1990

Foraging Behavior Of The Blue-Crab, Callinectes-Sapidus, On Juvenile Oysters, Crassostrea-virginica - Effects Of Prey Density And Size

DB Eggleson
Virginia Institute of Marine Science

Recommended Citation

Eggleson, DB, "Foraging Behavior Of The Blue-Crab, Callinectes-Sapidus, On Juvenile Oysters, Crassostrea-virginica - Effects Of Prey Density And Size" (1990). *VIMS Articles*. 1545.
https://scholarworks.wm.edu/vimsarticles/1545

BULLETIN OF MARINE SCIENCE, 46(1): 62–82, 1990

FORAGING BEHAVIOR OF THE BLUE CRAB, *CALLINECTES SAPIDUS*, ON JUVENILE OYSTERS, *CRASSOSTREA VIRGINICA*: EFFECTS OF PREY DENSITY AND SIZE

David B. Eggleston

ABSTRACT

Blue crabs (*Callinectes sapidus*) are major predators of juvenile oysters (*Crassostrea virginica*) in Chesapeake Bay, yet little information exists on the foraging behavior and predator–prey dynamics for this predator–prey system. Laboratory experiments assessed functional responses of blue crabs to six densities of three size-classes of juvenile American oysters. Behavioral subcomponents of the crabs' functional response were quantified: total and successful encounter rates, proportional attack success, persistence time in unsuccessful encounters, and breaking, eating and handling times in successful encounters. Specific opening techniques were used by crabs for the three oyster size-classes. Blue crabs exhibited a hyperbolic type II functional response regardless of oyster size, with an inverse relationship between predation rates and increasing oyster size. Crab persistence times with oysters were positively correlated with attack success rates at three oyster size-classes, and inversely related to prey density, suggesting higher selectivity by blue crabs at higher oyster densities. Oysters >30 mm shell-height may be near the critical size for crushing by large crabs as a result of increased variations in (1) shell to crab strength ratios, (2) opening techniques with oyster attachment site and growth geometry, and (3) oyster density. These findings indicate that crab acceptance or rejection sequences of bivalve prey depend on prey density and size, that predation by large male *C. sapidus* can lead to local extinction of juvenile oysters ($\bar{x}$ = 15–35 mm SH) regardless of density and, that increasing shell-height provides a refuge from predation.

Predation by the blue crab, *Callinectes sapidus* Rathbun, regulates marine bivalve mollusc populations in shallow (<10 m) unvegetated soft-bottom (Virnstein, 1977; 1979; Holland et al., 1980) and hard substrate (Peterson, 1979; Seed, 1980) communities. The American oyster, *Crassostrea virginica* (Gmelin), is a major component of estuarine benthos on the east coast of North America and supports commercial fisheries in many areas. However, the dynamics of predator–prey interactions between the blue crab and oyster remain unclear.

Experimental assessment of the functional response, which is the short-term dependence of a predator's feeding rate upon prey density (Solomon, 1949; Holling, 1959; 1965), has been used to determine mechanisms underlying predator–prey dynamics. Functional responses have been classified into three general types (Hassell, 1978; Taylor, 1984). In the type I response, which characterizes aquatic filter-feeding invertebrates, consumption rates increase linearly with prey density until satiation (Frost, 1972; Valiela, 1984). Satiation occurs when a predator cannot handle prey any faster; hence, ingestion remains constant despite increasing prey density (Valiela, 1984). In the type II response, consumption rates rise with prey density at a decelerating rate to an upper asymptote, reflecting increased costs or constraints associated with higher consumption rates (Valiela, 1984). The type III response is sigmoid, demonstrating density-dependent acceleration in consumption rates at low prey densities. The acceleration in feeding rates results from increased predator efficiency in the detection or capture of prey as prey density increases (Holling, 1965; Real, 1979). Recently, several examples of a type III response have been shown for invertebrates (Hassell et al., 1977; Lipcius and Hines, 1986; Eggleston, 1988). It is important to distinguish between type II and type III functional responses because of their very different effects upon population dynamics (Holling, 1959; 1965; Murdoch and Oaten, 1975; Hassell, 1978; Nunney, 1980; Abrams and Allison, 1982).

Functional Response Models.—Holling (1959) modeled the basic behavioral components of predation—the rate of successful search (attack coefficient) and handling time—with the equation:

$$N_e = a' \cdot T \cdot N_t / 1 + (a' \cdot T_h \cdot N_t) \qquad (1)$$

where the number of prey encountered (N_e) per predator equals a function of the instantaneous attack rate (a'), total time available for foraging (T), the number of prey available (N_t), and the prey handling time (T_h). Handling time includes the time from the initial encounter of the predator with prey, through the capture, ingestion and digestion of the prey, until searching resumes (Hassell, 1978). The instantaneous attack rate (a') is a measure of encounter success with prey in type II models (Hassell, 1978). Hence, a' and T_h are useful in comparing vulnerability of different prey. Holling's equation is a deterministic continuous-time model for a type II response, and assumes (1) constant prey handling times for all prey and (2) a fixed probability of prey encounter, thereby not allowing for prey depletion.

Discrete-time models integrate the instantaneous predation rate over the duration of the experiment (T), assuming an exponential decay in prey density, and are appropriate in experiments where eaten prey are not replaced. This model is the "random predator" equation (Royama, 1971; Rogers, 1972):

$$N_a = N_t[1 - e^{-a'}(T - T_h \cdot N_a)] \qquad (2)$$

where N_a is the number of prey eaten.

Continuous-time type III models account for variation in search rate (a') with density by substituting the parameters (b, c) for a' in equation 1 thus, yielding equation 3 (Hassell, 1978):

$$N_e = b \cdot T \cdot N_t^2 / 1 + (c \cdot N_t) + (b \cdot T_h \cdot N_t^2) \qquad (3)$$

The type III discrete-time model is obtained by substituting constants (b, c) for a' in equation 2 yielding equation 4 (Hassell et al., 1977):

$$N_a = N_t(1 - e\,[-b \cdot N_t / 1 + c \cdot N_t\,(T - T_h \cdot N_a]) \qquad (4)$$

It is unlikely that a' and T_h are constant and independent of prey density and feeding rate (Hassell, 1978). Each component is likely a function of several interacting factors (Holling, 1965; 1966). For example, T_h differs with varying biotic factors such as prey size and foraging tactics (Valiela, 1984). Other biotic factors affect a', such as the relative mobility of predator and prey, the perceptual field of the predator relative to the density and size of prey, and the ability of prey to avoid predation (Valiela, 1984). This paper examines the way in which a' and T_h vary with prey size for the blue crab feeding on juvenile oysters to provide essential information for the development of a general predator–prey model.

The objectives of this study were (1) to describe the foraging behavior of *C. sapidus* when preying on different sizes and densities of juvenile oysters, (2) to test and modify model-fitting procedures that differentiate statistically between continuous- and discrete-time functional response models, (3) to examine the effect of prey size on functional response parameter estimates, and (4) to compare empirically derived estimates of behavioral components with those predicted by functional response models.

METHODS AND MATERIALS

Experimental Predator–Prey System.—The blue crab, *Callinectes sapidus* (Arthropoda: Crustacea: Portunidae) is a large (up to 280 mm carapace width (CW)) epibenthic omnivore found throughout diverse habitats along the Atlantic and Gulf Coasts of North America (Van Engel, 1958; 1962; Williams, 1984). *C. sapidus* feeds upon a variety of prey, including bivalves, fish, small benthic infauna, algae, vascular plants and conspecifics (Odum and Heald, 1972; Laughlin, 1982; Alexander, 1986). The American oyster, *Crassostrea virginica* (Mollusca: Pelecypoda: Ostreidae), is an epibenthic suspension-feeding bivalve mollusc of commercial importance along the Atlantic and Gulf Coasts of North America. In Chesapeake Bay, *C. virginica* grows up to 18 cm in shell-height and occurs primarily on subtidal bars composed of shelly mud (Haven et al., 1981). Spawning is from late June to October. After larval attachment on suitable cultch materials (e.g., oyster shell) oysters may attain a shell-height of 40 mm (standard height (SH)) before the end of autumn (Kennedy and Briesch, 1981; pers. obs.). Density of spat ranges from 1–30 spat per 10-cm oyster shell (Kennedy and Briesch, 1981; pers. obs.).

Experimental Procedure.—Laboratory feeding studies were conducted from June–September 1987, with crabs captured in pots from the lower York River, Virginia, USA (37°14.5′N, 76°30.0′W). Only large (135–165 mm CW) male intermolt crabs that fed during the acclimation period were used in feeding trials. Crabs were fed oyster spat ad libitum for 1 week prior to feeding trials.

Juvenile oysters, ranging from 5–45 mm SH, were collected from Piankatank River, Virginia, USA (37°28.5′N, 76°15.0′W) by SCUBA divers. Animals were classified into three size categories: small ($\bar{x} = 15.0 \pm 2$ mm SH), medium ($\bar{x} = 25.0 \pm 2$ mm SH) and large ($\bar{x} = 35.0 \pm 2$ SH), based on preliminary laboratory experiments which indicated that large blue crabs were incapable of crushing juvenile oysters >45 mm SH. All oysters were attached to oyster shell cultch.

