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Foraging behavior of an estuarine predator, the blue crab *Callinectes sapidus* in a patchy environment

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To define general principles of predator-prey dynamics in an estuarine subtidal environment, we manipulated predator density (the blue crab, *Callinectes sapidus*) and prey (the clam, *Macoma balthica*) patch distribution in large field enclosures in the Rhode River subestuary of the central Chesapeake Bay. The primary objectives were to determine whether predators forage in a way that maximizes prey consumption and to assess how their foraging success is affected by density of conspecifics. We developed a novel ultrasonic telemetry system to observe behavior of individual predators with unprecedented detail.

Behavior of predators was more indicative of optimal than of opportunistic foraging. Predators appeared responsive to the overall quality of prey in their habitat. Rather than remaining on a prey patch until depletion, predators appeared to vary their patch use with quality of the surrounding environment. When multiple (two) prey patches were available, residence time of predators on a prey patch was shorter than when only a single prey patch was available. Predators seemed to move among the prey patches fairly regularly, dividing their foraging time between the patches and consuming prey from each of them at a similar rate. That predators more than doubled their consumption of prey when we doubled the number of prey (by adding the second patch) is consistent with optimizing behaviors – rather than with an opportunistic increase in prey consumption brought about simply by the addition of more prey. Predators at high density, however, appeared to interfere with each other's foraging success, reflected by their lower rates of prey consumption.

Blue crabs appear to forage more successfully (and their prey to experience higher mortality) in prey patches located within 15–20 meters of neighboring patch, than in isolated patches. Our results are likely to apply, at least qualitatively, to other crustacean-bivalve interactions, including those of commercial interest; their quantitative applicability will depend on the mobility of other predators and the scale of patchiness they perceive.

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The evolution of foraging behaviors that result in optimized energy intake has occurred in many patchy environments (Hassell and May 1974, Iwasa et al. 1981, Stephens and Krebs 1986, Alonso et al. 1995). When foraging on prey resources with patchy distributions, predators that optimize energy intake should select the most rewarding patches and concentrate their foraging efforts there. Given that predators experience diminishing energy returns as they continue to deplete prey from a patch, those that optimize must decide when to depart from a patch and seek a new one. Predators may make this decision by using knowledge of the immediate environment, "rules of thumb" developed from past experience, or a combination of both (Hassell and May

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1974, Iwasa et al. 1981, Stephens and Krebs 1986, Alonso et al. 1995). Predators using knowledge of the immediate surroundings should abandon a prey patch only when prey density falls below the overall mean density (marginal value) for the environment (Charnov 1976, Alonso et al. 1995). Predators that are not omniscient regarding prey resource densities should leave prey patches according to optimality rules developed over ecological and evolutionary time scales based on the predator population's past experience of the quality, variability, and distribution of prey patches (Iwasa et al. 1981, Green 1984, Alonso et al. 1995). Predators across a diverse array of species have been shown to employ such rules, effectively maximizing long-term energy intake despite short-term uncertainty about prey resources.

Foragers that exhibit behaviors characteristic of optimal foraging may modify them to reduce the risk of injury or mortality when under threat of predation or of intraspecific agonism (reviewed in Lima and Dill 1990). Agonism sometimes becomes intense as foragers aggregate on a prey patch (Beddington 1975, Ens and Goss-Custard 1984, Palumbi and Freed 1988, Goss-Custard et al. 1992). Foragers that are highly agonistic and capable of inflicting serious damage or cannibalism upon conspecifics may modify behavior to minimize risk of intraspecific interference. If predators direct time and energy into nonforaging behaviors and/or shift foraging activity to times and places of lower profitability, they may become less efficient foragers (Ens and Goss-Custard 1984). Impaired foraging success may be expected especially during interference with conspecifics as direct aggressive encounters and territorial defense further divert time from foraging (Vines 1980, Jaeger et al. 1983, Ens and Goss-Custard 1984).

Marine and estuarine systems should make good models to study both optimization behaviors among prey patches and the consequences of interactions among predators as a function of their density. Foragers in such environments have probably evolved ways to optimize foraging among patchily distributed prey. On the other hand, many foragers in these systems are highly agonistic and are likely to interfere with each other's foraging as they aggregate at high densities on the richest patches. While many studies of birds on estuarine shores have examined foraging behavior in a patchy environment (Goss-Custard 1977, Goss-Custard et al. 1982, 1984), controlled studies in the subtidal estuarine environment are limited because of the difficulty in directly observing animals in turbid water. Yet studies in estuarine subtidal systems could be especially important because they could reveal whether principles governing utilization of resource patches that have been demonstrated in other terrestrial and aquatic settings (Hassell and May 1974, Goss-Custard 1977, Stephens and Krebs 1986, Gotceitas 1990, Alonso et al. 1995) generalize to the estuarine environment, in which the relative importances of sensory modalities underlying patch-use behaviors may differ from those in other systems.

