

Effects of hypoxia on an estuarine predator-prey interaction: foraging behavior and mutual interference in the blue crab *Callinectes sapidus* and the infaunal clam prey *Mya arenaria*

David L. Taylor*, David B. Eggleston

North Carolina State University, Department of Marine, Earth, and Atmospheric Sciences Box 8208, Raleigh, North Carolina 27695-8208, USA

ABSTRACT: The effects of hypoxia on trophic interactions could vary dramatically depending on whether the benthos is experiencing the onset of a hypoxic event (decreasing dissolved oxygen concentrations from normoxia), or its dissipation (increasing dissolved oxygen concentrations from hypoxia). Predator-prey dynamics between the blue crab *Callinectes sapidus* and an infaunal clam prey *Mya arenaria* were examined to assess the impact of hypoxia upon predator foraging rates and prey mortality. Laboratory experiments quantified the behavioral response of *M. arenaria* to varying dissolved oxygen levels through the analyses of (1) sediment burial depth, and (2) siphon extension above the sediment surface. Moreover, the functional response (relationship between predator consumption rates and prey density) of single and 2 adult blue crabs to 2 densities of *M. arenaria* (6 and 24 clams tank⁻¹) was examined across 3 dissolved oxygen treatments: (1) normoxia (≥ 6.0 mg DO l⁻¹); (2) moderate hypoxia (3.0 to 4.0 mg DO l⁻¹), subsequent to clam acclimation at high oxygen conditions (≥ 6.0 mg DO l⁻¹), and (3) moderate hypoxia (3.0 to 4.0 mg DO l⁻¹), subsequent to clam acclimation at low oxygen conditions (≤ 1.5 mg DO l⁻¹). *M. arenaria* sediment burial depth decreased and siphon extension increased during exposure to severe hypoxia. Initiation of moderate hypoxia following normoxia altered blue crab foraging behavior from a destabilizing, type II functional response, to a partially stabilizing, type I functional response. Conversely, blue crabs exhibited a type II functional response under moderate hypoxia subsequent to clam exposure to severe hypoxia. Therefore, low dissolved oxygen concentrations appear to affect the predator-prey interaction between *C. sapidus* and *M. arenaria* by either hindering blue crab foraging, or alternatively, increasing clam vulnerability by altering their siphon extension and depth distribution within the sediment column. Moreover, the inclusion of a second blue crab in experimental trials further modified functional responses through both mutual interference and agonistic behavior or cooperative foraging between predators. The collective results indicate that fluctuations in dissolved oxygen concentrations, as well as both predator and prey density, must be examined jointly to understand their impact upon predator-prey dynamics in marine systems.

KEY WORDS: Hypoxia · Trophic dynamics · *Callinectes sapidus* · Blue crab · *Mya arenaria* · Predator-prey interaction · Functional response · Mutual interference

INTRODUCTION

The ecological impacts of hypoxia and anoxia in marine environments can be extensive but difficult to

evaluate due to the inherent variability of natural biological communities, which respond continuously to a multitude of biological and environmental factors (Sandberg 1994). Nevertheless, severe oxygen deficiency in estuarine and coastal waters is one of the few environmental perturbations that leads to massive mortality of benthic organisms (Sandberg 1994, reviewed by Diaz & Rosenberg 1995 and refer-

*Present address: Graduate School of Oceanography, University of Rhode Island, Narragansett, Rhode Island 02882, USA. E-mail: dtaylor@gso.uri.edu

ences therein). Even if the benthic community does not suffer extensive mortality, functionally important biological interactions such as predator-prey relationships may be fundamentally altered (Breitburg et al. 1994, Sandberg 1994, Nestlerode & Diaz 1998). Although chronic and large-scale hypoxia is prevalent in estuaries worldwide, little information exists on its direct and indirect effects on benthic predator-prey dynamics.

Species inhabiting oxygen-depleted waters vary considerably in their responses to hypoxia. For example, physiological and behavioral responses to oxygen deficiency are highly dependent upon the magnitude, duration, and frequency of hypoxia, and the life-history stage and age of the exposed species (Breitburg 1992, Diaz & Rosenberg 1995). Additionally, most species of marine macroinvertebrates exhibit different tolerances to hypoxia depending upon their taxonomic position (Rosenberg et al. 1991, Desprez et al. 1992, Diaz & Rosenberg 1995). Benthic macrofaunal species that are most resistant to prolonged exposure to severe hypoxia are bivalves and gastropods, followed by polychaetes, echinoderms, and crustaceans (Hagerman & Uglow 1985, Kapper & Stickle 1987, Rosenberg et al. 1991, Diaz & Rosenberg 1995). These taxonomic patterns of tolerance to hypoxia correspond to differences in activity level and metabolic rate (Stickle et al. 1989, Diaz & Rosenberg 1995). For example, sessile and infaunal species generally have a high tolerance to anoxia and hypoxia, due in part to a reduction in activity and hence energy use (Stickle et al. 1989). Conversely, more mobile organisms, such as crustaceans, are less effective in suppressing metabolic rates during exposure to hypoxia, and therefore exhibit a lower capacity for anaerobic metabolism, which in turn leads to a decreased tolerance to oxygen depletion (Stickle et al. 1989, Das & Stickle 1993, 1994).

A progression of hierarchical shifts in an organism's behavior occurs with the onset of hypoxia (Diaz & Rosenberg 1995). The first response to declining oxygen concentrations is an increase in ventilation rates that facilitates more efficient oxygen extraction from the surrounding water (Batterton & Cameron 1978, DeFur et al. 1990). Organisms that are mobile begin to migrate away from oxygen depleted areas when concentrations fall below 3.0 mg DO l^{-1} (Loesch 1960, May 1973, Renaud 1986, Pihl et al. 1991, Das & Stickle 1993, 1994). For example, certain species of demersal fish and crustaceans migrate from relatively deep, hypoxic waters towards more oxygenated shoreward areas (Pihl et al. 1991). Moreover, demersal fish and crustaceans may exhibit vertical escape behavior towards oxygenated surface waters. For example, anecdotal observations by fishermen suggest that blue crabs ex-

hibit vertical migration from hypoxic and anoxic bottom waters.

Sessile and infaunal species, unable to avoid or escape oxygen-depleted waters, initiate a series of responses to hypoxia according to its severity (Diaz & Rosenberg 1995). Typically, feeding and other activities unrelated to ventilation will decrease to reduce metabolism (Diaz & Rosenberg 1995). Infaunal species capable of limited mobility may also attempt an escape response by migrating vertically toward the sediment surface (Trevallion 1971, Jørgensen 1980, Diaz & Rosenberg 1995). Numerous studies propose that many species of bivalves, echinoderms, and annelids will leave the refuge provided by soft sediments as oxygen concentrations decrease to near lethal levels (Jørgensen 1980, Rosenberg et al. 1991, Nilsson & Rosenberg 1994, Diaz & Rosenberg 1995). Some bivalves also react to hypoxia by extending their siphons upward into the water column in search of higher oxygen concentrations (Jørgensen 1980, Diaz & Rosenberg 1995). As a consequence of the redistribution of macrobenthic fauna in response to hypoxia, the population structure of marine benthic communities may also be drastically altered (Jørgensen 1980, Breitburg 1992, Pihl et al. 1992, Diaz & Rosenberg 1995). If hypoxia persists or intensifies, selective mortality may occur, first among the more sensitive taxa such as crustaceans and echinoderms and, eventually, in even the most tolerant species (Diaz & Rosenberg 1995).

The prevalence of hypoxia in estuarine habitats is extremely dynamic spatially and temporally due to wind-driven upwelling events (Haas 1977, Officer et al. 1984, Blumberg & Goodrich 1990). Bottom waters can change nearly instantaneously from normoxic to hypoxic conditions, or vice versa, and are sustained episodically (minutes/hours) or chronically (weeks/months) (Breitburg 1992, Nestlerode & Diaz 1998, Taylor 1998). The effects of hypoxia on trophic interactions, and more specifically on the behavior of mobile epibenthic predators foraging upon infaunal prey, may vary dramatically depending on whether the benthos are experiencing declines in oxygen concentrations from normoxia to hypoxia, or an increase in oxygen concentrations from hypoxia to normoxia.

This paper describes the effects of episodic hypoxia on a key estuarine predator-prey relationship between the blue crab *Callinectes sapidus* and the infaunal clam prey *Mya arenaria*. We examined the behavioral response of *M. arenaria* prey to moderate and severe hypoxia under laboratory conditions by quantifying (1) sediment burial depth, and (2) siphon extension into the water column. Additionally, predator-prey experiments assessed foraging behavior and mutual interference in *C. sapidus* to ascertain whether or not hypoxia alters predator-prey dynamics.

Functional response

Analysis of functional responses

The relationship between the consumption rate of a predator and the density of its prey is known as the predator's functional response. The type of functional response may identify potential behavioral mechanisms leading to oscillations in prey populations (Murdoch & Oaten 1975), or to the local extinction or persistence of certain prey (Lipcius & Hines 1986, Eggleston 1990a, Eggleston et al. 1992). Examination of a predator's functional response is a powerful, quantitative method for examining predator-prey dynamics under varying environmental conditions (Lipcius & Hines 1986, Eggleston 1990b, Eggleston et al. 1992), and can provide an effective framework for identifying the importance of predation in regulating marine and estuarine benthic communities (Abrams et al. 1990).

When the number of prey consumed is plotted against prey density, a continuum of patterns may emerge from which 3 primary types of functional responses are typically characterized (Holling 1959, Hassell 1978). In the type I functional response, consumption rates increase linearly with increasing prey density until reaching a plateau at satiation. Satiation occurs when a predator cannot handle prey any faster; hence, ingestion remains constant despite increasing prey density (i.e. prey mortality is density-independent) (Hassell 1978). In the hyperbolic type II functional response, inversely density-dependent consumption rates rise at a decelerating rate to an upper asymptote, reflecting increased costs or constraints associated with higher consumption rates (Hassell 1978). The type III functional response is sigmoid, demonstrating density-dependent acceleration in consumption rates at low to moderate prey densities (Hassell 1978). The acceleration in feeding rates results from increased predator efficiency in the detection or capture of prey as prey density increases (Hassell 1978). Thus, a type III functional response imparts stability to predator-prey dynamics via a relative refuge at low prey densities (Lipcius & Hines 1986, Eggleston et al. 1992). Similarly, a type I functional response could be considered partially stabilizing to predator-prey dynamics relative to a destabilizing, type II functional response.

The ability to distinguish among functional responses may be difficult when analyses rely on predator consumption rates. When the number of prey consumed is converted to the proportion of prey eaten per predator, however, distinct differences appear among types I, II, and III functional responses. A constant mortality rate across prey densities is indicative of a type I

functional response. In the types II and III functional responses there is a change from an increasing to a decreasing risk of mortality as prey density decreases, respectively. The drastic differences occurring among the functional responses at low prey densities facilitate differentiation among types I, II, and III functional responses (Lipcius & Hines 1986, Eggleston et al. 1992). Moreover, if the 'low density' range for a particular species is known, then the difference between functional responses can be determined from as few as 2 data points within that range. For example, at low and moderate prey densities, a pattern illustrating no significant difference in proportional mortality across 2 prey densities demonstrates a density-independent, type I functional response. Conversely, significantly higher proportional mortality at low prey densities characterizes an inversely density-dependent, type II functional response, whereas a pattern of significantly lower proportional mortality at low prey densities defines a density-dependent, type III functional response (Lipcius & Hines 1986, Eggleston et al. 1992).