Six experimental tanks measuring 60 cm·55 cm·25 cm deep (72 liters) were filled with ground oyster shell to a level 8 cm above the tank bottom. This layout allowed six concurrent feeding trials and randomized interspersion of oyster density treatments (Underwood, 1981; Hurlbert, 1984). Each crab was exposed to a specific density only once in order to meet experimental design assumptions for the functional response (Houck and Strauss, 1985). Influent water from the York River ranged in salinity from 19–23‰. Temperatures were maintained at 26–27°C and artificial lights regulated photoperiod at 14 h L:10 h D.

Crabs were starved for 24 h before each trial to standardize hunger levels. Cultch with oysters were scattered on the tank bottom and the spatial arrangement noted. Cultch with oysters was cleaned of fouling organisms (potential alternate prey) by "dipping" in a concentrated salt solution (Provenzano, 1959). Feeding trials were initiated at 1300 hours when a single *C. sapidus* was introduced into a tank, and ended upon removal of the crab 24 h later. Six to 18 replicates at densities of 5, 10, 20, 30, 40, and 50 oysters/tank were run for medium and large oysters. As a result of increased feeding rates on small oysters, 6–10 replicates at 10, 20, 40, 80, 120, 250 and 350 oysters·tank^{-1} were required to assess the functional response. Since oysters were obtained from the field, potential variations in the distribution and abundance of oyster spat on each piece of cultch was not controlled. The density of oysters on each piece of cultch ranged as follows: 15 mm SH, 10–30 oysters·cultch^{-1}; 25 mm SH, 1–10 oysters·cultch^{-1}; 35 mm SH, 1–5 oysters·cultch^{-1}. Thus, only overall density within tanks was controlled. The numbers of oysters eaten were recorded following each experimental trial.

Behavioral Observations.—Crabs were observed during the first hour of each feeding trial through portholes in an opaque plastic canopy surrounding experimental tanks to avoid possible satiation effects which can reduce success rates and increase handling times (Bence and Murdoch, 1986).

The following dependent variables and parameters were quantified as contributing directly or indirectly to behavioral subcomponents of the functional response (i.e., a' and T_h): (1) breaking time (T_b), the time from the crab's first physical contact with an oyster, through the period of recognition and shell crushing, to the first bite of exposed flesh; (2) eating time (T_e), the period from the end of T_b to the completion of the meal and abandonment of the empty shell, including intermittent periods of shell breakage and inspection of shell debris; (3) handling time (T_h), the sum of T_b and T_e; (4) predator persistence time (T_p), the time from the initial encounter of the crab with the prey (e.g., manipulation of the prey with the chelae) until rejection; (5) total encounter rate (E_t), the number of active encounters; (6) successful encounter rate (E_s), the total number of encounters that resulted in feeding; and, (7) attack success (S), the proportion of active encounters resulting in consumption (E_s/E_t). In addition, initiation of foraging, oyster breaking methods, eating techniques and, relative vulnerability of oysters as a function of within-cultch settlement sites (herein termed "attachment sites") and growth geometries were noted. Behavioral observations were quantified at densities of 5, 20, and 50 oysters·tank^{-1} for medium and large oysters, and at 20, 40, 120 and 250 oysters·tank^{-1} for small oysters.

Analyses.—Daily consumption and proportional mortality (number eaten·density^{-1}) rates for each oyster size experiment were analyzed with a one-way ANOVA with oyster density as the independent factor. To meet assumptions of normality and homogeneity of variance, consumption rates were log transformed and proportional mortality rates were angular transformed (arc-sine square-root) as needed (Underwood, 1981). Proportions were used to allow for a more accurate definition of the shape (type) of the functional response curve at low prey densities (Peterman, 1977; Lipcius and Hines, 1986). Therefore, initial determination of the type of functional response (type II or III) was based on results from the ANOVA of proportional mortality rates. Multiple comparisons were performed with a Student-Newman-Keuls (SNK) test (Underwood, 1981).

Heterogeneity of functional responses among crabs within each density experiment was tested with a non-parametric log-likelihood ratio, *G*, applying Williams (1976) correction for continuity (Sokal and Rohlf, 1981). A hierarchical loglinear model (SPSSX Inc., 1986) generated expected distributions and provided contrasts.

Total and successful encounter rates for each density experiment were analyzed using a one-way ANOVA with density as the independent variable. Breaking (T_b), eating (T_e) and handling times (T_h) in successful encounters, and persistence times (T_p) in unsuccessful encounters were analyzed by an analysis of covariance (ANCOVA) with oyster height as the covariate and density as the independent variable. The assumption of equal slopes (Underwood, 1981) was met in the full data set, as evidenced by non-significant density by oyster height interaction effects. One-way ANOVA was employed when there was a nonlinear relationship between oyster height and density (Underwood, 1981). Fisher's transformation (Zar, 1984) indicated that exponential and power functions did not significantly improve the fit to either T_b, T_e, or T_h data for each oyster size treatment over linear functions (all $P > 0.19$).

Modeling.—A general functional response model (Real, 1977; 1979) was used to test the form of the functional response, free from the potential problems associated with analysis of specific functional response models (Eqs. 1–4) (Hassell, 1978; Livdahl and Stiven, 1983; Williams and Juliano, 1985; Trexler et al., 1988):

$$F = kA^n/X + A^n \qquad (5)$$

where F = the feeding rate, k = the maximum feeding rate (saturation), A = the density of food items, X = the density of food items that generate half-maximal feeding, and n = the parameter associated with the amount of increase in the rate of detection of a prey item with an increase in prey density. When n = 1, the functional response is a type II hyperbolic curve, and when n > 1 a type III (sigmoid) response is indicated (Real, 1979). To test the form of the functional response, estimates of n were compared against the null hypotheses $\hat{n} = 0$, $\hat{n} = 1$, $\hat{n} = 2$ with standard *t*-tests. The general functional response model was analyzed by linear regressions of the log-transformation of Eq. 5 (Real, 1979), and tested for appropriate fit as described in Lipcius and Hines (1986). The predicted type of functional response was then compared with results from the ANOVA of proportional mortality rates.

Non-linear least squares analyses (SAS Institute, 1985) were used to estimate a' and T_h, and fit the data to the appropriate functional response model (Eqs. 1–4).

The statistical fit of continuous- and discrete-time functional response models was examined with an *F*-test employing the ratio of the "lack-of-fit" mean square to the "pure error" mean square (Draper and Smith, 1981; Neter and Wasserman, 1974; Colton, 1987; Trexler et al., 1988). A significant *F*-ratio indicated a statistically inadequate fit of the data to a model.

The criteria for determining a statistically valid conceptual functional response model, listed in decreasing priority, were: (1) *F*-value of the regression significant; (2) "Lack-of-fit" error non-significant; (3) Lowest residual sum of squares of all models; and (4) Residuals about the predicted values distributed randomly for partial and complete data sets.

RESULTS

Foraging Behavior.—Foraging behavior of *C. sapidus* was generally prefaced by increased antennule flicking and gill bailing rates, followed by vigorous movements of the mouthparts. The dactyls of the first and second anterior walking legs, and the chelipeds were used to probe for and manipulate oyster spat attached to cultch. Although the setae on the inner edges of the walking legs are especially sensitive to tactile stimuli (Shepheard, 1974), their contact with oyster spat did not always result in an active encounter. In some instances, contact with cultch illicited attack responses in which a crab crushed shell devoid of oysters. The majority (97%, N = 35) of crabs used the right chela as the crusher. Prey handling usually began with an attempt to crush the oyster regardless of oyster height. During this process an oyster was held by one chela while force was applied by the other chela, usually to the umbonal region. The umbo or posterior end of the oyster affords a higher mechanical advantage to the chela (Blundon and Kennedy, 1982). After a series of force applications the oyster was reoriented using the chelae and maxillipeds, and different opening techniques were employed.

The vulnerability of a given oyster and the opening technique used appeared to be a function of oyster height, shell thickness, attachment site and growth geometry. For instance, oyster attachment to depressions on the surface of the cultch limited the ability of crabs to reach oysters with the chelae, whereas attachment along the outside edge of the cultch facilitated crushing. Growth geometry limits the positions available for crabs to exert sufficient force without the chelae slipping. Oysters growing parallel to the plane of the cultch were harder to reach, especially when attached to the smooth side of the oyster cultch, compared to those growing out of the plane. The majority of small juvenile oysters (15 mm SH) were growing parallel to the plane of the cultch and a large proportion were attached to the outside edge of the cultch compared to larger oysters. As oyster height increased up to 25 mm SH, growth geometry became increasingly heterogeneous with a concomitant decrease in numbers attached to the outside edges of the cultch. This was especially true at low within-cultch densities. At a mean size of 35 mm SH, very few oysters were attached at high vulnerability sites and growth geometry was extremely variable, when compared to smaller size classes.

Crabs used two major techniques to open large ($\bar{x} = 35 \pm 2$ mm SH) juvenile oysters. In the first technique, the teeth on the dactyl of the crusher chela were scraped back and forth along the umbonal region shearing off small shell-flakes. The cutter chela was then used in attempts to puncture the weakened area. This sequence was repeated until puncturing of the weakened area, followed by severing of the adductor muscle and separating of the valves. This technique was usually employed when oyster growth geometry caused the chelae to slip during initial crushing attempts. Where growth geometry facilitated an adequate grip, a second technique was employed, whereby crabs attempted to pry the oyster from the cultch with the crusher chela while the cutter chela gripped the cultch. Thereafter, the posterior edges of the oyster were chipped gradually until the cutter chela could be forced between the valves to tear the adductor muscle allowing separation of the valves.