To understand general principles of predator-prey dynamics in an estuarine subtidal environment, we need to determine, at field scale, whether major predators forage in a way consistent with optimization and whether optimization is compromised as predator density increases. To this end, we studied the foraging behavior of an important estuarine predator, the blue crab *Callinectes sapidus*, feeding on the tellinid clam *Macoma balthica*, in the Rhode River subestuary of the central Chesapeake Bay. Past studies in aquatic environments have drawn inferences about the foraging behavior of predators from prey censusing, from post hoc analysis of predators' stomach contents, and/or from periodic static "snap-shots" of predators' distribution. While our study included censusing of prey patches as one means of evaluating patch use, we also developed an ultrasonic telemetry system that allowed us to make more direct measurements.

Because blue crabs aggregate on patchy food resources and are highly agonistic, they are a good model to study foraging strategy and effects of intraspecific interference on behavior. They also tolerate telemetry transmitters without obvious behavioral artifacts (Wolcott and Hines 1990, Wolcott 1995, Hines et al. 1995). In large field enclosures, the density of predators as well as the distribution of their bivalve prey *Macoma balthica* were manipulated. The patch-use behavior of all crabs in enclosures was determined by censusing of prey patches. A subset of experimental crabs was telemetered, allowing us to record behavior with unprecedented detail. Because of the labor-intensive nature of the telemetry preparations, a single telemetered crab was used during each experiment as an index of the activity of all crabs in the enclosure. The Rhode River's simple predator-prey complex allows experimental manipulations under controlled, yet realistic, conditions (Hines et al. 1990). *Macoma balthica* were selected as prey because of their abundance and ecological importance, having major effects on recruitment of infaunal species (Hines et al. 1989). Clams are preferred prey items of crabs, composing up to 50% of their diets (Hines et al. 1990).

We hypothesized that the behavior of blue crabs would be consistent with an optimal foraging pattern, in that crabs' use of a prey patch would be influenced by the surrounding prey environment and would ultimately lead to increased prey intake. An alternative foraging pattern is described by the "component approach," in which foraging behavior of a predator in any prey patch is simply defined by the interaction of the predator's functional and aggregative responses (Holling 1959). In this more "opportunistic" model, a forager's behavior in a given prey patch is affected only by the inherent qualities of that patch (e.g., prey den-

sity, number of other predators on patch, prey type, sediment), and not by any decisions based on the quality of the surrounding prey environment.

These two theoretical approaches to foraging, although not always mutually exclusive, can be distinguished in our simple study design of one prey patch versus two identical prey patches by observing how predators partition time between the patches and the rate at which they consume prey. Optimal foraging models predict that predators will make relatively brief visits to prey patches when the marginal value of surrounding prey resources (mean value including background prey and other prey patches) is high (reviewed in Stephens and Krebs 1986). If crabs in our study can detect the presence of the alternative patch (e.g., presumably by chemoreception) while they are feeding on one patch, they may recognize that the environment has a higher marginal value than when no other patch is detectable (i.e., trials with only one experimental patch). Optimal foraging theory also predicts that predators will abbreviate visits to prey patches when the distance between patches is relatively short (reviewed in Stephens and Krebs 1986). If crabs can indeed "smell" the alternative patch, they may also respond to the apparent short travel time between patches versus that in trials with only one experimental patch, where the nearest substantial patch of background prey would be located somewhere well outside of the experimental enclosure. As overall environmental quality increases and perceived travel time between patches decreases (i.e., when a second prey patch is added), crabs would be expected to spend less time on a patch per visit. Ultimately, crabs, in an optimal foraging model, would be predicted to move back and forth among two prey patches, depleting them at a comparable rate. On the other hand, if crabs are responding only to the characteristics of the prey patch on which they are currently foraging, the length of patch visits should not vary between trials with one versus two prey patches.

Opportunistic and optimal foraging approaches also yield different predictions regarding prey consumption in the one- versus two-patch prey designs. The former approach would suggest that an unsatiated predator presented with twice the number of prey, through the addition of a second patch, will consume approximately twice as many simply because of an increased encounter rate (assuming that handling time is negligible). The latter approach would suggest that, by moving among the two prey patches, a predator will effectively delay patch "depression" and ultimately consume more than twice the number of prey. However, we hypothesized that, regardless of the foraging approach exhibited by crabs, interactions among crabs at high density on a prey patch would interfere with foraging success.

Methods

Study site

During the summers of 1991–1993, we conducted experiments in the Rhode River (38°51′ N, 76°32′ W), a 485 ha subestuary of the central Chesapeake Bay.

To regulate densities of large predatory blue crabs, all experiments were conducted in 20×20 m field enclosures. The walls were 4 cm mesh that extended above the high-tide line and were edged on the bottom with galvanized wire that extended several centimeters below the sediment surface. Enclosures were located near shore (water depth = 1–2.5 m) in the upper reaches of the river. Sediment in enclosures was primarily fine, silty mud with some sandy areas in the corners nearest shore.

The enclosures were effective in allowing us to control density of predators. Adult crabs in enclosures in addition to those deliberately introduced were frequently captured by crab pots deployed following experiments, but the majority of these animals were newly molted. This suggests that they had passed through the mesh as juvenile instars and hence were of a size-class that would not have interacted competitively with experimental animals during the experiments.

