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Predator-Prey Dynamics between the Blue Crab: Callineates sapidus Rathbun, and Juvenile Oysters Crassostrea virginica (Gmelin)

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Archives

Predator-prey dynamics between the blue crab, Callinectes sapidus Rathbun, and juvenile oysters Crassostrea virginica (Gmelin)

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Master of Arts

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APPROVAL SHEET

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DEDICATION

To my mother, Jean, for preparing me for success, and in memory of a good friend, my father, Duane.

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ABSTRACT

The functional response, which quantifies the short-term dependence of predator feeding rates on prey density, was used to infer basic mechanisms underlying predator-prey dynamics of a subtidal oyster reef in Chesapeake Bay. Laboratory feeding experiments assessed the relative effects of temperature, oyster length, crab carapace width, and sexual differences in cheliped morphology on the character and intensity of functional responses for blue crabs feeding on juvenile (5-45 mm SL) oysters attached to cultch. The data were fitted to various type II (inversely density-dependent) and type III (density-dependent, sigmoid response) functional response models. Behavioral observations quantified the effects of temperature, oyster length and density on the following functional response subcomponents: total and successful encounter rate, proportional attack success, persistence time in unsuccessful encounters, breaking, eating and handling times in successful encounters. The relative effects of temperature and oyster size-class on prey size-specific profitability, in terms of yield of flesh/handling time, were estimated. A field mark-recapture study assessed the impact of temperature, oyster length and density on total and crab-attributable mortality rates of juvenile oysters at two shell-plant sites in the lower Chesapeake Bay.

Field and laboratory predation rates were positively correlated with prey density and temperature with 14^{o} C being the critical temperature below which predation rates were significantly depressed. Large blue crabs (135-165 mm CW) preying on medium oysters (25 mm SL) exhibited a destabilizing type II response at $26\text{-}27^{o}$ C, and stabilizing type III and "displaced" type II responses at $19\text{-}20^{o}$ C and $13\text{-}14^{o}$ C, respectively. The positive correlation between persistence time and probability of successful encounter suggests that a reduction in persistence times with decreasing temperature is responsible for the partial and total prey refuges observed at the lowest prey density at medium and low temperatures, respectively. Breaking and eating times decreased significantly with temperature, whereas handling time did not. Reliable estimates of profitability were calculated by incorporating persistence times in unsuccessful encounters, and did not vary significantly between 20 and 26^{o} C.

Field and laboratory predation rates were positively correlated with decreasing oyster lengths. Large blue crabs exhibited a type II response when preying on small ($\bar{x}$=15 mm SL), medium ($\bar{x}$=25 mm SL), and large ($\bar{x}$=35 mm SL) oysters. The functional response for small oysters appeared atypical of the "traditional" type II response and was probably a consequence of differential space availability for architectural refuges as a function of increasing within-cultch densities. Persistence times were positively correlated with attack success rates at three oyster size-classes. Breaking and handling times of large oysters were significantly higher and more variable compared to small and medium oyster lengths. Large oysters (>30 mm) may be near the critical size for crushing by large crabs due to increased variability in (a) shell thickness and (b) attachment geometry. Profitability estimates indicated small oysters to be the most profitable in terms of E/Th.

Large and medium (100-125 mm CW) blue crabs preying on large oysters exhibited type II and type III responses, respectively. Small crabs (60-80 mm CW) were unable to feed on large oysters. Decreasing chelal height with carapace width is the probable explanation for the stabilizing effect of decreasing carapace width. All three size-class crabs exhibited a type II response when preying on medium oyster lengths. Medium and small blue crabs exhibited a type III response when preying on small oysters, whereas large crabs exhibited a type II response. Large crabs employed a "random" crushing technique at low prey densities to feed on small oysters attached to depressions on the cultch.

Sex-related differences in the form of the functional response were only apparent for large crabs preying on large oysters, in which males exibited a type II response and females a type III response. Chelal heights of similar-sized male and female crabs were significantly higher for the former. These results suggest that the stabilizing effect observed for large female crabs preying on medium oysters is probably a consequence of sex-related differences in cheliped morphology.

These results suggest potential prey refuges (1) in time at low prey densities, in which blue crab prey persistence times and predation levels are reduced following declining autumn water temperatures, and (2) in space, whereby oysters achieve an architectural refuge by attaching to depressions on the surface of the cultch or attain a size beyond which they are unprofitable prey items, or potential refuges (3) in time and space in which specific oyster lengths achieve a potential refuge in accordance with variations in carapace widths or crab sex (chelae height) of the predator field.

Theoretical implications of results of predator-prey modeling techniques and the applicability of results to oyster enhancement operations are discussed.

PREDATOR-PREY DYNAMICS BETWEEN THE BLUE CRAB *CALLINECTES SAPIDUS* RATHBUN, AND JUVENILE OYSTERS *CRASSOSTREA VIRGINICA* (GMELIN)

INTRODUCTION

Numerous manipulative and mensurative field investigations have yielded novel results concerning the role brachyuran decapod crustaceans play in the regulation and maintenance of local marine bivalve mollusc populations in shallow (< 10 m) unvegetated soft bottom (Virstein 1977, 1979; Holland, et al., 1980, Peterson 1982), deep (10 - 50 m) unvegetated soft bottom (Berge and Valderhauge 1983, Thrush 1986), rocky intertidal (Kitching et al. 1959, Ebling et al. 1964, Seed 1969, Harger 1972, Peterson 1979a), saltmarsh (West and Williams 1986), and seagrass (Young et al. 1976, Young and Young 1978, Heck and Orth 1980, Heck and Thoman 1981, Summerson and Peterson 1984) communities. These studies primarily employed cages to exclude large epibenthic predators such as crabs and fishes from natural densities of infaunal and epifaunal prey. The results for shallow unvegetated soft bottom and rocky intertidal manipulations were typically the same; increased numerical abundance within exclusion cages compared to uncaged controls.

By excluding predators from pier pilings at Barnegat Inlet, New Jersey, Peterson (1979a) found that predation by the blue crab, Callinectes sapidus, the mud crab, Neopanope texana sayi, and the oyster drill, Urosalpinx cinerea, disrupted the competitive monopolization of mid and low intertidal space by the mussel, Mytilus edulis, demonstrating that predation had a direct effect upon temporal and spatial heterogeneity, and supported the rocky intertidal paradigm suggested by previous investigators (reviews Dayton 1971, Connell 1972, Menge 1976, Menge and Lubchenco 1981).

This apparent organizational process is not as clearly demonstrable in unvegetated soft bottom communities owing to uncontrolled artifacts associated with caging (eg., physical, chemical, and biological differences between the caged microenvironment and the natural bottom) which complicate the interpretation of the results (Virstein 1978, Peterson 1979b, Hulberg and Oliver 1980, Dayton and Oliver 1980, Butman 1987). Experiments performed in the Chesapeake Bay (Virnstein 1977) demonstrated significant increases in density for the bivalves, *Mulinia lateralis*, *Mya arenaria*, and *Lyonsia hyalina*, as well as an overall increase in species diversity within two months after exclusion of spot, *Leiostomus xanthurus*, and blue crabs. This study was novel in that it did not reveal the competitive dominant found in rocky intertidal manipulations (review Peterson 1979b, 1982).

In contrast, the physical presence of seagrass blades, roots, and rhizomes has been used to explain the reduced effectiveness of crab predation on local bivalve populations within seagrass communities by releasing the benthos from the usual predatory controls operating in unvegetated sediments (Orth 1977, Peterson 1979b, Blundon and Kennedy 1982b, Orth et al. 1984, Summerson and Peterson 1984). A similar mechanism has been reported as operating within *Spartina alterniflora* communities (Ropes 1968, West and Williams 1986).

Recent field evidence indicates that prey density-dependent mortality mechanisms operate for crab-bivalve predator-prey systems as well (Peterson 1982, Boulding and Hay 1984). Boulding and Hay (1984) found that field mortality rates of littleneck clam, *Protothaca staminea* due to predation by the crab, *Cancer productus* increased with clam density. In a field experiment with *P. staminea* in enclosures, Peterson

(1982) found that the proportion of missing clams appeared to be density-dependent 3 out of 12 times. Although he attributed the loss of these clams partly to emigration of the clams themselves, he found that the missing proportion was significantly reduced (from 33 to 2%) by the presence of complete cages (Peterson 1982).

The great commercial importance of many bivalve species combined with the ecological significance of brachyuran crabs in regulating bivalve community structure is supported by an extensive literature directed towards examining both the feasibility of artificially enhancing natural bivalve numbers via commercial hatchery operations and determining the mechanisms underlying crab-bivalve predator-prey interactions. Early enhancement studies measured the intensity of crab predation on oyster and hard clam beds throughout the East and Gulf Coasts of North America. Lunz (1947), working at Wadmalaw Island, South Carolina, found that over 80 % of young-of-the-year oyster spat (5-30 mm) attached to cement partitions were eaten by C. sapidus during a single season. McDermott and Flower (1952) suggested that the mud crab, Panopeus herbstii was an active predator of one and two year old oysters in New Jersey.

Menzel and Hopkins (1955) estimated the potential destruction to oysters in Louisiana by the stone crab, Menippe mercenaria, while cage experiments demonstrated a mortality rate of 19 spat per day for the blue crab. During blue crab exclusion experiments in Rhode Island, Landers (1954), found that protected outplants of the juvenile hard clam, Mercenaria mercenaria, were reduced from 2000 to 258 individuals in one year following accidental introduction of the mud crab, Neopanope texana (probably N. texana sayi sensu McDermott 1960). Carriker (1959), examining oyster and hard clam culture in salt water ponds on Gardiners Bay, New York, discovered dramatic reduction of hard clam numbers from 3,453 to 18 individuals in just 6 days. Predation was attributed to C. sapidus.

The blue crab and stone crab have been suspected of causing 100 % mortality of hard clams planted in unprotected plots in Georgia and Florida (Menzel and Sims 1962, Godwin 1968). Castagna et al. (1970) suggested that predation by blue crabs is the major constraint in the culture of hard clams on natural bottoms.

Krantz and Chamberlain (1978) observed high oyster spat (3-40 mm) mortalities (79-99%) due to blue crab predation within one month after placement on natural bottom or in trays without closed tops. This experiment demonstrated that cultchless spat may be of little value when planted on natural bottoms.

In attempts to improve the hard clam fishery in South Carolina, Whetstone and Eversole (1978) investigated predation by Panopeus herbstii within protected trays in order to determine some important factors influencing predation. Clam mortalities were found to decrease with increasing clam size and decreasing water temperature. More clam shells were found in the cardiac stomachs of larger crabs than small crabs. The apparent size selection process operating in this system was used to suggest management strategies to effectively reduce predation (Eldridge et al. 1979).

Mechanisms regulating the character and intensity of predation

Recent laboratory feeding studies have focused on the mechanisms responsible for regulating the intensity of bivalve predation as a function of biotic and abiotic factors. These factors have included but are not limited to prey shell size and morphology, prey burial depth, crab size, crab sex and chelae morphology, temperature, substrate type, habitat complexity, prey density, and patch size. These findings have been used to infer distribution and abundance patterns of natural bivalve populations as well as to minimize predation losses during enhancement on natural bottoms.

Prey shell length, morphology, and crab size appear to be the most commonly manipulated factors in laboratory feeding studies (Walne and Dean 1972, Elner and Hughes 1978, Krantz and Chamberlin 1978, Elner and Jamieson 1979, Seed 1980, Hughes and Seed 1981, Whetstone and Eversole 1981, Seed 1982, Elner and Lavoie 1983, Jubb et al. 1983, Arnold 1984, Boulding 1984, apRheinhalt 1986, Bisker and Castagna 1987, Sanchez-Salazar et al. 1987). In general, for a given sized crab there is an optimal prey size at which prey value (energy content/handling time) is at a maximum. This optimal size usually increases with increasing crab size. Laboratory observations of the shore crab, <u>Carcinus</u> <u>meanas</u> feeding on the mussel, <u>Mytilus</u> <u>edulis</u> demonstrated that crabs accept or reject prey items actively according to their value (Elner and Hughes 1978).

Prey acceptance/rejection sequences suggest that foraging crabs have very short term memories which cause suboptimal prey to be rejected at first but accepted if optimal prey are not soon encountered. This flexible mechanism rapidly adjusts the feeding response to small scale changes in prey availability such as would occur in natural mussel beds (Elner and Hughes 1978). It remains uncertain whether <u>Carcinus</u> evaluates mussels by measuring some aspect of size and vulnerability or adopting a certain persistence time (Elner and Hughes 1978, Hughes and Seed 1981).

Jubb et al. (1983) addressed this question with two alternative behavioral hypotheses: "prey evaluation" and "relative stimulus". The prey evaluation hypothesis states that small (1.25 cm standard length, SL) mussels are rejected on the basis of size, gauged during a brief manipulatory period, while medium (2.25 cm SL) and large (2.75 cm SL) mussels are rejected on the basis of strength indicated by their resistence to crushing. The relative stimulus hypothesis states that retention or rejection of a mussel grasped in the chelae depends on the strength of the chelal stimulus relative to stimuli caused simultaneously by other mussels touching the periopods. Both hypotheses assume that prey selectivity increases with decreasing hunger level and that the average food intake is maximized when foraging on natural mussel beds where prey are extremely variable in strength and accessibility (Jubb et al. 1983).

Hughes and Seed (1981) found that _C_. _sapidus_ preferred small (2-2.5 cm SL) over large (3.5-4 cm SL) _Geukensia_ _demissa_ when fed mixed ratios of the two, thereby simultaneously minimizing the time spent handling prey and maximizing the net rate of energy intake. Seed (1982) attributed the bimodality of natural mussel, _Geukensia_ _demissa_ size frequencies within a _Spartina_ marsh, to preferential predation by _C_. _sapidus_ on _Geukensia_ of less than 3 cm SL. Laboratory experiments (Seed 1982) indicated that large mussels (> 3 cm SL) were generally avoided due to their low profitability.

Blundon and Kennedy (1982a,b) used results from field and laboratory examinations of prey refuges in shell structure and burial depth to explain infaunal bivalve species persistence in the Chesapeake Bay. They found that blue crabs ate significantly fewer Mya arenaria buried below 10 cm sediment depths compared to those above 10 cm. Mya reaches its maximum burial depth (25 cm) and size (40 mm) during August following winter and spring settlement pulses (Blundon and Kennedy 1982b). Burial depth combined with siphon extensibility, substrate type, time of settlement, and growth may explain Mya persistence (Blundon and Kennedy 1982b, Lipcius and Hines 1986) despite intense predation levels (Lucy 1976, Holland et al. 1980).

Similar observations have been used to explain the significant correlation of gaping and non-gaping bivalve species with burial depth in nature (Vermeij and Veil 1978, Boulding 1984, Haddon et al. 1987). Boulding (1984) examined the vulnerability of four burrowing clam morphs to shell-breaking predation by the cancrid crab, Cancer productus. She 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 large size, 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).

Crab feeding rates have been shown to dramatically increase with increased water temperatures (Landers 1954, Walne and Dean 1972, Wallace 1973, Elner 1980, Whetstone and Eversole 1981, Gibbons 1984, Sanchez-Salazar et al. 1987). Consumption rates of C. maenus feeding on cockels, Cerastoderma edule, increased ca. 1.7 fold between 6.0 and 9.5^{0} C for a Q_{10} of 6.4, and ca. 3.5 fold between 9.5 and 15.5^{0} C giving a

Q_{10} of 5.2 (Sanchez-Salazar et al. 1987). Elner (1980) indicated that although temperature greatly increased C. maenus feeding rates on mussels, it appeared to have no effect on preferred mussel size.

The majority of laboratory studies, in which predator sex is stated, have used only male crabs in order to avoid potential bias associated with sexual differences in feeding behavior and cheliped morphology (Elner and Hughes 1978, Seed 1980, Hughes and Seed 1981, Blundon and Kennedy 1982b, Seed 1982, Jubb et al. 1983, Arnold 1984, Bisker and Castagna 1986, Lipcius and Hines 1986). In the male shore crab, for example, the major chelae is larger and more robust and serves to crush prey, while the cutter, or small pincher chelae is longer, thinner and acts to hold and manipulate prey (Elner 1980, apRheinalt and Hughes 1985). These differences are much less marked in female shore crabs where both chelae are more cutter like (Elner 1980).

Laboratory examinations of crab feeding rates as a function of sexually dimorphic chelae have yielded different results depending on the crab species examined. Elner (1980) found that the prey preference pattern in female shore crabs was as well defined as in males, although prey sizes preferred by females were smaller than those of equivalent males. Female Carcinus have smaller chelae than males, yet when preferred prey size was expressed as a function of major chelae height there were no significant differences in foraging behavior (Elner 1980).

In contrast, no discernible sexual differences existed in prey size selection or mean predation rates, even without chelae height adjustments, for the rock crab, Cancer irroratus, and the mud crab, Neopanope sayi, feeding on attached oysters (Elner and Lavoie 1983).

Using a slightly different approach, Blundon and Kennedy (1982a) found that there were no sexual differences in mechanical advantage of grip strength for blue crabs, although crusher claws of both sexes had significantly greater mechanical advantage and strength than cutter claws.

Early studies implied a relationship between sediment composition and the intensity of predation on hard clam populations (Carriker 1956, Walne and Dean 1972). Recent laboratory studies have examined the mechanisms responsible for such regulation in light of both commercial enhancement operations (Castagna et al. 1970, Kraeuter and Castagna 1977, Arnold 1984) and species persistence in nature (Lipcius and Hines 1986). Arnold (1984) indicated that hard clams, M. mercenaria, were more vulnerable to predation by blue crabs in sand and sand/mud than in oyster shell or gravel substrates. He suggested that use of a fine gravel substrate would enhance the commercial exploitation of hard clams by minimzing losses due to blue crab predation (Arnold 1984). Lipcius and Hines (1986) demonstrated increased blue crab consumption rates of the soft clam, Mya arenaria in mud substrates compared to sand.

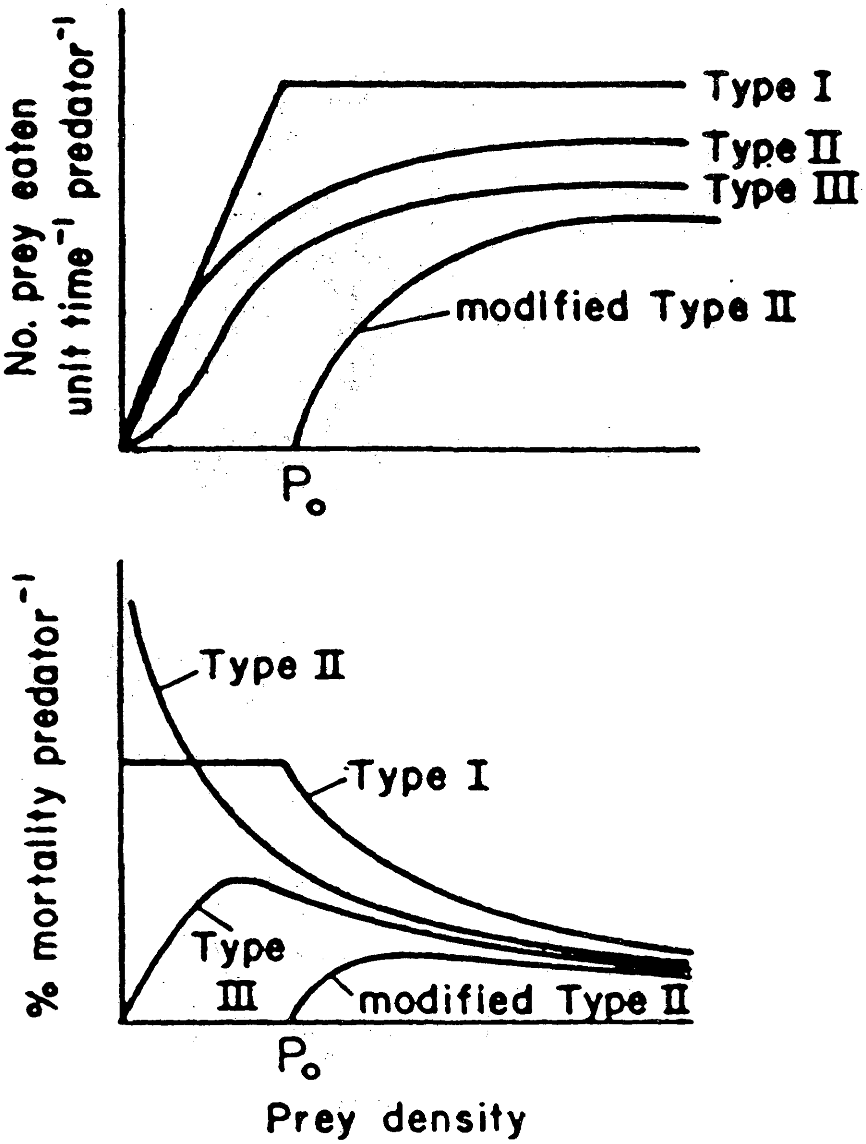
The previous examples have described the importance of crab predation in regulating bivalve community structure, distribution and diversity, and have illustrated partial prey refuges based on prey characteristics (eg. shell length, shell morphology, burial depth, etc.) and abiotic factors (eg. substrate type and temperature). Despite this extensive literature, very little is known about the effect brachyuran decapod predators have on the population dynamics of bivalve communities. For example, crab predation may drive some communities locally extinct, or allow coexistence. Previous experiments demonstrated that blue crabs exhibit both a theoretically stabilizing (eg., type III response) and destabilizing response (eg., type II response) to low prey densities in sand and mud substrates respectively. This lowered risk of mortality in sand may help to explain Mya arenaria persistence in the upper Chesapeake Bay despite intense blue crab predation levels (Lipcius and Hines 1986). With the exception of one previous study (Lipcius and Hines 1986), it is not known whether brachyuran predators tend to stabilize or destabilize bivalve prey dynamics.

Functional response models

The functional response, which describes the short-term dependence of the predators feeding rate on prey density (Solomon 1949, Holling 1959, 1965), can be used to infer basic mechanisms underlying predator-prey dynamics (Hassell 1978). Functional responses have traditionally been classified into four general types (Fig. 1) (Hassell 1978, Valiela 1984). The type I response is characteristic of aquatic filter-feeding invertebrates in which consumption rates increase linearly with prey density until satiation is reached (Frost 1972, Valiela 1984). Satiation occurs because the predator cannot handle prey any faster; hence ingestion remains constant despite increasing prey density (Valiela 1984).

Consumption rates for the type II response rise at a decelerating rate with increasing prey density to an upper asymptote, reflecting increased costs or constraints associated with increased consumption

Figure 1. Shape of hypothetical functional response curves (top) and the percent mortality expected per predator by each type of functional response (bottom). Adapted from Valiela (1984).


No. prey eaten
unit time⁻¹ predator⁻¹
Type I
Type II
Type III
modified Type II
P₀
% mortality predator⁻¹
Type II
Type I
Type
III
modified Type II
P₀
Prey density

rates (Valiela 1984). The type II response is typical of invertebrates due to their limited learning capacity (Hassell 1978), in which either the mechanism of prey capture becomes increasingly inefficient or the motivation for increased consumption may be reduced, as prey density increases (Valiela 1984).

Parsons et al. (1967, 1969) demonstrated a "modified" type II response for zooplankton feeding on varying concentrations of phytoplankton in which a feeding threshold was reached, below which no feeding took place. Inclusion of a hypothetical feeding threshold in a type II response could provide a mechanism for recovery of a depleted prey population.

Recently, Hassell et al. (1977) identified several examples of a type III response in invertebrates. The type III response is sigmoid, demonstrating density-dependent acceleration in consumption rates at low prey densities. The acceleration in feeding rates could result from an increase in predator efficiency in the detection and/or capture of prey as prey density increases (Holling 1965, Real 1979). This response is most common in vertebrates due to their ability to "learn" (Hassell 1978). The initial accelerating portion of the type III response has considerable theoretical implications because of its possible role in the maintenance of ecosystem stability (Nunney 1980, Abrams and Allison 1982) and in the regulation of prey populations by predators (Holling 1959, 1965; Murdoch and Oaten 1975).

The key difference between the type II and type III responses is that in the type II response, the risk of mortality increases with decreasing prey density, whereas in a type III response, there is a change from an increasing to decreasing risk of mortality as prey density diminishes to a low level (Lipcius and Hines 1986). Theoretically, a type II response is destabilizing to predator-prey dynamics (Hassell and May 1973) due to increased mortality with decreasing prey density (Holling 1959, Murdoch and Oaten 1975) while a type III response imparts stability at low prey densities in deterministic models (Hassell 1978) and limits population bounds and fluctuations in stochastic models (Murdoch 1979).

These conceptual functional response models can be grouped into continuous-time (Holling 1959, Hassell 1978) and discrete-time models (Royama 1971, Rogers 1972, Hassell et al. 1977, Hassell 1978). Contiuous-time models relate the number of successful and unsuccessful encounters with prey (Ne) as a function of prey density (Hassell 1978). Discrete-time models relate the number of prey eaten (Na) to prey density (Hassell 1978). The most widely discussed and elementary model from which more complex models are derived is Holling's (1959) "disc-equation":

$$Ne = \frac{a' * T * Nt}{1 + (a' * Th * Nt)} \qquad (1)$$

which states that the number of prey encountered (Ne) per predator is equal to the product of the instantaneous attack rate (a'), total time available for foraging (T), and the number of prey available (Nt), divided by 1 + the product of a', Nt, and prey handling time (Th). Holling's equation is a deterministic continuous-time model which describes a type II response. It assumes constant prey handling times for all prey items and a fixed probability of prey encounter, thereby not allowing for prey depletion. Continuous-time models best describe those feeding periods through which density remains nearly constant (Hassell 1978). Continous-time type III models account for variations in search rate (a') with density by substituting constants (b,c) for a' in equation 1 thus, yielding equation 2 (Hassell 1978):

$$Ne = \frac{b * T * Nt^2}{1 + (c * Nt) + (b * Th * Nt^2)} \qquad (2).$$

Discrete-time models integrate the instantaneous predation rate over the duration of the experiment (T), assuming an exponential decay in prey density, and are therefore appropriate for long-term "closed-system" experiments in which prey are not replaced as eaten. This model, commonly known as the "random predator" equation (Royama 1971, Rogers 1972), describes a type II response:

$$Na = Nt \; [1 - e^{-a'(T-Th*Na)}] \qquad (3)$$

where, Na is the number of prey eaten. The type III discrete-time model is obtained by again substituting constants (b,c) for a' yielding equation 4 (Hassell et al. 1977):

$$Na = Nt \; \{1 - e[\frac{- b * Nt}{1 + c * Nt} \; (T - Th * Na)]\} \qquad (4).$$

These general models have been developed in order to characterize a specific response as well as estimate biologically meaningful parameters. In order to understand the relationships between environmental factors and predator-prey dynamics, the form of the functional response must be specified for predator-prey systems (Murdoch et al. 1984, Lipcius and Hines 1986).

Behavioral components: functional response and optimization models

Handling time (Th) and the instantaneous attack rate (a') are central components of both functional response and optimization models, and influence the character and intensity of predation. Handling time (Th) is defined as 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 the encounter success of with prey in type II models, and, when b and c are substituted for a' in type III models, accounts for the dependence of search rate upon prey density (Hassell 1978). Hence, a' can be used to determine the comparative vulnerability of different prey types. A fundamental difference between the two responses is the tendency for a' to increase over an initial range of low prey densities in a type III response, and remain constant at low prey densities in a type II response (Hassell et al. 1977).

Optimization models attempt to predict the foraging strategies of predators which maximize the energy gained per unit time (Pyke et al. 1977, Krebs 1978, Hughes 1980, Pyke 1984). The major underlying assumptions are that an animals fitness is a function of foraging efficiency, usually measured in terms of energy (Schoener 1971), and that natural selection has resulted in animals that forage so as to maximize their net rate of energy intake (Pyke et al. 1977, Hughes 1980).

This energy maximization premise has frequently been used as a theoretical tool in describing the mechanisms underlying potential stabilizing properties of predator-prey systems. It is divided in its most simple form into foragers of two classes: time minimizers and energy maximizers (Hughes 1980). Time minimizers are animals that have a fixed energy requirement and require time to perform other activities; therefore they should maximize their fitness by minimizing the time spent acquiring energy. In contrast, energy maximizers are limited by a fixed amount of foraging time and should maximize energy intake in the time available.

Numerous laboratory investigations on the size selection of molluscs by crabs have contributed to the development and empirical testing of predictions based on energy maximization premises (Elner and Hughes 1978, Hughes 1979, Hughes and Elner 1979, Hughes and Seed 1981, Blundon and Kennedy 1982a, Jubb et al. 1983, Arnold 1984, Lawton and Hughes 1985). It still remains uncertain, however, whether crabs forage optimally, and if so whether they evaluate bivalve mollusc prey by measuring some aspect of size and vulnerability (passive mechanical mechanism) or adopt a certain persistence time (active behavioral mechanism).

Optimization models predict that mean handling time should increase with decreasing prey densities (Giller 1980), whereas functional response models assume a constant Th (Hassell 1978). The handling time of individual prey can, however, differ substantially with varying biotic factors such as prey type, foraging tactic and predator hunger level (Valiela 1984). Several other biotic factors have been shown to mediate the instantaneous attack rate (a'): (1) relative mobility of predator and prey, (2) the size of the perceptual field of the predator relative to the density and size of prey and, (3) the ability of the prey to inhibit predation (Valiela 1984). Abiotic factors such as temperature can be important in determining the intensity of functional responses. For example, consumption rates may increase with temperature, because warm temperatures allow faster movement of invertebrate poikilotherms leading to reduced handling times (Valiela 1984). This in turn facilitates a fast attack rate and concurrent increase in the functional response to prey density (Valiela 1984). Thus, parameter estimates from functional response models combined with empirically derived behavioral observations can be a valuable tool in the study of complex factor interactions for invertebrate predator-prey systems.

Recently, the form of the functional response has been shown to be dependent not only on prey density, but also on the relative distribution of predator and prey in time (Collins et al. 1981) and space (Kaiser 1983, de Lafontaine and Leggett 1987), habitat heterogeneity (Kaiser 1983, Folsom and Collins 1984, Lipcius and Hines 1986) and learning (Landenberger 1968, Draulans 1987). An understanding of how various biotic and abiotic factors affect a predator’s functional response within a given habitat, is of fundamental importance in interpreting the behavior and ecology of predator and prey (Real 1979).

The main and interactive effects of varying biotic and abiotic factors to density dependent mortality are relatively unexplored with respect to crab-bivalve predator-prey dynamics. In particular, only three studies (eg., Walne and Dean 1972, Boulding and Hay 1984, Lipcius and Hines 1986) have examined density-dependent mortality processes for crab-bivalve systems, and no reasearch has been performed on the effects of various factors (eg., temperature, prey size, predator size and sex) upon the functional response of C. sapidus feeding on C. virginica. In addition, the crowding effects of oyster spat attached to cultch may have an important bearing on the rate of crab predation (McDermott 1960). Of the relatively few studies that have examined crab predation on the oyster, Crassostrea virginica, under laboratory conditions (McDermott 1960, Krantz and Chamberlain 1978, Elner and Lavoie 1983, Bisker and Castagna 1987), only one has observed blue crab predation on oyster-shell cultch (Krantz and Chamberlain 1978), whereas others have used single-spat oysters obtained using hatchery techniques (Krantz and Chamberlain 1978, Bisker and Castagna 1987).

Field investigations of crab predation on oysters have assessed mortality rates of hatchery-reared cultchless oysters (Krantz and Chamberlain 1978), or spat attached to cement partitions (Lunz 1947) without taking into account the effects of varying biotic and abiotic factors. Natural within-cultch densities in field experiments may also affect juvenile survivorship in a manner yet to be determined.

In addition, very few studies have statistically tested the form of the functional response, nor the fit of continuous or discrete-time models.

The aim of the present study is to (1) investigate the effects of various biotic and abiotic factors on the character and intensity of functional responses for the blue crab, Callinectes sapidus, feeding on the oyster, Crassostrea virginica, attached to oyster shell cultch under laboratory conditions, (2) statistically test the form of the functional response and the fit of continuous and discrete-time models, (3) quantify the relative influence of crab predation upon seasonal field levels of oyster mortality for a subtidal oyster community and, (4) to infer the basic mechanisms underlying predator-prey dynamics of a subtidal oyster reef in the lower Chesapeake Bay based on field and laboratory results. More specifically this study addresses the following objectives:

1. Quantification of the level of oyster spat mortality due to blue crab predation under laboratory conditions.
2. Description of blue crab foraging behavior when preying on juvenile oysters.
3. Measurement of the relationship between prey density, feeding rates, and number of spat consumed (functional response).
4. Determination of the functional response for size specific predator-prey combinations.
5. Evaluation of the existence of a prey-size refuge within a given size range of blue crab.
6. Comparison of the effects of varying crab-size and oyster length on functional responses of male and female blue crabs.
7. Evaluation of differences in crusher chelal heights between large male and female crabs.
8. Quantification of the seasonal variation in blue crab functional responses under laboratory conditions.
9. Measurement of the effects of temperature, prey density, and prey size on total and successful encounter rates, prey handling times (Tb /Te) for successful encounters, persistence

times (Tp) for unsuccessful encounters, instantaneous attack rates (a'), and proportional attack success (S).

10. Comparison of observed prey specific Ht and a' with estimated values from predator equations.
11. Examinations of predictions based on optimal foraging premises by determining if mean handling times increase with decreasing prey densities.
12. Estimation of prey size profitability and generation of profitability curves based on breaking and handling times in successful encounters, and mean persistence times in unsuccessful encounters, as a function of temperature and oyster length.
13. Quantification of seasonal predation rates by xanthid and blue crabs on young-of-the-year oysters at VMRC and private shell-planting sites, Milford Haven, Piankatank River Estuary, Virginia.
14. Comparison of field and laboratory generated feeding rate data as a function of prey density, oyster length and water temperature.

METHODS AND MATERIALS

Experimental design for functional response model assumptions

The following elements of design, taken from Houck and Strauss (1985), are sufficient to satisfy simultaneously the assumptions of

Holling's model and provide adequate resolution of functional response curves to allow for quantitative comparison.

1) Total time of exposure of the predator to the prey should be held constant within trials and across all experimental densities tested. The exposure time per trial must be long enough to test fully the feeding response of the predator but short enough to preclude the possibility of satiation.

2) Either prey density, the size and shape of the experimental arena, or both of these factors should be held constant across all trials.

3) Careful choice at low prey densities will allow for a more accurate definition of the curve because the hyperbolic function has an initially steep rise that gradually decreses to near-zero. A few prey densities chosen at the higher end of the density scale will allow an accurate estimation of the predators maximum feeding rate.

4) All predators should be consistently exposed to some standardized set of pre-trial conditions, and individual predators should be tested only once to avoid secondary experimental conditioning and allow for independence of experimental trials.

5) Appropriate statistical procedures reflecting the design should be used to fit the model to the data.

6) Parameter values determined empirically (eg. observed encounter rates and handling times) may subsequently be compared with estimates derived from fitting the model. Some effort should be made to determine whether these values differ with prey density. If so, discrete-time models may provide a better statistical fit and interpretation.

Laboratory experimental animals and procedures

The blue crab, Callinectes sapidus Rathbun (Arthropoda: Crustacea: Portunidae) is a large (up to 200 mm carapace width) epibenthic omnivore found throughout diverse habitats along the East and Gulf Coasts of North America (Van Engel 1958, 1962; Williams 1984). The feeding ecology of Callinectes has been the the focus of several recent studies (Odum and Heald 1972, Laughlin 1982, Alexander 1986) which indicate a variety of principle food items including bivalve molluscs, fish, small benthic infauna, algae, vascular plants and conspecifics. Bivalve molluscs have been shown to form a major component of the diet (Laughlin 1982, Alexander 1986). In the Chesapeake Bay, Callinectes is abundant and actively forages from late spring through autumn, after which it overwinters buried in subtidal areas (Van Engel 1958, Hines et al. 1986).

The oyster, Crassostrea virginica Gmelin (Mollusca: Pelecypoda: Ostreidae), is an epibenthic suspension feeding bivalve mollusc of considerable commercial importance along the Atlantic and Gulf Coasts of North America. In Chesapeake Bay, Crassostrea may grow up to 18 cm in length and is found primarily on subtidal (1.5-7 m) bars composed of shelly mud (Haven et al. 1981). Spawning usually occurs from late June to October. After larval attachment on suitable cultch materials (eg., oyster shell) oysters may attain a length of 40 mm SL before the end of autumn (Kennedy and Briesch 1981, personal observation). Density of spat may range from 1 to 30 spat per 10 cm oyster shell at this time (Kennedy and Briesch 1981, personal observation).

Laboratory feeding studies were performed at the Virginia Institute of Marine Science (VIMS), Gloucester Point, Virginia, from July-December

1986 and April-October 1987. Experiments used crabs captured with either pots suspended from the "oyster pier" at VIMS or by otter trawl in seagrass beds in the lower York River Estuary, Virginia. Only intermolt crabs that actively fed were used in feeding trials. Crabs appeared to go through a learning process (preliminary observations) and were therefore fed oyster spat ad libitum for one week prior to feeding trials. Size ranges, grouped by maximum carapace width (between the prominent spines) were assigned as follows: small (60-85 mm), medium (100-125 mm), and large (135-165 mm).

Juvenile oysters, which ranged from 5-45 mm SL, were collected by SCUBA divers from Virginia Marine Resource Commission (VMRC) and private shell planting sites, Milford Haven, Piankatank River Estuary, Virginia. Oyster spat attached to cultch as collected in the field were classified as either medium ($\bar{x}$ = 25.0 ± 2 mm SL) or large ($\bar{x}$ = 35.0 ± 2 mm SL). A third small size-class ($\bar{x}$ = 15.0 ± 2 mm SL) was collected from remote setting operations in the East River, Virginia. These spat were attached to oyster shell cultch and demonstrated the same within-cultch densities observed on Milford Haven cultch (4-30 oysters/cultch) (Bohn, personal communication; personal observation). The increased growth rate of small oysters relative to large individuals did not facilitate their use in laboratory experiments. The use of remotely set oysters, however, allowed an adequate supply of small oysters for completion of the study objectives.

A flow-through seawater system was used in which the seasonal changes in temperature was the physical variable influencing predation rates. Three water temperatures were chosen which approximated early spring and late fall (13-14° C), early summer and fall (19-20° C), and summer (26-27° C) and were termed low, medium, and high respectively. Ambient salinity of York River water ranged from 16-23 ppt.

There were two water tables, each containing six opaque experimental tanks measuring 60cm X 55cm X 25cm (72 liters). Each tank was filled with ground oyster shell to a level 8cm above the tank bottom. One water table was used for feeding trials and the second for holding crabs. This layout allowed six concurrent feeding trials and randomized interspersion of oyster density treatments (Underwood 1981, Hurlbert 1984) such that each crab was exposed to a specific density only once.

Influent water was filtered to 50 microns in order to minimize the accumulation of fouling organisms. During periods of high plankton density and particulate concentrations (summer months) filters were changed every 8-12 hours in order to maintain adequate filtration. Influent flowed to a 200 l header tank where it was heated, as desired, by two 2,000 watt Vycor immersion heaters. Crabs were gradually acclimated to experimental temperatures. Twenty-four delivery tubes (2 per aquaria) with a flow rate of 0.5 liter/min/tube provided 90% flushing every 2.5 hours according to Rainey's (1967) guidelines. Artificial lights were regulated to seasonal photoperiod: 26-27° C, 14L-10D; 19-20° C, 13L-11D; and 13-14° C, 12L-12D.

Crabs were starved for 24 hours before each replicate trial in order to standardize hunger levels. Cultch and/or oysters were scattered onto the bottom of the tank and the overall spatial arrangement noted. Oysters and/or cultch were cleaned by "dipping" in a concentrated salt solution (Provenzano 1959) in order to eliminate additional prey items. Feeding trials were typically initiated at 1300 hours when a single Callinectes was introduced into a tank, and ended upon removal of the crab 24 h later. Six to eighteen replicates at densities of 5, 10, 20, 30, 40, and 50 oysters/tank were taken for medium and large oyster lengths. Due to increased feeding rates at small oyster lengths, 6-10 replicates at 10, 20, 40, 80, 120, 250 and 350 oysters/tank were required in order to assess the functional response. Temperature was recorded at the initiation and termination of each 24 h experimental period. Following each experimental trial the numbers eaten were recorded.

The significance of addressing the complexities of biotic and abiotic interactions within multifactorial laboratory and field experiments of predation has been described by numerous experimental marine ecologists (Menge and Lubchenco 1981, Underwood 1981, Choat 1982, Peterson 1982, Menge 1983). Due to logistical constraints, however, the use of a full factorial design in this study was not permitted. Hence, the relative effect of a single factor (eg., temperature) on the functional response was assessed within separate density experiments. Therefore, I have refrained from direct statistical comparisons of the various factor interactions in order to avoid "simple pseudoreplication" (sensu Hurlbert 1984).

A summary matrix of biotic and abiotic factors examined in the laboratory is shown by Table 1. In order to examine the relative effects of each factor on the functional response, density experiments were compared by:

Table 1. Summary Matrix Of Laboratory Experiments Performed

		Temp. Low	Temp. Med	Temp. High		
Spat Size		Med	Med	Lg	Med	Small
Crab Sex	Crab Size					
Male	Large	☐	☐	☐	☐	☐
	Medium			☐	☐	☐
	Small			☐	☐	☐
Female	Large			☐	☐	
	Medium			☐		

(1) Temperature - large male crabs feeding on medium length oysters at low, medium and high temperatures.

(2) Oyster length - large male crabs feeding on small, medium and large oysters.

(3) Crab size - large, medium and small male crabs exposed to small, medium and large oysters.

(4) Crab sex - large male and female crabs exposed to large and medium oysters. Medium male and female crabs exposed to large oysters.

General analysis of functional responses

Two independent variables were quantified:

(1) Consumption rate - the number of oysters consumed * crab^{-1} * $[24\ \text{h}]^{-1}$.

(2) Proportional mortality rate - the proportion of oysters consumed * crab * $[24\ \text{h}]^{-1}$.

All dependent variables in this study were examined for normality with normal and stem-leaf plots, and tested for equality of variances with Cochran's C-Test (Zar 1984, SPSSX 1986). Proportions were used to allow for a more accurate definition of the shape (type) of the functional response curve at low prey densities (Lipcius and Hines 1986). When appropriate, a oneway ANOVA (Zar 1984) with density as the independent variable was used. When transformations were unsuccessful, a non-parametric Kruskal-Wallis ANOVA was employed (Zar 1984). Multiple comparisons were performed by using an *a priori* Student-Newman-Kuels Test (SNK) or non-parametric Mann-Whitney Test (M-W) set at an experiment-wise error rate (EWER) of 0.05 (Zar 1984). For all statistical tests, the null hypothesis of no effect was rejected at $P \leq 0.05$.

Individual crab functional responses within each density experiment were tested with a non-parametric log likelihood ratio, G, applying Williams (1976) correction for continuity. A Hiloglinear model (SPSSX 1986) was used to generate expected distributions and to provide the appropriate contrasts.

Analysis of general functional response models

In order to statistically 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, Lipcius and Hines 1986), I used the general functional response model derived by Real (1977, 1979):

$$F = \frac{kA^n}{X + A^n} \qquad (5),$$

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. Thus, n is roughly equivalent to the amount of "learning" exhibited by the predator (Real 1979, Emlen 1984). When $\hat{n} = 0$, the functional response curve becomes linear (eg., type I). When $\hat{n} = 1$, the rate of detection is constant producing a type II hyperbolic functional response (Real 1979). The degree to which $\hat{n} > 1$ reflects the rate that detection is influenced by increasing prey density (Real 1979). Therefore, when $n > 1$ the curve is type III (sigmoid) (Real 1979). In order to statistically test the form of functional response, estimates of $\hat{n}$ were tested against the following null hypotheses with standard t-Tests (Neter and Wasserman 1974): Ho: $\hat{n} = 0$, $\hat{n} = 1$, $\hat{n} = 2$.

The general functional response models were analyzed by linear regressions of the log-transformation of Eq. 5 (Real 1979, Lipcius and Hines 1986), and tested for appropriate fit as determined by the following criterea: (1) the F-value of the regression had to be significant at the 0.05 level and, (2) the residuals about the predicted values had to be distributed randomly, as determined by binomial Z-Tests (Zar 1984) of the partial and complete data sets. Partial binomial tests were performed in order to avoid the effects of systematic end distributions cancelling each other out in the complete test (Lipcius and Hines 1986). Hartley's F-Max procedure (Neter and Wasserman 1974) assessed the validity of linearization by testing the assumption of homogeneity of variance of the transformed dependent variable.

Determination of the type of functional response (eg., type II or III) was based on (1) results from the ANOVA of proportional mortality rates, followed in decreasing priority by (2) results from general functional response model fitting procedures.

Analysis of conceptual functional response models

Partial consumption of oysters was not observed in any experiment, thereby precluding the need for nontraditional functional response models (Abrams 1982) developed to account for "wasteful killing" (Johnson et al. 1975).

In order to estimate a' and Ht, and fit the data to the appropriate functional response model (Eqs. 1-4), non-linear least squares analysis (SAS Institute, 1982) was employed. The use of linearized functional response models has been shown to yield biased and statistically invalid parameter estimates (Zar 1968, Hassell 1978, Williams and Juliano 1985). Marquart's (1963) algorithm method, with specified partial derivatives, allows estimation of asymptotic standard errors and correlations of parameters, and was thereby used to analyze continous-time models (Williams and Juliano 1985). Analysis 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 (Na) on both sides of the equation (Eqs. 3, 4).

To provide a statistical test of the fit of continuous and discrete-time models in describing the functional response, an F-Test employing the ratio of the "lack-of-fit" mean square to the "pure error" mean square was used (Draper and Smith 1966, Neter and Wassermen 1974, Colton 1987). The "pure error" term is an unbiased estimator of the error variance and does not rely on assumptions regarding the regression relation (Neter and Wassermen 1974). The "lack-of-fit" and "pure error" sums of squares were calculated by comparing predicted responses with observed cell means obtained from nonlinear regression analysis described above. A significant F-ratio indicated a statistically inadequate fit to the data and therefore inappropriate model.

The criteria for determining the most appropriate and statistically valid conceptual functional response model, listed in decreasing priority, were as follows:

(1) The F-value of the regression had to be significant at the 0.05 level.

(2) The "lack-of-fit" error could not be significant at the 0.05 level.

(3) The residual sums of squares had to be the lowest of the possible models.

