

# Density-dependent foraging and mutual interference in blue crabs preying upon infaunal clams

Randa A. Mansour, Romuald N. Lipcius\*

College of William and Mary, School of Marine Science, Virginia Institute of Marine Science, Gloucester Point, Virginia 23062,  
USA

**ABSTRACT:** Predator-prey dynamics between the blue crab *Callinectes sapidus* and an infaunal soft-shelled clam, *Macoma balthica*, were examined in laboratory experiments to assess the joint effects of varying predator and prey densities upon predator foraging rates and prey survival. A full-factorial experimental design involved 2 prey densities (4 and 16 clams m<sup>-2</sup>) and 3 predator densities (1, 2 and 4 crabs m<sup>-2</sup>) with 6 trials per treatment combination. Blue crabs exhibited density-dependent foraging under all conditions: proportionally more clams were consumed at the higher clam density. Furthermore, at the higher crab densities mutual interference was evident in the incidence of wounds and deaths to crabs resulting from cannibalism or intraspecific aggression. Thus, the combined impact of varying crab and clam densities resulted in (1) the maintenance of a density-dependent refuge from blue crab predation for large infaunal clams, irrespective of crab density, and (2) intraspecific aggression resulting in injury and mortality of blue crabs at high crab densities. The collective results indicate that both predator and prey densities must be examined experimentally for their joint impact upon predator-prey dynamics in marine systems.

## INTRODUCTION

In marine systems, predation regulates community structure and varies in intensity in many rocky and soft-sediment marine benthic habitats (Connell 1975, Peterson 1979a, Paine 1980, Menge et al. 1986a, b, Hall et al. 1990). Predator-prey interactions in marine soft-bottom communities are particularly complex because they are dominated by guilds of generalist predators capable of switching among diverse prey (Hines et al. 1990), and because there are few communities with competitively dominant prey capable of monopolizing resources (Peterson 1979a, Dayton 1984). Menge (1983) defined key components of predation intensity, which are fundamentally based on the effectiveness and the abundance of individual predators (i.e. functional and aggregative responses). Though a quantitative focus on these basic components and their joint effects is required to understand marine benthic predator-prey dynamics, few, if any, studies have attempted to integrate the influence of functional and aggregative responses.

The functional response describes a short-term behavioral phenomenon where predators increase prey consumption as prey abundance increases (Solomon 1949, Holling 1959). This response may be linear, hyperbolic (inversely density-dependent) or sigmoid (density-dependent), each with specific effects upon predator-prey dynamics (Murdoch 1973). Analyses of functional responses have yielded useful results concerning the regulation of prey populations by predators in marine benthos systems (Boulding & Hay 1984, Katz 1985, Lipcius & Hines 1986, Eggleston 1990a, b, Sponaugle & Lawton 1990).

The numerical response, the relationship between the number of predators and prey abundance, is a function of predator behavior (e.g. aggregative response), fecundity and survivorship patterns (Holling 1959). In the aggregative response predators may regulate prey populations by congregating in areas of high prey density and by leaving those prey patches where the rate of prey capture falls below a threshold (Readshaw 1973). The general aggregative response is sigmoid in form, and tends to stabilize predator-prey systems (Hassell & May 1974). Predator aggregation around high density patches can provide a partial refuge for prey in low density patches

\* Author for correspondence

(Hassell 1978). Aggregative responses have been described for various marine vertebrates and invertebrates (Hill 1979, Decho & Fleeger 1988, Fairweather 1988, Friedland et al. 1989, Piatt et al. 1989).

Predator aggregation can also enhance the foraging rates of individual predators if they are attracted to prey patches by the foraging of conspecifics, or when mutual attacks are more successful than individual attacks (Hassell & May 1973, 1974, Anger et al. 1977). Conversely, mutual interference resulting from predator aggregation may adversely affect either a predator's searching efficiency or its feeding rate. The general interference response describes the relationship between searching efficiency or attack rate and predator density, and is curvilinear with interference becoming negligible at low predator densities (Hassell 1978). The combination of aggregation and interference may stabilize predator-prey dynamics by providing partial refuges for prey in low density patches, and by promoting dispersal of predators from patches in which prey have been heavily exploited (Hassell 1978).

Blue crabs affect local population densities of their bivalve prey (Virnstein 1977, 1979, Peterson 1979b, Holland et al. 1980, Seed 1980, Blundon & Kennedy 1982a, b, Arnold 1984, Lipcius & Hines 1986, Sponaugle & Lawton 1990) and play a major role in energy transfer within estuaries (Baird & Ulanowicz 1989). However, little is known about the combined role of predator and prey densities in predator-prey interactions, especially the aggregative response and intraspecific competition or interference. The objective of this study was to quantify the combined effect of the functional, aggregative, and interference (i.e. intraspecific competition) responses upon prey and predator survival and predator foraging rates in a marine predator-prey system, specifically that between the blue crab *Callinectes sapidus* Rathbun and the infaunal clam *Macoma balthica* (L.), in Chesapeake Bay.