To allow installation of clam patches at random locations in enclosures, we buried ten fixed wooden frames of ca 1 m^2 within the central 10×10 m area of the enclosure. These frames allowed us to emplace plastic bins filled with 30 cm of control or prey-enriched sediment, such that the sediment surface of the "patch" was flush with the adjacent natural sediment.

Naturally occurring ("background") prey were scarce in the enclosures. The most common bivalve species, *Macoma balthica* and the smaller *Macoma mitchelli* (individuals of both species were < 1.5 cm shell width), occurred at low densities of only a few clams per square meter as estimated by random sediment cores. Juvenile crabs were rare within enclosures and, being much smaller than experimental predators, were considered potential prey rather than competitors (Hines and Ruiz 1995).

Experimental animals

Crabs were collected by trap and otter trawl. Intermolt males (130–170 mm carapace width) that possessed at least both chelipeds, both swimming paddles, and most walking legs were selected for experiments. In some trials, an individual crab possessing all limbs was outfitted with a transmitter to telemeter its location. Prior to experiments, crabs were held in 2000 l outdoor tanks with 10 cm deep flowing estuarine water and observed periodically for ca 48 h to verify health and vigor. Crabs were fed ad libitum with clams and frozen fish up

until 24 h before they were added to experimental enclosures.

The ultrasonic telemetry system used in these studies allowed us to monitor agonistic behavior (as indicated by the stereotypical spreading of chelae in the "lateral merus" display) and crab location; however, the meral spread data are discussed elsewhere (Clark et al. 1999b). The transmitters were derived from those used in previous experiments to detect molting (Wolcott and Hines 1990, Shirley and Wolcott 1991). The electronics were packaged in electrical sleeving ("shrink tubing"), contoured to conform to the dorsal carapace to minimize drag, and filled with corn oil to couple sound from the transducer to the water. Transmitters were lashed transversely on the dorsal carapace using copper wire twisted around the lateral spines. Transmitters weighed ca 20 g in air (7 g in water), and had no obvious effects on behavior of crabs.

Clams were collected by suction dredge. Only intact individuals of 20–30 mm shell width with a vigorous siphon-retraction reflex were selected for experiments. Clams were held on sea tables irrigated by flowing estuarine water until they were deployed in experimental enclosures.

Study design

The study design included two treatments of prey patch availability: 1) a single clam patch (1 m^2 patch of 45 clams), and 2) a pair of patches (two 1 m^2 patches of 45 clams each, separated by ca 15 m). The single patch was deployed in one site randomly chosen from the ten fixed patch sites. A patch to control for clam mortality not due to predation was placed in another randomly selected site, and covered with 1 cm galvanized wire mesh. The two-patch experiments were set up using diagonally opposed corner patch sites, and placement of prey patches in successive experiments alternated between the two possible diagonal configurations; occasionally, a third patch (control) was deployed in another of the ten fixed patch sites. Clams in both treatments were planted ca 10 cm deep into the sediment by divers. Patches were then covered with 1 cm galvanized wire mesh for 24 h, so that clams had time to bury deeper and to extend their siphons to the sediment surface while protected from predation. At the end of this acclimation period, patch covers were removed from the experimental (but not control) patches.

The study design also included two treatments of predator density: 1) low density (two crabs per enclosure), and 2) high density (eight crabs per enclosure). Crabs were added to enclosures after the clam patches were installed and covered, and given 24 h to acclimate before patch covers were removed to begin the experiments.

Fourteen trials using the single-patch treatment were conducted in September 1991 and during July and August 1992. Seven trials were conducted at low crab density, and seven at high crab density. (Five pilot trials using an intermediate predator density of four crabs per enclosure were executed within the single-patch design. However, this treatment level was not significantly different from the high crab density in terms of per capita prey consumption, so it was dropped to allow us to run more trials at the low and high crab densities.) We collected telemetry data from eight of the single-patch trials, four at low crab density and four at high density.

Forty-two trials using the two-patch treatment were conducted during June through September 1993, with interspersion of the two treatments of crab density. Twenty trials were conducted at low crab density, and 22 at high crab density. We collected telemetry data from eight of the two-patch trials, four at low crab density and four at high density.

Observations

To observe the movement pattern of predators, we monitored the signal coming from the telemetered crab in the enclosure during the time periods of 0600–0830 and 1530–1900; these are periods previously identified as peaks of feeding and aggressive activity of crabs in the field (Clark et al. 1999a). During each trial, a single telemetered crab was used as an index of the activity of all crabs in the enclosure. To track movements of crabs, the observer used an ultrasonic receiver and directional hydrophone from a small boat just outside the enclosure fencing, triangulating on the crab's transmitter. The observer manually recorded the movement of crabs on a waterproof chart of the enclosure. (Fig. 1 shows a sample movement track of a crab in the enclosure.) Foraging success was evaluated using divers to excavate bins of clams after crabs had fed from them for 24 h. Clams were censused (number live and number dead from causes other than predation) by sieving the sediment of each patch through 1 cm wire mesh. (Because mortality in control patches was uniformly low [$< 5\%$], no correction factor for mortality due to causes other than predation by experimental predators was ultimately used in analyses of prey consumption.)