(4) The residuals about the predicted values had to be distributed randomly for partial and complete data sets.

To compare instantaneous attack rates (a') between type II and type III models, I approximated a' from an equation derived by Hassell et al. (1977):

$$a' = \frac{bNt}{1 + cNt} \qquad (6)$$

where b and c are constants and Nt = prey density. To calculate the way in which the attack rate (a') was related to prey density, I inserted the predicted Th, Na and/or Ne from nonlinear regression analysis, along with the specific Nt, and solved for a' using the appropriate model (Eqs. 1-4).

Behavioral observations

Behavioral observations were made during the first hour of each feeding trial by viewing crabs through portholes in an opaque plastic canopy surrounding the water table. Crabs were viewed during the first hour of each feeding trial in order to avoid possible satiation effects which can reduce success rates and increase handling times (Bence and Murdoch 1986). Optimal diet theory assumes that the predator is maximizing its food intake, and starved crabs most closely match this assumption. Observations were performed on two adjacent tanks during concurrent feeding trials and were recorded with a hand held audio cassette recorder.

The following independent variables were quantified: (1) breaking time (Tb), which is the time from the crab's first physical contact with the oyster, through the period of recognition and shell crushing, to the first bite of exposed flesh; (2) eating time (Te), which is defined as the period from the end of Tb to the completion of the meal and abandonment of the empty shell, including intermittent periods of shell breakage and inspection of shell debris towards the end of the meal; (3) handling time (Th), which is the sum of Tb and Te; (4) persistence time (Tp), which is the time from the moment the crab actively encounters the prey (eg. manipulation of the prey with the chelae) until rejection, (5) total encounter rate, which is the number of active encounters, (6) successful encounter rate, which is the total number of encounters that resulted in feeding and, (7) attack success (S), which is the proportion of active encounters resulting in consumption. All behavioral components were matched with the appropriate oyster length, except for total and successful encounter rates. The short duration (1-2 s) of numerous encounters did not allow adequate determination of prey-specific length.

Qualitative observations recorded the following behaviors: a) initiation of foraging, b) oyster breaking methods and, c) eating techniques. Behavioral observations were only quantified for large male

Callinectes within temperature and oyster length treatments at densities of 5, 20, and 50 oysters/tank for medium and large oysters, and at 20, 40, 120 and 250 oysters/tank for small oysters. The overall spatial arrangement of the cultch was noted upon termination of the trial.

General analysis of behavioral observations

Total and successful encounter rates for each density experiment were analyzed using a oneway ANOVA (Zar 1984) with density as the independent variable (SPSSX 1986). Breaking (Tb), eating (Te) and handling times (Th) in successful encounters, and persistence times (Tp) in unsuccessful encounters were analyzed by an analysis of covariance (ANCOVA) with oyster length as the covariate and oyster density as the independent variable. The assumption of equal slopes (Underwood 1981) was met if the density X oyster length interaction was not significant (SPSSX 1986). In instances where there was a nonlinear relationship between oyster length and density, a oneway ANOVA was employed (Underwood 1981, SPSSX 1986).

Tb, Te and Th were normally distributed and homoscedastic for the entire data set (normal plot and Cochran's C-Test, SPSSX 1986). Additionally, the density X oyster length interaction was not significant for the entire data set, thus the assumption of equal slopes was met.

Prey profitability

Prey value was estimated by drying oyster spat of known length (5-45 mm SL) to a constant weight at 60° C for 24 h, enabling a regression equation of dry flesh weight (mg) on shell length (mm SL) to be calculated. Yield of flesh was related to C. virginica length by the regression equation $Y = 2.27\ x - 3.02$, $n = 67$, $r^2 = 0.82$, where y = log (dry flesh weight, mg) and $x = \log_e$(shell length, mm). Prey profitability was then calculated in two ways. First, the profitabilities for each of three oyster size classes were estimated as dry weight (mg)/breaking time (sec) and dry weight (mg)/handling time (sec) for successful encounters (a'). The second method incorporated persistence times in unsuccessful encounters by the following equation:

$$P = \frac{M}{f\ Tp + Th} \qquad (7)$$

where M = dry weight (mg) per individual prey item, f = proportion of unsuccessful encounters (eg., 1-S), Tp = average persistence time per failed attack, and Th = average handling time per successful attack. Thus, profitability estimated by this second method is a more reliable estimator of the total energetic cost associated with a specific oyster length because it depends upon success rates (S), handling times for successful and unsuccessful encounters, and the biomass of the prey.

To determine the best fit to Tb, Te and Th data for subsequent profitability computations, initial regression analysis involved determining the fit of linear, exponential and power functions to observations from each temperature and oyster length treatment. Differences between the correlation coefficients of these functions were compared using Fisher's transformation (Zar 1984). Fisher's transformation indicated that exponential and power functions did not significantly improve the fit to either Tb, Te, or Th data over linear functions for both temperature (all P>0.25) and oyster length (all P>0.19) treatments. Hence, profitability curves were derived by dividing the regression equation for dry flesh weight on shell length by linear regression functions for each dependent variable (Tb, Te, Th).

To determine if linear regression functions used in profitability estimates (eg., Tb, Te, Th) varied significantly as a function of temperature and oyster length, slopes and elevations were compared using standard t-Tests (temperature effects) and an ANCOVA (oyster length effects) (Zar, 1984).

Statistical analysis within specific factors:

Temperature

At 26-27° C, logarithmically (log) transformed consumption rates, arcsine transformed proportions, and log-transformed persistence times (Tp) were homoscedastic. At 19-20° C, consumption rates, arcsine transformed proportions and log transformed Tp resulted in homoscedasticity. Consumption rates at 13-14° C were also homoscedastic. Despite the use of several common transformations (ln, log, sqrt, arcsine), proportional mortality rates at 13-14° C remained heteroscedastic. Log transformation of Tp at 13-14° C resulted in homoscedasticity.

Oyster length

Consumption rates, arcsine transformed proportions, and log transformed Tp for large oysters were homoscedastic. For medium oysters, log-transformed consumption rates and Tp, as well as the arcsine transformed proportions were homoscedastic. For small oysters, proportions, Tp and log transformed consumption rates were homoscedastic.

Crab size

Consumption rates and arcsine-transformed proportions for large crabs feeding on large oysters were homoscedastic. For medium crabs feeding on large oysters, log transformed consumption rates and arcsine transformed proportions were homoscedastic.

Log transformations of consumption rates of large, medium and small crabs feeding on medium oysters resulted in homoscedasticity. For large and medium crabs, the arcsine transformed proportions were homoscedastic.

Log transformation of consumption rates for large, medium and small crabs feeding on small oysters resulted in homoscedasticity. Arcsine transformation of proportional mortality rates for small crabs, and the raw proportions for medium and large crabs feeding on small oysters were homoscedastic.

Crab sex

For large male and female crabs feeding on large oysters, consumption rate and log-transformed consumption rate variances were homogeneous, respectively. The arcsine-transformed proportions were homoscedastic for both sexes.

For large male and female crabs feeding on medium oysters, log transformed consumption rates as well as the raw numbers were homoscedastic, respectively. Arcsine transformed proportions were homoscedastic for both sexes.

For medium male and female crabs feeding on large oysters, log transformed consumption rates and arcsine transformed proportions were homoscedastic.

To determine if any sexual differences in cheliped morphology existed between large adult male and female crabs, crusher chela heights (mm) of 30 male and 37 female crabs were regressed against carapace width, with the resulting slopes compared by standard t-Tests (Zar 1984). The crusher chelae was assumed to be the more bluntly toothed and larger of the two chelipeds. Chelal height was measured in a straight line from the dorsal propodus next to the dactylus, to the ventral propodus.

Field Site

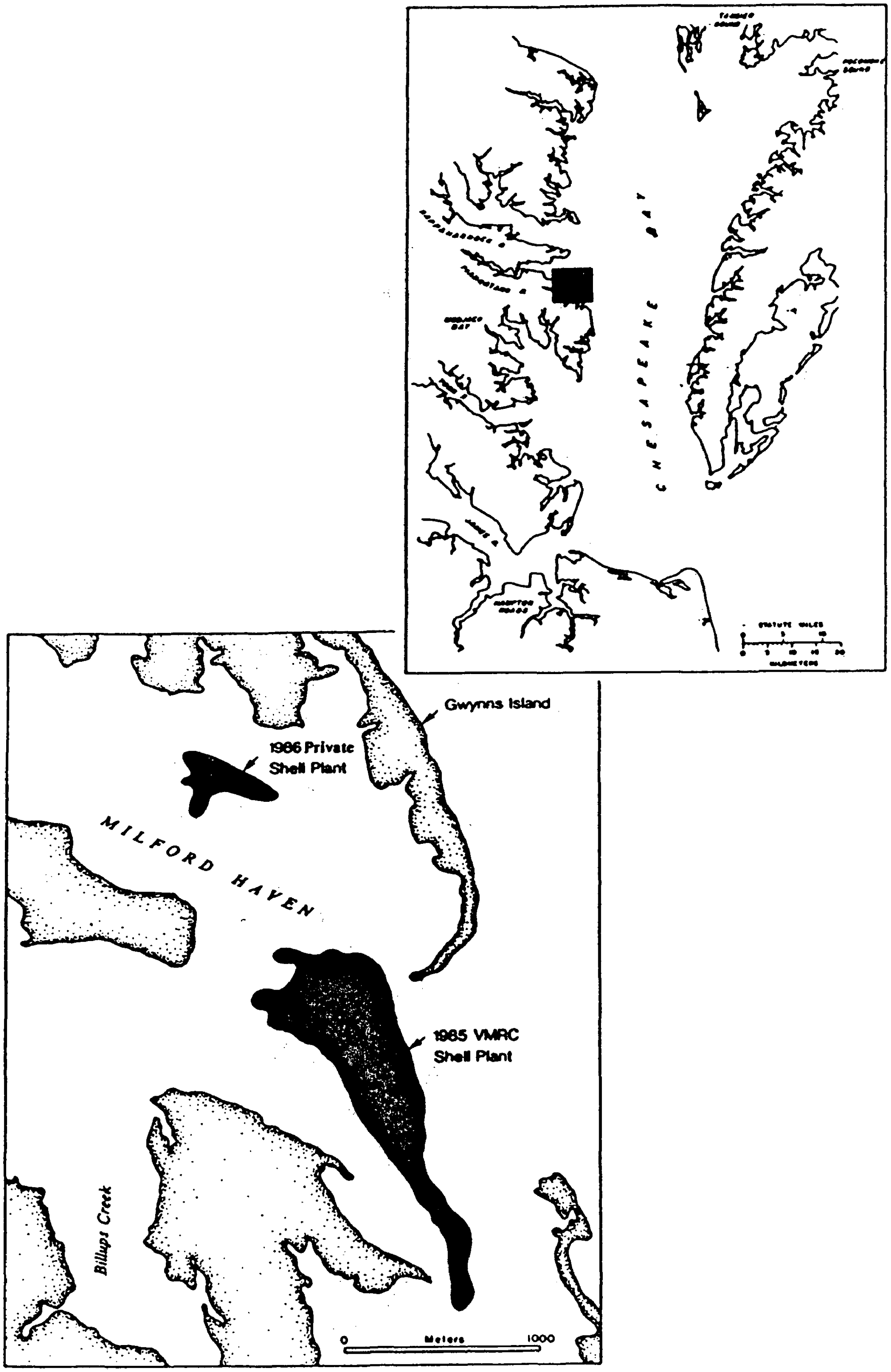
Milford Haven is part of the Piankatank River Estuary located on the western shore of the Chesapeake Bay just below Gwynn's Island, VA (Fig. 2). The Piankatank River is rural with forests, wetlands, or farms occupying most of its watershed of 466 km^2 (Chen et al. 1977). The waters of this system are considered to be the least modified of Virginia's oyster growing areas and has been, and still is highly productive for seed and market oysters (Haven et al. 1981). Milford Haven has a total acreage of 509 acres of which 2.6% is oyster rock, 65.6% soft mud, and the remainder primarily shelly mud. This area has been shelled extensively by the Virginia Marine Resources Commission (VMRC) with oyster setting rates ranging from moderate to heavy over the past 40 years (Haven et al. 1981). All bottoms in this area are in less than 5.5 m depth of water. Salinity averages 15 ppt (Chen et al. 1977) and oyster growth is classed as normal (Haven et al. 1981). The primary crab species found in this system are _Panopeus herbstii_ Milne-Edwards, _Hexapanopeus angustifrons_ Benedict and Rathbun, _Neopanopeus texana sayi_ Smith, _Eurypanopeus depressus_ Smith, and _Callinectes sapidus_ Rathbun (Ryan 1956, Wass et al. 1972).

Field study

The field component of this study used a mark and recapture method to quantify seasonal levels of crab predation at both the 1985 Milford Haven "Hole in the Wall" VMRC shell plant area and an adjacent 1986 private shell plant. The 1985 shell-plant site was sampled from April 30 to October 7, 1986 in order to assess temporal survivorship of the 1985 oyster year-class. Sampling was transferred to the 1986 site on October 7 because the 1985 cohorts began to reach lengths > 45 mm SL, and thus achieved a relative prey-size refuge from crab predation. Sampling of the 1986 cohorts began on October 7 when oysters averaged 15 mm SL, and was terminated on December 9 when water temperatures sufficiently reduced crab activity levels (13^{o} C).

Spat and cultch materials were obtained by haphazardly placing a square 0.25 m^2 grid directly on the bottom with subsequent collection by two SCUBA divers. This haphazard approach was chosen over a randomized design because of the heterogenous nature of the bottom. Both the 1985 and 1986 shell planting bottoms were found to have clumped and patchy

Figure 2. Location of field study. Milford Haven, Piankatank River Estuary, Virginia.


CHESAPEAKE BAY
Gwynns Island
1986 Private Shell Plant
MILFORD HAVEN
1985 VMRC Shell Plant
Billups Creek
0
Meters
1000

distributions of shells as a consequence of the planting technique; therefore only clumps of shells were sampled.

Each sample was placed on a plastic tray (0.25 m^2) and covered. This procedure was performed three times while temperature and salinity were recorded. The cultch with attached oysters from each quadrat were marked with marine epoxy and numbered. The maximum length of the right valve of each spat was measured to the nearest 0.1 mm. The number of spat and their corresponding sizes were then recorded. In addition to oyster spat, potential prey items found in the oyster fouling community as well as oysters larger than 45.0 mm were maintained in the laboratory (same approximate ambient temperature and salinity as the field site) during the three week marking period. By replacing the marked sample on the bottom with the original density of potential epifaunal prey items, the approximation of natural levels of spat mortality in the field should be enhanced.

Before replacement of the marked sample on the bottom two SCUBA divers collected a 0.25 m^2 sample for the next treatment as described above. The marked sample was then placed on the cleared bottom and relocated by a float attached to a reinforcing rod driven into the substrate. The marked spat were left on the bottom for three weeks. I used this technique successfully in preliminary trials during the summer of 1985. During those trials it was observed that the marked sample resembled very closely that of the surrounding oyster community after a two week replacement period, in terms of algal coverage and sedimentation, therefore I chose a three week sampling regime in order to allow for "reestablishment" and yet still account for any temporal changes in mortality.

Predation due to crabs was then quantified by recording the number of mortalities demonstrating any of the following features: chipped or cracked valve margins, puncture holes within the umbo region, crushing of the umbo region, and complete crushing of the valves themselves. These "signatures" are representative of both blue crab and mud crab predation, thus the two are indistinguishable. Mortality that cannot be attributed to crabs was quantified as well. In many instances I have observed laboratory mortalities in which the right valve was completely removed, therefore this approach most likely underestimates crab attributable mortality. In addition, preliminary laboratory observations indicated that the right valves of oysters < 10 mm SL were completely crushed, without exception, by both _P_. _herbstii_ and _C_. _sapidus_. Therefore, oysters < 10.0 mm SL were excluded from this study. With the exception of the first sample (May 13 A), which was on the bottom for only two weeks, this mark-recapture procedure was performed every three weeks from April through December, 1986,

Analysis of field data

The following dependent variables were quantified:

(1) Oyster mortality due to crabs - number of oyster mortalities displaying a distinct crab signature 21 d^{-1}.

(2) Proportional mortality due to crabs - proportion of oyster mortalites displaying a distinct crab signature 21 d^{-1}.

(3) Proportional mortality due to unknown causes - proportion of oyster mortalities not displaying a distinct crab signature 21 d^{-1}.

(4) Oyster density before and after recapture - oysters (5-45 mm SL) * $[0.25\ m^2]^{-1}$.

(5) Oyster length - shell length (mm) before replacement.

(6) Temperature (^{o} C).

Descriptive statistics (eg., mean, S.E.) were calculated for oyster mortality and proportional mortality due to crabs, proportional mortality due to unknown causes, oyster density before and after recapture, and oyster length. In addition, mortality due to crabs, recapture density, oyster length and arcsine transformed proportions for both sample sites, were each appropriate for oneway ANOVA (Zar 1984) with sample date as the independent variable.

RESULTS

General foraging behavior

Foraging behavior of large male 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. The setae on the inner edges of the walking legs or periopods are especially sensitive to tactile stimulus (Shepheard 1974). When these came into contact with a suitable prey item an active encounter did not always result. In some instances, contact with the cultch itself illicited an attack response in which the crab crushed areas of the shell devoid of oysters.

Although not markedly heterochelous, each cheliped serves as either a crusher or cutter. In this instance, an overwhelming majority (97%, n = 35) of observed crabs used the right chelae as the crusher.

Prey handling by C. sapidus usually began with an attempt to crush the oyster with the crusher cheliped, regardless of oyster length or temperature. During this process the prey was held by one cheliped while force was applied, usually to the umbone region, by the other cheliped. The umbone or posterior end of the oyster affords a higher mechanical advantage to the cheliped. After a series of force applications the prey was reoriented using the chelae and maxillipeds, and different techniques were employed. The type of handling technique used appeared to be a function of oyster length and thickness, and the geometry of oyster attachment. Attachment geometry limits the poitions available for crabs to exert sufficient force without the chelae slipping.

Crabs used two major techniques to open large oysters ($\bar{x} = 35 \pm 2$ mm SL). In the first technique, the dactyl teeth of the crusher chelae were scraped back and forth along the umbone region shearing off small flakes of shell. The cutter chelae was then used as a "punch" in an attempt to puncture the weakened area. This sequence was repeated until the cutter chelae punctured the weaker area and the adductor muscle was severed such that the valves could be pulled apart. This technique was usually employed when oyster attachment geometry caused the chelae to slip during initial crushing attempts. In instances where attachment geometry facilitated an adequate grip, a second technique was employed. Crabs using this second technique attempted to remove the oyster from the cultch by prying it off with the crusher chelae while the cutter chelae gripped the cultch. Upon removal from the cultch, the posterior edges of the oyster were gradually chipped until the cutter chelae could be forced between the valves, tearing the adductor muscle. The valves were then grasped by the chelae and pulled apart in order to expose the flesh.

Crabs feeding on medium-length oysters ($\bar{x}$ = 25 ± 2 mm SL) 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 large oyster lengths.

Once the valves of large and medium-length 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. The valves were discarded only after they had been thoroughly gleaned, after which the chelae would sweep the floor of the tank searching for any shell fragments that may have been missed.

Small-length oysters ($\bar{x}$ = 15 ± 2 mm SL) 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 (eg., 10 oysters/tank). A small proportion of small oysters were located within depressions on the surface of the cultch achieving a potential architectural refuge from crab predation. As a consequence of this random crushing technique, these architectural refuges became vulnerable to crab predation. During these directed and random opening attempts, crabs would lower themselves on top of the cultch and use their third maxillipeds to feed on the crushed aggregate of shell and oyster tissue, while the periopods continued probing the substrate and cultch materials. Once feeding was initiated, crabs became less sensitive to visual stimulus, regardless of oyster length, density, or temperature.

Complete spatial rearrangement of the cultch was generally observed upon termination of feeding trials.

Temperature effects: functional responses

Consumption rates of *C. sapidus* within each of three temperature treatments increased significantly with oyster density (ANOVA; 26-27^o C: F = 32.9, df = 5,45, P<0.0001; 19-20^o C: F = 12.3, df = 5,35, P<0.0001; 13-14^o C: F = 6.0, df = 5,35, P<0.0006), and with temperature (Fig. 3). Significantly more oysters were consumed at the upper 5 densities (10,20,30,40 and 50 oysters/tank) relative to the lowest prey density (5 oysters/tank) regardless of temperature (SNK: EWER = 0.05) (Fig. 3). Consumption rates decreased greatly at 13-14 ^{o} C for all prey densities, with no mortalities in the lowest prey density treatment at 13-14^o C (Fig. 3).

Differences in the functional responses at different temperatures were determined by analyzing proportional mortality rates as a function of oyster density (Fig. 4). Proportional mortality rates of *C. virginica* within the high and intermediate temperature experiments differed significantly with oyster density (ANOVA; 26-27^o C: F = 3.0, df

= 5,45, $P<0.02$; 19-20° C: F = 3.6, df = 5,35, $P<0.01$). At 26-27° C, proportional mortality was significantly higher at the lowest prey density ($\bar{x}$ = 80%) relative to increased densities ($\bar{x}$ = 62-52%) (SNK: EWER = 0.05) (Fig. 4). This pattern typifies an inversely density-dependent relationship between predation rate and prey density (eg., a type II functional response; Hassell 1978). In contrast, at 19-20° C, proportional mortality was significantly higher at intermediate densities of 10 and 20 oysters/tank (both $\bar{x}$ = 58%) relative to lower and higher densities ($\bar{x}$ = 23-43%) (SNK: EWER = 0.05) (Fig. 4). The reduction in proportional mortality at the lowest prey density implies a density-dependent sigmoid relationship between predation rate and prey density (eg., a type III or modified type II functional response). Hence, the existence of a partial prey refuge from predation below densities of approximately 5 oysters/tank or 15.2 oysters/m^2 at 19-20° C. Similarly, existence of a prey refuge below a density of 5 oysters/tank was evident at 13-14° C in which no oysters were eaten (Fig. 4). At 13-14° C, proportional mortality rates differed significantly with oyster density (K-W Test; X^2= 21.98, df = 35, $P<0.0005$), with highest proportional mortality rates at intermediate densities of 10 and 20 oysters/tank ($\bar{x}$ = 15%) (M-W Test: EWER = 0.05) (Fig. 4). The pattern of proportional mortality rates as a function of density resembles a displaced, inversely density-dependent, modified type II functional response rather than a density-dependent, sigmoid, type III response (Figs. 1 and 4).

Figure 3. Functional responses of _C_. _sapidus_ at different temperatures. Each point represents the mean feeding rate over 24h. Vertical bars equal 1 S.E. N = 6-10 replicates per prey density.

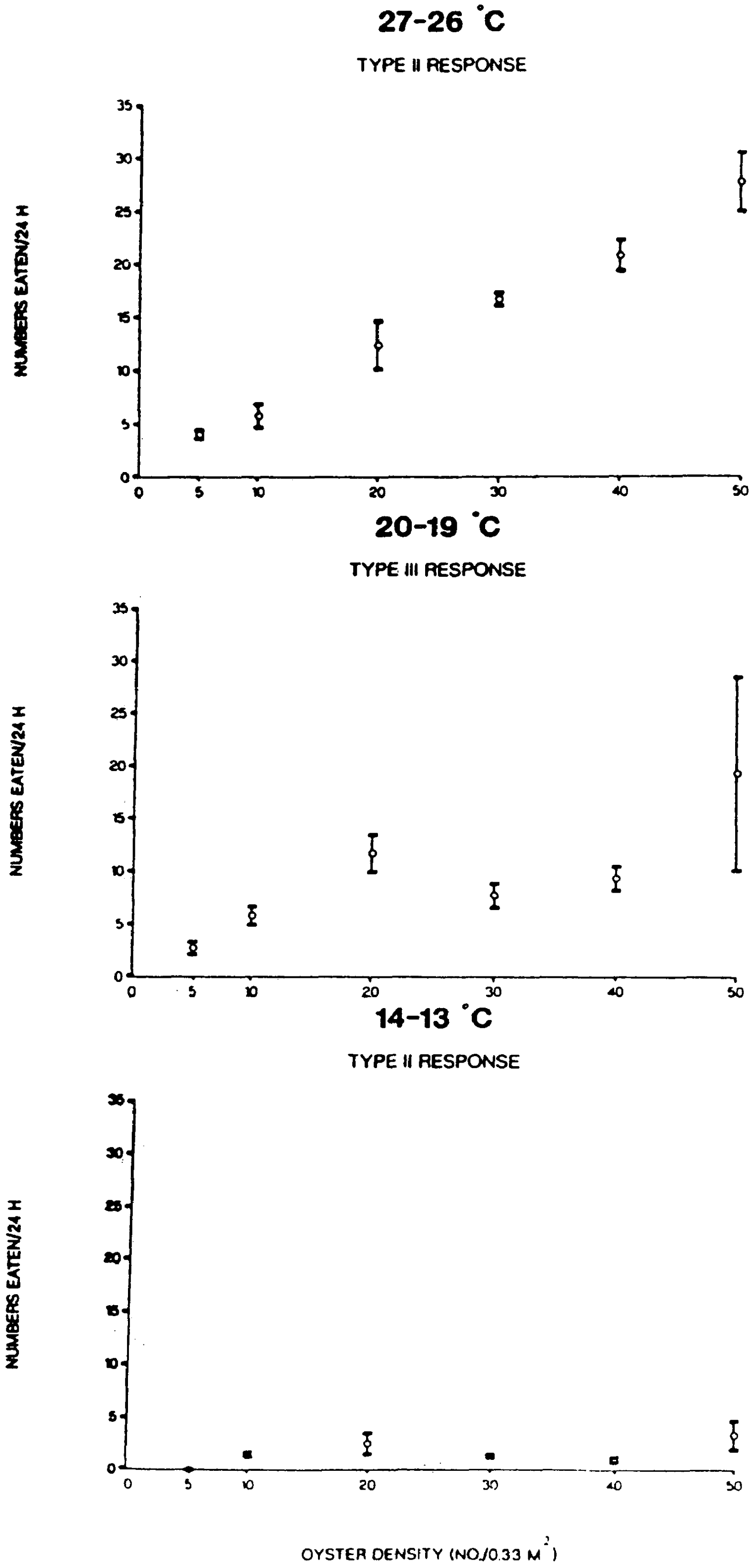
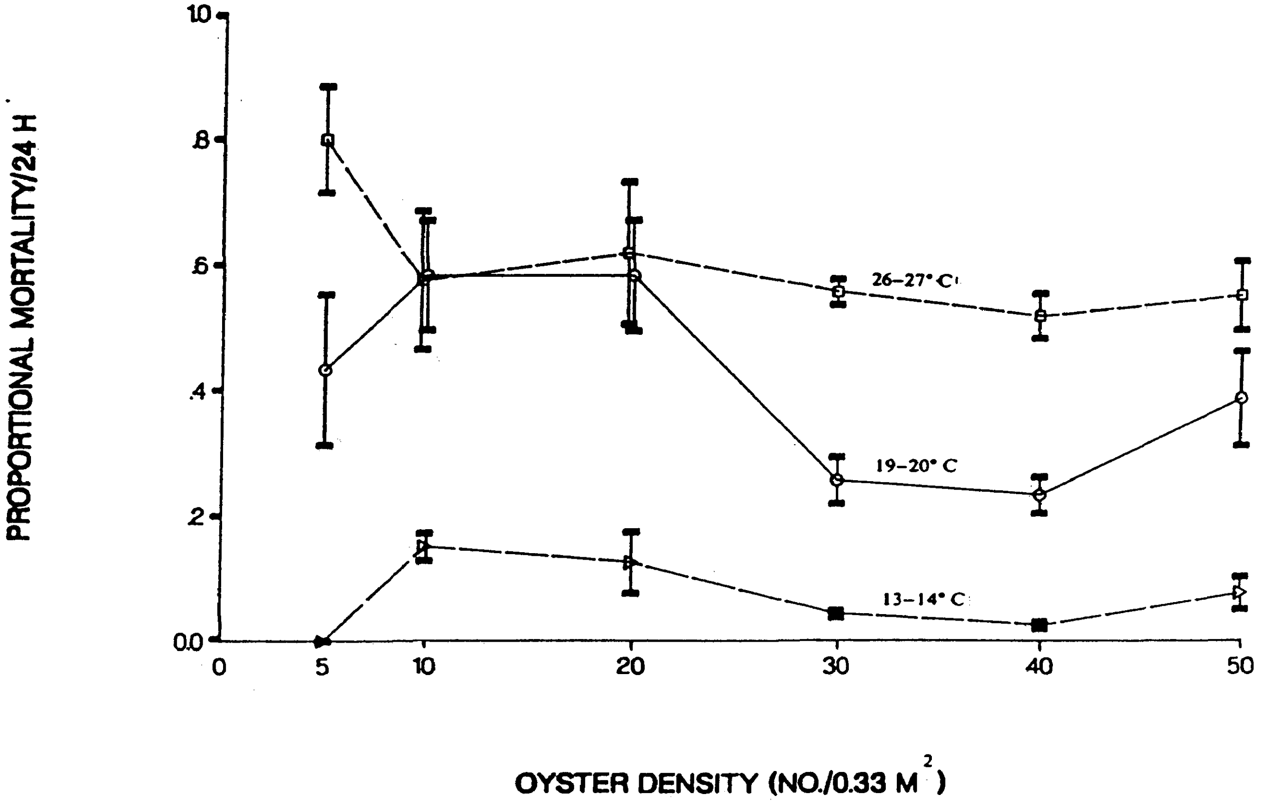

27-26 °C
TYPE II RESPONSE
NUMBERS EATEN/24 H
0
5
10
15
20
25
30
35
0
5
10
20
30
40
50
20-19 °C
TYPE III RESPONSE
NUMBERS EATEN/24 H
0
5
10
15
20
25
30
35
0
5
10
20
30
40
50
14-13 °C
TYPE II RESPONSE
NUMBERS EATEN/24 H
0
5
10
15
20
25
30
35
0
5
10
20
30
40
50
OYSTER DENSITY (NO./0.33 M²)

Figure 4. Proportional mortality of _C_. _virginica_ at six densities as a function of temperature. Each point represents the mean proportional mortality over 24h. Vertical bars equal 1 S.E. N = 6-10 replicates per prey density.


PROPORTIONAL MORTALITY/24 H
1.0
.8
.6
.4
.2
0.0
0
5
10
20
30
40
50
26–27° C
19–20° C
13–14° C
OYSTER DENSITY (NO./0.33 M 2)

Although a displaced type II response (Parsons et al. 1967, 1969) provides the same relative prey refuge at low prey densities as a type III response, there is a decreasing risk of mortality at intermediate densities (eg., 20 spat/tank) rather than the increased risk associated with a type II response (Figs. 1 and 4).

Individual crabs at 26-27^{o} C and 13-14^{o} C did not differ significantly from each other in their functional responses (Heterogeneity G-Test; 26-27^{o} C: $G = 18.5$, $df = 20$, $P = 0.55$; 13-14^{o} C: $G = 18.9$, $df = 20$, $P = 0.53$), whereas at 19-20^{o} C, individual crab responses were not all similar ($G = 45.2$, $df = 25$, $P<0.008$).

<u>Temperature effects</u>: <u>functional response models</u>

<u>General Model</u>

Consumption rates of <u>C</u>. <u>sapidus</u> within each temperature treatment were fitted to a general functional response model (Eq. 5) (Real 1977, 1979). At 26-27^{o} C, the residuals about the fitted model were distributed randomly and non-randomly for partial and complete data sets, and sample variances for the transformed dependent variable were unequal (Table 2). Despite this, the model corroborated the results from the ANOVA of proportional mortality indicating a hyperbolic, type II response with $\hat{n}$ not significantly different from 1 ($\hat{n} = 0.90$) (Table 2). At 13-14^{o} C, the model again corroborated the results from the ANOVA of proportional mortality, indicating a type II response with $\hat{n}$ not significantly different from 1 ($\hat{n} = 0.96$) (Fig. 1). In this experiment the residuals were distributed randomly and variances were equal (Table 2). At 19-20^{o} C; however, the model indicated a type II response with $\hat{n}$ not significantly different from 1 ($\hat{n}$ = 1.0) (Table 2), whereas the ANOVA of proportional mortality rates determined a type III response (Fig. 4). Since the residuals were distributed randomly and the variances were equal (Table 2), this discrepancy is probably due to mathematical constraints of the functional response model; it is unable to accomodate the effect a single point (eg., the low proportional mortality at an oyster density of 5 (Fig. 4). Examination of the residuals at the lowest prey density indicated a consistent distribution above the predicted value. Thus, at 19-20^{o} C, a significant decrease in proportional mortality at 5 oysters/tank, and increases at intermediate densities of 10 and 20 oysters/tank (Fig. 4) appear to be responsible for the type III response.

Conceptual models

The fit of continuous and discrete-time conceptual models varied with temperature (Table 3). At 26-27^{o} C, the functional response (Fig. 3) was best described by a type II discrete time model:

$$Na = Nt[1-e^{-.04(24-0.1Na)}]$$

as indicated by the (1) nonsignificant "lack-of-fit" error, (2) low residual sums of squares relative to the continuous-time model, and (3) biological relavance of a model which accounts for decreases in prey density as crabs consume prey (Table 3). At 19-20^{o} C, the functional response of *C. sapidus* was sigmoid type III (Fig. 3). Partial examination of the residuals for both continuous and discrete time models indicated a systematic distribution above and below the predicted values at prey densities of 10 and 30 oysters/tank, respectively (Table 3). Both models provided a statistically adequate fit as indicated by the nonsignificant "lack-of-fit" error (Table 3). However, the discrete-time type III model explained more (95%) of the variance in consumption and was characterized by lower residual sums of squares (Table 3). Therefore, the functional response at 19-20^{o} C is best described by a discrete-time type III model:

$$Na = Nt\{1-e[\frac{-.04Nt}{1+2.0Nt}(24-0.1Na)]\}$$

At 13-14^{o} C neither model adequately described the data. The continuous-time type II model explained only 50% of the variance, and was characterized by a systematic distribution of residuals below the predicted values (Table 3). The discrete-time type II model indicated a significant "lack-of-fit" error and systematic distribution of residuals above the predicted values (Table 3), though it described 84% of the variance in consumption rates and displayed the lower residual sums of squares of the two models. Hence, the functional response at 13-14^{o} C is best described by a continuous-time type II model:

$$Na = \frac{0.12Nt}{1 + 0.027Nt}.$$

Temperature and density effects: behavioral components

Nonlinear regressions with functional response models (Table 3) estimated mean handling time per oyster by C. sapidus to be 0.1 hour at 26-27° C and 19-20° C, and 5.4 hours at 13-14° C (Table 4). Observed mean handling times were 12-31% less than estimated values, and increased as temperature decreased (Table 4). Attack rate (a') estimates ranged from 0.037 (26-27°C) to 0.005 (13-14°C) for type II models; a' computed from eqn (6) with nonlinear regression estimates of b and c, equaled 0.043 (19-20°C) for the type III model. The estimated attack rate (a') was highest at 19-20° C; however, when a' was related to prey density, it was higher at 26-27°C at the lowest prey density (Fig. 5a). The tendency for a' to increase over an initial range of low prey densities at 19-20° C, but remain constant at low prey densities at 26-27° C and 13-14° C, illustrates the fundamental difference between the type III and type II responses (Fig. 5a).

Encounter rates (total) were increasing functions of prey density (Fig. 5b); however, the trends were only significant at 13-14° C (ANOVA; 26-27° C: $F = 3.1$, df = 2, 17, $P = 0.07$; 19-20° C: $F = 2.5$, df = 2, 19, $P = 0.11$; 13-14° C: $F = 74.8$, df = 2, 10, $P<0.001$). At 13-14° C, highest significant encounter rates occurred at prey densities of 20 and 50 oysters/tank (SNK: EWER = 0.05) (Fig. 5b). The trend in observed encounter rates at 5 oysters/tank was similar to that estimated from nonlinear model fitting procedures because (1) high encounter rates at 19-20° C were consistent with model predictions of an increased a' relative to the remaining temperatures, and (2) encounter rates decreased at 26-27^{0} C and 13-14^{0} C in the same order as predicted by the models (Fig. 5b). In contrast, at 19-20^{0} C encounter rates increased with prey density as in a type II response, rather than decreasing as predicted (Fig. 3b). The significant increase in a' with density at 13-14^{0} C, is contrary to model predictions of a constant a' (Hassell 1976, 1977). This is not suprising given that no successful encounters were observed within this temperature, hence more time was available for non-feeding activities (eg., searching for and encountering prey).

I examined proportional attack success and successful encounter rates as a function of prey density to determine how a partial prey refuge from predation could be achieved (eg., type III response), despite an increased encounter rate at 5 oysters/tank. Attack success rates decreased with increasing prey density at 26-27^{0} C and 19-20^{0} C (Fig. 6a). At 13-14^{0} C there were no observed successful encounters. Successful encounter rates did not vary significantly with oyster density at 19-20^{0} C and 26-27^{0} C (ANOVA; 26-27^{0} C: F = 0.7, df = 2,17, P = 0.53; 19-20^{0} C: F = 1.2, df = 2,19, P = 0.35). Although total encounter rates at 5 oysters/tank were higher at 19-20^{0} C versus 26-27^{0} C, the attack success rate at 26-27^{0} C was more than twice that at 19-20^{0} C (Fig. 6a). In addition, the successful encounter rate at 26-27^{0} C was nearly twice that of 19-20^{0} C (Fig. 6b). At 5 oysters/tank and 19-

Figure 5. (A) Proportional instantaneous attack (a’) rates related to oyster density at three temperatures. Rates are estimates from nonlinear functional response models. (B) Mean number of oyster encounters (total) per 1 hr observation at three different temperatures. Vertical bars equal 1 S.E.

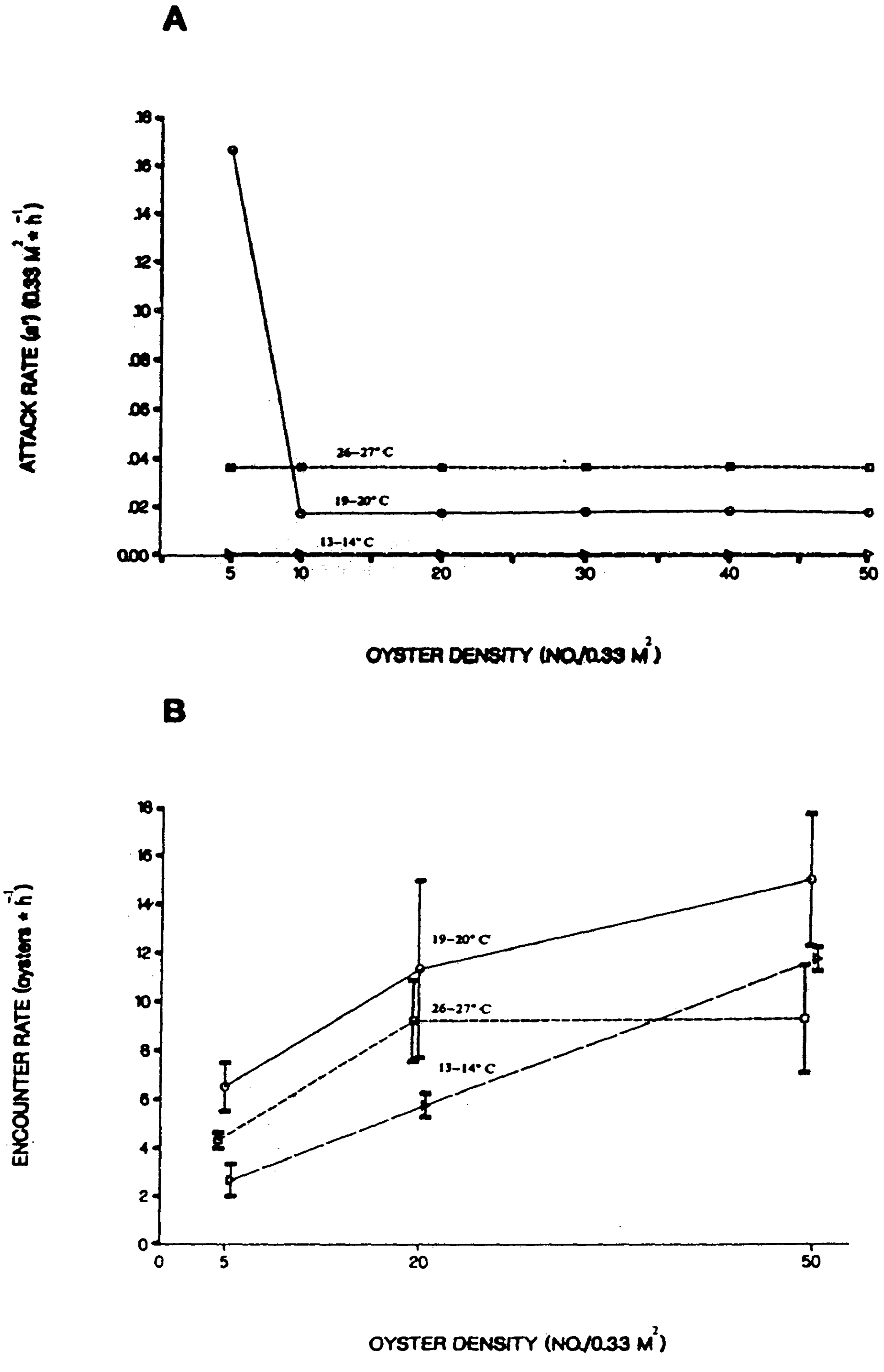
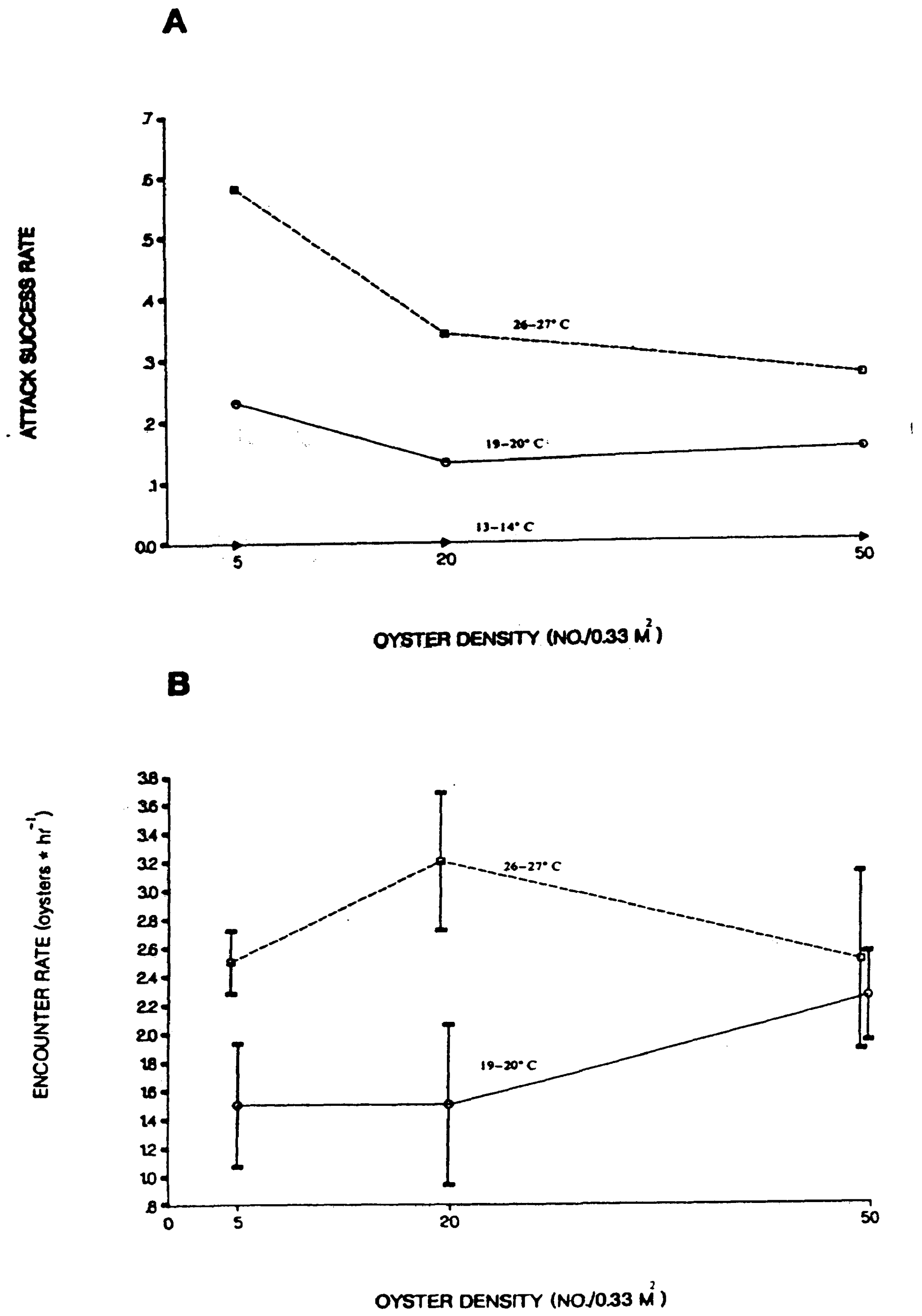

A
ATTACK RATE (a') (0.33 M^2 * h^{-1})
.18
.16
.14
.12
.10
.08
.06
.04
.02
0.00
26–27° C
19–20° C
13–14° C
5
10
20
30
40
50
OYSTER DENSITY (NO./0.33 M^2)
B
ENCOUNTER RATE (oysters * h^{-1})
18
16
14
12
10
8
6
4
2
0
19–20° C
26–27° C
13–14° C
0
5
20
50
OYSTER DENSITY (NO./0.33 M^2)

Figure 6. (A) Proportion of successful encounters per 1 h observation period related to oyster density at three temperatures. (B) Mean number of successful oyster encounters at three different temperatures per 1 h observation period. Vertical bars equal 1 S.E.


A
ATTACK SUCCESS RATE
.7
.6
.5
.4
.3
.2
.1
0.0
26–27° C
19–20° C
13–14° C
5
20
50
OYSTER DENSITY (NO./0.33 M²)
B
ENCOUNTER RATE (oysters * hr⁻¹)
3.8
3.6
3.4
3.2
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
.8
0
5
20
50
26–27° C
19–20° C
OYSTER DENSITY (NO./0.33 M²)

20^{o} C, decreases in the attack success rate and mean successful encounter rate, overcome the effect on an increased total encounter rate and provide a partial prey refuge (type III response) relative to that at 26-27^{o} C (type II response). At an intermediate density of 20 oysters/tank, mean successful encounter rates at 26-27^{o} C were approximately twice that at 19-20^{o} C, whereas at 50 oysters/tank, they were approximately equal (Fig. 6b). These results suggest the maximum feeding rate for C. sapidus to be between 2 and 3 oysters ($\bar{x}$ = 25 mm SL)/hour (Fig. 6b).