Factors affecting functional responses

The aggregation of foraging predators can have a significant impact on their individual functional responses. For example, predator aggregation can promote a type II functional response by enhancing the foraging efficiency of individual predators if they are attracted to prey patches by foraging conspecifics, or when mutual attacks are more successful than individual attacks (Hassell & May 1973, 1974, Mansour & Lipcius 1991). Conversely, predator aggregation may regulate prey populations if predators congregate in areas of high prey density, and leave those prey patches when the rate of prey capture falls below a threshold necessary to sustain constant foraging efforts (Mansour & Lipcius 1991). Aggregative responses could also promote agonistic interactions and mutual interference among predators, which could adversely affect either their searching efficiency or feeding rates (Mansour & Lipcius 1991, Clark 1997). The combination of predator aggregation and mutual interference may stabilize predator-prey dynamics by promoting a type III functional response. A type III functional response could provide a partial refuge for prey in low density patches, as well as promote dispersal of predators from patches in which prey have been heavily exploited (Mansour & Lipcius 1991). In a study that examined the density-dependent foraging of *Callinectes sapidus* upon the infaunal clam *Macoma balthica*, Mansour & Lipcius (1991) found evidence that mutual interference and intraspecific aggression between crabs increased with predator density. Agonistic interactions between

blue crabs—which resulted in mortality, carapace wounds, and loss of appendages—also promoted the maintenance of a density-dependent refuge (type III functional response) for large infaunal clams, rather than leading to a destabilizing, type II functional response (Mansour & Lipcius 1991).

Changes in abiotic and biotic factors can also significantly alter the functional response of a predator (Lipcius & Hines 1986, Eggleston 1990a, Sandberg 1994). For example, oxygen-deficient conditions can affect predator-prey interactions by altering spatiotemporal abundance patterns of both predator and prey. Moreover, the varying physiological responses by predators and prey to low dissolved oxygen concentrations potentially enhance or impede predation efficiency (Gade 1983, Breitburg et al. 1994). Hypoxic conditions could be beneficial to a predator if the primary effect were to increase the vulnerability of its prey. For example, when severe hypoxia forces infaunal species to emerge from the sediment to the substrate-seawater interface, it increases their vulnerability to predators able to exploit hypoxic areas (Jørgensen 1980, Pihl et al. 1992, Nestlerode & Diaz 1998). Additionally, bivalves that respond to hypoxia by extending their siphons above the sediment surface increase their susceptibility to sublethal predation (i.e. siphon cropping and nipping) by epibenthic foragers (Jørgensen 1980, Pihl et al. 1992, Nestlerode & Diaz 1998). In a study on the diet of bottom-feeding fish and crustaceans, Pihl et al. (1992) found that predators achieved optimal prey exploitation during or immediately after hypoxia as a result of increased prey availability due to changes in the depth distribution of infaunal organisms in the sediment.

Low oxygen concentrations can also have a detrimental effect on predators that require higher oxygen levels for efficient prey capture than their prey require for efficient escape behavior. For example, Sandberg (1994) determined that the foraging efficiency of the predatory isopod *Saduria entomon* on the amphipods *Corophium volutator* and *Bathyporeia pilosa* decreased significantly as a function of decreased dissolved oxygen levels. Because the physiology and behavior of marine predators and prey varies to such a large extent in response to depleted oxygen levels (Stickle et al. 1989, Breitburg 1992), hypoxic events can lead to either increased or decreased prey capture, thereby affecting predators' functional responses and ultimately food web dynamics within marine and estuarine communities.

Predator-prey system

Predator-prey interactions are extremely complex in many benthic communities due to the dominance of

generalized, omnivorous predators and the absence of a single, competitively dominant prey species capable of monopolizing resources (Virnstein 1977, Hines et al. 1990, Eggleston et al. 1992). In certain marine and estuarine systems, however, trophic complexities can be simplified to a relatively few strong interactions (Paine 1980, Menge 1983, Eggleston et al. 1992, Wooten 1994).

The blue crab *Callinectes sapidus* Rathbun (Arthropoda: Crustacea: Portunidae) is an ecologically and commercially important species that inhabits estuarine and coastal waters along the Atlantic and Gulf coasts of North America (Van Engel 1958, Laughlin 1982, Williams 1984). Serving as an epibenthic omnivore and prey resource, blue crabs are critical to energy transfer across trophic levels within estuarine and coastal ecosystems (Baird & Ulanowicz 1989). Despite its characterization as an omnivore (Laughlin 1982, Moksnes et al. 1997), blue crabs preferentially consume bivalves such as the infaunal, soft-shelled clam *Mya arenaria* (Lipcius & Hines 1986).

Mya arenaria Linnaeus (Mollusca: Bivalvia: Myacidae) is an abundant, deep-burrowing (ca 10 to 30 cm; Hines & Comtois 1985) suspension-feeding clam that occurs predominantly in sandy-mud habitats of temperate waters of the western North Atlantic coast (Hines & Comtois 1985). Blue crabs and *M. arenaria* exhibit discordant population cycles. For example, in Chesapeake Bay, USA, *M. arenaria* typically exhibit 2 recruitment pulses: a relatively weak winter settlement pulse, and a marked spring pulse after which the population declines rapidly in July and August at the time of increased crab abundance and intense predation (Blundon & Kennedy 1982a,b).

The contrasting oscillations that occur between populations of predatory *Callinectes sapidus* and *Mya arenaria* strongly suggest that blue crabs are capable of limiting the abundance of soft-shelled clams (Seitz unpubl.). Nevertheless, large adult clams persist at great burial depths (ca 20 to 30 cm; Hines & Comtois 1985) and low densities (0.2 to 19 clams m⁻²; Hines et al. 1990) within sandy but not muddy habitats. The low density refuge for *M. arenaria* in sand is attributed to *C. sapidus* exhibiting a density-dependent, type III functional response to *M. arenaria* in sandier substrates (Lipcius & Hines 1986). Conversely, blue crabs foraging in muddy sediments exhibit an inversely density-dependent, type II functional response, which precludes a refuge at low prey densities (Lipcius & Hines 1986). The suggested mechanism resulting in the change in predatory behavior across varying sediment compositions was an increase in crab encounter rates with clam siphons in muddy versus sandy sediments (Lipcius & Hines 1986). Blue crabs search for prey by probing the substrate with the tips of their walking

legs (Lipcius & Hines 1986), where chemosensory and tactile setae are located. The ease in which crabs can penetrate the surface of mud substrates with their walking legs enhances the detection of clam siphons and hence increases predation (Lipcius & Hines 1986, Eggleston et al. 1992).

Regardless of how subtle differences in the physical structure of microhabitats alter predator-prey dynamics, the local persistence of *Mya arenaria* may also be affected by other environmental factors such as the occurrence of hypoxia. Low dissolved oxygen concentrations potentially alter predator-prey dynamics between *Callinectes sapidus* and *M. arenaria* by either hindering foraging efficiency of blue crabs, or alternatively, by increasing vulnerability of clams to crabs by altering their siphon extension and depth distribution within the sediment column. For example, *C. sapidus* has a greater sensitivity to hypoxia than does its clam prey (Das & Stickle 1993, 1994, Diaz & Rosenberg 1995), yet the mobility of blue crabs may allow them to follow the spatially dynamic transition zone between normoxic and hypoxic waters, and exploit clams that have been stressed by severe bouts of hypoxia (Pihl et al. 1991, Das & Stickle 1993, 1994, Nestlerode & Diaz 1998). The ecological impact of the initiation and relaxation of hypoxia on predator-prey dynamics between *C. sapidus* and *M. arenaria* remains unknown. Moreover, the effects of mutual interference on the functional response of blue crabs to *M. arenaria*, or how this response is further modified by dissolved oxygen levels, are unknown. Research identifying the influence of hypoxia on predator-prey relationships is critical for predicting the effects of changes in water quality on trophic interactions and food web dynamics in marine and estuarine systems.

MATERIAL AND METHODS

Collection and maintenance. Adult *Callinectes sapidus* were purchased from local seafood dealers or captured with an otter trawl from seagrass beds along the Neuse River, a major tributary of Pamlico Sound (North Carolina, USA). Crabs were transferred to a large outdoor holding tank (5 m × 1 m × 2 m) where they were fed frozen fish and *Mya arenaria* *ab libitum* each day. Only male, intermolt crabs measuring 115 to 155 mm carapace width (representative of the dominant size class in Chesapeake Bay, USA; Hines et al. 1990) were used during this investigation. The use of male, intermolt crabs eliminated any potential variation in feeding due to sexual differences in behavior or chela morphology (Eggleston 1990c), and any additional stresses imposed upon molting crabs that could lead to higher rates of agonistic interactions or canni-

balism (Jachowski 1973, Hines & Ruiz 1995). *M. arenaria* were purchased from seafood distributors located in Auburn, Maine, USA. Only clams measuring 54 to 70 mm along the anterior-posterior axis and exhibiting vigorous siphon-withdrawal reflexes were used in experiments. Clams were maintained in a flow-through seawater system, with ambient phytoplankton as a food source.

Laboratory experiments were conducted at the National Marine Fisheries Service Laboratory in Beaufort, North Carolina, USA, from July 15 to October 10, 1998. Experimental conditions were manipulated to match local field conditions in mid-June to late August. Therefore, all experiments described below were conducted at 22–28°C, 33–37 psu, with a light:dark cycle of approximately 14:10 h. These conditions are typical of those encountered by estuarine organisms in temperate coastal areas of the western Atlantic during the summer, when episodes of hypoxia are most common (Officer et al. 1984).