### THE PREDATOR-PREY SYSTEM

The blue crab *Callinectes sapidus* is a large [males up to 227 mm carapace width (CW)] epibenthic omnivore occurring in various habitats along the Northwest Atlantic Ocean, Gulf of Mexico and Caribbean Sea (Williams 1984). Blue crabs serve as both prey and consumers, and are abundant and actively foraging from late spring through autumn in Chesapeake Bay, USA (Hines et al. 1987, 1990). The diet of Chesapeake Bay blue crabs consists of bivalves (predominantly *Macoma balthica*), crabs (both blue crabs and xanthids), fish and polychaetes, and to a lesser extent amphipods and isopods (Hines et al. 1990, R. Mansour & R. Lipcius unpubl.).

The tellinid *Macoma balthica* is an infaunal, soft-shelled clam commonly occurring in muddy and sandy habitats along both sides of the North Atlantic (from the Arctic Sea to Georgia along the western Atlantic) and along the Pacific coast from polar regions to its southern limit in San Francisco Bay (Beukema & Meehan 1985, Martini & Morrison 1987). In Chesapeake Bay, *M. balthica* is an abundant, deep-burrowing (depth to 40 cm), deposit or suspension feeder, and occurs predominantly in mud substrates of meso-polyhaline regions (Hines & Comtois 1985, Hines et al. 1989, 1990). Two settlement pulses occur: a relatively weak winter pulse and a marked spring pulse peaking in May, ceasing in June, and with populations declining rapidly in July and August primarily in association with intense blue crab predation (Holland et al. 1980, 1987, Blundon & Kennedy 1982b, Holland 1985, Hines et al. 1989, 1990). Large adults find at least partial refuge through greater burial depth (> 10 cm) (Blundon & Kennedy 1982b) and possibly through a low-density refuge, as observed in another soft-shelled infaunal clam, *Mya arenaria* (Lipcius & Hines 1986). The combined effect of varying predator and prey densities upon the dynamics of this system remains unquantified.

### MATERIALS AND METHODS

We used a full-factorial experimental design with 2 prey densities of 4 and 16 clams  $m^{-2}$  (i.e. clams tank $^{-1}$ ) and 3 predator densities of 1, 2 and 4 crabs  $m^{-2}$  (i.e. crabs tank $^{-1}$ ). Experimental clam densities resemble low to moderate field densities (Hines et al. 1990, D. Eggleston, R. Lipcius & A. Hines unpubl.), while crab densities are similar to moderate and high blue crab densities (> 25 mm CW, 6.9 crabs  $m^{-2}$ ) in Chesapeake Bay (Orth & van Montfrans 1987). Controls included both clam densities but without crabs. Experiments were conducted under natural photoperiod from mid-July through mid-October 1989 (mean water temperature  $\pm$  SE:  $22.1 \pm 0.3^\circ C$ ).

Six circular tanks 1.13 m in diameter ( $1 m^2$ ) were filled with fine muddy sand (97.3 % sand, 1.5 % silt, 1.3 % clay) to a depth of 15 cm and unfiltered, ambient York River (Virginia, USA) water to a level 25 cm above the sediment surface. Blue crabs were captured in traps, whereas *Macoma balthica* were collected by suction-dredge from local muddy and sandy habitats. Male intermolt crabs, 115 to 160 mm CW, were held separately, fed ad libitum with live *M. balthica* and mussels *Geukensia demissa*, and acclimated to laboratory conditions for 1 wk. *M. balthica*, 27 to 39 mm SL (shell length), were held in open-system tanks and also acclimated for 1 wk.

Crabs were matched for size to within 10 % CW. All

crabs were exposed to randomly chosen combinations of crab and clam densities to avoid learning specific treatment combinations (Murdoch & Oaten 1975). Crabs were checked daily; any crabs that died overnight, either from unknown causes or cannibalism, were replaced by similarly sized new crabs and treated in the same manner as their predecessors. All sizes of crabs used in this investigation were equally capable of excavating and feeding on the size classes of clams offered (Blundon & Kennedy 1982a, b). All sizes of experimental clams bury to similar depths (Blundon & Kennedy 1982b, Hines & Comtois 1985), and were therefore equally available to crabs. We only used crabs that fed during acclimation, and clams that exhibited a healthy siphon-withdrawal reflex.

The experimental procedure involved introduction of clams and crabs into tanks during daylight hours (11:00 to 14:00 h). *Macoma balthica* were randomly buried 10 cm below the sediment surface and allowed 48 h prior to crab introduction to acclimate to experimental conditions and bury to a natural depth (Hines & Comtois 1985). Crabs starved for 48 h were released into the center of each tank at the start of a trial. Trials ended with removal of crabs after 72 h, and determination of clam mortality through counts of survivors and umbos of eaten clams. Between each trial, experimental tank water was replaced with ambient river water, while the sediment was vigorously aerated. Twenty-four hours prior to clam introduction, water inflow was discontinued and sediment aeration reduced.