Examination of persistence times in unsuccessful encounters, as a function of density and temperature, with oyster length as a covariate, provides insight into the behavioral mechanisms affecting successful encounter rates. At 13-14^{o}C, persistence time indicated a positive linear relationship with oyster length, but the trend was not statistically significant (Table 5). Persistence time at 26-27^{o} C varied significantly with oyster density (Table 5). At 5 and 20 oysters/tank, persistence times decreased with temperature (SNK: EWER = 0.05) (Fig. 7). There was a positive relationship between persistence time and successful encounters (compare Figs. 6b and 7).

Breaking (Tb), eating (Te) and handling times (Th) of oysters increased significantly with oyster length, except for Tb at 19-20^{o} C (Table 5, Fig. 8). This relationship is most apparent for Te (Fig. 8b), and probably reflects the volume of flesh ingested or the surface area of shell gleaned. Oyster density did not significantly affect any

Figure 7. Mean persistence times of C. sapidus in unsuccessful encounters with C. virginica related to oyster density at three temperatures per 1 h observation period. Vertical bars equal 1 S.E.

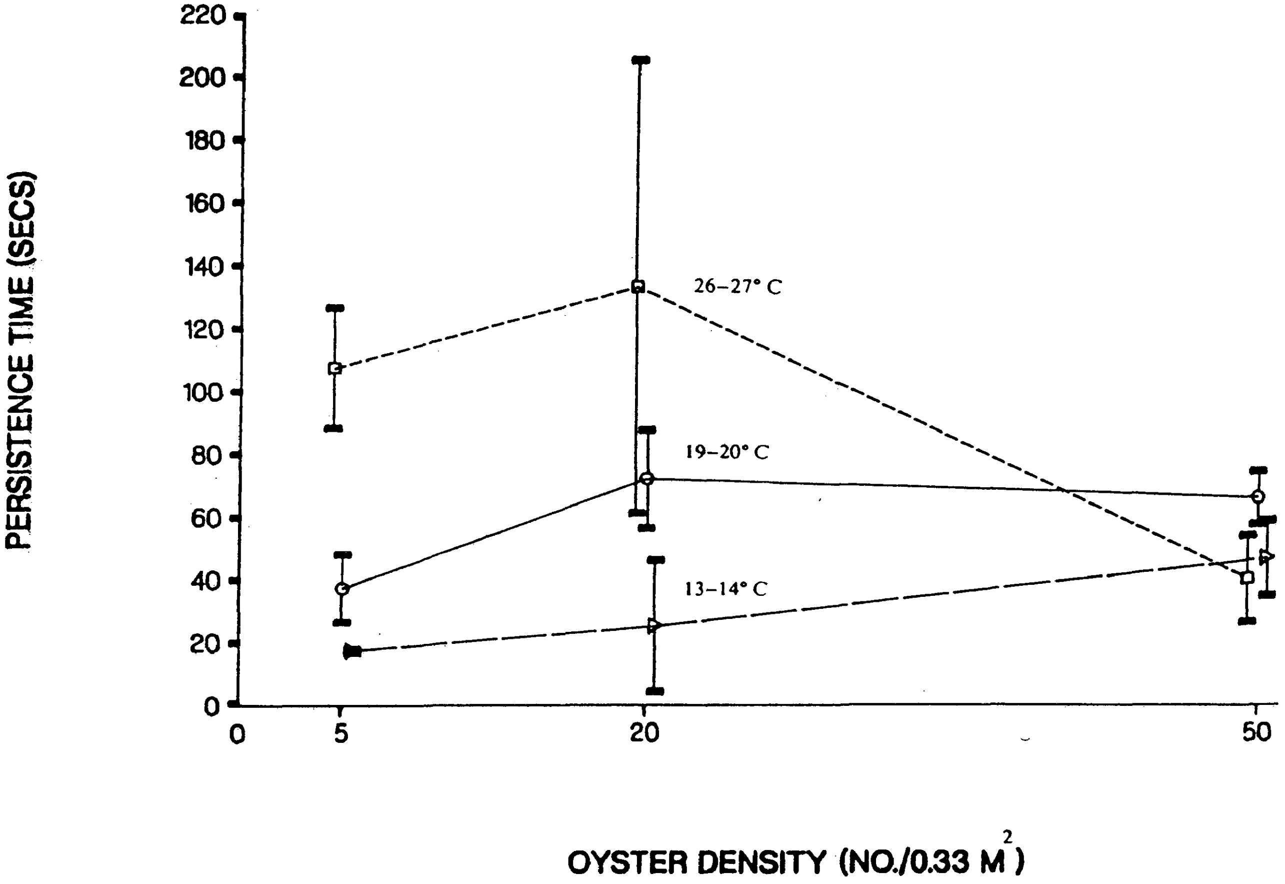

PERSISTENCE TIME (SECS)
220
200
180
160
140
120
100
80
60
40
20
0
0
5
20
50
26–27° C
19–20° C
13–14° C
OYSTER DENSITY (NO./0.33 M^2)

Figure 8. Handling time components of successful encounters per 1 h observation period, compared against oyster length at two temperatures.

(A) Breaking time (secs):

26-27^{o} C: $y = -69.5+6.9x$ ($r^2=.29$, $n = 26$)

19-20^{o} C: $y = 33.5+3.2x$ ($r^2=.03$, $n = 28$)

(B) Eating time (secs):

26-27^{o} C: $y = -124.1+12.8x$ ($r^2=.44$, $n = 26$)

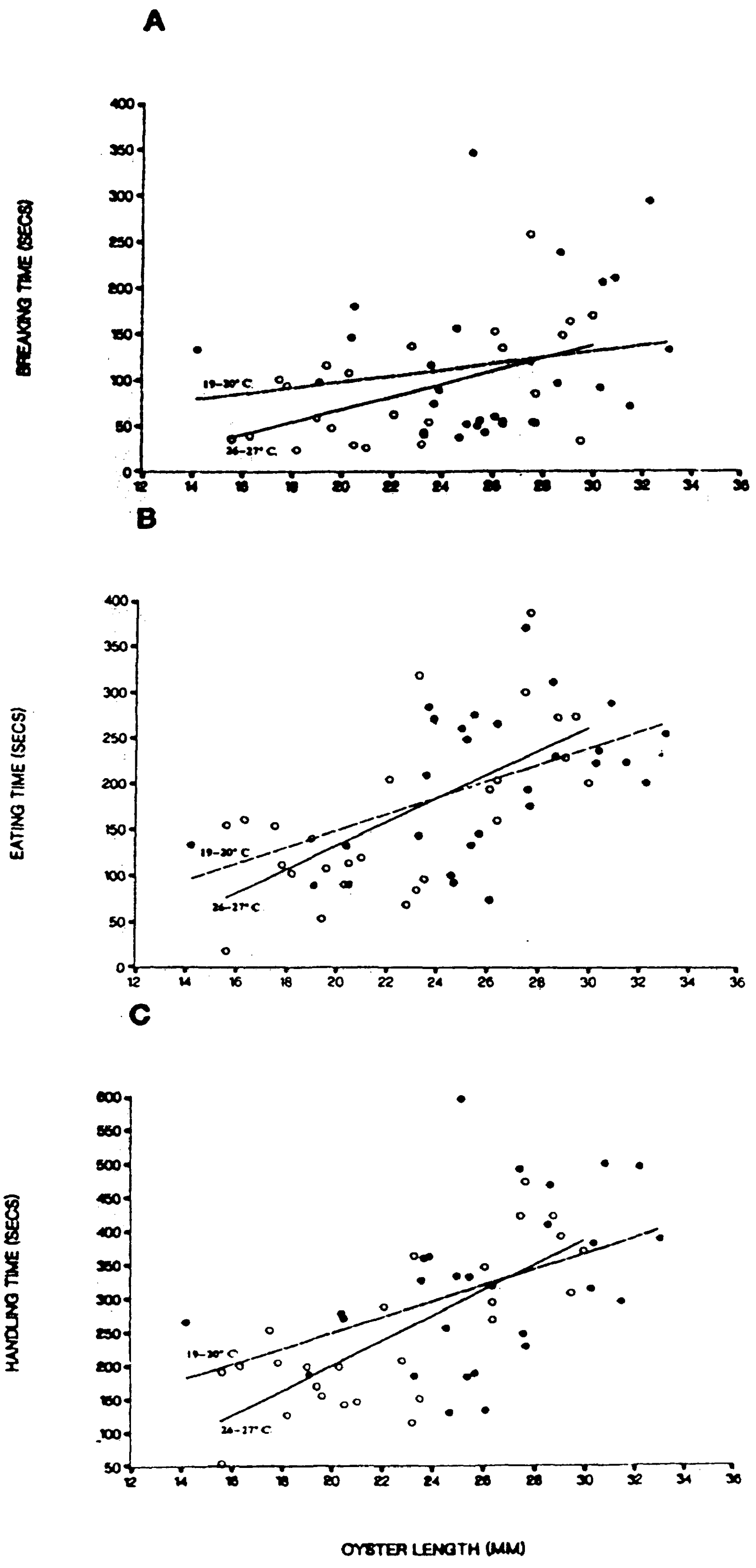
19-20^{o} C: $y = -30.6+9.0x$ ($r^2=.23$, $n = 28$)

(C) Handling time (secs):

26-27^{o} C: $y = -170.1+18.5x$ ($r^2=.52$, $n = 26$)

19-20^{o} C: $y = 16.9+11.6x$ ($r^2=.17$, $n = 28$)

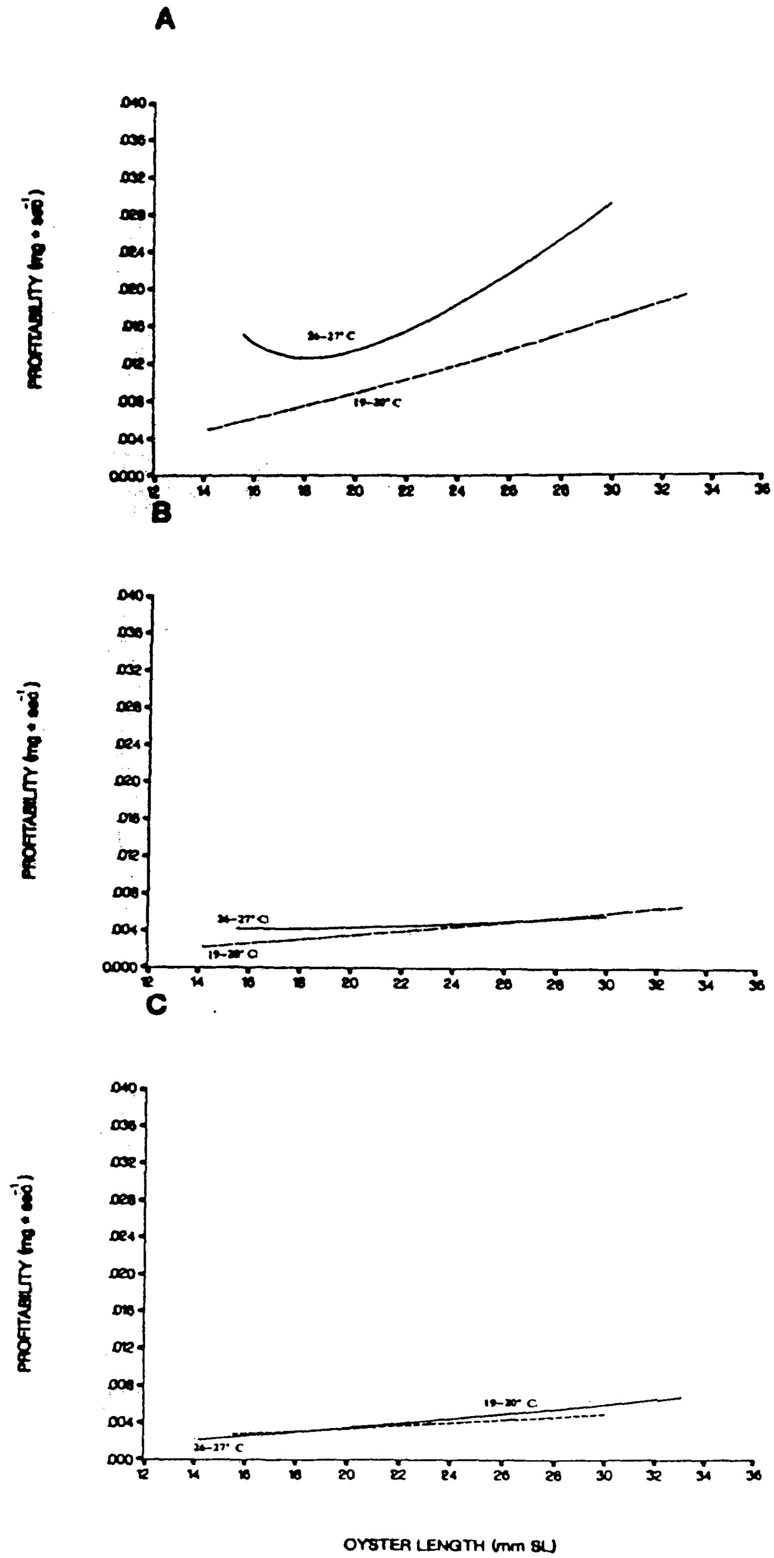
See Table 5 for significance levels.


A
BREAKING TIME (SECS)
400
350
300
250
200
150
100
50
0
19–30° C
26–27° C
12
14
16
18
20
22
24
26
28
30
32
34
36
B
EATING TIME (SECS)
400
350
300
250
200
150
100
50
0
19–30° C
26–27° C
12
14
16
18
20
22
24
26
28
30
32
34
36
C
HANDLING TIME (SECS)
600
550
500
450
400
350
300
250
200
150
100
50
19–30° C
26–27° C
12
14
16
18
20
22
24
26
28
30
32
34
36
OYSTER LENGTH (MM)

behavioral component (Table 5). Below an oyster length of approximately 25-26 mm, behavioral components tend to decrease with increasing temperature, above 27 mm they were approximately equal (Fig. 8). Linear regression coefficients of breaking times differed significantly with temperature (slopes; t = 2.2, df = 2,50, $P<0.05$) (Fig. 8a). In contrast, the slopes of eating times did not differ significantly with temperature (t = 0.02, df = 2,50, $P>0.95$), but elevations did (t = 0.09, df = 2,50, $P<0.0001$) (Fig. 8b). Handling times were equal regardless of temperature (slopes; t = 0.09, df = 2,50, $P>0.95$; elevations; t = 0.96, df = 2,51, $P>0.95$) (Fig. 8c).

Inclusion of profitability estimates illustrate the potential effects of temperature on profitability, and thus the effect on preferred oyster size within the context of optimal foraging tactics. When calculated with breaking time, prey profitability appeared to be increasing asymptotic and linear functions of oyster length at 26-27^0 C and 19-20^0 C, respectively (Fig. 9a). At 26-27^0 C and 19-20^0 C, observed profitabilty peaked at approximately 30 mm SL and 33 mm SL, respectively (Fig. 9a). Incorporation of eating time in profitability estimates reduced the optima by a factor of approximately 4.2 for each temperature, and tended to dampen the transition between the two temperatures (Fig. 9b). This suggests that digestion is a major component in oyster handling times, and does not vary from 26^0 C to 20^0 C. Adjustments for persistence times in the proportion of unsuccessful encounters did not greatly decrease profitability estimates at either

Figure 9. Profitability of C. *virginica* calculated as the ratio of predicted yield (mg dry weight) to observed handling time components (secs) at two temperatures. Curves were derived from regressions of yield on oyster length. Ratios of predicted yield to observed (A) breaking times, (B) handling times, and (C) handling times incorporating mean persistence times in unsuccessful encounters.


A
PROFITABILITY (mg • sec^{-1})
.040
.036
.032
.028
.024
.020
.016
.012
.008
.004
0.000
12
14
16
18
20
22
24
26
28
30
32
34
36
24–27° C
19–30° C
B
PROFITABILITY (mg • sec^{-1})
24–27° C
19–30° C
C
PROFITABILITY (mg • sec^{-1})
19–30° C
24–27° C
OYSTER LENGTH (mm SL)

temperature (Fig. 9c). Incorporation of Tp in unsuccessful encounters had the same net effect on profitability estimates at each temperature. At 26-27^{o} C, the proportion of unsuccessful encounters was low relative to 19-20^{o} C, but increased Tp and therefore energetic expense was higher. In comparison, at 19-20^{o} C, the energetic expense associated with Tp was low relative to 26-27^{o} C, but the proportion of unsuccessful encounters was higher.

Oyster length effects: functional responses

Blue crab consumption rates per 24-h generally increased with prey density and decreasing shell length (Fig. 10). At 26-27^{o} C, consumption rates of C. sapidus within each of three oyster size classes differed significantly with oyster density (ANOVA; $\bar{x} \pm 15$ mm SL: F = 221.6, df = 6,42, P<0.0001; $\bar{x} \pm 25$ mm SL: F = 32.9, df = 5,45, P<0.0001; $\bar{x} \pm 35$ mm SL: F = 5.0, df = 5,89, P<0.0005). At an oyster size class of 15 mm SL, consumption rates greatly increased relative to 25 and 35 mm SL oysters, reaching an asymptote at approximately 142 oysters * crab^{-1}* [24 h]$^{-1}$(Fig. 10). Within this size class significantly more oysters were consumed at the upper 6 densities (20, 40, 80, 120, 250, 350 oysters/tank) than at the lowest (SNK: EWER = 0.05). At shell lengths of 25 and 35 mm, highest consumption rates were approximately 27 and 7 oysters * crab^{-1}* [24 h]$^{-1}$, respectively (Fig. 10). In addition, significantly more oysters were consumed at the upper 4 densities (20, 30, 40, 50 oysters/tank) relative to the lowest two (5 and 10 oysters/tank) for both size classes (SNK: EWER = 0.05) (Fig. 10).

The trends in proportional mortality rates of C. virginica as a function of prey density were analagous for all three oyster size classes. Proportional mortality rates increased significantly with decreasing oyster density (ANOVA; $\bar{x}$ = 15 mm SL: F = 6.67, df = 6,42, $P<0.0001$; $\bar{x}$ = 25 mm SL: F = 3.0, df = 5,45, $P<0.02$; $\bar{x}$ = 35 mm SL: F = 4.9, df = 5,89, $P<0.0005$). At a mean shell length of 15 mm, proportional mortality rates were significantly higher at the lowest two prey densities ($\bar{x}$ = 82 and 81%, respectively), and at 120 oysters/tank ($\bar{x}$ = 81%) compared to the remaining densities ($\bar{x}$ = 41-66%) (SNK: EWER = 0.05) (Fig. 11). This pattern in proportional mortality rates appears to be atypical of the traditional type II or III typology; there is an increasing risk of mortality at the two lowest prey densities, a decreased risk at intermediate densities of 40 and 80 oysters/tank, an increased risk at 120 oysters/tank, and a decreasing risk as prey density is increased (Fig. 11). Therefore, these results support the possible use of nontraditional functional response models which account for "foraging time adjustments" as a function of different environmental cost/benifit ratios (Abrams 1982).

At a mean shell length of 25 mm, proportional mortality rates were significantly higher at the lowest prey density ($\bar{x}$ = 80%) than at higher densities ($\bar{x}$ = 52-62%) (SNK: EWER = 0.05), and is characteristic of a type II response. Consistent with results from the 25 mm SL size

Figure 10. Functional responses of C. sapidus at three oyster size-classes. Each point represents the mean feeding rate over 24h. Vertical bars equal 1 S.E. N = 6-18 replicates per prey density. Note the difference in X- and Y-values at 15 mm SL relative to other size classes.

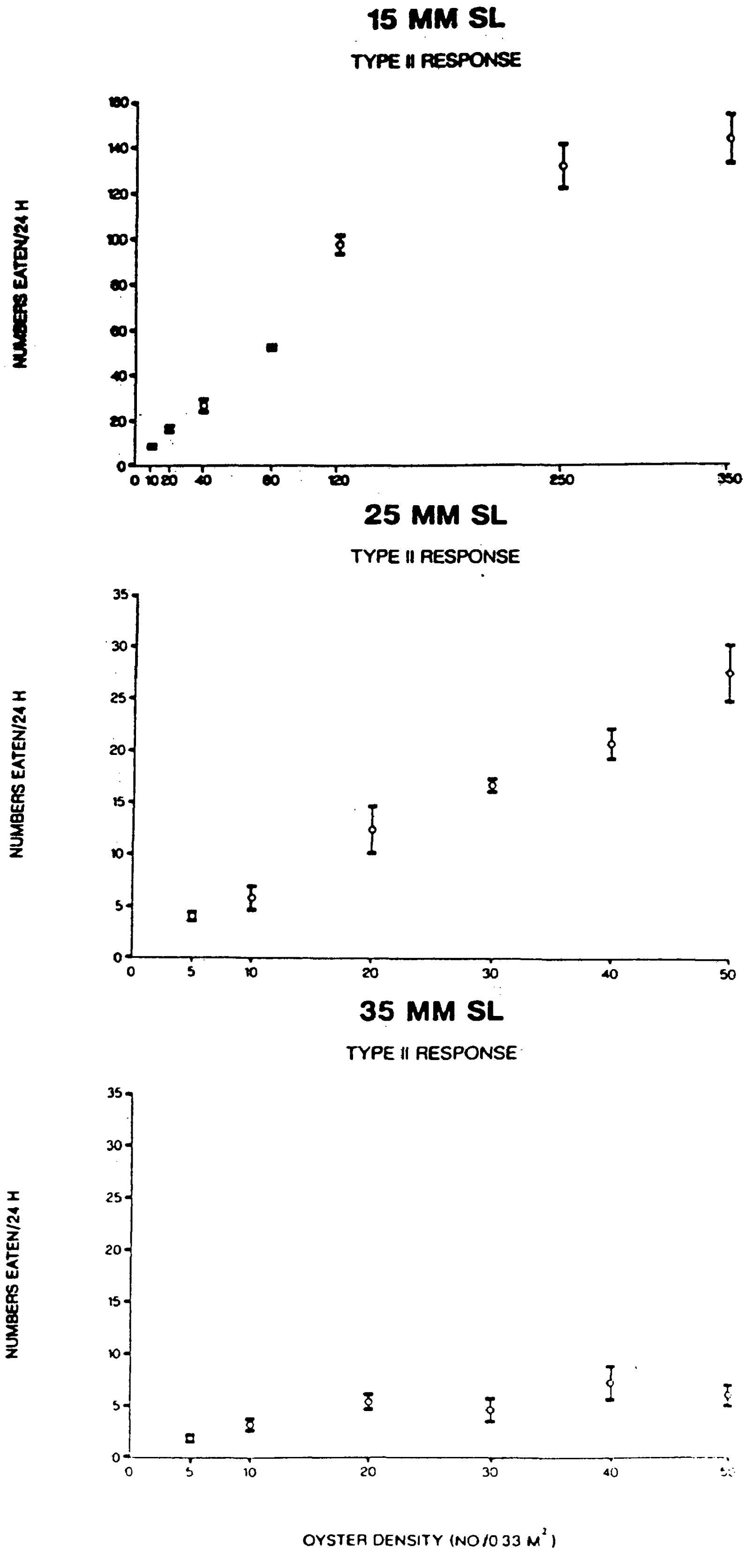
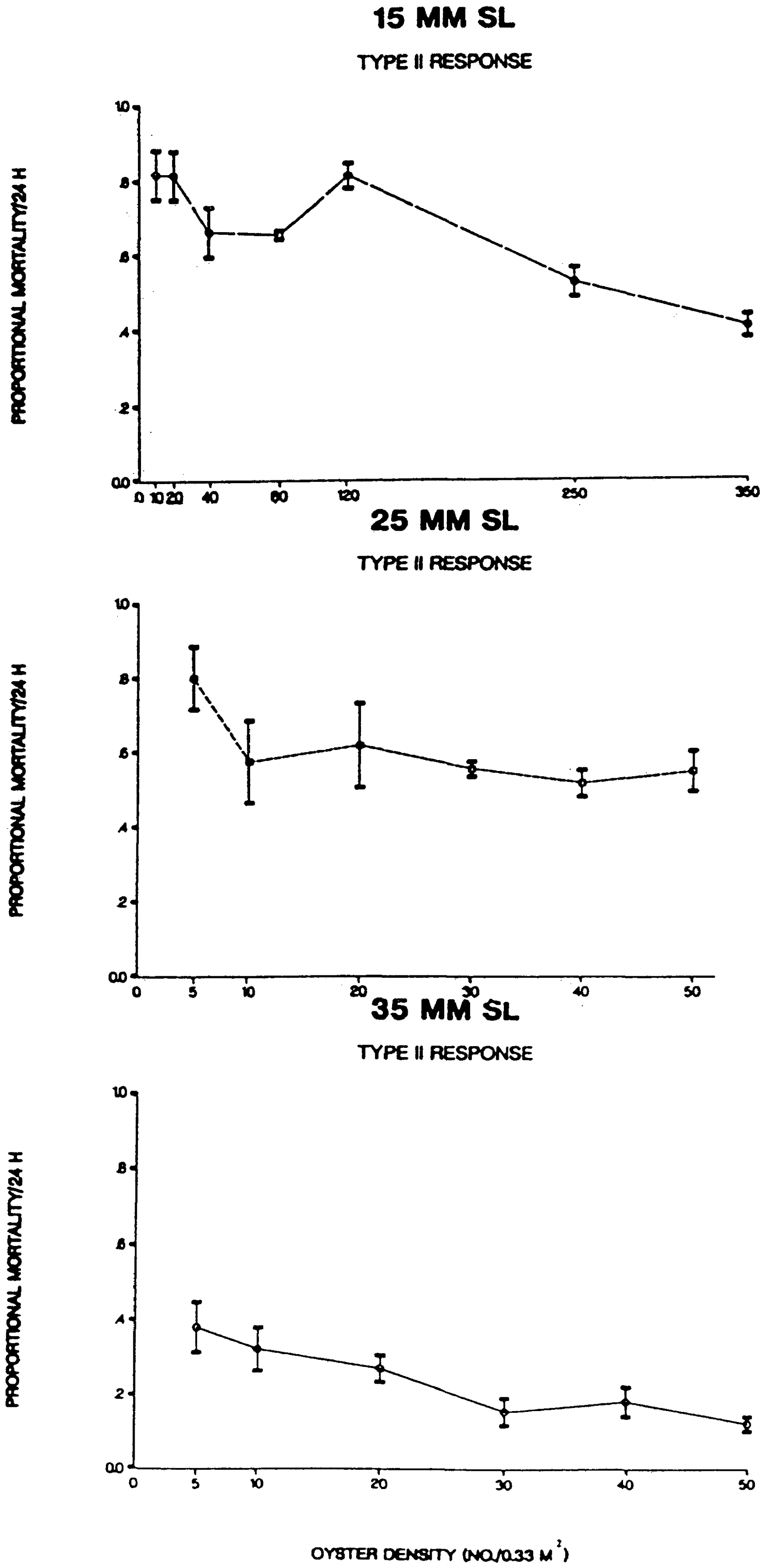

15 MM SL
TYPE II RESPONSE
NUMBERS EATEN/24 H
0
20
40
60
80
100
120
140
160
0
10
20
40
80
120
250
350
25 MM SL
TYPE II RESPONSE
NUMBERS EATEN/24 H
0
5
10
15
20
25
30
35
0
5
10
20
30
40
50
35 MM SL
TYPE II RESPONSE
NUMBERS EATEN/24 H
0
5
10
15
20
25
30
35
0
5
10
20
30
40
50
OYSTER DENSITY (NO/0 33 M²)

Figure 11. Proportional mortality of C. *virginica* at six densities as a function of oyster size-class. Each point represents the mean proportional mortality over 24h. Vertical bars equal 1 S.E. N = 6-18 replicates per prey density.


15 MM SL
TYPE II RESPONSE
PROPORTIONAL MORTALITY/24 H
1.0
.8
.6
.4
.2
0.0
0
10
20
40
60
120
250
350
25 MM SL
TYPE II RESPONSE
PROPORTIONAL MORTALITY/24 H
1.0
.8
.6
.4
.2
0.0
0
5
10
20
30
40
50
35 MM SL
TYPE II RESPONSE
PROPORTIONAL MORTALITY/24 H
1.0
.8
.6
.4
.2
0.0
0
5
10
20
30
40
50
OYSTER DENSITY (NO./0.33 M²)

class experiment, the pattern of proportional mortality at 35 mm SL was typical of a type II response (Fig. 11). In this case, significantly higher proportional mortality rates occurred at the two lowest densities of 5 and 10 oysters/tank ($\bar{x}$ = 38 and 32%, respectively) relative to remaining densities (12-27%) (SNK: EWER = 0.05) (Fig. 11).

Individual crabs at 35 mm and 15 mm SL differed significantly from each other in their functional responses (Heterogeneity G-Test; 35 mm SL: $G = 55.5$, $df = 25$, $P<0.0004$; 15 mm SL: $G = 143.0$, $df = 30$, $P<0.0001$), whereas individual crab responses were similar at 25 mm SL ($G = 18.5$, $df = 20$, $P = 0.55$).

Oyster length effects: functional response models

General model

Analysis according to the general functional response model (Eq. 5) (Real 1977, 1979) corroborated the results from the ANOVA of proportional mortality for both the 15 mm and 25 mm SL size classes, indicating a hyperbolic type II response. At a size class of 15 mm SL, the residuals about the fitted model were distributed randomly for both partial and complete data sets (Table 6); however, variances for the transformed dependent variable were unequal (Hartley's F-Max Test). Despite unequal sample variances and supportive evidence for a nontraditional functional response model at this size class, the general functional response model (Real 1977, 1979) explained 95.5% of the total variance and indicated a type II response with $\hat{n}$ not significantly different from 1 ($\hat{n} = 0.99$) (Table 6). At a size class of 25 mm SL, the residuals about the fitted model were distributed randomly and nonrandomly for partial and complete data sets, respectively (Table 6). In addition, unequal sample variances were found for the transformed dependent variable (Hartley's F-Max Test). The model however verified a type II reponse for the 25 mm size class with $\hat{n}$ not significantly different from 1 ($\hat{n}$ = 0.89) (Table 6). In contrast, for the 35 mm size class, the model explained only 22.7% of the total variance and was unable to adequately predict a response type as indicated by $\hat{n}$ being significantly different from 0, 1 and 2 ($\hat{n}$ = 0.58) (Table 6). This is somewhat surprising given that the residuals for both partial and complete data sets were distributed randomly (Table 6), and sample variances were equal (Hartley's F-Max Test). Therefore, interpretation of a type II response at this prey size class is based solely on the results from the ANOVA of proportional mortality rates.

Conceptual models

The fit of continuous and discrete-time conceptual models varied with oyster length (Table 7). For the 15 mm size class, the functional response was best described by a type II continuous-time model:

$$Na = \frac{0.919\ Nt}{1 + (0.0038)\ Nt}$$

as indicated by the (1) low residual sums of squares and (2) random distribution of residuals about the predicted values, relative to the discrete-time model (Table 7). This traditional type II model described 96.4% of the total variance at this prey size class, despite supportive evidence for a more nontraditional model. Although both continuous and discrete-time models adequately described the functional response for the 25 mm size class experiment (Fig. 10), the discrete-time model was chosen:

$$Na = Nt[1-e^{-.04(24-0.1Na)}]$$

because of the slightly lower residual sums of squares compared to the continuous time-model. For the 35 mm size class, the functional response of C. sapidus displayed a hyperbolic (destabilizing) type II response (Fig. 10). Complete examination of the residuals for both contiuous- and discrete-time models indicated a systematic distribution below the predicted values (Table 7). For the discrete-time model, partial examination of residuals indicated a systematic distribution below the predicted values (Table 7). Both models, however, provided a statistically adequate fit to the data as indicated by the nonsignificant "lack-of-fit" error (Table 7). When compared to the continuous-time model, the discrete-time model explained 85.5% of the variance in consumption rates and was characterized by the lower residual sums of squares (Table 7). Hence, the functional response of C. sapidus within the 35 mm size class experiment is best described by a discrete-time type II model:

$$Na = Nt[1-e^{-.005(24-0.1Na)}].$$

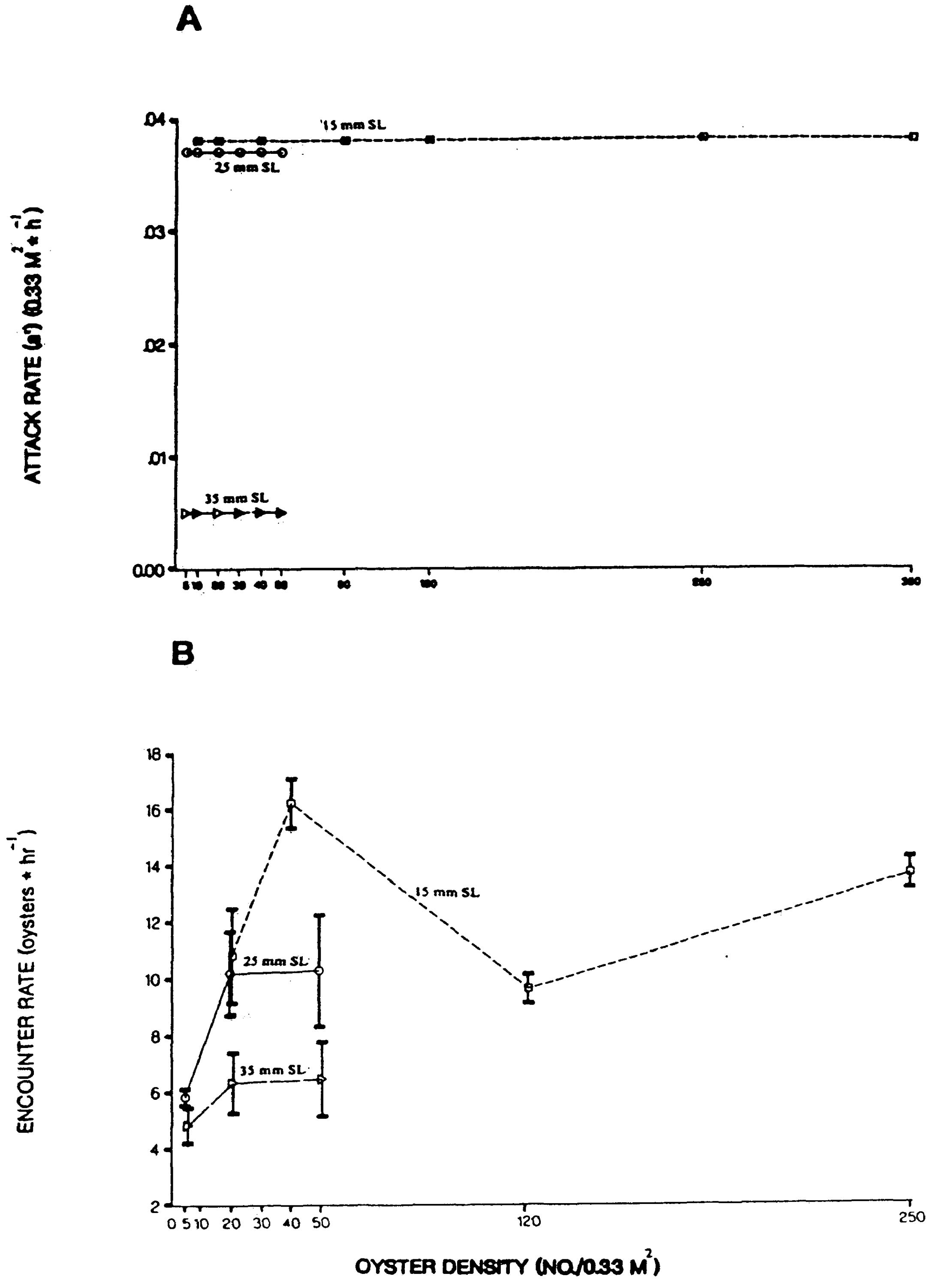
Oyster length effects: behavioral components

Nonlinear regressions with functional response models (Table 7) estimated the mean handling time per oyster by C. sapidus to be 0.1 hour, regardless of prey length (Table 8). Estimated instantaneous attack rates (a’) were equal for size classes of 15 and 25 mm SL but decreased, with increasing oyster length (Table 8). Figure 12a illustrates the substantial decrease in a’ with increasing prey length, and consistent a’ as a function of prey density (eg., type II response).

Handling time estimates decreased with decreasing oyster length (Table 8). Handling times were 97 and 31% lower than model estimates at size classes of 15 and 25 mm SL respectively, whereas mean handling times for the 35 mm SL were approximately three times higher (Table 8). Total and successful observed encounter rates were decreasing functions of increasing oyster length (Table 8). While this trend is similar to that estimated from nonlinear regression analysis, the transition in encounter rates between 25 mm and 35 mm is not as marked (Fig. 12b). When related to prey density, total encounter rates within the 15 mm size class experiment were significantly different; at 25 mm and 35 mm SL they were not (ANOVA; 15 mm SL: F = 8.73, df = 3,19, P<0.001; 25 mm SL: F = 3.1, df = 2,17, P = 0.07; 35 mm SL: F = 0.66, df = 2,19, P = 0.53). At 15 mm SL, highest encounter rates occurred at a prey density of 40 oysters/tank followed by 250, 20 and 120 (SNK: EWER = 0.05). The significant variation in encounter rates with density at 15 mm, is contrary to model predictions of a constant a’ (Hassell 1976, Hassell et al. 1977).

Attack success rates and successful encounter rates varied as function of oyster length and density (Fig. 13). The highest proportion of successful attacks occurred at the smallest prey size class, which

Figure 12. (A) Proportional instantaneous attack rates (a') related to oyster density at three oyster size-classes. Rates were estimates from nonlinear functional response models. (B) Mean number of encounters (total) per 1h observation period at three oyster size-classes. Vertical bars equal 1 S.E.


A
ATTACK RATE (a') (0.33 M² * h)⁻¹
.04
.03
.02
.01
0.00
15 mm SL
25 mm SL
35 mm SL
5 10 20 30 40 50 80 120 250 300
B
ENCOUNTER RATE (oysters * hr⁻¹)
18
16
14
12
10
8
6
4
2
15 mm SL
25 mm SL
35 mm SL
0 5 10 20 30 40 50 120 250
OYSTER DENSITY (NO./0.33 M²)

ranged from 80 to 54% (Fig. 13a). At 25mm and 35 mm SL, attack success rates declined steeply with increasing prey density ranging from 58 to 27% and 31 to 14%, respectively (Fig. 13a). At 25 mm and 35 mm SL, the trend in attack success rates and proportional mortality rates, as a function of increasing prey density were very similar (compare Figs. 11 and 13a). In this instance, increased proportional mortality rates correspond to an increase in the proportion of successful attacks/encounters (Fig. 13). In contrast, at 15 mm SL the pattern appears to be reversed. These results suggests that the 1-hr observation period during the 15 mm size class experiment, may not be adequate to quantify behaviors indicative of the total successful encounter rate response over a 24-h period.

Successful encounter rates within the 15 mm SL experiment differed significantly by density, but not at 25 mm and 35 mm SL (ANOVA; 15 mm SL: $F = 31.16$, $df = 3,19$, $P<0.0001$; 25 mm SL: $F = 0.67$, $df = 2,17$, $P = 0.53$; 35 mm SL: $F = 1.10$, $df = 2,19$, $P = 0.36$). At 15 mm SL, highest successful encounter rates occurred at a prey density of 20 oysters/tank followed in decreasing order by densities of 40, 250 and 120 oysters/tank (SNK: EWER = 0.05). At 25 mm SL, an apparent prey size threshold was reached, below which successful encounter rates significantly increased (Fig. 13b).

To evaluate any potential behavioral mechanisms regulating proportional attack success or successful encounter rates, I compared persistence times in unsuccessful encounters as a function of oyster length and density. The 15 mm size class experiment had a significant linear relationship with oyster length, and only persistence times at 25

Figure 13. (A) Proportion of successful encounters per 1h observation period related to oyster density at three oyster size-classes. (B) Mean number of successful encounters at three oyster size-classes per 1h observation period. Vertical bars equal 1 S.E.

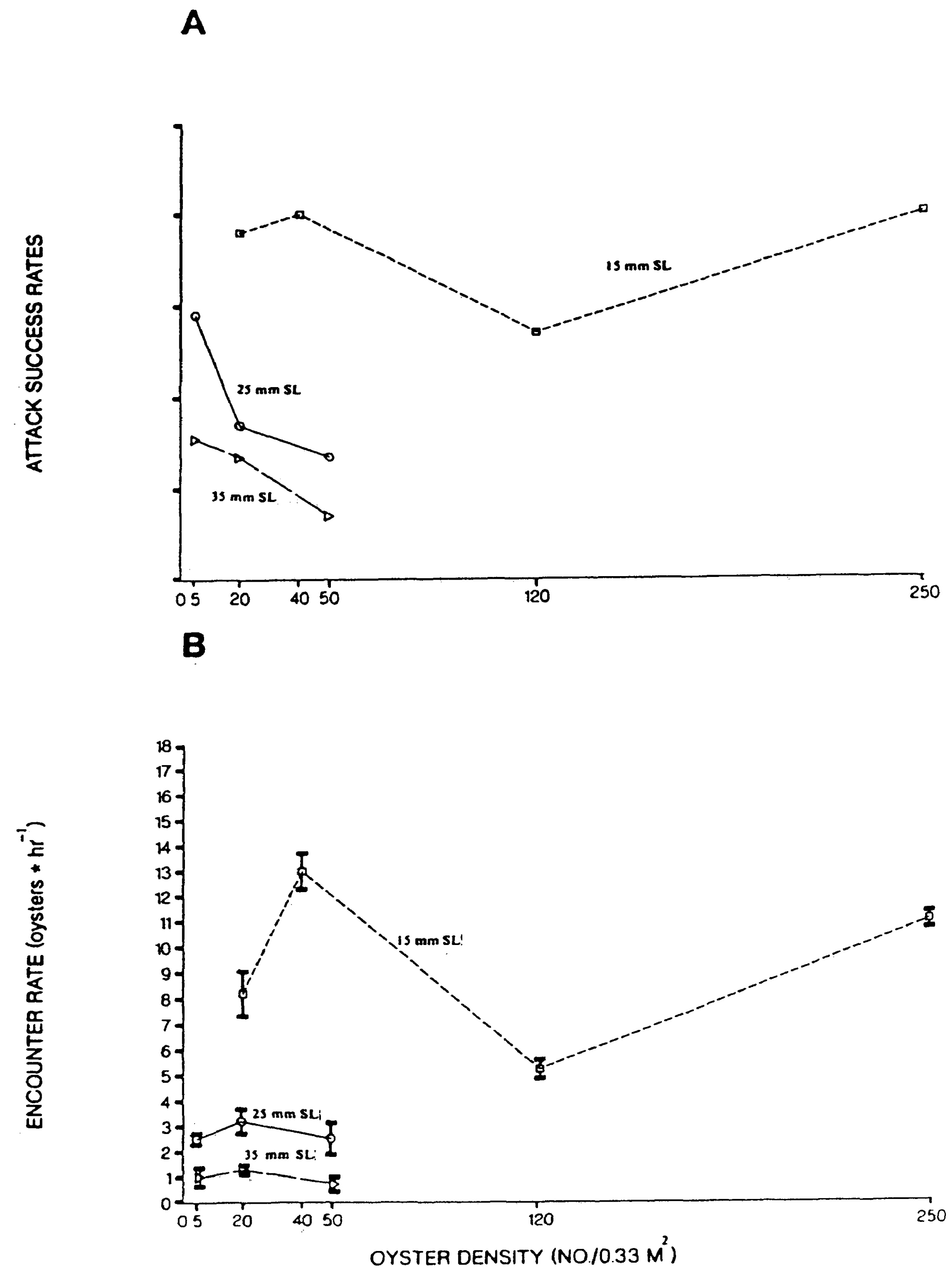
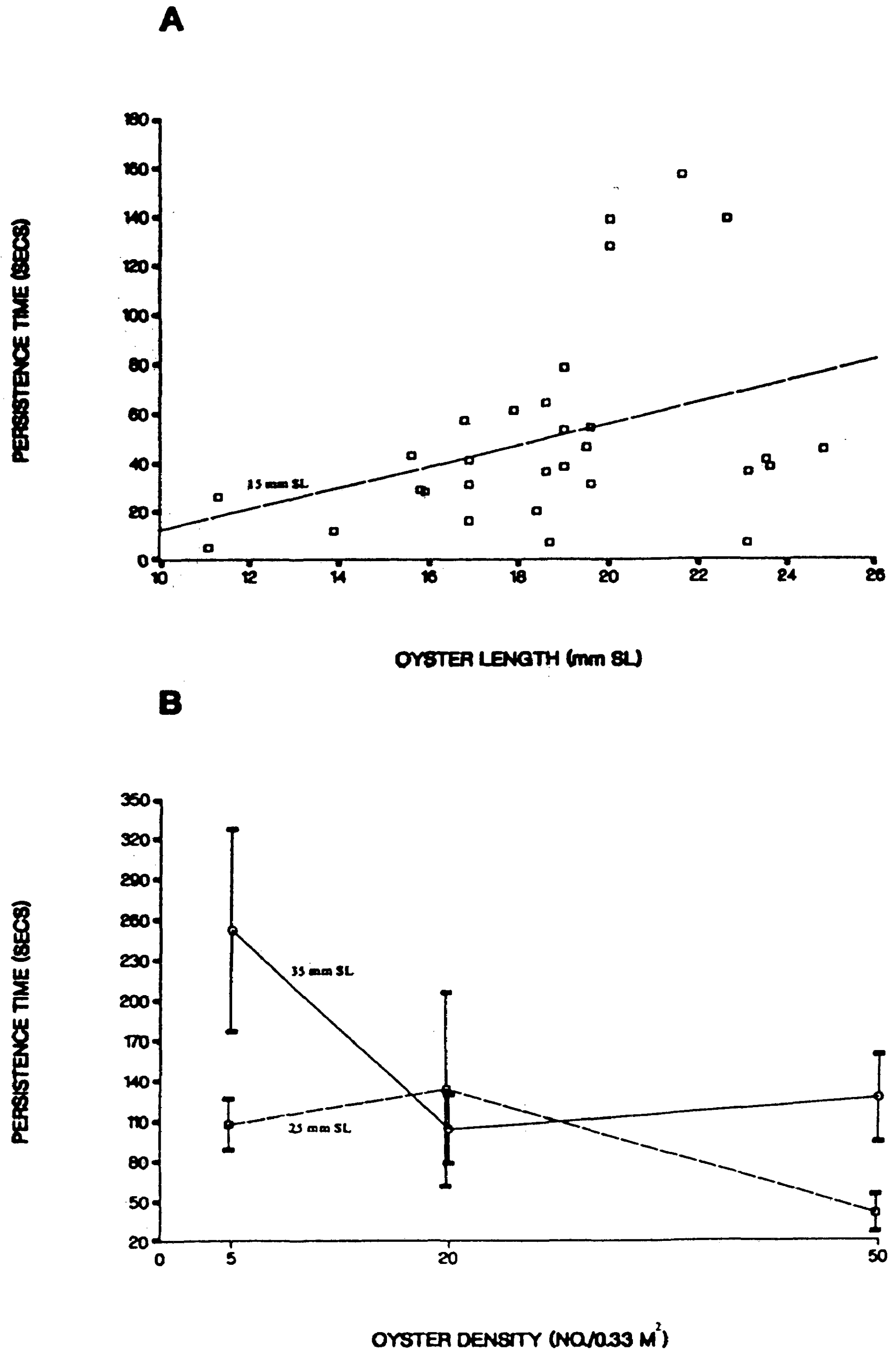

A
ATTACK SUCCESS RATES
15 mm SL
25 mm SL
35 mm SL
0 5
20
40
50
120
250
B
ENCOUNTER RATE (oysters * hr^{-1})
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
15 mm SL
25 mm SL
35 mm SL
0 5
20
40
50
120
250
OYSTER DENSITY (NO./0.33 M^2)

Figure 14. (A) Persistence times of _C_. _sapidus_ in unsuccessful encounters with small (15 mm SL) _C_. _virginica_ compared against oyster length. (B) Mean persistence times of _C_. _sapidus_ in unsuccessful encounters with _C_. _virginica_ at two oyster size-classes per 1h observation period. Vertical bares equal 1 S.E.


