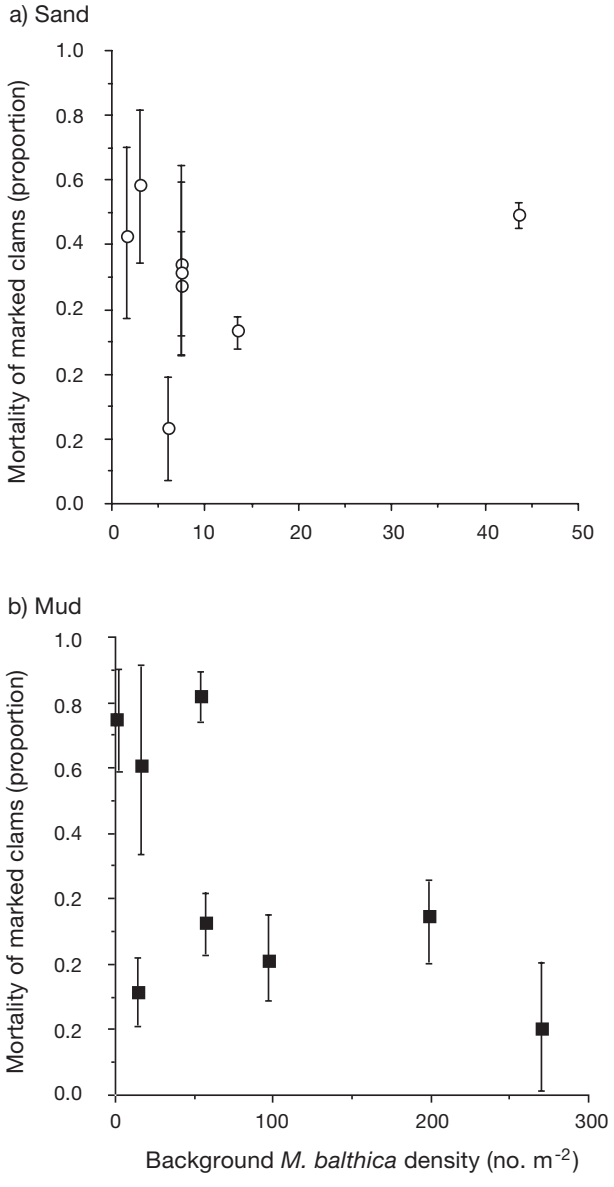

Fig. 3. *Macoma balthica*. Mean (±1 SE) proportional mortality of marked clams as a function of background clam density at (a) sand and (b) mud sites. Each point represents mean mortality for N = 4 patches at a single site. Means and standard errors are backtransformed from $Y' = \mathrm{Log}_{10}(Y + 1)$

Crab behavior

Crab behavior was successfully recorded for 59 to 137 min (mean = 109.56 ± 2.96 min) per trial. Observation time per trial did not differ among treatments (ANOVA, all $p > 0.2$). Crab behavior was unobservable because of glare, heavy rain, and other obstructions for 0 to 24% of each trial (mean = 3.97 ±

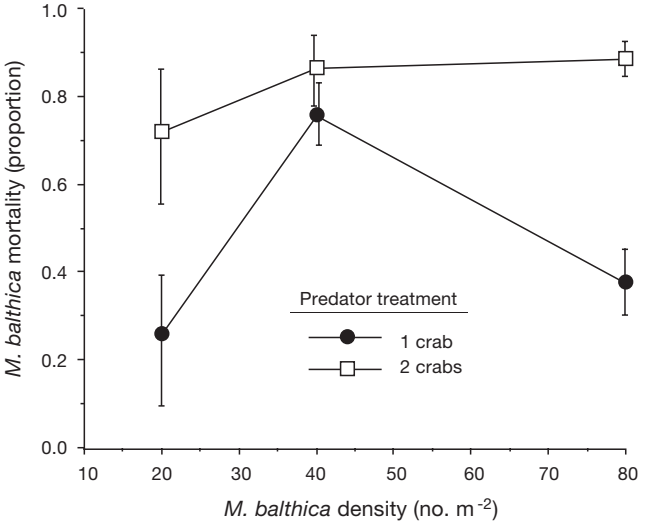

Fig. 4. *Macoma balthica*. Mean (± 1 SE) mortality as a function of clam and crab density in the mesocosm experiment. Means and standard errors are backtransformed from $Y' = \sin^{-1}(\sqrt{Y})$. N = 6 –10