Six trials were conducted for each combination of crab and clam density with systematic interspersion of each treatment combination (Underwood 1981, Hurlbert 1984). The numbers and proportions of eaten clams were analyzed as a function of clam and crab density in a 2-way fixed-factor analysis of variance (ANOVA). Prior to analyses, the raw numbers were log-transformed, while proportional mortality data were arc-sine square-root transformed to normalize the data and remove heteroscedasticity (Cochran's test; Sokal & Rohlf 1981, Underwood 1981, SPSS Inc. 1988). In 3 instances, 1 trial each of a treatment combination (i. e. 3 of 36 trials) was lost due to system failure. In these cases, we substituted the mean of the treatment combination for that trial to maintain a balanced experimental design, and reduced the error MS df accordingly before calculating *F* values (Underwood 1981). Means were back-transformed for graphical presentation.

Variations in proportional mortality with prey density can be used to distinguish density-dependent (i. e. relatively lower proportional mortality at low clam density) from inversely density-dependent (i. e. relatively higher proportional mortality at low clam density) predation (Lipcius & Hines 1986). Usually, 3 to 6 prey densities are required to determine the general shape

of a functional response curve, although the type of functional response is detectable only at low to moderate prey densities. However, 2 prey densities permit statistical differentiation among density-independent, inversely density-dependent and density-dependent functional response curves at low to moderate prey densities (Lipcius & Hines 1986). Other investigations (D. Eggleston, R. Lipcius & A. Hines unpubl.) indicated the range of *M. balthica* densities required to distinguish between functional response curves and described the general shape of the curves for the blue crab-*Macoma* predator-prey system. We therefore selected a subset of clam densities from within this range for this investigation.

Crab mortality resulting from cannibalism and intraspecific aggression was analyzed with Dunnett's multiple comparison procedure, which compares 2 or more proportions to a control proportion (Zar 1984).

## RESULTS

There was 100 % survivorship of control clams. Proportional mortality of clams and consumption rates of blue crabs differed significantly by clam density (Fig. 1A, B, Table 1). Blue crabs exhibited density-dependent foraging in all treatments: proportionally more clams were consumed at the high clam density (Fig. 1B). The data for consumption rates and proportional mortality of clams as a function of crab density suggested a decreasing trend (Fig. 1A, B); however, our power to detect a significant crab density effect was low (a posteriori test; Zar 1984; power < 0.20) for both the numbers eaten and proportional mortality. The interaction effect between crab density and clam density was not significant (Table 1).

Consumption rates and proportional mortalities standardized by crab density (number eaten and proportional mortality divided by crab density per treatment; Fig 1c, d) differed significantly by clam density and crab density (Table 2). Again, crabs exhibited density-dependent foraging, with highest clam mortalities per crab and consumption rates per crab at the higher clam density (Fig. 1C, D). The interaction effect between clam and crab density was not significant in either case (Table 2).

Cannibalism and intraspecific aggression by blue crabs, as indicated by crab deaths, carapace wounds and loss of appendages, occurred in both the 2-crab and 4-crab density treatments at both clam densities. The results of other investigations (Lipcius & Hines 1986, Martin et al. 1989, D. Eggleston, R. Lipcius & A. Hines unpubl.) using similar crab densities and tanks indicate that the crab densities used in this investigation were not likely to result in mortality associated