A
PERSISTENCE TIME (SECS)
180
160
140
120
100
80
60
40
20
0
10
12
14
16
18
20
22
24
26
35 mm SL
OYSTER LENGTH (mm SL)
B
PERSISTENCE TIME (SECS)
350
320
290
260
230
200
170
140
110
80
50
20
0
5
20
50
35 mm SL
25 mm SL
OYSTER DENSITY (NO./0.33 M²)

mm SL demonstrated significant variation with respect to density (Table 9, Fig. 14). At 25 mm SL, Tp was significantly lower at a density of 50 oysters/tank followed in increasing order by densities of 5 and 20 (SNK: EWER = 0.05) (Fig. 14b).

Handling time components in successful encounters generally increased with increasing oyster length, with no significant effect of prey density manipulations (Table 9). Breaking times (Fig. 12) of large oysters were significantly higher than small and medium oysters (slopes; F = 40.3, df = 2,129, P<0.0001; Tukey-Test EWER = 0.05). Although slopes for breaking times of 15 mm and 25 mm SL oysters were equal, elevations were not (t = 24.0, df = 2,100, P<0.0001) (Fig. 15a). At 15 mm and 25 mm SL, Tb averaged 35.5 and 116.0 seconds respectively, and displayed a significant positive linear relationship with oyster length (Fig. 15a, Table 9). At 35 mm SL, Tb averaged 709 seconds and was extremely variable resulting in a nonsignificant linear relationship with oyster length (Fig. 15a, Table 9). This lack of linearity for Tb of large oysters corresponds well with the nonsignificance in observed persistence times as a function of oyster length and density at 35 mm SL (Table 9). Eating times (Te) displayed a significant positive linear relationship with oyster length at all three prey size classes and averaged 69.0 secs (15 mm SL), 201.1 secs (25 mm SL), and 427.3 secs (35 mm SL) (Fig. 15b, Table 9). Linear regression coefficients of eating times (Fig. 15) increased significantly for large oysters relative to small and medium oysters (ANCOVA; F = 82.6, df = 2,129, P<0.0001; Tukey-Test: EWER = 0.05). Although slopes for eating times of 15 mm and 25 mm SL oysters were equal, the elevations were not (T-Test; t = 2.6, df =

Figure 15. Handling time components of successful encounters per 1 h observation period, compared against oyster length within three oyster size classes ($\bar{x} \pm 2$ mm SL).

(A) Breaking time (secs):

15: $y = -94.9+7.9x$ ($r^2=.42$, n = 81)

25: $y = -69.5+6.9x$ ($r^2=.29$, n = 26)

35: $y = -1131.6+53.6x$ ($r^2=.11$, n = 28)

(B) Eating time (secs):

15: $y = -107.8+10.8x$ ($r^2=.40$, n = 81)

25: $y = -124.1+12.8x$ ($r^2=.44$, n = 26)

35: $y = -598.0+29.9x$ ($r^2=.47$, n = 28)

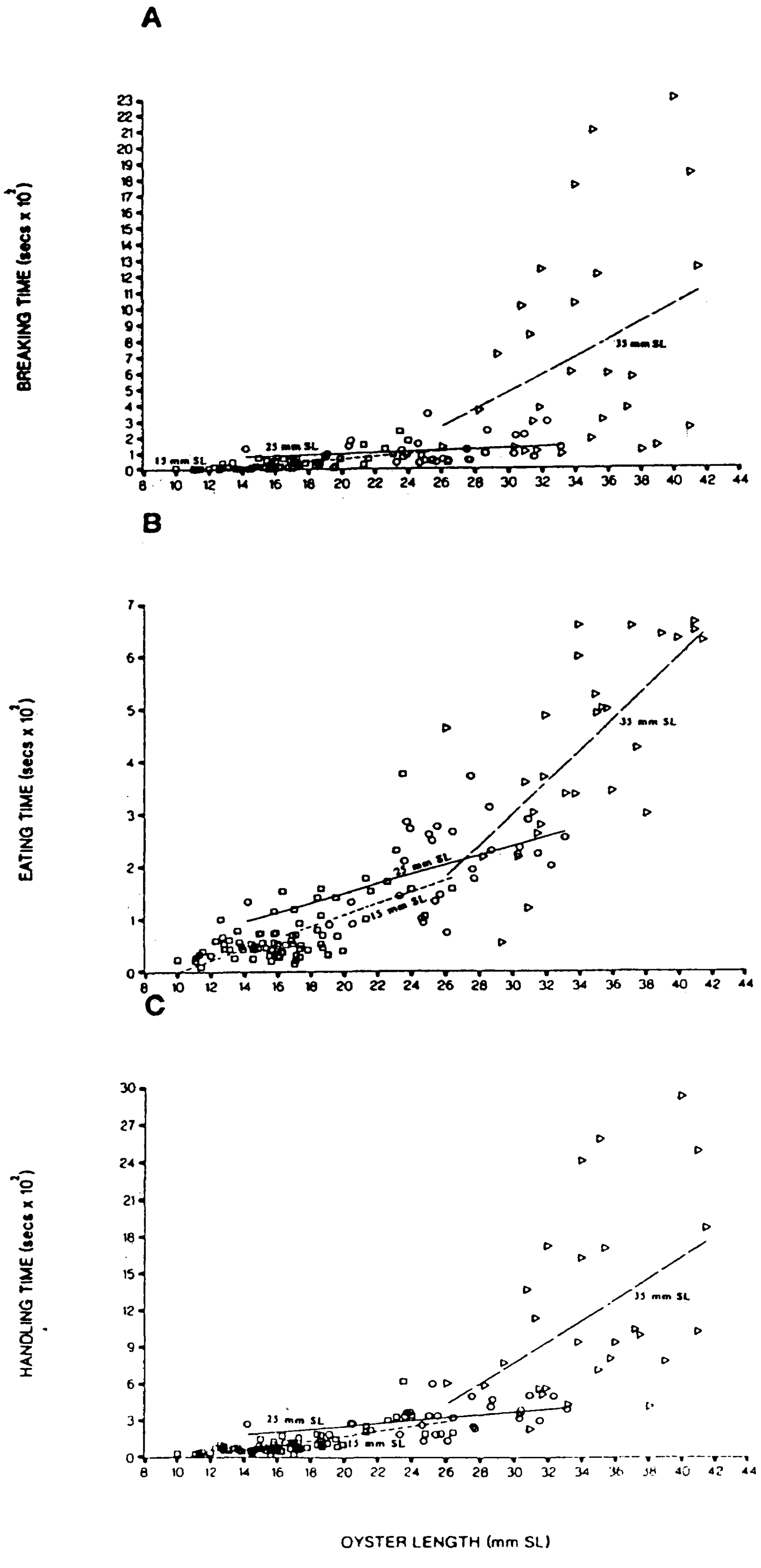
(C) Handling time (secs):

15: $y = -202.6+18.7x$ ($r^2=.52$, n = 80)

25: $y = -170.1+18.5x$ ($r^2=.52$, n = 26)

35: $y = -1803.05+85.7x$ ($r^2=.21$, n = 28)

See Table 9 for significance levels.


A
BREAKING TIME (secs x 10^3)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
15 mm SL
25 mm SL
35 mm SL
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
42
44
B
EATING TIME (secs x 10^3)
0
1
2
3
4
5
6
7
25 mm SL
15 mm SL
35 mm SL
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
42
44
C
HANDLING TIME (secs x 10^3)
0
3
6
9
12
15
18
21
24
27
30
25 mm SL
15 mm SL
35 mm SL
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
42
44
OYSTER LENGTH (mm SL)

2,100, P<0.005) (Fig. 15b). Variability in Te at oyster lengths greater than 25 mm was greatly reduced relative to Tb (Fig. 15b). The reduced variability in Te probably reflects the volume of flesh ingested or surface area of shell gleaned rather than differences in shell thickness or oyster attachment geometry. Comparison of Tb and Te ratios for each size class indicated that Tb was approximately twice that of Te at 35 mm SL, while at 15 mm and 25 mm they were approximately half. This suggests that Tb is a major component in oyster handling times above 25 mm SL and should decrease prey profitability estimates compared to smaller (eg. < 15 mm) oyster lengths. Handling times (Th) generally increased asymptotically with oyster length (Fig. 15c). Size classes of 15 mm and 25 mm SL demonstrated a significant positive linear relationship with oyster length, while 35 mm SL did not (Table 9). Linear regression coefficients of handling times (Fig. 15) increased significantly for large oysters relative to small and medium oysters (ANCOVA; F = 17.9, df = 2,129, P<0.0001; Tukey-Test: EWER = 0.05). Although slopes for eating times of 15 mm and 25 mm SL oysters were equal, elevations were not (T-Test; t = 3.6, df = 2,100, P<0.0001) (Fig. 15c).

Profitability curves derived from single regressions of yield and breaking time of C. virginica peaked at approximately 12 mm SL and decreased greatly with increasing oyster length (Fig. 16a). For 25 mm and 35 mm SL oysters, estimated profitability was highest at approximately 30 mm and 26 mm SL, respectively (Fig. 16b). Incorporation of eating time into profitability estimates did not change the previously indicated size optima for each size class, but greatly

Figure 16. Profitability of C. virginica calculated as the ratio of predicted yield (mg dry weight) to observed breaking time (secs). Curves were derived from regressions of yield on oyster length at three oyster size-classes: (A) 15 mm SL and (B) 25 and 35 mm SL.

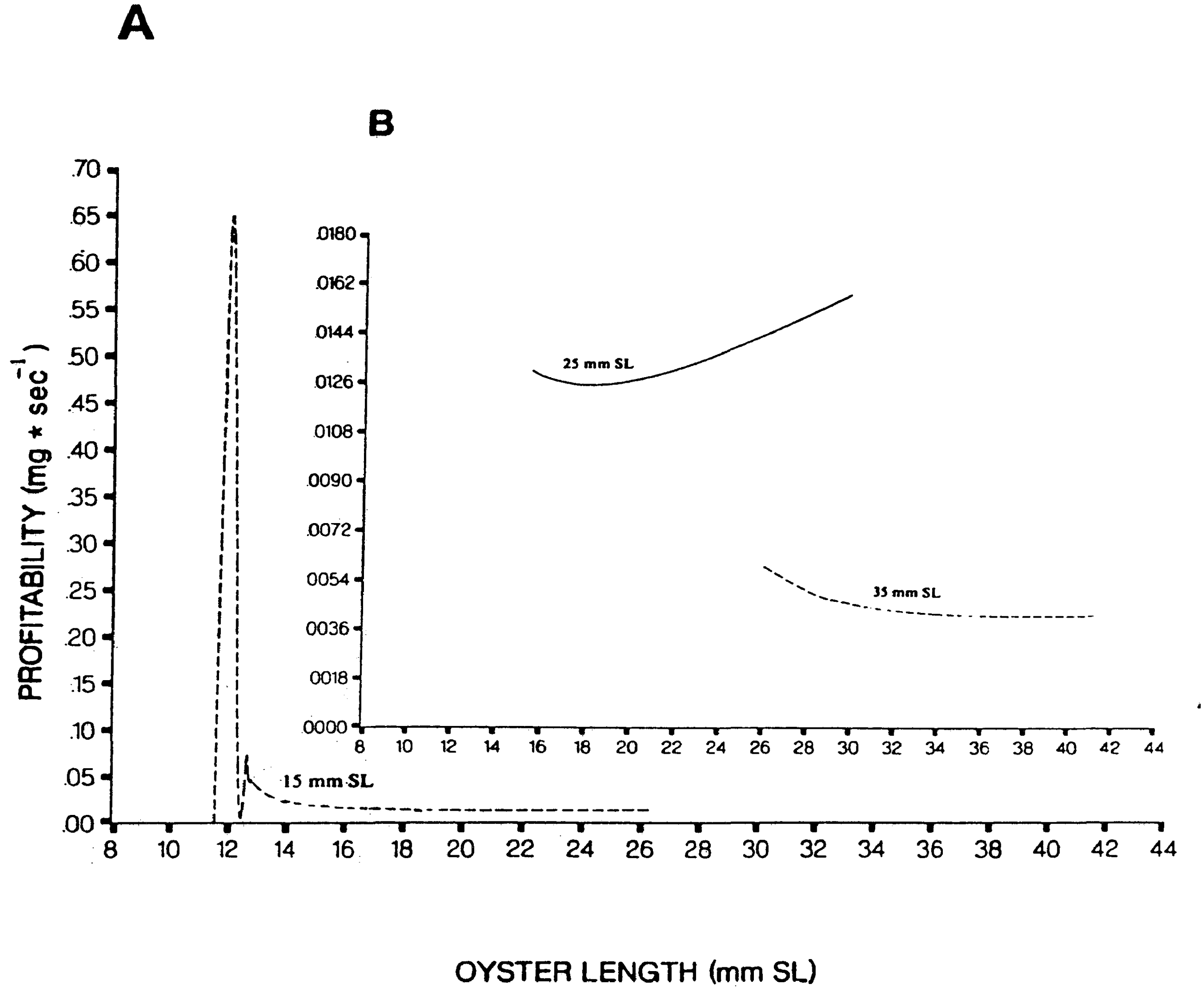

A
B
PROFITABILITY (mg * sec-1)
.70
.65
.60
.55
.50
.45
.40
.35
.30
.25
.20
.15
.10
.05
.00
15 mm SL
.0180
.0162
.0144
.0126
.0108
.0090
.0072
.0054
.0036
.0018
.0000
25 mm SL
35 mm SL
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
42
44
OYSTER LENGTH (mm SL)

Figure 17. Profitability of *C. virginica* calculated as the ratio of predicted yield (mg dry weight) to observed handling time (secs). Curves were derived from regressions of yield on oyster length at three oyster size-classes: (A) 15 mm SL and (B) 25 and 35 mm SL.

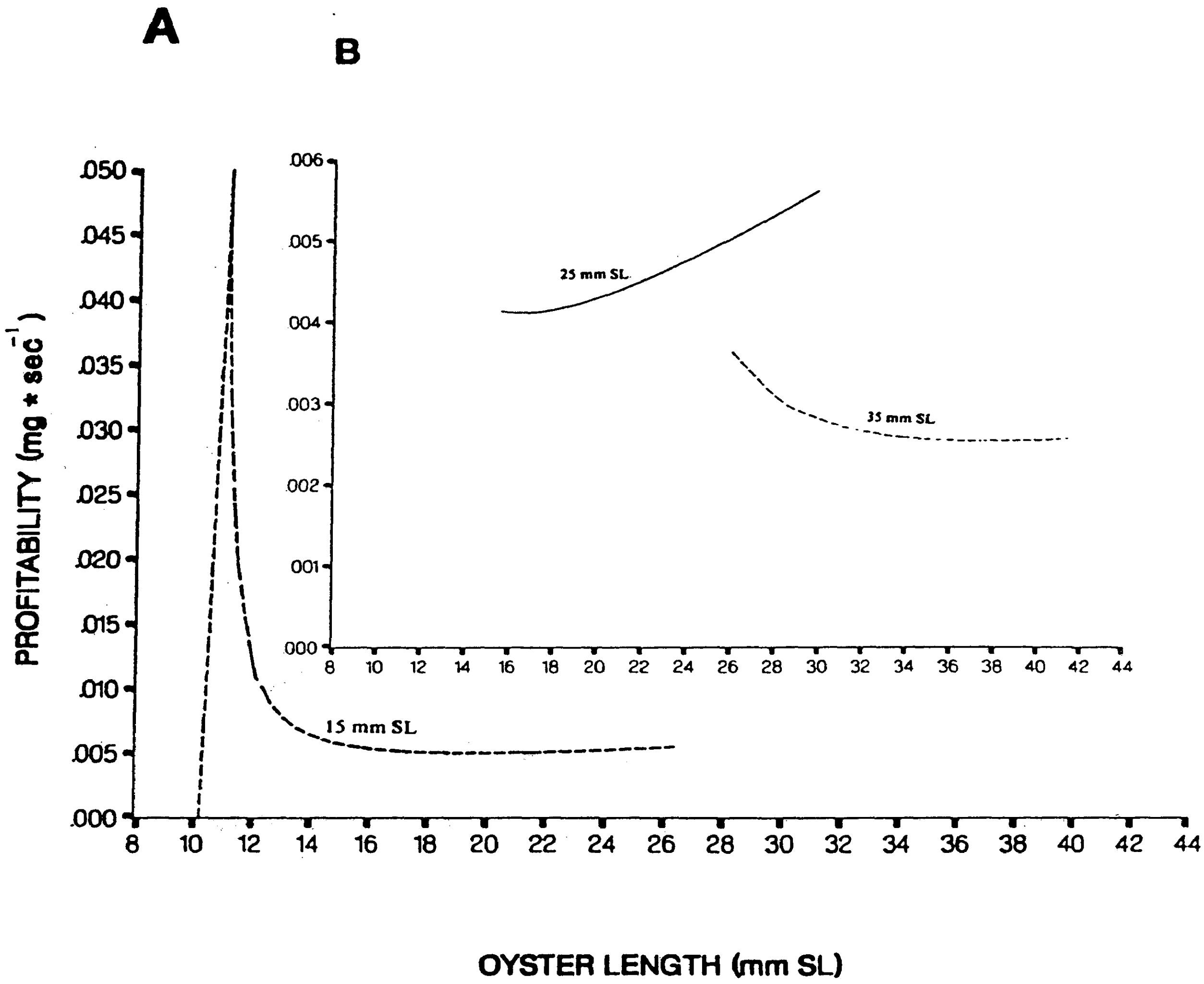
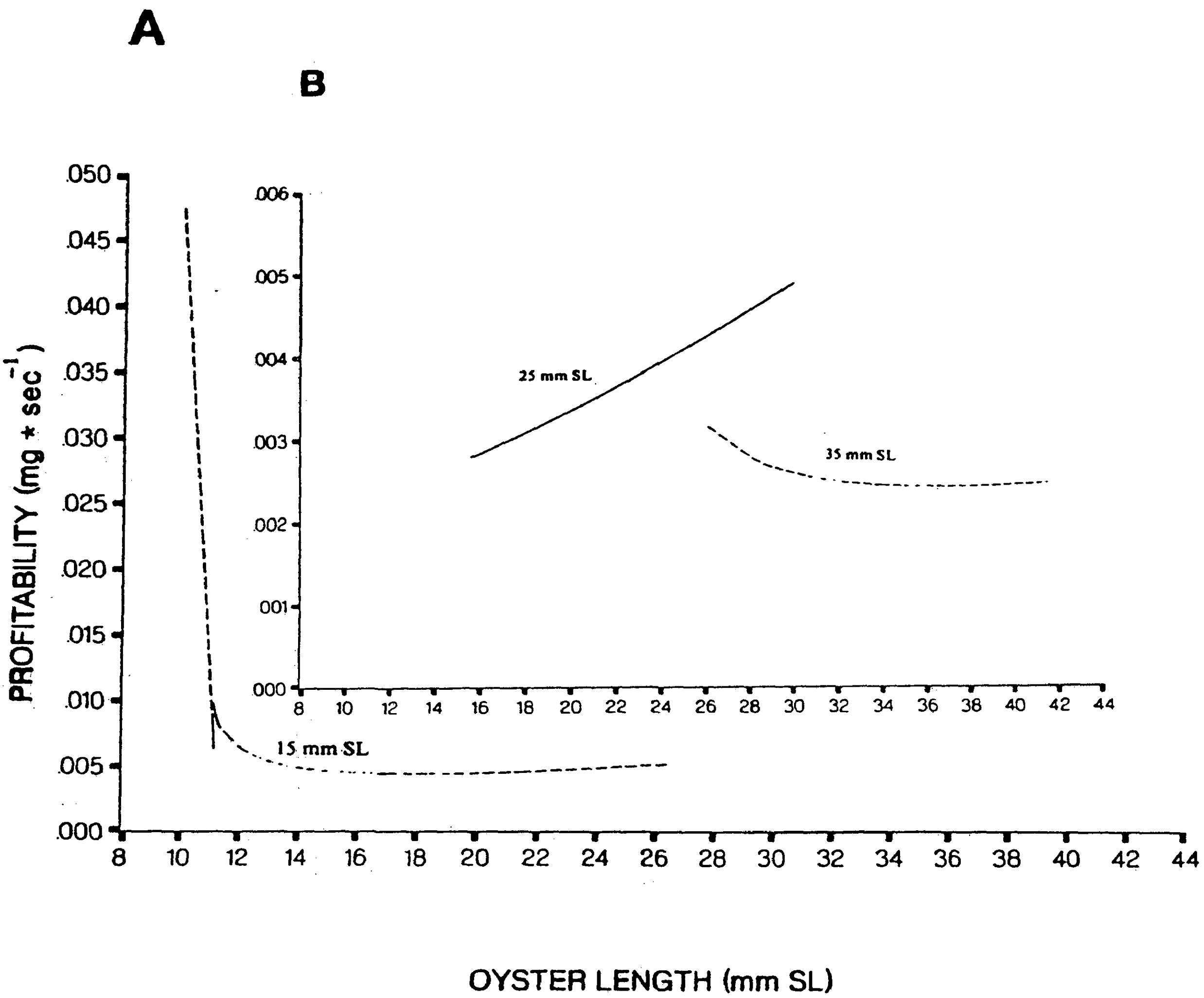

A
B
PROFITABILITY (mg * sec^{-1})
.050
.045
.040
.035
.030
.025
.020
.015
.010
.005
.000
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
42
44
15 mm SL
.006
.005
.004
.003
.002
.001
.000
25 mm SL
35 mm SL
OYSTER LENGTH (mm SL)

Figure 18. Profitability of _C_. _virginica_ calculated as the ratio of predicted yield (mg dry weight) to observed handling time incorporating mean persistence time in unsuccessful encounters (secs). Curves were derived from regressions of yield on oyster length at three oyster size-classes: (A) 15 mm SL and (B) 25 and 35 mm SL.

A
B
PROFITABILITY (mg * sec^{-1})
.050
.045
.040
.035
.030
.025
.020
.015
.010
.005
.000
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
42
44
OYSTER LENGTH (mm SL)
15 mm SL
.006
.005
.004
.003
.002
.001
.000
25 mm SL
35 mm SL

reduced profitability estimates. At 15 mm SL, profitability was reduced nearly 13 times, while estimates at 25 mm and 35 mm SL decreased approximately 3 and 2 times, respectively (Figs. 17a,b). When adjusted for the persistence times in proportional unsuccessful encounters, profitability estimates at 15 mm SL peaked at an oyster length of approximately 11 mm SL. Profitability declined steeply beyond 10 mm and leveled off at approximately 14 mm SL (Fig. 18a). Profitability at 25 mm displayed a more linear relationship with oyster length compared to unadjusted estimates (Fig. 18b). Estimates at 35 mm SL were relatively unaffected by incorporation of Tp in profitability estimates (Fig. 18b).

Crab size effects: functional responses

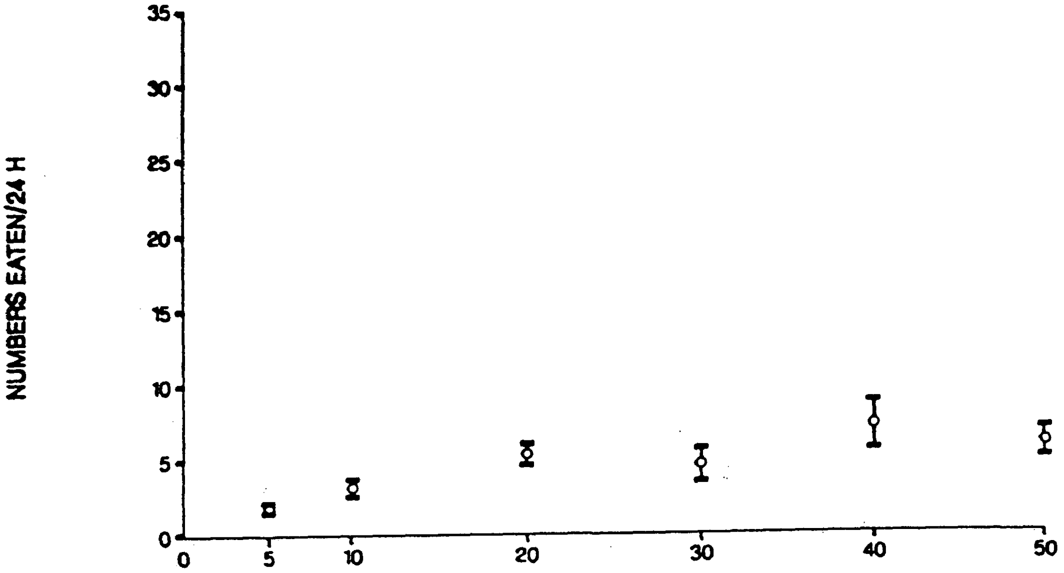
Large oysters

Crab consumption rates of large oysters ($\bar{x}$ = 35 ± 2 mm SL) within two crab size classes increased significantly with oyster density (ANOVA; 135-165 mm CW: $F = 5.0$, df = 5,89, $P<0.0005$; 100-125 mm CW: $F = 6.2$, df = 5,45, $P<0.0002$) and increasing carapace widths above 80 mm (Fig. 19). Of the six small crabs (60-80 mm CW) exposed to large oysters, none were capable of a successful encounter. This experiment was terminated after 4 replicates (24 individual feeding trials) in which numerous unsuccessful opening techniques were attempted. To verify that these crabs could actively feed they were systematically exposed to smaller length oysters until a successful encounter was observed for each individual. This occurred at an oyster length of approximately 29 mm. For medium crabs, consumption rates were

Figure 19. Functional responses of two *C. sapidus* size-classes feeding on large oysters ($\bar{x}$ = 35 mm SL). Each point respresents the mean feeding rate over 24h. Vertical bars equal 1 S.E. N = 6-10 replicates per prey density.

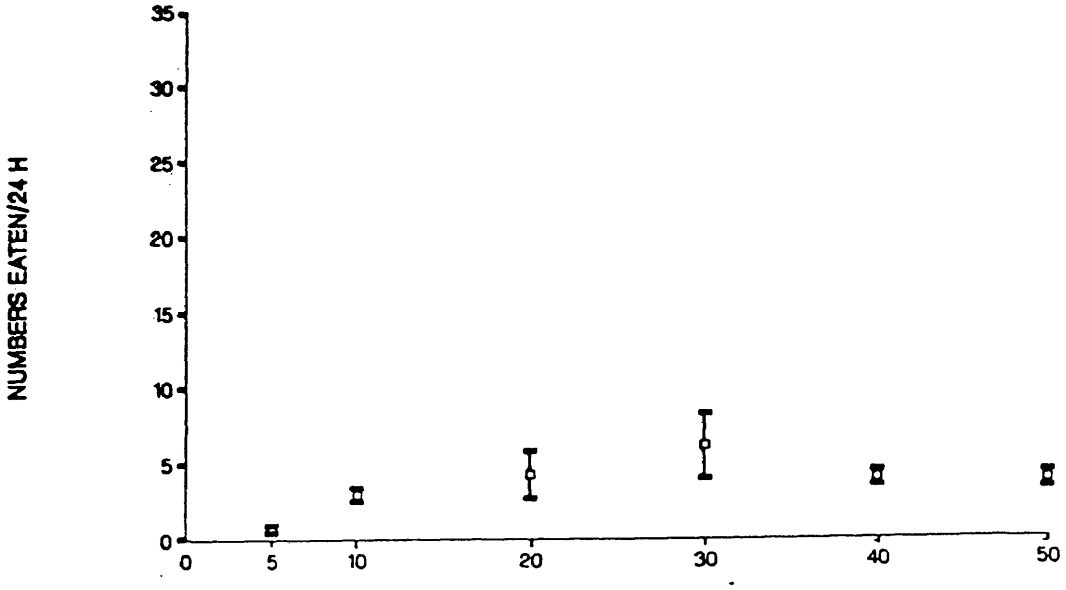
135-165 mm CW

TYPE II RESPONSE



100-125 mm CW

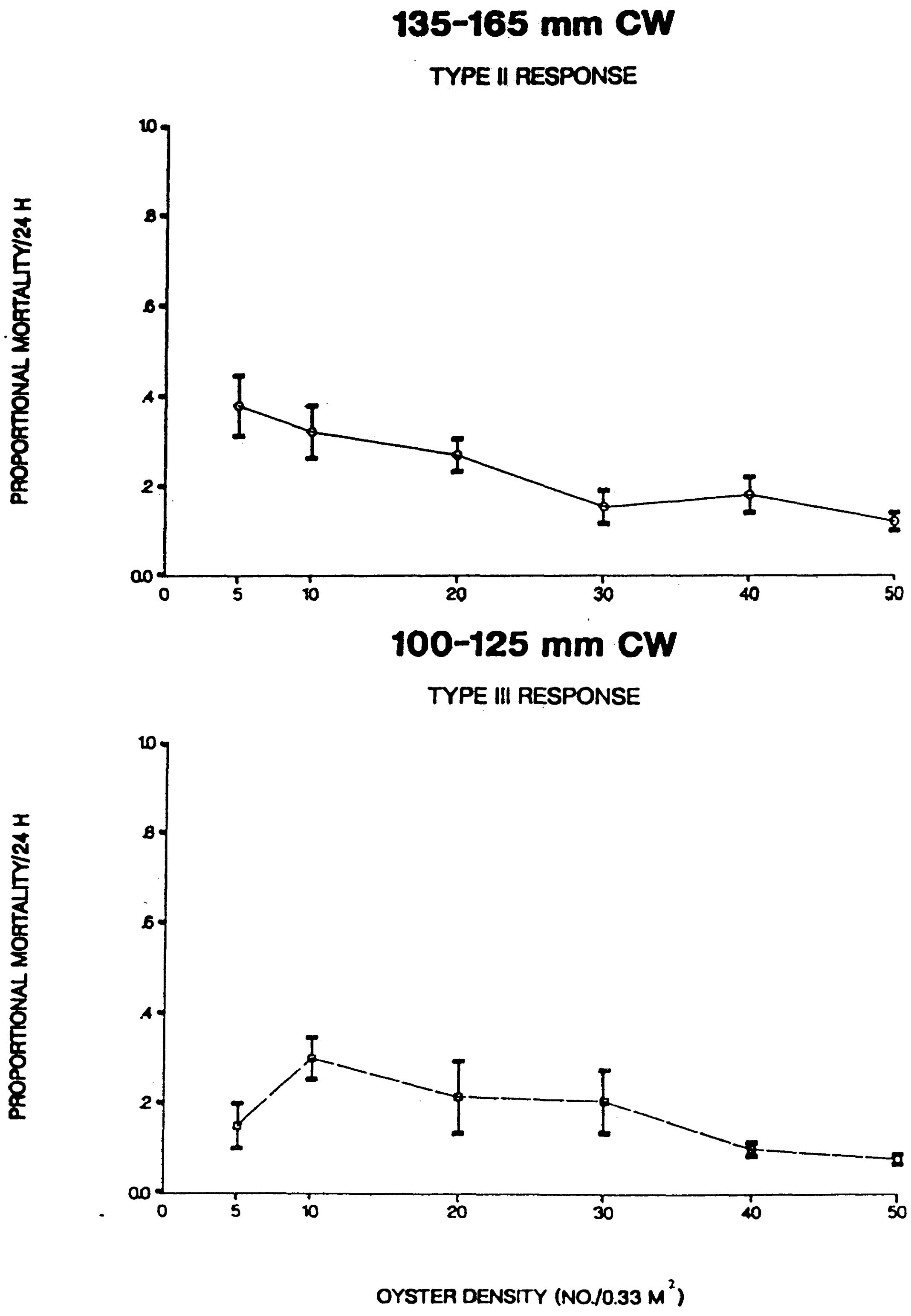
TYPE III RESPONSE



OYSTER DENSITY (NO./0.33 M^2)

LARGE OYSTER LENGTH

Figure 20. Proportional mortality of large ($\bar{x}$ = 35 mm SL) _C_. _virginica_ at six densities as a function of crab carapace width. Each point represents the mean proportional mortality over 24h. Vertical bars equal 1 S.E. N = 6-10 replicates per prey density.



LARGE OYSTER LENGTH

significantly lower at 5 oysters/tank compared to higher densities (SNK: EWER = 0.05) (Fig. 19). Consumption rates for large crabs were significantly lower at 5 and 10 oysters/tank relative to increased densities (SNK: EWER = 0.05) (Fig. 19).

Differences in functional responses at two different crab size-classes were determined by analyzing proportional mortality rates as a function of oyster density (Fig. 20). Proportional mortality rates of C. virginica for large and medium size-class crabs differed significantly with oyster density (ANOVA; 135-165 mm CW: F = 4.9, df = 5,89, $P<0.0005$; 100-125 mm CW: F = 0.06, df = 5,45, $P<0.031$). For 135-165 mm CW crabs, significantly higher proportional mortality rates occurred at the lowest densities of 5 and 10 oysters/tank ($\bar{x}$ = 38 and 32%, respectively) than at increased densities ($\bar{x}$ = 12-27%) (SNK: EWER = 0.05) (Fig. 20). This pattern typifies an inversely density-dependent relationship characterized by a type II functional response. For 100-125 mm CW crabs, proportional mortality rates were significantly higher at an intermediate density of 10 oysters/tank ($\bar{x}$ = 30%) than at lower and higher densities ($\bar{x}$ = 7-21%) (SNK: EWER = 0.05) (Fig. 20). This pattern of decreasing proportional mortality rates at the lowest prey density typifies a density-dependent sigmoid relationship characteristic of a type III response. Hence, the existence of a partial prey refuge from predation by medium-size crabs below densities of approximately 5 oysters/tank or 15.2 oysters/m^2.

Individual crabs within large and medium size-classes differed significantly from each other in their functional responses

(Heterogeneity G-Test; 135-165 mm CW: $G = 55.5$, $df = 25$, $P<0.0004$; 100-125 mm CW: $G = 22.2$, $df = 12$, $P<0.034$).

Crab size effects: functional response models

General model

The general functional response model (Eq. 5) (Real 1977, 1979) was unable to adequately describe response types for consumption rates at either crab size-class treatment. For 135-165 mm CW crabs, the model explained only 22.7% of the total variance and was unable to predict a response type as indicated by $\hat{n}$ being significantly different from 0, 1 and 2 ($\hat{n} = 0.58$) (Table 10). The ANOVA of proportional mortality rates indicated a type II response (Fig. 20). For 100-125 mm CW crabs, the model indicated a type II response with $\hat{n}$ not significantly different from 1 ($\hat{n} = 0.81$) (Table 10), whereas the ANOVA of proportional mortality rates determined a type III response (Fig. 20). For the medium-size crabs, the residuals about the predicted values were distributed randomly (Table 10) and variances were equal (Hartley's F-Max Test). Similar to results found for general model fitting procedures at 19-20^{o} C, the functional response model for medium-size crabs does not fit the lowered proportional mortality rate at 5 oysters/tank (Fig. 20). Examination of the residuals at the lowest prey density indicated a consistent distribution above the predicted mean. Thus, for the 100-125 mm CW treatment, a decrease in proportional mortality at 5 oysters/tank, and a significant increase at an intermediate density of 10 oysters/tank (Fig. 20) appear to be responsible for the type III response. For the 135-165 mm CW treatment, the significant increase in proportional mortality rates at the lowest prey density (Fig. 20) appears to be responsible for a type II response.

Conceptual models

The type of functional response exhibited by C. sapidus eating large oysters varied as function of crab carapace width (Fig. 19), but the fit of continuous- and discrete-time models was similar (Table 11). For 135-165 mm and 100-125 mm CW crabs, both continuous- and discrete-time nonlinear models provided a statistically adequate fit as indicated by the nonsignificant "lack-of-fit" error (Table 11). The discrete-time models for both large and medium-size crabs, however explained more (85.5 and 88.5%, respectively) of the variance in consumption and were characterized by lower residual sums of squares (Table 11). Therefore, the functional response for 135-165 mm CW crabs is best described by a type II discrete-time model:

$$Na = Nt[1-e^{-.005(24-0.1Na)}],$$

and for 100-125 mm CW crabs, is best described by a type III discrete-time model:

$$Na = Nt\{1-e^{\frac{-0.01Nt}{[1+2.0Nt\ (23.9Na)]}}\}.$$

Nonlinear regressions with functional response models (Table 11) estimated handling times per oyster by C. sapidus to be 0.1 hr, irrespective of crab carapace width (Table 12). Attack rate estimates were 0.005 for the type II model (135-165 mm CW crabs) and, when a' was computed from eqn (6), with nonlinear regression estimates of b and c, equaled 0.005 for the type III model as well (100-125 mm CW crabs) (Table 11).

Crab size effects: functional responses

Medium oysters

Blue crab consumption rates of medium oysters ($\bar{x}$ = 25 ± 2 mm SL) within three crab-size-classes increased significantly with oyster density (ANOVA; 135-165 mm CW: F = 32.9, df = 5,45, P<0.0001; 100-125 mm CW: F = 12.3, df = 5,44, P<0.0001; 60-80 mm CW: F = 40.0, df = 5,41, P<0.0001). For 135-165 mm CW crabs, consumption rates were significantly highest at 50 oysters/tank (SNK: EWER = 0.05), and averaged 27 oysters * crab^{-1}* [24 h]$^{-1}$, at this density (Fig. 21). For both 60-80 mm CW and 100-125 mm CW crabs, highest consumption rates were reduced relative to large crabs, reaching an asymptote at approximately 20 oysters * crab^{-1}* [24 h]$^{-1}$(Fig. 21). For small and medium-size crabs, consumption rates were significantly higher at 40 and 50 oysters/tank, followed in decreasing order by two subgroups comprised of 30, 20 and 10 oysters/tank, and 5 oysters/tank (SNK: EWER = 0.05) (Fig. 21).

The trends in proportional mortality rates of _C_. _virginica_ as a function of prey density were analogous for all three crab size-classes, indicating an inversely density-dependent relationship between feeding rates and prey density (type II response) (Fig. 22). Proportional mortality rates significantly increased with decreasing oyster density

Figure 21. Functional responses of three C. sapidus size-classes feeding on medium oysters ($\bar{x}$ = 25 mm SL). Each point respresents the mean feeding rate over 24h. Vertical bars equal 1 S.E. N = 6-10 replicates per prey density.

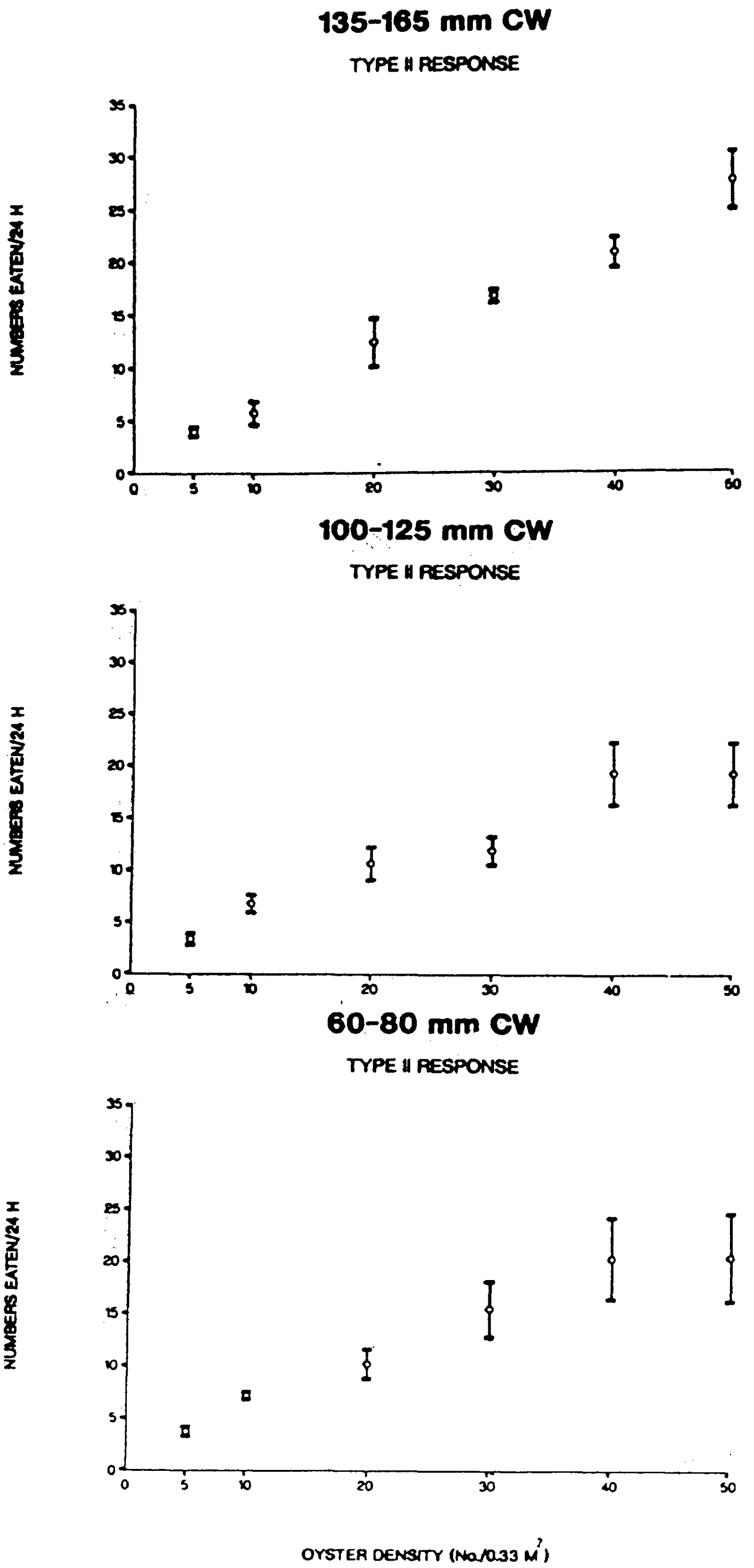
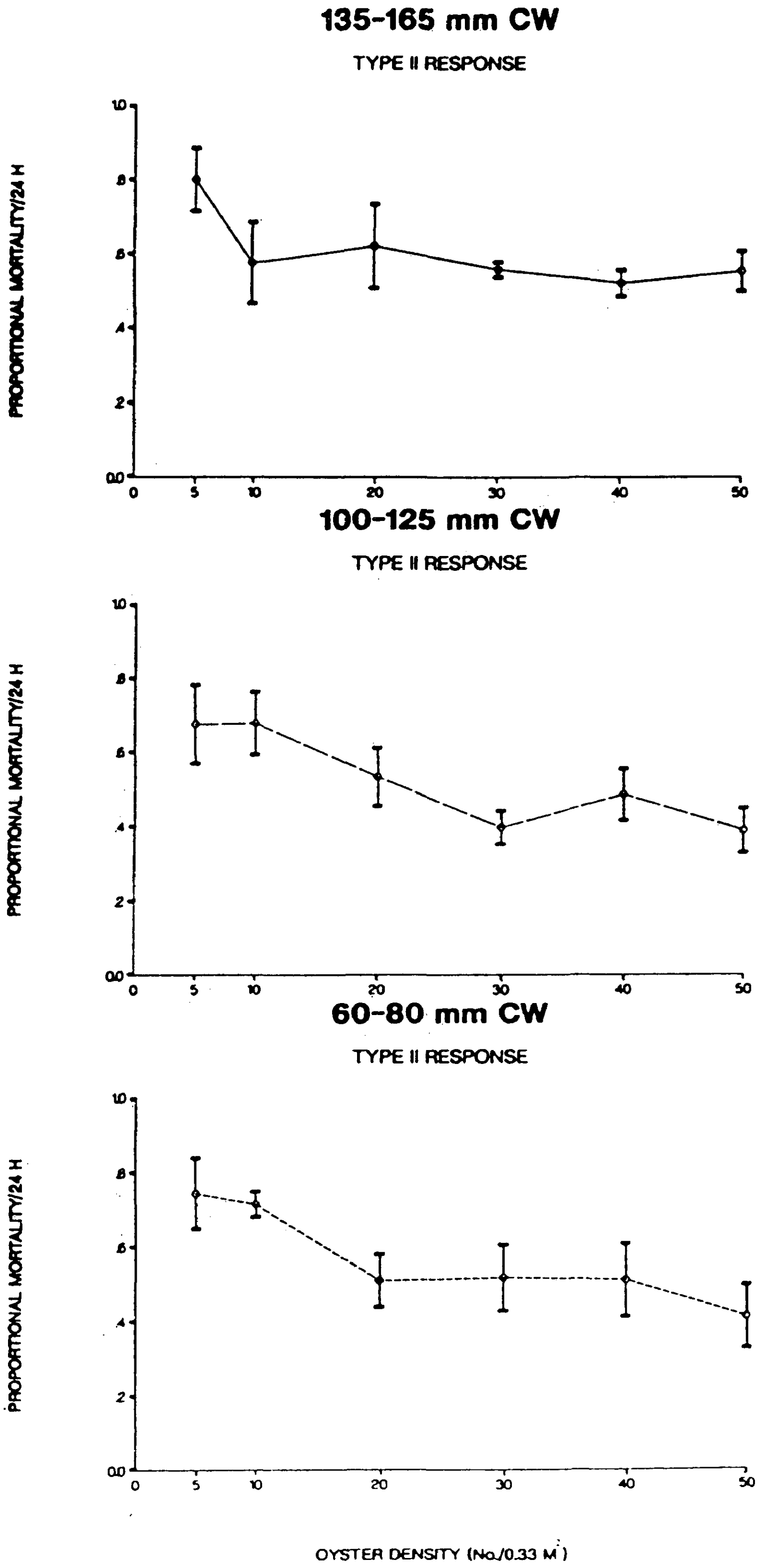

135-165 mm CW
TYPE II RESPONSE
NUMBERS EATEN/24 H
0
5
10
15
20
25
30
35
0
5
10
20
30
40
50
100-125 mm CW
TYPE II RESPONSE
NUMBERS EATEN/24 H
0
5
10
15
20
25
30
35
0
5
10
20
30
40
50
60-80 mm CW
TYPE II RESPONSE
NUMBERS EATEN/24 H
0
5
10
15
20
25
30
35
0
5
10
20
30
40
50
OYSTER DENSITY (No./0.33 M²)

Figure 22. Proportional mortality of medium ($\bar{x}$ = 25 mm SL) C. *virginica* at six densities as a function of crab carapace width. Each point represents the mean proportional mortality over 24h. Vertical bars equal 1 S.E. N = 6-10 replicates per prey density.



