ABSTRACT

Bell, Geoffrey. Behavioral response of free-ranging blue crabs to episodic hypoxia. (Under the direction of David B. Eggleston)

Hypoxia is increasing in frequency and magnitude in estuarine and coastal systems throughout the world. Very little is known about how periodic hypoxic intrusions into shallow, nearshore habitats influence local migration patterns and trophic dynamics of mobile species such as the blue crab, *Callinectes sapidus*. Studying these behavioral responses is important because hypoxic events may cause direct and indirect mortality of crabs and alter key trophic interactions. Moreover, when crabs recolonize deeper water habitats during the relaxation of hypoxic events they may increase consumption rates by feeding on slow-recovering infaunal prey, thus, altering higher level trophic dynamics. We used 1) biotelemetry techniques with concurrent water quality measurements to monitor movement and feeding responses of free-ranging crabs to spatiotemporal dynamics of water quality, and 2) a trawl survey to determine how periodic hypoxic upwelling events alter distribution and abundance patterns of blue crabs in nearshore habitats. Free-ranging blue crabs were moderately successful at avoiding drops in DO concentrations to hypoxic levels. They generally moved to higher DO concentrations and shallower depths but sometimes remained within hypoxic water for hours. Similarly, from our trawling study, most blue crabs were collected in relatively shallow water during hypoxic upwelling events, however, some crabs remained within near-anoxic mid-depth zones during these events. Although crabs fed within hypoxic water, most did not feed when DO concentrations dropped to or from hypoxic levels. The frequency of feeding did not increase when DO concentrations increased as was originally hypothesized, and is likely due to: 1) crabs foraging on prey other than sessile benthic infauna or 2) the duration of upwelling events which may not last

long enough for infauna to migrate close enough to the sediment surface to be vulnerable to predation from blue crabs. One telemetered crab died after only a few hours of exposure to near-anoxic water during a hypoxic upwelling event. Thus, hypoxic upwelling events can kill even highly mobile species if they are not successful at avoiding rapidly dropping DO levels. Understanding the direct and indirect impacts of episodic hypoxic disturbance on free-ranging blue crabs will help to predict how poor water quality impacts blue crab population and trophic dynamics.

BEHAVIORAL RESPONSE OF FREE-RANGING BLUE CRABS TO EPISODIC HYPOXIA

by

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DEDICATION

To my mother, for her constant support, encouragement, and faith in me.

Thank you

BIOGRAPHY

Geoffrey Weszely Bell was born on July 14, 1973 and raised by his mother in Berkshire Valley, NJ. He spent much of his summers near the water, either at Lake Ariel, PA fishing, swimming, and boating or at the Jersey Shore. Geoffrey graduated from high school in May of 1991 and entered college in the following fall without a major, but soon realized that he was particularly interested in marine science. He accepted a summer internship at the Rutgers University Marine Field Station (RUMFS) in Tuckerton, NJ where he participated in fish ecology fieldwork and developed an independent research project describing the metamorphosis of Conger eel leptocephali. This project later became an undergraduate honors thesis and marked the beginning of his career in marine science. Finally, after three different schools and six short years of college education Geoffrey finally graduated with a BS degree from Rutgers University in 1997. Thereafter, he briefly interned for the National Marine Fisheries Service in Sandy Hook, NJ, studying the cannibalistic behavior of bluefish, before returning to RUMFS to work as a technician.

Geoffrey left his home state in 1999 and moved south to Raleigh, NC to enroll in the Master's degree program in biological oceanography at North Carolina State University. Although his yankee heritage has made it impossible for him to embrace some aspects of southern culture including country music, NASCAR, and the John Boy and Billy morning show, Geoffrey can not resist the allure of pig pickens and sweet tea. Since starting graduate school three years ago he has focused the majority of his time researching the impact of episodic hypoxia on blue crab behavior in the Neuse River. But in his precious free time Geoffrey plays Ultimate Frisbee with the hopes of one day executing the coveted maneuver: "The Greatest".

Geoffrey has decided to continue his research on blue crabs and will enroll in the PhD program at NC State University in the fall of 2002.

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INTRODUCTION

Ecological impacts of hypoxia

Hypoxia (low dissolved oxygen; < 2 mg DO/l) and anoxia (no DO; = 0.0 mg DO/l) are often a consequence of eutrophication and are increasing in frequency, magnitude, and duration in ecosystems throughout the world (Diaz & Rosenberg 1995). Hypoxia is generally a seasonal phenomenon in temperate estuaries, and is usually restricted to deeper water basins, which remain hypoxic for most of the summer. These hypoxic "dead zones" often form in deep channels (Officer et al. 1984), thus reducing the amount of usable habitat for organisms and concentrating them along the shallower banks of rivers where oxygen concentrations are relatively high (Pihl et al. 1991, Breitburg 1992, Lenihan et al. 2001). The spatial and temporal extent of hypoxic water can be very dynamic because wind and tidal forcing periodically cause hypoxic bottom water to upwell onto shallow, nearshore habitat (Breitburg 1990, Sanford et al. 1990, Luettich et al. in press). The impact of hypoxic disturbance on relatively sessile marine benthic macrofaunal communities has been well documented (Arntz 1981, Pearson 1981, Dauer & Ranasinghe 1992, Llanso 1992, Diaz & Rosenberg 1995); however, little is known about the direct and indirect effects of hypoxia on mobile species.

Inferences concerning the effects of hypoxia on movement patterns of mobile species have come from repeated sampling of estuarine habitats using fish traps and periodic trawls (Pihl, et al. 1991, Breitburg 1992, Lenihan & Peterson 1998, Lenihan, et al. 2001). Although these approaches have identified large-scale distribution and abundance patterns of mobile species in relation to water quality, they provide little to no information on fine-scale behavioral responses of free-ranging animals to episodic hypoxia. In this study we

used biotelemetry with concurrent water quality measurements to track the movement and foraging response of free-ranging blue crabs (*Callinectes sapidus*) to episodic hypoxia in a highly eutrophic river. Accurate information on fine-scale behavioral responses of free-ranging animals to hypoxia is essential in estimating the population level and trophic consequences of hypoxia in coastal ecosystems.

Hypoxic events can modify the distribution and abundance patterns of large mobile fish and some crustaceans. In general, mobile organisms emigrate from areas of hypoxic or anoxic water to shallow refuge habitats where DO concentrations are higher and reinvade previously hypoxic deeper water after DO concentrations improve (Pihl, et al. 1991, Breitburg 1992, Lenihan, et al. 2001). For example, certain species of fish [e.g. pinfish (*Lagodon rhomboides*), silver perch (*Bairdiella chrysoura*), and toadfish (*Opsanus tau*)] associated with oyster reefs in the Neuse River, NC migrated from relatively deep reefs exposed to hypoxia/anoxia to shallower refuge reefs where DO concentrations were higher (Lenihan, et al. 2001). Moreover, some demersal fish [e.g. spot (*Leiostomus xanthurus*) and croaker (*Micrpogonius undulatus*)] and crustaceans [e.g. blue crabs and mantis shrimp(*Squilla empusa*)] also migrate to shallower water when deeper habitats become hypoxic or anoxic (Pihl et al. 1991). The migratory response of mobile fish and crustaceans to hypoxia concentrates large numbers of these organisms within shallow refuge habitats, thereby, causing crowding (Loesch 1960) and intensifying biological interactions (Lenihan et al. 2001).

Hypoxia can affect other ecological processes such as predator-prey dynamics if predators and prey have varying physiological and behavioral responses to hypoxia. For example, exposure to hypoxia often forces infaunal species to emerge from the substrate to

the sediment surface thereby increasing their vulnerability to predators able to exploit hypoxic areas (Pihl et al. 1992, Diaz & Rosenberg 1995, Taylor & Eggleston 2000). Immediately following a hypoxic intrusion, some bottom-feeding fish (e.g. spot and croaker), as well as mantis shrimp, were able to feed on additional benthic prey species (e.g. deep burrowing polychaetes and anemones) and larger prey that were not previously available to them during normoxic conditions (Pihl, et al. 1992). Because the physiological and behavioral response of marine predators and prey to low DO varies to such a large extent (Breitburg 1992) hypoxic events can lead to either increased or decreased prey capture, thereby affecting a predator's functional response (Taylor & Eggleston 2000) and food web dynamics within marine and estuarine communities (Breitburg et al. 1994).

Effects of hypoxia on blue crab behavior

The blue crab is an important estuarine benthic predator that often occurs in estuarine areas prone to hypoxia (e.g. Chesapeake Bay, USA, Mobile Bay, Alabama, USA). Predation by blue crabs determines distribution and abundance patterns of certain species of thin-shelled infaunal clams within Chesapeake Bay (Lipcius & Hines 1986, Eggleston et al. 1992, Seitz et al. 2001). Laboratory studies suggest that blue crabs are capable of detecting and avoiding hypoxic water (Das & Stickle 1994). Moreover, field trawling studies suggest that blue crabs do not occupy hypoxic water (Pihl, et al. 1991, Eby 2001). During periodic hypoxic intrusions into nearshore habitats adult blue crabs are hypothesized to migrate from deeper water habitats where DO concentrations are lowest towards shallower water where DO concentrations are higher (Pihl, et al. 1991). When hypoxic water recedes from shallower nearshore areas blue crabs presumably emigrate back towards deeper water where they may take advantage of infaunal prey that are slow to recover from hypoxic stress (Pihl,

et al. 1991). Our study tested three hypotheses concerning blue crab movement response to episodic hypoxia: 1) free-ranging crabs would avoid hypoxia and move to shallower water when DO dropped to hypoxic concentrations (i.e., upwelling), 2) free-ranging crabs would move to deeper water when DO increased to normoxic concentrations (i.e. relaxation events), and 3) the greatest relative abundance of blue crabs would occur in shallow water during upwelling events as the local population migrates to shallow refuge habitats.

Infaunal clams that remain within hypoxic or anoxic areas respond to low DO stress by migrating vertically to the sediment surface (Diaz & Rosenberg 1995, Taylor & Eggleston 2000, Tallqvist 2001). These clams attain a partial refuge from predation by foraging blue crabs because of their ability to bury deep within the sediment (Blundon & Kennedy 1982, Lipcius & Hines 1986, Eggleston, et al. 1992). When hypoxia forces clams to reside closer to the sediment surface they are more vulnerable to predation from blue crabs (Taylor & Eggleston 2000). A recent series of laboratory studies suggest that blue crabs may increase their consumption rate of infaunal clams immediately after periods of hypoxic stress because clams lose their depth refuge when they decrease their sediment burial depth and increase their siphon extension when exposed to hypoxia (Taylor & Eggleston 2000). Thus, periodic hypoxia can alter the trophic dynamics between a key benthic predator and its prey. We tested two hypotheses concerning the feeding response free-ranging blue crabs to episodic hypoxia: 1) free-ranging crabs would decrease their feeding frequency, relative to their overall frequency of feeding, when DO dropped to hypoxic concentrations (i.e., upwelling), and 2) free-ranging crabs would increase their feeding frequency, relative to their overall frequency of feeding, when they moved to deeper water after DO increased to normoxic concentrations (i.e., relaxation events).

Water quality dynamics in the Neuse River Estuary

The Neuse River Estuary (NRE) is a highly eutrophic (Bricker et al. 1999), shallow, mesohaline, estuary located in eastern North Carolina, USA that experiences seasonal bottom water hypoxia during summer months. The development of summer-time hypoxia is due to the increased oxygen demand of bottom water and strong vertical density stratification of the water column that restricts the supply of oxygen to benthic habitats. Hypoxic bottom water develops most frequently in the deeper upstream portions of the Neuse R. and commonly covers 20% to 40% of the bottom (Eby 2001). The extent of hypoxic bottom water in the NRE can cover 100 km^2 and is thought to be an important cause of the near complete mortality of infaunal clams (*Macoma sp*.) in some areas (Buzzelli et al. 2002). Clams are an important benthic prey for many demersal fish and crustaceans in this system; poor water quality and the loss of a food source in these areas has presumably restricted fish and crabs to shallower nearshore habitats (Eby 2001, McClellan 2001).

Water circulation patterns in the NRE are controlled primarily by winds (Luettich, et al. in press). The prevailing regional northeast-southwest wind pattern during the summer is aligned cross-channel for the section of the Neuse R. located between Minnesott Beach and New Bern (Fig. 1). Changes in wind direction often produce relatively rapid upwelling of bottom waters during summer months (Sweet 2000, Luettich et al. in press). Winds from the northeast cause upwelling on the northern shore, while winds from the southwest cause upwelling on the southern shore (Fig. 1). Upwelled hypoxic water may remain in shallow habitats from hours to days, depending on wind patterns, until it recedes back to the deep basins of the river (relaxation of hypoxia). These expansion and relaxation events are frequent during the summer and fall (pers. obs.). Thus, this section of the Neuse River is

ideal for measuring the behavioral response of mobile animals, such as free ranging blue crabs, to periodic hypoxic events.

The objectives of this study were to: 1) describe fine spatial (< 1 km) and temporal (hourly) scale dynamics of periodic hypoxic upwelling events, 2) identify movement and feeding responses of individual, free-ranging blue crabs to dynamic hypoxia, 3) determine how periodic hypoxic upwelling events alter local blue crab distribution and abundance patterns, and 4) describe diel patterns of crab movement and feeding behavior.

METHODS

Study Site

The study was conducted along the northern shore of the Neuse River, just upriver of Minnesott Beach, and near the mouth of Beards Creek (Fig. 1). The study area was approximately 2.15 km^2 with a mean depth of 2.4 m and summer salinities ranging from 10-17 psu. Sediment is mostly sand in nearshore habitats and mud in the deeper mid sections of the river (McClellan 2001). There is no tidal signal (Luettich, et al. in press) or submerged aquatic vegetation within the study site.