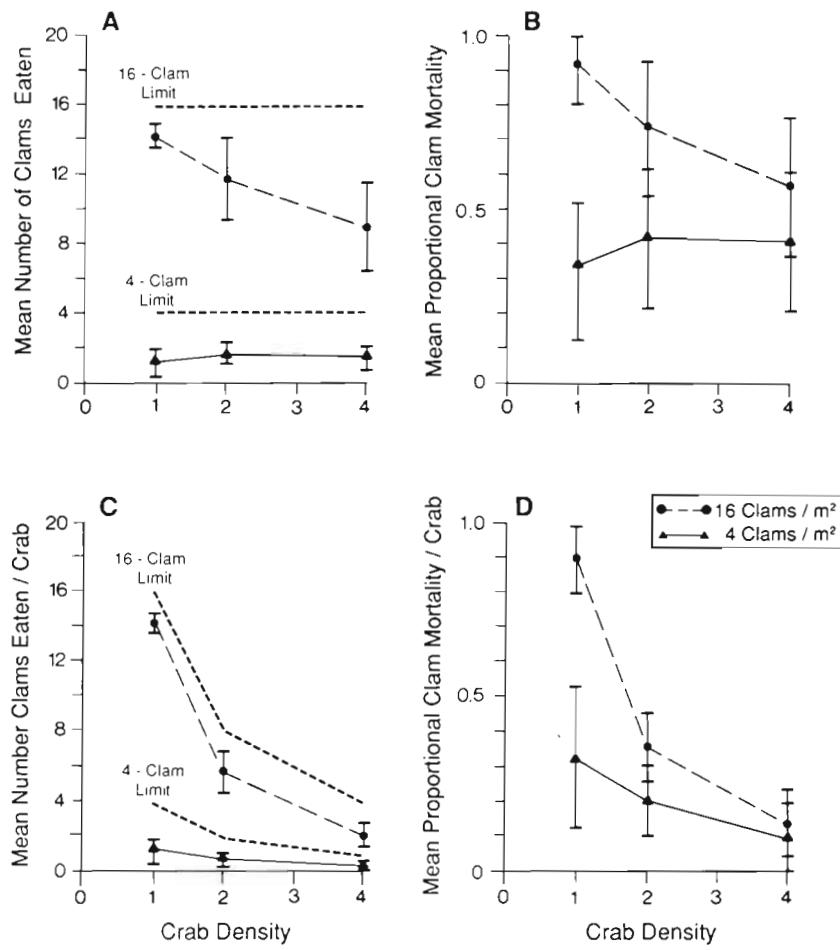


Fig. 1. *Callinectes sapidus* preying on *Macoma balthica*. Mortality of clams as a function of crab and clam density for (A) mean number of clams eaten ( $\pm$  SE), (B) mean proportional clam mortality ( $\pm$  SE), (C) mean number of clams eaten per crab ( $\pm$  SE), (D) mean proportional clam mortality per crab ( $\pm$  SE)

Table 1. Two-way fixed factor ANOVA of number eaten and proportional clam mortality as a function of clam and crab density

Source of variation	SS	df	MS	F
<b>Number Eaten</b>				
Clam density	9.756	1	9.756	22.13****
Crab density	0.314	2	0.157	0.36 ns
Clam $\times$ Crab interaction	0.838	2	0.419	0.95 ns
Error	11.905	27	0.441	
<b>Proportional mortality</b>				
Clam density	2.072	1	2.072	6.20*
Crab density	0.167	2	0.084	0.25 ns
Clam $\times$ Crab interaction	0.360	2	0.180	0.54 ns
Error	9.028	27	0.334	

\* p < 0.05. \*\*\*\* p < 0.001, ns: p > 0.05

with adverse abiotic conditions. Furthermore, since only hard intermolt crabs were used in each trial and none of these crabs molted during the trials, it is unlikely that any crabs were more susceptible to cannibalism than others in the same tank. Thus, we assumed that death from causes other than cannibalism or intraspecific aggression occurred at the proportional

mortality rate observed in the 1-crab treatments ( $0.083 \text{ crabs tank}^{-1} 72\text{h}^{-1}$ ; Table 3). This rate was adjusted for the number of crabs in each tank (see Table 3), yielding 4 hypothetical proportional mortalities due to sources other than cannibalism and intraspecific aggression in the 2-crab and 4-crab treatments. The 4 observed proportional mortalities were then compared with these

Table 2. Two-way fixed factor ANOVA of consumption rate and proportional clam mortality standardized by crab density (see text) as a function of clam and crab density

Source of variation	SS	df	MS	F
<b>Number eaten per crab</b>				
Clam density	8.596	1	8.596	28.87****
Crab density	2.070	2	1.035	3.47*
Clam × Crab interaction	1.136	2	0.568	1.91 ns
Error	8.040	27	0.298	
<b>Proportional mortality per crab</b>				
Clam density	1.060	1	1.060	8.28**
Crab density	2.158	2	1.079	8.43****
Clam × Crab interaction	0.732	2	0.366	2.86 ns
Error	3.453	27	0.128	

\* p < 0.05, \*\* p < 0.01, \*\*\*\* p < 0.001, ns: p > 0.05

Table 3. Mortalities of crabs as a function of crab and clam density. Hypothetical proportional mortalities were calculated for each treatment combination by multiplying crab density by 0.083 (i.e. the value derived from the 1-crab, 4-clam and 16-clam density treatments, which reflected the proportion dead due to causes other than cannibalism or intraspecific aggression). In 2-crab trials the hypothetical proportional mortality =  $0.083 \times 2 = 0.166$ ; in 4-crab trials,  $0.083 \times 4 = 0.332$ . \* p < 0.05, Dunnett's multiple comparison procedure for comparing proportions with a hypothetical proportion (Zar 1984). In this procedure, the observed proportions in the column 'Proportion with a dead crab' were compared with those in the column 'Hypothetical proportional mortality'. The procedure accounts for the number of comparisons. ns: p > 0.05, Dunnett's procedure

Clam density	Crab density	Trials with a dead crab	Total trials	Proportion with a dead crab	Hypothetical proportional mortality	Proportion cannibalized
4 or 16	1	1	12	0.083	0.083	0.000
4	2	3	6	0.333 ns	0.166	0.167 ns
4	4	3	5	0.600 *	0.332	0.268 *
16	2	4	6	0.333 ns	0.166	0.167 ns
16	4	2	5	0.400 ns	0.332	0.068 ns

hypothetical proportional mortalities with Dunnett's multiple comparison test (Zar 1984). The resulting tests showed mortality significantly higher than the hypothetical proportions in the 4-crab, 4-clam treatment, which had the lowest ratio of clam:crab abundance, but not in the remaining 3 treatments (Table 3), though these were also greater than zero.

## DISCUSSION

Blue crabs exhibited density-dependent foraging in all treatment combinations of crab and clam densities. Although the occurrence of a density-dependent functional response was not unexpected given the outcomes of previous studies (i.e. with the soft-shelled infaunal clam *Mya arenaria* in sand, Lipcius & Hines 1986; with *Macoma balthica* in mud and sand, D. Eggleston, R. Lipcius & A. Hines unpubl.), the results were novel in that the density-dependent refuge for

clams was maintained irrespective of crab density. Thus, adult *M. balthica* obtain a refuge from blue crab predation at low densities (i.e. ca 1 to 4 clams per tank), and this refuge appears to be retained even when crab densities are high.