Effects of hypoxia on clam behavior. To investigate the response of *Mya arenaria* to depleted oxygen concentrations, one 110 l aquarium (78 cm × 60 cm × 30 cm) was filled with 20 cm of muddy, fine-sand substrate (composition: 9.7% fine sand, 75.3% very fine sand, and 15.0% silt; 125–250, 62.5–125, and 3.9–62.5 µm, respectively; Folk 1974), and 20 cm of overlying seawater. Sediment composition and characterization (i.e. muddy, fine-sand substrate) were consistent with previous investigations that have examined predator-prey dynamics between *Callinectes sapidus* and *M. arenaria* (Lipcius & Hines 1986). Three *M. arenaria* were buried approximately 10 cm below the sediment surface and located 20 cm apart from each other and the periphery of the experimental tank. Clams were allowed 24 h prior to the initiation of any treatment to acclimate under high oxygen conditions (≥ 6.0 mg DO l⁻¹) and bury to natural depths (ca 10 to 20 cm; Hines & Comtois 1985). After initial measurements of temperature, salinity, and dissolved oxygen, an experimental trial was initiated by rendering tank water either normoxic (≥ 6.0 mg DO l⁻¹), moderately hypoxic (3.0 to 4.0 mg DO l⁻¹), or severely hypoxic (≤ 1.5 mg DO l⁻¹) for 24 h. Desired dissolved oxygen concentrations, monitored continuously with YSI Model 57 and YSI Model 55 handheld dissolved oxygen meters, were maintained by balancing the inflow of air and nitrogen. Four replicates of each 24 h oxygen treatment were conducted. Two response variables were quantified for *M. arenaria*: (1) burial depth and (2) siphon extension above the sediment surface. Burial depth was quantified by measuring the sediment penetration of a predetermined length of monofilament line (11.35 kg test) glued to the anterior tip of the clam's shell surface prior to its introduction into

the sediment. Siphon extension of the protruding inhalent/exhalent siphon was measured from the sediment-seawater interface to the siphon tip with a metric ruler. Burial depths and siphon extensions were averaged across the 3 clams in each trial. Mean differences in the response variables among dissolved oxygen concentrations (≤ 1.5 mg DO l⁻¹, 3.0 to 4.0 mg DO l⁻¹, and ≥ 6.0 mg DO l⁻¹) were analyzed with a 1-way, fixed factor analysis of variance (ANOVA) model using dissolved oxygen concentration as a factor. The natural log of ($x + 1$) transformation was used when variances were heteroscedastic. When data transformations were unsuccessful in achieving homoscedasticity, hypotheses were rejected at alpha values lower than the p-values of F_{\max} tests for homogeneity of variance (Underwood 1981). Means were contrasted with a Tukey's multiple comparison test.

Effects of hypoxia on clam behavior—real time. To gain perspective on the rate of change in burial depth and siphon extension of *Mya arenaria* in response to fluctuating dissolved oxygen concentrations, as indicative of field conditions, 3 clams were acclimated according to the experimental protocol described in the previous section. Following the completion of a 24 h high oxygen acclimation period, dissolved oxygen levels were lowered to severe hypoxia (≤ 1.5 mg DO l⁻¹) over a 2 h interval. Values were maintained at this level for 22 h, after which dissolved oxygen levels were returned to normoxia (≥ 6.0 mg DO l⁻¹) over a 2 h interval and maintained for an additional 22 h. During each of 4 replicate trials, burial depth and siphon extension were measured 4, 8, and 24 h after the onset of both the low and high dissolved oxygen treatments (≤ 1.5 mg DO l⁻¹ and ≥ 6.0 mg DO l⁻¹, respectively). Experimental dissolved oxygen concentrations (intensity, rate of change, and duration) simulated field data collected by the US Geological Survey, North Carolina District, from the bottom waters of the Neuse River, North Carolina, USA, during mid-August 1998 (Taylor 1998).

Blue crab satiation levels. Satiation experiments were conducted to assess maximum consumption rates of *Mya arenaria* by *Callinectes sapidus* over a 48 h time interval. These rates were required to define an appropriate experimental period and upper density of *M. arenaria* that allowed for some degree of prey survival, and hence comparison of clam mortality rates across experimental densities. Satiation levels of blue crabs were determined by placing individual crabs within a 1 m diameter polyethylene tank containing 12 uniformly distributed *M. arenaria*. The experimental arena had 20 cm of normoxic (≥ 6.0 mg DO l⁻¹) seawater, but no sediment to prevent clam burial and therefore any constraints on crab searching and foraging rates. Six trials were conducted by introducing an individual blue crab for 48 h. Satiation

levels were taken as the mean rate at which *M. arenaria* were consumed (no. of clams eaten per 48 h) across the 6 trials.

Effects of hypoxia and mutual interference on predator-prey dynamics. To evaluate predator responses to prey density, dissolved oxygen concentrations, and mutual interference, 2 densities of *Mya arenaria* (6 and 24 clams tank⁻¹; 7.8 clams m⁻² and 31.1 clams m⁻², respectively) were exposed to 2 densities of predatory *Callinectes sapidus* (1 and 2 crabs tank⁻¹) across 2 dissolved oxygen concentrations (moderate hypoxia: 3.0 to 4.0 mg DO l⁻¹; and normoxia: ≥ 6.0 mg DO l⁻¹). The experimental densities of crabs and clams used in this investigation represent a moderate to lower range of natural densities of *C. sapidus* (Orth & van Montfrans 1987) and *M. arenaria* (Hines et al. 1990) in Chesapeake Bay, USA. The experimental clam densities correspond to the 'low density' range for blue crabs preying on *M. arenaria* (Fig. 1).

Eight circular (1 m diameter) polyethylene tanks were filled with 20 cm of muddy, fine-sand substrate (composition: 9.7% fine sand, 75.3% very fine sand, and 15.0% silt; 125–250, 62.5–125, and 3.9–62.5 μ m, respectively; Folk 1974), and 20 cm of overlying seawater. The sediment composition chosen for this experiment was similar to that used in a previous study that identified a type II functional response by *Callinectes sapidus* to *Mya arenaria* (Lipcius & Hines 1986). Three dissolved oxygen treatments were used: (1) normoxia (≥ 6.0 mg DO l⁻¹), (2) moderate hypoxia (3.0 to 4.0 mg DO l⁻¹) subsequent to 24 h clam acclimation at high oxygen conditions (≥ 6.0 mg DO l⁻¹), and (3) moderate hypoxia (3.0 to 4.0 mg DO l⁻¹) subsequent to 24 h clam acclimation at low oxygen conditions (≤ 1.5 mg DO l⁻¹) (Fig. 2).

Clams were buried approximately 10 cm below the sediment surface, and allowed 24 h to acclimate under high or low oxygen conditions (≥ 6.0 mg or ≤ 1.5 mg DO l⁻¹, respectively) and bury to natural depths. *Mya arenaria* were also positioned at least 10 cm from the sides of the tank to avoid edge effects on predation rates (Eggleston et al. 1992). *Callinectes sapidus* were starved for 48 h to standardize hunger levels prior to their release into the center of each tank. Six to ten 48 h trials were conducted for each treatment. Prey mortality was quantified by counting surviving clams and umbones of eaten clams.

Consumption (no. of clams eaten per 48 h) and proportional mortality rates (no. of clams eaten per clam density per 48 h) of *Mya arenaria* by either 1 or 2 blue crabs were analyzed with separate 2-way, fixed-factor ANOVA models using clam density and dissolved oxygen concentration as factors. Predator density (1 vs 2 crabs tank⁻¹) was not incorporated as a factor in these analyses since the feeding experiments with different

predator densities were not conducted simultaneously (considered separate experiments; sensu Hurlbert 1984). Qualitative comparisons between the functional responses exhibited by 1 versus 2 blue crabs, however, may suggest behavioral mechanisms leading to the

local persistence or extinction of prey populations exposed to different predator densities and varying dissolved oxygen concentrations. Mean consumption and proportional mortality of clams across 2 levels of prey density and 3 levels of dissolved oxygen treat-

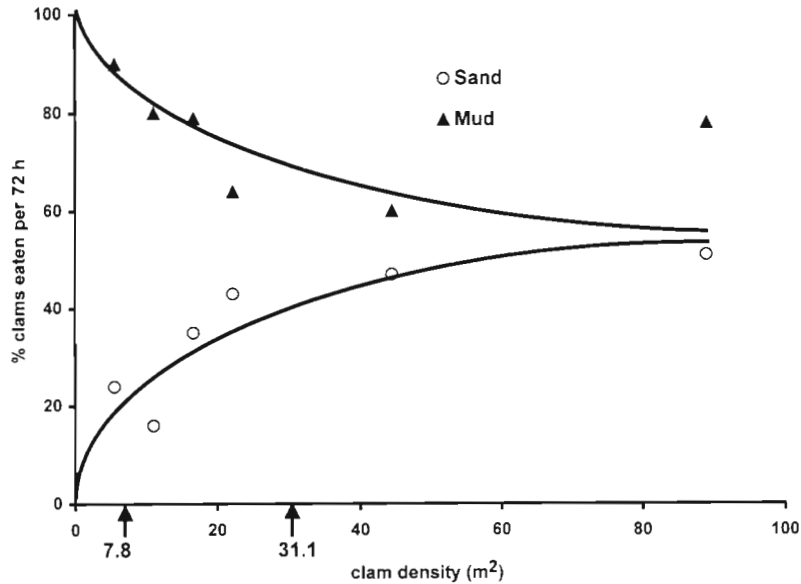


Fig. 1. Proportional mortality rates of *Mya arenaria* clams to blue crab predation as a function of clam density and sediment type (after Lipcius & Hines 1986). This figure is used to justify the choice of the 'low range' of experimental prey densities so that differences between functional responses can be distinguished with only 2 data points. Clam densities (x-axis) used in Lipcius & Hines (1986) were standardized to no. of clams m⁻². The experimental clam densities chosen for this study (denoted by the solid black arrows) encompassed low to moderate prey densities and therefore permit efficient statistical differentiation among functional responses based on 2 data points

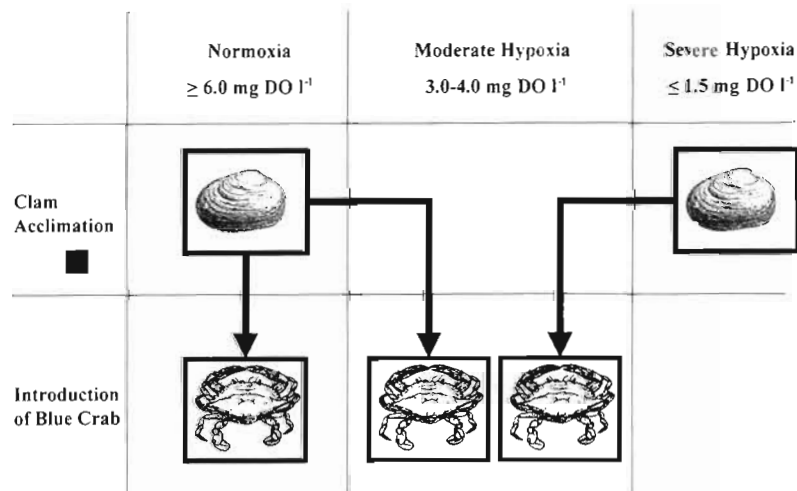


Fig. 2. Schematic of the predator-prey experimental design, which simulates 2 densities of *Mya arenaria* (6 and 24 clams tank⁻¹) acclimated under normoxia (≥ 6.0 mg DO l⁻¹) or severe hypoxia (≤ 1.5 mg DO l⁻¹) for 24 h. Dissolved oxygen concentrations were then maintained or raised to either normoxia (≥ 6.0 mg DO l⁻¹) or moderate hypoxia (3.0 to 4.0 mg DO l⁻¹), respectively, after which 1 or 2 blue crabs were introduced into the experimental arena. Following a 48 h predation period, counts of surviving *M. arenaria* and umbones of eaten clams were used to calculate consumption rates (no. of clams eaten per 48 h) and proportional mortality rates (no. of clams eaten per clam density per 48 h). The experimental design simulates drastic fluctuations in dissolved oxygen concentrations characteristic of numerous estuarine systems during summer months

ments were contrasted with a 2-way ANOVA model and Ryan-Einot-Gabriel-Welsch (Ryan's Q) multiple comparison tests, respectively. A Ryan's Q multiple comparison test was used in cases with unequal sample sizes (i.e. predator-prey experiments), as opposed to the Tukey's multiple comparison test, which was used in situations with equal sample sizes (as recommended by Day & Quinn 1989).