Water Quality

We measured discrete DO, temperature, and salinity with two YSI model 6920 Sondes that were deployed seven times during July – September, 2001 (Appendix 1). Sondes were deployed separately at two fixed locations (shallow and mid-depth) for 3-5 days and were randomly assigned to a location prior to each deployment. The mid-depth location was a US Coast Guard channel marker (1.9 – 2.4 m deep) and the shallow station was a private resident's dock (0.5 – 1.1 m deep). Each Sonde was fastened vertically to pilings with stainless steel hose clamps such that the probes were approximately 10 cm off the sediment

surface. The sondes were programmed to record water temperature, salinity, DO, and depth every 10 min; calculated hourly averages are reported in this paper. After each deployment the sondes were retrieved, cleaned thoroughly, and recalibrated before redeployment.

Fine-scale movement and foraging of free-ranging crabs

Measurements

We used a multichannel biotelemetry system to simultaneously monitor movement and feeding behavior of individual free-ranging blue crabs within the Neuse River. A total of 14 adult, intermolt, male crabs (135-175 mm CW) were outfitted with transmitters (see below) and tracked from July – September of 2001 (n = 8) and 2002 (n = 6) within the Beards Creek study site (Table 1). All telemetered crabs were collected from the study site using crab pots baited with dead fish. After being outfitted with a transmitter (approximately 1 hr of preparation time) each crab was held in a 113 L aquarium for 12-24 hr prior to release to ensure that the crab did not sustain any injuries during the tagging process and that the transmitter was functioning properly. Crabs were tracked continuously for 72-96 hr with occasional interruptions due to severe weather or boat problems. Tracking was terminated early (< 42 hr) for four crabs because of either transmitter failure, death of the crab, crabs were observed mating (consequently not feeding), or the crab had not moved or taken a bite in over 12 hr. Four observers, working in 8-20 hr shifts of two, tracked the movement and feeding behavior of individual crabs aboard a 6 m boat using a Sonotronics USR-5W ultrasonic receiver and unidirectional hydrophone.

Mark-recapture data from this area suggests that adult blue crab migration patterns are primarily downriver (E.G. Johnson pers. comm.), therefore, telemetered crabs were released at upriver locations within the study site (near the mouth of Beards Creek) to reduce the risk

of crabs leaving the study site. Crabs were released during daylight and nighttime hours at locations that varied in DO concentration (3-8 mg/l) and depth (1–4m). Crabs were relocated every 40 - 60 minutes, or earlier if it appeared that they would move out of listening range. As soon as a crab was relocated, we measured initial surface and bottom water temperature, DO, and salinity with a YSI Model 85 handheld instrument, and recorded the date, time, depth (to the nearest 0.3 m), and the boat's location using differential GPS. The time interval between successive relocations was used to record feeding behavior data sent by the transmitter (see below). Final bottom water quality measurements were recorded prior to moving to the next relocation point so that changes in DO could be calculated by subtracting final from initial measurements (see below).

The biotelemetry system was adapted from previous designs used to observe behavior of free-ranging blue crabs (Wolcott & Hines 1989, Clark et al. 1999a, Clark et al. 1999b, Clark et al. 2000). The electronic circuitry of the transmitter was packaged in pliable electrical sleeving (shrink tubing) which was molded to conform to the dorsal surface of the carapace (to reduce drag), and filled with mineral oil to couple sound between the transducer and water. The packaged transmitter was bonded to the dorsal surface of the carapace using cyanoacrylate glue and fastened with metal wire to the lateral spines (see Fig. 2 in Clark et al. 1999a). Transmitters were approximately 85 mm long x 16 mm in diameter and weighed about 24 g in air. Previous biotelemetry studies have shown that transmitters of similar design do not interfere with common blue crab behaviors such as feeding, agonism, and mating (Nye 1989, Wolcott & Hines 1989, Wolcott & Hines 1990, Clark et al. 1999b, Clark, et al. 2000).

Transmitters monitored consumption rates of free-ranging crabs by measuring biopotentials of the mandible adductor muscle with two stainless steel electrodes inserted into the muscle; activity of this muscle is a definitive indicator of feeding (Wolcott & Hines 1989). The location on the carapace where the two electrodes were inserted through the exoskeleton was first cleaned with a paper towel to dry the area and remove algal growth. We used a Dremel tool to drill two holes (diameter ≈ 0.5 mm) partially through the exoskeleton at the origin of the mandible adductor muscle. The electrodes were inserted through the holes and into the muscle, then covered with cyanoacrylate glue and a rubber membrane (dental dam) to hold the wires in place and waterproof the insertion site. Transmitters recorded individual bites, stored this information in three, 10 minute time bins (t, t-1, t-2), and used binary encoded pulses of ~ 75 kHz (low pitched tone = 0, low-high pitched tone = 1) to transmit feeding data. The data were transmitted in a repeating loop of: 1) the number of bites in the current 10 minute period (time bin *t*), which was updated every 1.5 min and reset every 10 minutes, 2) the number of bites taken in the ten minutes prior to time bin *t* (time bin *t*-1), updated every 10 minutes, and 3) the number of bites taken in the ten minutes prior to time bin *t*-1 (time bin *t*-2), updated every 10 min. Crabs were considered to be feeding when the number of bites within a time bin exceeded three because nonfeeding blue crabs can take up to three bites over a 10 min period (Wolcott & Hines 1989).

Analyses

In all statistical tests significance was determined using an alpha level of 0.05 and the assumption of normality was tested with a Kolmogorov-Smirnov (K-S) test. In instances where data were not normal for paired sample t-tests, a nonparametric Wilcoxon rank test

was used instead. For one sample t-tests, when transformations were not successful at achieving normality we used the raw data because 1) normal probability plots did not suggest severe skewness in most cases and 2) t-tests are robust to deviations from normality (Zar 1984). The assumption of homogeneity of variance was tested with a Levene Median test for 1-way ANOVA and regression analyses, and with an F_{max} test for the split-plot ANOVA. In instances where the data were either non-normal or the variances heterogeneous, the log transformation was generally successful in achieving model assumptions. In instances where transformations were unsuccessful hypotheses were rejected at a lower alpha level (0.01) (Underwood 1981).

To assess how free-ranging blue crabs responded to increasing or decreasing DO, the change in DO observed at each crab relocation point (i.e., final – initial DO measurements; see measurements section) was grouped into six DO scenarios. DO could 1) decrease from hypoxia to more severe hypoxia (H↓H), 2) decrease from normoxia to lower normoxic concentrations (N↓N), or 3) decrease from normoxia to hypoxia (N↓H). DO could also 4) increase from hypoxia to less severe hypoxia (H↑H), 5) increase from normoxia to greater normoxic concentrations (N↑N), or 6) increase from hypoxia to normoxia (H↑N). Upon encountering a specific DO scenario, crabs could: 1) move to higher or lower DO (DO change), 2) move to deeper or shallower depths (depth change), and 3) move to hypoxic or normoxic water (new location DO). We measured the three movement responses of crabs (DO change, depth change, and new location DO) to changes in DO by subtracting final DO and depth measurements at each location from the initial DO and depth measurements at each subsequent location.

In instances where crabs exhibited a movement response to changing DO (e.g. move to different depths and DO concentrations), which was ~ 60% of the time depending on the DO scenario, we hypothesized that crabs would respond to decreasing DO concentrations by moving to shallower, more oxygenated, normoxic water, and that crabs would respond to increasing DO concentrations by moving to deeper, less oxygenated, normoxic water. We used separate one sample t-tests to test the overall null hypothesis that the proportion of times crabs responded to a given DO scenario was greater or less than (1-sided test) a random response (50%). For example, although we expected crabs to respond to decreasing DO at each relocation by moving to relatively shallow water at the subsequent relocation, we tested the null response that the proportion of times that crabs moved to shallower water when DO decreased was greater than 50%. The proportion of times that each crab exhibited the hypothesized movement response to each of the three DO scenarios was calculated and used as a single replicate in each t-test. Thus each crab was a replicate and sample sizes varied from two to eleven among tests because some crabs did not experience all six DO scenarios (e.g., H↑N) or display a measurable response (e.g. no depth change).

The analysis of blue crab feeding response to DO change was similar to that of the movement analysis. For each crab location, DO change was calculated and classified into one of the six DO scenarios (as described previously), then the number of bites were averaged across 10 minute time bins (see biotelemetry measurements section) that corresponded to a period of no more than 60 minutes after each initial crab relocation time. Each location was then classified as either nonfeeding or feeding (mean number of bites per 10 min > 3; Wolcott & Hines 1989). For each crab and within each DO scenario we calculated the percentage of relocations where feeding occurred. For each crab we also

calculated the overall percent of locations where feeding occurred (irrespective of DO scenario). We hypothesized that 1) when DO concentrations decreased to or increased from hypoxic levels feeding frequency would drop below the overall frequency, 2) when DO increased from normoxia to normoxia, feeding frequency would increase relative to overall feeding frequency, and 3) blue crabs that moved to deeper water after experiencing an increase in DO would feed more often than their overall feeding frequency. We used separate, paired t-tests to test the null hypothesis that the difference between the percent feeding occurrence for a given DO scenario and the overall percent feeding occurrence would be greater or less than zero. For example, although we expected crabs to feed more frequently when DO increased from normoxia to greater normoxic concentrations, we tested the null response that the difference between the percent feeding occurrence during the N↑N DO scenario and the overall percent feeding occurrence was greater than zero. Some of the observations (~ 15%) used to calculate the overall percent feeding occurrence for each crab were also used to calculate each crab's percent feeding occurrence during all six DO scenarios. Therefore, comparisons between these two groups are not independent and paired t-test results are more conservative (less likely to find significance) than if the groups were independent.

To determine if free-ranging crabs displayed diel patterns in speed, feeding occurrence, and feeding rate, relocation points and feeding measurements within 10-minute bins were classified according to: 1) day (1 hr after sunrise to 1hr before sunset), 2) night (1 hr after sunset to 1 hr before sunrise), and 3) twilight (1 hr before and after sunrise and sunset). Speed was defined as distance traveled per hour (m/h), and quantified using ArcView 3.1 software. We computed distances between sequential relocations and then divided each

distance by the time between relocations to obtain an estimate of speed. For each crab we calculated: 1) the mean speed, 2) the percent of 10 minute time bins where feeding (> 3 bites) occurred, 3) the mean feeding rate (mean number of feeding bites / 10 min) during each of the three diel periods, and 4) the overall mean for all three responses. We used a paired-sample t-test to determine whether each response differed significantly between diel period means and the overall means (n = 14).

Distribution and abundance patterns of the local crab population

Measurements

During 2001, we conducted a trawl survey to quantify distribution and abundance patterns of the local blue crab population in our study site relative to water quality. This component of the study allowed us to 1) determine how episodic hypoxia changes the distribution and abundance patterns of the local blue crab population, and 2) make qualitative comparisons between these distribution and abundance patterns and fine-scale behavioral responses of individual crabs to episodic hypoxia. The study site was divided into three depth strata (Fig. 1) based on the occurrence of hypoxia within each stratum. The deep stratum (3.0 – 4.6 m deep; $\bar{x}$ = 3.7m) was always hypoxic if hypoxia was present, the mid-depth stratum (1.7 – 3.0 m deep; $\bar{x}$ = 2.2m) only experienced hypoxia during upwelling events, and the shallow stratum (0.9 – 1.7 m deep; $\bar{x}$ = 1.3 m) was rarely hypoxic. Thus, the shallow depth stratum should represent a refuge for crabs avoiding hypoxia during upwelling events.

Trawl collections were made on 11 days from August - September 2001. During each collection date all 3 depth strata were sampled using a 3.9m otter trawl (15 mm mesh

wings and body, 5 mm mesh cod end) that was towed behind a 5.5 m boat at speeds of 3.6 – 4.8 kn ($\bar{x}$ = 4.4 kn) for a period of 7 to 15 minutes. Blue crab abundance was standardized for tow time by calculating the number of crabs collected per 10 min trawl. Trawling was only conducted during daylight hours and trawls were always towed into the wind. Within each depth stratum, two to three subsample trawls were collected along each of three randomly generated transects. After the completion of a trawl, water quality data (temperature, salinity, and DO) were recorded at four randomly chosen points along each of the three depth-discrete transects using a hand-held YSI Model 85 Environmental Monitoring System. Water depth was also recorded for each transect. For each subsample trawl, all crabs were identified, enumerated, and measured to the nearest 1 mm carapace width (CW; to tips of lateral spines).

Collections were timed to coincide with three different hypoxic conditions. "Normoxia" (n=3), was characterized by DO > 2 mg/l at all depth strata. This condition typically occurred after wind-driven mixing events reoxygenated deeper bottom waters. "Moderate hypoxia" (n = 5) occurred when hypoxia was present only in the deepest depth stratum. This condition was the most common condition because deeper sections of the river were hypoxic for most of the summer (see study site section). "Strong hypoxia" (n = 3) occurred when hypoxia was present in the deep and middle depth strata. This condition denotes periods of hypoxic upwelling. Every sample date was assigned to one of these three hypoxic conditions, thus making each date a replicate

Analyses

Catch rates of blue crabs from each trawl were standardized to number of crabs collected per 10 minutes, which served as a relative measure of abundance. The mean

relative abundance of crabs declined significantly from August to September ($\bar{x}$ = 12.90 crabs/10 min. trawl and 2.85 crabs/10 min. trawl, respectively; 1-way ANOVA, df=1; F = 5.46; p = 0.04), and mean carapace width increased significantly from August to September ($\bar{x}$ = 113.1 mm and 143.5 mm, respectively; F = 31.0; p < 0.001). These monthly differences confounded the interpretation of depth-discrete abundance and size distribution patterns under different DO scenarios over time. Therefore, we first normalized abundance and size data by dividing each replicate measure of crab abundance and carapace width by its corresponding monthly mean and used these normalized values as response variables in the split-plot and linear regression models described below.