Crabs feeding on medium-sized ($\bar{x} = 25 \pm 2$ mm SH) juvenile oysters were usually successful after a series of force applications and reorientations. If this method failed, crabs attempted to remove the oyster from the cultch as described above for larger oysters.

Once the valves of large and medium-sized oysters were opened, the flesh of the left valve was torn away by the third or outer maxillipeds while the cultch was steadied with the chelipeds and anterior walking legs. Valves were discarded once they were thoroughly gleaned. Afterwards, the chelae swept the floor of the tank in search of shell fragments containing flesh.

Small ($\bar{x} = 15 \pm 2$ mm SH) juvenile oysters were easily opened by simple crushing attempts directed at individual oysters, or by randomly crushing the cultch itself. This latter technique was primarily employed at low densities (i.e., 10 $\text{oysters} \cdot \text{tank}^{-1}$). A small proportion of small oysters located within depressions on the cultch achieved a refuge from crab predation. As a consequence of this random crushing technique, these attachment site refuges became accessible to crab predation.

Functional Responses.—Consumption rates increased significantly with oyster density and decreasing shell-height (Fig. 1). Maximum daily consumption rates

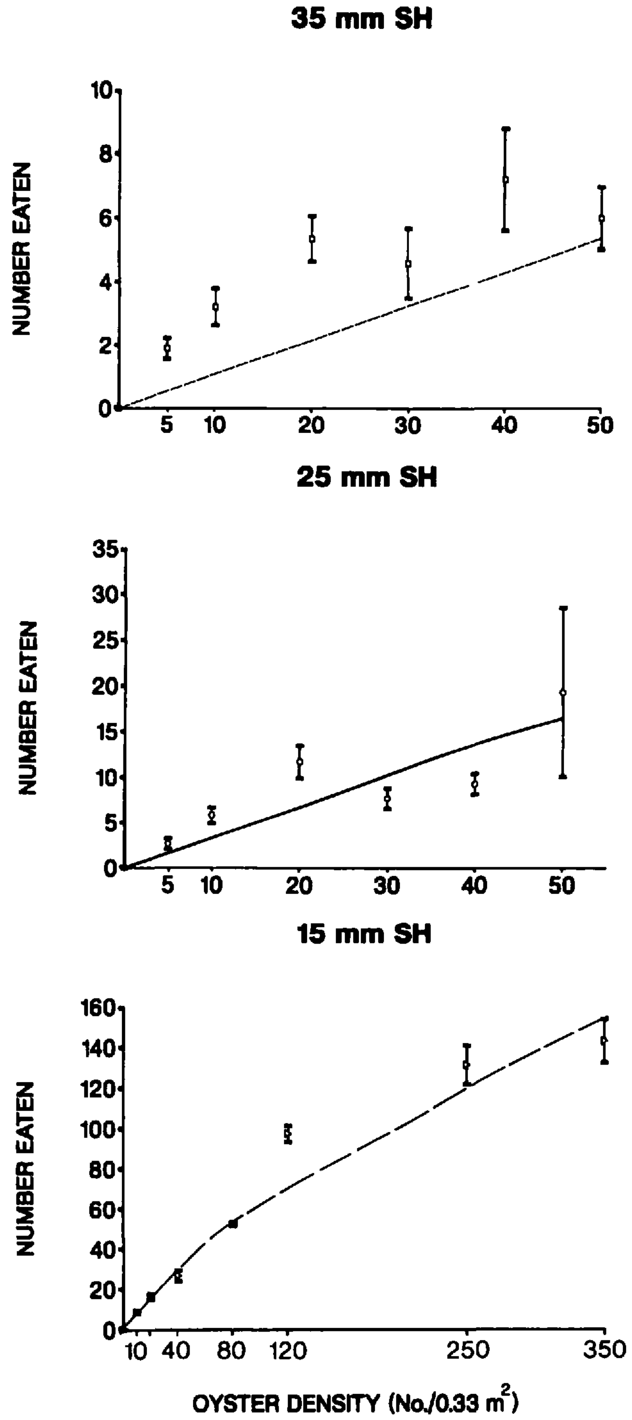

Figure 1. Functional responses of *C. sapidus* at three oyster size-classes (ANOVA; $\bar{x}$ = 15 mm SH: $F = 221.6$, df = 6,42, $P < 0.0001$; $\bar{x}$ = 25 mm SH: $F = 32.9$, df = 5,45, $P < 0.0001$; $\bar{x}$ = 35 mm SH: $F = 5.0$, df = 5,89, $P < 0.0005$). Each point represents the mean feeding rate over 24 h. Vertical bars equal 1 SE. N = 6–18 replicates per prey density. Note the difference in X-values at 15 mm SH relative to other size classes. Solid lines represent the fit to a discrete-time type II functional response model.

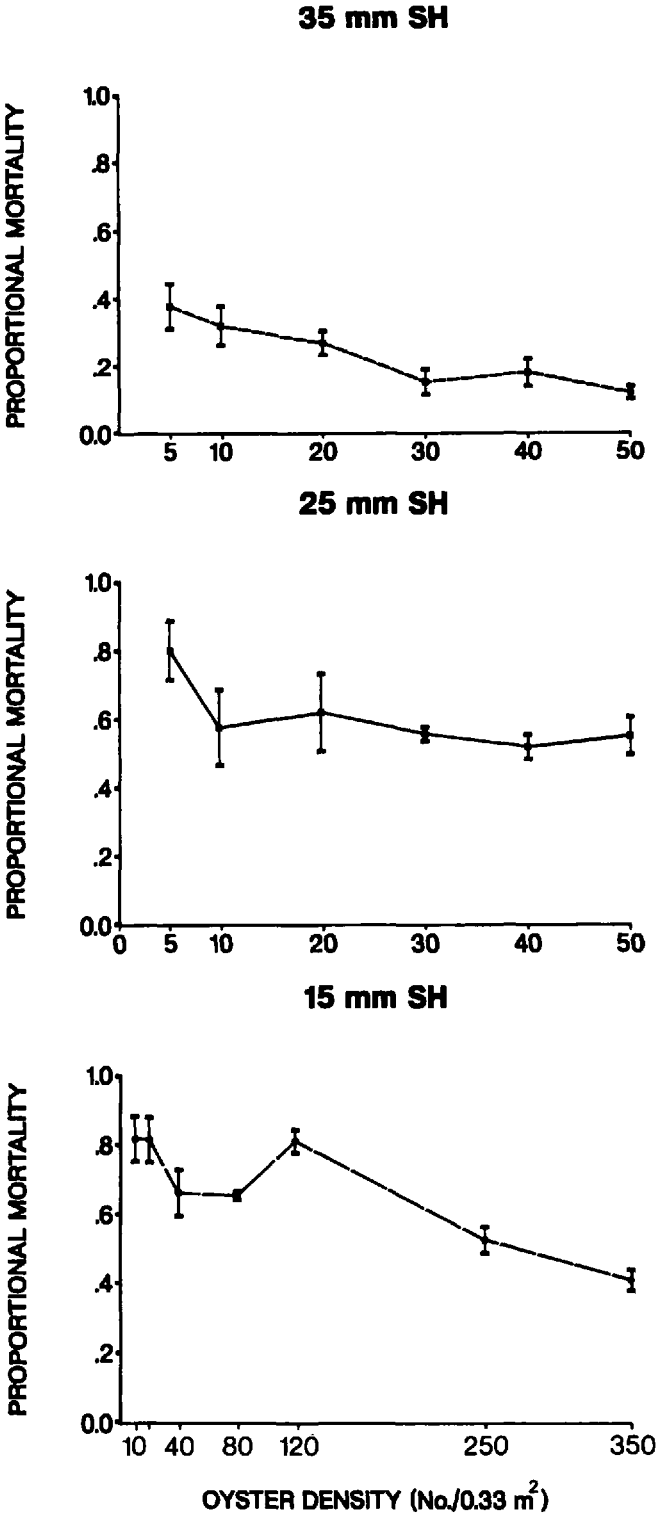
35 mm SH
PROPORTIONAL MORTALITY
1.0
.8
.6
.4
.2
0.0
5
10
20
30
40
50
25 mm SH
PROPORTIONAL MORTALITY
1.0
.8
.6
.4
.2
0.0
0
5
10
20
30
40
50
15 mm SH
PROPORTIONAL MORTALITY
1.0
.8
.6
.4
.2
0.0
10
40
80
120
250
350
OYSTER DENSITY (No./0.33 m²)

Table 1. Results of linear regression of the log-transformed general functional response model (Real, 1977; 1979) for oyster shell height effects

Feature	Oyster size-class ($\bar{x} \pm 2$ mm SH)		
	15	25	35
Parameter Estimates			
Intercept	−2.62	−2.65	−1.88
Slope	1.00	0.90	0.58
Slope standard error	0.03	0.09	0.12
Summary Statistics			
Regression SS (df)	11.6 (1)	4.9 (1)	3.8 (1)
Residual SS (df)	0.5 (41)	2.1 (44)	13.0 (86)
F-value	867.9	104.6	25.3
P-values	<0.0001	<0.0001	<0.0001
R^2 (%)	95.5	70.4	22.7
Binomial test (partial)	NS	NS	NS
Binomial test (complete)	NS	$P < 0.005$	NS
Tests of Hypothesis			
H_0: slope = 0	$P < 0.0005$	$P < 0.0005$	$P < 0.0005$
H_0: slope = 1	NS	NS	$P < 0.0005$
H_0: slope = 2	$P < 0.0005$	$P < 0.0005$	$P < 0.0005$

of 142 oysters·crab^{-1} were observed with the smallest oysters (Fig. 1). At shell-heights of 25 and 35 mm, highest daily consumption rates were approximately 27 and 7 oysters·crab^{-1}, respectively (Fig. 1). The trends in proportional mortality rates of *C. virginica* as a function of prey density were similar for all three oyster size-classes, decreasing significantly with increasing oyster density (Fig. 2). This pattern typifies a hyperbolic relationship between predation rate and prey density (type II response) (Hassell, 1978).