We analyzed the clam survival data to see 1) if clam consumption in one of the two patches was positively correlated with clam consumption in the other patch, and 2) whether a plot of clam mortality in one patch against mortality in the other patch would form a continuous distribution (i.e., consistent with movement between patches and optimal foraging) rather than the clumped distribution of points hypothesized if crabs did not move between the two patches, but simply remained on the first patch they encountered (i.e., consistent with the component approach to foraging). Steps

used to estimate where these hypothetical points would lie were as follows: 1) we calculated the probability of trials having each possible distribution of crabs between two clam patches (e.g., the possible initial crab distributions were 0:8, 1:7, 2:6, 3:5, and 4:4 for high crab density) using the probability equation:

$(a + b)!/a!b! = N(a:b)$; where "a" and "b" are the number of crabs on each of the two patches, and "N" = the fraction of trials in which a given distribution "a:b" should appear.

The total number of trials was then multiplied by the above probabilities to yield an expected number of trials in which each crab distribution would appear. 2) We estimated the expected clam consumption in each of the above distributions if crabs never moved from their initial patches. We plotted per capita clam consumption (y) versus crab density (x) for 2, 4, and 8 crabs provided with a single clam patch, and extrapolated for the other densities (1, 3, 5, 6, and 7 crabs per patch). The expected depletion of a patch was calculated by multiplying the expected per capita clam consumption by the number of crabs on that patch.

Statistical analyses

Because we were interested in the potential interaction between predator density and prey patch distribution, our analyses combined the data across years (i.e., single-patch trials from 1991–1992 and two-patch trials from 1993). Although this is not the ideal design, we feel that analyzing the data as a single set is justifiable for the following reasons: 1) key variables were uniform among years. Most importantly, densities of background alternative prey (clams, juvenile crabs) were uniformly low among years. The physical layout of the experimental system and techniques were identical. Physical variables (e.g., temperature, salinity, turbidity) showed more seasonal variability within years than variability among years. 2) Overall responses of crabs (e.g., rate of movement, temporal pattern of agonism) were similar between years. 3) In statistical analyses, we included a lower-level ANOVA where the two-way ANOVA indicated a significant interaction term between main effects, so that possible confounding effects between years were partitioned before conclusions were drawn from the experimental results. A two-way ANOVA procedure, with crab density (low and high) and clam patch distribution (single patch and two patches) as factors, was used to analyze the following response variables: duration of each visit to the clam patch by crabs (min) and per capita clam consumption rate (number of clams consumed per crab in 24 h). Where the interaction of factors was significant, a one-way ANOVA was used to analyze the response variables for each factor. A t-test was used to compare the observed and hypothesized proportions of time that crabs spent on clam patches. A t-test was also used to compare the actual and hypothesized values of per capita clam consumption rate when a second patch was added. Linear regression was used to analyze the correlation between: 1) total time a crab spent on one clam patch (y) and total time spent on the other patch of the two (x), and 2) proportional clam mortality in one prey patch (y) and that in the other patch (x). Proportional mortality was arc-sine square-root transformed to meet assumptions of homogeneity of variance and normality. Data are presented in the text as mean $\pm$ standard error.

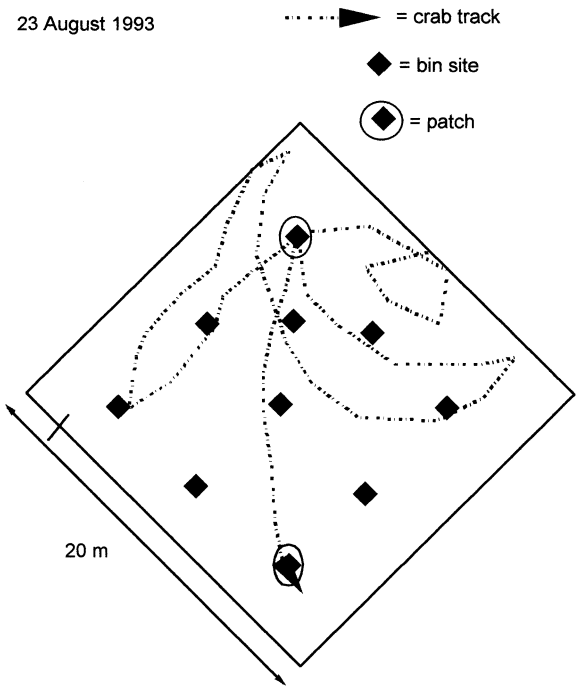

Fig. 1. Movement pattern of crabs within enclosures: sample track.