Furthermore, several observations strongly suggest the existence of mutual interference and intraspecific aggression between crabs with increased predator density. First, crab mortality and injury occurred at a significant rate in at least one of the crab density treatments, and may have been statistically non-significant in the other treatments due to our low statistical power (ca 0.20). A similar result was observed by Martin et al. (1989) in enclosures of equal area as those used in our experiment, and a density of 2 crabs per enclosure (ca 1 m<sup>2</sup>). Second, we noted the frequency with which clam densities in the 16-clam trials remained above the low-density refuge (i.e. 1 to 4 clams per tank), and thereby were not reduced substantially. The data showed an increase in the number

of trials remaining above the low-density refuge as crab density increased (i.e. 0 of 5 with 1 crab, 2 of 6 with 2 crabs, and 3 of 5 with 4 crabs), suggesting that mutual interference between crabs further enhanced the low-density refuge. Third, although a single blue crab could consume all experimental clams, the numbers of clams eaten decreased, though not significantly, in the 2-crab and 4-crab treatments.

Other field and laboratory studies also indicate that cannibalism is common in blue crabs (Darnell 1959, Tagatz 1968, Laughlin 1982, Martin et al. 1989, Peery 1989, Hines et al. 1990, R. Mansour & R. Lipcius unpubl.). In the Apalachicola estuary, Florida, USA, Laughlin (1979) observed an inverse relationship between blue crab recruitment levels and subsequent population abundance, and suggested that high densities of juveniles may stimulate cannibalism and exploitative competition. Blue crabs constituted 11 % of the total diet of large crabs (> 61 mm) in that estuary (Laughlin 1982). Cannibalism is an extreme form of interference competition, occurring in a wide variety of vertebrates and invertebrates. It is most frequent during periods of low availability of alternative prey or high predator density, and acts as a density-dependent regulator of population size (Fox 1975, Polis 1981).

In Chesapeake Bay, blue crabs and their prey exhibit seasonal cycles in abundance. The blue crab population is composed of 2 year-classes that are actively foraging in the tributaries of Chesapeake Bay from April through December (Hines et al. 1987, Lipcius & Van Engel 1990). Therefore, the potential for intra-specific agonistic interactions leading to cannibalism is high, especially as alternative prey are depleted later in the season. Further evidence that density-dependent rates of cannibalism may regulate blue crab populations includes: density-dependent autotomy (Smith 1990), increased occurrence of crabs in blue crab stomachs in late summer when alternative (bivalve) prey availability and densities are reduced (Hines et al. 1990, R. Mansour & R. Lipcius unpubl.), cannibalism of tethered juvenile blue crabs (L. D. Smith unpubl.), the highly developed and complex intraspecific agonistic behaviors of blue crabs (Jachowski 1974), and the significant effect of previous year-classes on the stock-recruitment relationship for blue crabs in Chesapeake Bay (Lipcius & Van Engel 1990).

Our results indicate that the interactive effects of prey density and predator density are also important for clam persistence in prey patches. Furthermore, our results show how the aggregative and interference responses may affect the magnitude of predation intensity. The aggregative and interference responses are strongly interrelated (Hassell 1978): by congregating in patches of high prey density, the probability of interference is enhanced, which then modifies the functional and

aggregative responses. Crowley & Martin (1989) derived 2 functional response models of interference, and applied them to data on cannibalistic functional responses of dragonfly larvae. In a distraction model a predator's attention is divided between other predators and the prey, whereas in a preemption model the predator's response to other predators takes precedence over feeding. Both models fit the data well: there was an inverse relationship between feeding rate and predator density, indicating strong interference among these cannibalistic predators (Crowley & Martin 1989). MacLeod & Valielas (1975) found a similar trend of decreasing prey consumption with increasing predator density for nudibranch predators. At the highest predator density, nudibranchs spent more time in small inactive groups rather than actively searching for prey. For blue crabs, it is unclear whether agonistic interactions lead primarily to avoidance responses (as in some starfish; Palumbi & Freed 1988) and hence predator dispersal, or if cannibalism is the relatively more frequent response to low alternative prey availability or high conspecific population density. Behavioral studies are required to quantify the nature of these interactions between blue crabs.