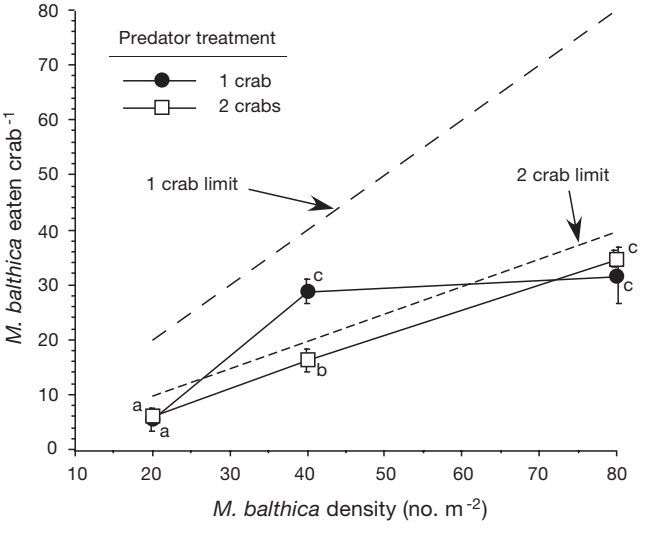

Fig. 5. Mean (±1 SE) number of *Macoma balthica* eaten per crab as a function of clam and crab density in the mesocosm experiment. Letters indicate the results of post-hoc mean comparison (SNKtest). Means sharing the same letter are not significantly different. Dashed lines indicate the total number of clams available per crab in each of the crab-density treatments. N = 6 –10

Table 5. Multivariate and univariate analyses of clam mortality, crab activity and foraging behavior variables in the mesocosm functional response experiment

a) MANOVA

Effect	Pillai's Trace	*F*	Hypothesis df	Error df	p
Clam density	1.049	6.620	12	72	<0.001
Crab density	0.598	8.679	6	35	<0.001
Clams × crabs	0.404	1.521	12	72	0.137

b) Univariate ANOVAs

Dependent variable	Source	df	MS	*F*	p
Clam mortality (proportion)[a]	Clam density	2	1587.692	3.528	0.039
	Crab density	1	5657.815	12.571	0.001
	Clams × crabs	2	558.117	1.240	0.300
	Error	40	450.071		
Clams eaten per crab	Clam density	2	3100.752	50.874	<0.001
	Crab density	1	94.759	1.555	0.220
	Clams × crabs	2	240.891	3.952	0.027
	Error	40	60.949		
Feeding frequency[b]	Clam density	2	0.196	3.026	0.060
	Crab density	1	0.012	0.185	0.669
	Clams × crabs	2	0.149	2.291	0.114
	Error	40	0.065		
Foraging time (proportion)[a]	Clam density	2	133.701	0.740	0.484
	Crab density	1	519.727	2.876	0.098
	Clams × crabs	2	557.112	3.083	0.057
	Error	40	180.728		
Active time (proportion)[a]	Clam density	2	174.105	0.710	0.498
	Crab density	1	330.608	1.347	0.253
	Clams × crabs	2	365.100	1.488	0.238
	Error	40	245.362		
Active time on clam patch (proportion)	Clam density	2	77.650	0.550	0.581
	Crab density	1	139.181	0.985	0.327
	Clams × crabs	2	187.594	1.328	0.276
	Error	40	141.234		

[a]Angular transformed ($Y' = \sin^{-1}[\sqrt{Y}]$)
[b]Log transformed ($Y' = \mathrm{Log}_{10}[Y + 1]$)

0.88%) and did not differ among treatment levels (ANOVA, all $p > 0.18$).