MEDIUM OYSTER LENGTH

(ANOVA; 135-165 mm CW: F = 3.0, df = 5,45, $P<0.02$, 100-125 mm CW: F = 2.7, df = 5,44, $P<0.034$, 60-80 mm CW: F = 3.0, df = 5,41, $P<0.023$). For large crabs (135-165 mm CW), proportional mortality rates were significantly higher at 5 oysters/tank ($\bar{x}$ = 80%) than at increased densities ($\bar{x}$ = 52-62%) (SNK: EWER = 0.05) (Fig. 22). For 100-125 mm CW crabs, proportional mortality rates were significantly higher at 5 and 10 oysters/tank (both 68%) compared to increased densities ($\bar{x}$ = 39-54%) (SNK: EWER = 0.05) (Fig. 22). Proportional mortality rates for small blue crabs (60-80 mm CW) were significantly higher at the lowest prey density (74%) compared to increased densities ($\bar{x}$ = 41-71%) (SNK: EWER = 0.05) (Fig. 22).

Individual crabs within the 100-125 mm and 60-80 mm size-class treatments differed significantly from each other in their functional responses (Heterogeneity G-Test; 100-125 mm CW: G = 124.5, df = 35, $P<0.0001$; 60-80 mm CW: G = 101.3, df = 30, $P<0.0001$), whereas individual crab responses within the 135-165 mm CW treatment were similar (G = 18.5, df = 20, P = 0.55).

Crab size effects: functional response models

General model

Analysis according to the general functional response model (Eq 5) (Real 1977, 1979) corroborated the results from the ANOVA of proportional mortality indicating a hyperbolic, type II functional response for all three crab size-classes (Table 13). For 135-165 mm CW crabs, the residuals about the predicted values were distributed randomly and nonrandomly for partial and complete data sets (Table 13), and sample variances for the transformed dependent variable were unequal (Hatley's F-Max Test). The model, however, did verify a type II response with $\hat{n}$ not significantly different from 1 ($\hat{n}$ = 0.90) (Table 13). For 100-125 mm CW crabs, the residuals were distributed randomly (Table 13) and variances were equal (Hartley's F-Max Test). The general model indicated a type II response with $\hat{n}$ not significantly different from 1 ($\hat{n}$ = 0.93) (Table 13). For the small size-class crabs, the residuals were distributed randomly, but variances for the transformed dependent variable were unequal (Table 13). The general model; however, indicated a type II response with $\hat{n}$ not significantly different from 1 ($\hat{n}$ = 0.93) (Table 13).

Conceptual models

For medium size-class oysters, continuous-time conceptual models provided the best fit to consumption rates, regardless of carapace width (Table 14). For 135-165 mm CW crabs, the functional response (Fig. 21) was best described by a type II continuous-time model:

$$Na = \frac{0.919\ Nt}{1 + (0.0038)\ Nt}$$

as indicated by the (1) low residual sums of squares, and (2) random distribution of residuals for both partial and complete data sets, relative to the discrete-time model (Table 14).

For 100-125 mm CW crabs, the continuous-time type II model explained 88.2% of the variance, and was characterized by a random distribution of residuals about the predicted values (Table 14). The discrete-time type II model indicated a significant "lack-of-fit" error and systematic distribution of residuals above the predicted values, though it described 92.2% of the variance in consumption rates and displayed the lower residual sums of squares of the two models (Table 14). Hence, the functional response for 100-125 mm CW crabs feeding on medium-size oysters is best described by a continuous-time type II model:

$$Na = \frac{0.72\ Nt}{1 + (0.015)Nt.}$$

For 60-80 mm CW crabs, the continuous-time type II model explained 82.5% of the variance, and was characterized by a random distribution of residuals about the predicted values (Table 14). The discrete-time type II model indicated a significant "lack-of-fit" error and systematic distribution of residuals above the predicted values, though it described 93.5% of the variance in consumption rates and displayed the lower residual sums of squares of the two models (Table 14). Hence, the functional response for 60-80 mm CW crabs feeding on medium-size oysters is best described by a continuous-time type II model:

$$Na = \frac{0.72\ Nt}{1 + (0.015)Nt.}$$

Nonlinear regression with functional response models (Table 14) estimated handling times per medium oyster by large crabs to be approximately 5 times less than for medium and small size crabs (0.53 and 0.49h, respectively) (Table 15). Attack rate (a’) estimates were nearly equal, regardless of carapace width (Table 15).

Crab size effects: functional responses

Small oysters

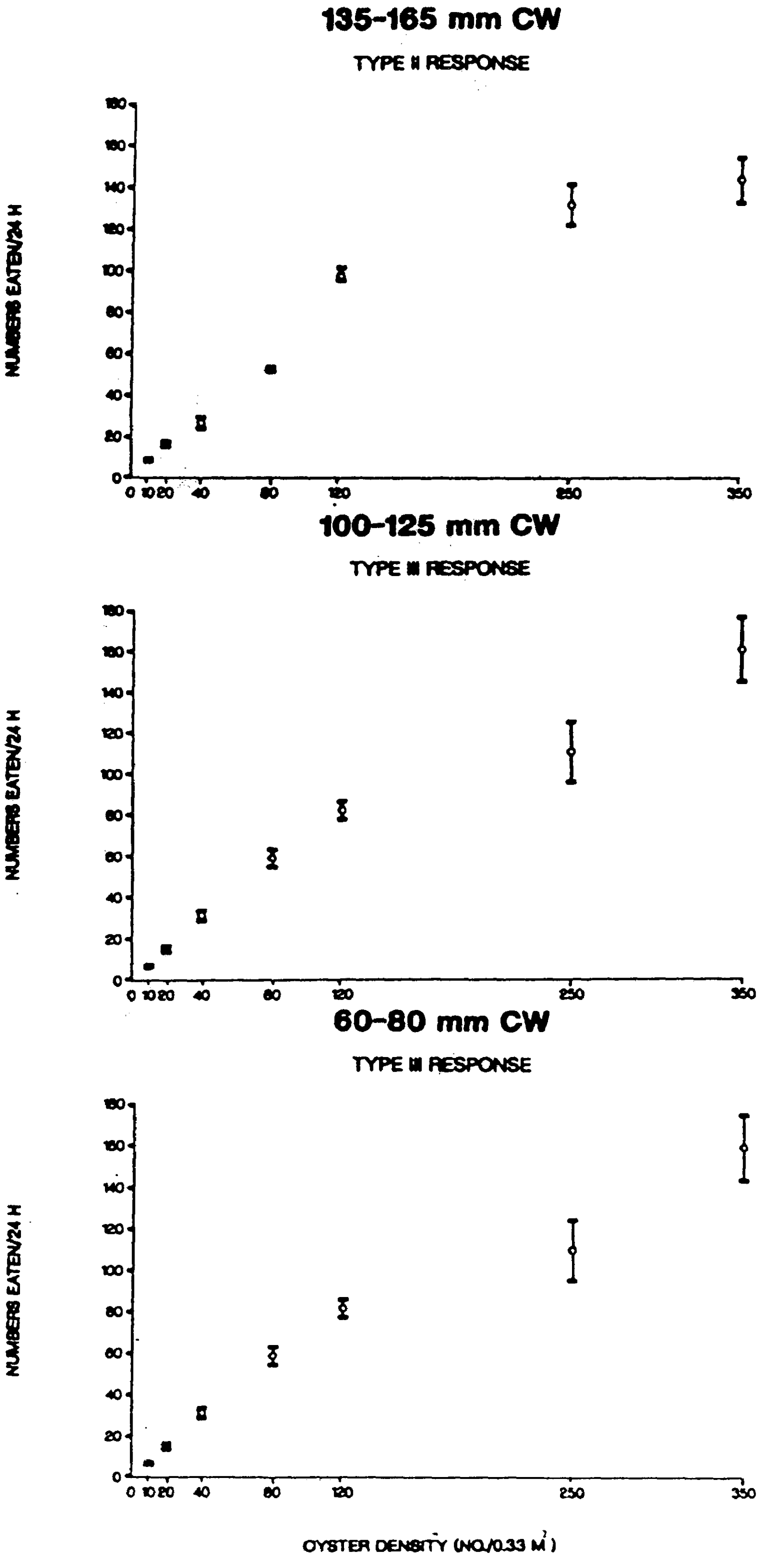
Crab consumption rates of small oysters ($\bar{x}$ = 15 ± 2 mm SL) within three crab size-classes increased significantly with oyster density (ANOVA; 135-165 mm CW: F = 221.6, df = 6,42, $P<0.0001$; 100-125 mm CW: F = 0.022, df = 6,42, $P<0.0001$; 60-80 mm CW: F = 0.014, df = 6,42, $P<0.0001$), with no apparent effect of carapace width (Fig. 23). For 135-165 mm and 100-125 mm CW crabs, consumption rates were significantly higher at 350 and 250 oysters/tank, followed in decreasing order by 120, 80, 40, 20, and 10 oysters/tank (SNK: EWER = 0.05) (Fig 23). Consumption rates of 60-80 mm CW crabs were significantly highest at 350 oysters/tank, followed in decreasing order by a subset comprised of 250 and 120 oysters/tank, followed by 80, 40, 20, and 10 oysters/tank (SNK: EWER = 0.05) (Fig. 23).

Differences in functional responses at three different crab size-classes were determined by analyzing proportional mortality rates as a function of oyster density (Fig. 24). Proportional mortality rates of _C_. _virginica_ at each of three crab size-class treatments differed significantly with oyster density (ANOVA; 135-165 mm CW: F = 6.7, df = 6,42, $P<0.0001$; 100-125 mm CW: F = 8.1, df = 6,42, $P<0.0001$; 60-80 mm CW: F = 5.5, df = 6,42, $P<0.0004$). For 135-165 mm CW crabs, proportional mortality rates were significantly higher at the two lowest prey densities of 10 and 20 oysters/tank ($\bar{x}$ = 82 and 81%, respectively), and at 120 oysters/tank ($\bar{x}$ = 81%) versus remaining densities ($\bar{x}$ = 66-41%) (SNK: EWER = 0.05) (Fig 24). This response, as previously described for 15 mm SL oysters under the subheading "Oyster length effects: functional responses", appeared atypical of the traditional type II and III responses. The pattern of proportional mortality rates at low prey densities, inferred a type II response (Fig. 24).

Proportional mortality rates for 100-125 mm CW crabs were significantly higher at intermediate densities of 20 and 40 oysters/tank, followed in decreasing order by two groups comprised of 120, 80, and 10 oysters/tank, and 250 and 350 oysters/tank (SNK: EWER = 0.05). For blue crabs of 60-80 mm CW, proportional mortality rates were significantly higher at an intermediate density of 20 oysters/tank followed in decreasing order by two subgroups comprising 40, 80, 120 and 10 oysters/tank, followed by 350 and 250 oysters/tank (SNK: EWER = 0.05) (Fig. 24). For both medium and small size-class crabs, the reduction in proportional mortality at the lowest prey density implies a density-dependent sigmoid relationship between predation rate and prey density characterized by a type III functional response. These results indicate a partial prey refuge from predation below densities of approximately 10 oysters/tank or 30.3 oysters/m^2.

Individual crabs within each size class differed significantly from each other in their functional response, regardless of carapace width (Heterogeneity G-Test; 135-165 mm CW: G = 143.0, df = 30, P,0.0001; 100-125 mm CW: G = 109.2, df = 30, P<0.0001; 60-80 mm CW: G = 93.8, df = 30, P<0.0001).

Figure 23. Functional responses of three C. sapidus size-classes feeding on small ($\bar{x}$ = 15 mm SL) oysters. Each point respresents the mean feeding rate over 24h. Vertical bars equal 1 S.E. N = 6-10 replicates per prey density.

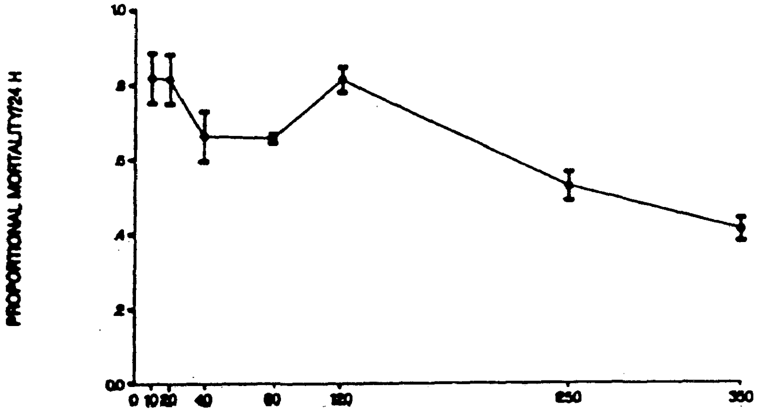


SMALL OYSTER LENGTH

Figure 24. Proportional mortality of small ($\bar{x}$ = 15 mm SL) _C_. _virginica_ at six densities as a function of crab carapace width. Each point represents the mean proportional mortality per 24h. Vertical bars equal 1 S.E. N = 6-10 replicates per prey density.

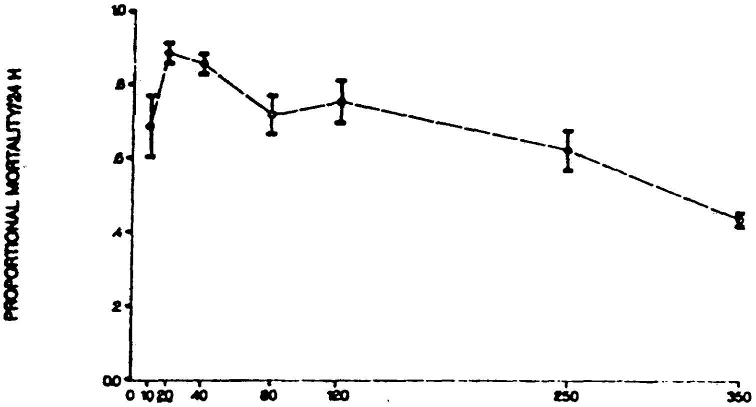
135-165 mm CW

TYPE II RESPONSE



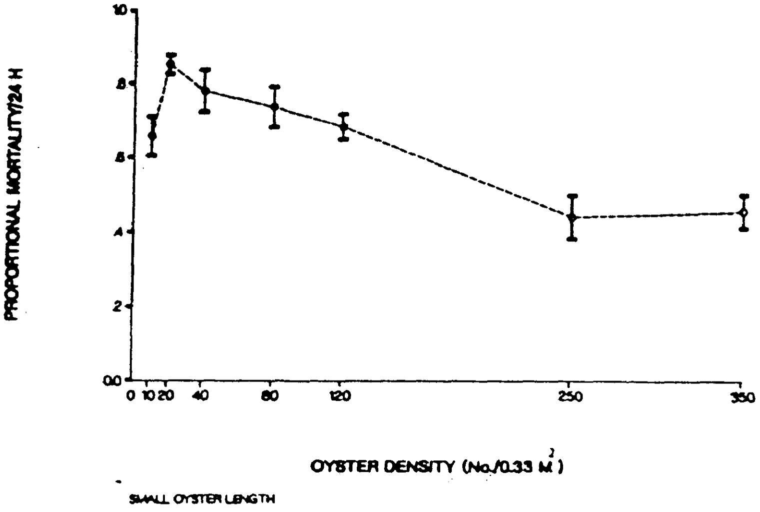
100-125 mm CW

TYPE III RESPONSE



60-80 mm CW

TYPE III RESPONSE



Crab size effects: functional response models

General model

Analysis according to the general functional response model (Eq 5) (Real 1977, 1979) corroborated the results from the ANOVA of proportional mortality for both the 135-165 mm and 60-80 mm CW crabs, indicating a hyperbolic type II response. For 135-165 mm CW crabs, the residuals about the fitted model were distributed randomly for both partial and complete data sets (Table 16); however, variances for the transformed dependent variable were unequal (Hartley's F-Max Test). Despite unequal sample variances and supportive evidence for a nontraditional functional response model at this size class, the general functional response model (Real 1977, 1979) explained 95.5% of the total variance and indicated a type II response with $\hat{n}$ not significantly different from 1 ($\hat{n}$ = 0.99) (Table 16). For 100-125 mm CW crabs, the general functional response model indicated a type II response with $\hat{n}$ not significantly different from 1 ($\hat{n}$ = 1.1) (Table 16), whereas the ANOVA of proportional mortality rates determined a type III response. The residuals about the fitted model were distributed randomly and nonrandomly for complete and partial data sets, respectively (Table 16). Additionally, unequal sample variances were found for transformed dependent variables (Hartley's F-Max Test). Examination of the residuals at the lowest prey density indicated a consistent distribution above the predicted value. For small size-class crabs (60-80 mm CW), the model indicated a type II response with $\hat{n}$ not significantly different from 1 ($\hat{n}$ = 1.0) (Table 16), whereas the ANOVA of proportional mortality rates indicated a type III response. Complete examination of the residuals indicated a sytematic distribution above the predicted mean, while partial examination indicated a random distribution. Sample variances for the transformed dependent variable were equal. Thus, for the 100-125 mm and 60-80 mm crab-size treatments, a significant decrease in proportional mortality at 10 oysters/tank, and increases at intermediate densities of 20 and 40 oysters/tank (Fig. 24) appear to be responsible for the type III response.

Conceptual models

The type of functional response exhibited by _C_. _sapidus_ eating small _C_. _virginica_ varied as function of crab carapace width (Fig. 23); however, continuous-time conceptual models provided the best fit regardless of carapace width (Table 17). For 135-165 mm CW crabs, the functional response was best described by a type II continuous-time model:

$$Na = \frac{0.92\ Nt}{1 + (0.0038)Nt}$$

as indicated by the (1) low residual sums of squares and (2) random distibution of residuals relative to the discrete-time model (Table 17). For 100-125 mm CW crabs, the discrete-time type III model was characterized by a systematic distribution of residuals above the predicted mean and indicated a significant "lack-of-fit" error (Table 17). Therefore, the functional response for medium size-class crabs eating small oysters is best described by a type III continuous-time model:

$$Na = \frac{.24\ Nt^2}{1 + 0.10Nt + 0.24Nt^2}$$

as indicated by the (1) nonsignificant "lack-of-fit" error and, (2) random distribution of residuals relative to the discrete-time model (Table 17). For 60-80 mm CW crabs, the continuous-time type III model indicated a systematic distribution of residuals below the predicted mean (Table 17). Despite this, the continuous-time type III model explained more (88.2%) of the variance in consumption and was characterized by lower residual sums of squares (Table 17). Therefore, the functional response for small size-class crabs eating small oysters is best described by a continuous-time type III model:

$$Na = \frac{.24\ Nt^2}{1 + 0.10Nt + 0.24Nt^2}.$$

Nonlinear regressions with functional response models (Table 17) estimated handling times per small oyster by large crabs, to be 200 times less (0.01h) than estimates for medium and small sized crabs (both 0.20h) (Table 18). Attack rate (a') estimates were 0.038 for 135-165 mm CW crabs (Type II model); and, when a' was computed from eqn (6), with nonlinear regression estimates of b and c, it equaled 0.083 for both 100-125 mm and 60-80 mm CW crabs (both type III models) (Table 18).

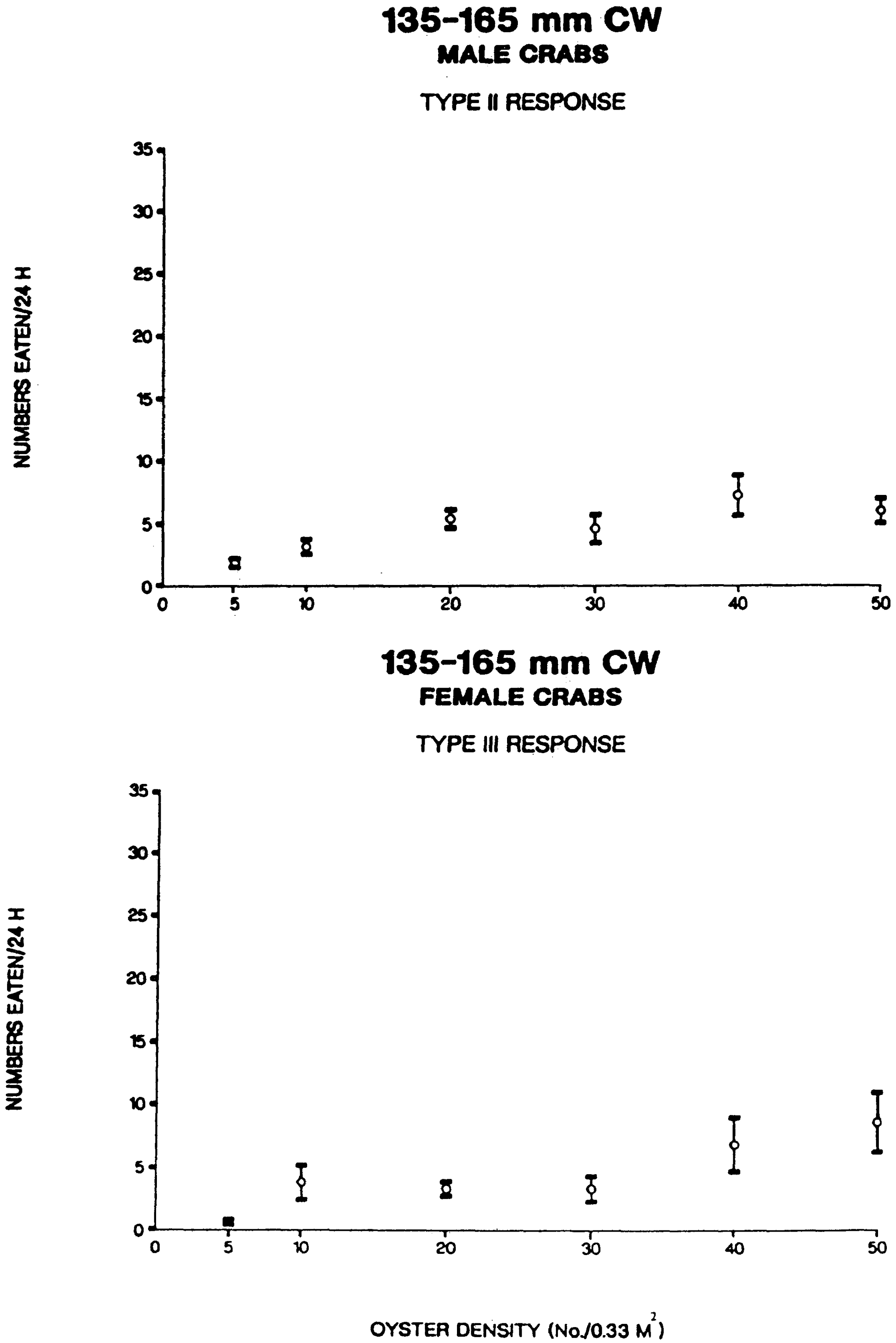
Crab sex effects: functional responses

Large oysters-Large crabs

Consumption rates of large male and female C. sapidus (135-165 mm CW) feeding on large oysters ($\bar{x}$ = 35 ± 2 mm SL) increased significantly with oyster density (ANOVA; Male crabs: F = 5.0, df = 5,89, P<0.0005; Female crabs: F = 13.4, df = 5,35, P<0.0001), with no apparent effect of sex, except at 5 oysters/tank in which consumption rates of females were lower (Fig. 25). For large male crabs, consumption rates were significantly higher within a subset comprised of (listed in decreasing order) 40, 50, 20 and 30 oysters/tank, followed by 10 and 5 oysters/tank (SNK: EWER = 0.05) (Fig. 25). Consumption rates of large female crabs were significantly higher at 50 oysters/tank, followed in decreasing order by two subgroups comprised of 20, 30, 10 and 40 oysters/tank, and 50 oysters/tank (SNK: EWER = 0.05) (Fig. 25).

Proportional mortality rates for male and female crabs differed significantly with oyster density (ANOVA; Male crabs: F = 4.9, df = 5,89, P<0.0005; Female crabs: F = 7.8, df = 5,35, P<0.0001). For male crabs, significantly higher proportional mortality rates occurred at the two lowest densities of 5 and 10 oysters/tank ($\bar{x}$ = 38 and 32%, respectively) relative to remaining densities ($\bar{x}$ = 12-27%) (SNK: EWER = 0.05) (Fig. 26). This pattern typifies an inversely density-dependent relationship (eg., a type II functional response; Hassell 1978). In contrast, for female crabs, proportional mortality was significantly higher at an intermediate density of 10 oysters/tank ($\bar{x}$ = 47%), followed in decreasing order by two subgroups comprised of 20 oysters/tank ($\bar{x}$ = 33%), and 5, 30, 50 and 40 oysters/tank (30-10%, respectively) (SNK: EWER = 0.05) (Fig. 26). The reduction in proportional mortality at the

Figure 25. Functional responses of large (135-165 mm CW) male and female *C. sapidus* feeding on large ($\bar{x}$ = 35 mm SL) oysters. Each point respresents the mean feeding rate over 24h. Vertical bars equal 1 S.E. N = 6-10 replicates per prey density.



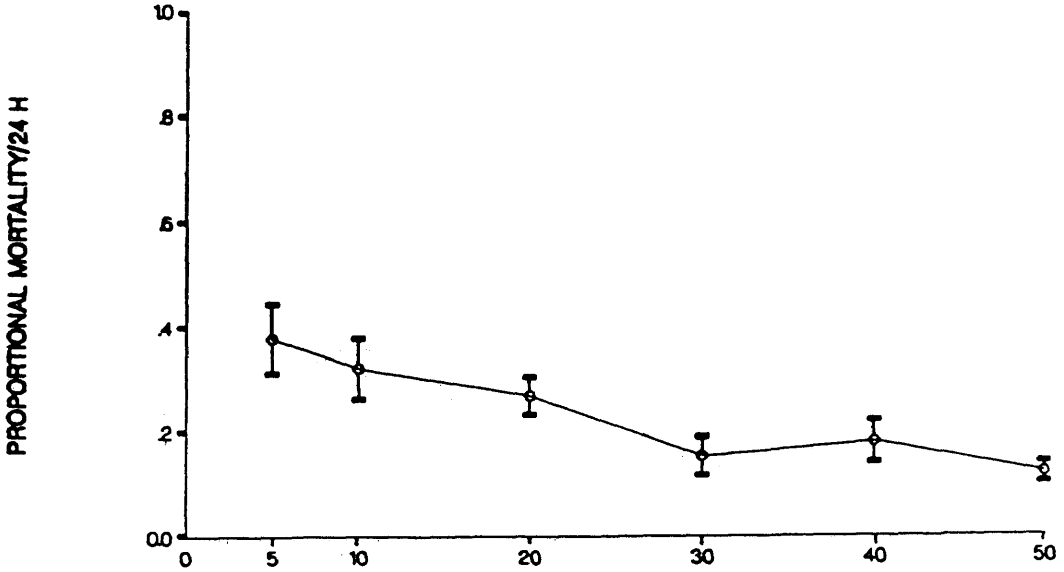
LARGE OYSTER LENGTH

Figure 26. Proportional mortality of large ($\bar{x}$ = 35 mm SL) C. *virginica* at seven densities as a function of crab sex. Each point represents the mean proportional mortality over 24h. Vertical bars equal 1 S.E. N = 6-10 replicates per prey density.

135-165 mm CW

MALE CRABS

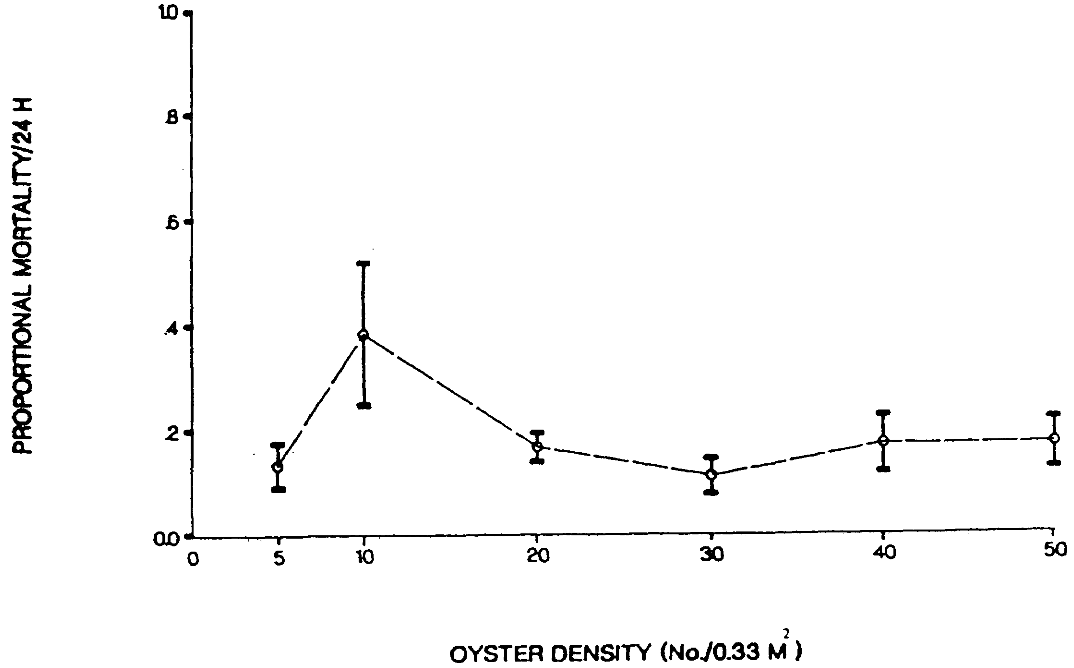
TYPE II RESPONSE



135-165 mm CW

FEMALE CRABS

TYPE III RESPONSE



LARGE OYSTER LENGTH

lowest prey density implies a density-dependent sigmoid relationship between predation rate and prey density (eg., a type III response; Hassell 1978). Hence, the existence of a partial prey refuge from predation by large female crabs below densities of approximately 5 oysters/tank or 15.2 oysters/m^2.

Individual male and female crabs differed significantly from each other in their functional responses (Heterogeneity G-Test; Males: G = 55.5, df = 25, P<0.0001; Females: G = 41.1, df = 25, P<0.022).

Crab sex effects: functional response models

General Model

The general functional response model (Eq. 5) (Real 1977, 1979) was unable to adequately describe response types for consumption rates for either crab sex treatment. For male crabs, the model explained only 22.7% of the total variance and was unable to predict a response type as indicated by $\hat{n}$ being significantly different from 0, 1 and 2 ($\hat{n}$ = 0.58) (Table 19). In this instance, the ANOVA of proportional mortality rates indicated a type II response (Fig. 26). For female crabs, the model predicted a type II response with $\hat{n}$ not significantly different from 1 ($\hat{n}$ = 1.0) (Table 19), whereas the ANOVA of proportional rates determined a type III response (Fig. 26). For female crabs, the residuals about the predicted values were distributed randomly (Table 19), and variances were equal (Hartley's F-Max Test). Thus, for female crabs eating large oysters, a significant decrease in proportional mortality at 5 oysters/tank, and increases at intermediate densities of 10 and 20 oysters/tank (Fig. 26) appear to be responsible for the type III response.

Conceptual models

The type of functional response exhibited by large *C. sapidus* eating large *C. virginica* varied as a function of crab sex (Fig. 25), but discrete-time conceptual models provided the best fit regardless of sex (Table 20). For male crabs, the continuous-time type II model described less (69.3%) of the variance, and was characterized by higher residual sums of squares, when compared to a discrete-time model (Table 20). Therefore, the functional response for male crabs is best described by a discrete-time type II model:

$$Na = Nt[1-e^{-0.005(24-0.1Na)}].$$

Similarly, for female crabs, the continuous-time type III model explained less (65.6%) of the the variance and was characterized by higher residual sums of squares relative to the continuous-time model (Table 20). Hence, the functional response is best described by a discrete-time type III model:

$$Na = \frac{-0.018Nt}{Nt\{1-e\ [1 + 2.0Nt\ (23.9Na)]\}}.$$

Nonlinear regressions with functional response models (Table 20) estimated handling time per oyster by *C. sapidus* to be 0.01h and 0.1h for males and females, respectively (Table 21). Attack rate (a') estimates equaled 0.0005 for males (type II response); and, when a' was computed from eqn (6), with nonlinear regression estimates of b and c, it equaled 0.009 for females (type III responses) (Table 21). Thus, compared to male crabs, females are spending a greater amount of time, per unit area (0.33 m^2), searching for prey (0.0009), and are taking 10 times as long to handle individual oysters after the encounter (Table 21).

Crab sex effects: chelae height to carapace width ratios

Comparison of linear regression coefficients indicated that chelae height to carapace width ratios were significantly higher for males than females (slopes; $t = 78.0$, $df = 2,65$, $P<0.0001$) (Fig. 27).

Crab sex effects: functional responses

Medium oysters-Large crabs

Consumption rates of large male and female *C. sapidus* (135-165 mm CW) feeding on medium oysters ($\bar{x} = 25 \pm 2$ mm SL) increased significantly with oyster density (ANOVA; Male crabs: $F = 32.9$, $df = 5,45$, $P<0.0001$; Female crabs: $F = 8.6$, $df = 5,38$, $P<0.0001$), with no apparent effect of sex (Fig. 28). For male crabs, significantly more oysters were consumed at 50 oysters/tank, followed in decreasing order by 40 oysters/tank, and two subgroups comprised of 30 and 20 oysters/tank, and 10 and 5 oysters/tank (SNK: EWER = 0.05) (Fig. 28). For female crabs, significantly more oysters were consumed at 40 and 50 oysters/tank,

Figure 27. Chelae height (mm) compared against carapace width (mm) for large (135-165 mm CW) male and female crabs, where x = carapace width (mm) and y = chelae height (mm).

Males: $y = 0.15x + 0.77$ ($r^2=0.63$, $n = 30$, $P<0.0001$)

Females: $y = 0.11x + 0.80$ ($r^2=0.49$, $n = 37$, $P<0.0001$)

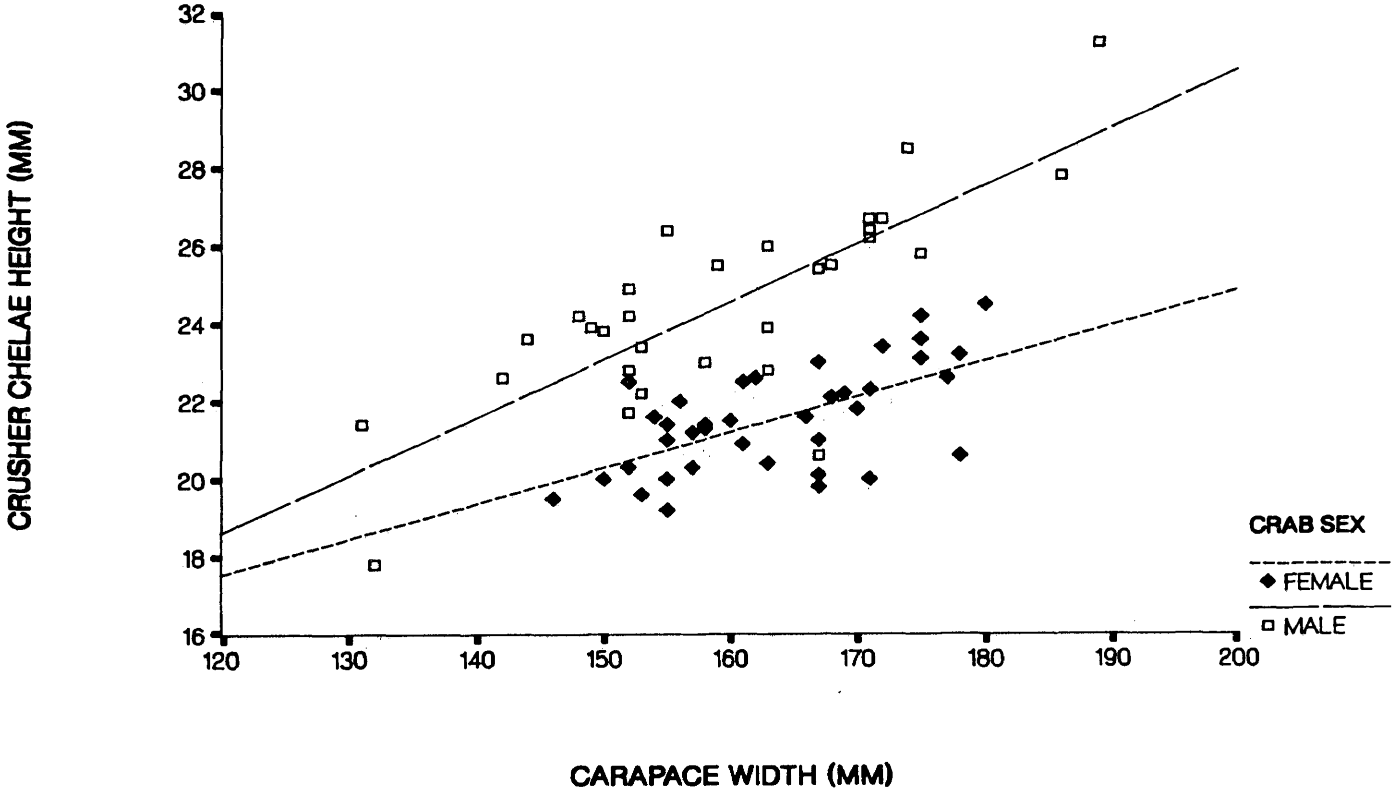
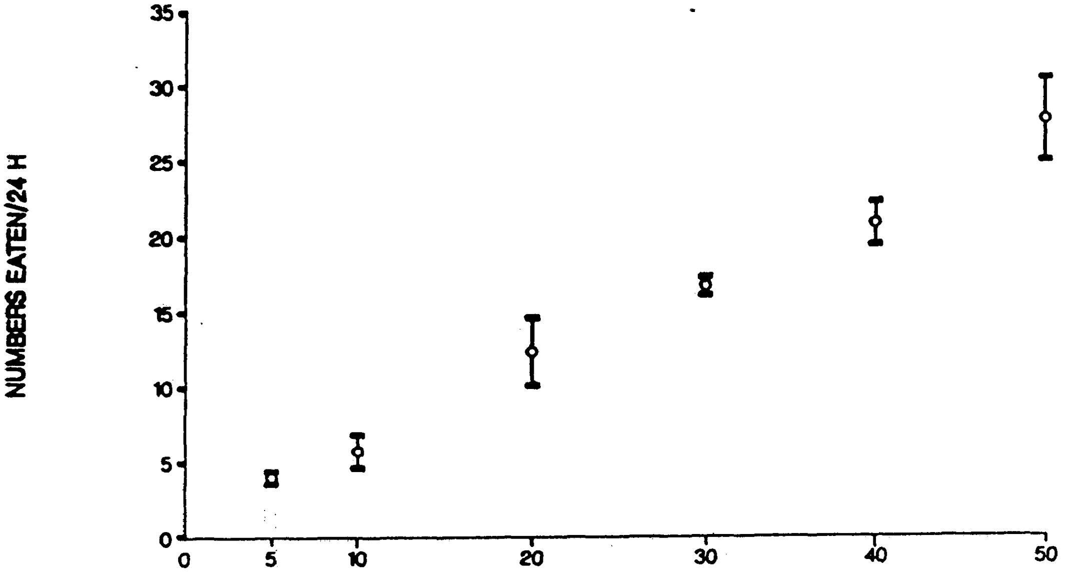

CRUSHER CHELAE HEIGHT (MM)
32
30
28
26
24
22
20
18
16
120
130
140
150
160
170
180
190
200
CARAPACE WIDTH (MM)
CRAB SEX
◆ FEMALE
□ MALE

Figure 28. Functional responses of large (135-165 mm CW) male and female C. sapidus feeding on medium ($\bar{x}$ = 25 mm SL) oysters. Each point respresents the mean feeding rate over 24h. Vertical bars equal 1 S.E. N = 6-10 replicates per prey density.

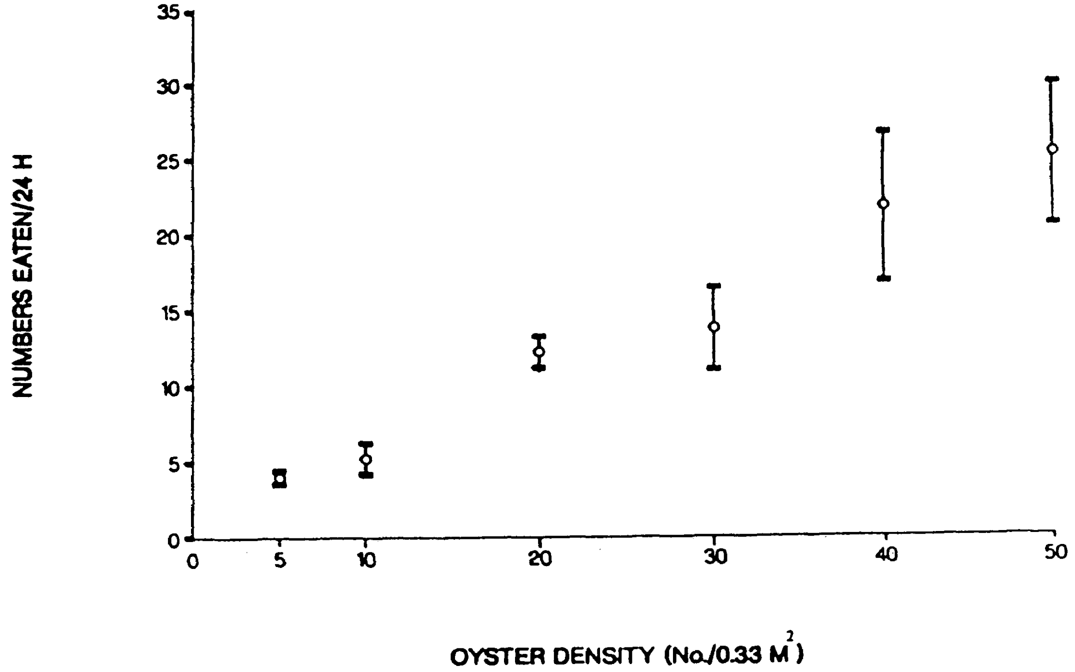
135-165 mm CW
MALE CRABS

TYPE II RESPONSE



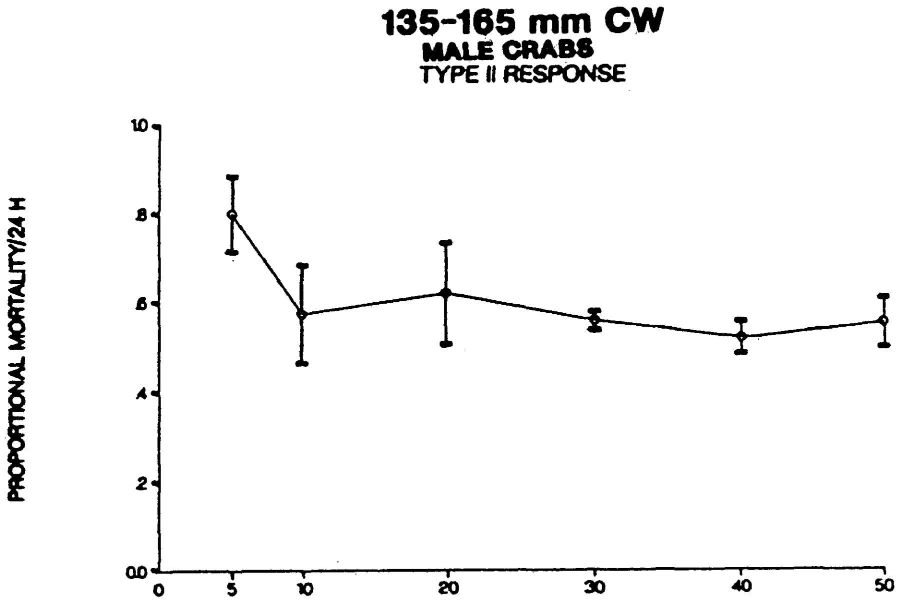
135-165 mm CW
FEMALE CRABS

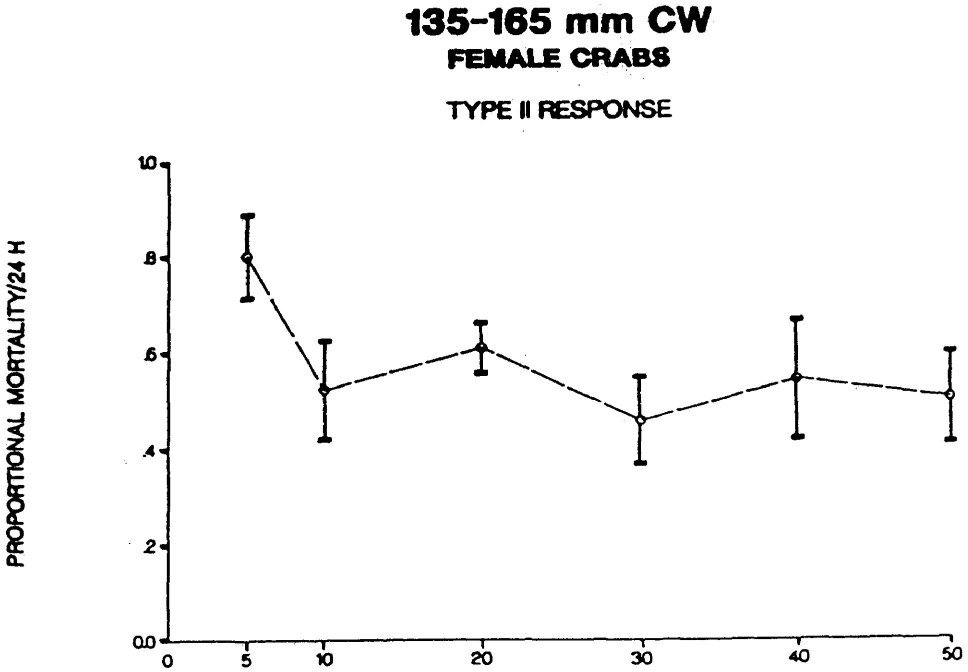
TYPE II RESPONSE



MEDIUM OYSTER LENGTH

Figure 29. Proportional mortality of medium ($\bar{x}$ = 25 mm SL) C. virginica at seven densities as a function of crab sex. Each point represents the mean proportional mortality over 24h. Vertical bars equal 1 S.E. N = 6-10 replicates per prey density.