To examine how water quality affected the distribution and abundance patterns of the local blue crab population we used a combination of analyses that used categorical (ANOVA) and continuous (regression) explanatory variables. We used a split-plot mixed-model ANOVA to examine the interactive effects of depth stratum and hypoxic condition on the relative abundance and size distribution of crabs. In a split-plot design all levels of the split-plot factor (in this case, depth) are sampled within a single replicate (date) of the whole plot factor (hypoxic condition). Pairwise contrasts tested differences in normalized abundance and carapace width among depth strata within a particular hypoxic condition and within a depth stratum across different hypoxic conditions. We also used simple linear, nonlinear, and principal components regressions analyses to determine the functional relationship between normalized catch rates of blue crabs and abiotic factors (DO, temperature, salinity, and depth). Normalized abundances were first fit to least squares nonlinear (3 parameter sigmoidal curves) and linear regression models for each of the

abiotic variables separately. The nonlinear model explained significantly more variability than the linear model for DO (F-ratio test; F = 4.42; num df = 1; den df = 30; p = 0.04) but not for salinity or depth (F-ratio test; p > 0.05). To incorporate all abiotic factors into a multiple regression framework, principal components analysis (PCA) was used to create new uncorrelated independent variables, each of which was a linear combination of the original colinear variables. These new variables replaced the original explanatory variables (DO, temperature, salinity, and depth) in a regression analysis of the functional relationship between environmental factors and adjusted catch rates.

RESULTS

Water quality

During July – September 2001 at the mid-depth station (1.9 – 2.4 m depth) we recorded a total of 32 hypoxic events throughout the 35 day monitoring period. These hypoxic events were highly variable in terms of mean DO concentration ($\bar{x}$ = 1.1 mgDO/l; range = 0.27 – 1.94 mg/l) and duration ($\bar{x}$ = 5.6 hr; range = 1 – 30 hr) (Appendix 1). The onset of hypoxic events was characterized by a rapid drop in DO (as fast as 5.81 mgDO/l/hr) and temperature, as well as a rapid increase in salinity (Fig. 2). The increase in salinity and decrease in DO and temperature indicates that mid-depth hypoxia is associated with upwelled bottom water from the deep basins of the Neuse R. (Sweet 2000). Relaxation of these hypoxic events resulted in a relatively slow rate of change back to pre-event levels of DO, temperature and salinity (Fig. 2). Hypoxia was detected at the shallow station (0.5 – 1.1 m depth) on only two of the 32 mid-depth hypoxic events (9/6/01, 0700 h. and 9/11/01, 0600 h.). During these two events, the shallow station remained hypoxic for three and five hours,

respectively, whereas the mid-depth station remained hypoxic for 11 and 30 hours, respectively (Appendix 1). The proportion of total hourly observations that were hypoxic for the mid and shallow stations were 23% and 1%, respectively. Thus, although hypoxic events were highly variable in space and time there were numerous episodic hypoxic events with which to assess crab behavioral response to dynamic water quality, particularly at mid-depths.

The percentage of hourly, mid-depth station observations within a month that were hypoxic increased from July to September. The mean duration of hypoxic events also increased throughout the field season; hypoxic events lasted longer and were more variable in September than other months. The mean DO concentration per hypoxic event was lowest during August ($\bar{x}$ = 0.80 ± 0.10) and highest in July ($\bar{x}$ = 1.58 ± 0.13) and September ($\bar{x}$ = 1.37 ± 0.16).

Fine-scale movement and foraging of free-ranging crabs

Movement

Telemetered crabs exhibited two general types of movement patterns: 1) slow meandering within relatively small areas, and 2) relatively fast directional movements that covered large distances (Appendix 2). Meandering lasted for hours to days whereas rapid movements lasted only a few hours. Individual crabs were highly variable with respect to mean speed ($\bar{x}$ = 49.1 m/h ± 6.7; range = 13.91 – 93.24 m/h) and maximum distance traveled in one hour (48.09 – 606.82 m) (Table 1). Although crabs were relocated across all depths within the study site, they occurred more frequently in shallow areas (< 1.7m) than mid (1.7 – 3.0 m) or deep locations (3.0 – 4.6m). For example, the percent of crab

relocations that occurred in deep, mid, and shallow areas were 18%, 24%, and 58%, respectively when averaged across crabs. During all 14, 4-day tracking periods, crabs never moved to the other side of the river (southwest) but had a tendency to move downstream (Appendix 2).

Crab encounters with hypoxia were rare along the nearshore zone of the Neuse River (Appendix 2). For each crab, the percent of crab observations that were hypoxic ranged from 0 – 17.3% and averaged 6.3% across all crabs. Crab encounters with hypoxia occurred at all depth strata but were most common at mid depths. For example, the percent of observations that were hypoxic for shallow (0.9 – 1.7 m deep), mid (1.7 – 3.0 m deep) and deep (3.0 – 4.6 m deep) strata averaged 6.1%, 13%, and 7% across crabs, respectively. Exposure of individual crabs to hypoxia lasted from less than one hour to six hours.

As hypothesized, crabs generally moved to higher DO concentrations, shallower depths, and normoxic water after encountering a decrease in DO; however, whether these movement responses were significantly different from random depended upon the particular DO scenario (Fig. 3A). For example, when DO concentrations decreased, crabs moved to higher DO levels significantly more often than random irrespective of the DO scenario (one sample t-tests; N↓H: $t = 8.10$, $df = 8$, $p < 0.001$; N↓N: $t = 3.9$, $df = 10$, $p = 0.003$; H↓H: 100% moved, no statistics necessary) (Fig. 3A). The proportion of time that crabs moved to shallower water, however, was significantly greater than 50% only when DO concentrations decreased from normoxia to hypoxia (i.e. hypoxic upwelling; Fig. 3A) ($t = 9.5$ $df = 8$, $p < 0.001$). The proportion of times that crabs moved to normoxic water was significantly greater than 50% ($t = 26.5$, $df = 10$, $p < 0.001$) only when DO concentrations dropped from normoxia to lower normoxic concentrations (N↓N) (Fig. 3A).

The movement response of crabs to increases in DO also depended upon whether initial and final DO measurements were hypoxic or normoxic. For example, the proportion of times that crabs moved to lower DO and deeper water was significantly greater than 50% (one sample t-test, $t = 2.08$, $df = 10$, $p = 0.03$) only when DO increased from normoxia to greater normoxic concentrations (Fig. 3B). Crabs moved to normoxic waters a significantly greater proportion of times than random when DO increased from hypoxia to normoxia ($t = 4.0$, $df = 4$, $p = 0.016$) and from normoxia to greater normoxic concentrations ($t = 4.3$, $df = 10$, $p = 0.001$; Fig. 3B). Finally, when DO increased from hypoxia to less severe hypoxia the proportion of times that crabs moved to deeper depths and normoxic water was significantly less than random (0% moved to deeper water, no statistics necessary; $t = -3$, $df = 3$, $p = 0.03$; Fig. 3B).

Foraging

Crabs usually fed continuously for periods of 20 – 40 minutes; these feeding bouts could occasionally persist for up to 2 hours (Fig. 4). The duration of nonfeeding periods was highly variable, averaging ~ 1 hour and ranging from 10 min to 26 hours (Fig. 5). The number of feeding bouts per day ranged from 0 to 8. Feeding rate (number of bites per 10 min time bin) was highly variable among crabs ($\bar{x} = 37.9 \pm 3.9$; range = 16.9 – 71; Table 2). Within the 10 minute time bins, the number of bites occasionally reached or exceeded the capacity of the transmitter's "bite counter" (255). The proportion of time crabs spent feeding was also highly variable. For each crab, the proportion of time spent feeding ranged from 3.4% - 50% and averaged 20% across all crabs (Table 1). Crabs fed more frequently when in shallow areas relative to mid and deep depths. For example, crabs spent an average

of 23% of their time feeding when in shallow areas as compared to 16% and 10% in mid and deep depths respectively, therefore

Crabs fed in hypoxic water where DO concentrations were as low as 1.01 mgDO/l. The percent feeding occurrence at hypoxic relocations was highly variable among crabs, ranging from 0% to 75% and averaging 26.9% ± 9.3 across crabs. In comparison, percent feeding occurrence at normoxic relocations was less variable; ranging from 3.3% to 66.7% and averaging 30.3% ± 4.19 across crabs. Therefore, crabs fed only somewhat less frequently when in hypoxic than normoxic water. Only under certain DO scenarios did crabs change how often they fed relative to their overall frequency of feeding. For example, when DO decreased the mean percent feeding occurrence was not significantly different from the overall mean for any of the three DO scenarios (paired t-tests; H↓H: $t = 0.68$, $df = 4$, $p = 0.53$; N↓H: $t = 0.39$, $df = 8$, $p = 0.71$; N↓N: $t = -0.78$. $df = 10$, $p = 0.45$) (Fig. 5A). Crabs did feed significantly less frequently than their overall mean percent feeding occurrence when DO increased from hypoxia to normoxia (H↑N: $t = 2.49$, $df = 4$, $p = 0.03$) and from hypoxia to less severe hypoxia (H↑H: $t = 2.88$, $df = 3$, $p = 0.03$) (Fig. 5B). Crabs that moved to deeper water after experiencing an increase in DO, however, did not feed more frequently than their overall feeding occurrence ($t = 0.03$; $df = 10$; $p = 0.98$).

Diel patterns in movement and feeding

Telemetered crabs exhibited differences in speed and feeding rate among certain diel periods; no diel patterns were detected for feeding occurrence. Mean speed was greatest during daytime hours ($\bar{x}$ = 57.3 m/h ± 7.4) and was significantly different than the overall mean speed (paired sample t-test; $t = -2.47$; $df = 13$; $p = 0.03$) (Fig. 6A). There were no

significant differences between the overall mean percent feeding occurrence and the mean percent feeding occurrence for any of the diel periods (day: $t = 0.11$, $df = 13$, $p = 0.92$; night: $t = -0.11$ $df = 13$, $p = 0.91$; twilight: $t = -1.15$, $df = 13$, $p = 0.27$) (Fig. 6B). Mean feeding rate was lowest during twilight hours ($\bar{x} = 25.4$ bites per 10 min $\pm$ 5.14) and was significantly different than the overall mean feeding rate ($t = 3.25$; $df = 13$; $p = 0.01$) (Fig. 6C).

Distribution and abundance patterns of the local crab population

Blue crab depth distribution and abundance patterns differed according to the spatial extent of hypoxic bottom water within the study site. Although there was a significant main effect of depth on crab abundance (split-plot ANOVA; $F = 16.37$; $df = 2$; $p < 0.001$), the interaction term between depth and hypoxic condition was also significant ($F = 2.92$; $df = 4$; $p = 0.05$). Although crabs were collected in the deep stratum during normoxic conditions, they were absent from this stratum during moderate and strong hypoxia (Fig. 7). At the mid-depth stratum, crabs were collected during all three hypoxic conditions, however, normalized abundances during strong hypoxic conditions (i.e. upwelling) were significantly less than normalized abundance during normoxia (split-plot ANOVA; $F = 10$; $df = 16$; $p = 0.003$) and moderate hypoxia ($F = 7.4$; $df = 16$; $p = 0.008$) (Fig. 7). Crabs were collected in the shallow depth stratum during all hypoxic conditions; there were no significant differences in normalized abundance between these three conditions (all $p > 0.05$; Fig. 7). Under strong hypoxic conditions normalized crab abundance was significantly greater in shallow than deep ($F = 16.1$; $df = 16$; $p < 0.001$) and mid-depth strata ($F = 14$; $df = 16$; $p = 0.001$) (Fig. 7), suggesting that crabs relocate to shallow water habitats during hypoxic upwelling events.

Blue crab abundance varied significantly according to most of the measured abiotic variables. Normalized crab abundance decreased significantly with both depth (least squares regression; $F = 24.5$; $df = 1$; $p < 0.001$) and salinity ($F = 19.9$; $df = 1$; $p < 0.001$) (Fig. 8). The significant ($F = 17.0$; $df = 2$; $p < 0.001$), positive sigmoidal curve for oxygen suggests a threshold at about 2 mgDO/l, below which crabs are not collected and above which normalized abundance is greater but unchanging with increasing DO (Fig. 8). There was no significant trend in crab abundance with temperature ($F = 1.7$; $df = 1$; $p = 0.21$), therefore, it was not included as a response variable in the principal components regression analysis. PCA could not remove collinearity among the remaining abiotic variables (DO, salinity, and depth), therefore, we did not do the principal components regression.

The size distribution of blue crabs was not affected by depth or the spatial extent of hypoxic bottom water in the study site. For example, there were no significant differences in normalized carapace width among depth strata (split-plot ANOVA; $df = 2$; $F = 0.03$; $p = 0.97$) or hypoxic condition ($df = 2$; $F = 2.33$; $p = 0.16$). Moreover, none of the pairwise contrasts among and within depth strata and hypoxic conditions were significant. When crabs were present in trawls, carapace width ranged from 40 mm CW to 175 mm CW at shallow, mid, and deep depths during most hypoxic conditions (Table 3), thus, smaller individuals were not restricted to shallow, nearshore habitats, as expected.

DISCUSSION

Results from our study of free-ranging blue crab movement response to dynamic hypoxia indicate that: 1) during hypoxic upwelling events blue crabs migrate to shallow refuge habitats, 2) during hypoxic upwelling events blue crabs are successful at migrating to normoxic water 60% of the time, and 3) blue crabs may reinvade deeper water habitats

during relaxation events. When DO decreased to hypoxic concentrations free-ranging crabs avoided hypoxia by moving to shallower, more oxygenated water, but were only moderately successful at moving to normoxic water (60% of the time), and could remain within hypoxic water for hours. Similarly, the relative abundance of blue crabs was significantly greater in the shallow than the mid-depth and deep stratum during hypoxic upwelling events, however, some crabs remained within near-anoxic, mid-depth zones during these events. Conversely, blue crabs responded to increases in DO to normoxic concentrations by moving to deeper water. This general inshore-offshore migratory response of free-ranging crabs to hypoxia is consistent with other studies of blue crabs and fish that occur in other nearshore areas prone to periodic intrusions of hypoxia (Pihl, et al. 1991, Breitburg 1992, Lenihan & Peterson 1998, Lenihan, et al. 2001).