Across all treatments, crabs were inactive for most of the time they were observed (sitting or buried: mean = 65.78 ± 3.45%) (Fig. 6a,b). Agonistic behaviors only occurred in the 2 crab treatments and only occupied 3.03 ± 0.74% of a crab's time. Foraging and locomotion occupied 13.42 ± 2.46% and 15.43 ± 2.10% of the observed time, respectively.

Feeding frequency showed the same general pattern as proportional clam mortality. With 1 crab, feeding frequency increased sharply between 20 and 40 clams m^{-2} and then dropped, while with 2 crabs feeding frequency increased slightly as clam density increased (Fig. 7a). The main effect of clam density was nearly significant (Table 5b), although crab density and the interaction were not.

Foraging time did not differ significantly with clam density or crab density, but the crab × clam interaction was nearly significant (Table 5b), so we conducted post-hoc means comparisons within each treatment level. At 20 clams m^{-2}, foraging time was significantly higher with 2 crabs than with 1 and intermediate at all other clam densities (Fig. 7b). Since the interaction term was slightly non-significant ($p = 0.057$), these post-hoc test should be interpreted cautiously.

None of the main or interaction terms were significant for the remaining 2 behavior variables, active time and time active on the patch (Table 5b). Both of these variables showed the same general pattern as foraging time, having relatively large differences between the crab density treatments only at the lowest clam density (Fig. 7c,d).

The multivariate effect of clam density on the crab agonistic behavior variables (Table 3) in the 2 crab trials was not significant (MANOVA: Pillai's Trace = 1.53; $F = 0.441$; df = 6, 32; $p = 0.846$), so we did not conduct univariate tests on individual variables. As we ex-

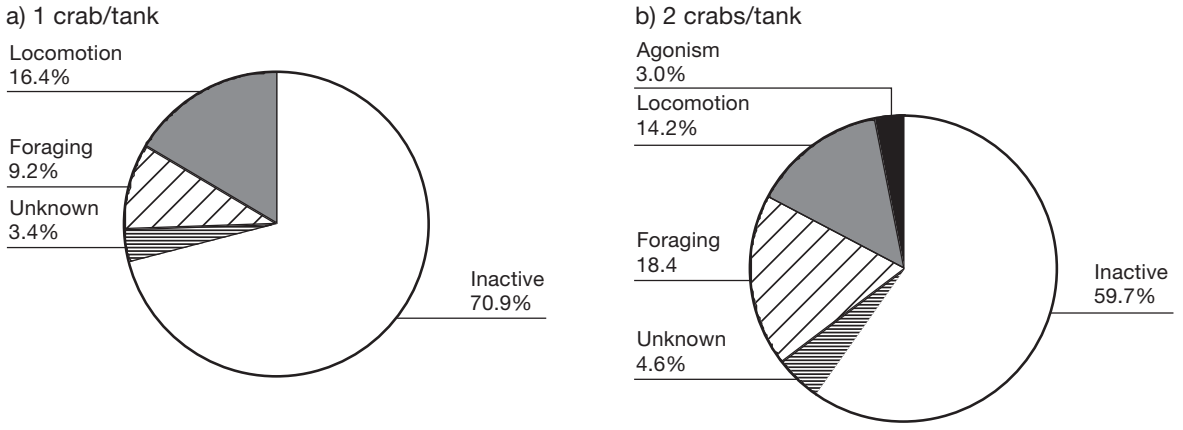

Fig. 6. *Callinectes sapidus*. Activity budgets (percent of total time observed) of blue crabs in the mesocosm experiment. (a) 1 crab/tank and (b) 2 crabs/tank. Data are means pooled across all clam density treatments