Some individual crabs eating 35-mm and 15-mm oysters differed significantly in their functional responses (i.e., consumption·prey density^{-1}·[24 h^{-1}]) from other crabs within their respective prey-size treatments (Log-likelihood *G*-Test; 35 mm SH: $G = 55.5$, df = 25, $P < 0.0004$; 15 mm SH: $G = 143.0$, df = 30, $P < 0.0001$), whereas all crabs eating 25-mm oysters had similar responses ($G = 18.5$, df = 20, $P = 0.55$).

Modeling.—Analysis according to the general functional response model (Eq. 3) (Real, 1977; 1979) corroborated the results from the ANOVA of proportional mortality for all oyster size-classes, indicating a hyperbolic type II response (Table 1).

Continuous- and discrete-time models provided a statistically adequate fit, irrespective of oyster shell-height, as indicated by the non-significant lack-of-fit error (Table 2). For 25-mm and 35-mm SH oysters, discrete-time models explained more of the variance in consumption and were characterized by lower residual sum of squares than continuous-time models (Table 2). For 15-mm SH oysters, the continuous-time model explained more of the variance than the discrete-time model (96.4% versus 92.2%, respectively, Table 2); however, the

←

Figure 2. Proportional mortality of *C. virginica* at six densities as a function of oyster size-class (ANOVA; $\bar{x}$ = 15 mm SH: $F = 6.67$, df = 6,42, $P < 0.0001$; $\bar{x}$ = 25 mm SH: $F = 3.0$, df = 5,45, $P < 0.02$; $\bar{x}$ = 35 mm SH: $F = 4.9$, df = 5,89, $P < 0.0005$). Each point represents the mean proportional mortality over 24 h. Vertical bars equal 1 SE. N = 6–18 replicates per prey density.

Table 2. Summary statistics for nonlinear least squares analysis of continuous- and discrete-time functional response models

Oyster size-class ($\bar{x} \pm 2$ mm SH)	Source	SS (df)	MS	F	P	R^2	Binomial test	
							Partial	Complete
15	Continuous-time type II model:					96.4	NS	NS
	Regression	300,941.5 (2)	150,470.7	542.4	<0.0005			
	Residual	11,374.5 (41)	277.4					
	Lack-of-fit	740.0 (6)	123.3	0.4	NS			
	Pure error	10,634.6 (35)	303.8					
	Total	312,316.0 (43)						
	Discrete-time type II model:					94.5	$P < 0.0005$	NS
	Regression	287,937.3 (1)	287,937.3	596.1	<0.0005			
	Residual	24,378.7 (42)	580.4					
	Lack-of-fit	1,036.3 (7)	148.0	0.2	NS			
	Pure error	23,342.3 (35)	666.9					
	Total	312,316.0 (43)						
25	Continuous-time type II model:					93.5	NS	NS
	Regression	11,610.6 (2)	5,805.3	322.5	<0.0005			
	Residual	810.4 (44)	18.4					
	Lack-of-fit	3.9 (5)	0.8	0.04	NS			
	Pure error	806.4 (39)	20.7					
	Total	12,421.0 (46)						
	Discrete-time type II model:					95.2	NS	NS
	Regression	11,820.2 (2)	5,910.1	432.8	<0.0005			
	Residual	600.8 (44)	13.7					
	Lack-of-fit	4.5 (5)	0.9	0.1	NS			
	Pure error	596.3 (39)	15.3					
	Total	12,421.0 (46)						
35	Continuous-time type II model:					69.3	NS	$P < 0.05$
	Regression	2,107.1 (2)	1,053.6	97.0	<0.0005			
	Residual	933.9 (86)	10.9					
	Lack-of-fit	2.8 (4)	0.7	0.1	NS			
	Pure error	931.0 (81)	11.4					
	Total	3,041.0 (88)						
	Discrete-time type II model:					85.8	$P < 0.001$	$P < 0.005$
	Regression	2,609.2 (2)	1,304.6	259.9	<0.0005			
	Residual	431.8 (86)	5.0					
	Lack-of-fit	27.1 (4)	6.8	1.4	NS			
	Pure error	404.6 (81)	5.0					
	Total	3,041.0 (88)						

discrete-time model was chosen to compare parameter estimates between oyster sizes and in the interest of uniformity.

Behavioral Components.—Regression estimates (Table 2) of mean handling time per oyster were 0.1 h, regardless of prey size (Table 3). Experimental handling time estimates increased significantly with oyster height, in contrast to the constant regression estimates (Table 3). Regression estimates of instantaneous attack rates (a′) decreased with increasing oyster height (Table 3). Similarly, experimental estimates of total and successful encounter rates were decreasing functions of oyster height (Table 3). Total encounter rates for the 15-mm size-class experiment differed significantly by oyster density, whereas for 25-mm and 35-mm size-classes they did not (Fig. 3A). However, the pattern for all three size-classes was similar by prey density, increasing to an asymptote (Fig. 3A). The significant variation in encounter rates with density for 15-mm oysters is contrary to model predictions of a constant a′ (Hassell et al., 1977; Hassell, 1978).

Successful encounter and attack success rates varied as a function of oyster height and density (Fig. 3B, C). The highest proportion of successful attacks occurred at the smallest prey size-class, ranging from 54–80% (Fig. 3B). At 25 mm and 35 mm SH, attack success rates declined steeply with prey density from 58–27% and 31–14%, respectively (Fig. 3C). At 25 mm and 35 mm SH, attack success rates and proportional mortality rates varied similarly as a function of prey density (compare Figs. 2 and 3B, C)—high proportional mortality rates corresponded to high proportions of successful encounters and attacks. In contrast, the pattern is reversed at 15 mm SH. Successful encounter rates differed significantly by density for 15-mm oysters, but not for 25-mm and 35-mm oysters.

Predator persistence times in unsuccessful encounters were analyzed as a function of oyster height and density to evaluate any potential behavioral mechanisms regulating proportional attack success or successful encounter rates. Persistence times varied linearly with oyster length among smaller oysters (Table 4, Fig. 4A), and only medium-sized oysters demonstrated significant variation with density, although a similar decrease in T_p with density was observed for 35-mm oysters (Table 4, Fig. 4B).

Handling time components in successful encounters generally increased with oyster height, but did not vary significantly with prey density (Table 4, Fig. 5). Thus, handling time components (T_h, T_b, T_e) were only compared as a function of oyster shell-height. Breaking times of large oysters were significantly higher than small and medium oysters (Fig. 5; slopes; $F = 40.3$, df = 2,129, $P < 0.0001$; Tukey-Test). Although slopes for breaking times of 15-mm and 25-mm SH oysters were equal, elevations were not ($t = 24.0$, df = 2,100, $P < 0.0001$). At 15 mm and 25 mm SH, T_b averaged 35.5 and 116.0 seconds respectively, and displayed a significant positive linear relationship with oyster height (Fig. 5A, Table 4). At 35 mm SH, T_b averaged 709 seconds and was extremely variable resulting in a nonsignificant linear relationship with oyster height, despite various transformations (Fig. 5A, Table 4). This lack of linearity for T_b of large oysters corresponds well with the nonsignificance in observed persistence times as a function of oyster height and density at 35 mm SH (Table 4). Eating times correlated positively with oyster height for all prey size-classes and averaged 69.0 sec (15 mm SH), 201.1 sec (25 mm SH), and 427.3 sec (35 mm SH) (Fig. 5B, Table 4). Linear regression coefficients of eating times increased significantly for large oysters relative to small and medium oysters (ANCOVA; $F = 82.6$, df = 2,129, $P < 0.0001$; Tukey-Test). Slopes of eating times for 15-mm and 25-mm SH oysters were equal; however, elevations differed ($t = 2.6$, df = 2,100, $P < 0.005$). Variability in T_e