A predator's combined aggregative, functional and interference response must be defined in investigations of predator-prey dynamics and community organization in marine soft-bottom benthic communities. In our system, the combination of responses allows prey to persist, despite intense predation, by affecting the magnitude of predation in prey patches. Previous work on the blue crab-bivalve (i.e. *Macoma balthica* and *Mya arenaria*) predator-prey system in Chesapeake Bay has concentrated on the interactive effects of prey species, prey density and habitat type (e.g. sediment) on clam survivorship (Lipcius & Hines 1986, Hines et al. 1990, D. Eggleston, R. Lipcius & A. Hines unpubl.). The field and laboratory evidence accumulated thus far indicates that predator foraging and prey mortality rates vary significantly across gradients in prey availability, and the physical properties of microhabitats (Blundon & Kennedy 1982a, b, Arnold 1984, Lipcius & Hines 1986, West & Williams 1986, Hines et al. 1990, Sponaugle & Lawton 1990). The results of this study suggest differences in the magnitude of the functional response resulting from predator density, such that prey mortality and predator foraging rates may be reduced within prey patches where predators aggregate. Other studies have shown that interference between predators is important to the outcome of interactions between predators and prey, and determines predator dispersion and prey persistence (Beddington 1975, MacLeod & Valielas 1975, Sih 1981, Eveleigh & Chant 1982, Ens & Goss-Custard 1984, Palumbi & Freed 1988). This study further indicates that predator density and interference may be impor-

tant in the population dynamics of marine species, by affecting foraging rates and perhaps promoting cannibalism when alternative food resources are limited. Further field investigations are required to quantify these components of predation and determine effects on both predator and prey population dynamics, and community organization in marine systems.

**Acknowledgements.** We thank D. Eggleston, P. Gerdes, T Leggett, and K. Metcalf for help with field collections of clams and crabs. Critical reviews of the manuscript were provided by D. Eggleston, A. H. Hines, R. Mann, J. Sutherland, D. Sved and 2 anonymous reviewers. We are especially thankful to C. H. Peterson for his thorough and insightful criticisms. This work was supported by funds from the National Science Foundation (Biological Oceanography grants OCE 87-00414 to R. Lipcius & A. Hines, and OCE 90-00483 to A. Hines, R. Lipcius, T Wolcott & D. Wolcott), VIMS Minor Research Grants Program, the Commonwealth of Virginia, the Smithsonian Institution, and a generous contribution by L. L. Glucksman. Contribution No. 1656 from the Virginia Institute of Marine Science. This paper is dedicated (by R.A.M.) to Marzell Deans and to the memory of Doris Deans.

#### LITERATURE CITED

- Anger, K., Rogal, U., Schriever, G., Valentin, C. (1977). In-situ investigations on the echinoderm *Asterias rubens* as a predator of soft-bottom communities in the western Baltic Sea. *Helgoländer wiss. Meeresunters.* 29: 439-459
- Arnold, S. K. (1984). The effects of prey size, predator size, and sediment composition on the rate of predation of the blue crab, *Callinectes sapidus* Rathbun, on the hard clam, *Meretrix mercenaria* (Linne). *J. exp. mar. Biol. Ecol.* 80: 207-219
- Baird, D., Ulanowicz, R. E. (1989). The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecol. Monogr.* 59: 329-364
- Beddington, J. R. (1975). Mutual interference between parasites or predators and its effect on searching efficiency. *J. Anim. Ecol.* 44: 331-340
- Beukema, J. J., Meehan, B. W. (1985). Latitudinal variation in linear growth and other shell characteristics of *Macoma balthica*. *Mar. Biol.* 90: 27-33
- Blundon, J. A., Kennedy, V. S. (1982a). Mechanical and behavioral aspects of blue crab, *Callinectes sapidus* (Rathbun), predation on Chesapeake Bay bivalves. *J. exp. mar. Biol. Ecol.* 65: 47-65