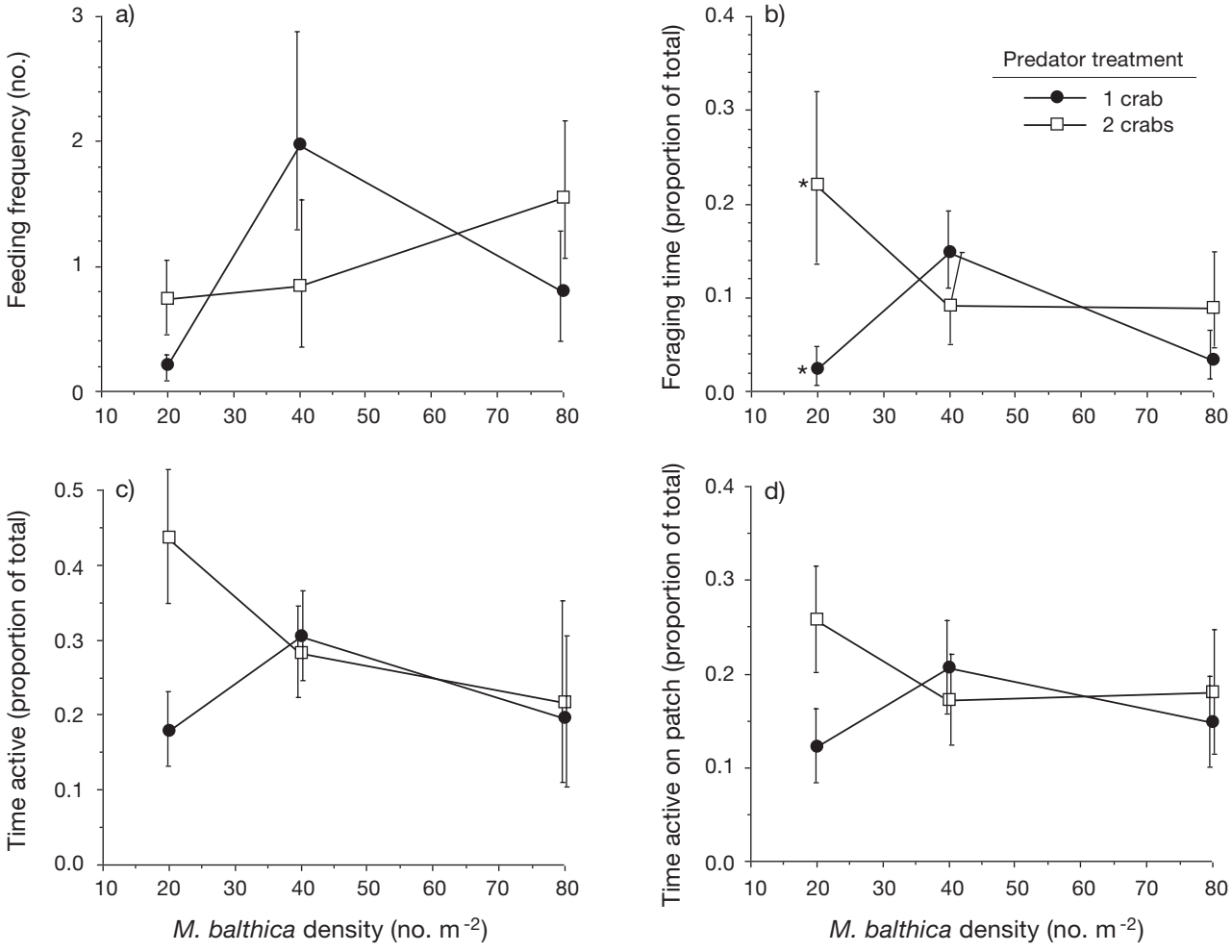

Fig. 7. *Callinectes sapidus*. Behavior as a function of clam and crab density in the mesocosm experiment. Data are means ±1 SE of N = 6 –10 replicates. (a) Feeding frequency. Means and standard errors are backtransformed from $Y' = \mathrm{Log}_{10}(Y + 1)$. (b) Proportion of total time blue crabs foraged. Asterisks indicate means that are significantly different from each other (SNK test $p < 0.05$). (c) Proportion of total time spent active. Means and standard errors are backtransformed from $Y' = \sin^{-1}(\sqrt{Y})$. (d) Proportion of total time blue crabs spent active (see Table 3) on the clam patch side of the mesocosm