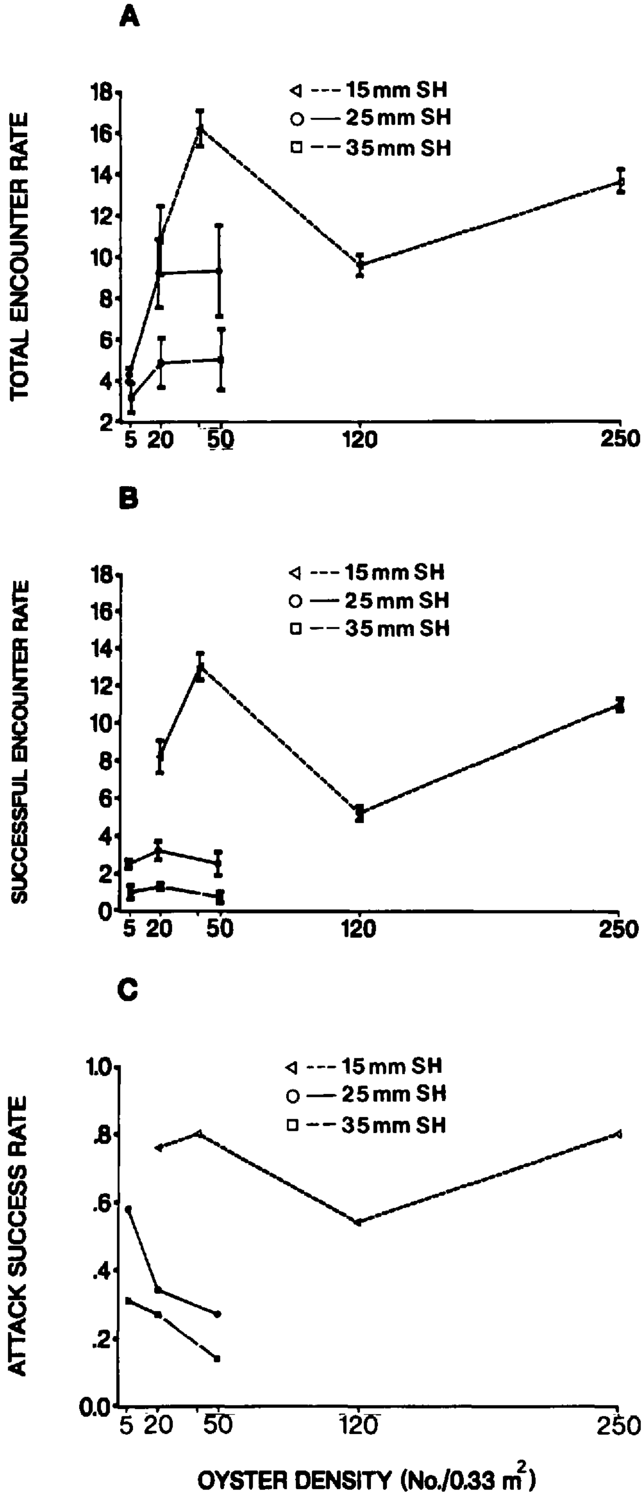

Figure 3. (A) Mean number of encounters (total) related to oyster density at three oyster size-classes (ANOVA; 15 mm SH: $F = 8.73$, df = 3,19, $P < 0.001$; 25 mm SH: $F = 3.1$, df = 2,17, $P = 0.07$; 35

Table 3. Estimated model parameters and observed behavioral components of *C. sapidus* functional responses (Values are means ± 1 SE)

Oyster size-class ($\bar{x}$ ± 2 mm SH)	Model parameters a'*	Th	Observed behavioral components encounter rates† Total	Successful	Th‡
15	0.061 ± 0.015	0.1 ± 0.01	12.55 ± 0.75	9.4 ± 0.73	0.03 ± 0.003
25	0.037 ± 0.005	0.1 ± 0.13	7.61 ± 1.04	2.7 ± 0.27	0.07 ± 0.006
35	0.005 ± 0.001	0.1 ± 0.43	4.40 ± 0.69	1.0 ± 0.16	0.33 ± 0.040

* a' = attack rate = the area a predator searches for prey per unit time. Th = the time taken to break open and eat a single prey, and is a decimal fraction of 1.0 h.

† $\text{Oysters}\cdot h^{-1}$.

‡ $\text{Oyster}\cdot h^{-1}$.

at oyster heights greater than 25 mm was low relative to T_b (Fig. 5B). Breaking times were approximately twice T_e values at 35 mm SH, while at 15 mm and 25 mm they were approximately half. This suggests that T_b is a major component in oyster handling times above 25 mm SH and should decrease prey profitability estimates compared to smaller (i.e., <15 mm) oyster heights. Handling times (T_h) generally increased asymptotically with oyster height (Fig. 5C). Size-classes of 15 mm and 25 mm SH correlated significantly with oyster height, whereas the 35-mm size-class did not (Table 4). Linear regression coefficients of handling times increased significantly for large oysters relative to small and medium oysters (ANCOVA; $F = 17.9$, df = 2,129, $P < 0.0001$; Tukey-Test).

DISCUSSION

Foraging Behavior.—Increasing variations in oyster attachment sites and growth geometries with height appeared to be the key factor in determining both the type of opening method used and the potential for success. If initial crushing attempts were unsuccessful, crabs usually attempted to remove the oyster from the cultch. Once oysters were removed from the cultch, the prey handling methods and shell breaking "signatures" were similar to those of *C. sapidus* feeding on cultchless oyster spat (Krantz and Chamberlin, 1978; Elner and Lavoie, 1983; Bisker and Castagna, 1987), and those of lobsters, *Homarus americanus* and rock crabs, *Cancer irroratus* feeding on Atlantic deep-sea scallops, *Placopecten magellanicus* (Elner and Jamieson, 1979). If the crab was unable to remove the oyster from the cultch, the cultch was discarded and the crab resumed foraging. The majority of blue crabs feeding on small oysters at low densities displayed a unique random crushing technique to feed on oysters that had attached to depressions on the cultch. Crabs sometimes encountered oysters with attachment geometries that enabled them to exert force without the chelae slipping, but did not initiate shell-opening behavior. Conversely, crabs sometimes probed cultch devoid of oysters, followed by several crushing attempts. Thus, the sensitivity or efficiency of the dactyls in foraging may be a function of complex interactions involving such factors as (1) hunger level, (2) the density of prey available to simultaneous probing

←

mm SH: $F = 0.66$, df = 2,19, $P = 0.53$). (B) Mean number of successful encounters related to oyster density at three oyster size-classes (ANOVA; 15 mm SH: $F = 31.16$, df = 3,19, $P < 0.0001$; 25 mm SH: $F = 0.67$, df = 2,17, $P = 0.53$; 35 mm SH: $F = 1.10$, df = 2,19, $P = 0.36$). (C) Proportion of successful attacks (E_t/E_s) related to oyster density at three oyster size-classes. All observations per 1 h. Vertical bars equal 1 SE.

Table 4. Results from the analysis of covariance of oyster height (covariate), density and prey size-class effects on observed A) Persistence Times, B) Breaking Times, C) Eating Times, and D) Handling Times: degrees of freedom (df), mean squares (MS), *F*-ratio (*F*) and probabilities (*P*) associated with the *F*-ratio tests for variability accounted for by regression against oyster height and the main effect, oyster density

Oyster size-class	Regression against oyster height				Oyster density effects				Density by oyster height interaction			
($\bar{x}$ ± 2 mm SH)	df	MS	*F*	*P*	df	MS	*F*	*P*	df	MS	*F*	*P*
A) Persistence Time:												
15	1,22	6,108.36	4.72	<0.04	3,22	477.78	0.37	0.78	3,22	3,397.48	2.63	0.08
25*	1,39	0.01	0.06	0.82	2,39	2.20	8.65	<0.00	2,39	0.18	0.70	0.50
35*	1,69	0.17	0.43	0.51	2,69	0.98	2.50	0.09	2,69	0.21	0.53	0.59
B) Breaking Time:												
15	1,73	55,366.37	57.47	<0.00	3,73	1,033.23	1.07	0.37	3,73	885.53	0.92	0.44
25	1,20	24,785.95	9.37	<0.01	2,20	3,026.77	1.15	0.34	2,20	1,287.93	0.49	0.62
35	1,22	1,454,447.1	1.24	<0.28	2,22	2,461,632.6	1.26	0.31	2,22	2,843,575.8	2.30	0.13
C) Eating Time:												
15	1,73	101,747.55	55.09	<0.00	3,73	1,084.89	0.59	0.63	3,73	4,035.10	2.19	0.10
25	1,20	86,652.44	18.97	<0.00	2,20	3,023.06	0.66	0.53	2,20	7,499.98	1.64	0.22
35	1,16	1,284,366.2	14.89	<0.00	2,16	29,113.83	1.53	0.25	2,16	15,728.39	0.82	0.46
D) Handing Time:												
15	1,73	307,225.79	88.56	<0.00	3,73	2,812.45	0.81	0.49	3,73	7,358.91	2.12	0.11
25	1,20	179,615.84	43.28	<0.00	2,20	12,052.09	2.90	<0.08	2,20	8,506.03	2.05	0.16
35	1,22	11,628,322.4	3.58	<0.08	2,22	2,654,784.0	1.44	0.27	2,22	2,648,835.9	1.42	0.27

* Logarithmically transformed.