- Blundon, J. A., Kennedy, V. S. (1982b). Refuges for infaunal bivalves from blue crab, *Callinectes sapidus* (Rathbun), predation in Chesapeake Bay. *J. exp. mar. Biol. Ecol.* 65: 67-81
- Boulding, E. G., Hay, T. K. (1984). Crab response to prey density can result in density-dependent mortality of clams. *Can. J. Fish. Aquat. Sci.* 41: 521-525
- Connell, J. H. (1975). Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In: Cody, M. L., Diamond, J. (eds.) *Ecology and evolution of communities*. Belknap Press, Cambridge, Massachusetts, p. 460-490
- Crowley, P. H., Martin, E. K. (1989). Functional responses and interference within and between year classes of a dragonfly population. *J. N. Am. Benthol. Soc.* 8: 211-221
- Darnell, R. M. (1959). Studies of the life history of the blue crab (*Callinectes sapidus* Rathbun) in Louisiana waters. *Trans. Am. Fish. Soc.* 88: 294-304
- Dayton, P. K. (1984). Processes structuring some marine communities: are they general? In: Strong, D. R. Jr., Simberloff, D., Abele, L. G., Thistle, A. B. (eds.) *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, New Jersey, p. 181-197
- Decho, A. W., Fleeger, J. W. (1988). Microscale dispersion of meiobenthic copepods in response to food-resource patchiness. *J. exp. mar. Biol. Ecol.* 118: 229-243
- Eggleston, D. B. (1990a). Foraging behavior of the blue crab, *Callinectes sapidus*, on juvenile oysters *Crassostrea virginica*: effects of prey density and size. *Bull. mar. Sci.* 46: 62-82
- Eggleston, D. B. (1990b). Behavioural mechanisms underlying variable functional responses of blue crabs, *Callinectes sapidus* feeding on juvenile oysters, *Crassostrea virginica*. *J. Anim. Ecol.* 59: 615-630
- Ens, B. J., Goss-Custard, J. D. (1984). Interference among oyster catchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*, on the Exe estuary. *J. Anim. Ecol.* 53: 217-231
- Eveleigh, E. S., Chant, D. A. (1982). Experimental studies on acarine predator-prey interactions: the effects of predator density on prey consumption, predator searching efficiency, and the functional response to prey density (Acarina: Phytoseiidae). *Can. J. Zool.* 60: 611-629
- Fairweather, P. G. (1988). Correlations of predatory whelks with intertidal prey at several scales of space and time. *Mar. Ecol. Prog. Ser.* 45: 237-243
- Fox, L. R. (1975). Cannibalism in natural populations. *Ann. Rev. Ecol. Syst.* 6: 87-106
- Friedland, K. D., Ahrenholz, D. W., Guthrie, J. F. (1989). Influence of plankton on distribution patterns of the filter-feeder *Brevoortia tyrannus* (Pisces: Clupeidae). *Mar. Ecol. Prog. Ser.* 54: 1-11
- Hall, S. J., Raffaelli, D., Robertson, M. R., Basford, D. J. (1990). The role of the predatory crab, *Liocarcinus depurator*, in a marine food web. *J. Anim. Ecol.* 59: 421-438
- Hassell, M. P. (1978). *The dynamics of arthropod predator-prey systems. Monographs in population biology*. Princeton University Press, Princeton, New Jersey
- Hassell, M. P., May, R. M. (1973). Stability in insect host-parasite models. *J. Anim. Ecol.* 42: 693-736
- Hassell, M. P., May, R. M. (1974). Aggregation of predators and insect parasites and its effect on stability. *J. Anim. Ecol.* 43: 567-594
- Hill, B. J. (1979). Aspects of the feeding strategy of the predatory crab *Scylla serrata*. *Mar. Biol.* 55: 209-214
- Hines, A. H., Comtois, K. L. (1985). Vertical distribution of infauna in sediments of a subestuary of central Chesapeake Bay. *Estuaries* 8: 296-304
- Hines, A. H., Haddon, A. M., Weichert, L. A. (1990). Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 67: 105-126
- Hines, A. H., Lipcius, R. N., Haddon, A. M. (1987). Population dynamics and habitat partitioning by size, sex, and molt stage of blue crabs (*Callinectes sapidus*) in a subestuary of Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 36: 55-64
- Hines, A. H., Posey, M. H., Haddon, P. J. (1989). Effects of adult suspension- and deposit-feeding bivalves on recruitment of estuarine infauna. *Veliger* 32: 109-119
- Holland, A. F. (1985). Long-term variation of macrobenthos in a mesohaline region of Chesapeake Bay. *Estuaries* 8: 93-113