Effects of agonism on blue crab functional responses.

The effect of physical injury, resulting from intraspecific aggression, on rates of predation by *Callinectes sapidus* was determined *a posteriori* by categorizing the 2-predator, moderate hypoxic oxygen treatment (clams acclimated under severe hypoxia; Fig. 2) as either lacking or demonstrating visible evidence of crab mortality, carapace wounds, or loss of appendages. This 'physical evidence of crab agonism' treatment (present, absent) was chosen *a posteriori* because there was clear evidence of injury or lack thereof in 50% of the trials. Consumption and proportional mortality rates were each analyzed with a 2-way, fixed-factor ANOVA model using clam density (low, high) and evidence of crab agonism (present, absent) as factors.

RESULTS

Effects of hypoxia on clam behavior

As dissolved oxygen concentrations decreased, *Mya arenaria* migrated toward the sediment surface and

extended their siphons above the substrate-seawater interface. Clam burial depths differed significantly according to dissolved oxygen levels (1-way ANOVA: $F = 17.18$, $df = 2, 11$, $p < 0.01$), and were significantly shallower at low dissolved oxygen concentrations than at moderate or high concentrations (Fig. 3a, Tukey's multiple comparison test). To eliminate potential biases in clam burial depth measurements (resulting from differences in size or initial burying of clams), 'changes' in burial depth were calculated by subtracting the burial depth of clams after a specified dissolved oxygen treatment from the depths achieved after the 24 h acclimation period. A positive change in depth indicates a decrease in burial depth (i.e. movement to sediment surface), whereas negative values denote an increase in burial depth. Changes in the sediment burial depths of *M. arenaria* differed significantly according to dissolved oxygen concentrations (1-way ANOVA: $F = 17.76$, $df = 2, 11$, $p < 0.01$), and were significantly greater at low dissolved oxygen levels (depth change = +5.04 cm at ≤ 1.5 mg DO l⁻¹) than at moderate (depth change = -0.08 cm at 3.0 to 4.0 mg DO l⁻¹) or high (depth change = -0.07 cm at ≥ 6.0 mg DO l⁻¹) oxygen concentrations (Tukey's multiple comparison test).

Siphon extension into the water column also differed significantly across dissolved oxygen levels (1-way ANOVA: $F = 56.67$, $df = 2, 11$, $p < 0.01$), and was significantly greater at low dissolved oxygen concentrations than at moderate or high concentrations (Fig. 3b, Tukey's multiple comparison test). To eliminate potential biases in siphon extension measurements associ-

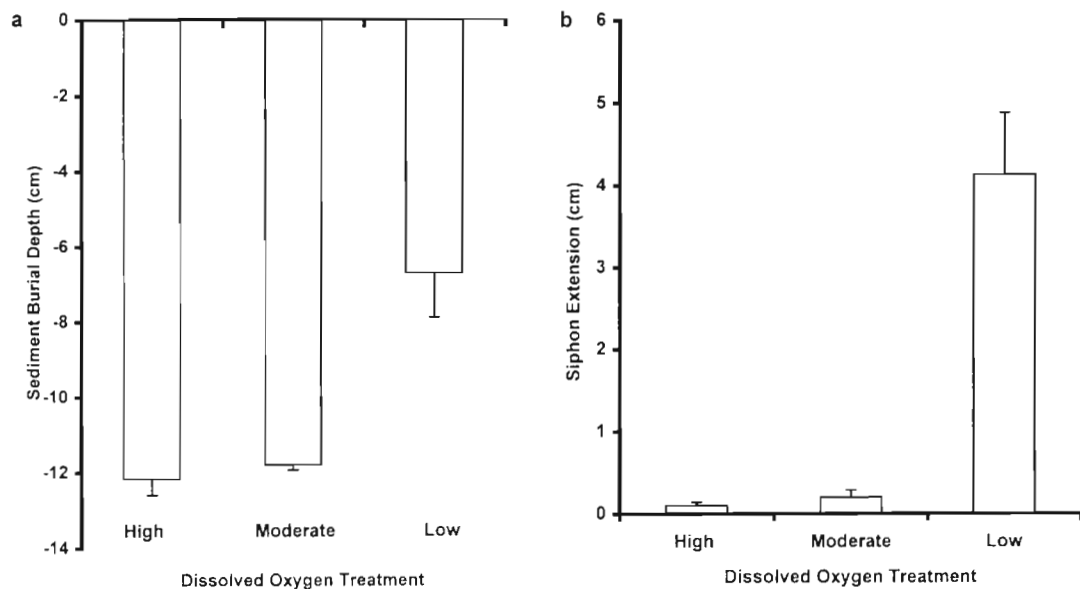


Fig. 3. (a) Sediment burial depth and (b) siphon extension of *Mya arenaria* in response to a 24 h exposure period to 3 oxygen concentrations: high, moderate, and low (≥ 6.0 , 3.0 to 4.0, and ≤ 1.5 mg DO l⁻¹, respectively). Means (+SE) at each dissolved oxygen treatment are plotted ($n = 4$). See text for significant levels

ated with clam size, 'changes' in siphon extension were calculated by subtracting the values achieved after a given dissolved oxygen treatment from those recorded after the 24 h acclimation period. A positive change in siphon extension indicates an increase in extension (i.e. protrusion into the water column), whereas negative values denote a withdrawal in siphon extension. Changes in clam siphon extension differed significantly according to dissolved oxygen levels (1-way ANOVA: $F = 99.14$, $df = 2, 11$, $p < 0.01$), and were significantly greater at low dissolved oxygen levels (extension change = +3.61 cm at ≤ 1.5 mg DO l⁻¹) than at moderate (extension change = -0.05 cm at 3.0 to 4.0 mg DO l⁻¹) or high (extension change = -0.02 cm at ≥ 6.0 mg DO l⁻¹) oxygen concentrations (Tukey's multiple comparison test).

Effects of hypoxia on clam behavior — real time

The initiation and persistence of severe hypoxia (≤ 1.5 mg DO l⁻¹) resulted in the nearly continuous extension of *Mya arenaria* siphons into the water column (Fig. 4). The behavioral response of clams to hypoxia was immediate; siphon extension occurred at a rate of 0.32 cm h⁻¹ over the first 4 h of exposure to dis-

solved oxygen levels less than 1.5 mg DO l⁻¹ (Fig. 4). The rate of siphon extension gradually decreased with increased exposure time to hypoxia (Fig. 4). Between the fourth and eighth hour of exposure to hypoxia, siphon extension occurred at a rate of 0.13 cm h⁻¹ (Fig. 4). Between the eighth and twenty-fourth hour of exposure to hypoxia, siphon extension rates decreased to 0.08 cm h⁻¹ (Fig. 4). The return to normoxic conditions (≥ 6.0 mg DO l⁻¹) resulted in siphon withdrawal back into the sediment (Fig. 4). The rate of siphon withdrawal was greatest at the onset of normoxia, and gradually decreased with time (0.44 cm h⁻¹ from 0 to 4 h; 0.13 cm h⁻¹ from 4 to 8 h; 0.03 cm h⁻¹ from 8 to 24 h).

Mya arenaria burial depth decreased with the initiation and persistence of hypoxia (Fig. 4), and occurred at a rate of 0.17 cm h⁻¹. The return to normoxia resulted in a steady rate of sediment reburial of 0.10 cm h⁻¹ over the 24 h period (Fig. 4).

Blue crab satiation levels

Callinectes sapidus consumed an average of 7.83 *Mya arenaria* per 48 h when foraging was unimpeded by sediment. Therefore, the experimental period of

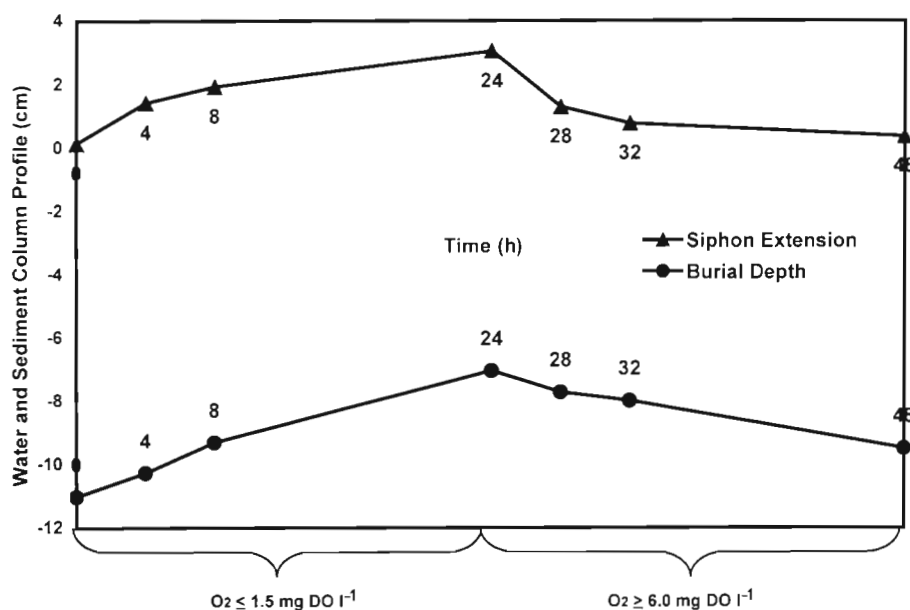


Fig. 4. Rate of change in *Mya arenaria* burial depth (cm) and siphon extension (cm) in response to fluctuating dissolved oxygen concentrations. Following a 24 h acclimation period under normoxia, dissolved oxygen levels were lowered to severe hypoxia (≤ 1.5 mg DO l⁻¹) over a 2 h interval. Dissolved oxygen was maintained at this level for 22 h, after which it was returned to normoxia (≥ 6.0 mg DO l⁻¹) over a 2 h interval and maintained for an additional 22 h. The response variables, burial depth (●) and siphon extension (▲), were measured 4, 8, and 24 h after the onset of both the low and high dissolved oxygen treatment (≤ 1.5 and ≥ 6.0 mg DO l⁻¹, respectively). Experimental dissolved oxygen concentrations (intensity, rate of change, and duration) simulated field data collected by the US Geological Survey, North Carolina District, from the bottom waters of the Neuse River, North Carolina, USA (latitude 34° 56' 56", longitude 76° 48' 36") during mid-August 1998

48 h and densities of *M. arenaria* used in predator-prey experiments (6 and 24 clams tank⁻¹) did not bias the results against differentiating clam consumption and proportional mortality rates across high and low prey density treatments, since crabs were presumably below satiation.

