VARIABLE FUNCTIONAL RESPONSES OF A MARINE PREDATOR IN DISSIMILAR HOMOGENEOUS MICROHABITATS[1]

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Abstract. Adult soft-shelled clams (*Mya arenaria*) persist at low densities in Chesapeake Bay sandy habitats despite intense predation by blue crabs (*Callinectes sapidus*). Clam persistence may be a consequence of variation in blue crab foraging rates as a function of clam density and sediment composition. In laboratory aquaria, we measured the functional responses (prey consumption per predator as a function of prey density) of large blue crabs to six densities of adult soft-shelled clams buried at natural depths in two sediment types (mud and sand). Functional responses in sand and mud were differentiated statistically by analyses of (1) residuals and residual sums of squares of discrete and continuous-time models, and (2) the exponent β of a general functional response model.

Crab predation rates were significantly higher in mud than sand, and functional responses differed significantly between these two substrates. Blue crabs displayed type III (sigmoid) density-dependent functional responses in sand, and type II (decelerating rise to an upper asymptote) inversely density-dependent responses in mud. Risk of mortality for clams decreased sharply in sand at low densities similar to those observed in the field near the end of the annual period of active predation. These observations (1) suggest that variable blue crab functional responses result in microhabitat-specific mortality rates of benthic prey, and (2) indicate that functional responses can differ significantly according to the physical properties of topographically simple habitats.

Key words: blue crabs; Callinectes sapidus; *foraging behavior; functional responses; habitat variation;* Mya arenaria; *predation; predator-prey dynamics.*

INTRODUCTION

Quantitative analyses of the functional response, the relationship between prey consumption per predator and prey density (Solomon 1949, Holling 1959, 1965), provide information on the mechanisms underlying predator-prey dynamics. Functional responses are conveniently classified into four general types (Hassell 1978, Taylor 1984), although there are numerous theoretically possible forms (Abrams 1982). The type I response increases linearly to a plateau, and has been observed in aquatic filter-feeding invertebrates (Hassell 1978). The type II response rises at a decelerating rate to an upper asymptote, and was thought to be characteristic of invertebrates because of their limited learning capacity until Hassell et al. (1977) identified several examples of the type III response in invertebrates. The type III response is sigmoid, density dependent, and most common in vertebrates (Hassell 1978). The key difference between type II and type III responses is that in the type III response there is a change from an increasing to a decreasing risk of mortality as prey density diminishes to a low level, whereas the risk of mortality increases with decreasing prey density in the type II response. Hence, a type III response imparts stability to predator-prey dynamics at low prey densities in deterministic models (Hassell

1978), and limits population bounds and fluctuations in stochastic models (Murdoch 1979). The type IV response is dome-shaped, with decreasing rates of predation at high densities (Taylor 1984). In order to understand the relationships between environmental conditions and predator-prey interactions, the form of the functional response must be specified for predator-prey systems.

Until recently, functional responses were considered to be invariant for specific predator-prey combinations (see Murdoch and Oaten 1975, Hassell 1978). That is, a predator could display a type II response with prey species A, and type III response with prey species B, but the responses remained unchanged for each of the prey species in all situations. However, the form of the functional response varies according to environmental conditions (Murdoch and Oaten 1975, Hassell 1978, Abrams 1982). In particular, increased habitat heterogeneity resulted in a shift from type II to type III responses in a net-spinning caddis larva (Hildrew and Townsend 1977), a larval dragonfly (Folsom and Collins 1984), and a predatory mite (Kaiser 1983).

Environmental variation also includes gradual changes in physical properties across topographically simple habitats (e.g., the transition from mud to sand upon approach from subtidal areas to a beach). Despite the abundant evidence for modifications in species composition across such habitat gradients (Gray 1974, Rhoads 1974, Pearson and Rosenberg 1978), research is lacking on the effects of these gradients upon functional responses. In addition, most analyses of func-

tional responses have not differentiated statistically between type II and type III responses; rather, most curves are fitted by visual inspection (see review by Livdahl and Stiven 1983).

In this paper we investigate the functional responses of the blue crab, *Callinectes sapidus,* to the soft-shelled clam, *Mya arenaria.* We (1) examine the variation in form of functional responses in laboratory microhabitats differing by sediment composition, (2) describe model-fitting and curve-fitting approaches that differentiate statistically between type II and type III responses, (3) use Monte Carlo simulation techniques to determine whether prey mortality within microhabitats is random, and (4) relate these results to the abundance and distribution patterns of the predator and prey in nature.