OYSTER DENSITY (No./0.33 M^2)

MEDIUM OYSTER LENGTH

followed in decreasing order by two subgroups comprised of 30 and 20 oysters/tank, and 10 and 5 oysters/tank (SNK: EWER = 0.05) (Fig. 28).

The trend in proportional mortality rates of C. virginica as a function of prey density were similar for both crab sexes indicating an inversely density-dependent relationship between feeding rates and prey density (type II response) (Fig. 29). Proportional mortality rates increased significantly with decreasing oyster density (ANOVA; Males: F = 3.0, df = 5,45, $P<0.02$; Females: F = 2.7, df = 5,43, $P<0.04$). Proportional mortality rates for male and female crabs were significantly higher at the lowest prey density (both $\bar{x}$ = 80%), relative to increased densities ($\bar{x}$ = 52-62% and 46-61%, respectively) (SNK: EWER = 0.05) (Fig. 29).

Individual male and female crabs did not differ significantly from each other in their functional responses (Heterogeneity G-Test; Males: G = 18.5, df = 20, P = 0.55; Females: G = 13.7, df = 25, P = 0.83).

Crab sex effects: functional response models

General model

Analysis according to the general functional response model (Eq. 5) (Real 1977, 1979) corroborated the results from the ANOVA of proportional mortality for both crab sexes, indicating a hyperbolic type II response (Table 22). For male crabs, the residuals about the fitted model were distributed randomly and nonrandomly for partial and complete data sets, respectively (Table 22), and unequal sample variances were found for the transformed dependent variable (Hartley's F-Max Test). The model, however, did verify a type II reponse with $\hat{n}$ not significantly different from 1 ($\hat{n} = 0.89$) (Table 22). For female crabs, the residuals were distributed systematically above the predicted values (Table 22), and unequal sample variances were indicated for the transformed dependent variable (Hartley's F-Max Test). The model, again verified a type II response with $\hat{n}$ not significantly different from 1 ($\hat{n} = 1.0$) (table 22).

Conceptual models

The fit of continuous and discrete-time conceptual models varied with crab sex (Table 23). For male crabs, the functional response (Fig. 28) was best described by a type II discrete-time model:

$$Na = Nt[1-e^{-.04(24-0.1Na)}]$$

as indicated by the (1) low residual sums of squares relative to the continuous-time model (Table 23) and (2) the biological relevance of a model which accounts for decreases in prey density s crabs consume prey without replacement (Table 23). For female crabs, the discrete-time type II model indicated a significant "lack-of-fit" error and systematic distribution of residuals above the predicted values, though it described 93.8% of the variance in consumption rates and displayed the lower residual sums of squares of the two models (Table 23). In contrast, the continuous-time model provided a statistically adequate fit as indicated by the nonsignificant "lack-of-fit" error (Table 23). Thus, the functional response was best described by a type II continuous-time model:

$$Ne = \frac{0.552\ Nt}{1 + 0.0023Nt.}$$

Nonlinear regressions with functional response models (Table 23) estimated handling time per oyster by C. sapidus to be 0.10 hr regardless of sex (Table 24). Attack rate (a') estimates equaled 0.037 and 0.023 for males and females respectively (Table 24). Thus prey search rates and individual oyster handling times are approximately equal for male and female crabs feeding on medium oysters (Table 24).

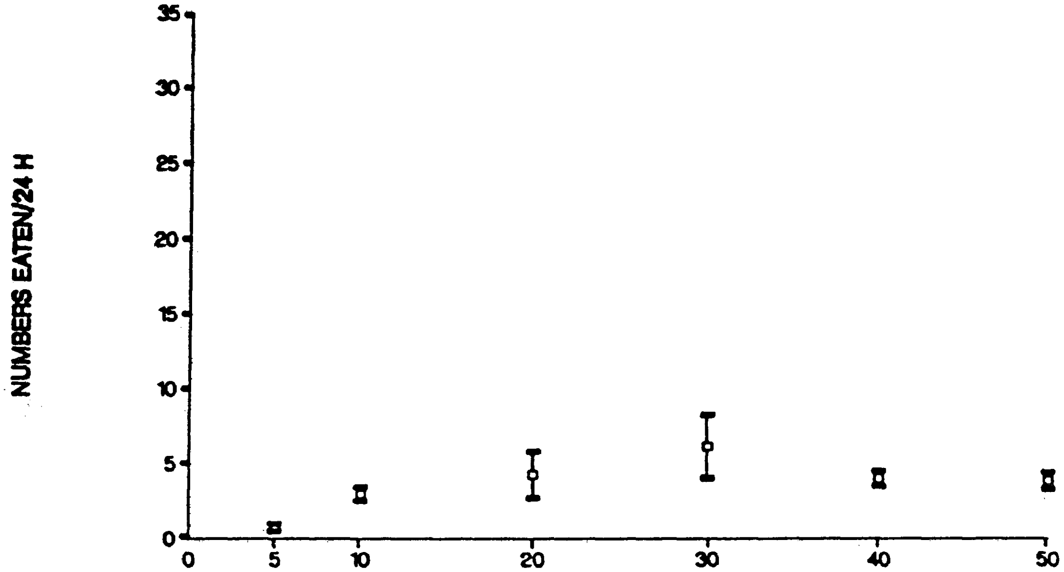
Crab sex effects: functional responses

Large oysters-Medium crabs

Consumption rates of medium (100-125 mm CW) male and female C. sapidus feeding on large oysters ($\bar{x}$ = 35 mm SL) increased significantly with oyster density (ANOVA; Males: F = 6.2, df = 5,45, P<0.0002; Females: F = 13.4, df = 5,35, P<0.0001), with no apparent effect of sex (Fig 30). For males, consumption rates were significantly higher at the 5 highest densities, relative to 5 oysters/tank (SNK: EWER = 0.05) (Fig. 30). Consumption rates of females were significantly higher at 50 oysters/tank, followed in decreasing order by two subgroups comprised of 20, 30, 10 and 40 oysters/tank, and 5 oysters/tank (SNK: EWER = 0.05) (Fig. 30).

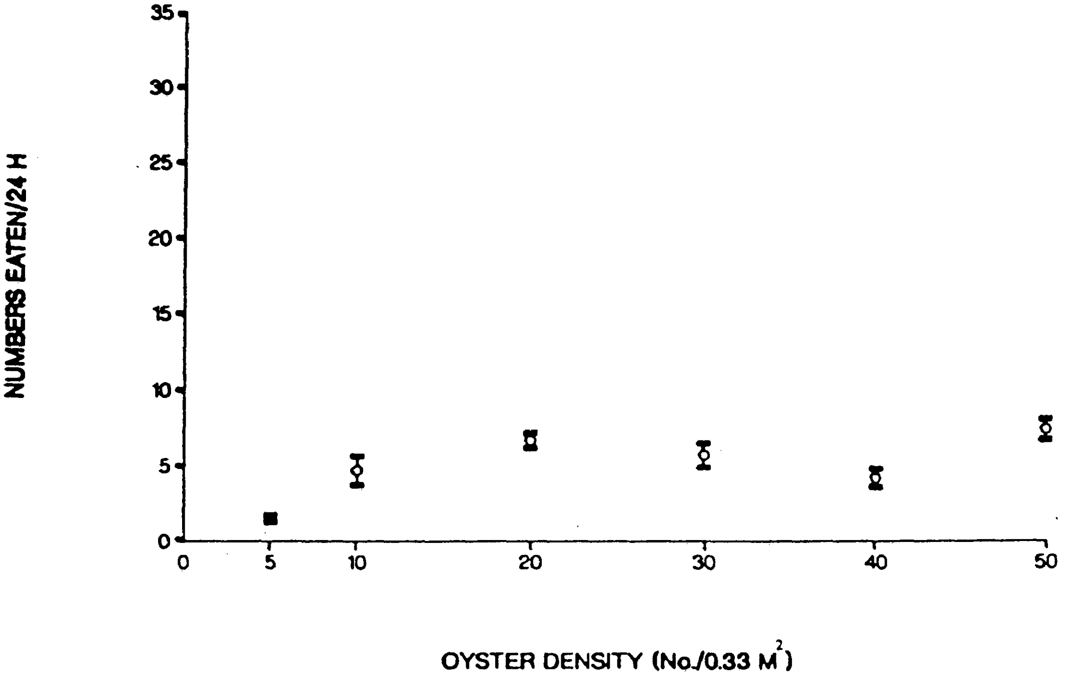
Proportional mortality rates of C. virginica as a function of oyster density were analogous for both crab sexes indicating a density-dependent sigmoid relationship between predation rate and prey density (type III response) (Fig. 31). For male crabs, proportional mortality rates were significantly highest at an intermediate density of 10

Figure 30. Functional responses of medium (100-125 mm CW) male and female C. sapidus feeding on large ($\bar{x}$ = 35 mm SL) oysters. Each point respresents the mean feeding rate over 24h. Vertical bars equal 1 S.E. N = 6-10 replicates per prey density.



100-125 mm CW
MALE CRABS

TYPE III RESPONSE



100-125 mm CW
FEMALE CRABS

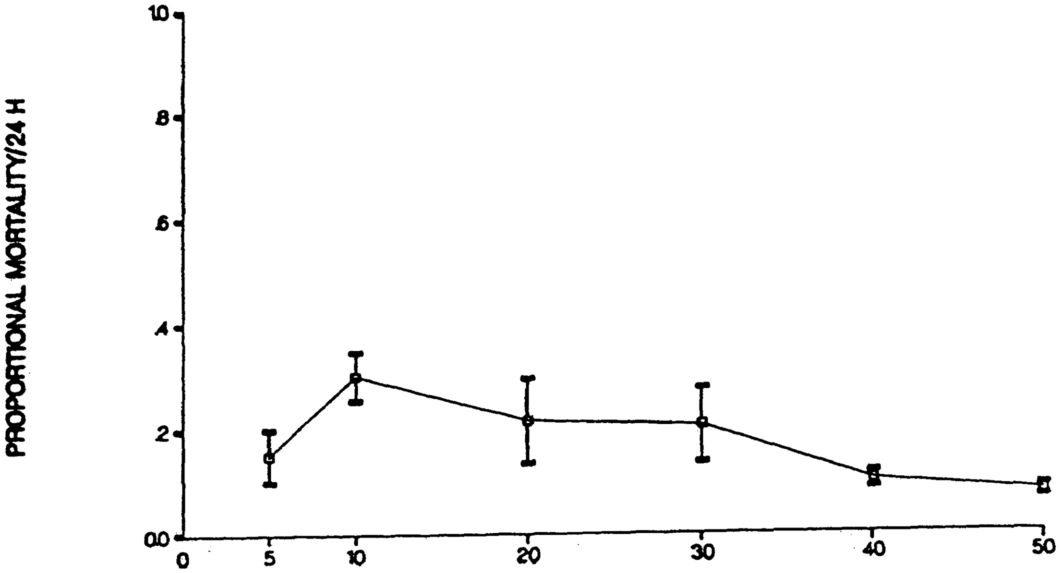
TYPE III RESPONSE

LARGE OYSTER LENGTH

Figure 31. Proportional mortality of large ($\bar{x}$ = 35 mm SL) _C_. _virginica_ at seven densities as a function of crab sex. Each point represents the mean proportional mortality over 24h. Vertical bars equal 1 S.E. N = 6-10 replicates per prey density.

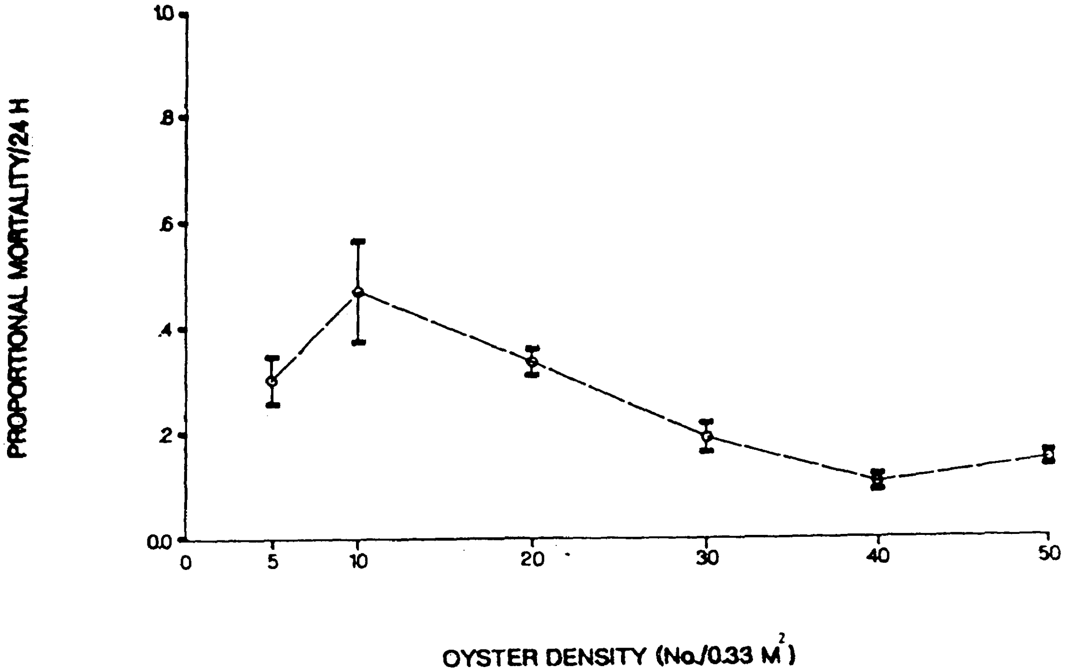
100-125 mm CW
MALE CRABS

TYPE III RESPONSE



100-125 mm CW
FEMALE CRABS

TYPE III RESPONSE



LARGE OYSTER LENGTH

oysters/tank ($\bar{x}$ = 30%) relative to lower and higher densities ($\bar{x}$ = 7-21%) (SNK: EWER = 0.05) (Fig. 31). For female crabs, proportional mortality rates were significantly highest at 10 oysters/tank ($\bar{x}$ = 47%), followed by 20 oysters/tank ($\bar{x}$ = 33%), relative to lower and higher densities ($\bar{x}$ = 10-30%) (SNK: EWER = 0.05) (Fig. 31). Hence, the existence of a partial prey refuge, for large oysters, from predation by medium-size male and female crabs below densities of approximately 5 oysters/tank or 15.2 oysters/m^2.

Individual male crabs differed significantly from each other in their functional response (Heterogeneity G-Test; G = 22.2, df = 12, $P<0.034$) whereas females were similar (G = 12.6, df = 25, P = 0.98).

Crab sex effects: functional response models

General model

The general functional response model (Eq. 5) (Real 1977, 1979) was unable to adequately describe response types for consumption rates at either crab size-class treatment. For male crabs, the model indicated a type II response with $\hat{n}$ not significantly different from 1 ($\hat{n}$ = 0.81) (Table 25), whereas the ANOVA of proportional mortality rates determined a type III response (Fig. 24). For the medium-size crabs, the residuals about the predicted values were distributed randomly (Table 25) and variances were equal. Despite equal variances for the transformed dependent variable (Hartley's F-Max Test), and a random distribution of residuals about the predicted values for females (Table 25), the model was unable to predict a response type as indicated by $\hat{n}$ being significantly different from 0, 1 and 2 ($\hat{n} = 0.55$) (Table 25). Thus, for medium male and female blue crabs eating large oysters, a significant decrease in proportional mortality at 5 oysters/tank, and increases at intermediate densities of 10 and 20 oysters/tank (Fig. 31) appear to be responsible for the type III response.

Conceptual models

The fit of continuous and discrete-time conceptual models varied with crab sex (Table 26). For male crabs, the discrete-time type III model explained more (88.5%) of the variance in consumption and was characterized by lower residual sums of squares, relative to the continuous-time model. Therefore, the functional response for male crabs is best described by a type III discrete-time model:

$$Na = \frac{-0.01Nt}{Nt\{1-e\ [1+2.0Nt\ (23.9Na)]\}}.$$

In contrast, for female crabs, the discrete-time type III model indicated a systematic distribution of residuals below the predicted values (partial data set), and displayed the higher residual sums of squares, though it explained more (96.7%) of the variance in consumption rates (Table 26). Therefore, the functional response for female crabs is best described by a type III continuous-time model:

$$Ne = \frac{24Nt^2}{1 + 0.014Nt + 4.0Nt^2}.$$

Nonlinear regression with functional response models (Table 26) estimated handling times per oyster by C. sapidus to be 0.1 and 4.0h for males and females, respectively (Table 27). When attack rate (a') estimates were computed from eqn (6), with nonlinear regression estimates of b and c, it equaled 0.0005 and 0.12, respectively (Table 27). Similar to results for large male and female crabs eating large oysters, medium females are spending an estimated 24 times as long to search for prey (0.12), and taking 40 times as long to handle individual oysters after the encounter, compared to males (Table 27).

Field Study

Percent recapture of marked field samples averaged 86.4% and 89.4% for the 1985 and 1986 oyster shell-plant sites, respectively (Table 28). Losses of marked individuals were most likely due to, but not limited to, the following environmental conditions: (1) recapture by visual observation was usually impossible due to low water visibility (1-3"), (2) surface swells associated with high winds impaired efficient transport of recaptured oysters from the water to the boat, and (3) in one instance where water clarity allowed visible observation, a blue crab was observed removing a marked oyster from the plot. With the exception of two replicates within the 1985 site, all samples were recovered (Table 29). The two unrecovered replicate samples were not found because the location-markers (see methods) were missing and visibility was reduced.

Field mortality rates of juvenile C. virginica due to crab predation varied significantly by sample date for both the 1985 and 1986 shell-plant sites (ANOVA; 1985 site: $F = 10.6$, $df = 7,21$, $P<0.0001$; 1986 site: $F = 10.2$, $df = 2,8$, $P<0.012$). For the 1985 site, oyster mortality rates were significantly higher for the May 13, June 3 and June 24 sample dates ($\bar{x}$ = 10.7, 9.5 and 8.7 oysters eaten/21 days, respectively), compared to later dates ($\bar{x}$ = 1.3-3.7 oysters eaten/21 days) (SNK: EWER = 0.05) (Fig. 32, Table 28). For the 1986 site, oyster mortality was significantly higher for the October 28 sample date ($\bar{x}$ = 21.3 oysters eaten/21 days), compared to later dates ($\bar{x}$ = 2.7-5.7 oysters eaten/21 days) (Fig. 32, Table 28).

Oyster mortality rates generally decreased with increasing water temperature for the 1985 site, whereas the converse was true for the 1986 site (compare Figs. 32 and 33). These results illustrate the potential importance of biotic factors (oyster density and size) in regulating crab predation intensity from late-spring through early-fall at the 1985 site, and the effects of decreasing temperature during the fall to winter transition period within the 1986 site.

Oyster mortality rates demonstrated a positive correlation with density at both sites (Figs. 32 and 34). Oyster density at the 1985 and 1986 sites varied significantly with sampling date (ANOVA; 1985 site: F = 8.3, df = 7,21, $P<0.0005$; 1986 site: F = 6.0, df = 2,8 $P<0.037$). For the 1985 site, oyster density was significantly highest on May 13 and June 3 ($\bar{x}$ = 133.7 and 132.5 oysters/0.25 m^2, repectively) compared to the June 24 to September 16 dates ($\bar{x}$ = 52-94 oysters/0.25 m^2) (SNK: EWER = 0.05) (Fig. 34, Table 28). For the 1986 site significantly higher densities occurred on October 28 ($\bar{x}$ = 690 oysters/0.25 m^2) compared to later dates ($\bar{x}$ = 490-567 oysters/0.25 m^2) (SNK: EWER = 0.05) (Fig. 34, Table 28).

Figure 32. Mean field mortality rates of juvenile oysters (10-45 mm SL) due to crab predation per 21 days at two shell-plant sites. Vertical bars equal 1 S.E. Note: Mortality rates for the May 13 sample date (quadrat A) are over 14 days.

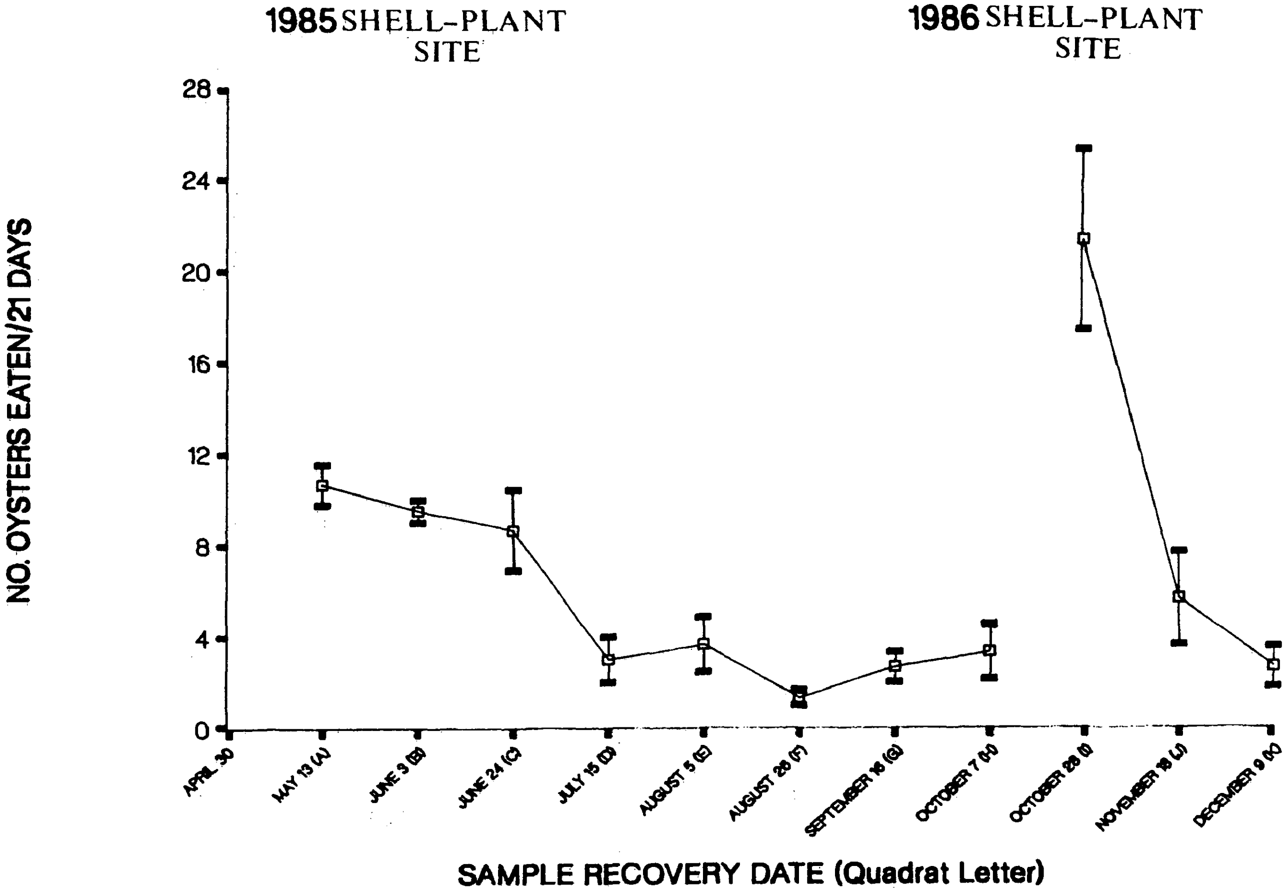

1985 SHELL-PLANT SITE
1986 SHELL-PLANT SITE
NO. OYSTERS EATEN/21 DAYS
28
24
20
16
12
8
4
0
APRIL 30
MAY 13 (A)
JUNE 3 (B)
JUNE 24 (C)
JULY 15 (D)
AUGUST 5 (E)
AUGUST 26 (F)
SEPTEMBER 16 (G)
OCTOBER 7 (H)
OCTOBER 28 (I)
NOVEMBER 18 (J)
DECEMBER 9 (K)
SAMPLE RECOVERY DATE (Quadrat Letter)

Figure 33. Ambient water temperature per sample date at two shell-plant sites.

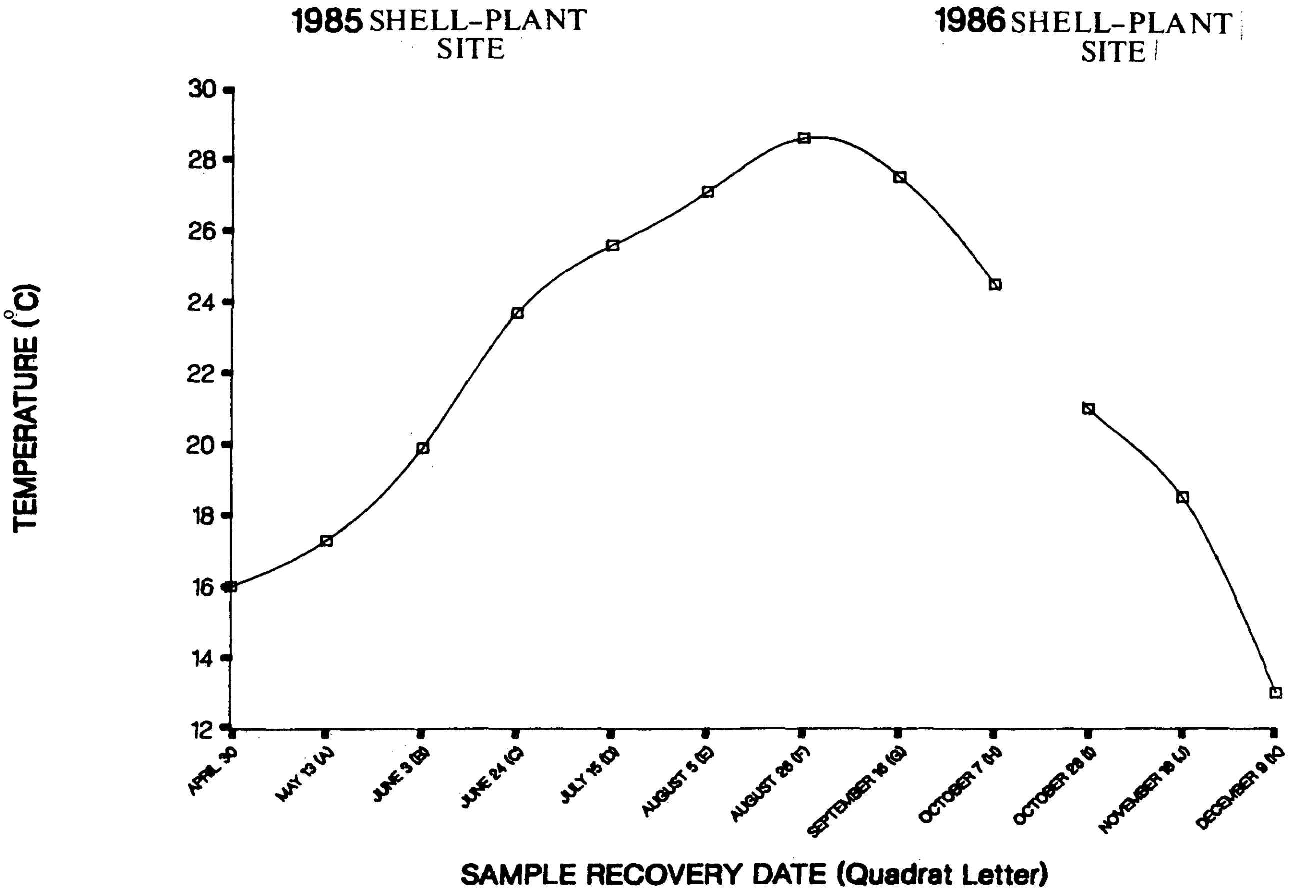
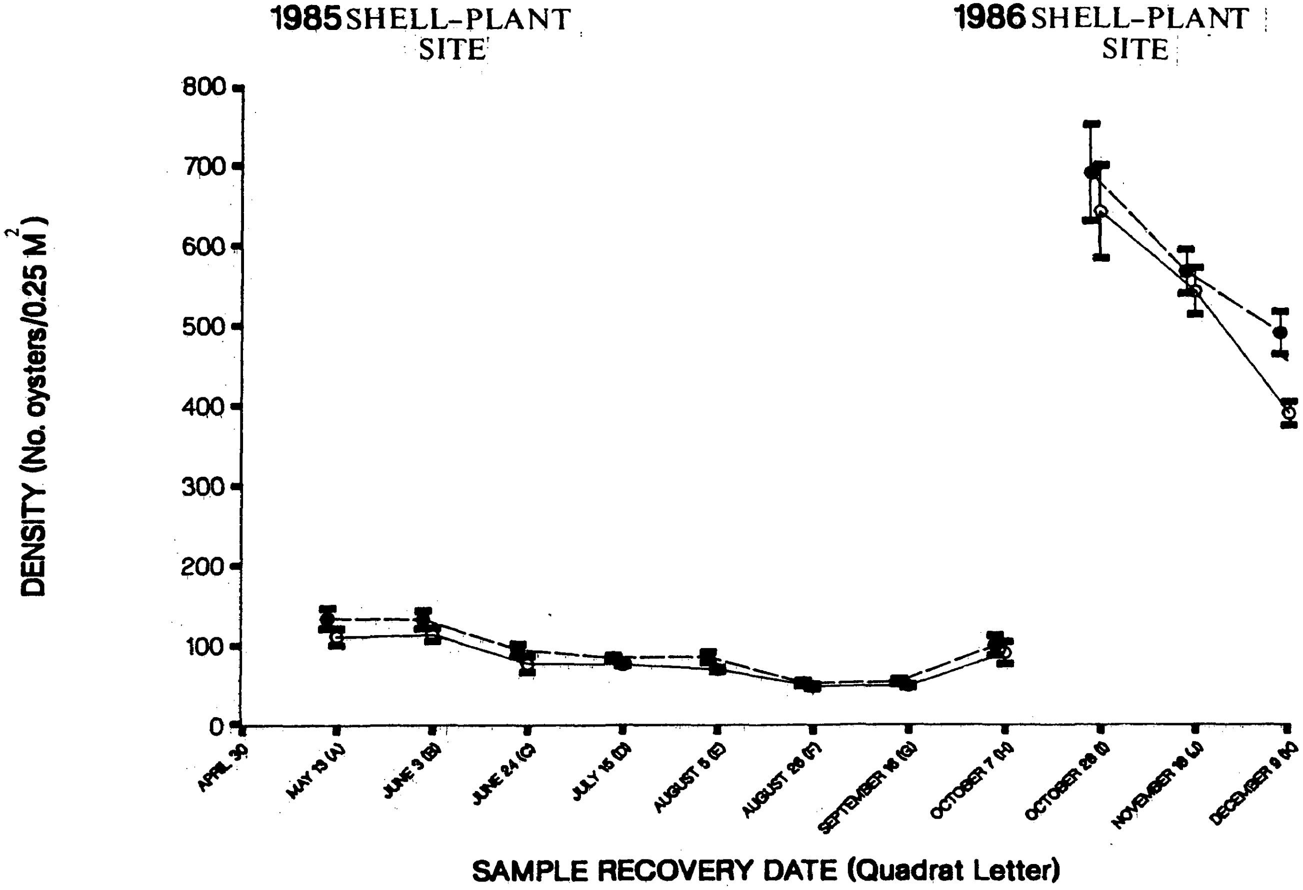
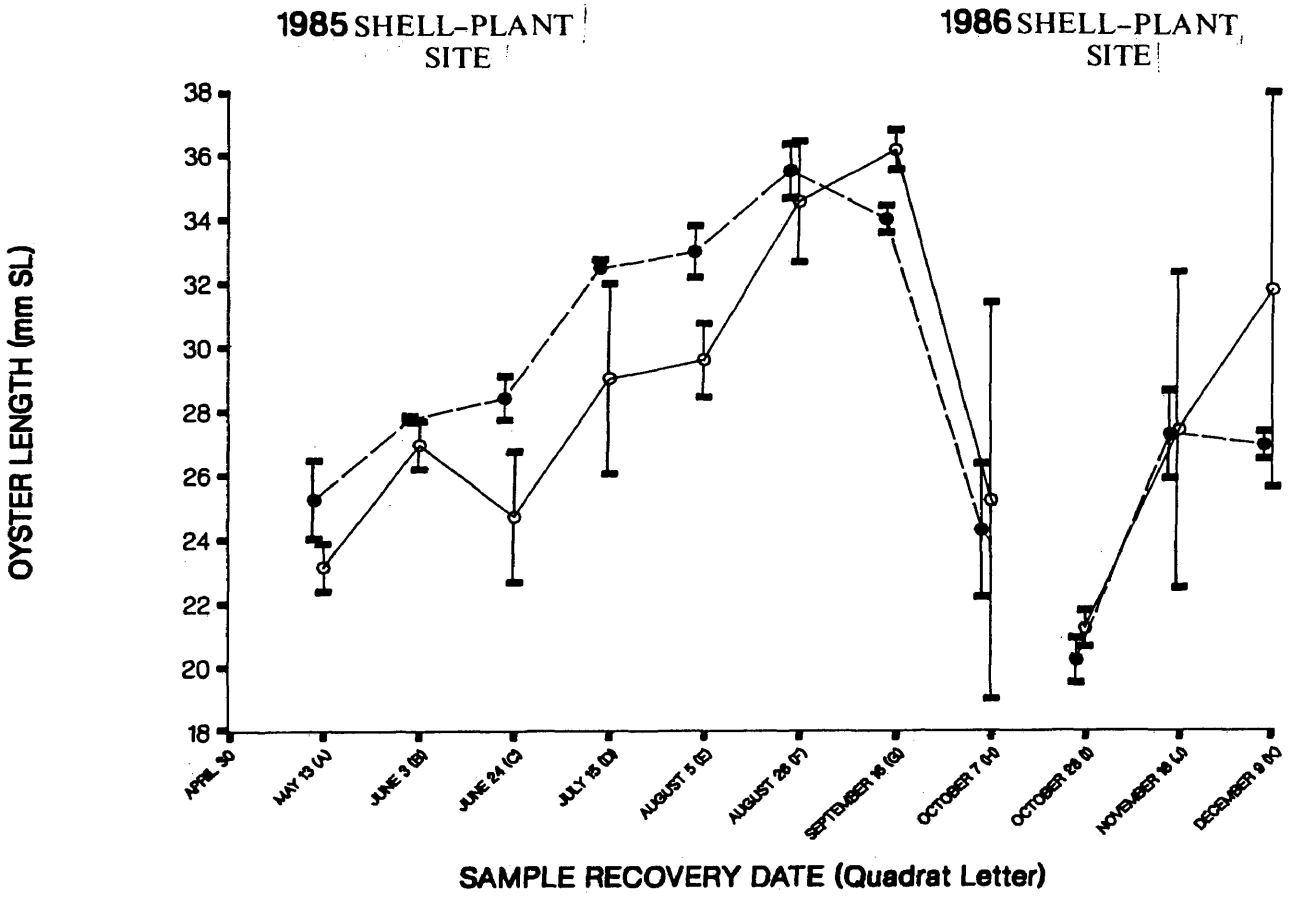

1985 SHELL-PLANT SITE
1986 SHELL-PLANT SITE
TEMPERATURE (°C)
30
28
26
24
22
20
18
16
14
12
APRIL 30
MAY 13 (A)
JUNE 3 (B)
JUNE 24 (C)
JULY 15 (D)
AUGUST 5 (E)
AUGUST 26 (F)
SEPTEMBER 16 (G)
OCTOBER 7 (H)
OCTOBER 28 (I)
NOVEMBER 18 (J)
DECEMBER 9 (K)
SAMPLE RECOVERY DATE (Quadrat Letter)

Figure 34. Mean juvenile oyster (10-45 mm SL) density per 0.25 m^2 at two shell-plant sites. Broken lines and closed circles represent the initial marked density, and solid lines and open circles represent the recaptured density. Vertical bars equal 1 S.E.


1985 SHELL-PLANT SITE
1986 SHELL-PLANT SITE
DENSITY (No. oysters/0.25 M^2)
800
700
600
500
400
300
200
100
0
APRIL 30
MAY 13 (A)
JUNE 3 (B)
JUNE 24 (C)
JULY 15 (D)
AUGUST 5 (E)
AUGUST 26 (F)
SEPTEMBER 16 (G)
OCTOBER 7 (H)
OCTOBER 28 (I)
NOVEMBER 18 (J)
DECEMBER 9 (K)
SAMPLE RECOVERY DATE (Quadrat Letter)

Oyster mortality rates at the 1985 and 1986 sites appeared to be a decreasing function of increasing oyster length, with the lowest mean number of oysters eaten per 21 days ($\bar{x}$ = 1.3-2.7 and 2.7-5.7, respectively) corresponding to the largest mean oyster lengths ($\bar{x}$ = 33.0-37.0 mm and 26.9-27.7 mm SL, respectively) (Figs. 32 and 35). Oyster length at both sites varied significantly with sampling date (ANOVA; 1985 site: F = 6.9, df = 7,21, $P<0.0012$; 1986 site: F = 18.7, df = 2,8, $P<0.0026$). For the 1985 site, oyster lengths were significantly higher within two subgroups comprised of September 16 ($\bar{x}$ = 37 mm SL) and August 26 and August 6 ($\bar{x}$ = 35.5 and 33.0, respectively), than on earlier dates ($\bar{x}$ = 24.9-32.5 mm SL) (SNK: EWER = 0.05) (Figs. 32 and 35). For the 1986 site, oyster length was significantly higher on November 18 and December 9 ($\bar{x}$ = 27.3 and 26.9 mm SL, respectively) compared to October 28 ($\bar{x}$ = 20.0 mm SL) (SNK: EWER = 0.05) (Fig. 35). From May 13 to August 5, crabs generally fed on oysters that were smaller than the sample mean oyster length, whereas on August 26 and October 8, consumption lengths and sample lengths were approximately equal (Table 28, Fig. 35). On September 16, oysters larger than the mean sample length were eaten (Table 28, Fig. 35). For the 1986 site, crabs generally fed on the sample mean oyster length (Table 28, Fig. 35). Average oyster lengths at the 1985 site ranged from 25.3 mm SL on May 13 to 35.5 mm SL on August 26, demonstrating an average growth rate of 0.10 mm SL/day. For the 1986 site, average oyster lengths ranged from 20.2 mm SL on October 28 to 27.3 mm SL on November 18 for an

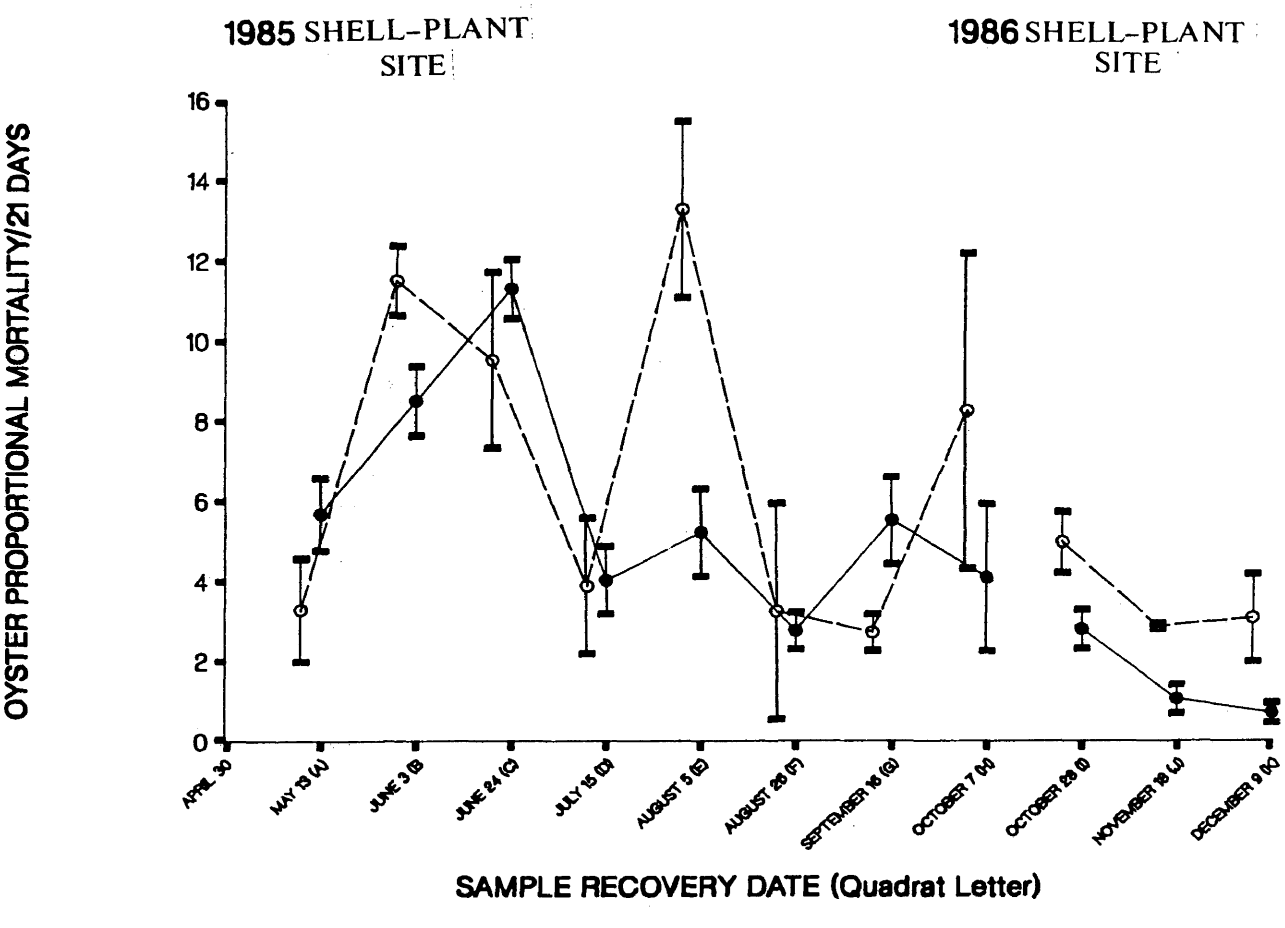
Figure 35. Mean length of juvenile oysters (10-45 mm SL) after marking and before exposure (broken line and closed circles), and eaten by crabs (solid line and open circle) at two shell-plant sites. Vertical bars equal 1 S.E.


1985 SHELL-PLANT SITE
1986 SHELL-PLANT SITE
OYSTER LENGTH (mm SL)
38
36
34
32
30
28
26
24
22
20
18
APRIL 30
MAY 13 (A)
JUNE 3 (B)
JUNE 24 (C)
JULY 15 (D)
AUGUST 5 (E)
AUGUST 26 (F)
SEPTEMBER 16 (G)
OCTOBER 7 (H)
OCTOBER 28 (I)
NOVEMBER 18 (J)
DECEMBER 9 (K)
SAMPLE RECOVERY DATE (Quadrat Letter)

average growth rate of 0.34 mm SL/day. No measurable growth occurred after November 14 (Table 28, Fig. 35).

Field proportional mortality rates of juvenile oysters due to crab predation varied significantly by sample date for both the 1985 and 1986 shell-plant sites (ANOVA; 1985 site: $F = 4.8$, df = 7,21, $P<0.006$; 1986 site: $F = 8.7$, df = 2,8, $P<0.017$). For the 1985 site, proportional mortality was significantly higher on June 24 ($\bar{x} = 11.3$) than on earlier and later sample dates ($\bar{x} = 2.8$-8.5) (SNK: EWER = 0.05) (Fig. 36). During this time oyster length did not significantly vary and oyster density significantly decreased (Figs. 34 and 35), but temperature increased 6.4^{o} C (Fig. 33). These results suggest that from May 13 to June 24, predation rates were inversely density-dependent (type II response) and that predation intensity was regulated primarily by temperature, with relatively little influence of oyster length. From June 24 to July 15 there was a significant decline in proportional mortality rates (Fig. 36). During this time there was a small increase in temperature (1^{o} C) (Fig. 33) and no significant change in oyster density and size (Figs. 34 and 35). During this period, however, there was a massive set of sessile tunicates, <u>Molgula</u> <u>manhattensis</u> covering 90-100% of cultch materials and oysters. I have observed both <u>C</u>. <u>sapidus</u> and <u>P</u>. <u>herbstii</u> feeding on <u>M</u>. <u>manhattensis</u> in the laboratory. Therefore, I suggest that the significant decline in proportional mortality during this period is due either to crabs exhibiting a prey switching behavior (eg., Murdoch and Oaten 1975) from oysters to

Figure 36. Mean proportional mortality of juvenile oysters per 21 days due to crab predation (solid line and solid circle) and due to unknown causes (broken line and open circles). Vertical bars equal 1 S.E. Note: Proportional mortality rates for the May 13 sample date (quadrat A) are over 14 days.