Effects of hypoxia and mutual interference on predator-prey dynamics

Single predator — effects of hypoxia on crab foraging behavior

Consumption rates of individual blue crabs differed significantly according to dissolved oxygen concentration and *Mya arenaria* density (2-way ANOVA; dissolved oxygen treatment: $F = 11.36$, $df = 2$, 44 , $p < 0.01$; clam density: $F = 6.84$, $df = 1$, 44 , $p = 0.01$); the interaction effect was not significant ($F = 2.51$, $df = 2$, 44 , $p = 0.09$) (Fig. 5a). Consumption rates were significantly higher during normoxia (≥ 6.0 mg DO l⁻¹) and moderate hypoxia (3.0 to 4.0 mg DO l⁻¹) when clams were acclimated to severe hypoxia (≤ 1.5 mg DO l⁻¹), than during moderate hypoxia when clams were acclimated to normoxia (Fig. 5a, Ryan's *Q* multiple comparison test). In addition, significantly more *M. arenaria* were consumed at the high clam density (24 clams tank⁻¹) than the low density (6 clams tank⁻¹) (Fig. 5a, lower-level ANOVA).

The proportion of *Mya arenaria* consumed by a single blue crab also differed significantly by dissolved oxygen concentration and clam density (2-way ANOVA; dissolved oxygen treatment: $F = 29.92$, $df = 2$, 44 , $p < 0.01$; clam density: $F = 53.26$, $df = 1$, 44 , $p < 0.01$); however, the interaction effect was also significant (2-way ANOVA, $F = 18.46$, $df = 2$, 44 , $p < 0.01$) (Fig. 5b), precluding contrasts across the main effects. The interaction effect was due to significantly higher proportional mortality rates of *M. arenaria* at low versus high experimental clam densities in normoxia and moderate hypoxia (low dissolved oxygen acclimation for clams) (indicative of a type II functional response); and no difference in proportional mortality rates between clam densities (indicative of a type I functional response) in moderate hypoxia (high dissolved oxygen acclimation for clams) (Fig. 5b, lower-level ANOVA). Thus, during the transition from normoxia to hypoxia, crab foraging behavior was altered drastically such that it was no longer destabilizing to predator-prey dynamics at low prey densities (Fig. 5b). Conversely, as dissolved oxygen concentrations for acclimating clams increased from severe hypoxia (≤ 1.5 mg DO l⁻¹) to moderate hypoxia (3.0 to 4.0 mg DO l⁻¹), crab foraging behavior changed from a type I functional

response to a type II functional response; stressed clams with increased siphon extension resided closer to the sediment-water interface and suffered disproportionately high predation-induced mortality at low prey densities (Fig. 5b).

Two predators — effects of hypoxia and mutual interference on crab foraging behavior

Total consumption rates by 2 *Callinectes sapidus* differed significantly according to dissolved oxygen concentration and *Mya arenaria* density (2-way ANOVA; dissolved oxygen treatment: $F = 8.05$, $df = 2$, 39 , $p < 0.01$; clam density: $F = 17.66$, $df = 1$, 39 , $p < 0.01$); however, the interaction effect was also significant ($F = 9.69$, $df = 2$, 44 , $p < 0.01$) (Fig. 5c), precluding contrasts across the main effects. The interaction effect was due to significantly higher clam mortality at high than low clam densities under moderate hypoxia (3.0 to 4.0 mg DO l⁻¹), when clams were acclimated to severe hypoxia (≤ 1.5 mg DO l⁻¹), and no significant difference in clam mortality rates between clam densities for the remaining dissolved oxygen treatments (Fig. 5c, lower-level ANOVA).

Proportional mortality of *Mya arenaria* also differed significantly by dissolved oxygen concentrations and clam density (2-way ANOVA; dissolved oxygen treatment: $F = 8.08$, $df = 2$, 39 , $p < 0.01$; clam density: $F = 5.67$, $df = 1$, 39 , $p = 0.02$); however, the interaction effect was also significant (2-way ANOVA, $F = 9.34$, $df = 2$, 39 , $p < 0.01$) (Fig. 5d), precluding contrasts across the main effects. The interaction effect was due to significantly higher proportional mortality rates of clams at low versus high clam densities under moderate hypoxia, when clams were acclimated to normoxia (indicative of a type II functional response), and no difference in proportional mortality rates (indicative of a type I functional response) between clam densities under normoxia, or moderate hypoxia when clams were acclimated to severe hypoxia (Fig. 5d, lower-level ANOVA).

Mutual interference between 2 large *Callinectes sapidus* altered the functional response of crabs across all dissolved oxygen treatments (Fig. 5). For example, under normoxia, a single blue crab exhibited a type II functional response to *Mya arenaria*, whereas 2 crabs exhibited a type I functional response (Fig. 5). Similarly, although a single crab exhibited a type II functional response to *M. arenaria* under moderate hypoxia when clams were acclimated to severe hypoxia, 2 crabs exhibited a type I functional response (Fig. 5). Lastly, under moderate hypoxia, a single blue crab exhibited a type I functional response to *M. arenaria* when clams had been acclimated to normoxia, whereas

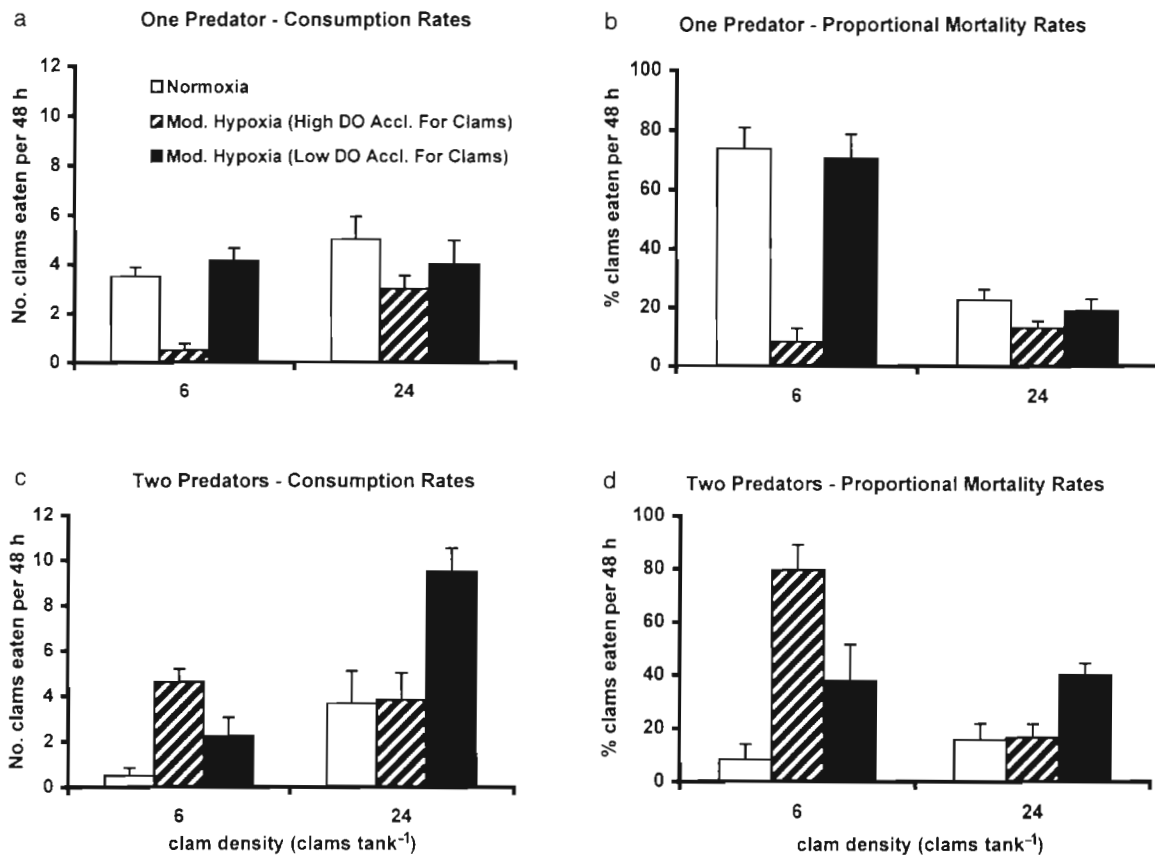


Fig. 5. Summary of (a) consumption rates (no. of clams eaten per 48 h) and (b) proportional mortality rates (no. of clams eaten per clam density per 48 h) of *Mya arenaria* by a single *Callinectes sapidus*, and (c) consumption rates (no. clams eaten per 48 h) and (d) proportional mortality rates (no. of clams eaten per clam density per 48 h) of *M. arenaria* by 2 *C. sapidus* across 2 clam densities (6 and 24 clams tank⁻¹) and 3 dissolved oxygen treatments: normoxia (≥ 6.0 mg DO l⁻¹); moderate hypoxia (3.0 to 4.0 mg DO l⁻¹), with clams acclimated to high oxygen conditions (≥ 6.0 mg DO l⁻¹); and moderate hypoxia (3.0 to 4.0 mg DO l⁻¹), with clams acclimated under low oxygen conditions (≤ 1.5 mg DO l⁻¹). Means (+SE) at each clam density and dissolved oxygen treatment are plotted. See text for significant levels

2 crabs exhibited a type II functional response under such conditions (Fig. 5).

Effects of agonism on blue crab functional responses

Physical evidence of agonism between *Callinectes sapidus* in the experiments with 2 predators significantly affected proportional mortality rates of *Mya arenaria*, altering the functional response of blue crabs (Fig. 6). Total consumption rates of 2 *C. sapidus* differed significantly according to whether or not physical evidence of blue crab agonism was present, as well as *M. arenaria* density (2-way ANOVA; agonism: $F = 10.33$, $df = 1, 13$, $p < 0.01$; clam density: $F = 50.00$, $df = 1, 13$, $p < 0.01$); the interaction effect was not significant ($F = 0.81$, $df = 1, 13$, $p = 0.38$) (Fig. 6a). Consumption rates of *M. arenaria* by *C. sapidus* bearing evidence of physical injury were significantly lower than

for undamaged blue crabs (Fig. 6a, lower-level ANOVA). In addition, significantly more *M. arenaria* were consumed at the high versus low clam density (Fig. 6a, lower-level ANOVA).