The predator-prey system

The experimental system comprises the blue crab, *Callinectes sapidus* (Arthropoda: Crustacea: Portunidae), and the soft-shelled clam, *Mya arenaria* (Mollusca: Bivalvia: Myacidae). *Callinectes* is a large (up to 200 mm carapace width) epibenthic omnivore that inhabits soft-bottom coastal areas in the northwest Atlantic Ocean, Gulf of Mexico, and Caribbean Sea (Williams 1984). Blue crabs consume fish, crabs, shrimp, mollusks, plant matter, and conspecifics, although infaunal bivalve mollusks such as *Mya* form a major component of the diet (Laughlin 1982). In Chesapeake Bay, *Callinectes* is abundant and actively foraging from late spring through autumn, after which it overwinters buried in subtidal areas (Van Engel 1958).

Mya is a temperate-water infaunal suspension feeder that ranges up to 80 mm in shell length, and is found most abundantly in sandier substrates of Chesapeake Bay (Hines and Comtois 1985). *Mya* abundance increases in late winter and spring after recruitment periods, and decreases sharply when predators become active in late spring and summer (Holland et al. 1980). The distinct and discordant population cycles of *Callinectes* and *Mya* suggest that *Callinectes* predation reduces *Mya* abundance significantly. However, some large, adult *Mya* persist in nature (Virnstein 1977, 1979, Holland et al. 1980), suggesting that factors associated with large size, such as burial depth or low density, provide protection from predation. In addition, natural populations of *Mya* exhibit a Deevey (1947) type III survivorship curve, indicating that juveniles suffer heavy mortality, while larger adults have increased survivorship (Brousseau 1978*b,* Commito 1982). Thus the field studies indicate that a key issue in understanding the interaction between *Callinectes* and *Mya* is to determine those factors promoting persistence of adult *Mya* despite intense predation by *Callinectes.*

In laboratory experiments, large *Mya* attain a partial refuge from *Callinectes* predation by deep burial (Blundon and Kennedy 1982*b*), but not by size or shell strength (Blundon and Kennedy 1982*a*). Since deeper burial does not provide an absolute refuge (Blundon and Kennedy 1982*b*), it appears that other factors promote persistence of large *Mya.* In nature, *Mya* is more abundant in sand than mud (Holland et al. 1977, Mountford et al. 1977, Hines and Comtois 1985), suggesting that sediment composition may modify predation intensity upon *Mya.* In addition, low densities of adult *Mya* survive annually, indicating that density-dependent predation may be critical in the *Callinectes-Mya* interaction. Thus, we contrasted the form of *Callinectes* functional responses to *Mya* in sand and mud, and related our findings to natural fluctuations in prey abundance and distribution.

MATERIALS AND METHODS
Experimental animals and procedures

Adult *Mya arenaria* (48–60 mm shell length) from Chesapeake Bay were held in closed-system, indoor aquaria and gradually acclimated to the experimental temperature of $25° \pm 0.5°C$. Salinities in the field and laboratory remained at 10–13‰. Laboratory photoperiod was maintained at natural autumnal levels (L:D 12:12). Nighttime lighting for behavioral observations was provided by red fluorescent lights, which do not inhibit crustacean behavior patterns significantly (Lipcius and Herrnkind 1982). Clams were fed locally collected phytoplankton.

Adult *Callinectes sapidus* (130–140 mm carapace width, a representative dominant size class in Chesapeake Bay) were collected by otter trawl at the mouth of the Rhode River, Maryland. Ten intermolt males that were healthy and fed actively were chosen for experimental trials. These crabs were held under similar conditions to *Mya,* and fed ad libitum with live *Mya* and frozen fish.

There were six 220-L experimental tanks (1.2 m length × 0.3 m width); three of these held sand and three mud. Each tank was filled to a sediment level 25 cm above the tank bottom, and brackish water was added to a level 25 cm above the sediment surface. This layout allowed six concurrent trials and randomized interspersion of clam density treatments (Underwood 1981, Hurlbert 1984).

We used six experimental clam densities of 2, 4, 6, 8, 16, and 32 clams per tank (5.6–89.0 clams/m²), representing the lower range of natural *Mya* densities in Chesapeake Bay. Twenty-four hours before the initiation of a trial, healthy clams exhibiting vigorous siphon-withdrawal reflexes were buried in the tanks by covering them with sediment until their anterior (bottom) tips were ≈15 cm below the sediment surface. Sufficient time was provided for clam siphons to reach the sediment surface. The mud and sand in experimental and holding tanks were collected from field sites that differed significantly in sediment composition, and were known to harbor populations of *Mya* (Sand: 40% medium sand, 30% fine sand, 30% fine silt and clay;

TABLE 1. Burial depths and survivorship of *Mya arenaria* buried initially at ≈15 cm and held for 3 or 21 d without crabs. Burial depths were measured as the vertical distance from the bottom of the clam to the sediment surface.