Results

General behavior of predators in enclosures

There was little apparent artifact of enclosures upon crab behavior: crabs moved throughout enclosures and seldom walked along fencing (Fig. 1). When two experimental clam patches were available, crabs spent disproportionately more time on patches than in background areas ($t_8 = 2.32$, $p < 0.05$). This pattern is consistent with the "ideal free distribution" (IFD) theory (Fretwell and Lucas 1970, Kennedy and Gray 1993), although our study was not designed to test IFD predictions explicitly. When only one patch was available, however, the proportion of time that crabs spent on the patch, although averaging nearly 20% of observation

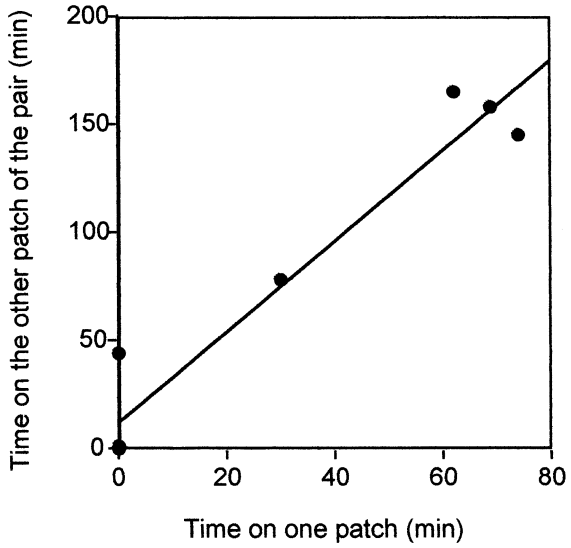

Fig. 2. Residence time of crabs on one clam patch (min) vs residence time on the other patch of the pair (min). $y = 12.86 + 2.08x$, $F_{1,6} = 86.10$, $r^2 = 0.93$, $p < 0.0001$. Each point on the graph represents the behavior of an individual telemetered crab.

time, did not differ significantly from the proportion of total enclosure area represented by the patch ($t_8 = 1.82$, $p = 0.11$). The reduced proportion of time spent on the patch in the single-patch design may reflect avoidance of high agonistic activity on the patch in this design (Clark et al. 1999b).

Responsiveness of predators to the overall quality of the prey environment

Crabs appeared responsive to changes in the overall quality of their immediate environment, making shorter patch visits when two patches were available (51.69 ± 13.31 min) than when only one patch was available (130.50 ± 21.74 min) ($F_{1,8} = 5.55$, $p < 0.05$). Predator density had no significant effect on duration of patch visits by crabs ($F_{1,8} = 0.01$, $p = 0.99$), and there was no significant interaction term ($F_{1,8} = 0.89$, $p = 0.37$).

Consistent with a prediction of the marginal value theory, residence time of crabs on one clam patch was significantly correlated with residence time on the other patch of the pair (ANOVA, y = Residence time on Patch # 1, x = Residence time on Patch # 2, $p < 0.0001$) (Fig. 2). Similarly, clam mortality was positively significantly correlated between patches (ANOVA, y = Mortality in Patch # 1, x = Mortality in Patch # 2, $p < 0.00001$) (Fig. 3). At both low and high crab density, the observed distribution of points was continuous, and did not resemble the clumped distribution of points expected if the crabs simply remained on the first patch they encountered (Fig. 4).

Foraging success as a function of predator density and overall quality of the prey environment

There was a nearly linear decrease in foraging efficiency of crabs when their density was increased from two, to four, to eight crabs per enclosure; there was no threshold effect (Fig. 5). However, we ran only a limited number of trials using the intermediate crab density.

Because prey distribution and predator density interacted significantly in their effect on the per capita feeding rate of crabs ($F_{1,52} = 9.20$, $p < 0.01$), these two factors were analyzed independently via one-way ANOVA. Crabs consumed significantly more clams per capita in two-patch trials (16.97 ± 1.97 clams $\times$ crab$^{-1} \times$ d^{-1}) than in single-patch trials (6.43 ± 3.41 clams $\times$ crab$^{-1} \times$ d^{-1}) ($F_{1,54} = 7.28$, $p < 0.01$). However, crabs appeared to interfere with each other at high predator density, consuming significantly fewer clams per capita (5.43 ± 1.83 clams $\times$ crab$^{-1} \times$ d^{-1}) than crabs at low density (23.85 ± 1.90 clams $\times$ crab$^{-1} \times$ d^{-1}) ($F_{1,54} = 48.78$, $p < 0.00001$).

Moreover, increases in crabs' foraging success when they had access to a second patch were depressed as density of crabs rose (Fig. 6). At low predator density, consumption was consistent with optimal foraging. At low density, mean per capita feeding rate of crabs (clam mortality) in two-patch trials (28.70 ± 2.84 clams $\times$ crab$^{-1} \times$ d^{-1}) rose to 2.87 times that in single-patch trials (10.00 ± 1.48 clams $\times$ crab$^{-1} \times$ d^{-1}), significantly greater than the doubling expected with doubling the number of clams available ($t_{19} = 3.07$, $p < 0.05$). At high predator density, on the other hand, mean per

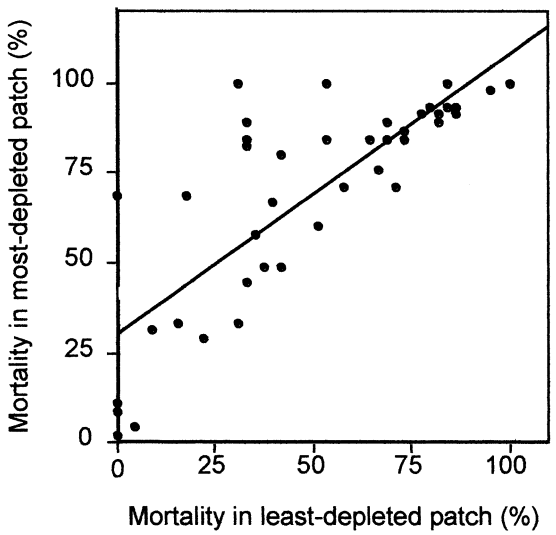

Fig. 3. Clam mortality in one prey patch (%) vs mortality in the other patch of the pair (%): both crab densities. Plot displays untransformed data. Using arc-sine square-root transformation: $y = 0.54 + 0.96x$, $F_{1,40} = 62.19$, $r^2 = 0.63$, $p < 0.00001$.