1985 SHELL-PLANT SITE
1986 SHELL-PLANT SITE
OYSTER PROPORTIONAL MORTALITY/21 DAYS
0
2
4
6
8
10
12
14
16
APRIL 30
MAY 13 (A)
JUNE 3 (B)
JUNE 24 (C)
JULY 15 (D)
AUGUST 5 (E)
AUGUST 26 (F)
SEPTEMBER 16 (G)
OCTOBER 7 (H)
OCTOBER 28 (I)
NOVEMBER 18 (J)
DECEMBER 9 (K)
SAMPLE RECOVERY DATE (Quadrat Letter)

tunicates or the crabs were unable to encounter oysters due to the physical barrier created by the tunicate mat. For the 1986 site, proportional mortality rates were significantly higher on October 28 ($\bar{x}$ = 2.8) than on later sample dates (SNK: EWER = 0.05) (Fig. 36). On October 28, water temperature was 3.5 to 8.0^{o} C higher, oyster density was significantly higher and, oyster length was significantly smaller (Fig. 35), relative to later dates. These results suggest that from October 28 to December 9, predation rates were density-dependent (type III response), and that predation intensity was reduced as a function of decreasing temperature and increasing oyster lengths.

Field proportional mortality rates of juvenile oysters due to unknown causes appeared to mirror that due to crabs (with the exception of the August 5 sample date) (Fig. 36), but the trend over time for both sites was not significant (ANOVA; 1985 site: F = 2.5, df = 7,21, $P<0.06$; 1986 site: F = 2.3, df = 2,8, $P<0.19$). On August 5, proportional mortality rates due to unknown causes appeared to be significantly higher than proportional mortality rates due to crabs (Fig. 36).

DISCUSSION

The significant finding in this thesis, with respect to predator-prey dynamics, is that the functional response of an invertebrate predator can exhibit both stabilizing and destabilizing features as a consequence of different temperatures, predator-prey size combinations, complex microhabitat features, and sex-related morphologies. For this relatively "simple" single predator-single prey system, free from the effects of a mobile prey escape response, it is apparent that a high degree of complexity exists when realistic biotic and abiotic factors are superimposed onto blue crab foraging behaviors. The key finding in relation to general foraging behavior, was that the type of opening technique used appeared to be a function of oyster length and thickness, and the geometry of oyster attachment.

Foraging behavior

Increased antennule flicking and gill bailing rates were observed at the initiation of foraging, in this study. The use of the dactyls and antennae as chemoreceptors in C. sapidus has been described by Hazlett (1971) and Pearson and Olla (1977). Shepheard (1974) suggested that among decapods, the dactyls have lower chemosensitivity and function as local contact chemoreceptors, while the more sensitive antennules are the site of distance chemoreception.

The efficiency with which the dactyls served as local tactile and chemoreceptors warrants further investigation. In many instances crabs encountered architecturally vulnerable oysters with the dactyls of the walking legs, without eliciting an opening attempt. Conversely, crabs sometimes probed cultch devoid of oysters, followed by several crushing attempts. Thus, the sensitivity and/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 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.

The degree of cheliped laterality (sensu Hamilton et al. 1976) observed in this study (95%) is high compared to previous work. Hamilton et al. (1976) found that 74% of the largest blue crabs examined possessed a crusher cheliped on the right. The increased degree of cheliped laterality observed in this study may be a function of the low sample size (n = 35) compared to that of Hamilton et al. (1976) (n = 60).

Increasing variation in oyster attachment geometry with length in 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. The increased energy and time expenditure associated with the predators' removal of the oyster from the cultch before repeated breaking, attempts supports the use of cultch in oyster seed planting operations.

Once the oysters were removed from the cultch, the prey handling methods and shell breaking "signatures" were similar to those displayed by _C_. _sapidus_ feeding on cultchless oyster spat (Krantz and Chamberlain 1978, Elner and Lavoie 1983, Bisker and Castagna 1987), and those displayed by lobsters and rock crabs feeding on Atlantic deep-sea scallops, _Pacopecten_ _magellanicus_ (Gmelin) (Elner and Jamieson 1979).

For small oysters ($\bar{x}$ = 15 mm SL) at low densities (eg., 10 oysters/tank), blue crabs displayed a unique random crushing technique in order to feed on oysters within depressions of the cultch. This technique allowed crabs to feed on otherwise invulnerable oysters.

Crabs in this study became less sensitive to visual stimuli once feeding was initiated. This was previously reported for C. sapidus feeding on the ribbed mussel, Geukensia demissa (Hughes and Seed 1983). Hughes and Seed (1983) suggested that, because of reduced visual sensitivity during feeding, it may be more important to minimize prey handling time by feeding on small mussels rather than to maximize the net rate of energy intake; C. sapidus feeding on mussels at high tide may be more vulnerable to predation by herons and egrets and to prey-robbing by conspecifics.

Temperature effects: functional responses

Before discussion of the various factor effects on the functional response of C. sapidus feeding on juvenile oysters, a cautionary note must be made regarding the relative comparisons of different factors (eg., temperature, oyster length, crab size and sex) incorporated into each density experiment. Because each experiment was performed at a different time, temporal variation and inherent variability among experimental units (sensu Hurlbert 1984) may have differed over the course of the study, and may lead to erroneous conclusions if these variations are not considered. However, meaningful comparisons can be made since the techniques in observation and measurement were standardized. This should eliminate both experimental bias and experimentally-generated variability, which have been implicated as a major source of confusion in previous ecological studies (Hurlbert 1984).

Blue crab consumption rates were positively correlated with oyster density and temperature, with 14° C being the critical temperature below which consumption rates were markedly reduced. Whetstone and Eversole (1981) also demonstrated that percent mortality of juvenile hard clams, Mercenaria mercenaria ($\bar{x}$ = 20 mm) due to P. herbstii predation decreased from 12.7% at 24° C and 17°C, to 3.7% at 10°C. Similarly, Elner (1980) found that the foraging rate of C. maenus, both in terms of mussels eaten per day and energy intake per day, was higher at 17° C than at 10° C.

The functional response of C. sapidus was shown to vary significantly in form as a function of temperature. Analysis of proportional mortality rates at the lowest prey density (5 oysters/tank) indicated that medium length oysters obtained a partial prey refuge from from crab predation below 20° C and a total refuge below 14° C. Previous experiments have demonstrated variations in the intensity of the functional response as a consequence of temperature (Fedorenko 1975, Thompson 1978, Chow et al. 1983, Cockrell 1984, Murdoch et al. 1984, Spitze 1985, Persson 1986), but not the form of the response. Thus, temperature not only affects consumption rates of aquatic poikilotherms, but has the potential to stabilize predator-prey dynamics as well (this study).

Differences in individual crab functional responses at 19-20° C suggest that this temperature range may represent a transition in blue crab feeding responses such that individual crabs may exhibit either a type II or type III response, this notion is consistent with the high variability in consumption rates at this temperature range (Fig. 3).

Temperature effects: modeling

The general functional response model (Real 1977, 1979) was used as a statistical test of the form of the functional response. This technique has been used successfully to differentiate type II and III responses for both mammalian (Real 1979) and invertebrate (Lipcius and Hines 1986) predators. Lipcius and Hines (1986) found that consumption rates of C. sapidus feeding on M. arenaria were significantly lower at the two lowest prey densities, regardless of sediment type. Thus, model predictions were based on differences in consumption rates between mud and sand at the two lowest prey densities (Lipcius and Hines 1986). In this study, model predictions were based on differences in consumption rates at the lowest prey density, and did not corroborate the type III response indicated by the ANOVA of proportional mortality rates at medium temperatures. The model corroborated the ANOVA results of proportional mortality rates indicating a type II response at both high and low temperatures despite unequal sample variances at 26-27^{0} C. Therefore, these results (a) add evidence to the supposition that the general functional response model is constrained in testing the form of a sigmoid type III response based on consumption rate differences at a single density, and (b) suggest that the general model is relatively insensitive to unequal sample variances. Results from Real's (1979) study did not allow assessment of consumption rate differences per prey density.

The suitability of discrete-time conceptual models in describing the functional response, in which prey were not replaced as eaten, was realized at both 26-27^{o} C and 19-20^{o} C. At 13-14^{o} C, a significant "lack-of-fit" error indicated the discrete-time model to be inappropriate. This result is important in that the discrete-time model described more (84%) of the variance in consumption rates and displayed the lower residual sums of squares of the two models. Previous studies (Lipcius and Hines 1986) have used the lower residual sums of squares as the primary criterion in choosing the most appropriate model. These results suggest that an F-Test, employing the ratio of the "lack-of-fit" mean square to the "pure error" mean square (Draper and Smith 1966, Neter and Wasserman 1974), be incorporated into criteria for determining the best fit of continuous and discrete-time models. The use of a continuous-time conceptual model (which assumes a constant prey density) in describing the functional response at 13-14^{o} C, rather than a discrete-time model, may be due to the mathematical structure of the model when fit to extremely low consumption rates, as observed at 13-14^{o} C.

Density and temperature effects: behavioral components

Increased temperature typically accelerates metabolic activity. Assuming capture efficiency remains nearly constant or increases, blue crab attack (a')/encounter rates with stationary oysters should increase with temperature. Handling time (Th) and its components, breaking time (Tb) and eating time (Te), should decrease as temperature increases. The trend in functional response model parameter estimates reflected these predictions and indicated a temperature threshold above which, a' and Th were relatively unaffected.

Nonlinear regressions estimated a constant handling time between temperatures of 19 and 27° C, suggesting that crabs at these temperatures were able to feed at their maximum rates at high prey densities. Hence, direct handling time of oysters (eg., breaking time, consumption, and gut clearance) was not increased above 19° C. The _ca_.-54 fold increase in Th at 13-14° C clearly illustrates the exponential increase in handling time components of individual oysters with decreasing temperature below 19° C. Thompson (1978) indicated that handling times per _Daphnia_ _magna_ by larvae of the damselfly _Ischnura elegans_ remained constant between 16 and 27.5° C, and greatly increased below 8° C. Thompson (1978) suggested that absence of growth for _Ischnura_ below 8° C may be due to the significant decrease in a' observed at this temperature.

Similarly, the attack coefficient shows relatively little change between 19 and 27° C, but decreases dramatically below 19° C. The marked decrease in a' below 19° C corresponds well with field evidence of reduced blue crab activity levels below 16° C (Van Engel 1958).

Before discussing results pertaining to the various observed behavioral components, a cautionary note must be made regarding the comparison of directly measured predation parameters with those estimated from nonlinear regressions. Estimates of a' represent a maximum theoretical rate of attack and are separate from the effects of feeding history (Hassell 1978). It is therefore not equivalent to quantification of a finite feeding rate, which includes pretreatment effects and the effect of prey handling during the experimental period (Spitze 1985). Estimates of Th are likely to yield values that do not conform well to direct observation (Hassell 1978). This is because the estimated Th also includes periods of non-searching activity induced, for example, by satiation of the predator (Hassell 1978). Incorporation of all subcomponents of prey handling time (eg., Tb, Te, Tp) in assessment of the relationship between prey capture and reduction in future foraging ability, however, should be appropriate when total cost is desired for profitability analysis and optimal foraging predictions.

Despite standardization of hunger levels, the observed behavioral components within crabs were quite variable, regardless of temperature. The high variability within the data points is consistent with previous laboratory observations of crab foraging behavior (Elner 1980, Hughes and Seed 1981, Lawton and Hughes 1985), and may be due to differences in shell strength, crab strength, chelal morphology, oyster attachment geometry, or variations in individual crab attack methods.

Direct observations indicated that the total encounter rate was an increasing function of oyster density, regardless of temperature. Density-dependent increases in a' have been shown for several predators and parasitoids exhibiting a type III response (Hassell 1978). In this study, blue crabs appeared to search more actively as oyster density increased, despite functional response model assumptions of a constant a' with density.

The decrease in the total encounter rate at 26-27^{o} C is probably a consequence of the increased proportion of successful attacks observed at this temperature. The reduction in attack success with decreasing temperature may be due to one or more of the following functions decreasing with temperature: (1) number of crushing attempts, (2) muscular efficiency and/or (3) muscular strength. At 26-27^{o} C, the reduction in attack success rates with increasing prey density may reflect increased oyster encounters by the crabs pereiopods as prey density and metabolic (activity) levels increased. This is not unlike the relative stimulus hypothesis postulated by Jubb et al. (1983).

The positive correlation between Tp and probability of a successful encounter provides strong evidence for a behavioral mechanism that would mediate temperature-dependent attack success at low prey densities, and therefore would explain the marked differences in the form of the functional response at each temperature. Thus incorporation of Tp into subcomponents of the functional response (eg., a' and Th) facilitates a mechanistic view of the variable functional response observed in this study, and demonstrates the need for concurrent behavioral observations in functional response experiments.

Within the context of optimization models, the density and temperature dependence of Tp interact to produce a much more complex picture of crab acceptance/rejection sequences of bivalve prey than has previously been put forth. Hughes and Seed (1981) discussed the problems inherent in distinguishing between active diet selection and passive selection resulting from mechanical properties of the predator and prey, and suggested that crabs evaluate mussels by (1) measuring some aspect of size and vulnerability, or (2) adopt a certain persistence time that is perhaps a function of hunger level. Results from this study indicate that within a single oyster size-class, persistence times were not constant but extremely variable, and may be a function of prey density and temperature as well. At 26-27^{o} C, the decrease in persistence time at high prey densities accounts for the reduction in attack success rate and adds further support for the relative stimulus hypothesis (Jubb et al. 1983) at this temperature and density. However, increasing Tp with density from 5 to 20 oysters/tank suggest that there is a prey density threshold below which prey evaluation may be more important. Thus, crab evaluation of bivalve prey may involve a complex series of prey evaluation at low prey densities and relative stimulus at higher densities, with prey evaluation behaviors moving towards a relative stimulus response, as temperature (activity level) increases.

Breaking and eating times decreased with increasing temperature as predicted, but handling times did not. Observed handling times were slightly less than nonlinear regression estimates, which was probably due to incorporation of non-searching activity in model estimates (sensu Hassell 1978). Observed handling times did not vary with prey density as predicted by optimization models (Giller 1980), but did support functional response model assumptions of a constant Th. In contrast, Collins et al. (1981) found that observed mean handling times of <u>Aphelinus</u> <u>thomsoni</u>, a predator and parasite of the aphid <u>Drepansiphium</u> <u>platanoidis</u>, decreased with prey density due to a decrease in feeding attacks. Although they concluded that the decreased handling time contributed to the density-dependent sigmoid functional response of A. thomsoni, they did not equate this phenomenon with predictions based on optimization models. These results further illustrate the need for concurrent behavioral observations in functional response experiments.

Breaking times of individual oysters were shown to decrease with increasing temperature emphasizing the need for a detailed assessment of the effect of temperature on the crushing capabilities of Callinectes. As a consequence of the reduced Tb associated with increasing temperature, profitability of medium oysters was markedly higher at 26-27^{0} C than at 19-20^{0} C. Profitability was highest at an oyster length of approximately 31 mm SL at both temperatures. These results are similar to those reported for C. sapidus feeding on mussels, G. demissa, in which profitability peaked at approximately 25 mm SL (Hughes and Seed 1981, Seed 1982). Inclusion of eating time into profitability estimates greatly reduced profitability and yielded handling times that did not vary significantly with temperature. Thus, at medium and high temperatures, profitability estimates based on oyster dry weight to handling time ratios were equal.

Incorporation of persistence time in unsuccessful encounters had the same net effect on profitability estimates at each temperature, but for different reasons (see Results). These results suggest that profitability estimates that incorporate the total energetic cost for consumming an oyster of specific shell length is a more reliable estimator of profitability and does not readily vary between 20 and 26^{0} C. Despite the importance of temperature effects on predation and parasitism (Fedorenko 1975, Thompson 1978, Elner 1980, Spitze 1985, Persson 1986), there is little data in the literature with which to compare changes in profitability as a function of temperature. Elner (1980) examined the foraging strategy of C. maenas feeding on mussels, Mytilus edulis at two temperatures, 10 and 17° C and concluded that temperature had no effect on preferred mussel size. Whereas this study examined profitability based on individual foraging behavioral components, Elner (1980) examined crab prey-size selectivity assuming a constant optimal size regardless of temperature. Hence, this study and Elner's (1980) have reached the same conclusion using quite different approaches.

Oyster length effects: functional responses

Consumption rates for large crabs ($\bar{x}$ = 135-165 mm CW) increased with density and decreasing oyster length as expected. An increase in predation rates with decreasing size is consistent with results from previous studies (Whetstone and Eversole 1981, Elner and Lavoie 1983, Bisker and Castagna 1986, Sanchez-Salazar et al. 1987); however, the dramatic increase in consumption rates observed for small oysters ($\bar{x}$ = 15 mm SL) in this study, are the highest documented feeding rates for laboratory decapod-bivalve studies. A prey density of 350 oysters/tank was required in order to assess the form of the functional response for small oysters. Increasing shell length from 15 to 25 mm, and 25 to 35 mm, reduced consumption rates approximately 4.6 and 3.9 fold, respectively. Shell lengths of 40-45 mm SL appeared to be the critical size for crushing by large Callinectes. Elner and Lavoie (1983) indicated that maximum feeding rates by large (94-107 mm) lobsters, Homarus americanus and rock crabs, Cancer irroratus were 28 and 4.5 oysters * crab^{-1}* day^{-1}, respectively. The oysters in their study were attached to cement partitions and ranged from 10 to 25 mm SL. Oysters of 30-35 mm SL appeared to be the critical size for crushing as very few oysters were preyed upon by lobsters and rock crabs (Elner and Lavoie 1983). Increased consumption rates of Callinectes relative to either H. americanus or C. irroratus is probably due to differences in cheliped morphology. The chelal dactyls of Callinectes are very thin with a fine point compared to the broad and blunt dactyls of H. americanus and C. irroratus. This would provide Callinectes with greater dexterity in preying on small attached oysters. In light of the reduced handling time associated with cultchless oysters reported by Bisker and Castagna (1987), the increased consumption rates observed for Callinectes in this study, is probably a consequence of the large size of crabs used ($\bar{x}$=135-165 versus 85.5 mm CW).

Analysis of proportional mortality rates as function of prey density indicated that large Callinectes exhibited a type II response, regardless of oyster size-class. Although the initial pattern of proportional mortality rates for small oysters is typical of a type II response, which is characterized by the greatest mortality risk at the lowest prey density, this response demonstrates how an increase in prey density could change the initial decelerating (destabilizing) functional response into an accelerating (stabilizing) one. For instance, there is a decreased risk in proportional mortality at 40 and 80 oysters/tank relative to lower and higher densities (Fig. 11). This is probably due to differences in oyster spat attachment sites, such that certain of these microhabitats are less vulnerable to predation by blue crabs than others. At the two lowest prey densities (10 and 20 oysters/tank), blue crabs usually crushed the cultch into small pieces in order to feed on oysters located within these architectural refuges. This would account for the significantly higher proportional mortality rates at these two densities. As the available space for these refuges becomes saturated with increasing densities per cultch, proportional mortality rates begin to increase with prey density up to 120 oysters/tank. As prey density increases, an increased proportion of foraging time per 24h is probably being taken up by prey encounter and handling time activities, with a subsequent reduction in proportional mortality rates.

Individual crab functional responses were similar for 25 mm SL oysters suggesting that at this prey length, a combination of homogeneous microhabitat and prey features (eg., attachment geometry, shell thickness) facilitated the use of a similar opening technique, irrespective of prey density. Differences in the functional response for 35 mm SL oysters are probably due to differences in attachment geometry and shell thickness, whereas differences for 15 mm SL oysters are probably due to differences in opening techniques in which certain crabs may not exhibit the "random" crushing technique at low prey densities.

Oyster length effects: modeling

Despite unequal sample variances for the transformed dependent variable at 15 and 25 mm SL, the general functional response model (Real 1977, 1979) corroborated the results from the ANOVA of proportional rates indicating a type II response. These results provide additional evidence to the supposition that the general model is relatively insensitive to unequal sample variances. Additionally, the general functional response model (Real 1977, 1979) indicated a type II response for 15 mm SL oysters despite an atypical response at this oyster length. For 35 mm SL oysters, the general model described only 22.7% of the variance in consumption rates and was unable to adequately predict a response type. This result is probably due to the high variance in consumption rates for this oyster size class.

Both continuous and discrete-time models provided a statistically adequate fit to the data, regardless of oyster size-class. Discrete-time models provided the best fit to the data at 25 and 35 mm SL. At 15 mm SL, a continuous-time model was chosen over the discrete-time model, despite changes in prey density over 24 h. Similar results were obtained by Lipcius and Hines (1986) in which both type II and III continuous-time models best described the functional response of *Callinectes*, even though prey were not replaced as eaten.

Oyster length effects: *behavioral components*

Prey size should affect a number of measureable components of predation (Thompson 1978). Decreasing prey size typically reduces prey handling times with a subsequent increase in profitability and attack/encounter rates. Therefore, decreasing prey size should maximize the net rate of energy intake by minimizing the time spent handling prey. The trend in model estimates of a’ clearly reflected these changes, whereas Th did not.

Nonlinear regressions estimated a constant handling time of 0.1 h per *C. virginica*, regardless of prey length. This is in marked contrast to results obtained through direct measurement. Fox and Murdoch (1978) discuss the potential sources of error in using regression techniques to estimate predation coefficients. Therefore, direct measurement serves as a check on the previous nonlinear regression estimates. The attack coefficient (a') changed very little from 15 to 25 mm SL, but decreased approximately 7.6 times from 25 to 35 mm. Thus, 25 mm SL represents a prey size threshold, below which instantaneous attack rates are markedly reduced. These results suggest that instantaneous attack rates are an increasing function of decreasing prey size, but a concomittant decrease in handling times did not occur as predicted. Spitze (1985) found that handling times per *Daphnia pulex* by larvae of *Chaoborus americanus* increased linearly with prey size, whereas the attack rate peaked at intermediate sizes. These results indicated that digestion was a major component in handling times (Spitze 1985). Cockrell (1974) examined predation of four arbitrary prey size classes of *Asellus aquaticus* by adult *Notonecta glauca* and found that a' declined linearly and Th increased exponentially as prey size increased. In contrast, Hewett (1988) examined the effects of predator and prey size on the behavior of the predatory ciliate, *Didinium nasutum* feeding on *Paramecium sp*., and found that searching times during capture were not significantly affected by prey size. Additionally, 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 *I. elegans* feeding on *D. magna*, a' increased with increasing prey size. Thus, the effect of varying prey size upon functional response sub-components appears to be largely a function of the particular predator-prey system examined.

Most models of foraging predict that a predator will spend more time foraging as prey density increases (Hassell and May 1974, Murdoch and Oaten 1975). This trend was evident for 25 and 35 mm SL oysters, in which observed encounter rates increased beyond an initial range of low prey densities; however, the trend was not statistically significant. Direct measurement indicated that total encounter rates were increasing functions of decreasing oyster length, which probably reflects the reduction in handling time associated with smaller oysters.

Total encounter rate observations for small oysters may be somewhat suspect in that encounters not involving active manipulation by the chelae were not quantified. Blue crab prey evaluation of small oysters might be accomplished through tactile stimulus by the periopods (eg., relative stimulus) rather than active manipulation with the chelae (eg., prey evaluation). This would help explain the confusing nature of both total and successful encounter rates since the two appear to be positively correlated, rather than inversely related as indicated in the temperature results. Film analysis of encounter rates for the oystercatcher, <u>Haematopus</u> <u>ostralegus</u> preying on the infaunal bivalve, <u>Scrobicularia</u> <u>plana</u> 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 Zwartz 1985).

Blue crabs reached maximum encounter rates at an intermediate density of 20 oysters/tank, demonstrating an average of 10 and 6 encounters/h for medium and large oysters, respectively. For medium and large oysters, attack success was inversely related to total encounter rates. The behavioral mechanism most likely regulating attack success is persistence time, which decreased with increasing prey density.

Therefore, as a consequence of increasing persistence times with decreasing density, crabs were more successful at opening oysters and therefore had less available time to encounter new prey.

The key finding in relation to behavioral components that regulate predation intensity is that persistence time appears to depend upon prey density, size and microhabitat, as well as temperature. The addition of prey size-dependence in Tp as a subcomponent of the functional response adds further complexity to the overall view of crab acceptance/rejection sequences of bivalve prey. At 5 oysters/tank, persistence times inidicated a significant linear relationship with oyster length. At 25 mm SL, there was a significant density effect, and at 35 mm SL, there was no significant effect of either oyster length or density. These results suggest that given a range of oyster lengths and densities, crab acceptance/rejection of bivalve prey involves a suite of complex foraging tactics which are regulated by changing oyster length and density plus microhabitat features (eg., attachment geometry, shell thickness). For example, at small oyster lengths (eg., 15 mm SL) with concurrent high within-cultch densities, Tp is mainly a function of oyster length. Within this small size class, oysters are probably more homogeneous with respect to shell thickness and a greater proportion of spat are located in high vulnerability areas, than are larger size classes. As oyster length increases up to 25 mm SL, individual shell thickness and attachment geometry become increasingly heterogeneous. This should be especially true at low prey densities where most of the vulnerable oysters, in terms of shell thickness and attachment geometry, have been eaten, hence the significant decrease in Tp at the highest prey density at 25 mm SL. At a mean size of 35 mm SL, the proportion of high vulnerability sites is at its lowest point, and shell thickness and oyster attachment geometry is most variable, when compared to smaller size classes. This corresponds well with the lack of significant variation in Tp at 35 mm SL, in terms of oyster length and density. Previous experiments have demonstrated a positive correlation between prey length 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 length as expected, with no significant effect of prey density. The lack of density-dependence disagrees with predictions based on optimization models (Giller 1980), and supports functional response model assumptions of a constant Th. Breaking times increased asymptotically with oyster length, and were significantly higher for large oysters than for small and medium length oysters, indicating a prey length threshold at 30 mm, above which breaking times greatly increased. The increased variability observed in breaking times above 30 mm SL reemphasizes the importance of shell thickness and attachment geometry in mediating attack methods, and suggests that 30-35 mm SL oysters are approaching the critical size for crushing by large _Callinectes_. 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). Lawton and Hughes (1985) found that _C. pagurus_ exhibited different opening techniques with increasing size of *N. lapillus*, with considerable variation in breaking times at large prey sizes.

Eating times displayed a more linear relationship with oyster length, reflecting the volume of flesh ingested or surface area of shell gleaned, rather than differences in varying shell thickness or attachment geometry. These results are consistent with previous studies, which describe a linear relationship between eating times and prey size (Elner and Hughes 1978, Lawton and Hughes 1985).

Optimal prey sizes calculated from profitability estimates must be interpreted with some degree of caution for, although different functions (eg., power or exponential) can be fitted equally well to handling time prey-size observations, the optimal prey values predicted from them can vary substantially (Lawton and Hughes 1985, Sanchez-Salazar et al. 1987). In reviewing the literature, there does not appear to be a consistent relationship between prey size and profitability. Sanchez-Salazar et al. (1987) found that the time required for *C. maenas* to open and consume individual cockles, *C. edule*, increased exponentially with prey size, with small cockles (<15 mm) being most profitable in terms of E/Th. Optimal size of prey increased with predator size (Sanchez-Salazar et al. 1987). Elner and Hughes (1978) found that as mussel, *M. edulis*, length increased, prey value (E/Th) reached a maximum which itself increased with crab size. Beyond the maximum, prey value declined because of the accelerating increase in Th. Spitze (1985) demonstrated that profitability, based on handling times of fourth-instar *C. americanus* preying on *D. pulex*, increased linearly with prey size, but concluded that *Chaoborus* did not selectively feed as predicted by optimal foraging models. Bence and

Murdoch (1986) examined prey size selection of Daphnia by the mosquitofish, Gambusia affinis, in an attempt to decouple profitability and detectability. They tested the assumption that prey profitability would decrease with increasing prey size, owing to difficulties in capture and handling, whereas detectability should increase monotonically (Bence and Murdoch 1986). Their results demonstrate that profitability decreases rather than increases with prey size, and that Gambusia actively selected certain size prey (Bence and Murdoch 1986). Similar results from this study indicated profitability to be an increasing function of decreasing oyster length, with a marked increase in profitability below an oyster length of 15 mm.

Incorporation of eating time into profitability estimates dramatically reduced (13 fold) profitability of small oysters and suggests that feeding, digestion and gut clearance are major components of oyster handling times. Profitability of medium and large oysters were relatively unaffected (3 and 2 fold, respectively) after incorporation of eating times, suggesting that the effects of varying shell thickness and attachment geometry are more important to handling times of large oysters than small oysters. Persistence time adjustments in profitability did not significantly affect profitability estimates as much as incorporation of eating times.

Crab size effects: functional responses

Zaret (1980) proposed that an increase in predator size should increase the range of prey species available to the predator and enhance predator success rate, encounter rate, and prey handling ability. Hewett (1988), examining predator-prey dynamics of a protozoan system, divided this generalization into two behavioral hypotheses: "large size" and "adaptive size". The large size hypothesis states that it is always advantageous for a predator to be large because they encounter prey more frequently, have a higher rate of capture and, for protozoan systems, divide more rapidly (Hewett 1988). The adaptive size hypothesis states that predation success is a direct function of the relative sizes of predator and prey. Under this hypothesis, small predators should be competitively superior to large predators on small prey and vice versa, with a higher rate of capture for each size of predator feeding on the appropriate prey size (Hewett 1988). Due primarily to differences in the preference of large and small predators on small prey, Hewett (1988) concluded that both hypotheses were partially supported.

Similar complex interactions between factors (size of predator and prey) were demonstrated for the intertidal predatory gastropod, Morula marginalla, feeding on barnacles, Tesseropa rosea (Moran 1985). Moran (1985) found that 15 mm Morula ate adult Tesseropora faster than did 12 mm Morula, and both sizes of whelks ate juvenile Tesseropora faster than they ate adults. Morula of 15 mm did not eat juvenile Tesseropora significantly faster than 12 mm Morula.

In this study consumption rates varied as a function of carapace width for large and medium oysters, but not small oysters. Small crabs were unable to feed on large oysters despite persistence times of nearly 20 minutes (personal observation). Thus, large oysters ($\bar{x}$ = 35 mm SL) are invulnerable to predation by blue crabs < 80 mm CW. Although medium size crabs were capable of opening large oysters, their consumption rates were lower than those for large crabs. At medium oyster lengths, consumption rates were higher for large crabs compared to medium and small size crabs, whereas there were no apparent carapace width related differences in consumption rates of small oysters. These results suggest that when foraging on large and medium oysters, the large size hypothesis is a plausible explanation for the observed variations in feeding rates with carapace width. At small oyster lengths, neither the large size nor adaptive size hypothesis adequately described the interaction effect between oyster length and carapace width. The ability of large crabs to successfully feed on small and large oysters suggests that large crabs are well suited to feed on a wide range of juvenile oyster lengths. This success may be due in part to increased crushing strength associated with a large chela height and/or use of variable attack methods (eg., random crushing).

The functional response of C. sapidus feeding on large oysters varied significantly in form due to crab carapace width, suggesting a significant interaction effect between carapace width, oyster length and oyster density. Analysis of proportional mortality rates at the lowest prey density (5 oysters/tank) indicated that large oysters achieved a partial prey refuge from predation by medium size crabs ($\bar{x}$ = 100-125 mm CW). Although the intensity of the functional response of Callinectes feeding on medium oysters increased with carapace width above 135 mm, the form of the response was a destabilizing type II response, regardless of crab size. For small oysters, analysis of proportional mortality rates at the lowest prey densities (eg., 10 and 20 oysters/tank) indicated that small oysters achieved a partial prey refuge from predation by medium and small size blue crabs. Differences in crusher chelae height as a function of carapace width may explain the observed differential stabilizing-destabilizing effects of various predator-prey size combinations. At low prey densities, the range of large ($\bar{x}$ = 35 mm SL) oyster lengths is reduced in order to achieve the desired mean of 35 mm. As prey density increases, there is a wide range in prey sizes with a concomittant increase in attachment geometry variability. Assuming crusher chelae height is a decreasing function of carapace width, medium size crabs would be at a mechanical disadvantage relative to large crabs, resulting in a lowered probability of success. Crusher chelae strength, which is directly proportional to chelae size in terms of height (Vermeij 1976, Elner 1978), determines the efficiency with which a prey item can be opened, and hence determines prey value and optimal size (Elner 1980).

Medium oysters were vulnerable to predation regardless of carapace width and oyster density. These results are consistent with the hypothesis that medium length ($\bar{x}$ = 25 mm SL) oysters represent a consistent combination of microhabitat and prey features (eg., attachment geometry, oyster length, shell thickness) that facilitates the use of a similar opening technique, irrespective of oyster density.

Similarly, results obtained for small oysters support the hypothesis that small oysters attain an architectural refuge from predation when attached to depressions on the surface of the cultch, and as a consequence, obtain a partial prey refuge (type III response) from small and medium size blue crabs that do not display the "random" crushing technique.

Previous experiments demonstrated variations in the intensity of the functional response as a consequence of different predator sizes (Thompson 1975, Moran 1985), but not the form of the response (this study). Thus, predator size not only affects consumption rates of invertebrate predators, but has the potential to stabilize predator-prey dynamics as well.

Crab size effects: modeling

The inability of the general functional response model to predict a response type for large crabs feeding on large oysters was previously discussed under the subheading "oyster length effects: modeling". The overall trend in model fitting procedures for crab-size effects, using the general functional response model (Real 1977, 1979), was similar to previous results; corroboration of the ANOVA results for type II responses, and an inability to predict a type III response based on consumption rate differences at a single prey density. The former was the case for all three crab size-classes feeding on medium oyster lengths, and for large crabs feeding on small oysters, while the latter occurred with medium crabs eating large oysters, and medium and small crabs feeding on small oysters. In numerous instances, where the general model corroborated the ANOVA results, variances were equal. Therefore, these results further support the supposition that (a) the general functional response model is constrained in describing the form of a sigmoid type III response based on consumption rate differences at a single prey density, and (b) the general model is relatively insensitive to unequal sample variances.

The suitability of discrete-time conceptual models to describe the functional response, in which prey were not replaced as eaten, was realized for large and medium crabs feeding on large oysters; however, both continuous and discrete-time models provided a statistically adequate fit. In contrast, continuous-time models best described the data for all three size-class crabs feeding on medium and small oysters. For medium and small crabs feeding on medium oysters, a significant "lack-of-fit" error indicated the discrete-time model to be inappropriate. These results are similar to results at 13-14^{0} C, in that the discrete-time model described more of the variance (medium crabs, 92.2%; small crabs, 93.5%) in consumption rates and displayed the lower residual sums of squares of the two models. These results further emphasize the need for incorporating an F-Test employing the ratio of the "lack-of-fit" mean square to the "pure error" mean square (Draper and Smith 1966, Neter and Wasserman 1974) into criteria for determining the best fit of continuous and discrete-time models.

For large crabs preying on medium and large oysters, and small crabs preying on small oysters, continuous-time models were chosen over discrete-time models, despite changes in prey density over 24h. These results are similar to those described by Lipcius and Hines (1986) and discussed under the subheading "oyster length effects:modeling". These results suggest that in many instances, models that assume a constant density over the experimental period, better describe the functional response in which prey were not replaced as eaten, compared to a discrete-time model.

Crab size effects: behavioral components

The trends in functional response model parameter estimates (a' and Th) were consistent with the notion that foraging behavior is a complex interaction of oyster length, carapace width, and oyster density; however, the trends do not correspond well with different predator-prey-size consumption rates. Nonlinear regressions estimated a constant a' and Th for large oyster lengths, regardless of carapace width. For medium oyster lengths, attack coefficients were approximately equal for all three size-class crabs, whereas handling time for large crabs was nearly 5 times less. At small oyster lengths, a' and Th were equal for small and medium size crabs, with both parameters increasing dramatically for large crabs. These results suggest that the large size hypothesis adequately explains the interaction of crab size and predator success for medium and small oysters, but not large oysters. Thompson (1975) examined the functional response of five instars of _I. elegans_ each preying on five sizes of _D. magna_. Attack coefficients increased with size of predator and decreased with increasing size of prey; handling times varied in an opposite manner to a'. Similar results were reported by Moran (1985) for _Morula_. Fairweather and Underwood (1983), using regression techniques, did not find a significant effect of size of _Morula_ on handling times with several prey types. The disagreement between results from this study and those of Thompson (1975) and Moran (1985) may be due to the inherent bias associated with using regression techniques to estimate predation coefficients (Fox and Murdoch 1978).

Crab sex effects: functional responses

The approach of this study was to segregate predators by sex and determine whether consumption rates and/or the functional response varied as a consequence of various predator-prey size combinations. Although potential behavioral differences were not directly measured, they can be inferred, with some degree of caution, from parameter estimates derived from nonlinear regressions with functional response models.

Crab sex appeared to have relatively little effect on consumption rates, regardless of oyster length and carapace width. In contrast, both male and female crabs exhibited much higher consumption rates on medium oysters than large oysters. These results are similar to those described by Elner and Lavoie (1983) in which mean predation rates for male and female _H_. _americanus_ and _C_. _irroratus_ feeding on _C_. _virginica_ attached to "chinese hat" collectors, were not significantly different.

The functional response of _C_. _sapidus_ was shown to vary significantly in form as a function of crab sex and oyster length. Analysis of proportional mortality rates at the lowest prey density (5 oysters/tank) indicated that large oysters achieve a partial prey refuge from predation by large and medium female crabs, and medium male crabs. These results are consistent with the observed stabilizing-destabilizing effects of various predator-prey-size combinations discussed under the subheading "crab size effects: functional responses". The significant difference in the form of functional response for large male and female crabs is probably due to the increased mechanical advantage afforded the larger chelae heights of males, compared to females. Variations in opening techniques for large oysters probably explains the significant differences in individual functional responses of large male and female crabs.

Medium oyster lengths were vulnerable to predation regardless of crab sex and thus potential differences in chelal heights. These results are consistent with results observed for three crab size classes feeding on medium oysters, and further suggest that medium oysters ($\bar{x}$ = 25 mm SL) represent a consistent combination of microhabitat and prey features (see discussion for "crab size effects: functional responses"). Individual functional responses of male and female crabs at this prey size class were found to be equal. These results support the supposition that medium oysters facilitate the use of a similar opening technique, irrespective of oyster density and carapace width. The type III functional response observed for medium male and female *Callinectes* preying on large oysters is probably a function of lowered chelal height to oyster length ratios associated with decreasing carapace widths. Hence, the form of the functional response can vary as a consequence of sexual differences in cheliped morphology. Previous work has not documented a change in the *form* of the functional response as a function of sex-related morphological differences.

Crab sex effects: *modeling*

The overall trend in results from model fitting procedures for crab-sex effects, using the general functional response model (Real 1977, 1979), was similar to previous results; corroboration of the ANOVA results for type II responses, and an inability to predict a type III response based on consumption rate differences at a single prey density.

The former was the case for large crabs feeding on medium oysters, whereas the latter occurred for large female and medium male crabs feeding on large oysters. The general functional response model was unable to adequately predict a response type for large crabs feeding on large oysters. Possible reasons for the inability of the general functional response model (Real 1977, 1979) to adequately describe the functional response were described above (see "temperature effects: modeling").

Descrete-time conceptual models provided the best fit for large crabs feeding on large oysters, regardless of crab sex. For large female crabs feeding on medium oysters, a significant "lack-of-fit" error indicated the discrete-time model to be inappropriate. This result is similar to results at 13-14^{o} C and for medium and small crabs eating medium oysters in that the discrete-time model described more (93.8%) of the variance in consumption rates and displayed the lower residual sums of squares of the two models. These results reemphasize the need for incorporating an F-Test, employing the ratio of the "lack-of-fit" mean square to the "pure error" mean square (Draper and Smith 1966, Neter and Wasserman 1974) into criteria for determining the best fit of continuous and discrete-time models. For medium female crabs feeding on large oysters, a continuous-time model best described the data despite density depletion over the experimental period.

Crab sex effects: behavioral components

Functional response model parameter estimates indicated that variations in the instantaneous attack rate (a') and handling time (Th) for Callinectes were a complex interaction of oyster length, crab sex (chelae height) and carapace width (chelae height). Based on nonlinear regressions, a' for large female crabs preying on large oysters was 18 times greater and Th 10 times higher than those parameters for similar size males. These results suggest that the critical size for crushing, and thus optimal size (Elner 1980), for large females may be reduced relative to males. Elner (1980) found that the prey preference pattern in female C. maenas was as well defined as in males; however, the preferred prey sizes for females were smaller than those for equivalent size males. Female Carcinus have smaller chelae than males and when preferred size was expressed as a function of crusher chelae height, there were no significant differences in foraging behavior (Elner 1980). For large crabs feeding on medium size oysters, a' and Th were found to be equal regardless of crab sex. These results provide further evidence for the role of chelae height in determining critical crushing size, and suggests that the efficiency of female crusher chelae in preying on medium size oysters is equivalent to that of the larger crusher chelae possessed by males.

For medium size males preying on large oysters, both a' and Th were markedly reduced compared to equivalent size females, despite no apparent differences in consumption rates or the form of the functional response. The disagreement between results for this predator-prey size combination (medium crabs-large oysters) and the previous one (large crabs-medium oysters), may be due to the inherent bias associated with using regression techniques to estimate predation coefficients (Fox and Murdoch 1978). In this instance, the estimated a' for medium crabs preying on large oysters was estimated from eqn (6) whereas a' for large crabs preying on medium oysters was estimated directly from nonlinear regressions with type II functional response models. Perhaps this indicates that the bias associated with estimating a' from eqn (6), and type III models in general, is greater relative to direct estimation from type II models.

Overview of complex factor effects

Temperature

Large blue crabs preying on medium length oysters exhibited a type II response at 26-27° C, a type III response at 19-20° C, and a "displaced" type II response at 13-14° C. The positive correlation between Tp and probability of a successful encounter provides strong evidence for a behavioral mechanism mediating attack success, and indicates that Tp should be incorporated into functional response model subcomponents for this particular predator-prey system. Decreasing temperature tended to stabilize predator-prey dynamics and is probably a consequence of the reduction in Tp with decreasing temperature. These results suggest that Callinectes possesses a flexible behavioral mechanism which rapidly adjusts to small scale changes in prey availability and temperature. If we assume that Callinectes is foraging within energy maximization premises (Pyke et al. 1977, Hughes 1980), we are left with the question of how a density and temperature dependent behavioral mechanism, such as prey persistence time, maximizes Callinectes net rate of energy intake. This question can only be addressed through detailed physiological measurements examining the energy expenditure of Tp versus the potential energy gain, given a specific temperature, prey density and associated encounter success probability.

Profitability estimates were calculated by incorporating Tp in unsuccessful encounters, and did not vary between 20 and 26^{0} C.

Overview: oyster length

Large blue crabs exhibited a type II response when preying on small ($\bar{x}$ = 15 mm SL), medium ($\bar{x}$ = 25 mm SL), and large ($\bar{x}$ = 35 mm SL) oysters. The functional response for small oysters appeared atypical of the "traditional" type II response, indicating how an increase in prey density could change the response from a destabilizing to a stabilizing response. This response was likely a consequence of the differential space availability for architectural refuges as a function of increasing within-cultch densities. These results suggest that future laboratory studies of crab-oyster predator-prey dynamics examine not only the effect of total density (eg., oysters/tank), but the effect of within-patch (eg., oysters/cultch) density as well. Results from such a study might indicate that density-dependent foraging responses are operating at both meso- and micro-spatial scales. Additionally, it is important to examine the effect of interannual differences in crab size-class frequencies on oyster juvenile mortality rates. For instance, in a year with many large crabs, oysters would likely suffer more than a year with many small crabs.

Persistence times were positively correlated with attack success at three oyster size-classes, and appeared to be prey density and prey size-dependent. Breaking and handling times of large oysters (>30 mm

SL) greatly increased and were more variable, relative to small and medium oyster lengths. These results suggest that oysters >30 mm SL are approaching the critical size for crushing due to increased variability in shell thickness and attachment geometry. Profitability estimates indicated small oysters to be the most profitable in terms of E/Th. The energy maximization premise requires that the predator is able to rank prey types according to their value defined as E/Th. The question now remains: given limited and unlimited availability of three oyster size-classes, would Callinectes "choose" the more profitable (15 mm SL) size class in accordance with energy maximization premises? Active selection of small oysters would simultaneously maximize net energy intake and minimize handling time. Examination of diet selection alone does not allow one to falsify optimization premises because of the inability to distinguish between active diet selection and passive selection resulting from mechanical properties of predator and prey (Hughes and Seed 1981).

Overview: crab size

Large and medium blue crabs preying on large oysters ($\bar{x}$ = 35 mm SL) exhibited type II and type III responses, respectively. The critical size for crushing by small crabs was approximately 29 mm SL. Decreasing chelal height and correspondingly reduced crushing forces likely explain the pattern with carapace width. All three sizes of crabs exhibited a type II response with medium oysters, which probably represent the most homogeneous size-class with respect to micro-habitat and prey features. This oyster size probably facilitated similar opening techniques regardless of prey density and carapace width. Medium and small blue crabs exhibited a type III response when preying on small oysters, whereas large crabs exhibited a type II response. The results here can be explained by different opening techniques in which large crabs employ a "random" cushing technique to feed on small oysters attached to depressions on the cultch. These results have important implications for both public and private oyster enhancement operations which might utilize various substrates for setting purposes. For example, use of a smooth-surfaced shell such as the surf clam, Spisulla solidissima, as cultch material, might not provide the stuctural complexity required to achieve the architectural refuge observed in this study. Conversely, increased structural complexity, either through use of "natural" or "artificial" cultch materials might effectively reduce the loss of small oysters ($\leq$ 15 mm SL) to crab predation. Structural complexity mediates predator-prey interactions by providing more refuges for prey species as well as reducing the foraging efficiency of the predator (Rosenzweig and MacArthur 1963, Murdoch and Oaten 1975). Future laboratory studies of crab-oyster predator-prey dynamics should examine the potential effects of varying stuctural complexity, associated with different cultch materials, in mediating prey dynamics.

Overview: crab sex

Large male and female blue crabs preying on large oysters exhibited type II and type III responses, respectively. When large male and female blue crabs were exposed to medium oysters, both exhibited a type II response. Medium male and female crabs preying on large oysters exhibited a type III response. These results are consistent with the observed stabilizing-destabilizing effects of various predator-prey size combinations described above, and are probably a consequence of different chelal height to carapace width ratios. These results suggest that the chelal heights of male and female blue crabs are approximately equal until the terminal molt, after which the chelae height of males is significantly greater, and support standardization by sex as done in studies of *C. sapidus* feeding upon bivalves (Elner and Hughes 1978, Seed 1980, Hughes and Seed 1981, Blundon and Kennedy 1982b, Seed 1982, Jubb et al. 1983, Arnold 1984, Bisker and Castagna 1986, Lipcius and Hines 1986).