	After 3 d		After 21 d	
	Sand	Mud	Sand	Mud
No. of clams	10	10	10	10
Survivorship (%)	100	100	100	90
Burial depths (cm)				
Mean	14.49	14.54	14.84	14.96
SE	0.28	0.30	0.39	0.48
Range	13.1–15.8	13.2–15.9	13.4–17.3	13.0–17.2

Mud: 30% fine sand, 70% fine silt and clay). Crabs were starved for 48 h prior to each trial. A trial began when a single *Callinectes* was introduced into a tank well before dark (about 1200–1300), and ended upon removal of that crab 72 h later. Five trials were conducted at each clam density. Surviving clams and umbos of eaten clams were counted to ensure that all clams were accounted for. Control trials were run under equivalent conditions, but without *Callinectes*. Satiation levels of *Callinectes* were determined by performing the feeding experiments as described previously, but with *Mya* spread uniformly across a hard bottom that prevented clam burial.

Tests of biological assumptions

We eliminated potentially confounding effects of sediment type upon *Mya* survivorship and burial depth by conducting control experiments without *Callinectes*. Clams buried at 15 cm for 3 and 21 d remained at those burial depths regardless of sediment type (Table 1). Survivorship after 72 h (3 d) was 100% in sand and mud, with surviving clams displaying healthy siphon-withdrawal reflexes (Table 1). In addition, clam length and burial depth were not correlated across the small size range used in the experiment (ANCOVA; grouping variable: sediment type; covariate: shell length; $F = 0.84$, df = 1,17, $P > .35$). These results indicated that our experimental differences in *Mya* survivorship were purely a consequence of variation in *Callinectes* predation intensity.

Analyses and specific models of functional responses

The numbers and proportions of eaten clams were analyzed by two-way ANOVA (SAS Institute 1982). Proportions were used in addition to the numbers eaten because the respective patterns for type II and type III curves differ significantly at low prey densities. Tests of normality and equality of variance (Sokal and Rohlf 1981) indicated that the raw numbers ($F' = 1.04$, df = 29,29, $P > .25$) and arcsine square-root transformed proportions ($F' = 1.55$, df = 29,29 $P = .24$) were both appropriate for ANOVA. In the absence of significant factor interactions, treatment means were contrasted by *t* tests set at a Bonferroni experimentwise error rate of 0.05 (Harris 1975).

Several functional response models have been developed to characterize the type of response, and to estimate biologically meaningful parameters (Table 2). These models can be grouped into continuous-time models (Holling 1959, Hassell 1978) and discrete-time models (Royama 1971, Rogers 1972, Hassell et al. 1977, Hassell 1978). Continuous-time models relate the number of encounters of a predator with prey (N_e), whether successful or not, to a function of prey density (N_t), whereas discrete-time models relate the number of prey eaten (N_a) to prey density (Table 2). The prey encounter and consumption functions of prey density involve several parameters. Handling time (T_h) is defined as the time from the initial encounter of the predator with a prey, through the capture, ingestion, and digestion of the prey, until a new search begins (Hassell 1978). The instantaneous search rate (a') is a measure of the success of encounters with prey in type II models, whereas *b* and *c* replace *a'* in type III models to account for the dependence of search rate upon prey density (Hassell 1978). Discrete-time models integrate over the total feeding period of a predator, and therefore account for significant decreases in prey density as the predator consumes prey (Royama 1971, Rogers 1972, Hassell 1978). In contrast, continuous-time models best represent situations where prey density remains nearly constant through the feeding period (Hassell 1978).

Regressions using linearized forms of the preceding functional response models may yield biased or statistically invalid parameter estimates (Hassell 1978, Livdahl and Stiven 1983). Hence, we used nonlinear least squares analyses (SAS Institute 1982) to estimate parameters and fit to the data. Analyses of continuous-time models used the Marquardt method (Marquardt 1963, SAS Institute 1982) with specified partial derivatives. Analyses of discrete-time models used the derivative-free multivariate secant method (Ralston and Jennrich 1979, SAS Institute 1982) because of the problem of deriving partial derivatives of a function with the dependent variable (N_a) on both sides of the equation (Table 2).

We established several criteria to determine the most appropriate and statistically valid functional response models:

1) The *F* value of the regression had to be significant at the .05 level.

TABLE 2. Nonlinear functional response models.

Equation type	Model type	Equation	References
Continuous	II	$N_e = \dfrac{a' \cdot T \cdot N_t}{1 + (a' \cdot T_h \cdot N_t)}$	Holling 1959
	III	$N_e = \dfrac{b \cdot T \cdot N_t^2}{1 + (c \cdot N_t) + (b \cdot T_h \cdot N_t^2)}$	Hassell 1978
Discrete	II	$N_a = N_t[1 - e^{-a'(T - T_h \cdot N_a)}]$	Royama 1971, Rogers 1972
	III	$N_a = N_t\left\{1 - e^{\left[\frac{-b \cdot N_t}{1 + c \cdot N_t}(T - T_h \cdot N_a)\right]}\right\}$	Hassell et al. 1977
	IIIb	$N_a = N_t\left(1 - e^{\frac{-b}{c}\left\{T - (T_h \cdot N_a) - \left[\frac{N_a}{b \cdot N_t(N_t - N_a)}\right]\right\}}\right)$	Hassell et al. 1977