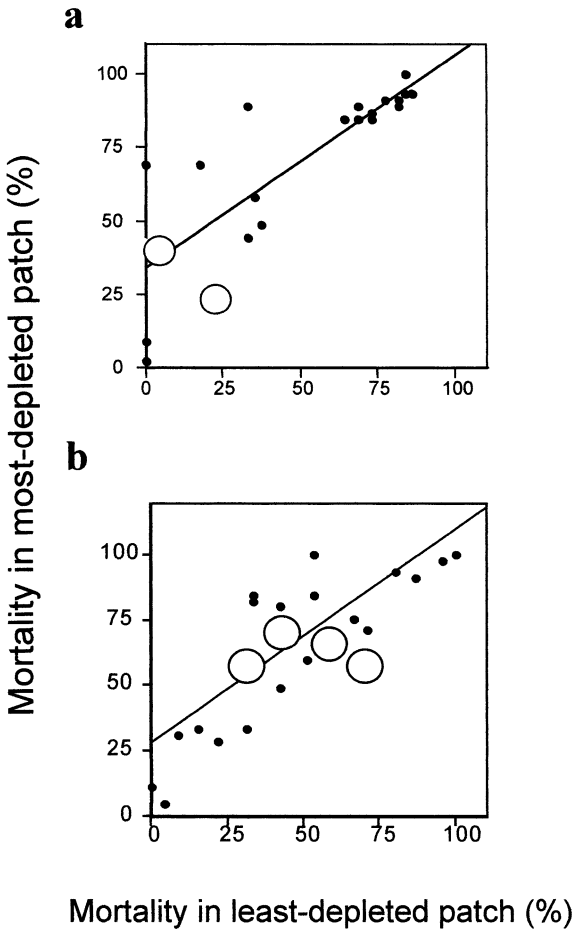

Fig. 4. Observed clam mortality in the paired prey patches vs that expected if crabs remained only on the first patch they encountered. Expected clam depletion was estimated by using probabilities of each crab distribution among the two clam patches, and by adjusting for per capita consumption of clams by crabs at each crab density on a clam patch as described in the Methods section. Small circles indicate observed points; large circles indicate expected point regions. a. Low crab density treatment: $y = 33.85 + 0.73x$, $r^2 = 0.67$, $p < 0.0001$. b. High crab density treatment: $y = 28.05 + 0.82x$, $r^2 = 0.60$, $p < 0.0001$. Expected point region corresponding to 0:8 crabs does not appear on plot because of the very low probability of this distribution occurring.

capita feeding rate of crabs (clam mortality) in two-patch trials (6.31 ± 0.66 clams $\times$ crab$^{-1} \times$ d^{-1}) was 2.36 times that in single-patch trials (2.67 ± 0.64 clams $\times$ crab$^{-1} \times$ d^{-1}), statistically indistinguishable from the doubling expected with twice the clams available ($t_{21} = 1.38$, $p = 0.18$).

Patterns of prey depletion by predators

Clam depletion did not limit foraging success of crabs. Although most of the clams were consumed in a few of the trials, overall, a substantial proportion of the clams

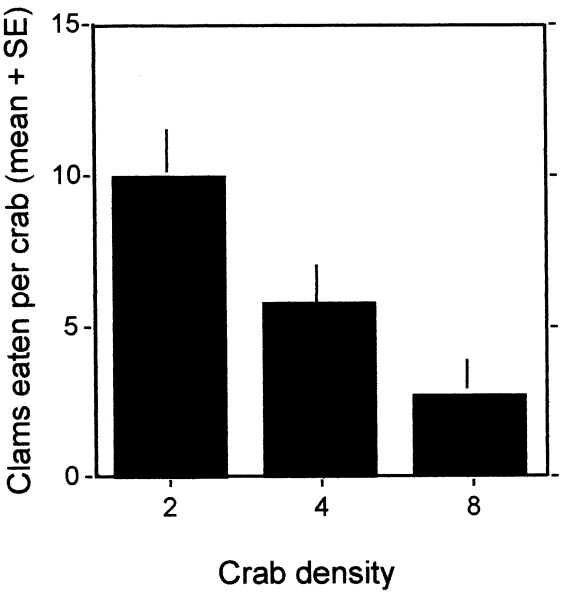

Fig. 5. Mean per capita consumption of clams as a function of predator density.

remained at the end of experiments: at low crab density, $36.22\% \pm 6.30\%$ of clams remained in the two-patch treatment and $55.56\% \pm 6.58\%$ in the single-patch treatment. At high crab density, $43.89\% \pm 5.86\%$ of clams remained in the two-patch treatment and $52.38\% \pm 11.31\%$ in the single-patch treatment.