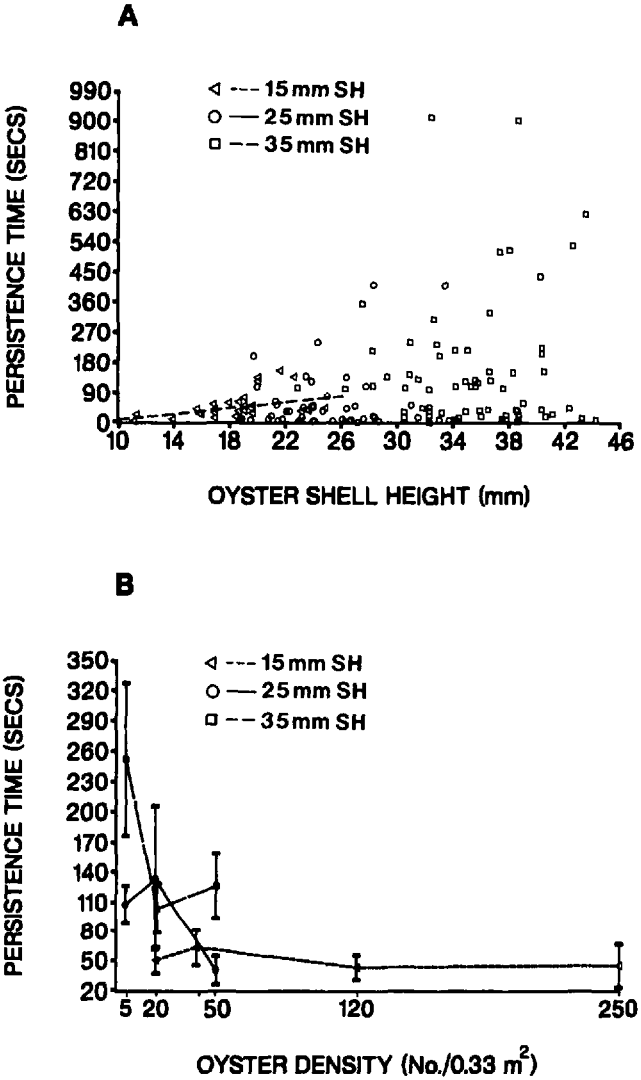

Figure 4. (A) Predator persistence times of *C. sapidus* in unsuccessful encounters with three oyster size-classes compared against oyster height. (B) Mean predator persistence times in unsuccessful encounters with *C. virginica* at three oyster size-classes related to oyster density. All observations per 1 h. Vertical bars equal 1 SE.

by all dactyls, and (3) the effect of varying flow rates in mediating the chemical stimulus of oysters both before and after opening by the crab.

Functional Responses.—Consumption rates for *C. sapidus* increased with oyster density and decreasing shell-height. Reduced predation rates with increasing prey size is consistent with previous laboratory studies of decapod–bivalve predator–prey systems (Whetstone and Eversole, 1978; Elner and Lavoie, 1983; Bisker and Castagna, 1987; Sanchez-Salazar et al., 1987); however, the consumption rates of small juvenile oysters in this study are the highest documented feeding rates for laboratory decapod–bivalve studies. A prey density of 350 oysters/tank was required to assess the form of the functional response for small juvenile oysters.

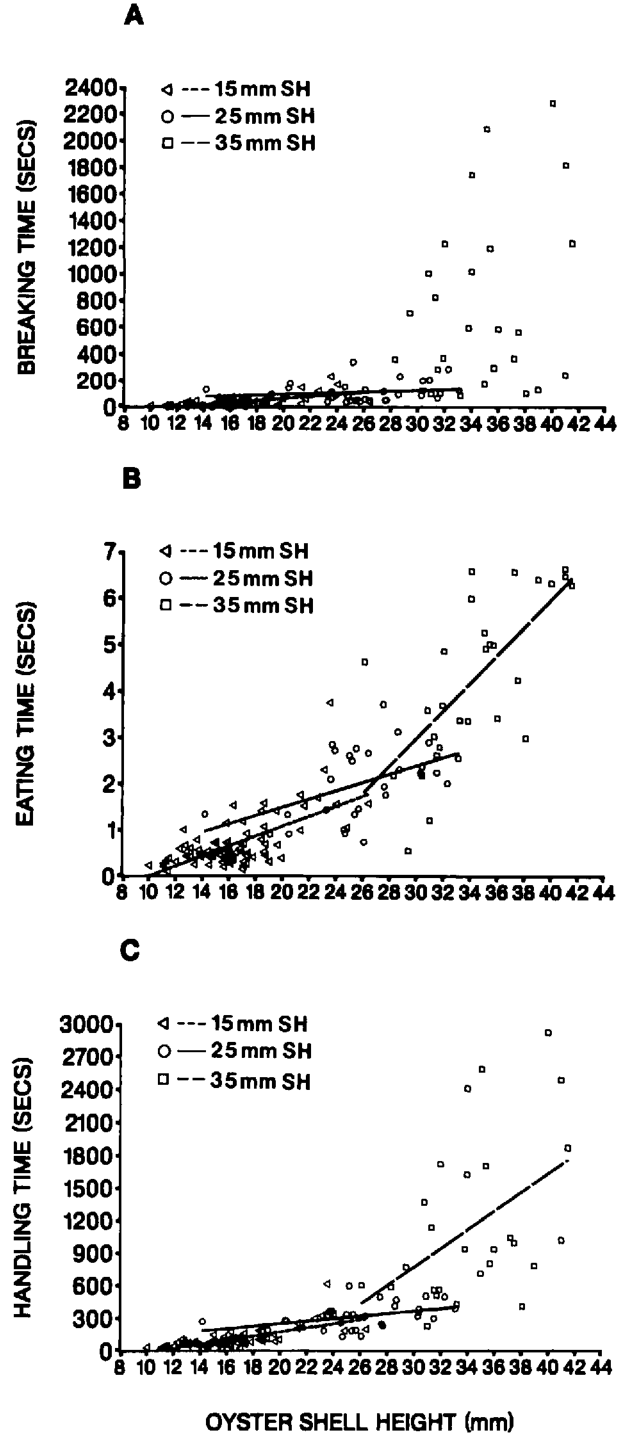

Figure 5. Handling time components of successful encounters per 1-h observation period, compared against oyster height within three oyster size-classes: (A) Breaking time (sec): 15: $y = -94.9 + 7.9x$ ($r^2 = 0.42$, N = 81); 25: $y = -69.5 + 6.9x$ ($r^2 = 0.29$, N = 26); 35: NS. (B) Eating time (sec): 15: $y = -107.8 + 10.8x$ ($r^2 = 0.40$, N = 81); 25: $y = -124.1 + 12.8x$ ($r^2 = 0.44$, N = 26); 35: y =

Elner and Lavoie (1983) indicated that maximum feeding rates by large (94–107 mm) *H. americanus* and *C. irroratus* were 28 and 4.5 oysters·crab^{-1}·day^{-1}, respectively.

Inversely density-dependent proportional mortality rates as a function of prey density indicated that large *C. sapidus* exhibited a type II response with oysters, irrespective of oyster size. Individual crab functional responses were similar for 25-mm SH oysters. Differences in crab functional responses for 35-mm SH oysters were probably due to variations in opening techniques as a function of attachment site and growth geometry. The inability to crush large juvenile oysters after initial opening attempts caused switching to alternate opening behaviors whereby certain crabs were unsuccessful (pers. obs.). Differences for 15-mm SH oysters were probably due to some crabs not displaying the random crushing technique at low oyster densities (pers. obs.).

Modeling.—The general functional response model (Real, 1977; 1979) corroborated the results from the ANOVA of proportional mortality rates of a type II response. In addition, the general model indicated a type II response for 15-mm SH oysters despite the atypical form of the functional response. Previous work has shown the general functional response model is useful in identifying both type II and type III functional responses (Lipcius and Hines, 1986).

Both continuous- and discrete-time models provided a statistically adequate fit to the data, regardless of oyster size. Discrete-time models provided the best fit to the data at 25 and 35 mm SH, whereas a continuous-time model fit the data best for 15-mm oysters. However, the discrete-time model was chosen primarily so that parameter estimates could be compared.

Behavioral Components.—Directly measured predation parameters cannot be compared with those from nonlinear regressions. Regression estimates of a′ represent a maximum theoretical rate of attack and are separate from the effects of feeding history (Hassell, 1978). These are not equivalent to quantitative measures of feeding rates, which include pretreatment effects and the effect of prey handling during experiments (Spitze, 1985). Regression estimates of T_h are not likely to equal estimates from direct observation because the T_h estimates from regression also include periods of non-searching activity induced, for example, by satiation of the predator (Hassell, 1978). However, qualitative features of the parameter estimates can be compared (e.g., constancy of T_h or a′ as a function of prey size and density).

Prey size affects many components of predation (Thompson, 1978). Increases in prey size typically increase prey handling times and decrease attack and encounter rates. Therefore, increasing prey size decreases profitability by decreasing the net rate of energy intake through increases in the time spent handling prey (assuming there is not a higher proportional increase in calorie reward).

The trend in functional response model parameter estimates partially reflected these predictions. Regression estimates of T_h were constant at all prey size-classes, whereas a′ decreased two-fold with increasing shell-height from 15 mm to 25 mm, and seven-fold from 25 mm to 35 mm. The apparently exponential decrease in a′ with increasing shell-height is in accord with the positive allometric relationship (Schmidt-Nielsen, 1984) between shell-height and surface area of oysters

---

←

−598.0 + 29.9x (r^2 = 0.47, N = 28). (C) Handling time (sec): 15: y = −202.6 + 18.7x (r^2 = 0.52, N = 80); 25: y = −170.1 + 18.5x (r^2 = 0.52, N = 26); 35: NS. See Table 4 for significance levels.

(Galtsoff, 1964). Thus, 25 mm SH appears to be a prey size threshold above which instantaneous attack rates decrease markedly.