Our results from the study of free-ranging blue crab feeding response to DO changes suggest that the proportion of time blue crabs spend feeding during hypoxic upwelling and relaxation events is no different than their overall feeding frequency. Although free-ranging crabs did not reduce their feeding frequency when DO decreased to hypoxic concentrations (i.e. upwelling events), as was hypothesized, most crabs did not feed during this DO scenario. Also free-ranging crabs did not increase their frequency of feeding when DO increased to normoxic concentrations (i.e. relaxation events) or when they moved to deeper water after experiencing an increase in DO. These results are somewhat inconsistent with prior laboratory studies of blue crab feeding response to hypoxia (Taylor & Eggleston 2000) and did not support our original hypotheses.

Some of the crabs we either tracked or collected in our trawl survey occurred in hypoxic and near-anoxic water, despite not being found in hypoxic water during nearby and quasi-

concurrent trawl surveys in the NRE (Eby 2001). The inconsistent results between this study and those of Eby (2001) might be explained by either differences in 1) gear efficiency within hypoxic water, or 2) the spatial and temporal scales of sampling. The mongoose trawl used in Eby's (2001) study is of similar design to our otter trawl, making gear efficiency an unlikely explanation. Because blue crabs respond to short-lived hypoxic upwelling events on hourly time scales, it is more likely that Eby's (2001) biweekly, system-wide trawl survey (large spatial and temporal scales) rarely sampled nearshore habitats during such events. Thus, collections of crabs in hypoxic water would be improbable because sampling did not occur at the same temporal and spatial scales as hypoxic upwelling events. The contrasting results between these two studies supports the theory that ecological processes are scale-dependent and that sampling outside space and time scales relevant to the ecological process of interest may reduce our ability to detect ecological patterns associated with these processes (Wiens 1989).

Behavioral response of crabs to hypoxic upwelling events

Free-ranging blue crabs responded to decreases in DO from normoxic to hypoxic levels (N↓H) by migrating towards shallower (~ 95% of the time), more oxygenated water (~ 90% of the time). This DO scenario best represents the behavioral response of free-ranging blue crabs to episodic hypoxia because 1) most hypoxic relocations of free-ranging crabs (79%) occurred in nearshore habitats (mid and shallow depth strata) and 2) drops in DO to hypoxic levels within these nearshore habitats occurred only during upwelling events. The local blue crab population showed a similar response to hypoxia; approximately 90% of crabs, sampled from our trawl survey, were collected in the shallow stratum (< 1 m depth) during hypoxic upwelling events. Relative crab abundance, however, was not significantly greater in the

shallow stratum during upwelling events when compared to normoxic and moderate hypoxic conditions, as was originally hypothesized. If a substantial number of crabs that remained within the hypoxic mid-depth stratum during hypoxic upwelling events were inaccessible to our trawl (i.e., reduced gear efficiency if crabs bury within the sediment during exposure to hypoxia) then this may explain our nonsignificant results. Alternatively, a considerable portion of the local crab population could have moved to shallower water that was not accessible by trawl. These shallow depths were rarely hypoxic and always had higher DO concentrations than mid-depth areas during upwelling events. Thus, shallow habitats represent suitable refuge habitat from episodic hypoxia.

Free-ranging blue crabs, however, were only moderately successful at avoiding hypoxia given that 1) the proportion of time that crabs moved to normoxic water after DO decreased to hypoxia (N↓H and H↓H) was not different than a random response, and 2) crabs could remain in hypoxic water for up to six hours. Moreover, one of the four free-ranging crabs that encountered near-anoxic DO concentrations (< 0.5 mgDO/l) during an upwelling event died. Although this crab migrated to the shallow depth stratum, DO concentrations were nearly anoxic even in areas less than 0.6 m deep. This crab died within a few hours of exposure to these lethal DO concentrations, which suggests that hypoxic upwelling events can kill even highly mobile organisms. Three mechanisms that may explain the occurrence of some crabs in hypoxic/anoxic water are that blue crabs: 1) may be able to tolerate or acclimate to low DO concentrations, 2) are unable to effectively avoid rapidly dropping DO, or 3) actively choose not to move to shallower water based on costs associated with refuge habitats. Since blue crabs experience physiological stress when exposed to hypoxia and show no obvious acclimation (i.e., increase in oxygen extraction efficiency) to low DO

concentrations (Batterton & Cameron 1978, Lowery & Tate 1986), the occurrence of free-ranging crabs in hypoxic water is more likely explained by the latter two hypotheses.

Laboratory results indicate that although juvenile blue crabs can detect low DO concentrations they move sporadically and do not exhibit clear avoidance behavior when exposed to hypoxia or anoxia (Lowery & Tate 1986, Das & Stickle 1994). Therefore, DO concentrations may drop so rapidly (as fast as 5.81 mgDO/l/hr) during hypoxic upwelling events that escaping crabs may not have enough time to find normoxic water before becoming trapped in hypoxic areas. Alternatively, some crabs may be forced into hypoxic areas during upwelling events by increased agonistic interactions, and/or predation risk in shallower refuge habitats. Hypoxic intrusions concentrate mobile organisms in shallower refuge habitats (Pihl, et al. 1991, Breitburg 1992, Lenihan, et al. 2001). When blue crabs occur at high densities they increase agonistic behavior which can cause carapace wounds, loss of appendages, and increased mortality rates of conspecifics (Mansour & Lipcius 1991, Taylor & Eggleston 2000). Anecdotal evidence from our trawling study and results from other field studies within the Neuse River Estuary help to support this hypothesis. For example, the only time that crabs occurred in hypoxic water during hypoxic upwelling events was when relative crab abundance within the study site was at its second highest point. Furthermore, demersal fish (spot and croaker) and blue crabs may reduce their avoidance threshold for DO as the spatial extent of hypoxia increases (Eby 2001). For example, during periods when hypoxic bottom water covered large areas in the NRE blue crabs and some fish were collected at lower DO concentrations than they were during periods when hypoxic bottom water was less extensive (Eby 2001). Eby (2001) suggested

that as the amount of oxygenated refuge area shrinks increased crowding of organisms into shallow refuge habitats forces some individuals to occupy low DO habitats.

Feeding by free-ranging crabs was not significantly reduced when DO dropped from normoxia to hypoxia (N↓H) (i.e., upwelling). This feeding pattern, however, does not necessarily suggest that crabs do not decrease their feeding frequency during hypoxic upwelling events. For example, five of the nine crabs that were included in the analysis of the N↓H DO scenario did not feed at all. Furthermore, one of the other crabs fed 100% of the time during this scenario but did not encounter hypoxia by means of an upwelling event, thus, this skewed our results toward an increase in feeding frequency. The remaining three crabs that fed during this DO scenario were able to successfully move to normoxic water. Blue crabs, therefore, are more likely to stop feeding as they migrate towards shallower water in response to rapidly dropping DO concentrations during upwelling events; those crabs that successfully reach normoxic refuge habitats can feed in these areas.

Behavioral response of crabs to relaxation of hypoxia

Free-ranging blue crabs may respond to the relaxation of hypoxic events by moving to deeper, less oxygenated water. Although the H↑N DO scenario best approximates changes in DO that occur during relaxation events physiological stress associated with exposure to hypoxia causes crabs to remain quiescent for hours after DO increases to normoxic levels (Lowery & Tate 1986). This may explain why most free-ranging crabs in this study that were exposed to hypoxia for more than a few hours did not move or feed until a few hours after exposure to normoxic concentrations. The large variability about the mean movement response for this DO scenario, however, suggests that at least some crabs, trapped in hypoxic water prior to relaxation events, do move to deeper water. Conversely, the

proportion of times that crabs moved to deeper water when DO increased from normoxia to greater normoxic concentrations (N↑N) was significantly greater than random. This result suggests that crabs, not exposed to hypoxia during upwelling events, will migrate back to deeper water during subsequent relaxation of hypoxia.

Free-ranging crabs showed no indication of increasing the frequency with which they fed during relaxation events as compared to their overall feeding frequency given that neither of our original hypotheses was supported. For example, feeding frequency, during scenarios when DO increased to normoxia (N↑N and H↑N), was not significantly greater than the overall frequency of feeding. Moreover, crabs that moved to deeper water after experiencing an increase in DO did not feed more frequently than their overall feeding frequency. Although Taylor and Eggleston (2001) suggest that blue crab feeding rates may be reduced during relaxation events because of mutual interference, two other alternative hypotheses may better explain these surprising results: 1) hypoxic upwelling events within our study site did not last long enough for infaunal prey to significantly reduce their burial depth, and 2) alternative prey (e.g., dead fish) may be a more significant source of food than infaunal clams for blue crabs in the NRE.

For example, blue crabs in laboratory studies, increased consumption rates of clams during simulated relaxation events only after clams had been allowed to vertically migrate in response to hypoxia for 24 hours (Taylor & Eggleston 2000). Moreover, nearshore habitats in Chesapeake Bay were hypoxic for several days before demersal fish could exploit infaunal prey that had reduced their burial depth in response to hypoxia (Diaz et al. 1992, Pihl, et al. 1992). Conversely, hypoxic upwelling events, within our study site, usually lasted about five hours and rarely persisted for more than 10 hrs. Therefore, hypoxic

upwelling events may not have lasted long enough for infauna to migrate vertically to shallow depths that make them more susceptible to predation by blue crabs. Alternatively, recent evidence suggests that 1) the biomass of infaunal clams in the NRE are insufficient to support the blue crab population, and 2) trawler by-catch may be an important food source for blue crabs in this area (G. Johnson, UNC-CH pers. com.). Furthermore, our free-ranging crabs consistently fed in areas that were devoid of infaunal prey and their consumption rates were not an increasing function of *in situ* clam density (Bell, Eggleston, & Wolcott unpubl. data). These results are inconsistent with previous blue crab functional response studies (Lipcius & Hines 1986, Mansour and Lipcius 1991, Eggleston et. al. 1992). Moreover, dead fish were collected in our trawl collections and free-ranging crabs fed in areas where dead and dying Menhadden (*Brevoortia tyrannus*) from fish kills were present. These results suggest that blue crabs may rely on alternative sources of prey, such as dead fish from trawler by-catch or fish kills, in the NRE. If infaunal clams are not a significant source of food for blue crabs this may explain why free-ranging blue crabs did not increase their feeding frequency during relaxation of hypoxia.

Understanding the direct and indirect impacts of episodic hypoxic disturbance on free-ranging blue crabs will help to predict how poor water quality impacts blue crab population and trophic dynamics. The behavioral responses of free-ranging crabs to changing water quality measured in this study can be used to parameterize movement and feeding rules in spatially explicit individual based models that predict crab population responses to varying water quality. These models are powerful tools for fisheries managers interested in predicting whether episodic hypoxia has population-level consequences and the impact of water quality on trophic dynamics. To fully understand the consequences of episodic

hypoxic disturbance on blue crabs, future field studies are needed to examine: 1) mortality rates of organisms within refuge habitats during upwelling events, 2) mortality rates of organisms trapped in hypoxic water during upwelling events, and 3) the significance of alternative prey in the diet of blue crabs.

LITERATURE CITED

Arntz, W. E. (1981). Zonation and dynamics of macrobenthos biomass in an area stressed by oxygen deficiency. In: Barrett, G. W. and Rosenberg, R. (eds.) Stress Effects on Natural Ecosystems. Wiley, New York, p. 215-225

Batterton, C. V. and Cameron, J. N. (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

Blundon, J. A. and Kennedy, V. S. (1982). Refuges for infaunal bivalves from the blue crab, Callinectes sapidus (Rathbun), predation in Chesapeake Bay. J. Exp. Mar. Biol. Ecol. 65, 67-81

Breitburg, D. L. (1990). Near-shore hypoxia in the Chesapeake Bay: patterns and relationships among physical factors. Est. Coast. Shelf Sci. 30, 593-609

Breitburg, D. L. (1992). Episodic hypoxia in Chesapeake Bay: interacting effects of recruitment, behavior, and physical disturbance. Ecol. Monogr. 62, 525-546

Breitburg, D. L., Steinberg, N. D., DuBeau, S., Cooksey, C. and Houde, E. D. (1994). Effects of low dissolved oxygen on predation on estuarine fish larvae. Mar. Ecol. Prog. Ser. 104, 235-246

Bricker, S. B., Clement, C. G., Pirhalla, D. E., Orlando, S. P. and Farrow, D. R. G. (1999). National Estuarine Eutrophication Assessment: effects of nutrient enrichment in the nation's estuaries. NOAA, National Ocean Service, Special Programs Office and the National Centers for Coastal Ocean Science. Silver Spring, MD: p. 67

Buzzelli, C. P., Luettich, R. A., Jr., Powers, S. P., Peterson, C. H., McNinch, J. E., Pinckney, J. L. and Paerl, H. W. (2002). Estimating the spatial extent of bottom-water hypoxia and habitat degradation in a shallow estuary. Mar. Ecol. Prog. Ser. 230, 103-112

Clark, M. E., Wolcott, T. G., Wolcott, D. L. and Hines, A. H. (1999a). Intraspecific interference among foraging blue crabs *Callinectes sapidus*: interactive effects of predator density and prey patch distribution. Mar. Ecol. Prog. Ser. 178, 69-78

Clark, M. E., Wolcott, T. G., Wolcott, D. L. and Hines, A. H. (1999b). Foraging and agonistic activity co-occur in free-ranging blue crabs (*Callinectes sapidus*): observation of animals by ultrasonic telemetry. J. Exp. Mar. Biol. Ecol. 233, 143-160

Clark, M. E., Wolcott, T. G., Wolcott, D. L. and Hines, A. H. (2000). Foraging behavior of an estuarine predator, the blue crab *Callinectes sapidus* in a patchy environment. Ecography 23, 21-31

Das, T. and Stickle, W. B. (1993). Sensitivity of crabs *Callinectes sapidus* and *C. similis* and the gastropod *Stramonita haemastoma* to hypoxia and anoxia. Mar. Ecol. Prog. Ser. 98, 263-274

Das, T. and Stickle, W. B. (1994). Detection and avoidance of hypoxic water by juvenile *Callinectes sapidus* and *C. similis*. Mar. Biol. 120, 593-600