Symbol	Type	Definition	Models
N_e	Variable	No. encounters with prey	Continuous II, III
N_a	Variable	No. prey eaten	Discrete II, III, IIIb
N_t	Variable	No. prey available	All
T	Constant	Total time available for foraging (h)	All
T_h	Parameter	Handling time (h)*	All
a'	Parameter	Instantaneous search rate	II
b, c	Parameters	Replace a' to estimate variable search rate	III, IIIb

* Handling time includes the time from attack initiation, through subjugation and feeding, and until initiation of the search for a subsequent prey (Hassell 1978).

2) The residual sum of squares had to be the lowest of the possible models.

3) The residuals about the predicted values had to be distributed randomly, as determined by binomial tests of the full data set and partial data set. Partial data sets consisted of the middle range (6, 8, and 16) of prey densities. These partial binomial tests were conducted because we noticed that in situations where the residuals appeared nonrandom, their systematic variation was positive at one end of the curve or line and negative at the other end, thereby cancelling out in the complete binomial test.

Analyses of general functional response models

In order to provide an unequivocal statistical test of the form of the functional responses, free of the potential problems associated with analyses of specific functional response models (Hassell 1978, Livdahl and Stiven 1983), we used the general functional response model derived by Real (1977, 1979):

$$N_a = \frac{K \cdot N_t^\beta}{X + N_t^\beta} \qquad (1)$$

where N_a = numbers of prey eaten,
K = the maximum feeding rate (satiation),
N_t = initial prey density,
X = the density of prey at which $N_a = 0.5K$, and
β = the parameter associated with the form

of the functional response curve (Real 1979, Emlen 1984).

When $\beta = 0$, the curve becomes linear, when $\beta = 1$, the curve is type II (decelerating rise to an asymptote), and when $\beta > 1$, the curve is type III (sigmoid) (Real 1979). Thus, a statistical test of the parameter β is also a test of the form of the functional response. We tested the estimates of β with standard t tests (Chatterjee and Price 1977).

The general functional response models were analyzed by linear regressions of the log transformation of Eq. 1 (Real 1979), and tested for appropriate fit as described for the specific functional response models. The assumption of homogeneity of variance of the transformed variable was tested with Hartley's F_{max} procedure (Sokal and Rohlf 1981), assuring statistical validity of the linearization.

Monte Carlo simulation analyses of clam spatial mortality patterns

We recorded the locations of dead and surviving clams in trials using 16 and 32 clams per tank in order to determine if blue crabs foraged randomly in the experimental tanks. Conventional analyses of spatial pattern (e.g., nearest neighbor analyses, Clark and Evans 1954) were inappropriate for our data because of constraints imposed by experimental procedures and crab feeding rates. That is, all clams were spaced uniformly in experimental tanks, and crabs consumed

varying numbers of clams in trials, ranging from 3–9 clams/72 h. Hence, we employed Monte Carlo simulation analyses (Hammersley and Handscombe 1964, Bard 1974) to test for spatial mortality patterns of *Mya* (Appendix).

RESULTS

Behavior

Most crab activity (foraging, prey capture, feeding, walking, and swimming) was observed during simulated darkness, and resembled natural behavior patterns (Halusky 1975, Nishimoto and Herrnkind 1978).

Feeding rates of the experimental crabs did not vary significantly among individuals (ANOVA; $F = 0.92$, df = 3,12, $P > .25$). Satiation was reached on the average at 8.25 clams·crab^{-1}·(72 h)$^{-1}$. Blue crab activity levels, as measured by hourly point scans of behavior (Lipcius and Herrnkind 1982), appeared to differ between mud and sand trials, being 30% higher in mud, but this difference was not statistically significant (Binomial Test; $Z = 1.13$, $P = .129$). In addition, there was no detectable edge effect (i.e., crabs potentially consuming more clams from the periphery of experimental tanks, as measured in the 32-clam trials). In sand, a nonsignificantly higher proportion of clams was eaten from the center than the edge, whereas in mud, a nonsignificantly higher proportion was eaten from the edge (ANOVA; sand: 0.20 vs. 0.11; mud: 0.14 vs. 0.28; $N = 5$, $P = .12$). Hence, the functional responses of *Callinectes* to *Mya* were a consequence only of sediment composition and *Mya* density.