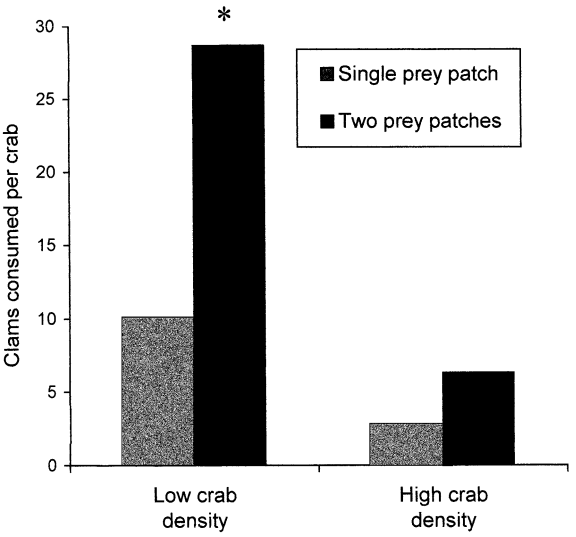

Fig. 6. Mean per capita consumption of clams by crabs: effect of crab density and distribution of prey patches. Within each crab density treatment, the expected (null) values in the two-patch treatment were simply a doubling of the values in the single-patch treatment. Asterisk indicates difference from the expected value is significant at 0.01 level.

Discussion

Blue crabs foraged among prey patches in a way that was more consistent with optimization than with an opportunistic approach. When a second prey patch was added, crabs consumed significantly more than the two-fold increase expected by doubling the number of clams available. Crabs appeared responsive to changes in their immediate environment. When a second clam patch was added, crabs made shorter visits to the patches and partitioned their time between patches. While crabs did not appear to divide their foraging time exactly equally between the two patches, this may have been a function of our relatively limited sampling periods (6 h out of each 24 h trial). Crabs also consumed clams from each of the two patches at a relatively even rate. The above are all predicted responses to the quality (i.e., marginal value) of the habitat (Charnov 1976). However, the presence of underlying "rules of thumb" (Stephens and Krebs 1986), governing departure from the patches, cannot be discounted. In fact, we speculate that such rules may exist based on the relatively high number of clams remaining in the single patch at the end of some of the experiments; crabs may depart a patch, even an isolated one, before they are satiated or have depleted prey to very low densities. Although if such patch-leaving rules were operative, they were obviously modified in the presence of a second patch. Rules of thumb in other animals have been shown to be responsive to instantaneous environmental cues (e.g., ovipositing parasitoids, cranes) (Waage 1979, Alonso et al. 1995). Perhaps, if crabs have underlying patch-leaving rules, these rules are modified when crabs "smell" other patches in the vicinity.

Distingushing this example of optimal foraging at the patch level from the many examples (e.g., insects, birds, fish) that have come before is the relative importance of sensory modalties underlying foraging behaviors (Hassell and May 1974, Goss-Custard 1977, Stephens and Krebs 1986, Gotceitas 1990, Alonso et al. 1995). In the highly turbid water of the central Chesapeake Bay, crabs are predicted to rely heavily, if not soley, on chemosensory cues during foraging (e.g., amino acids from torn clam flesh). Vision probably plays only a minimal role in this system, where nearly complete darkness prevails at depths >1 m. Blue crabs possess sensitive olfactory receptors, responding to concentrations of crushed clam extract as low as 10^{-15} M (Pearson and Olla 1977), and use chemoreception for foraging in the laboratory setting (Zimmer-Faust 1989, Zimmer-Faust et al. 1995). While chemosensory foraging clearly may be important for predators in other systems (e.g. insects), the extremely slow current regimes (≤ 1 cm s^{-1}) in the upper reaches of some estuaries should allow odor plumes to remain intact much better than in more turbulent aquatic and especially terrestrial flows (Weissburg and Zimmer-Faust 1993). Thus, in the Rhode River and similar slow-current environments, crabs and other benthic predators presumably use chemical cues to indicate location of prey patches (Weissburg and Zimmer-Faust 1993) and, perhaps, their quality.

Although all crabs fed more efficiently when given access to two clam patches, crabs at high density appeared to interfere with each other's foraging success. They had a lower per capita clam consumption rate and a smaller increase in foraging success with increasing clam availability, than did crabs at low density. Crabs at high density may have interfered with each other through direct agonistic activity or through evasive behaviors that wasted foraging time. It should be noted that our results are unlikely to have been confounded by differences in competitive ability among experimental crabs. For example, one factor that can account for differences in competitive ability is the status of individuals within a dominance hierarchy as in American lobsters *Homarus americanus* (Atema 1995). However, repeated encounters among individual blue crabs, sufficient to establish a dominance hierarchy, are unlikely given the high mobility of these crabs. A second possible explanation for differences among crustaceans is competitive "class" of an individual (Dingle 1983). In fact, large blue crabs generally dominate over smaller ones, and males over females (Jachowski 1974). However, given that all of our experimental crabs were large (minimum carapace width of 130 mm) intermolt males, potential for a class effect is low.