Dauer, D. M. and Ranasinghe, J. A. (1992). Effects of low dissolved oxygen events on the macrobenthos of the lower Chesapeake Bay. Estuaries 15, 384-391

Diaz, R. J., Neubauer, R. J., Schaffner, L. C., Pihl, L. and Baden, S. P. (1992). Continuous monitoring of dissolved oxygen in an estuary experiencing periodic hypoxia and the effect of hypoxia on macrobenthos and fish. Science of the Total Environment suppl. 1992, 1055-1068

Diaz, R. J. and Rosenberg, R. (1995). Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. Oceanogr. Mar. Biol. Ann. Rev. 33, 245-303

Eby, L. (2001). Response of a fish community to frequent and infrequent disturbances in an estuarine ecosystem. Ph.D. dissertation, Duke University, Durham

Eggleston, D. B., Lipcius, R. N. and Hines, A. H. (1992). Density-dependent predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. Mar. Ecol. Prog. Ser. 85, 55-68

Hines, A. H. and Ruiz, G. M. (1995). Temporal variation in juvenile blue crab mortality: nearshore shallows and cannibalism in Chesapeake Bay. Bull. Mar. Sci. 57, 884-901

Lenihan, H. S. and Peterson, C. H. (1998). How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. Ecol. Appl. 8, 128-140

Lenihan, H. S., Peterson, C. H., Byers, J. E., Grabowski, J. H., Thayer, G. W. and Colby, D. R. (2001). Cascading of habitat degradation: oyster reefs invaded by refuge fishes escaping stress. Ecol. Appl. 11, 764-782

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

Llanso, R. J. (1992). Effects of hypoxia on estuarine benthos: the lower Rappahannock River (Chesapeake Bay), a case study. Est. Coast. Shelf Sci. 35, 491-515

Loesch, H. (1960). Sporadic mass shoreward migrations of demersal fish and crustaceans in Mobile Bay, Alabama. Ecology 41, 292-298

Lowery, T. A. and Tate, L. G. (1986). Effect of hypoxia on hemolymph lactate and behavior of the blue crab *Callinectes sapidus* Rathbun in the laboratory and field. Comp. Biochem. Physiol. 85A, 689-692

Luettich, R. A., Jr., Reynolds-Fleming, J. V., McNinch, J. E. and Buzzelli, C. P. (in press). Circulation characteristics of the Neuse River Estuary, North Carolina. Estuaries

Mansour, R. A. and Lipcius, R. N. (1991). Density-dependent foraging and mutual interference in blue crabs preying upon infaunal clams. Mar. Ecol. Prog. Ser. 72, 239-246

McClellan, C. M. (2001). Mesoscale habitat use of juvenile southern flounder, Paralichthys lethostigma: responses to environmental variability. M.S. thesis, Duke University, Durham

Nye, L. A. (1989). Variation in feeding behavior of blue crabs (*Callinectes sapidus* Rathbun) measured by ultrasonic biotelemetry. M.S. thesis, North Carolina State University, Raleigh

Officer, C. B., Biggs, R. B., Taft, J. L., Cronin, L. E., Tyler, M. A. and Boynton, W. R. (1984). Chesapeake Bay anoxia: origin, development, and significance. Science 223, 22-27

Pearson, T. H. (1981). Stress and catastrophe in marine benthic ecosystems. In: Barrett, G. W. and Rosenberg, R. (eds.) Stress Effects on Natural Ecosystems. Wiley, New York, p. 201-214

Pihl, L., Baden, S. P. and Diaz, R. J. (1991). Effects of periodic hypoxia on distribution of demersal fish and crustaceans. Mar. Biol. 108, 349-360

Pihl, L., Baden, S. P., Diaz, R. J. and Schaffner, L. C. (1992). Hypoxia-induced structural changes in the diet of bottom-feeding fish and crustacea. Mar. Biol. 112, 349-361

Sanford, L. P., Sellner, K. G. and Breitburg, D. L. (1990). Covariability of dissolved oxygen with physical processes in the summertime Chesapeake Bay. J. Mar. Res. 48, 567-590

Seitz, R. D., Lipcius, R. N., Hines, A. H. and Eggleston, D. B. (2001). Density-dependent predation, habitat variation, and the persistence of marine bivalve prey. Ecology 82, 2435-2451

Sweet, W.V. (2000). The response of the halocline to physical forcing in the Neuse River Estuary. M.S. thesis, North Carolina State University, Raleigh

Tallqvist, M. (2001). Burrowing behaviour of the Baltic clam *Macoma balthica*: effects of sediment type, hypoxia and predator presence. Mar. Ecol. Prog. Ser. 212, 183-191

Taylor, D. L. and Eggleston, D. B. (2000). 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*. Mar. Ecol. Prog. Ser. 196, 221-237

Underwood, A. J. (1981). Techniques of analysis of variance in experimental marine biology and ecology. Oceanogr. Mar. Biol. Ann. Rev. 19, 513-605

Wiens, J. A. (1989). Spatial scaling in ecology. Functional ecology 3, 385-397

Wolcott, T. G. and Hines, A. H. (1989). Ultrasonic biotelemetry of muscle activity from free-ranging marine animals: a new method for studying foraging by blue crabs (*Callinectes sapidus*). Biol. Bull. 176, 50-56

Wolcott, T. G. and Hines, A. H. (1990). Ultrasonic telemetry of small-scale movements and microhabitat selection by molting blue crabs (*Callinectes sapidus*). Bull. Mar. Sci. 46, 83-94

Table 1. Tracking information for individual crabs including release date, carapace width (CW), and duration of tracking events. Also reported are data on individual movement rates (m/h) including the mean (± standard error) and range, the percent of 10 min time bins where feeding (> 3 bites) occurred, and feeding rate (mean # feeding bites / 10 min). Averages of movement rate, percent feeding occurrence, and feeding rate across crabs is also provided. Exact carapace width measurements for "Dale Earnhardt" and "George Dickel" were not available but were approximately the same size as other crabs.

Release Date	Crab ID	CW (mm)	Tracking Duration (h:min)	Mean movement rate (m/h) ± SE	Range (m/h)	Percent Feeding Occurrence	Feeding Rate (# bites/10 min)
7/24/00	Billy Bob	154	69:11	47.2 ± 6.4	0 – 202.4	24.1	23.1 ± 2.3
7/31/00	Billy Rae	149	60:07	13.9 ± 2.7	0 – 81.3	26.0	41.8 ± 10.7
8/7/00	Joe Bob	151	73:53	81.2 ± 12.3	0 – 334.1	14.4	32.2 ± 8.9
8/13/00	Cletus Lee	138	95:20	22.8 ± 3.9	0 – 243.5	3.4	22.1 ± 7.7
8/24/00	Clawed	135	85:41	51.6 ± 9.2	0 – 606.8	22.1	16.9 ± 2.6
9/11/00	Uncle Jessie	152	95:55	17.2 ± 3.8	0 – 232.2	7.1	61.4 ± 12.3
9/19/00	Boss Hog	140	73:37	46.2 ± 8.5	0 – 346.2	11.4	42.5 ± 6.9
9/24/00	Jethro	148	71:37	42.9 ± 6.7	0 – 347.8	10.9	71.0 ± 8.6
7/22/01	Dale Earnhardt	~ 150	67:22	29.6 ± 4.4	0 – 119.4	28.9	37.9 ± 5.4
8/8/01	George Dickel	~ 150	30:21	81.9 ± 17.1	0 – 271.3	50.0	39.7 ± 6.7
8/11/01	John Steinbeck	162	42:32	57.0 ± 13.3	0 – 291.0	14.0	36.4 ± 9.3
8/17/01	Crab Pitt	175	29:09	67.9 ± 12.7	0 – 353.7	15.2	24.6 ± 4.9
9/5/01	Cooter	170	26:34	93.2 ± 18.8	2.65 – 382.4	39.1	39.4 ± 8.2
9/8/01	Feeds Alot	159	38:12	35.0 ± 6.1	0 – 48.1	15.4	41.4 ± 10.3
Averages:				49.1 ± 6.7		20.1%	37.9 ± 3.9

Table 2. Depth-specific size distribution of blue crabs collected during different hypoxic conditions. The mean and range of blue crab carapace width measurements (mm) (± standard error) are reported in each cell; sample sizes (in parentheses) are also included. Size distribution data were not available (N/A) in the deep stratum during moderate and strong hypoxia because no crabs were collected.

		Depth Stratum		
		Shallow	Mid-depth	Deep
Hypoxic Condition	Normoxia	133.3 ± 8.6 (19) 39 – 181	107.1 ± 4.7 (58) 45 – 166	109.2 ± 9.6 (22) 40 – 170
	Moderate Hypoxia	132.7 ± 4.4 (58) 52 – 176	110.6 ± 4.29 (64) 42 – 186	N/A
	Strong Hypoxia	112.9 ± 5.6 (57) 34 – 175	153.3 ± 13.4 (4) 124 – 184	N/A

Fig. 1. Map of study site in the Neuse River, NC, USA. Panel A is the coastal region of North Carolina. Panel B is the Neuse River Basin. Panel C is the study site showing the three depth strata used in the trawling study (Shallow, Mid-depth, and Deep); asterisks denote the locations of the two in situ water quality instruments.

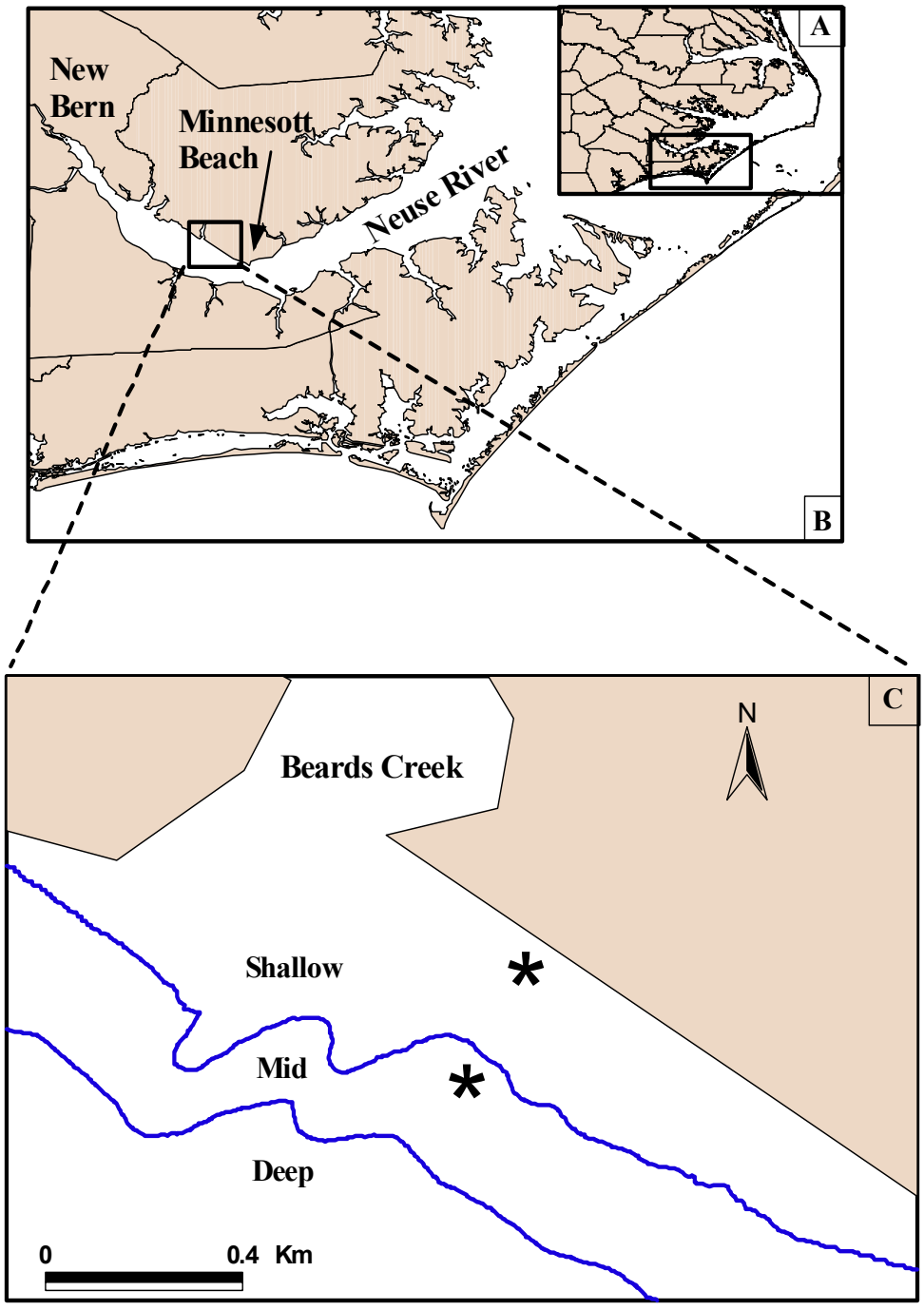

A
New
Bern
Minnesott
Beach
Neuse River
B
C
N
Beards Creek
Shallow
Mid
Deep
0
0.4 Km

Fig. 2. Time series of hourly DO (o), temperature (Δ), and salinity (+) measurements from (A) the mid-depth sonde (1.9 – 2.4 m deep) and (B) shallow sonde (0.5 – 1.1 m deep) from 9/5/01 to 9/10/01. Horizontal solid line represents the threshold DO for hypoxia (2 mgDO/l).