Analyses and specific models of functional responses

Consumption rates of *Callinectes* differed significantly by sediment type and clam density (ANOVA; Sediment type: $F = 45.7$, df = 1,48, $P < .0001$; Clam density: $F = 24.5$, df = 5,48, $P < .0001$); the interaction effect was not significant (ANOVA, $F = 1.1$, df = 5,48, $P > .25$). On average, *Callinectes* consumed significantly more clams over 72 h in mud than sand (Table 3). Consumption rates at high clam densities (8–32 clams per tank) were well below the mean satiation level (8.25 clams·crab^{-1}·[72 h]$^{-1}$) in sand, but approached the satiation level in mud (Table 3). In addition, significantly more clams were consumed at the upper three densities (8, 16, and 32 clams per tank) than at the lowest two (2 and 4 clams per tank), regardless of sediment type (Table 3).

The proportions of clams eaten differed significantly by sediment type, but not by clam density (ANOVA; Sediment type: $F = 43.0$, df = 1,48, $P < .0001$; clam density: $F = 0.67$, df = 5,48, $P > .5$). The interaction effect between sediment type and clam density was significant (ANOVA, $F = 3.2$, df = 5,48, $P < .025$), precluding contrasts among treatment means (Underwood 1981). *Callinectes* consumed proportionately

TABLE 3. The effects of sediment composition and clam density on crab consumption rates.

		Mean consumption rate* (clams·crab^{-1}·[72 h]$^{-1}$)
A.	Sediment composition	
	Sand	2.5
	Mud	4.5
B.	Clam density (clams/0.36-m^2 tank)	
	2	1.1
	4	1.9
	6	3.4
	8	4.2
	16	4.7
	32	5.8

* Results of Bonferroni contrasts at an experimentwise error rate of .05. Within each section of the table, consumption rates that are not significantly different share a common bracket.

more clams in mud (60–90%) than in sand (17–54%), with a pronounced interaction effect due to major differences in consumption rates at low clam densities. With only 2–6 clams per tank, much lower percentages of clams were eaten in sand (17–35%) than in mud (80–90%).

The functional responses of *Callinectes* were significantly different as a consequence of sediment composition (Fig. 1). In sand, the functional response was sigmoid (Fig. 1a), and best described by the type III continuous-time equation:

$$N_a = \frac{0.216N_t^2}{1 + 0.143N_t + 0.039N_t^2}$$

as indicated by the nonlinear least squares analyses (Table 4). Density-dependent consumption rates were evident at densities from 0–8 clams per tank (Fig. 1a). As indicated by the slope of the functional response curve, the maximum risk of mortality for *Mya* occurred at ≈4–8 clams per tank (Fig. 1a). Discrete-time models had higher residual sums of squares, and were characterized by nonrandom residuals about the predicted values when contrasted with continuous-time models (Table 4).

In mud, the functional response of *Callinectes* exhibited a decelerating rise to an asymptote (Fig. 1b), and was best described by the type II continuous-time equation:

$$N_a = \frac{1.512N_t}{1 + 0.193N_t}$$

as indicated by the nonlinear analyses (Table 4). The mortality risk of *Mya* decreased with increasing clam density (Fig. 1b).

The significant difference between the functional responses of *Callinectes* in sand and mud was reflected in the relationship between the mean proportional mortality rate of *Mya* and clam density (Fig. 2). In
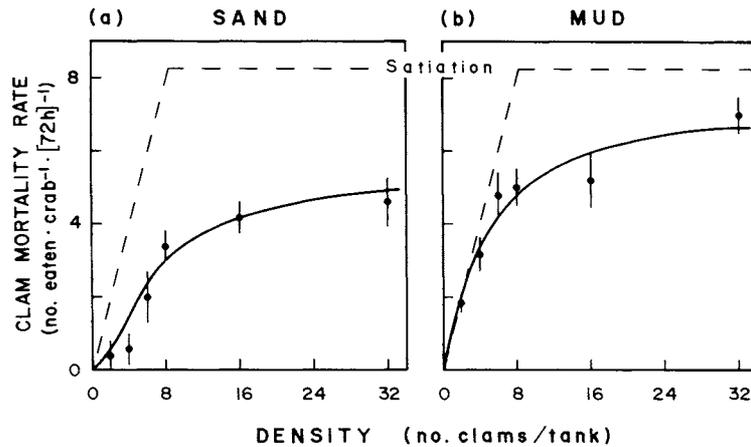
FIG. 1. Functional responses of blue crabs feeding at six densities of soft-shelled clams. The fitted curves are from the continuous-time models presented in the text. Predicted satiation levels ($-\ -\ -$) increase isometrically at a linear rate up to the average satiation level of 8.25 clams·crab^{-1}·(72 h)$^{-1}$. Means ($\pm$SE) of five trials conducted at each clam density are plotted for (a) sand and (b) mud.

TABLE 4. Results of nonlinear least squares analysis of functional responses (no. clams eaten). Equations of models given in Table 2. Underlined values indicate the selected model. Parameter estimates were significantly >0 in the selected models, as defined by 95% confidence intervals.