The interaction of optimal foraging behaviors and conspecific interference among crabs affected the survival of their patchy prey. Clams in our study survived best in isolated patches, having roughly the same chance of survival whether being preyed upon by a low or high density of crabs. Surprisingly, clams in patches that were near other patches had the greatest chance of survival when crab density was high, apparently because of interference among crabs. From the way that distribution of prey patches and density of predators interact to affect the foraging behavior of blue crabs and subsequent *Macoma balthica* survival, we can predict that these factors will have similar effects on other crustacean-bivalve predator-prey dynamics. Other factors affecting the success of crabs foraging on bivalves, like prey density and substrate type, have been shown to be generally applicable across a number of species (Peterson 1982, Blundon and Kennedy 1982, Arnold 1984, Sponaugle and Lawton 1990).

Like blue crabs, many other crustaceans probably forage most efficiently in habitats where prey patches are relatively closely spaced, although not to the point of being almost contiguous. This distribution of prey patches apparently enables foragers to optimize prey intake and may allow them to reduce agonistic interactions by moving to readily accessible alternative feeding

sites (Clark et al. 1999b). Both of these needs – to maximize intake of patchily distributed prey and to reduce agonistic interactions – are likely to shape the foraging behavior of many other crustaceans. Many crustacean predators consume patchy prey as a major part of their diet, and can probably move easily between prey patches using chemosensory foraging (Derby and Atema 1982, Zimmer-Faust 1989, Rebach et al. 1990). On the other hand, many crustaceans appear motivated to reduce agonistic encounters as evidenced in part by the evolution of ritualized threat displays (Dingle 1983). Presumably because of these competing needs, blue crabs forage most successfully among prey patches spaced 7–10 m apart (Hines et al. unpubl.). Wider spacing hinders detection of neighboring patches whereas closer spacing leads to greater agonistic interference. However, optimal interpatch distances are likely to be considerably shorter for species that are less mobile that blue crabs. Bivalve mariculture operations that suffer major losses from predation by blue crabs and other crustaceans (Elner and Jamieson 1979, Sponaugle and Lawton 1990, Barbeau and Scheibling 1994) may be able to reduce their losses by using relatively small, widely spaced outplanted patches, although for operations plagued by highly mobile predators, the distances required may well be impractical. The mobility of other predators and the scale of patchiness they perceive will determine the quantitative applicability of our findings.

The ecological impact of this predator-prey interaction is likely to be strong in the Rhode River system and similar estuaries, given that predation by blue crabs appears to regulate prey abundance throughout the Chesapeake Bay (Holland et al. 1980, Hines et al. 1990). If crabs are foraging optimally at the level of selecting individual prey items, they may also be affecting the size structure of bivalve populations. However, although crabs have been shown to actively select individual prey items in some studies (Hughes and Seed 1981, Eggleston 1990), it is unlikely in the Rhode River. If appreciable effort is required to evaluate a prey item, a predator will rarely reject any item (Seed and Hughes 1995). For example, blue crabs feeding on epifaunal bivalves such as oysters and mussels select only optimally sized prey (Hughes and Seed 1981, Eggleston 1990), but when presented with infaunal bivalves such as *Mya* and *Mercenaria*, crabs do not reject any item (Blundon and Kennedy 1982). Given that crabs in the Rhode River consume primarily infaunal bivalves (*Macoma* and *Mya*) (Hines et al. 1990), they are unlikely to reject prey items that they have excavated. Thus, it is likely that crabs here optimize at the prey patch level, but not at the prey item level.

In addition to blue crabs' direct influence on community structure through predation in bivalve patches, both blue crabs and *Macoma balthica* may have other indirect effects on the benthic community. Foraging crabs destabilize the sediment (Hines et al. 1990), favoring deposit-feeding animals at the expense of suspension feeders (Woodin 1976). Because of the interference among crabs at high density demonstrated in this study, the influence of crabs as bioturbators of the sediment cannot be assumed to be a linear function of crab density. *Macoma balthica* has major effects on recruitment of infaunal species, strongly reducing the abundances of a tube-building amphipod, *Corophium lacustre*, and polychaete, *Polydora ligni* – both competitively dominant species (Hines et al. 1989). Thus, by structuring the clam population, foraging blue crabs may in turn affect infaunal recruitment.

By assessing the fine-scale behavior of individual predators with our novel telemetry system, we have shown a significant interactive effect between the distribution of prey and the density of predators on the foraging behavior of a subtidal estuarine predator. These factors altered predators' use of prey resources, movement, and foraging efficiency – and ultimately, the survival of their prey. Determining the factors that influence the foraging behavior of this key estuarine predator can, in turn, lead to a better understanding of the mechanisms that define the make-up of estuarine soft-bottom communities. In a publication by Clark et al. (1999b), we further explore the behaviors that underlie the decrease in foraging success at high predator density and how such behaviors may depend on distribution of prey.

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