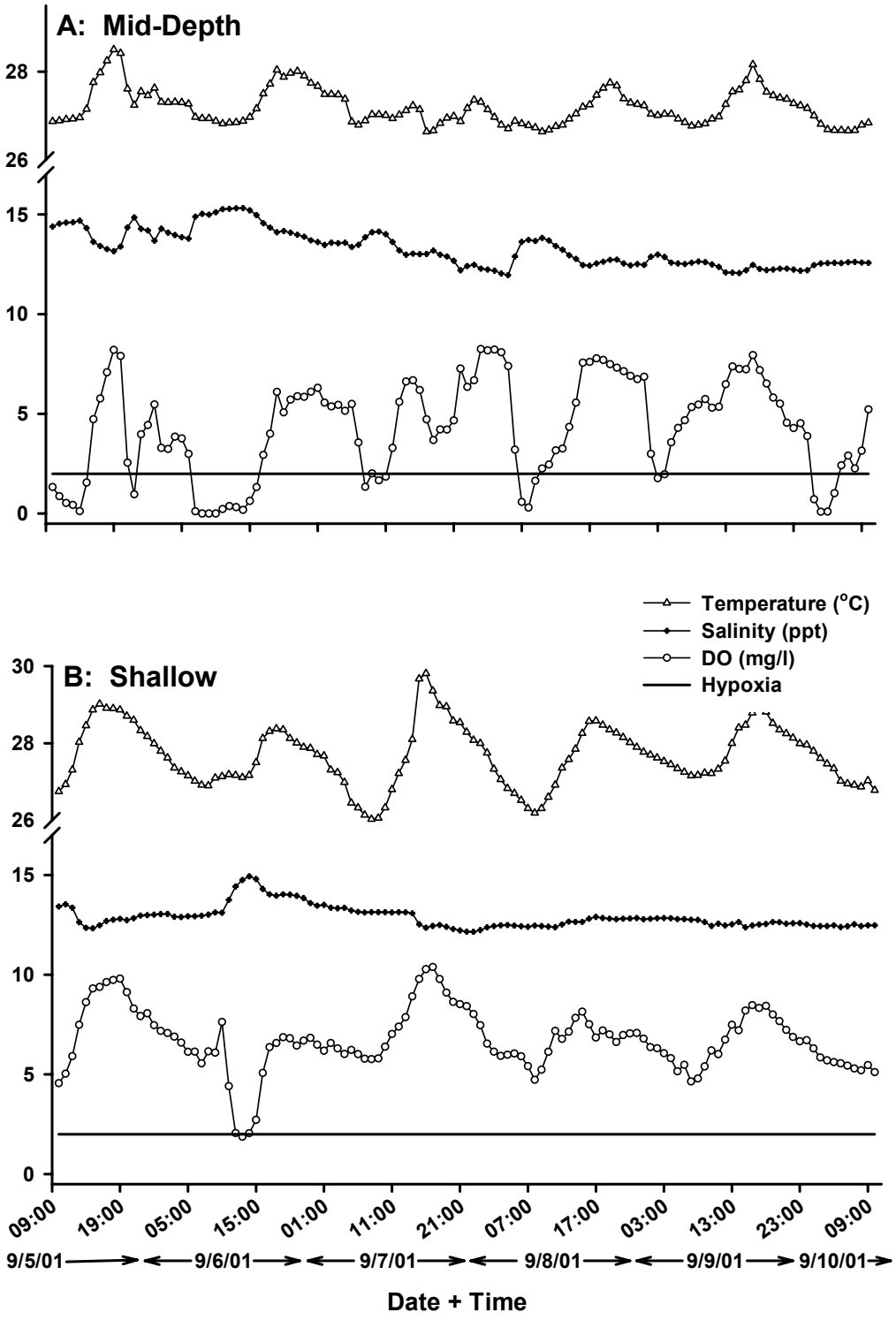

A: Mid-Depth
28
26
15
10
5
0
Temperature (°C)
Salinity (ppt)
DO (mg/l)
Hypoxia
B: Shallow
30
28
26
15
10
5
0
09:00
19:00
05:00
15:00
01:00
11:00
21:00
07:00
17:00
03:00
13:00
23:00
09:00
9/5/01
9/6/01
9/7/01
9/8/01
9/9/01
9/10/01
Date + Time

Fig. 3. Movement response of telemetered crabs to (A) decreasing and (B) increasing DO concentrations. (A) shows the mean percentage of encounters (± SE) in which crabs moved to higher DO (closed bars), shallower depths (hashed bars), and normoxic water (open bars) after DO decreased. (B) shows the mean percentage of encounters (± SE) in which crabs moved to lower DO (closed bars), deeper depths (hashed bars), and normoxic water (open bars) after DO increased. The three response types are grouped along the x-axis based on whether DO changed from/to hypoxia/normoxia (arrow indicates direction of change). Asterisks indicate significant differences from expected random behavior (50%) as tested with one sample t-tests.

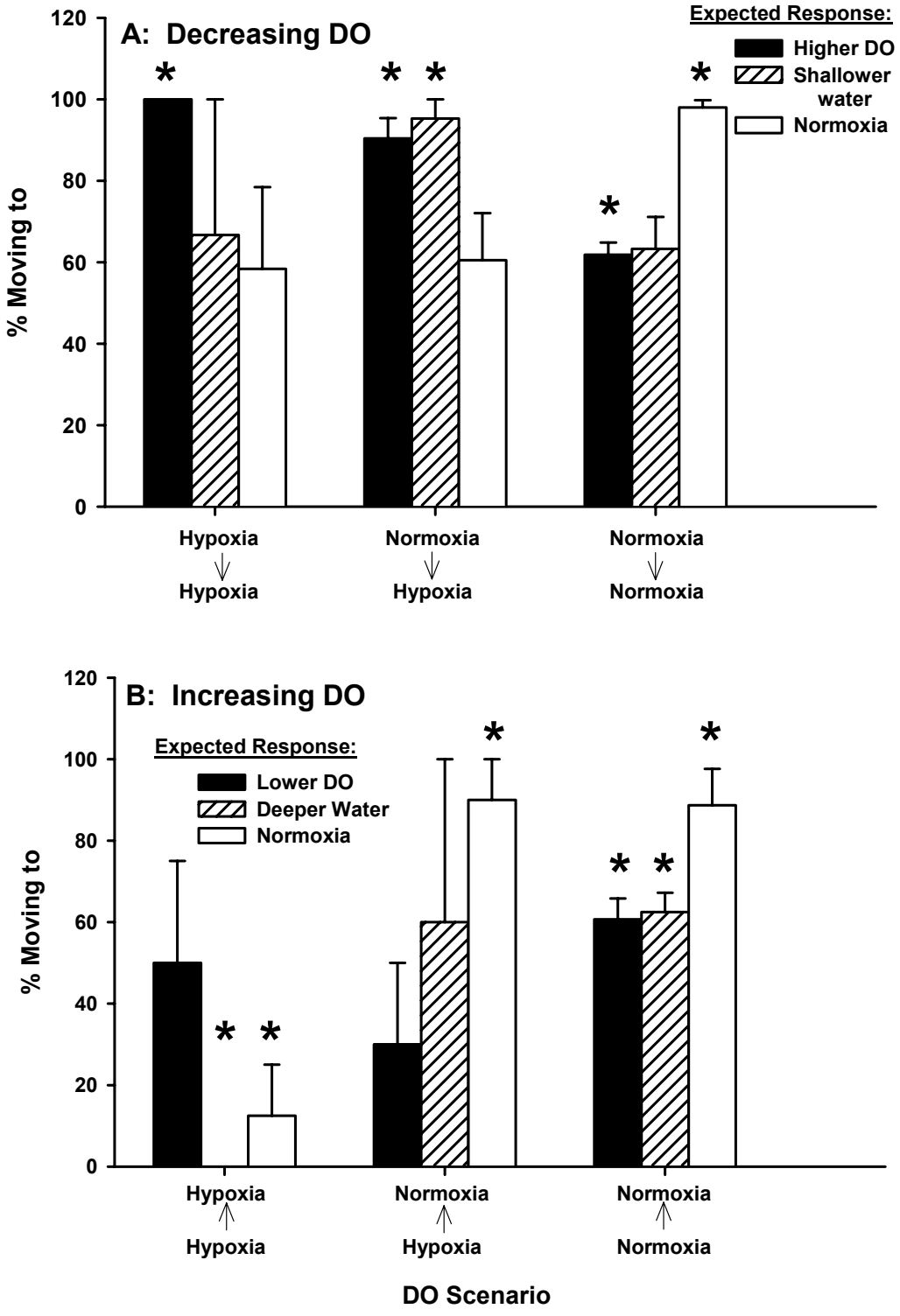

A: Decreasing DO
Expected Response:
Higher DO
Shallower water
Normoxia
% Moving to
120
100
80
60
40
20
0
Hypoxia
Hypoxia
Normoxia
Hypoxia
Normoxia
Normoxia
B: Increasing DO
Expected Response:
Lower DO
Deeper Water
Normoxia
% Moving to
Hypoxia
Hypoxia
Normoxia
Hypoxia
Normoxia
Normoxia
DO Scenario

Fig. 4. Complete feeding record (3 – 4 days) for two telemetered crabs ("Boss Hog" and "Jethro"). Each bar extending up from the x-axis represents the number of feeding bites (> 3) taken during a single 10 min time bin. Bars extending below the x-axis represent nonfeeding time bins where crabs took 0 – 3 bites. Zero values are periods of missing data.

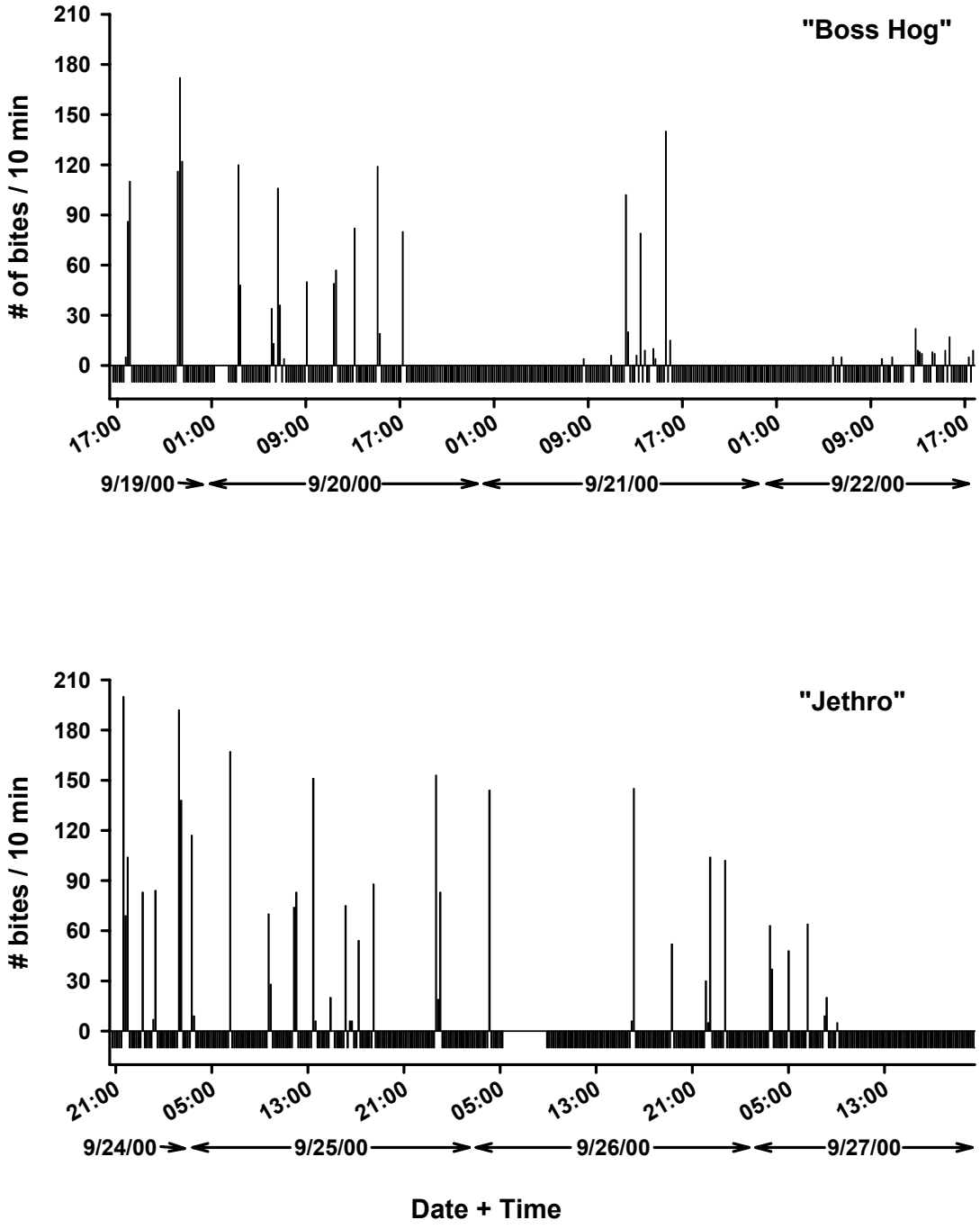
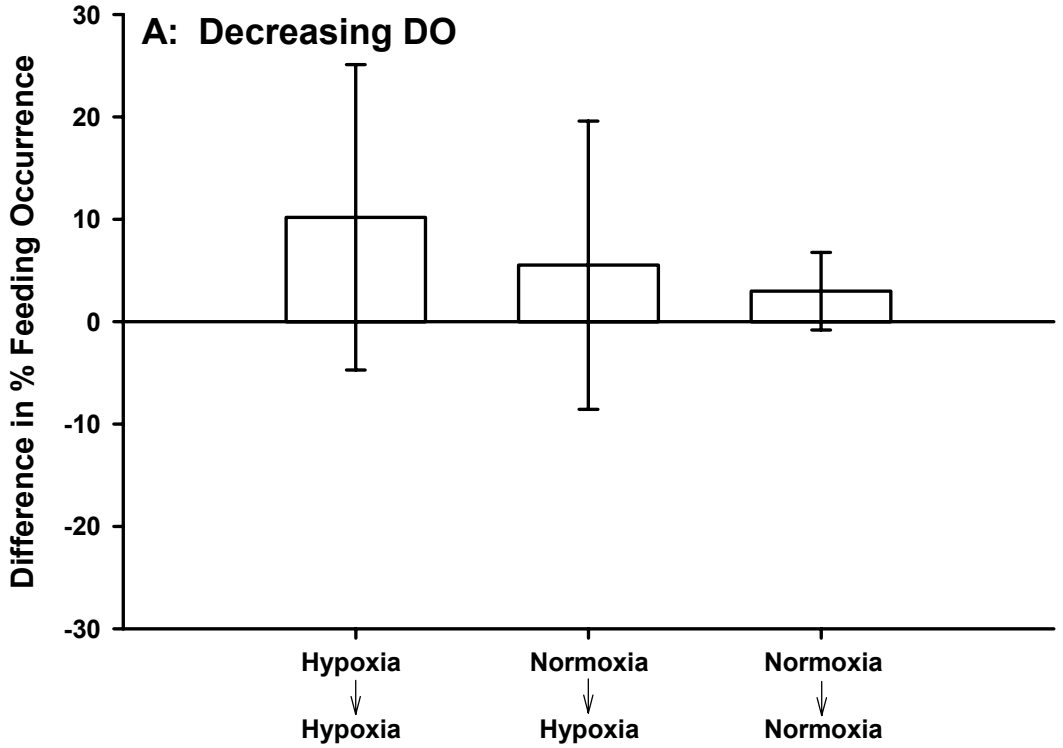