Sediment	Feature	Discrete-time models			Continuous-time models	
		Type II	Type III	Type IIIb	Type II	Type III
Sand	Parameter estimates					
	a'	0.003	$\cdots$	$\cdots$	0.007	$\cdots$
	b	$\cdots$	0.017	0.058	$\cdots$	0.003
	c	$\cdots$	2.0	20.0	$\cdots$	0.143
	T_h†	0.1	5.6	0.10	10.0	13.0
	Summary statistics					
	Regression ss (df)	240.0 (2)	261.3 (3)	236.4 (2)	263.6 (2)	268.6 (3)
	Residual ss (df)	66.0 (28)	44.7 (27)	69.6 (28)	42.4 (28)	37.4 (27)
	F value	50.9***	52.8***	47.5***	87.3***	64.4***
	Regression ss ÷ total ss (%)	78.4	85.4	77.3	86.1	87.8
	Binomial test (partial)	***	NS	***	NS	NS
	Binomial test (complete)	NS	*	NS	NS	NS
Mud‡	Parameter estimates					
	a'	0.007	$\cdots$	$\cdots$	0.021	$\cdots$
	b	$\cdots$	0.015	0.186	$\cdots$	0.015
	c	$\cdots$	2.0	20.0	$\cdots$	1.3
	T_h†	4.1	4.1	5.1	9.2	5.5
	Summary statistics					
	Regression ss (df)	556.9 (2)	552.1 (2)	471.7 (2)	681.9 (2)	642.8 (3)
	Residual ss (df)	160.1 (28)	164.9 (28)	245.3 (28)	35.1 (28)	74.2 (27)
	F value	48.7***	46.8***	26.8***	272.7***	77.9***
	Regression ss ÷ total ss (%)	77.7	77.0	65.8	95.1	89.7
	Binomial test (partial)	***	***	§	NS	NS
	Binomial test (complete)	***	***	***	NS	NS

* $P < .05$, ** $P < .01$, § $P < .005$, *** $P < .001$.

† T_h = handling time in hours. Includes time from attack initiation until initiation of the search for subsequent prey.

‡ In addition, a type II linear reciprocal-transformation model (Livdahl and Stiven 1983) was fit to the data from mud trials, but explained less of the total variance (69.2%) than the discrete-time or continuous-time models.
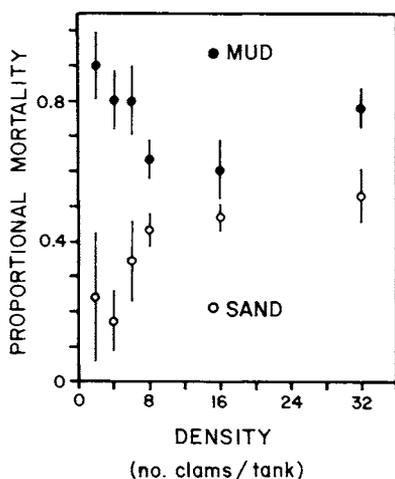
FIG. 2. Proportional mortality rates of *Mya* at six densities exposed to *Callinectes* predation. Data are means (±SE) of five trials conducted at each clam density.

sand, very few of the available clams were consumed at low densities, whereas greater percentages were eaten at high densities (Fig. 2). The reduction in the proportional mortality rate in sand at low densities signifies (1) a density-dependent sigmoid relationship between predation rate and prey density, and (2) the existence of a partial refuge from predation below some density. In this case, that density appears to be ≈4–8 clams per tank (11–22 clams/m²).

In mud, almost all available clams were consumed at low densities, with the proportional mortality rate decreasing at intermediate densities, and then increasing slightly at higher densities as the crabs approached their satiation level (Fig. 2). This pattern is indicative of an inversely density-dependent relationship, which is characterized by a type II functional response and lowest mortality risk at high prey densities. The increased proportional mortality rate at highest densities may have been "wasteful killing" (Johnson et al. 1975), since a few clams in the high-density treatments were only partially consumed, suggesting that nontraditional functional response models (Abrams 1982) may also be appropriate in this situation.

Analyses of general functional response models

Analyses using the general functional response model (Eq. 1) (Real 1977, 1979) corroborated the results of the preceding analyses. The functional response was sigmoid (type III) in sand, with $\hat{\beta}$ (2.29) significantly different from 0 and 1 (Table 5). In mud, the functional response was convex (type II), with $\hat{\beta}$ not significantly different from 1 ($\hat{\beta} = 0.81$) and significantly different from 0 and 2 (Table 5). Thus the tests of β, and hence, of the form of the functional responses, verified that the curves differed significantly according to sediment composition, with the type III response most appropriate in sand, and type II in mud (Table 5).

Monte Carlo simulation analyses of clam spatial mortality patterns

In the Monte Carlo simulation analyses of nearest neighbor distances (NND), significant deviations from a random distribution are identified by probability levels below 0.025 (indicating clumping) or above 0.975 (indicating overdispersion). Of the 14 testable trials in sand and mud at densities of 16 and 32 clams per tank, only one NND value was significant, suggesting overdispersion in that trial (Table 6). All other trials had nonsignificant probability levels (Table 6), without any general tendency, indicating that spatial mortality patterns of *Mya* in the tanks were random.