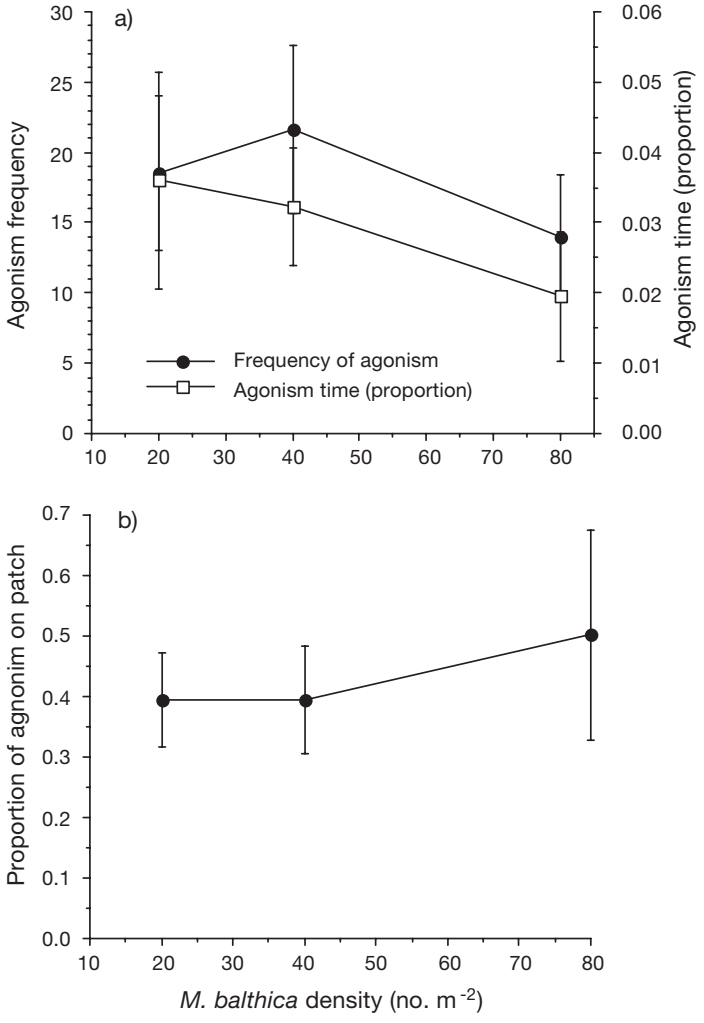

Fig. 8. *Callinectes sapidus*. Agonistic behavior (see Table 3) as a function of clam density in the 2 crab treatments of the mesocosm experiment. Data are means ±1 SE of N = 5 – 9 replicates. (a) Frequency of agonistic behaviors and proportion of total time spent in agonism. (b) Proportion of agonistic behaviors that occurred on the clam-patch end of the mesocosm

pected, agonism tended to be lowest at the highest prey density (Fig. 8a), although these trends were not statistically significant. Clam density had little effect on where agonistic interactions occurred (Fig. 8b).

DISCUSSION

Previous studies found that a single blue crab foraging on a clam patch in the lab showed a Type III functional response, causing significantly lower proportional prey mortality at lower prey density (Mansour & Lipcius 1991, Eggleston et al. 1992). Theory predicts that this type of functional response may create a low-density refuge from predation for the prey, allowing prey patches to persist. Our laboratory experiments with single crabs found a similar density-dependent, Type III functional response (Fig. 4). We predicted that the addition of a second crab would reduce density dependence. The difference in proportional mortality among clam densities was less with 2 crabs than with 1 (Fig. 4), but this trend was not statistically significant. However, when *Macoma balthica* patches were placed in the field, where the full range of predator responses, interactions among predators, and larger-scale factors could occur, we detected at best a very weak low-density refuge in sand but not in mud. Interestingly, a laboratory study of juvenile blue crab cannibalism on postlarvae found a similar shift from density dependence to density independence as predator abundance increased (Moksnes et al. 1997).