- Holland, A. F., Mountford, N. K., Hiegel, M. H., Kaumeyer, K. R., Mihursky, J. A. (1980). Influence of predation on infaunal abundance in upper Chesapeake Bay, USA. *Mar. Biol.* 57: 221–235
- Holland, A. F., Shaughnessy, A. T., Hiegel, M. H. (1987). Long-term variation in mesohaline Chesapeake Bay macro-benthos: spatial and temporal patterns. *Estuaries* 10: 227–245
- Holling, C. S. (1959). The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Can. J. Entomol.* 91: 293–320
- Hurlbert, S. (1984). Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54: 187–211
- Jachowski, R. L. (1974). Agonistic behavior of the blue crab, *Callinectes sapidus* Rathbun. *Behaviour* 50: 232–253
- Katz, C. H. (1985). A nonequilibrium predator-prey interaction. *Ecology* 66: 1426–1438
- Laughlin, R. A. (1979). Trophic ecology and population distribution of the blue crab, *Callinectes sapidus* Rathbun, in the Apalachicola estuary, Florida, USA. Ph. D. dissertation, Florida State University, Tallahassee
- Laughlin, R. A. (1982). Feeding habits of the blue crab, *Callinectes sapidus* Rathbun, in the Apalachicola estuary, Florida. *Bull. mar. Sci.* 32: 807–822
- Lipcius, R. N., Hines, A. H. (1986). Variable functional responses of a marine predator in dissimilar homogeneous microhabitats. *Ecology* 67: 1361–1371
- Lipcius, R. N., Van Engel, W. A. (1990). Blue crab population dynamics in Chesapeake Bay: Variation in abundance (York River, 1972–1988) and stock-recruit functions. *Bull. mar. Sci.* 46: 180–194
- MacLeod, P., Valiela, I. (1975). The effect of density and mutual interference by a predator: a laboratory study of predation by the nudibranch *Coryphella rufibranchialis* on the hydroid *Tubularia larynx*. *Hydrobiologia* 47: 339–346
- Martin, T. H., Wright, R. A., Crowder, L. B. (1989). Non-additive impact of blue crabs and spot on their prey assemblages. *Ecology* 70: 1935–1942
- Martini, I. P., Morrison, R. I. G. (1987). Regional distribution of *Macoma balthica* and *Hydrobia minuta* on the subarctic coasts of Hudson Bay and James Bay, Ontario, Canada. *Estuar. coast. Shelf Sci.* 24: 47–68
- Menge, B. A. (1983). Components of predation intensity in the low zone of the New England rocky intertidal region. *Oecologia (Ber.)* 58: 141–155
- Menge, B. A., Lubchenco, J., Ashkenas, L. R. (1986a). Experimental separation of effects of consumers on sessile prey in the low zone of a rocky shore in the Bay of Panama: direct and indirect consequences of food web complexity. *J. exp. mar. Biol. Ecol.* 100: 225–269
- Menge, B. A., Lubchenco, J., Gaines, S. D., Ashkenas, L. R. (1986b). A test of the Menge-Sutherland model of community organization in a tropical rocky intertidal food web. *Oecologia (Ber.)* 71: 75–89
- Murdoch, W. W. (1973). The functional responses of predators. *J. appl. Ecol.* 10: 335–342
- Murdoch, W. W., Oaten, A. (1975). Predation and population stability. In: MacFadyen, A. (ed.) *Advances in ecological research*, Vol. VIX. Academic Press, New York, p. 1–131
- Orth, R. J., van Montfrans, J. (1987). Utilization of a seagrass meadow and tidal marsh creek by blue crabs *Callinectes sapidus*. I. Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. *Mar. Ecol. Prog. Ser.* 41: 283–294
- Paine, R. (1980). Food webs: linkage, interaction strength and community infrastructure. *J. Anim. Ecol.* 49: 667–685
- Palumbi, S. R., Freed, L. A. (1988). Agonistic interactions in a keystone predatory starfish. *Ecology* 69: 1624–1627
- Peery, C. A. (1989). Cannibalism experiments with the blue crab (*Callinectes sapidus* Rathbun): potential effects of size and abundance. Masters thesis, School of Marine Science, Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, Virginia
- Peterson, C. H. (1979a). Predation, competitive exclusion, and diversity in the soft-sediment communities of estuaries and lagoons. In: Livingston, R. J. (ed.) *Ecological processes in coastal and marine systems*. Plenum Publishing Corporation, New York, p. 233–264
- Peterson, C. H. (1979b). The importance of predation and competition in organizing the intertidal epifaunal communities of Barnegat Inlet, New Jersey. *Oecologia (Ber.)* 39: 1–24
- Piatt, J. F., Methven, D. A., Burger, A. E., McLagan, R. L., Mercer, V., Creelman, E. (1989). Baleen whales and their prey in a coastal environment. *Can. J. Zool.* 67: 1523–1530
- Polis, G. A. (1981). The evolution and dynamics of intraspecific predation. *Ann. Rev. Ecol. Syst.* 12: 225–251
- Readshaw, J. L. (1973). The numerical response of predators to prey density. *J. appl. Ecol.* 10: 342–351
- Seed, R. (1980). Predator-prey relationships between the mud crab *Panopeus herbstii*, the blue crab, *Callinectes sapidus* and the Atlantic ribbed mussel *Geukensia* (= *Modiolus demissa*). *Estuar. coast. mar. Sci.* 11: 445–458
- Sih, A. (1981). Stability, prey density and age/dependent interference in an aquatic insect predator, *Notonecta hoffmanni*. *J. Anim. Ecol.* 50: 625–636
- Smith, L. D. (1990). Patterns of limb loss in the blue crab, *Callinectes sapidus*, and the effects of autotomy on growth. *Bull. mar. Sci.* 46: 23–36
- Sokal, R. R., Rohlf, F. J. (1981). *Biometry*, 2nd edn. W. H. Freeman and Co., New York
- Solomon, M. E. (1949). The natural control of animal populations. *J. Anim. Ecol.* 18: 1–35
- Sponaugle, S., Lawton, P. (1990). Opportunid crab predation on juvenile hard clams: effects of substrate type and prey density. *Mar. Ecol. Prog. Ser.* 67: 43–53
- SPSS Inc. (1988). *SPSS-X advanced statistics guide*, 2nd edn. SPSS Inc., Chicago, Illinois
- Tagatz, M. E. (1968). Biology of the blue crab, *Callinectes sapidus* Rathbun, in the St. Johns River, Florida. *Fish. Bull. U.S.* 67: 17–33
- Underwood, A. J. (1981). Techniques of analysis of variance in experimental marine biology and ecology. *Ocean. mar. Biol. A. Rev.* 19: 513–605
- Virnstein, R. W. (1977). The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. *Ecology* 58: 1199–1217
- Virnstein, R. W. (1979). Predation on estuarine infauna: response patterns of component species. *Estuaries* 2: 69–86
- West, D. L., Williams, A. H. (1986). Predation by *Callinectes sapidus* (Rathbun) within *Spartina alterniflora* (Loisel) marshes. *J. exp. mar. Biol. Ecol.* 100: 75–95
- Williams, A. B. (1984). Shrimps, lobsters and crabs of the east coast of the United States. Smithsonian Institution Press, Washington, D.C.
- Zar, J. H. (1984). *Biostatistical analysis*. Prentice-Hall, Inc., Englewood Cliffs, New Jersey