DISCUSSION

Blue crab predation intensity and prey persistence

The functional response analyses showed that adult *Mya* obtained refuge from *Callinectes* predation at low densities in sand, but not in mud. Our low *Mya* experimental densities (6–22 clams/m²) were similar to those reported for large *Mya* surviving in sandy sediments until autumn in Chesapeake Bay (0.2–12 clams/m², Cory and Redding 1977) and Essex Bay, Massachusetts (9–19 clams/m², Brousseau 1978b). In muddy sediments, *Mya* occur in low numbers and rarely survive through summer (A. Hines, *personal observation*). In addition, survivorship depends on the burial depth of clams (Blundon and Kennedy 1982b). Our mortality rates for Mya exposed to *Callinectes* were similar to those of Blundon and Kennedy (1982b) when compared at similar clam densities and burial depths (≈50% mortality at 15 cm depth and 50–60 clams/m²). However, their depth-dependent responses and our density-dependent responses suggest that clam density and

TABLE 5. Linear regression results of log-transformed general functional response models (Real 1977, 1979). The transformed dependent variable met assumptions of normality and equality of variance.

Feature	Sediment	
	Sand	Mud
Parameter estimates		
Intercept	−2.98	−0.74
Slope	2.29	0.81
Slope standard error	0.41	0.11
Summary statistics		
Regression ss (df)	24.06 (1)	2.78 (1)
Residual ss (df)	21.68 (28)	1.44 (27)
F value	31.1***	51.8***
Regression ss ÷ total ss (%)	52.6	65.8
Tests of hypotheses		
H_0: slope = 0	***	***
H_0: slope = 1	§	NS
H_0: slope = 2	NS	***
H_0: slope = 3	*	***

*$P < .05$, §$P < .005$, ***$P < .001$.

TABLE 6. Monte Carlo simulation analysis of spatial patterns of *Mya arenaria* mortality in treatments with 32 and 16 clams per 0.36-m² tank. The Monte Carlo simulations were run on the nearest neighbor distances (NND) between eaten clams.

Sediment	Clam density (no./tank)	Trial	No. clams eaten	Mean NND (cm)		Median NND (cm)	
				Observed	Monte Carlo probability	Observed	Monte Carlo probability
Sand	32	1	3	35.5	0.72	30.6	0.88
		2	3	40.4	0.85	30.6	0.88
		3	5	19.2	0.57	12.0	0.14
		4	6	12.2	0.14	6.0	0.10
		5	6	19.6	0.84	16.2	0.79
		all		25.4	0.88	16.2	0.86
	16†	1	4	16.5	0.27	16.5	0.50
		2	5	16.8	0.38	18.0	0.94
		all		16.7	0.16	17.3	0.61
Mud	32	1	6	18.6	0.76	12.0	0.27
		2	6	12.0	0.13	12.0	0.27
		3	7	9.6	0.04	6.0	0.19
		4	7	19.3	0.97	16.2	0.95
		5	9	12.7	0.55	12.0	0.54
		all		14.4	0.42	12.0	0.23
	16†	1	3	18.0	0.17	18.0	0.71
		2	5	26.1	0.99*	15.0	0.63
		all		22.1	0.41	16.5	0.56

* $P < .05$, two-sided test.
† Data on spatial mortality patterns are available for only 4 of the 10 trials in the 16-clam treatments.

burial depth interact to enhance the refugium potential of selected habitats. Hence, irrespective of potential recruitment differences across sandy and muddy sediments, the collective evidence suggests that natural populations of deeper dwelling adult *Mya* are more likely to persist at low densities in sandy habitats because of reduced predation rates by *Callinectes* in these habitats.

Local persistence of *Mya* may also be affected by a suite of other environmental and biotic factors throughout its range, including summer anoxia (Seliger et al. 1985), the combined effect of high temperatures and low salinities following intense tropical storms (Cory and Redding 1977), intraspecific competition (Peterson 1982*a, b*), edaphic parameters (Appeldoorn 1983), gradients in salinity and temperature (Ulanowicz et al. 1982, Appeldoorn 1983), hydrodynamic features (Matthiessen 1960), demersal fish (Orth 1975, Virnstein 1977, Kelso 1979, Holland et al. 1980), and predatory snails (Edwards and Huebner 1977, Wiltse 1980, Commito 1982). However, despite the numerous potential sources of disturbance and mortality, *Mya arenaria* populations recover (Cory and Redding 1977, Brousseau 1978*b*), probably due to the high fecundity of survivors (Brousseau 1978*a*). Hence the regional persistence of *Mya* appears to depend on density-dependent factors modified by local environmental conditions, the degree of disturbance by density-independent factors, and the life-history characteristics of local populations. (See Zajac and Whitlatch [1985] for a discussion of the potential interactions of these factors.)