The proportion of clams consumed also differed significantly according to whether or not there was physical evidence of blue crab agonism, but not by *Mya arenaria* density (2-way ANOVA; agonism: $F = 22.89$, $df = 1, 13$, $p < 0.01$; clam density: $F = 0.00$, $df = 1, 13$, $p = 0.95$); however, the interaction effect was also significant ($F = 12.23$, $df = 1, 13$, $p < 0.01$) (Fig. 6b), precluding contrasts across main effects. Foraging by intact (undamaged) blue crabs demonstrated a type II functional response, as clams suffered significantly greater proportional mortality at low versus high prey densities (Fig. 6b, lower-level ANOVA). *M. arenaria* suffered greater proportional mortality at high versus low clam densities when preyed upon by injured *Callinectes sapidus*, indicating that blue crabs exhibit a type III functional response under conditions that

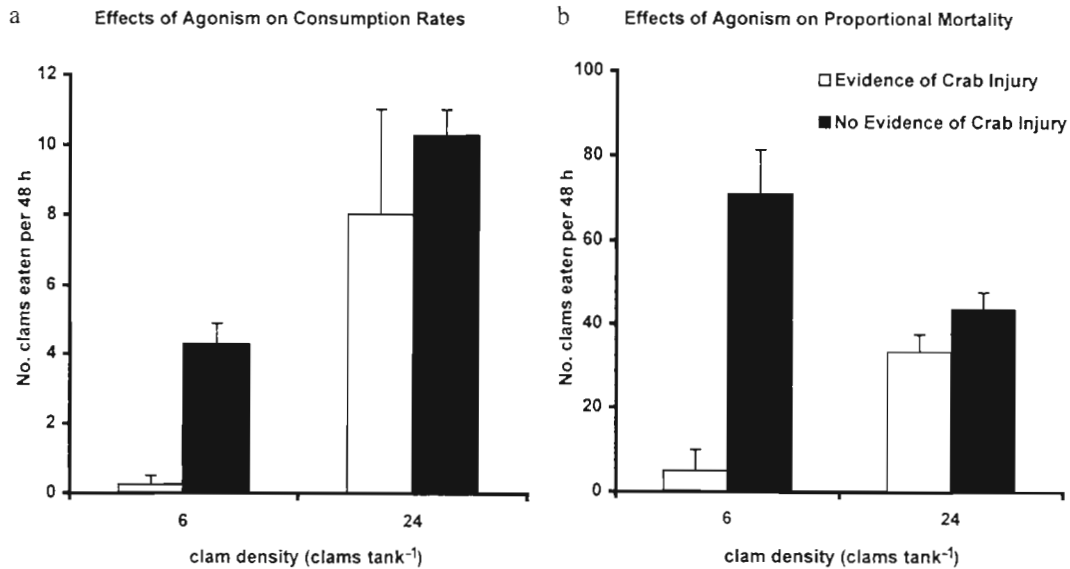


Fig. 6. Effects of *Callinectes sapidus* agonism (present and absent) and *Mya arenaria* density (6 and 24 clams tank⁻¹) on (a) consumption rates (no. of clams eaten per 48 h) and (b) proportional mortality rates (no. of clams eaten per clam density per 48 h) of *M. arenaria* under moderate hypoxia (3.0 to 4.0 mg DO l⁻¹), with clams acclimated to low oxygen conditions (≤ 1.5 mg DO l⁻¹). Means (+SE) at each clam density and dissolved oxygen treatment are plotted. See text for significant levels

result in agonism and physical damage (Fig. 6b, lower-level ANOVA)

DISCUSSION

Results from this study provide quantitative insight regarding the impact of fluctuations in dissolved oxygen levels on prey refuges for infaunal clam populations, as well as predator-prey dynamics between *Callinectes sapidus* and clam prey. *Mya arenaria* obtained a partial prey refuge from blue crab predation when dissolved oxygen concentrations decreased from normoxia to moderate hypoxia (≥ 6.0 mg to 3.0–4.0 mg DO l⁻¹), where the foraging behavior of blue crabs upon clam prey changed from a destabilizing, type II functional response, to a partially stabilizing, type I functional response (Table 1). *M. arenaria*'s low density prey refuge at moderate hypoxia was lost, however, when blue crabs preyed upon clams that were previously acclimated under severe hypoxia (≤ 1.5 mg DO l⁻¹) (indicative of a type II functional response) (Table 1).

The inclusion of a second blue crab predator in experimental trials further modified crab functional responses (Table 1). The initiation of moderate hypoxia from normoxia changed the foraging behavior of 2 blue crabs from a type I functional response to a type II response (Table 1). Conversely, 2 blue crabs exhibited a type I functional response under moderate hypoxia subsequent to clam exposure to severe hypoxia

(Table 1). The collective results indicate that fluctuations in dissolved oxygen concentrations, as well as both predator and prey density, must be examined jointly to understand their impact upon predator-prey dynamics in marine systems.

The underlying mechanism controlling the effects of hypoxia on the predator-prey dynamics between *Callinectes sapidus* and *Mya arenaria* is the behavioral response of clam prey to low oxygen conditions; i.e. prey behavioral responses that affect burial depth and siphon extension altering *M. arenaria*'s vulnerability to blue crab predation. In this study, very low dissolved oxygen concentrations (≤ 1.5 mg DO l⁻¹) significantly decreased the burial depth of *M. arenaria*, rendering clams more accessible to foraging blue crabs. The morphological characteristics (i.e. spines, varices, thickness of shells) of many molluscan prey species serve as a deterrent to predation (Vermeij 1978, Palmer 1979, Blundon & Kennedy 1982a). For example, large juvenile oysters *Crassostrea virginica* are able to attain an absolute prey refuge from foraging female blue crabs in conjunction with increases in size and shell thickness (Eggleston 1990b). Conversely, mature *M. arenaria* possess a relatively thin shell with a siphonal and pedal gape, lacking any prominent predator-resistant morphological features (Boulding 1984). Structural analyses of *M. arenaria* detected that their shells were never strong enough to confer resistance to crushing by blue crabs (i.e. provided no size refuge) (Blundon & Kennedy 1982a). The absence of anti-predator shell features in *M. arenaria* reflects the partial refuge pro-

Table 1 Results of *Callinectes sapidus-Mya arenaria* predator-prey experiments with 1 and 2 predators, demonstrating consumption rates (no. of clams eaten per 48 h) and proportional mortality rates (no. of clams eaten per clam density per 48 h) for prey across 2 clam densities (6 and 24 clams tank⁻¹) and 3 dissolved oxygen treatments: normoxia (≥ 6.0 mg DO l⁻¹), moderate hypoxia (3.0 to 4.0 mg DO l⁻¹), with clams acclimated under high oxygen conditions (≥ 6.0 mg DO l⁻¹); and moderate hypoxia (3.0 to 4.0 mg DO l⁻¹), with clams acclimated under low oxygen conditions (≤ 1.5 mg DO l⁻¹). The effect of blue crab agonism on consumption and proportional mortality rates for clams is reported for the moderate hypoxic (3.0 to 4.0 mg DO l⁻¹) treatment in which clams were acclimated under severe hypoxia (≤ 1.5 mg DO l⁻¹). The number of replicates (n) per treatment combination, the type of functional response under different experimental treatments, and the hypothesized behavioral mechanisms underlying variable functional responses are summarized

| Dissolved oxygen treatment | n | Clam density | Functional response | Hypothesized behavioral mechanism |
|--|----|--------------|---------------------|--|
| One crab | | | | |
| Normoxia | 8 | 6 | Type II | Relatively high encounter rates by crabs with clam siphons in mud |
| | 6 | 24 | | |
| Moderate hypoxia (high DO accl. for clams) | 10 | 6 | Type I | Decreased activity of blue crabs with exposure to low dissolved oxygen |
| | 7 | 24 | | |
| Moderate hypoxia (low DO accl. for clams) | 7 | 6 | Type II | Increased clam vulnerability due to shallow burial depth and increased siphon extension |
| | 7 | 24 | | |
| Two crabs | | | | |
| Normoxia | 6 | 6 | Type I | Mutual interference between crabs at low prey densities reduces predator foraging efficiency |
| | 6 | 24 | | |
| Moderate hypoxia (high DO accl. for clams) | 8 | 6 | Type II | Mutual attacks of crabs on prey enhances predator foraging efficiency |
| | 6 | 24 | | |
| Moderate hypoxia (low DO accl. for clams) | 8 | 6 | Type I | Mutual interference between crabs at low prey densities reduces predator foraging efficiency |
| | 6 | 24 | | |
| Agonism absent | | | | |
| Moderate hypoxia (low DO accl. for clams) | 4 | 6 | Type II | Mutual attacks of crabs on prey enhances predator foraging efficiency |
| | 6 | 24 | | |
| Agonism present | | | | |
| Moderate hypoxia (low DO accl. for clams) | 4 | 6 | Type III | Mutual interference between crabs at low prey densities reduces predator foraging efficiency |
| | 6 | 24 | | |

vided by their infaunal existence (Boulding 1984). Although predators such as blue crabs are capable of excavating moderately deep clams (ca 10 cm; Blundon & Kennedy 1982a), crabs forage more efficiently near the sediment surface (Blundon & Kennedy 1982b, Boulding 1984). Previous studies examining the effectiveness of possible refuges within the sediment in protecting *M. arenaria* from blue crab predation determined that crabs foraged less efficiently on clams residing deeper than 10 cm in the sediment column than on those closer to the surface (Blundon & Kennedy 1982b). Thus, factors eliminating the deep burial depths of *M. arenaria* appear detrimental to clam survival.

When blue crabs foraged upon *Mya arenaria* under normoxia (≥ 6.0 mg DO l⁻¹) in this study, clam prey suffered a higher risk of mortality at low versus high densities (indicative of a type II functional response) (Table 1). Thus, the observed pattern of inversely density-dependent mortality of clam prey under high oxygen conditions was consistent with the findings of Lip-

cius & Hines (1986). Accordingly, *M. arenaria* were incapable of attaining a low density, deep burial depth refuge from blue crab predation in muddy substrates. The absence of a low-density refuge for clams in mud was attributed to the increased penetration of the tips of the walking legs of blue crabs in mud versus sand sediments (Lipcius & Hines 1986) (Table 1). Furthermore, the physical attributes of mud may facilitate the excavation of *M. arenaria* because sand tends to refill holes faster during blue crab digging than in mud (pers. obs.) (Table 1).

The initiation of moderate hypoxia following normoxic conditions dramatically modified the functional response of *Callinectes sapidus* from a type II functional response to a type I response (Table 1). *Mya arenaria* attained a partial refuge at this lower oxygen level due to different tolerance levels of predatory blue crabs and their clam prey to hypoxia (Table 1). Blue crabs are highly sensitive to low oxygen conditions (Pihl et al. 1991, Das & Stickle 1993, 1994, Diaz

& Rosenberg 1995), decreasing their activity and becoming quiescent when exposed to even moderate hypoxia (pers. obs.). Conversely, burial depth and siphon extension of *M. arenaria* appeared unaffected by moderate hypoxia. Under lower oxygen concentrations, stressed blue crabs do not expend the energy required to excavate deeply buried clam prey. Moreover, in natural populations the mobility and resulting horizontal or vertical migration of *C. sapidus* away from hypoxic waters (3.0 to 4.0 mg DO l⁻¹) allow blue crabs to avoid the deleterious effects associated with severe oxygen limitation (Pihl et al. 1991, Nestlerode & Diaz 1998). Consequently, crab emigration under hypoxic conditions indirectly establishes a prey refuge for *M. arenaria* at oxygen concentrations below moderate hypoxia as clams benefit from the temporary absence of one of their key predators. Thus, *M. arenaria* indirectly utilizes hypoxic regimes as a refuge from blue crab predation through the maintenance of deep burial depths, and relative inactivity or absence of crabs.