"Boss Hog"
# of bites / 10 min
210
180
150
120
90
60
30
0
17:00
01:00
09:00
17:00
01:00
09:00
17:00
01:00
09:00
17:00
9/19/00
9/20/00
9/21/00
9/22/00
"Jethro"
bites / 10 min
210
180
150
120
90
60
30
0
21:00
05:00
13:00
21:00
05:00
13:00
21:00
05:00
13:00
9/24/00
9/25/00
9/26/00
9/27/00
Date + Time

Fig. 5. Feeding response (difference between the percent feeding occurrence during each DO scenario and each crabs' overall feeding occurrence) of telemetered crabs to (A) decreasing and (B) decreasing DO concentrations. Positive values indicate that crabs increased their frequency of feeding relative to their overall percent feeding occurrence and negative values indicate a decrease in percent feeding occurrence. Feeding response is classified along the x-axis based on whether DO changed from/to hypoxia/normoxia (arrow indicates direction of change). Asterisks indicate significant results from paired t-tests comparing observed mean response to the overall mean.


A: Decreasing DO
Difference in % Feeding Occurrence
30
20
10
0
-10
-20
-30
Hypoxia
Hypoxia
Normoxia
Hypoxia
Normoxia
Normoxia

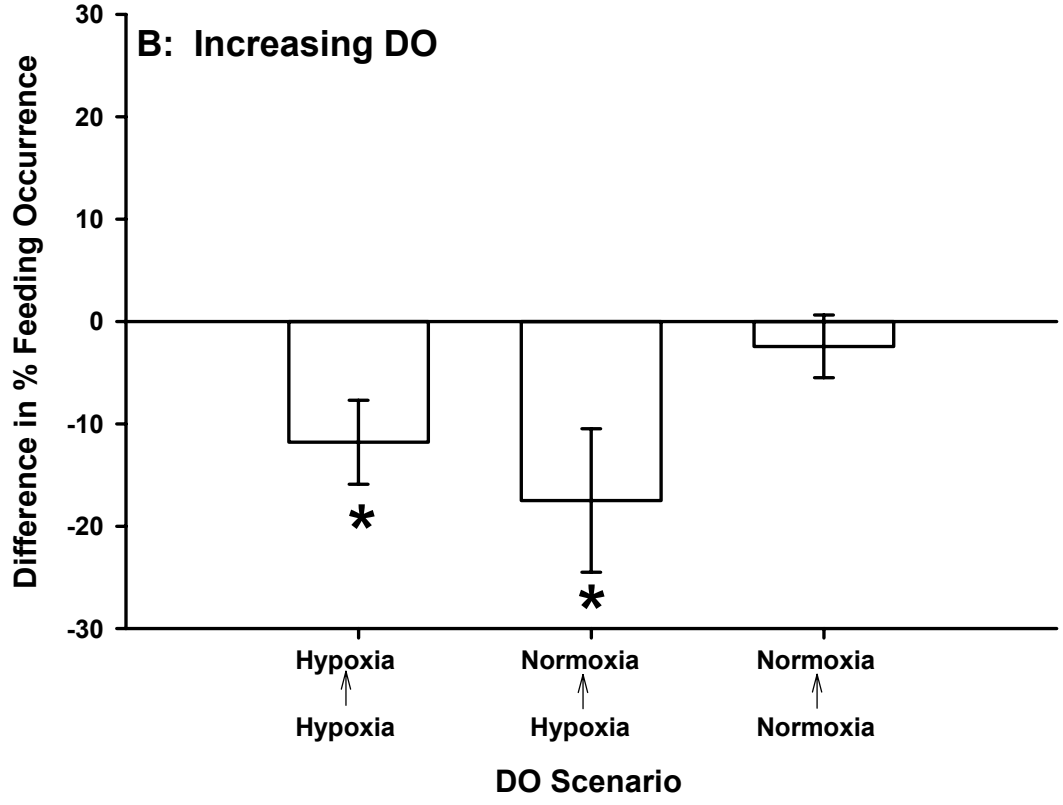

B: Increasing DO
Difference in % Feeding Occurrence
30
20
10
0
-10
-20
-30
*
*
Hypoxia
Hypoxia
Normoxia
Hypoxia
Normoxia
Normoxia
DO Scenario

Fig. 6. Diel patterns in telemetered crab (A) mean speed (m/h), (B) percent feeding occurrence (% of 10 min time bins where feeding occurred), and (C) feeding rate (# of bites / 10 min). Plotted are means of 14 crabs ± standard errror. Asterisks denote significant differences between observed mean and overall mean from paired t-tests.

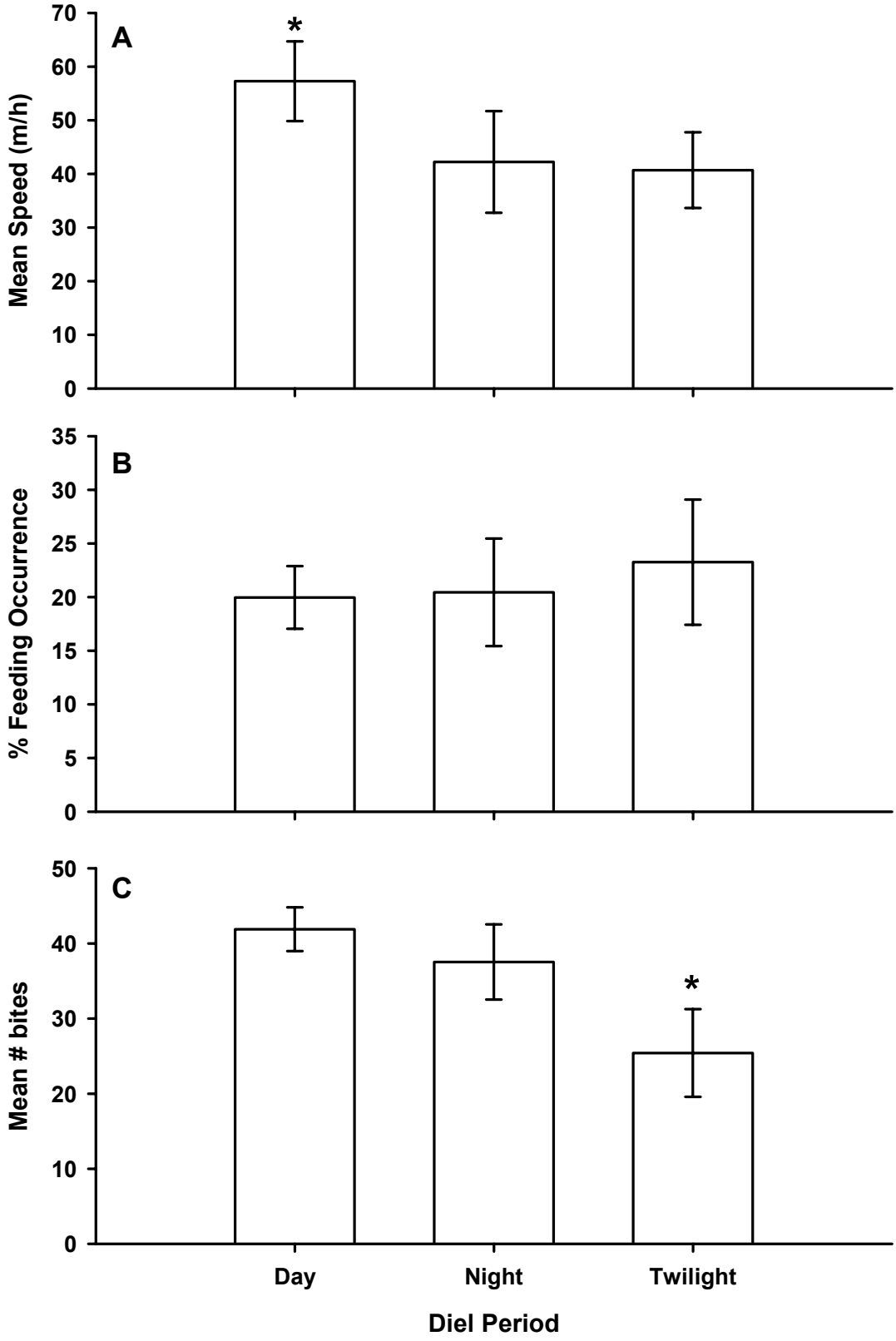

A
B
C
Mean Speed (m/h)
% Feeding Occurrence
Mean # bites
*
*
0
10
20
30
40
50
60
70
0
5
10
15
20
25
30
35
0
10
20
30
40
50
Day
Night
Twilight
Diel Period

Fig. 7. Log-transformed normalized mean abundance (number of crabs per 10 min tow; adjusted for monthly effect on crab abundance) of blue crabs (± SE) by depth [deep (3.0 – 4.6 m deep), mid (1.7 – 3.0 m deep), and shallow (0.9 – 1.7 m deep)] during normoxia, moderate hypoxia, and strong hypoxia (e.g. upwelling).