Predation intensity of blue crabs is in turn affected by various physical and biotic variables. Our results suggest that activity levels and prey encounter rates of

Callinectes differ according to sediment composition and are correlated with prey density. In nature, *Callinectes* may migrate from low-density to high-density prey patches, such that local patterns in prey abundance and distribution determine the diet of individual *Callinectes* (Laughlin 1982). Other factors such as anoxia (Seliger et al. 1985) may reduce the extent of available feeding areas, as may intraspecific interference (Ens and Goss-Custard 1984) when blue crab densities are high. Thus the character and intensity of predation by *Callinectes* will vary greatly according to local conditions, and conclusions regarding its predator–prey dynamics must be tailored to specific environmental circumstances.

Functional responses, habitat variability, and predator-prey dynamics

Our key finding in relation to predator-prey dynamics is that the functional response of an invertebrate predator can vary significantly in form as a consequence of subtle differences in microhabitat physical structure. Blue crabs preying upon soft-shelled clams exhibited a type II functional response in mud, and a type III response in sand. Reduced penetrability of sandy sediments probably reduces prey encounter rates because blue crabs search for prey by probing the substrate with the tips of their walking legs, where chemosensory and tactile setae are located. Reduced encounter rates may lead to lowered activity levels, which subsequently reduce encounter rates further, or result in emigration from areas of low prey density. Handling time did not appear to differ significantly in the two sediments, because blue crabs rapidly extracted and ate clams once a clam was detected. The proposed

differences in encounter rates have been observed in other predators, and have led to changes from type II to type III functional responses (Hassell 1978, Abrams 1982).

Previous experiments have documented alterations in functional responses as a consequence of differences in prey quality and habitat heterogeneity (Murdoch 1969, Hassell et al. 1977, Hildrew and Townsend 1977, Akre and Johnson 1979, Kaiser 1983, Folsom and Collins 1984, Ohman 1984), but not the physical properties characterizing microhabitats. A possible analogue to our findings may be fish foraging at different light levels, which affect the ability of visual predators to detect prey. The zooplanktivorous *Abramis brama* exhibited a change in response from type II to type III in decreased light, although the altered response may also have been due to differing prey distributions under various light regimes (Townsend and Risebrow 1982).

Several field experiments and observations show that prey density and differences in the physical structure of homogeneous microhabitats alter foraging rates of predators. Pacific shorebirds reduced densities of infaunal prey in mudflats with low sand content, but avoided foraging in nearby flats with higher sand content (Quammen 1982, 1984). Similar patterns occur in Atlantic shorebirds (Myers et al. 1980), and are likely due to the reduced penetrability of sediments with high sand content (Grant 1984). Sediment composition also affected predation rates by blue crabs on the hard clam, *Mercenaria mercenaria* (Arnold 1984). Adult littleneck clams, *Protothaca staminea,* inhabiting intertidal sand–gravel beaches suffered relatively higher mortality rates at higher densities when exposed to predation by cancrid crabs (Boulding and Hay 1984), as did an infaunal clam, *Chione cancellata,* exposed to whelk and blue crab predation (Peterson 1982a). Similarly, the biomass of amphipods, *Corophium volutator,* consumed by wading birds was positively correlated with amphipod density (Goss-Custard 1970). Hence, the collective field and laboratory evidence indicates that predator foraging and prey mortality rates vary significantly across gradients in prey availability, habitat heterogeneity, and the physical properties of microhabitats.

Varying mortality risks of prey as a function of the physical structure of habitat patches have been identified in populations residing in coral reefs (Kohn 1983) and seagrass meadows (Orth 1977, Heck and Orth 1980, Orth et al. 1984, Virnstein et al. 1984). This factor complements the role of habitat heterogeneity in modifying the susceptibility of prey to predators, and demonstrates the need to specify the precise and potentially subtle characteristics of the habitat and prey influencing predator-prey dynamics.

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APPENDIX

Separate Monte Carlo simulations of the nearest neighbor distance (NND) between eaten clams were run for each unique combination of number of clams eaten, clam density, and sediment type. Each simulation required the following steps:

1) Each of the 16 or 32 possible clam locations was assigned a unique set of Cartesian coordinates (x,y).

2) A random number generator drew the required number of sets of Cartesian coordinates, with the number of sets equal to the observed number of clams eaten.

3) The mean and median NND of that draw were computed using the sets of Cartesian coordinates.

4) Steps 1–3 were repeated for a total of 10 000 draws, resulting in frequency distributions of mean and median NND values.

5) The observed NND values were calculated using the Cartesian coordinates of the observed locations of eaten clams.

6) The cumulative probabilities of the observed NND values were determined directly from the frequency distributions derived from the Monte Carlo simulations.