Mya arenaria exposed to severe hypoxia (≤ 1.5 mg DO l⁻¹) decreased their sediment burial depth and increased their siphon extension. The rapid dissipation of low oxygen episodes in the field may allow blue crabs to return to affected areas and take predatory advantage of easily accessible clams. Under moderate hypoxia, blue crabs foraging upon clams previously acclimated under severe hypoxia exhibited a type II functional response (Table 1). The low-density prey refuge, previously achieved at moderate hypoxia when clams were acclimated under normoxia, was lost when oxygen concentrations recovered from severe hypoxia (as opposed to decreasing from normoxia) (Table 1). The decrease in clam burial depth under severe hypoxia probably facilitated excavation by blue crabs and subsequent predation (Table 1). Additionally, while increases in siphon extension did not evoke a high incidence of sub-lethal predation (siphon cropping), it is probable that prey encounter rates by foraging blue crabs were enhanced as a function of increased visual and tactile detection of protruding clam siphons (Table 1).

The inclusion of a second *Callinectes sapidus* predator altered the functional response of blue crabs through the initiation of mutual interference and intraspecific agonism (Table 1). Under normoxia, blue crabs exhibited a type I functional response to varying densities of clam prey (Table 1). The underlying mechanism shifting the foraging behavior of solitary blue crabs from a type II functional response to a type I response for 2 crabs was attributed to a higher incidence of agonism in 2 predator treatments at low versus high prey densities (Table 1). The observed patterns of reduced foraging efficiency due to predator

agonism were consistent with a previous study of the impact of mutual interference on blue crab predation upon the soft-shelled clam *Macoma balthica*, where agonistic interactions between blue crabs stabilized predator-prey dynamics at low clam densities (Mansour & Lipcius 1991). In this study, qualitative comparisons of consumption and proportional mortality rates of *Mya arenaria* across the 2 densities of *C. sapidus* (1 and 2 crabs tank⁻¹) suggest that interference responses by blue crabs at high predator densities significantly decrease the magnitude of predation intensity upon clam prey. First, mutual interference between predatory blue crabs potentially decreases crab searching, foraging, and prey handling efficiency. Mansour & Lipcius's (1991) study of mutual interference among blue crabs foraging upon *M. balthica* confirmed that increasing predator density resulted in a higher incidence of agonistic interactions, which subsequently decreased foraging efficiency of blue crabs upon infaunal clam prey. Second, the occurrence of cannibalism in 2 predator experiments may reduce the need to forage for clam prey as the consumption of conspecifics by blue crabs becomes an additional or alternative food resource. Previous field (Laughlin 1982) and laboratory (Mansour & Lipcius 1991) studies indicate that cannibalism is common in *C. sapidus*. Hence, consumption of conspecifics constitutes a major component of the diet of blue crabs, particularly in the late summer-early fall when the abundance of infaunal clam prey has dramatically declined (Fox 1975, Mansour 1992). Third, agonistic interactions resulting in the loss of blue crab appendages potentially hinder the excavation of *M. arenaria*. In a laboratory study that examined the effects of appendage loss on rates at which injured blue crabs forage on *M. arenaria*, Smith & Hines (1991) determined that crabs missing both chelipeds experience significantly lower consumption rates upon buried clams as compared to blue crabs whose chelipeds remained intact.

The joint foraging rate of 2 *Callinectes sapidus* was enhanced when dissolved oxygen levels decreased from normoxia to moderate hypoxia (Table 1). Thus, under moderate hypoxia, foraging by 2 predators on infaunal clam prey appears more successful than individual crab foraging responses. A similar response was detected in a field investigation that examined direct and indirect interactions between predatory blue crabs and the demersal fish, spot *Leiostomus xanthurus*, and their benthic prey (Martin et al. 1989). The foraging efficiency of spot was enhanced by the presence of additional blue crab predators, as crabs made copepods and amphipods more accessible to spot predation by grazing their algal prey refuge, *Enteromorpha intestinalis* (Martin et al. 1989). The behavior of one predator that minimizes the structural complexity of a

habitat can therefore lead to increased inter- and intraspecific predator efficiency (Crowder & Cooper 1982, Leber 1985, Martin et al. 1989). Similarly, blue crabs exposed to moderate hypoxia may forage upon deeply buried *Mya arenaria* for only short time intervals before becoming quiescent (Table 1). If these crabs, which may be stressed under hypoxic conditions, only partially excavate clams, the foraging efficiency by additional blue crabs may be enhanced if they feed in the same area on newly accessible prey. The combined foraging rates of 2 blue crab predators would be greater (compared to a single predator) if the net result were crabs unintentionally assisting in the excavation of clam prey (i.e. foraging at different times within the same area) without encountering agonistic interactions between each other (Table 1). A previous study that staged fighting contests between size-matched male shore crabs *Carcinus maenas* under a range of water oxygen tensions (between 10 and 100% oxygen saturation), determined that the initiation of hypoxic episodes minimized the frequency and duration of aggressive encounters between crabs (Sneddon et al. 1999). The analyses of physiological responses to fighting between 2 shore crabs suggest that contests staged under hypoxia were significantly shorter, whereby crabs exhibited elevated concentrations of haemolymph metabolites (L-lactate and glucose) in muscle tissue (Sneddon et al. 1999). Decreased fighting episodes between crabs under hypoxia imply that metabolite accumulation may be acting as a physiological constraint that limits crabs to a few minutes of activity under oxygen-stressed conditions (Sneddon et al. 1999).

Mya arenaria recovering from severe hypoxia in this study attained a partial prey refuge from the foraging of 2 blue crab predators when dissolved oxygen concentrations were raised to moderate levels (Table 1). The observed type I functional response in this situation was probably due to mutual interference between *Callinectes sapidus*, which imparted partial stability to crab-clam predator-prey dynamics at low clam densities (Table 1).

The effect of intraspecific aggression on blue crab foraging behavior in this study was determined by categorizing trials *a posteriori* according to whether or not there was visible evidence of damage and injury to blue crabs. Damaged blue crabs exhibited a type III functional response, whereas intact crabs demonstrated a type II functional response. These results imply that increased predator density and presumed mutual interference between foraging crabs (Mansour & Lipcius 1991) do not necessarily account for the stabilizing effect on clam prey populations. Instead, the foraging response of 2 blue crabs preying upon infaunal clams was inhibited only in conjunction with

intraspecific confrontations between agonistic crabs that resulted in mortality or physical injury.

The results of this laboratory investigation indicate that the interactive effects of prey and predator density are important factors in determining the local persistence of clams in prey patches. Furthermore, the results suggest that mutual interference between blue crabs affects the magnitude of predation intensity across all dissolved oxygen levels. In field conditions, however, it is unclear whether agonistic interactions lead primarily to avoidance responses and hence predator dispersal, or if predator aggregation persists at vulnerable prey patches despite the occurrence of intraspecific aggression leading to crab injury or mortality (Clark 1997). The distinction between the aggregative and avoidance response in blue crabs is critical in determining predator-prey dynamics and community organization in marine soft-bottom benthic communities (Clark 1997). This study was limited in that confinement within the experimental arena negated the opportunity for blue crabs to disperse in response to agonistic encounters with other blue crab predators. Thus, *in situ* behavioral studies are required to quantify aggregative and avoidance responses occurring between blue crabs when they are confronted with hypoxic situations.

Drastic fluctuations in dissolved oxygen concentrations have the ability to influence trophic dynamics between predators and their benthic prey. Moreover, trophic interactions under hypoxic conditions have important short- and long-term implications for energy flow within estuarine ecosystems. This study suggests that the initiation of moderate hypoxia from normoxic regimes has an inhibitory effect on individual blue crab foraging efficiency. The increased tolerance of infaunal clam prey to low oxygen conditions allows *Mya arenaria* to indirectly utilize moderate hypoxic situations as a refuge from blue crab predation through the maintenance of their deep burial depths. Accordingly, there may be decreased energy flow from clams (secondary producers) to upper trophic levels since stressed crabs do not expend the energy required to excavate and consume deeply buried clams.

Mya arenaria exposed to severe hypoxia require a recovery period on the order of hours or days to reburrow and resume normal activity (Jørgensen 1980, this study). The ability of blue crabs to avoid severe hypoxic regions, however, eliminates their need for a recovery time from oxygen stress before feeding can commence (Nestlerode & Diaz 1998). Blue crabs may be able to quickly move into affected areas as soon as oxygen levels are tolerable and take predatory advantage of susceptible *M. arenaria* before clams have time to recover and reburrow in the sediment. The immediate pulse of energy that follows a severe hypoxic

event, due to enhanced feeding by crabs on shallow dwelling clams, may temporarily benefit blue crab predators, but the long-term implication could leave crabs with reduced food resources later in the season or in following prey generations (Diaz & Rosenberg 1995, Nestlerode & Diaz 1998). For example, if significant numbers of prey are removed, either by blue crabs driving *M. arenaria* populations to local extinction (indicative of a type II functional response), or by hypoxia-induced clam mortality, the long-term predation rate and subsequent energy flow from clams to upper trophic levels may be drastically reduced.

Results of studies concentrating on the impact of anthropogenic perturbations on marine and estuarine systems are essential for predicting the effects of changes in water quality on trophic interactions and food web dynamics. This laboratory investigation emphasized the importance of quantifying the main and interactive effects of hypoxia on predator-prey interactions. Because macrobenthic fauna differ in their ability to tolerate and recover from oxygen stress, periods of benthic hypoxia could dramatically influence the structure of marine soft-bottom communities. To fully understand the effect of hypoxia on trophic dynamics, further *in situ* studies are required to examine the (1) recovery rates of prey species to hypoxia, (2) migratory behavior of mobile predators in response to oxygen-stressed areas, and (3) impact of predator aggregative or avoidance responses to predator-prey dynamics.

Acknowledgements. We thank the National Marine Fisheries Service and Duke Marine Laboratory, Beaufort, North Carolina for the allocation of laboratory space and equipment. We are also grateful to J. Rice and T. Wolcott for scientific and editorial reviews which greatly improved this manuscript. Financial support for this project was provided by North Carolina Sea Grant College Program (Grant NA46RC0087), and the National Science Foundation (OCE 97-34472).