The effect of varying prey size upon functional response sub-components appears to be largely a function of the particular predator–prey system examined. Spitze (1985) found that handling times per *Daphnia pulex* by larvae *Chaoborus americanus* increased linearly with prey size, whereas attack rate peaked at intermediate sizes, indicating that digestion affected handling times. Cockrell (1974) examined predation of four arbitrary prey size classes of *Asellus aquaticus* by adult *Notonecta glauca* and found that a′ declined linearly and T_h increased exponentially as prey size increased. In contrast, Hewett (1988) examined feeding by the predatory ciliate, *Didinium nasutum* on *Paramecium* sp., and found that searching times during capture were not significantly affected by prey size. Hewett (1988) contends that encounter rates should increase with increasing prey size because larger prey represent a large target and swim faster than small prey. Thompson (1975) found that for *Ischnura elegans* feeding on *Daphnia magna,* a′ increased with increasing prey size.

Most foraging models predict that predators spend more time foraging as prey density increases up to a certain prey density (Hassell and May, 1973; Murdoch and Oaten, 1975). This trend was evident for 15-, 25- and 35-mm SH oysters, in which observed encounter rates increased to an asymptote beyond an initial range of low prey densities.

Total encounter rates decreased with increasing oyster height, probably reflecting a reduction in handling time with smaller oysters. Total encounter rate observations for small oysters may be underestimates since encounters not involving active manipulation by the chelae were not quantified. Blue crab prey evaluation of small oysters might be accomplished through tactile stimulation of the pereopods (e.g., "relative stimulus," sensu Jubb et al., 1983), rather than active manipulation with the chelae (e.g., "prey evaluation," sensu Jubb et al., 1983). Film analysis of encounter rates for the oystercatcher, *Haematopus ostralegus* preying on the infaunal bivalve, *Scrobicularia plana* explained the lower than expected encounter rates at high densities, showing that a prey can be located and refused too quickly to be noticed by an observer (Wanink and Zwarts, 1985).

The key behavioral finding in this study is that persistence time appears to depend upon prey size and density. Persistence time decreased with increasing prey density, whereas encounter rates increased. For medium and large oysters, attack success was inversely related to total encounter rates. Thus, crabs were not as persistent with individual oysters at high prey densities, and therefore had more time available to encounter weaker prey.

The addition of prey size-dependence in T_p as a subcomponent of the functional response adds further complexity to the overall view of crab acceptance and rejection sequences with bivalve prey. Crab acceptance and rejection of bivalve prey appears to involve a suite of complex foraging tactics regulated by variations in factors such as shell to crab strength ratios, opening techniques with attachment site and growth geometry, and oyster density. For instance, at small oyster heights (i.e., 15 mm SH) with concurrent high within-cultch densities, Tp is probably a function of oyster height since growth geometry and attachment sites are relatively homogeneous irrespective of density (pers. obs.). At medium oyster sizes (25 mm SH), T_p was probably a function of oyster height at high densities and attachment site and growth geometry at low densities since the various factors influencing foraging tactics were variable at low within-cultch densities (pers. obs.). Hence, the significant decrease in T_p at the highest prey density at 25 mm SH. This high variability at low within-cultch densities may be a consequence of attaining oysters from the field after crabs had already reduced within-cultch densities, leaving only "hard-to-get" prey. This might bias the results making predation rates at low densities even lower. Similar variations in attachment sites and growth geometries were apparent for large juvenile oysters (35 mm SH), irrespective of oyster density (pers. obs.). These observations correspond well with the lack of significant variation in T_p at 35 mm SH, in terms of both oyster height and density. In addition, persistence times may be modified by crab hunger levels (Hughes and Elner, 1979). Previous experiments have demonstrated a positive correlation between prey height and persistence time in unsuccessful encounters (Hughes and Elner, 1979; Lawton and Hughes, 1985). Lawton and Hughes (1985) found that mean persistence time in unsuccessful attacks by *Cancer pagurus* on the gastropod *Nucella lapillus* increased with increasing prey size; however, there was much variation about the trend.

Handling time components in successful encounters increased with oyster height, with no significant effect of prey density. The lack of density-dependence supports the functional response model assumption of a constant T_h (Hassell, 1978). Breaking times increased asymptotically with oyster height, and were significantly higher for large oysters than for small and medium height oysters, indicating a prey height threshold at 30 mm. The increased variability observed in breaking times above 30 mm SH reemphasizes the importance of shell-height and various prey features (e.g., attachment site and growth geometry) in mediating attack methods. Boulding (1984) examined the vulnerability of four burrowing clam morphs to shell-breaking predation by the cancrid crab, *Cancer productus,* and concluded that the resistance of bivalves to crabs could best be explained as the sum of a number of shell features that greatly increase shell-breaking time rather than the attainment of a size refuge. These characteristics included a thick shell, an ability to close tightly, an inflated shape with a steep ventral margin, and an increased depth of burial in the sediment (Boulding, 1984). Previous experiments have demonstrated increased variability in breaking times at larger prey sizes (Elner and Hughes, 1978; Hughes and Elner, 1979; Lawton and Hughes, 1985). Elner and Hughes (1978) found that shore crabs, *Carcinus maenas,* were too weak to crush any but the smallest (i.e., 10–15 mm length) mussels, *Mytilus edulis,* with a single application of force to the shell, causing crabs to search out weak spots in the umbo of the shell by trial and error. Elner and Hughes (1978) suggested that this randomizing technique accounted for much of the variability in their data. Lawton and Hughes (1985) found that *C. pagurus* exhibited different opening techniques with increasing size of *N. lapillus,* leading to considerable variation in breaking times with increasing prey sizes. However, the possibility that some crabs may have benefited from previous experience with oysters prior to capture, or that slight differences in chela morphology influenced opening techniques cannot be ruled out.

I have identified several potential factors likely acting in concert to regulate the behavioral subcomponents of the functional response. Specific predictions regarding shell to crab strength ratios, attachment sites, growth geometry, and within-cultch densities require further investigation, because the effect of these factors was only casually observed within the experimental design. More detailed knowledge of the energetic costs and constraints of these specific behaviors might provide a useful perspective for understanding the foraging behavior of *C. sapidus* feeding upon juvenile oysters. In addition, the experimental predator–prey system used in this study appears ideal for addressing further questions regarding predictions based on the marginal value theorem (Charnov, 1976; Hughes, 1980), as well as examining patch-scale (e.g., within-cultch) dynamics of predator–prey interactions

(Hassell, 1978). Results from this study indicate that predation by large male *C. sapidus* can lead to local extinction of juvenile oysters (x̄ = 15–35 mm SH) regardless of prey density, and suggest that increasing shell-height is a refuge from predation.

ACKNOWLEDGMENTS

Special thanks is given to R. Mann, R. Lipcius and M. Luckenbach for their abundant advice and discussions during this project. Critical comments from R. Lipcius, M. Luckenbach, and two anonymous reviewers were very helpful in the revision of this manuscript. This paper is part of a thesis submitted in partial satisfaction of the requirements for the M.A. degree in Marine Science at the College of William and Mary. This work was funded in part by two Minor Research grants from the College of William and Mary, the Council on the Environment of the Commonwealth of Virginia, and National Science Foundation grant No. OCE 87-00414 to R. Lipcius and A. Hines. This is Contribution No. 1545 from the Virginia Institute of Marine Science.

LITERATURE CITED

Abrams, P. A. and T. D. Allison. 1982. Complexity, stability, and functional response. Am. Nat. 119: 240–249.

Alexander, S. K. 1986. Diet of the blue crab, *Callinectes sapidus* Rathbun, from nearshore habitats of Galveston Island, Texas. Texas J. Sci. 38(1): 85–89.

Bence, J. R. and W. W. Murdoch. 1986. Prey size selection by the mosquitofish: relation to optimal diet theory. Ecology 67: 324–326.

Bisker, R. and M. Castagna. 1987. Predation on single spat oysters, *Crassostrea virginica* Gmelin by blue crabs, *Callinectes sapidus* Rathbun and mud crabs, *Panopeus herbstii* Milne-Edwards. J. Shellfish. Res. 6(1): 37–40.

Blundon, J. A. and V. S. Kennedy. 1982. Mechanical and behavioral aspects of blue crab, *Callinectes sapidus* (Rathbun), predation on Chesapeake bay bivalves. J. Exp. Mar. Biol. Ecol. 65: 47–65.

Boulding, E. G. 1984. Crab-resistant features on shells of burrowing bivalves: decreasing vulnerability by increasing handling time. J. Exp. Mar. Biol. Ecol. 76: 201–223.

Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. Theor. Pop. Biol. 9: 129–136.

Cockrell, B. J. 1974. Effects of temperature and oxygenation on predator-prey overlap and prey choice of *Notonecta glauca*. J. Anim. Ecol. 53: 519–532.

Colton, T. F. 1987. Extending functional response models to include a second prey type: an experimental test. Ecology 68: 900–912.

Draper, N. R. and H. Smith. 1981. Applied regression analysis, 2nd ed. John Wiley and Sons, Inc., New York, London, Sydney. 709 pp.

Eggleston, D. B. 1988. Predator-prey dynamics between the blue crab *Callinectes sapidus* Rathbun, and juvenile oysters *Crassostrea virginica* (Gmelin). M.A. Thesis, The College of William and Mary, Williamsburg, Virginia. 222 pp.

Elner, R. W. and R. N. Hughes. 1978. Energy maximization in the diet of the shore crab, *Carcinus maenas*. J. Anim. Ecol. 47: 103–116.