These experiments provide a basis for including prey density and size, predator size and sex, and temperature as factors in models of foraging behavior of *Callinectes*, in modeling survivorship of young-of-the-year *Crassostrea*, and within functional response studies of other predator-prey systems.

Applicability of general and conceptual functional response models

Results from analyses with the general functional response model (Real 1977, 1979) suggest that the general model is (a) relatively insensitive to unequal sample variances, and (b) constrained in testing the form of a sigmoid type III response based on consumption rate differences at a single prey density. Since the primary goal of the general model was to test the form of the functional response, the latter point indicates that the model does not provide an adequate statistical test in all circumstances. Further, the results promote the use of other criteria for detecting the form of the functional response based on: (a) results of the ANOVA of proportional mortality rates as a function of density, followed in decreasing priority by (b) results from general functional response model fitting procedures. The added emphasis on ANOVA in determining the form of the functional response combined with the experimental design assumptions (Holling 1959, Houck and Strauss 1985), which state that individual predators should be tested only once to avoid secondary experimental conditioning and allow for independence of experimental trials, creates a perplexing situation regarding the error term in the ANOVA hypothesis test. When individual crabs are constrained to one density trial, the within-cell error term does not account for variations in individual crab responses, hence the F-ratio is conservatively biased (ie., decreased chance of a type I error) and may reducte statistical power. Use of the Heterogeneity G-Test (Sokal and Rohlf 1981) allowed assessment of individual feeding responses without replication, but the variance could not be incorporated into hypothesis tests. In order to assess the form of the functional response with a more appropriate error term, future studies might replicate each predator twice (assuming no secondary experimental conditioning) and employ a repeated measures design (Sokal and Rohlf 1981).

Nonlinear regressions with conceptual functional response models (Eqns 1-4) allowed estimation of biologically meaningful parameters (a' and Th). In several instances, continuous-time models, which assume a constant density, fit the data better than discrete-time models, which account for prey depletion over the experimental period. Additionally, models which described more of the variance in consumption rates and exhibited the lower residual sums of squares of the two models, in some instances indicated a significant "lack-of-fit" (Draper and Smith 1966, Neter and Wasserman 1974). These results suggest that future studies should incorporate an F-Test employing the ratio of the "lack-of-fit" mean square to the "pure error" mean square (Draper and Smith 1966, Neter and Wasserman 1974) into criteria for determining the best fit of continuous and discrete-time models.

Field study

To determine the accuracy with which the mark-recapture technique assessed temporal survivorship and identify any potential artifacts associated with handling and marking of juvenile oysters, I compared the final observed mean density for each site with a predicted density based on the cumulative proportional mortality rates due to crabs and unknown causes. For the 1985 site, the initial mean density of 133 oysters * $[0.25m^2]^{-1}$ (Table 28, quadrat A) was reduced to 54 oysters * $[0.25m^2]^{-1}$(Table 28, quadrat G) for a 59.6% reduction over a 140 day experimental period. Due to confounding effects of recruitment of the 1986 year class, the density associated with quadrat H and the proportional mortality rates measured for quadrat G were not used in the above comparisons. Cumulative proportional mortality rates predicted a 79.5% reduction over the experimental period for a final density of 27.7 oysters * $[0.25m^2]^{-1}$. A Student's t-Test (Zar 1984) indicated that the arcsine-transformed predicted (79.5%) and observed (59.6%) proportions were not significantly different (t = 0.2, df = 2, NS).

For the 1986 site, the initial mean density of 690.0 oysters * $[0.25m^2]^{-1}$(Table 28, quadrat I) was reduced to 490.3 oysters *

$[0.25m^2]^{-1}$ for a 28.9% reduction over a 63 day experimental period. Cumulative proportional mortality rates predicted a 15.5% reduction over the experimental period for a final density of 583.1 oysters * $[0.25m^2]^{-1}$. A Student's t-Test (Zar 1984) indicated that the arcsine-transformed predicted (15.5%) and observed (28.9%) proportions were not significantly different (t = 0.49, df = 2, NS). Results from both sites indicate that the mortality rate of juvenile oysters was not significantly enhanced due to handling and marking, and suggest that this mark-recapture technique accurately assessed temporal survivorship of juvenile oysters.

The identification of crab-related mortality was based upon identifying distinct crab "signatures" on the shells of eaten oysters. Laboratory observations indicated that the frequency with which Callinectes and Panopeus completely crushed the right valve increased with decreasing shell length (personal observation). In addition, the trend in proportional mortality rates appeared to mirror that due to crabs, with the exception of the August 5 sample date. Therefore, I suggest that a large proportion of the mortality for smaller oysters (eg., 20-27 mm) due to unknown causes is probably attributable to crabs. This would explain the increase in proportional mortality rates due to unknown causes for smaller oysters (20-27 mm SL) at the 1986 site (Fig. 36). The significant increase in unknown proportional mortality rates on August 5 is probably a consequence of the massive set of Molgula manhattensis around July 15. M. manhattensis is an epibenthic suspension-feeding ascidian that feeds on the same food items as Crassostrea. Molgula typically settle in dense mats on top of the oyster reefs and feed through extended siphons. Thus, competition between Molgula and Crassostrea may have effectively reduced the available food resources and/or smothered oysters to the point that they gaped allowing access to a variety of predators. The decreased growth rate observed between July 15 and August 28 (Table 28) adds further evidence to the postulation of limited food during this period.

Mortality due to unknown causes may also have been affected by a suite of other predators such as the polyclad turbellarian flatworm, Stylochus ellipticus (Landers and Rhodes 1970), oyster drills, Urosalpinx cinerea and Eupleura caudata (MacKenzie 1961), and the cownose ray, Rhinoptera bonansus (Smith and Merriner 1978). Other gastropod predators/parasites such as Odostomia impressa prefer older, larger oysters as prey rather than spat or small oysters (Loosanoff 1956). Although the oyster toadfish, Opsanus tau, is a probable predator, it also preys to a greater extent on mud crabs (McDermott 1964) and may be more of an oyster benefactor than predator (Gibbons and Castagna 1985).

Oyster diseases and anoxia/hypoxia were probably not significant mortality factors in this study. The shallow depth (3-4m) of Milford Haven probably facilitates wind-driven mixing of the water column such that low DO levels are seldom encountered by oysters. Should conditions become hypoxic, oysters can survive up to 5 days at 1.0 ppm oxygen (Sparks et al. 1958). Oyster diseases such as Michinia nelsoni (MSX) and Perkinsus marinus (Dermo) are usually not fatal until oysters are 2 to 3 years old (Sprague 1971).

Predation dynamics of blue crabs varied as a function of abiotic and biotic factors. Laboratory results suggested that prey persistence times and thus successful encounter rates varied according to temperature and oyster length and were both correlated with oyster density. Field results suggest that temperature, oyster length and density-dependent mortality mechanisms were operating for this subtidal oyster reef. Mortality rates appeared to be decreasing functions of increasing oyster length, and were positively correlated with density at both sites. At the 1985 site, the confounding nature of mortality rates as a function of temperature suggests that oyster density and length mediated crab predation intensity from late-spring through late-summer as 0+ oysters reached 1 year old. Local patterns in prey abundance and distribution determine the diet of individual _Callinectes_ such that crabs may migrate from low-density to high-density prey patches (Laughlin 1982). Boulding and Hay (1984) postulated that crabs are able to detect areas of higher prey density from a distance and actively forage there. Pearson et al. (1979) showed that _Cancer_ _magister_ uses its antennules as distance chemoreceptors and has the ability to detect extracts of the little neck clam, _Protothaca_ _staminea,_ at a concentration of 10^{-10}g/L; higher concentrations elicit foraging behaviors (Pearson et al. 1979). Hence, high clam densities would emit a greater concentration of metabolites than would fewer clams in the same area, thus more crabs would be attracted leading to higher mortality rates (Boulding and Hay 1984). Crabs might also cause density-dependent mortality by remaining longer in, or returning more often to patches of high density (Boulding and Hay 1984), as predicted by optimal foraging premises (Pyke et al. 1977). Intraspecific competion between large aggregations of crabs within high density patches might also reduce the extent of available feeding areas (Ens and Goss-Custard 1984) and the efficiency with which crabs forage.

The field results do not allow one to specifically test if crabs stabilize oyster populations in the mathematical sense of establishing locally or globally stable equilibria, or in the sense of the rate of return to equilibrium. Therefore, in discussing the field data, the term destabilizing refers to a situation in which mortality rates increase with decreasing prey prey density. Proportional mortality rates increased from May 13 to June 24 with a concomittant decrease in oyster density and increase in length. These results suggest that crab predation had a potentially destabilizing effect on prey dynamics over this period. Despite this destabilizing trend, oysters appear to persist after June 24 by attaining a length (>30 mm) beyond which they are relatively invulnerable to crab predation. These results agree with laboratory observations of increased handling time and decreasing profitability for oysters > 29 mm SL. The field results from May 13 to June 24 are consistent with the destabilizing predation shown by three sizes of blue crabs feeding on medium oysters at high temperatures. Due to the intense recruitment of Molgula, this trend probably began to stabilize as a consequence of prey switching and/or increased habitat complexity associated with the tunicate mat. However, competition for food resources may have enhanced oyster mortality and negated the stabilizing feature. Decreasing temperature associated with autumn appeared to be the key factor in reducing predation intensity at the 1986 site. Thus a suite of direct and indirect mortality factors combined with medium to high annual recruitment levels (Haven et al. 1981) probably interacted to enhance local and/or global stability of this oyster community, or cause density-dependent mortality (Murdoch and Oaten 1975, Hassell 1978).

Application to oyster enhancement operations

The cumulative laboratory and field evidence indicates that an outplanting strategy of oysters > 29 mm SL, attached to oyster cultch, during the fall when water temperatures reach approximately 15^{o} C would probably minimize losses due to crab predation. Increasing habitat complexity for small oysters <29 mm SL via rough-surfaced cultch may help mediate predation intensity as well. Additionally, proper manipulation of total and within-cultch densities might reduce losses due to density-dependent predation.

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Table 2. Results of linear regression with the log-transformed general functional response model (Real 1977, 1979) at each temperature.

	Temperature		
Feature	27-26° C	20-19° C	14-13° C
Parameter estimates			
Intercept	-2.65	-2.07	-2.94
Slope	0.90	1.00	0.96
Slope standard error	0.09	0.18	0.24
Summary Statistics			
Regression SS(df)	4.9(1)	4.4(1)	3.7(1)
Residual SS(df)	2.1(44)	4.6(34)	7.7(34)
F-value	104.6	33.0	16.4
P-values	<0.0001	<0.0001	<0.0001
R^2(%)	70.4	49.2	32.6
Binomial Test (Partial)	NS	NS	NS
Binomial Test (Complete)	P<0.005	NS	NS
Tests of Hypothesis			
Ho: slope=0	P<0.0005	P<0.0005	P<0.0005
Ho: slope=1	NS	NS	NS
Ho: slope=2	P<0.0005	P<0.0005	P<0.0005

Table 3. Summary statistics for nonlinear least squares analysis of continuous and discrete-time functional response models.

Temperature	Source	SS(df)	MS	F	P	R^2	Binomial Test	
							(partial)	(complete)
26-27° C	Continuous-time type II model:					93.5	NS	NS
	Regression	11610.6(2)	5805.3	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	12421.0(46)						
	Discrete-time type II model:					95.2	NS	NS
	Regression	11820.2(2)	5910.1	432.8	<0.0005			
	Residual	600.8(44)	13.7					
	Lack-of-fit	4.5(5)	0.9	0.06	NS			
	Pure error	596.3(39)	15.3					
	Total	12421.0(46)						
19-20° C	Continuous-time type III model:					79.5	P<0.0005	NS
	Regression	3814.1(3)	1271.4	42.7	<0.0005			
	Residual	981.9(33)	29.8					
	Lack-of-fit	79.2(4)	19.8	0.6	NS			
	Pure error	902.7(29)	31.1					
	Total	4796.0(36)						

Table 3. Continued

Temperature	Source	SS(df)	MS	F	P	R^2	Binomial Test	
							(partial)	(complete)
19-20° C								
	Discrete-time type III model:					94.5	P<0.0005	NS
	Regression	4530.4(1)	4530.4	596.1	<0.0005			
	Residual	265.6(35)	7.6					
	Lack-of-fit	64.5(6)	10.8	1.6	NS			
	Pure error	201.1(29)	6.9					
	Total	4796.0(36)						
13-14° C	Continuous-time type II model:					48.9	P<0.0005	P<0.0005
	Regression	124.7(2)	62.3	16.8	<0.0005			
	Residual	130.3(35)	3.7					
	Lack-of-fit	5.3(5)	1.1	0.3	NS			
	Pure error	125.0(30)	4.2					
	Total	255.0(37)						
	Discrete-time type II model:					84.3	P<0.0005	P<0.0005
	Regression	214.9(2)	107.4	94.2	<0.0005			
	Residual	40.1(35)	1.1					
	Lack-of-fit	13.9(5)	2.8	3.2	<0.05			
	Pure error	26.2(30)	0.9					
	Total	255.0(37)						

Table 4. Estimated model parameters and observed behavioral components of _C_. _sapidus_ functional responses. Values are means ± 1 S.E.

	Model Parameters				Observed Behavioral Components		
Temperature	a'	b	c	Th	Encounter Rates** (total)	(successfull)	Th*
26-27° C	.037 ± .005	-----	-----	0.1 ± .13	7.61 ± 1.04	2.7 ± .27	.069 ± .006
19-20° C	-----	.037 ± .06	2.0 ± .00	0.1 ± 0.0	11.35 ± 1.69	1.8 ± .25	.088 ± .006
13-14° C	.0009 ± .0003	-----	-----	0.1 ± 2.5	7.09 ± 1.2	0.0 ± .00	-----

* oyster * $[h]^{-1}$

** oysters * $[h]^{-1}$

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.
b = a constant.
c = a constant.

Table 5. Results from the analysis of covariance of oyster length (covariate), density and temperature effects on observed A) Persistence Times, B) Breaking Times, C) Eating Times, and D) Handling Times: degress 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 length and the main effect, oyster density.

	Regression against oyster length				Oyster density effects				Density by oyster length interaction			
Temperature	df	MS	F	P	df	MS	F	P	df	MS	F	P
A) Persistence Times:												
26-27° C[*]	1,39	0.01	0.06	0.82	2,39	2.20	8.65	<0.001	2,39	0.18	0.70	.504
19-20° C[*]	1,118	0.19	0.60	0.44	2,118	0.04	0.12	.887	2,118	0.06	0.17	.843
13-14° C	1,15	3603.27	4.16	0.06	2,15	1993.75	2.30	.135	2,15	903.00	1.04	.377
B) Breaking Times:												
26-27° C	1,20	24785.95	9.37	<0.006	2,20	3026.77	1.15	.338	2,20	1287.93	0.49	.622
19-20° C	1,22	4947.05	0.82	.376	2,22	9956.45	1.64	.216	2,22	6956.63	1.15	.336
C) Eating Times:												
26-27° C	1,20	86652.44	18.97	<0.000	2,20	3023.06	0.66	.527	2,20	7499.98	1.64	.219
19-20° C	1,22	38567.41	7.17	<0.014	2,22	3373.96	0.63	.543	2,22	951.27	0.18	.839

[*] Persistence Times logarithmically transformed.

Table 5 continued.

	Regression against oyster length				Oyster density effects				Density by oyster length interaction			
Temperature	df	MS	F	P	df	MS	F	P	df	MS	F	P
D) Handling Times:												
26-27° C	1,20	179615.84	43.28	<0.000	2,20	12052.09	2.90	.078	2,20	8506.03	2.05	.155
19-20° C	1,22	64331.93	5.66	<0.026	2,22	16145.65	1.42	.263	2,22	13993.32	1.23	.311

Table 6. Results of linear regression with the log-transformed general functional response model (Real 1977, 1979) at each oyster size-class.

	Oyster size class (x ± 2 mm SL)		
Feature	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			
Ho: slope=0	P<0.0005	P<0.0005	P<0.0005
Ho: slope=1	NS	NS	P<0.0005
Ho: slope=2	P<0.0005	P<0.0005	P<0.0005

Table 7. Summary statistics for nonlinear least squares analysis of continuous and discrete-time functional response models.

Oyster size class (x ± 2 mm SL)	Source	SS(df)	MS	F	P	R^2	Binomial Test (partial)	Binomial Test (complete)
15	Continuous-time type II model:					96.4	NS	NS
	Regression	300941.5(2)	150470.7	542.4	<0.0005			
	Residual	11374.5(41)	277.4					
	Lack-of-fit	740.0(6)	123.3	0.4	NS			
	Pure error	10634.6(35)	303.8					
	Total	312316.0(43)						
	Discrete-time type II model:					94.5	P<0.0005	NS
	Regression	287937.3(1)	287937.3	596.1	<0.0005			
	Residual	24378.7(42)	580.4					
	Lack-of-fit	1036.3(7)	148.0	0.2	NS			
	Pure error	23342.3(35)	666.9					
	Total	312316.0(43)						
25	Continuous-time type II model:					93.5	NS	NS
	Regression	11610.6(2)	5805.3	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	12421.0(46)						

Table 7. Continued

Oyster size class ($x \pm 2$ mm SL)	Source	SS(df)	MS	F	P	R^2	Binomial Test (partial)	Binomial Test (complete)
25								
	Discrete-time type II model:					95.2	NS	NS
	Regression	11820.2(2)	5910.1	432.8	<0.0005			
	Residual	600.8(44)	13.7					
	Lack-of-fit	4.5(5)	0.9	0.06	NS			
	Pure error	596.3(39)	15.3					
	Total	12421.0(46)						
35	Continuous-time type II model:					69.3	NS	P<0.05
	Regression	2107.1(2)	1053.6	97.0	<0.0005			
	Residual	933.9(86)	10.9					
	Lack-of-fit	2.8(4)	0.7	0.06	NS			
	Pure error	931.0(81)	11.4					
	Total	3041.0(88)						
	Discrete-time type II model:					85.8	P<0.001	P<0.0005
	Regression	2609.2(2)	1304.6	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	3041.0(88)						

Table 8. Estimated model parameters and observed behavioral components of *C. sapidus* functional responses. Values are means ± 1 S.E.

	Model Parameters		Observed Behavioral Components		
Oyster size class	a'	Th	Encounter Rates**		Th*
(x ± 2 mm SL)			(total)	(successfull)	
15	.038 ± .005	0.1 ± .01	12.55 ± 0.75	9.4 ± .73	0.03 ± .003
25	.037 ± .005	0.1 ± .00	7.61 ± 1.04	2.7 ± .27	0.07 ± .006
35	.005 ± .001	0.1 ± .43	4.40 ± 0.69	1.0 ± .16	0.33 ± .040

* oyster * $[h]^{-1}$

** oysters * $[h]^{-1}$

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.

Table 9. Results from the analysis of covariance of oyster length (covariate), density and prey size class effects on observed A) Persistence Times, B) Breaking Times, C) Eating Times, and D) Handling Times: degress 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 length and the main effect, oyster density.

	Regression against oyster length				Oyster density effects				Density by oyster length interaction			
Temperature	df	MS	F	P	df	MS	F	P	df	MS	F	P
A) Persistence Times (secs):												
15	1,22	6108.36	4.72	<0.04	3,22	477.78	0.37	.78	3,22	3397.48	2.63	.08
25*	1,39	0.01	0.06	0.82	2,39	2.20	8.65	<0.00	2,39	0.18	0.70	.50
35*	1,69	0.17	0.43	0.51	2,69	0.98	2.50	0.09	2,69	0.21	0.53	.59
B) Breaking Times (secs):												
15	1,73	55366.37	57.47	<0.00	3,73	1033.23	1.07	.37	3,73	885.53	0.92	.44
25	1,20	24785.95	9.37	<0.01	2,20	3026.77	1.15	.34	2,20	1287.93	0.49	.62
35	1,22	1454447.1	1.24	<0.28	2,22	2461632.6	1.26	.31	2,22	2843575.8	2.30	.13
C) Eating Times (secs):												
15	1,73	101747.55	55.09	<0.00	3,73	1084.89	0.59	.63	3,73	4035.10	2.19	.10
25	1,20	86652.44	18.97	<0.00	2,20	3023.06	0.66	.53	2,20	7499.98	1.64	.22
35	1,16	1284366.2	14.89	<0.00	2,16	29113.83	1.53	.25	2,16	15728.39	0.82	.46

*Persistence Times logarithmically transformed.

Table 9 continued.

	Regression against oyster length				Oyster density effects				Density by oyster length interaction			
Temperature	df	MS	F	P	df	MS	F	P	df	MS	F	P
D) Handling Times (secs):												
15	1,73	307225.79	88.56	<0.00	3,73	2812.45	0.81	.49	3,73	7358.91	2.12	.11
25	1,20	179615.84	43.28	<0.00	2,20	12052.09	2.90	<0.08	2,20	8506.03	2.05	.16
35	1,22	11628322.4	3.58	<0.08	2,22	2654784.0	1.44	.27	2,22	2648835.9	1.42	.27

Table 10. Results of linear regression with the log-transformed general functional response model (Real 1977, 1979) for large oysters at each crab size-class.

	Crab size class (mm CW)	
Feature	135-165	100-125
Parameter estimates		
Intercept	-1.88	-2.31
Slope	0.58	0.81
Slope standard error	0.12	0.17
Summary Statistics		
Regression SS(df)	3.8(1)	3.8(1)
Residual SS(df)	13.0(86)	7.3(44)
F-value	25.3	23.2
P-value	<0.0001	<0.0001
R^2(%)	22.7	34.5
Binomial Test (Partial)	NS	NS
Binomial Test (Complete)	NS	NS
Tests of Hypothesis		
Ho: slope=0	$P<0.0005$	$P<0.0005$
Ho: slope=1	$P<0.0005$	NS
Ho: slope=2	$P<0.0005$	$P<0.0005$

Table 11. Summary statistics for nonlinear least squares analysis of continuous- and discrete-time functional response models.

Crab size class (mm CW)	Source	SS(df)	MS	F	P	R^2	Binomial Test	
							(partial)	(complete)
135-165	Continuous-time type II model:					69.3	NS	P<0.05
	Regression	2107.1(2)	1053.6	97.0	<0.0005			
	Residual	933.9(86)	10.9					
	Lack-of-fit	2.8(4)	0.7	0.06	NS			
	Pure error	931.0(81)	11.4					
	Total	3041.0(88)						
	Discrete-time type II model:					85.8	P<0.001	P<0.0005
	Regression	2609.2(2)	1304.6	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	3041.0(88)						
100-125	Continuous-time type III model:					62.5	NS	NS
	Regression	660.4(3)	220.1	23.9	<0.0005			
	Residual	395.6(43)	9.2					
	Lack-of-fit	13.0(3)	4.3	0.4	NS			
	Pure error	382.6(39)	9.8					
	Total	1056.0(46)						

Table 11. Continued

Crab size class (mm CW)	Source	SS(df)	MS	F	P	R^2	Binomial Test (partial)	Binomial Test (complete)
100-125	Discrete-time type III model:					88.5	NS	NS
	Regression	935.0(2)	467.5	170.0	<0.0005			
	Residual	121.0(44)	2.8					
	Lack-of-fit	19.3(5)	3.9	1.5	NS			
	Pure error	101.7(39)	2.6					
	Total	1056.0(46)						

Table 12. Estimated model parameters for conceptual nonlinear functional response model results for large oysters by crab carapace width. Values are means ± 1 S.E.

Crab size class	Model parameters			
(mm CW)	a'	b	c	Th*
135-165	.005 ± .001	-----	-----	0.01 ± 0.43
100-125	-----	.010 ± .001	2.00 ± 0.0	0.01 ± 0.56

*$[h]^{-1}$ * oyster

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.

b = a constant.

c = a constant.

Table 13. Results of linear regression with the log-transformed general functional response model (Real 1977, 1979) for medium oysters at each crab size-class.

Feature	Crab size-class (mm CW) 135-165	100-125	60-80
Parameter estimates			
Intercept	-2.65	-1.81	-1.75
Slope	0.90	0.93	0.93
Slope standard error	0.09	0.19	0.14
Summary Statistics			
Regression SS(df)	4.9(1)	4.8(1)	4.4(1)
Residual SS(df)	2.1(44)	3.3(43)	4.0(40)
F-value	104.6	62.1	43.8
P-values	<0.0001	<0.0001	<0.0001
R^2(%)	70.4	59.1	52.2
Binomial Test (Partial)	NS	NS	NS
Binomial Test (Complete)	P<0.005	NS	NS
Tests of Hypothesis			
Ho: slope=0	P<0.0005	P<0.0005	P<0.0005
Ho: slope=1	NS	NS	NS
Ho: slope=2	P<0.0005	P<0.0005	P<0.0005

Table 14. Summary statistics for nonlinear least squares analysis of continuous and discrete-time functional response models.

Crab size class (mm CW)	Source	SS(df)	MS	F	P	R^2	Binomial Test (partial)	Binomial Test (complete)
135-165	Continuous-time type II model:					93.5	NS	NS
	Regression	11610.6(2)	5805.3	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	12421.0(46)						
	Discrete-time type II model:					95.2	NS	NS
	Regression	11820.2(2)	5910.1	432.8	<0.0005			
	Residual	600.8(44)	13.7					
	Lack-of-fit	4.5(5)	0.9	0.06	NS			
	Pure error	596.3(39)	15.3					
	Total	12421.0(46)						
100-125	Continuous-time type II model:					88.2	NS	NS
	Regression	7164.3(2)	3582.2	160.0	<0.0001			
	Residual	962.7(43)	22.4					
	Lack-of-fit	11.0(5)	2.2	0.09	NS			
	Pure error	951.6(38)	25.0					
	Total	8127.0(44)						

Table 14. Continued

Crab size-class (mm CW)	Source	SS(df)	MS	F	P	R^2	Binomial Test	
							(partial)	(complete)
100-125								
	Discrete-time type II model:					92.2	P<0.0001	P<0.0001
	Regression	7494.4(2)	3747.2	254.7	<0.0001			
	Residual	632.6(43)	14.7					
	Lack-of-fit	322.1(5)	64.4	7.9	<0.0001			
	Pure error	310.5(38)	8.2					
	Total	8127.0(45)						
60-80	Continuous-time type II model:					82.5	NS	NS
	Regression	8601.9(2)	4301.0	94.4	<0.0001			
	Residual	1822.1(40)	45.6					
	Lack-of-fit	5.7(5)	1.1	0.02	NS			
	Pure error	1816.4(35)	51.9					
	Total	10424.0(42)						
	Discrete-time type II model:					93.5	P<0.0001	P<0.0001
	Regression	9743.0(2)	4871.5	286.1	<0.0001			
	Residual	681.0(40)	17.0					
	Lack-of-fit	402.3(5)	80.5	10.1	<0.0001			
	Pure error	278.8(35)	8.0					
	Total	10424.0(42)						

Table 15. Estimated model parameters for conceptual nonlinear functional response model results for medium oysters by crab carapace width. Values are means ± 1 S.E.

Crab size class (mm CW)	Model parameters a'	Th*
135-165	0.037 ± 0.005	0.10 ± 0.00
100-125	0.029 ± 0.007	0.53 ± 0.22
60-80	0.031 ± 0.010	0.49 ± 0.28

$^{*}[h]^{-1}$ * oyster

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.

Table 16. Results of linear regression with the log-transformed general functional response model (Real 1977, 1979) for small oysters at each crab size-class.

	Crab size-class (mm CW)		
Feature	135-165	100-125	60-80
Parameter estimates			
Intercept	-2.62	-2.71	-2.65
Slope	1.00	1.06	1.00
Slope standard error	0.03	0.04	0.04
Summary Statistics			
Regression SS(df)	11.6(1)	13.7(1)	12.3(1)
Residual SS(df)	0.5(41)	0.6(41)	0.8(41)
F-value	867.9	893.1	655.7
P-values	<0.0001	<0.0001	<0.0001
R^2(%)	95.5	95.6	94.1
Binomial Test (Partial)	NS	P<0.05	NS
Binomial Test (Complete)	NS	NS	P<0.05
Tests of Hypothesis			
Ho: slope=0	P<0.0005	P<0.0005	P<0.0005
Ho: slope=1	NS	NS	NS
Ho: slope=2	P<0.0005	P<0.0005	P<0.0005

Table 17. Summary statistics for nonlinear least squares analysis of continuous and discrete-time functional response models.

Crab size class (mm CW)	Source	SS(df)	MS	F	P	R^2	Binomial Test (partial)	Binomial Test (complete)
135-165	Continuous-time type II model:					96.4	NS	NS
	Regression	300941.5(2)	150470.7	542.4	<0.0005			
	Residual	11374.5(41)	277.4					
	Lack-of-fit	740.0(6)	123.3	0.4	NS			
	Pure error	10634.6(35)	303.8					
	Total	312316.0(43)						
	Discrete-time type II model:					94.5	P<0.0005	NS
	Regression	287937.3(1)	287937.3	596.1	<0.0005			
	Residual	24378.7(42)	580.4					
	Lack-of-fit	1036.3(7)	148.0	0.2	NS			
	Pure error	23342.3(35)	666.9					
	Total	312316.0(43)						
100-125	Continuous-time type III model:					88.2	NS	NS
	Regression	327117.4(3)	109039.1	100.3	<0.0001			
	Residual	43602.6(40)	1090.1					
	Lack-of-fit	5844.7(5)	1168.9	1.08	NS			
	Pure error	37757.9(35)	1078.8					
	Total	370720.0(43)						

Table 17. Continued

Crab size-class (mm CW)	Source	SS(df)	MS	F	P	R^2	Binomial Test (partial)	Binomial Test (complete)
100-125								
	Discrete-time type III model:					98.7	P<0.0001	P<0.0001
	Regression	365787.2(3)	121929.1	988.7	<0.0005			
	Residual	4932.8(40)	123.3					
	Lack-of-fit	4775.2(5)	955.0	212.0	<0.0001			
	Pure error	157.7(35)	4.5					
	Total	370720.0(43)						
60-80	Continuous-time type III model:					88.2	P<0.0005	P<0.0005
	Regression	272536.5(3)	90845.5	99.7	<0.0001			
	Residual	36439.5(40)	911.0					
	Lack-of-fit	3583.3(5)	716.7	0.08	NS			
	Pure error	32856.2(35)	938.8					
	Total	308976.0(43)						
	Discrete-time type III model:					84.5	NS	NS
	Regression	261193.9(2)	130597.0	112.1	<0.0001			
	Residual	47782.1(41)	1165.4					
	Lack-of-fit	1455.3(6)	242.6	0.2	NS			
	Pure error	46326.7(35)	1323.6					
	Total	308976.0(43)						

Table 18. Estimated model parameters for conceptual nonlinear functional response model results for small oysters by crab carapace width. Values are means ± 1 S.E.

Crab size class	Model parameters			
(mm CW)	a'	b	c	Th*
135-165	.038 ± .005	-----	-----	0.01 ± 0.01
100-125	-----	0.01 ± 0.004	0.10 ± 0.01	0.20 ± 0.003
60-80	-----	0.01 ± 0.004	0.10 ± 0.01	0.20 ± 0.003

*$[h]^{-1}$ * oyster

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.

b = a constant.

c = a constant.

Table 19. Results of linear regression with the log-transformed general functional response model (Real 1977, 1979) for large male and female crabs eating large oysters.

	Crab sex	
Feature	Male	Female
Parameter estimates		
Intercept	-1.88	-2.50
Slope	0.58	1.00
Slope standard error	0.12	0.19
Summary Statistics		
Regression SS(df)	3.8(1)	4.5(1)
Residual SS(df)	13.0(86)	6.0(35)
F-value	25.3	26.7
P-value	<0.0001	<0.0001
R^2(%)	22.7	43.2
Binomial Test (Partial)	NS	NS
Binomial Test (Complete)	NS	NS
Tests of Hypothesis		
Ho: slope=0	P<0.0005	P<0.0005
Ho: slope=1	P<0.0005	NS
Ho: slope=2	P<0.0005	P<0.0005

Table 20. Summary statistics for nonlinear least squares analysis of continuous and discrete-time functional response models.

Crab sex	Source	SS(df)	MS	F	P	R^2	Binomial Test (partial)	Binomial Test (complete)
Male	Continuous-time type II model:					69.3	NS	P<0.05
	Regression	2107.1(2)	1053.6	97.0	<0.0005			
	Residual	933.9(86)	10.9					
	Lack-of-fit	2.8(4)	0.7	0.06	NS			
	Pure error	931.0(81)	11.4					
	Total	3041.0(88)						
	Discrete-time type II model:					85.8	P<0.001	P<0.0005
	Regression	2609.2(2)	1304.6	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	3041.0(88)						
Female	Continuous-time type III model:					65.6	NS	NS
	Regression	972.1(3)	324.0	21.6	<0.0001			
	Residual	509.9(34)	15.0					
	Lack-of-fit	8.0(4)	2.0	0.12	NS			
	Pure error	501.9(30)	16.7					
	Total	1482.0(37)						

Table 20. Continued

Crab sex	Source	SS(df)	MS	F	P	R^2	Binomial Test (partial)	Binomial Test (complete)
Female								
	Discrete-time type III model:					95.1	NS	NS
	Regression	1409.8(3)	469.9	221.3	<0.0001			
	Residual	72.2(34)	2.1					
	Lack-of-fit	10.0(4)	2.5	1.2	NS			
	Pure error	62.2(30)	2.1					
	Total	1482.0(37)						

Table 21. Estimated model parameters for conceptual nonlinear functional response model results for large male and female crabs eating large oysters. Values are means ± 1 S.E.

	Model parameters			
Crab sex	a'	b	c	Th*
Male	.005 ± .001	-----	-----	0.01 ± 0.43
Female	-----	0.018 ± 0.11	2.0 ± 12.64	0.01 ± 0.21

*$[h]^{-1}$ * oyster

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.

b = a constant.

c = a constant.

Table 22. Results of linear regression with the log-transformed general functional response model (Real 1977, 1979) for large male and female crabs eating medium oysters.

	Crab sex	
Feature	Male	Female
Parameter estimates		
Intercept	-2.65	-1.94
Slope	0.90	1.04
Slope standard error	0.09	0.20
Summary Statistics		
Regression SS(df)	4.9(1)	5.6(1)
Residual SS(df)	2.1(44)	8.5(42)
F-value	104.6	27.6
P-value	<0.0001	<0.0001
R^2(%)	70.4	39.7
Binomial Test (Partial)	NS	P<0.005
Binomial Test (Complete)	P<0.005	P<0.0001
Tests of Hypothesis		
Ho: slope=0	P<0.0005	P<0.0005
Ho: slope=1	NS	NS
Ho: slope=2	P<0.0005	P<0.0005

Table 23. Summary statistics for nonlinear least squares analysis of continuous and discrete-time functional response models.

Crab sex	Source	SS(df)	MS	F	P	R^2	Binomial Test (partial)	Binomial Test (complete)
Male	Continuous-time type II model:					93.5	NS	NS
	Regression	11610.6(2)	5805.3	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	12421.0(46)						
	Discrete-time type II model:					95.2	NS	NS
	Regression	11820.2(2)	5910.1	432.8	<0.0005			
	Residual	600.8(44)	13.7					
	Lack-of-fit	4.5(5)	0.9	0.06	NS			
	Pure error	596.3(39)	15.3					
	Total	12421.0(46)						
Female	Continuous-time type II model:					81.2	NS	P<0.05
	Regression	9667.1(2)	4833.6	90.8	<0.0001			
	Residual	2236.9(42)	53.3					
	Lack-of-fit	9.3(4)	2.3	0.04	NS			
	Pure error	2227.6(37)	60.2					
	Total	11904.0(44)						

Table 23. Continued

Crab sex	Source	SS(df)	MS	F	P	R^2	Binomial Test (partial)	Binomial Test (complete)
Female								
	Discrete-time type II model:					93.8	P<0.0001	P<0.0001
	Regression	11175.5(2)	5587.7	322.1	<0.0001			
	Residual	728.5(42)	17.3					
	Lack-of-fit	541.4(5)	108.3	21.4	<0.0001			
	Pure error	187.1(37)	5.1					
	Total	11904.0(44)						

Table 24. Estimated model parameters for conceptual nonlinear functional response model results for large male and female crabs feeding on medium oysters. Values are means ± 1 S.E.

	Model parameters	
	a'	Th*
Male	0.037 ± 0.005	0.10 ± 0.00
Female	0.023 ± 0.007	0.10 ± 0.31

*$[h]^{-1}$ * oyster

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.

Table 25. Results of linear regression with the log-transformed general functional response model (Real 1977, 1979) for medium male and female crabs eating large oysters.

	Crab sex	
Feature	Male	Female
Parameter estimates		
Intercept	-2.31	-1.73
Slope	0.81	0.55
Slope standard error	0.17	0.11
Summary Statistics		
Regression SS(df)	3.8(1)	1.3(1)
Residual SS(df)	7.3(44)	1.7(34)
F-value	23.2	26.6
P-value	<0.0001	<0.0001
R^2(%)	34.5	43.9
Binomial Test (Partial)	NS	NS
Binomial Test (Complete)	NS	NS
Tests of Hypothesis		
Ho: slope=0	P<0.0005	P<0.0005
Ho: slope=1	NS	P<0.0005
Ho: slope=2	P<0.0005	P<0.0005

Table 26. Summary statistics for nonlinear least squares analysis of continuous and discrete-time functional response models.

Crab sex	Source	SS(df)	MS	F	P	R^2	Binomial Test (partial)	Binomial Test (complete)
Males	Continuous-time type III model:					62.5	NS	NS
	Regression	660.4(3)	220.1	23.9	<0.0005			
	Residual	395.6(43)	9.2					
	Lack-of-fit	13.0(3)	4.3	0.4	NS			
	Pure error	382.6(39)	9.8					
	Total	1056.0(46)						
	Discrete-time type III model:					88.5	NS	NS
	Regression	935.0(2)	467.5	170.0	<0.0005			
	Residual	121.0(44)	2.8					
	Lack-of-fit	19.3(5)	3.9	1.5	NS			
	Pure error	101.7(39)	2.6					
	Total	1056.0(46)						
Female	Continuous-time type III model:					88.8	NS	NS
	Regression	986.1(3)	328.7	87.6	<0.0001			
	Residual	123.9(33)	3.8					
	Lack-of-fit	7.4(4)	1.8	0.46	NS			
	Pure error	116.5(29)	4.0					
	Total	1110.0(36)						

Table 26. Continued

Crab sex	Source	SS(df)	MS	F	P	R^2	Binomial Test (partial)	Binomial Test (complete)
Female								
	Discrete-time type III model:					96.7	P<0.0001	NS
	Regression	12009.6(3)	4003.2	418.4	<0.0001			
	Residual	411.4(43)	9.6					
	Lack-of-fit	30.1(3)	10.0	1.0	NS			
	Pure error	381.3(39)	9.8					
	Total	12421.0(46)						

Table 27. Estimated model parameters for conceptual nonlinear functional response model results for medium male and female crabs feeding on large oysters. Values are means ± 1 S.E.

	Model parameters		
Crab sex	b	c	Th*
135-165	0.010 + 0.001	2.00 + 0.0	0.01 ± 0.56
100-125	0.007 ± 0.003	0.01 ± 0.002	3.98 ± 0.01

$^*[h]^{-1} * \text{oyster}$

Th = the time taken to break open and eat a single prey, and is a decimal fraction of 1.0 h.

b = a constant.

c = a constant.

Table 28. Summary statistics of field data according to treatments. Each treatment represents a 21 day exposure period (except the A quadrats which were over 14 days). Values are means ± 1 S.E.

Quadrat Letter	No. oysters marked/recovered	Mortality due to crabs (no./21 days)	% Mortality due to crabs (%/21 days)	% Mortality due to unknown causes (%/21 days)	Oyster length offerred/eaten (mm)
1985 Shell-plant site					
A	133.7 ± 12.7/ 110.7 ± 10.6	10.9 ± 0.9	5.7 ± 0.9	3.3 ± 1.3	25.3 ± 1.2/ 23.1 ± 0.7
B	132.5 ± 11.2/ 113.5 ± 8.4	9.5 ± 0.5	8.5 ± 0.9	11.5 ± 0.9	27.8 ± 0.1/ 27.0 ± 0.8
C	94.0 ± 7.7/ 76.3 ± 10.3	8.7 ± 1.8	11.3 ± 0.7	9.5 ± 2.2	28.4 ± 0.7/ 24.7 ± 2.0
D	84.5 ± 2.6/ 75.5 ± 1.4	3.0 ± 1.0	4.0 ± 0.8	3.9 ± 1.7	32.5 ± 0.3/ 29.0 ± 3.0
E	84.7 ± 6.6/ 69.0 ± 2.4	3.7 ± 1.2	5.2 ± 1.3	13.3 ± 2.2	33.0 ± 0.8/ 29.6 ± 1.2
F	52.0 ± 3.4/ 47.7 ± 2.8	1.3 ± 0.3	2.8 ± 0.5	3.3 ± 2.7	35.5 ± 0.8/ 34.6 ± 1.9
G	54.0 ± 3.3 48.3 ± 1.9	2.7 ± 0.7	5.52 ± 1.1	2.7 ± 0.5	34.0 ± 0.4/ 36.2 ± 0.6
H	99.7 ± 12.5/ 90.0 ± 14.0	3.3 ± 1.2	4.1 ± 1.8	8.3 ± 3.9	24.3 ± 2.1/ 25.2 ± 6.2
1986 Shell plant site					
I	690.0 ± 60.2/ 641.7 ± 58.1	21.3 ± 3.9	2.8 ± 0.5	5.0 ± 0.8	20.2 ± 0.7/ 21.2 ± 0.6

Table 28 continued.

Quadrat Letter	No. oysters marked/recovered	Mortality due to crabs (no./21 days)	% Mortality due to crabs (%/21 days)	% Mortality due to unknown causes (%/21 days)	Oyster length offerred/eaten (mm)
J	567.1 ± 27.2/	5.7 ± 2.0	1.1 ± 0.4	2.9 ± 0.1	27.3 ± 1.4/
	542.3 ± 28.9				27.4 ± 4.9
K	490.3 ± 26.6/	2.7 ± 0.9	0.7 ± 0.3	3.1 ± 1.1	26.9 ± 0.4/
	389.3 ± 14.8				31.8 ± 6.2

Table 29. Field data grouped according to replicates within each treatment. Each treatment represents a 21 day exposure period for marked individuals (except the A quadrats which were over 14 days) while each replicate represents a 0.25 m^2 quadrat.

Quadrat #	Total Spat marked/recovered	No. spat eaten (no./day)	% Mortality due to crabs (%/day)	% Unknown mortality (%/day)	Mean size offered/eaten (mm)	Size ranges offered/eaten (mm)
1985 Shell-plant site						
1A	112/93	0.58	0.36	0.31	28.0/22.3	12.3-44.8/15.0-34.8
2A	165/136	0.42	0.18	0.07	22.8/22.1	9.0-42.3/16.4-31.2
3A	124/103	0.50	0.27	0.09	25.0/25.0	8.8-41.4/9.0-36.1
1B			This sample was not recovered			
2B	113/99	0.48	0.47	0.62	27.6/25.7	10.5-44.4/16.0-35.2
3B	152/128	0.43	0.33	0.48	27.9/28.3	10.0-43.6/17.4-36.7
1C	111/94	0.57	0.61	0.71	26.8/22.0	13.0-44.4/14.1-36.0
2C	79/52	0.29	0.55	0.37	29.3/22.4	14.0-45.0/14.0-31.2
3C	92/83	0.38	0.46	0.29	29.2/29.7	13.0-43.7/17.9-41.0

Table 29 continued.

Quadrat #	Oysters marked/recovered	Mortality due to crabs (no./day)	% Mortality due to crabs (%/day)	% Unknown mortality (%/day)	Mean size offered/eaten (mm)	Size ranges offered/eaten (mm)
1D	This sample was not recovered					
2D	80/73	0.19	0.26	0.33	33.0/34.2	14.8-45.0/28.4-42.6
3D	89/78	0.10	0.12	0.06	32.0/23.9	15.0-44.2/19.1-28.6
1E	71/63	0.10	0.15	0.38	35.0/32.3	17.1-45.0/29.9-34.7
2E	99/72	0.14	0.20	0.73	31.8/29.0	15.1-42.6/25.6-33.0
3E	84/72	0.29	0.40	0.79	32.3/27.6	17.3-45.0/19.1-34.8
1F	45/41	0.05	0.12	0.46	37.4/39.0	23.4-45.0/-39.0-
2F	59/52	0.10	0.18	0	33.9/33.4	13.5-43.8/30.0-36.7
3F	52/50	0.05	0.10	0	35.3/31.3	13.4-44.6/-31.3-
1G	61/52	0.10	0.18	0.18	33.0/35.1	11.5-44.9/28.6-41.5
2G	57/49	0.19	0.39	0.10	34.2/37.5	10.2-45.0/32.6-42.8
3G	47/44	0.10	0.22	0.11	34.8/35.5	12.5-45.0/30.3-40.6

Table 29 continued.

Quadrat #	Total Spat marked/recovered	No. spat eaten (no./day)	% Mortality due to crabs (%/day)	% Unknown mortality (%/day)	Mean size offered/eaten (mm)	Size ranges offered/eaten (mm)
1H	115/104	0.24	0.23	0.23	20.0/25.1	10.2-41.4/10.8-44.2
2H	76/66	0.19	0.29	0.72	27.0/14.5	10.8-45.0/12.5-17.9
3H	112/107	0.05	0.05	0.18	27.8/36.0	10.0-45.0/-36.0-
1986 Shell-plant site						
1I	765/728	1.24	0.17	0.20	20.9/20.5	6.0-44.7/12.5-30.5
2I	571/531	0.76	0.14	0.20	20.9/20.7	4.0-41.7/5.4-39.7
3I	734/666	0.62	0.09	0.31	18.8/22.3	4.9-40.5/14.8-31.2
1J	522/510	0.43	0.08	0.14	25.3/19.7	6.8-44.5/11.1-29.8
2J	616/600	0.29	0.05	0.13	26.6/26.0	5.3-44.7/20.4-31.1
3J	563/517	0.10	0.02	0.14	29.9/36.6	6.1-41.9/31.4-40.8
1K	471/378	0.05	0.01	0.10	27.5/43.0	9.8-45.0/-43.0-
2K	457/408	0.19	0.05	0.25	26.1/30.5	7.8-44.8/24.0-37.1
3K	543/382	0.14	0.04	0.09	27.2/21.8	9.5-45.0/12.0-28.1

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