An earlier field study of blue crab predation on *Macoma balthica* found density dependence in both sand and mud in 1 yr, but, as in our study, in neither substrate a second yr (Seitz et al. 2001). Thus, blue crab predation on *M. balthica* in the Rhode River appears to be density dependent only at some times or in some places.

The reduction in the density-dependence of prey mortality with increasing degrees of complexity (i.e. 1 predator vs. 2 predators vs. a predator population) may be explained partly by behavioral changes observed in our mesocosm experiment. The biggest difference in clam mortality between the 1 and 2 crab treatments occurred at the lowest prey density, where doubling the number of crabs led to a nearly 3-fold increase in clam mortality (Fig. 4) and an increase in per-crab consumption (Fig. 5) (1 crab: 5.70 ± 2.19 clams, 2 crabs: 6.44 ± 1.31 clams). Significantly, the only effects of crab number on crab behavior also appeared at the lowest clam density. While we expected agonism to detract from foraging, especially when prey were scarce, crabs foraging on the lowest density of clams spent as much or more time active (Fig. 7c), on the clam patch (Fig. 7d), and foraging (Fig. 7b) in the 2 crab treatments than in the single-crab treatments. These results suggest that, at low prey density, crabs facilitate rather than interfere with each other's foraging. Facilitation could occur if the chemical cues of crabs macerating clams stimulate other crabs to forage in the same area (Clark et al. 2000).

Contrary to our expectations, we found no significant effects of clam density on the frequency of or the amount of time spent on agonistic behaviors. Although threat displays and physical contact between crabs were frequently observed in 2 crab trials, agonism accounted for a relatively small percentage of a crab's time (Fig. 6b). In addition, there were no deaths and only 1 injury attributable to aggressive encounters during our study.

In contrast, a similar study of blue crabs foraging on *Macoma balthica* in laboratory tanks by Mansour & Lipcius (1991) found frequent injuries and deaths from agonism, with the highest death rates occurring at the lowest per-crab clam density. The level of agonism was much lower in our study, probably because we used larger tanks (2 m^2 vs. 1 m^2), lower crab densities, and somewhat higher clam densities. In the field, blue crabs can aggregate at high densities on prey patches (Clark et al. 1999b), but they are not restricted there and can quickly retreat if threatened. Crabs could, to some extent, do the same in our experiment because the tanks were relatively large and the clam patch only covered one end of the tank. Although injuries (e.g. missing limbs) are common on crabs in the field, limb autotomy frequencies are highest in small crabs, reflecting attempted predation by larger conspecifics (Smith & Hines 1991, Ruiz et al. 1993, Dittel et al. 1995, Hines & Ruiz 1995) rather than competitive interactions. Because agonistic behaviors between equal-sized individuals are highly ritualized (Jachowski 1974) and, in nature, a crab can retreat from a conspecific, competitive interactions usually do not result in injuries. Thus, the level and effects of agonism that we observed may be more representative of what happens in the field than studies done using more crowded conditions.

While the change in the pattern of prey mortality is consistent with the changes we observed in the within-patch foraging behavior of crabs when conspecifics were present, patch choice and other factors affecting predator behavior and distribution, which we were unable to observe in this study, are also likely to contribute to prey mortality. Given the statistical weakness of the within-patch behavioral patterns we found in the mesocosm experiment, between-patch factors may be more important in producing patterns of clam mortality in the field. For example, Anderson (2001) found that the Type II (inversely density-dependent) functional response of a predatory fish measured in the laboratory was overridden in the field by its aggregative response, resulting in density-dependent prey mortality. Blue crabs appear to aggregate on prey patches (Clark et al. 1999a,b), although the exact form of this response is unknown. Predicting the total response of blue crabs on prey populations is further complicated by behavioral interactions between individuals. For example, at high crab densities, agonistic interactions interfere with foraging (Mansour & Lipcius 1991, Clark et al. 1999b) and blue crabs may respond to agonistic encounters by moving to a different prey patch (Clark et al. 1999b). How these other types of responses and behavioral interactions contribute to the predator population's total response to changes in prey density remain to be explored.