——— and G. S. Jamieson. 1979. Predation of sea scallops, *Placopecten magellanicus*, by the rock crab, *Cancer irroratus*, and the American lobster, *Homarus americanus*. J. Fish. Res. Board Can. 36: 537–543.

——— and R. E. Lavoie. 1983. Predation on American oysters (*Crassostrea virginica* [Gmelin]) by American lobsters (*Homarus americanus* Milne-Edwards), rock crabs (*Cancer irroratus* Say), and mud crabs (*Neopanope sayi* [Smith]). J. Shellfish Res. 3(2): 129–134.

Frost, B. W. 1972. Effects of size and concentration of food particles on the feeding behaviour of the marine planktonic copepod, *Calanus pacificus*. Limnol. Oceanogr. 17: 805–815.

Galtsoff, P. S. 1964. The American oyster, *Crassostrea virginica* Gmelin. U.S. Fish and Wildlife Ser. Fish. Bull. 64: 1–480.

Hassell, M. P. 1978. The dynamics of arthropod predator-prey systems. Monographs in Population Biology 13. Princeton University Press, Princeton. 237 pp.

———, J. H. Lawton and J. R. Beddington. 1977. Sigmoid functional responses by invertebrate predators and parasitoids. J. Anim. Ecol. 46: 249–262.

——— and R. M. May. 1973. Stability in insect host-parasite models. J. Anim. Ecol. 46: 693–736.

Haven, D. S., J. P. Whitcomb and P. C. Kendall. 1981. The present and potential productivity of the Baylor Grounds in Virginia. I. VIMS Spec. Report No. 243 in Applied Mar. Sci. and Ocean Engineering. 167 pp.

Hewett, S. W. 1988. Predation by *Didinium nasutum*: effects of predator and prey size. Ecology 69: 135–145.

Holland, A. F., N. K. Mountford, M. H. Hiegel, K. R. Kaumeyer and J. A. Mihursky. 1980. Influence of predation on infaunal abundance in upper Chesapeake Bay, USA. Mar. Biol. 57: 221–235.

Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can. Entomol. 91: 293–320.

———. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Mem. Ent. Soc. Can. 45: 3–60.

———. 1966. The functional response of invertebrate predators to prey density. Mem. Ent. Soc. Can. 48: 1–86.

Houck, M. A. and R. E. Strauss. 1985. The comparative study of functional responses: experimental design and statistical interpretation. Can. Ent. 117: 617–629.

Hughes, R. N. 1980. Optimal foraging theory in the marine context. Oceanogr. Mar. Biol. Ann. Rev. 18: 423–481.

——— and R. W. Elner. 1979. Tactics of a predator, *Carcinus maenas*, and morphological responses of the prey, *Nucella lapillus*. J. Anim. Ecol. 48: 65–78.

Hurlbert, S. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54: 187–211.

Jubb, C. A., R. N. Hughes and T. ap Rheinalt. 1983. Behavioural mechanisms of size selection by crabs, *Carcinus maenas* (L.) feeding on mussels, *Mytilus edulis* L. J. Exp. Mar. Biol. Ecol. 66: 81–87.

Kennedy, V. S. and L. L. Briesch. 1981. Maryland's oysters: research and management. Maryland Sea Grant Publication.UM-SG-TS-81-04. 286 pp.

Krantz, G. E. and J. F. Chamberlin. 1978. Blue crab predation on cultchless oyster spat. Proc. Natl. Shellfish. Assoc. 68: 38–41.

Laughlin, R. A. 1982. Feeding habits of the blue crab, *Callinectes sapidus* Rathbun, in the Apalachicola Estuary, Florida. Bull. Mar. Sci. 32: 807–822.

Lawton, P. and R. N. Hughes. 1985. Foraging behavior of the crab, *Cancer pagurus* feeding on the gastropods *Nucella lapillus* and *Littorina littorea*: comparisons with optimal foraging theory. Mar. Ecol. Prog. Ser. 27: 143–154.

Lipcius, R. N. and A. H. Hines. 1986. Variable functional responses of a marine predator in dissimilar homogeneous microhabitats. Ecology 67: 1361–1371.

Livdahl, T. P. and A. E. Stiven. 1983. Statistical difficulties in the analysis of predator functional response data. Can. Entomol. 115: 1365–1370.

Murdoch, W. W. and A. Oaten. 1975. Predation and population stability. Adv. Ecol. Res. 9: 2–131.

Neter, J. and W. Wasserman. 1974. Applied linear statistical models: regression, analysis of variance, and experimental design. Irwin, Homewood, Illinois. 842 pp.

Nunney, L. 1980. The stability of complex model ecosystems. Am. Nat. 115: 639–649.

Odum, W. E. and E. J. Heald. 1972. Trophic analysis of an estuarine mangrove community. Bull. Mar. Sci. 22: 671–738.

Peterman, R. M. 1977. A simple mechanism that causes collapsing stability regions in exploited salmonid populations. J. Fish. Res. Board Can. 34: 1130–1142.

Peterson, C. H. 1979. The importance of predation and competition in organizing the intertidal epifaunal communities of Barnegat Inlet, New Jersey. Oecologia 39: 1–24.

Provenzano, A. J. 1959. Effects of the flatworm *Stylochus ellipticus* (Girard) on oyster spat in two salt water ponds in Massachusetts. Proc. Natl. Shellfish. Assoc. 50: 83–88.

Real, L. A. 1977. The kinetics of functional response. Am. Nat. 111: 289–300.

———. 1979. Ecological determinants of functional response. Ecology 60: 481–485.

Rogers, D. 1972. Random search and insect population models. J. Anim. Ecol. 41: 369–383.

Royama, T. 1971. A comparative study of models for predation and parasitism. Researches in Population Ecology, Supplement 1: 1–91.

Sanchez-Salazar, M. E., C. L. Griffiths and R. Seed. 1987. The effect of size and temperature on the predation of cockles, *Cerastoderma edule* (L.) by the shore crab, *Carcinus maenas* (L.). J. Exp. Mar. Biol. Ecol. 111: 181–193.

SAS Institute. 1985. SAS user's guide: statistics. Version 5 ed. SAS Institute, Cary, North Carolina. 957 pp.

Schmidt-Nielsen, K. 1984. Scaling: why is animal size so important? Cambridge University Press, Cambridge. 241 pp.

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*. Estuarine Coastal Mar. Sci. 2: 445–458.

Shepheard, P. 1974. Chemoreception in the antennule of the lobster, *Homarus americanus*. Mar. Behav. Physiol. 2: 261–273.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry, 2nd ed. W. H. Freeman, New York. 859 pp.
Solomon, M. E. 1949. The natural control of animal populations. J. Anim. Ecol. 18: 1–35.
Spitze, K. 1985. Functional response of an ambush predator: *Chaoborus americanus* predation on *Daphnia pulex*. Ecology 66: 938–949.
SPSS Inc. 1986. SPSSX user's guide: statistics, 2nd ed. McGraw-Hill, Chicago, Ill. 806 pp.
Taylor, R. J. 1984. Predation. Chapman and Hall, New York. 166 pp.
Thompson, D. J. 1975. Towards a predator-prey model incorporating age-structure: the effects of predator and prey size on the predation of *Daphnia magna* by *Ischnura elegans*. J. Anim. Ecol. 44: 907–916.
———. 1978. Towards a realistic predator-prey model: the effect of temperature on the functional response and life history of the damselfly, *Ischnura elegans*. J. Anim. Ecol. 47: 757–767.
Trexler, J. C., C. E. McCullogh and J. Travis. 1988. How can the functional response best be determined? Oecologia 76: 206–214.
Underwood, A. 1981. Techniques of analysis of variance in experimental marine biology and ecology. Oceanogr. Mar. Biol. Ann. Rev. 19: 513–605.
Valiela, I. 1984. Marine ecological processes. Springer-Verlag, Inc., New York. 545 pp.
Van Engel, W. A. 1958. The blue crab and its fishery in the Chesapeake Bay, Part 1. Reproduction, early development, growth and migration. Comm. Fish. Rev. 20(6): 6–17.
———. 1962. The blue crab and its fishery in the Chesapeake Bay, Part 2. Types of gear for hard crab fishing. Comm. Fish. Rev. 24(9): 1–10.
Virnstein, R. J. 1979. Predation on estuarine infauna: response patterns of component species. Estuaries 2: 69–86.
Virnstein, R. W. 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. Ecology 58: 1199–1217.
Wanink, J. and L. Zwarts. 1985. Does an optimally foraging oystercatcher obey the functional response? Oecologia 67: 98–106.
Whetstone, J. M. and A. G. Eversole. 1978. Predation on hard clams, *Mercenaria mercenaria* by mud crabs, *Panopeus herbstii*. Proc. Natl. Shellfish. Assoc. 68: 42–48.
Williams, A. B. 1984. Shrimps, lobsters, and crabs of the Atlantic Coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, D.C. 550 pp.
Williams, D. A. 1976. Improved likelihood ratio tests for complete contingency tables. Biometrika 63: 33–37.
Williams, F. M. and S. A. Juliano. 1985. Further difficulties in the analysis of functional-response experiments and a resolution. Can. Ent. 117: 631–640.
Zar, J. H. 1984. Biostatistical analysis, 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. 718 pp.

DATE ACCEPTED: June 14, 1989.

ADDRESS: *The College of William and Mary, School of Marine Science, Virginia Institute of Marine Science, Gloucester Point, Virginia 23062.*