LITERATURE CITED

- Abrams P, Hill C, Elmgren R (1990) The functional response of the predatory polychaete, *Harmothoe sarsi*, to the amphipod, *Pontoporeia affinis*. *Oikos* 59:261–269
- Baird D, Ulanowicz RE (1989) The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecol Monogr* 59(4):329–364
- Batterton CV, Cameron JN (1978) Characteristics of resting ventilation and response to hypoxia, hypercapnia, and emersion in the blue crab, *Callinectes sapidus* (Rathbun). *J Exp Zool* 203:403–418
- Blumberg AF, Goodrich DM (1990) Modeling of wind-induced destratification in Chesapeake Bay. *Estuaries* 13:236–249
- Blundon JA, Kennedy VS (1982a) Mechanical and behavioral aspects of blue crab, *Callinectes sapidus* (Rathbun), predation on Chesapeake Bay bivalves. *J Exp Mar Biol Ecol* 65:47–65
- Blundon JA, Kennedy VS (1982b) Refuges for infaunal bivalves from blue crab *Callinectes sapidus* predation in Chesapeake Bay. *J Exp Mar Biol Ecol* 65:67–81
- Boulding EG (1984) Crab-resistant features of shells of burrowing bivalves: decreasing vulnerability by increasing handling time. *J Exp Mar Biol Ecol* 76:201–233
- Breitburg DL (1992) Episodic hypoxia in Chesapeake Bay: interacting effects of recruitment behavior, and physical disturbance. *Ecol Monogr* 62(4):525–546
- Breitburg DL, Steinberg N, DuBeau S, Cooksey C, Houde ED (1994) Effects of low dissolved oxygen on predation on estuarine fish larvae. *Mar Ecol Prog Ser* 104:235–246
- Clark ME (1997) Foraging behavior and intraspecific interactions of blue crabs (*Callinectes sapidus*) in a patchy environment: observation of individuals by ultrasonic telemetry. PhD dissertation, North Carolina State University, Raleigh
- Crowder LB, Cooper WE (1982) Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63:1802–1813
- Das T, Stickle WB (1993) Sensitivity of crabs *Callinectes sapidus* and *C. similis* and the gastropod *Stramonita haestoma* to hypoxia and anoxia. *Mar Ecol Prog Ser* 98:263–274
- Das T, Stickle WB (1994) Detection and avoidance of hypoxic water by juvenile *Callinectes sapidus* and *C. similis*. *Mar Biol* 120:593–600
- Day RW, Quinn GP (1989) Comparisons of treatments after an analysis of variance in ecology. *Ecol Monogr* 59(4):433–463
- DeFur PL, Mangum CP, Reese JE (1990) Respiratory responses of the blue crab *Callinectes sapidus* to long-term hypoxia. *Biol Bull* 178:46–54
- Desprez M, Rybaczynski H, Wilson JG, Ducrotoy JP, Sueur F, Olivieri R, Elkaim B (1992) Biological impact of eutrophication in the Bay of Somme and the induction and impact of anoxia. *Neth J Sea Res* 30:149–159
- Diaz RJ, Rosenberg R (1995) Marine benthic hypoxia: a review of its ecological effects and behavioral responses of benthic macrofauna. *Oceanogr Mar Biol Annu Rev* 33:245–303
- Eggleston DB (1990a) Foraging behavior of the blue crab *Callinectes sapidus*, on juvenile oysters, *Crassostrea virginica*: effects of prey density and size. *Bull Mar Sci* 46:62–82
- Eggleston DB (1990b) Behavioural mechanisms underlying variable functional responses of blue crabs, *Callinectes sapidus* feeding on juvenile oysters, *Crassostrea virginica*. *J Anim Ecol* 59:615–630
- Eggleston DB (1990c) Functional responses of blue crabs *Callinectes sapidus* Rathbun feeding on juvenile oysters *Crassostrea virginica* (Gmelin): effects of predator sex and size, and prey size. *J Exp Mar Biol Ecol* 143:73–90
- Eggleston DB, Lipcius RN, Hines AH (1992) Density-dependent predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. *Mar Ecol Prog Ser* 85:55–68
- Folk RL (1974) Petrology of sedimentary rocks. Hemphills Publishing Co, Austin
- Fox LR (1975) Cannibalism in natural populations. *Annu Rev Ecol Syst* 6:87–106
- Gade G (1983) Energy metabolism of arthropods and mollusks during environmental and functional anaerobiosis. *J Exp Zool* 228:415–429
- Haas LW (1977) The effect of the spring-neap tidal cycle on the vertical salinity structure of the James, York, and Rappahannock rivers, Virginia, U.S.A. *Estuar Coast Mar Sci* 5:485–496

- Hagerman L, Uglow RF (1985) Effects of hypoxia on the respiratory and circulatory regulation of *Nephrops norvegicus*. *Mar Biol* 87:273–278
- Hassell MP (1978) The dynamics of arthropod predator-prey systems. Princeton University Press, Princeton, NJ
- Hassell MP, May RM (1973) Stability in insect host-parasite models. *J Anim Ecol* 42:693–736
- Hassell MP, May RM (1974) Aggregation of predators and insect parasites and its effect on stability. *J Anim Ecol* 43:567–594
- Hines AH, Comtois KL (1985) Vertical distribution of infauna in sediments of a subestuary of Central Chesapeake Bay. *Estuaries* 8:296–304
- Hines AH, Ruiz GM (1995) Temporal variation in juvenile blue crab mortality: nearshore shallows and cannibalism in Chesapeake Bay. *Bull Mar Sci* 57(3):884–901
- Hines AH, Haddon AM, Wiechert LA (1990) Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. *Mar Ecol Prog Ser* 67:105–106
- Holling CS (1959) Some characteristics of simple types of predation and parasitism. *Can Entomol* 91:385–398
- Hurlbert S (1984) Pseudoreplication and the design of ecological field experiments. *Ecol Monogr* 54:187–211
- Jachowski RL (1973) Agonistic behavior of the blue crab, *Callinectes sapidus* Rathbun. *Behaviour* 50:232–253
- Jørgensen BB (1980) Seasonal oxygen depletion in the bottom waters of a Danish fjord and its effect on the benthic community. *Oikos* 34:68–76
- Kapper MA, Stickle WB (1987) Metabolic responses of the estuarine gastropod *Thais haemastoma* to hypoxia. *Physiol Zool* 60:159–173
- Laughlin RA (1982) Feeding habits of the blue crab, *Callinectes sapidus* Rathbun, in the Apalachicola Estuary, Florida. *Bull Mar Sci* 32(4):807–822
- Leber KM (1985) The influence of predatory decapods, refuge, and microhabitat selection on seagrass communities. *Ecology* 66:1951–1964
- Lipcius RN, Hines AH (1986) Variable functional response of a marine predator in dissimilar homogenous microhabitats. *Ecology* 67:361–371
- Loesch H (1960) Sporadic mass shoreward migrations of demersal fish and crustaceans in Mobile Bay, Alabama. *Ecology* 41:292–298
- Mansour RA (1992) Foraging ecology of the blue crab, *Callinectes sapidus* Rathbun, in lower Chesapeake Bay. PhD dissertation, College of William and Mary, Virginia Institute of Marine Science, Gloucester Point
- Mansour RA, Lipcius RN (1991) Density-dependent foraging and mutual interference in blue crabs preying upon infaunal clams. *Mar Ecol Prog Ser* 72:239–246
- Martin TH, Wright RA, Crowder LB (1989) Non-additive impact of blue crabs and spot on their prey assemblages. *Ecology* 70(6):1935–1942
- May EB (1973) Extensive oxygen depletion in Mobile Bay, Alabama. *Limnol Oceanogr* 18(3):353–366
- Menge BA (1983) Components of predation intensity in the low zone of the New England rocky intertidal region. *Oecologia* 58:141–155
- Moksnes PO, Lipcius RN, Pihl L, van Montfrans J (1997) Cannibal-prey dynamics in young juveniles and postlarvae of the blue crab. *J Exp Mar Biol Ecol* 215:157–187
- Murdoch WW, Oaten A (1975) Predation and population stability. *Adv Ecol Res* 9:1–125
- Nestlerode JA, Diaz RJ (1998) Effects of periodic environmental hypoxia on predation of a tethered polychaete, *Glycera americana*: implications for trophic dynamics. *Mar Ecol Prog Ser* 172:185–195
- Nilsson HC, Rosenberg R (1994) Hypoxic response of two marine benthic communities. *Mar Ecol Prog Ser* 115:209–217
- Officer CB, Biggs RB, Taft JL, Cronin LE, Tyler MA, Boynton WR (1984) Chesapeake Bay anoxia: origin, development and significance. *Science* 223:22–27
- Orth RJ, van Montfrans J (1987) Utilization of a seagrass meadow and tidal marsh creek by blue crabs *Callinectes sapidus*. I. Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. *Mar Ecol Prog Ser* 41:283–294
- Paine R (1980) Food webs: interaction strength and community infrastructure. *J Anim Ecol* 49:667–685
- Palmer AR (1979) Fish predation and the evolution of gastropod shell sculpture: experimental and geographical evidence. *Evolution* 33:697–713
- Pihl L, Baden SP, Diaz RJ (1991) Effects of periodic hypoxia on distribution of demersal fish and crustaceans. *Mar Biol* 108:349–360
- Pihl L, Baden SP, Diaz RJ, Schaffner LC (1992) Hypoxia-induced structural changes in the diet of bottom-feeding fish and Crustacea. *Mar Biol* 112:349–361
- Renaud ML (1986) Detecting and avoiding oxygen deficient seawater by brown shrimp, *Penaeus aztecus* (Ives), and white shrimp *Penaeus setiferus* (Linnaeus). *J Exp Mar Biol Ecol* 98:283–292
- Rosenberg R, Hellman B, Johansson B (1991) Hypoxic tolerance of marine benthic fauna. *Mar Ecol Prog Ser* 79:127–131
- Sandberg E (1994) Does short-term oxygen depletion affect predator-prey relationships in zoobenthos? Experiments with the isopod *Saduria entomon*. *Mar Ecol Prog Ser* 103:73–80
- Smith LD, Hines A (1991) The effect of cheliped loss on the blue crab *Callinectes sapidus* Rathbun foraging rate on soft-shelled clams *Mya arenaria* L. *J Exp Mar Biol Ecol* 151:245–256
- Sneddon LU, Taylor AC, Huntingford FA (1999) Metabolic consequences of agonistic behavior: crab fights in declining oxygen tensions. *Anim Behav* 57:353–363
- Stickle WB, Kapper MA, Liu L, Gnaiger E, Wang SY (1989) Metabolic adaptations of several species of crustaceans and molluscs to hypoxia: tolerance and microcalorimetric studies. *Biol Bull* 177:303–312
- Taylor J (1998) United States Geological Survey, North Carolina District: Neuse River water quality plots — dissolved oxygen. BB-MER accessed: July–September 1998; available at <http://sgl1dnrcrlg.er.usgs.gov/>
- Trevallion A (1971) Studies on *Tellina tenuis* Da Costa. III. Aspects of general biology and energy flow. *J Exp Mar Biol Ecol* 7:95–122
- Underwood AJ (1981) Techniques of analysis of variance in experimental marine biology and ecology. *Oceanogr Mar Biol Annu Rev* 19:513–605
- Van Engel WA (1958) The blue crab and its fishery in Chesapeake Bay. *Commer Fish Rev* 20:6–17
- Vermeij GJ (1978) Biogeography and adaptation: patterns of marine life. Harvard University Press, Cambridge, MA
- Virnstein RW (1977) The importance of predation by crabs and fishes on benthic fauna in Chesapeake Bay. *Ecology* 58:1199–1217
- Williams AB (1984) Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, DC
- Wooten JT (1994) Predicting direct and indirect effects: an integrated approach using experiments and path analysis. *Ecology* 75(1):151–165