Because we did not remove existing clams before creating the experimental patches in the field experiment, it is also possible that density dependence was diminished in the field as the total clam density (planted clams + background clams) within many of the patches was above the refuge prey level, particularly at the mud sites where background density was high. In this case, planted clam density would affect mortality at low but not high background clam densities, creating an interaction between planted clam density and background clam density. In the sand experiment, where many of the sites had low background clam densities (Table 1), our data met the ANCOVA assumption of equal slopes, so there was no interaction between the 2 clam density factors. Therefore, we conclude that predators responding to the existing clams within the patches did not cause the diminished density dependence in sand. In the mud experiment, only 1 site had experimental patches with a total clam density <20 clams m^{-2} (Table 1), so it is not possible to definitively rule this effect out. Nevertheless, regardless of the exact cause, the pattern of clam mortality at the mud sites was influenced more by the environment in which it was placed than by our experimental manipulation.

Our study clearly shows the importance of considering the effects of larger-scale factors on the outcome of small-scale field experiments. Because we conducted our field experiments at numerous sites spanning a range of prey densities, we were able to detect a larger-scale effect of variation in *Macoma balthica* density, as indicated by the significant effect of clam density at the site scale in mud (i.e. background clam density: Fig 3b). Thus, prey mortality is affected by prey density, but not at the scale we manipulated. At the site scale, clam mortality rate was inversely density dependent, which was contradictory to predictions from small-scale laboratory functional response experiments (Eggleston et al. 1992, Fig. 4). This pattern of prey mortality could lead to local extinction, rather than persistence, of small prey patches (Lipcius & Hines 1986, Eggleston et al. 1992, Seitz et al. 2001). This effect of background clam density was not observed in sand, but the range of densities among those sites was much less than in the mud sites, perhaps precluding its detection. The full range of background clam density in sand (~1.5 to 50 clams m^{-2}) reflected only the lowest clam densities in mud (~1.5 to 300 clams m^{-2}) and the proportional mortality at those low densities (<50 clams m^{-2}) was similar for both substrates (Fig. 3). Refuge prey densities may also be lower than our experiments detected, as some earlier studies found density-dependent effects mainly at <10 clams m^{-2} (e.g. Seitz et al. 2001).

Many other differences between these 2 substrate types could also affect the predator's foraging response. For example, a blue crab locates individual clams by probing the substrate with its walking legs. Because sand is less penetrable than mud, encounter rates may vary between the 2 substrates independent of actual prey density (Lipcius & Hines 1986), affecting the foraging behavior of the predator. In addition, natural patch size, or the 'grain' component of scale (Thrush et al. 1997), may vary between these 2 substrates. Patch size has been shown to affect foraging behavior in a variety of ways (Sih & Baltus 1987, Bach 1988, Whitlatch et al. 1997, Fulton & Bellwood 2002, Wellenreuther & Connell 2002).

Our study highlights the importance of considering scale when conducting and drawing inference from ecological experiments. Here, we found that patterns of prey mortality observed in simplified laboratory conditions did not occur in the more complicated natural system. Predator responses, such as the effects of conspecifics on foraging and patch choice, that were lacking in the laboratory appear to be key in determining prey mortality patterns in the field. In addition, we found that large scale (among sites) patterns of prey density variation were more important in determining prey mortality rates than the small-scale variation represented by the experimentally manipulated patches. Thus, care must be taken when extrapolating from simple, small-scale experiments to larger ecological domains or spatio-temporal scales (Thrush et al. 1997). Additional studies specifically addressing issues related to scaling up from small experiments to larger ones are urgently needed.

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