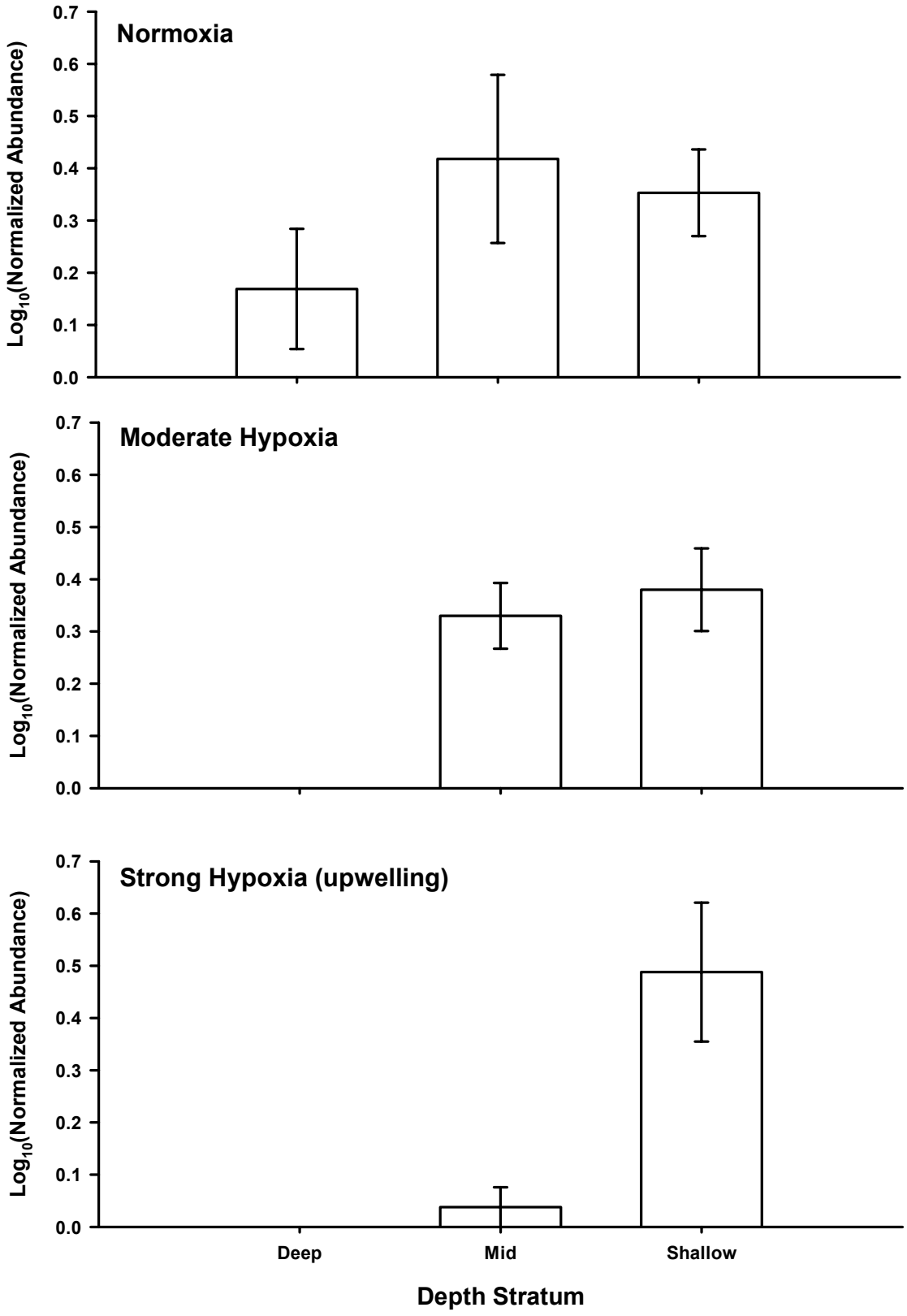
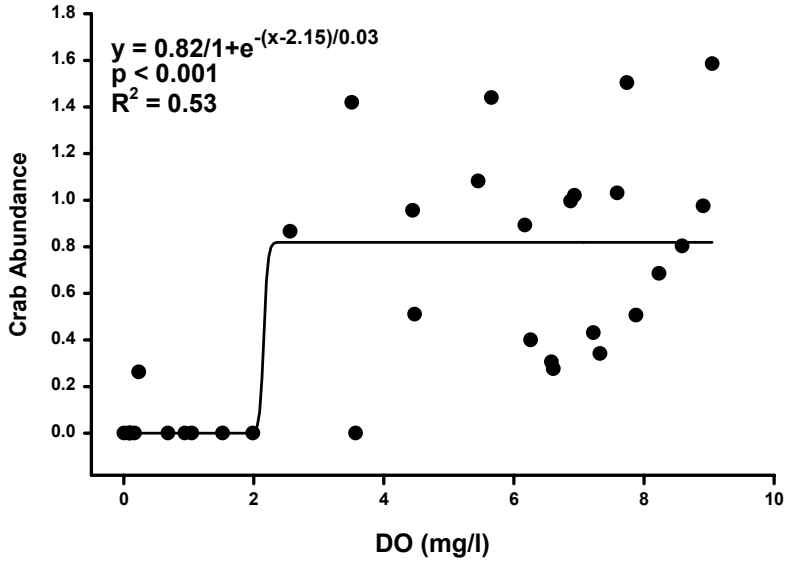
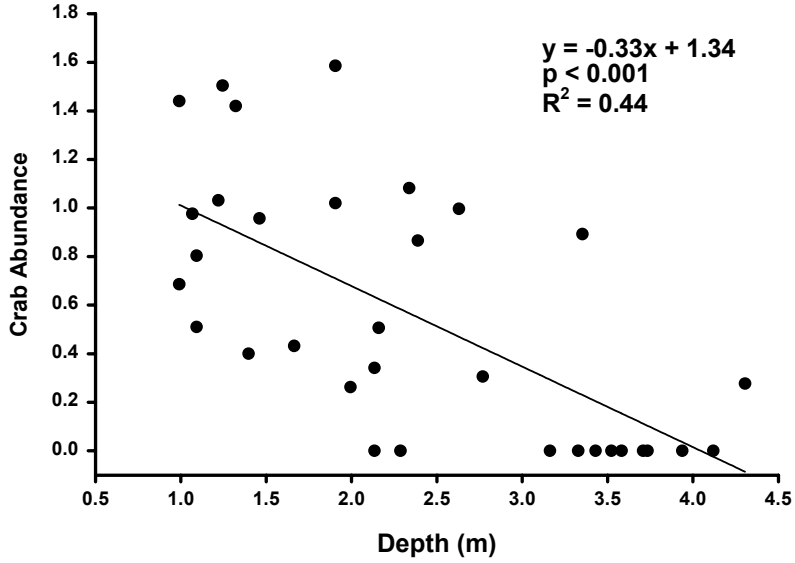
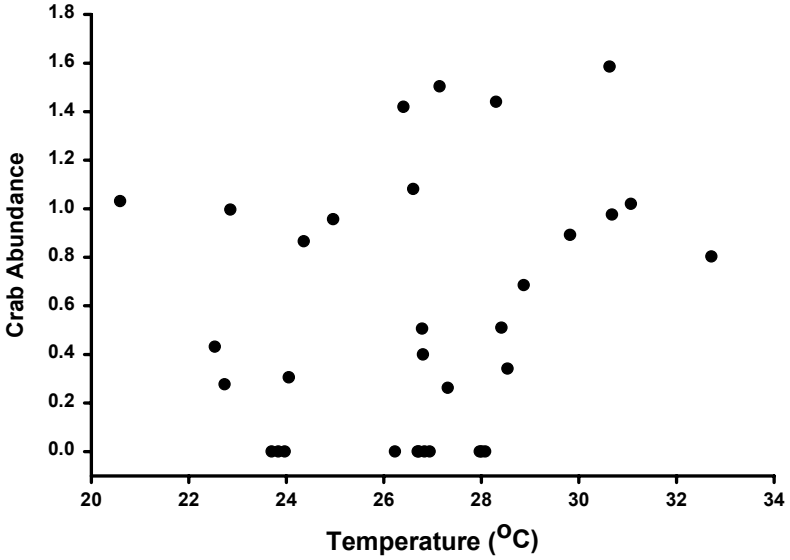
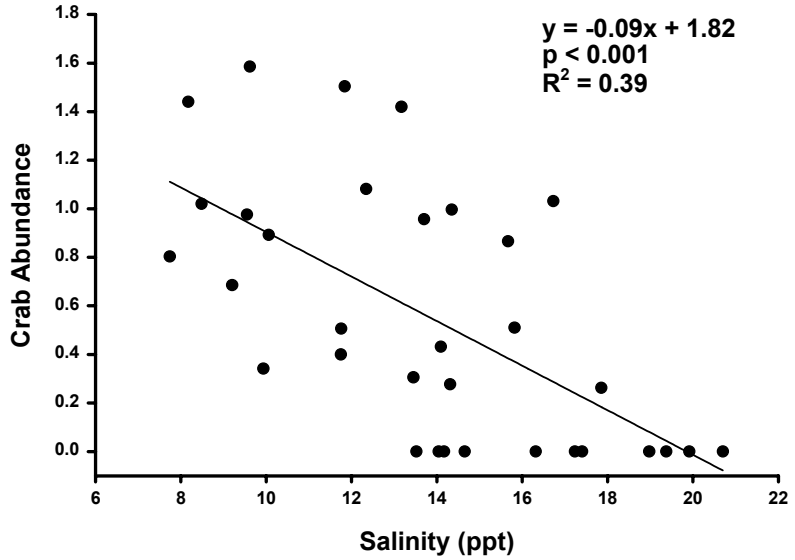

Normoxia
Moderate Hypoxia
Strong Hypoxia (upwelling)
Log10(Normalized Abundance)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Deep
Mid
Shallow
Depth Stratum

Fig. 8. Relationship between abiotic factors (DO, temperature, depth, and salinity) and log-transformed normalized catch rates (number of crabs per 10 min tow; adjusted for monthly effect on crab abundance) of blue crabs. Lines are significant least squares regression trends; included are regression equations, as well as p and R^2 values.


y = 0.82/1+e-(x-2.15)/0.03
p < 0.001
R2 = 0.53
Crab Abundance
DO (mg/l)


y = -0.33x + 1.34
p < 0.001
R2 = 0.44
Crab Abundance
Depth (m)


Crab Abundance
Temperature (OC)

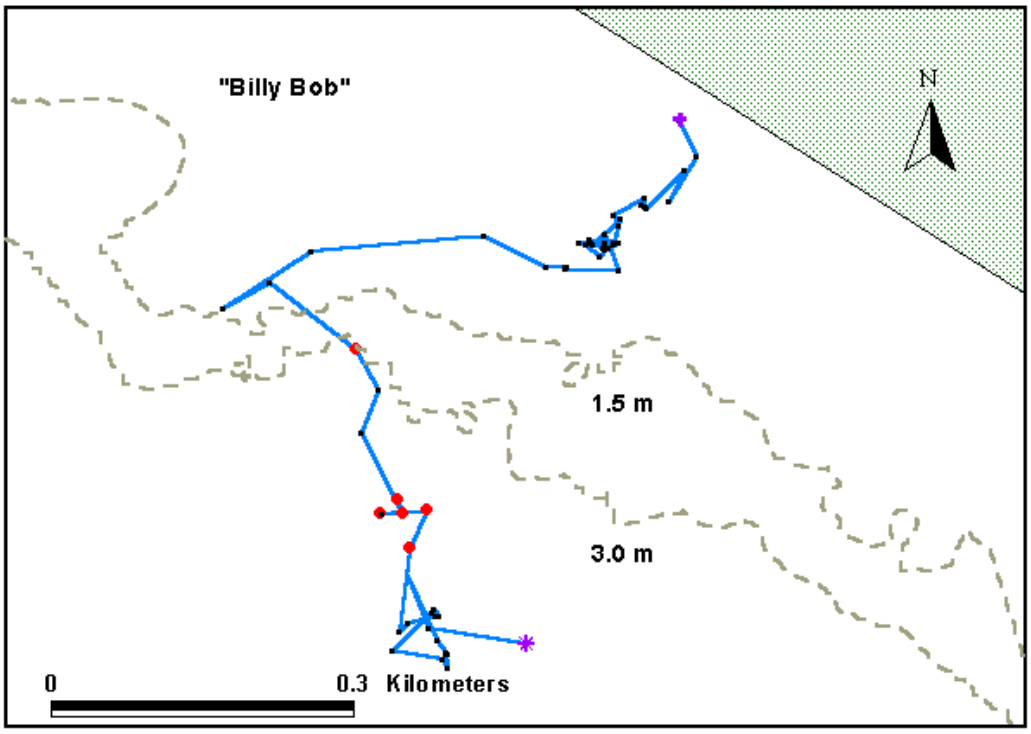

y = -0.09x + 1.82
p < 0.001
R2 = 0.39
Crab Abundance
Salinity (ppt)

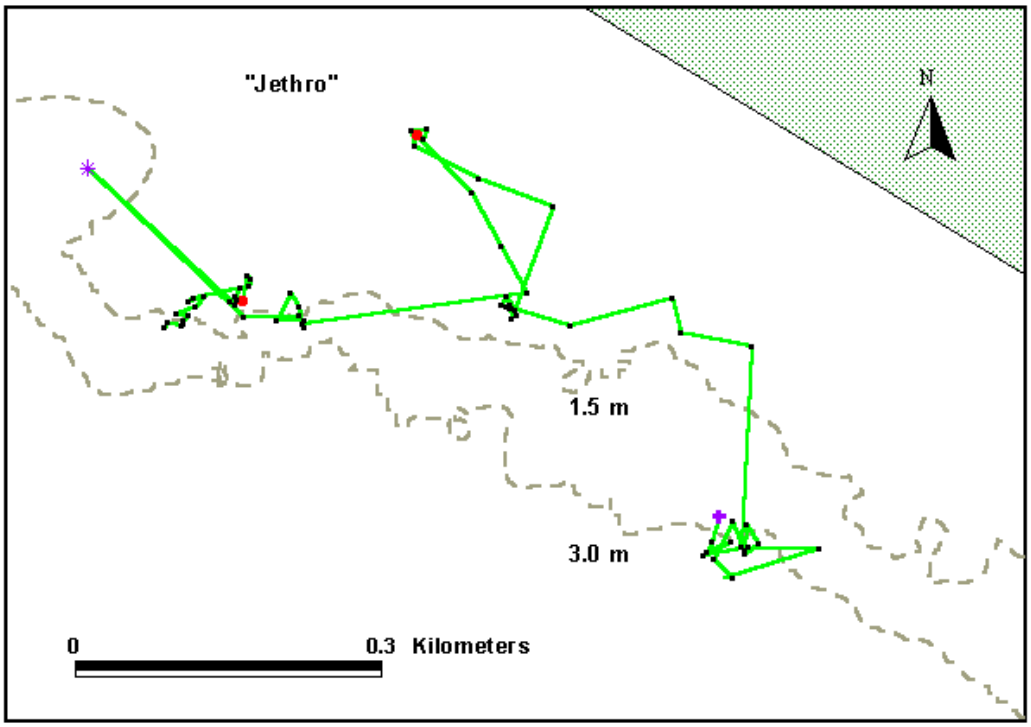
APPENDICES

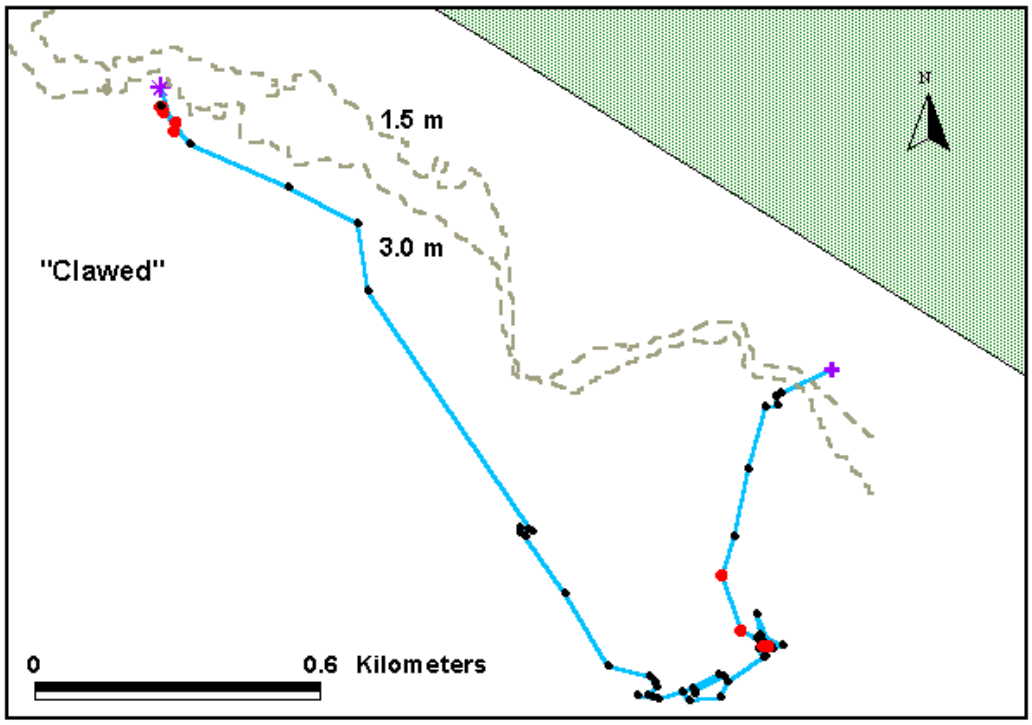
Appendix 1. List of Sonde deployment dates (number of days deployed for in parentheses) and hypoxic upwelling events during each deployment. The duration of each event, as well as the lowest recorded DO and mean DO (± standard error) for both the mid-depth and shallow sites are provided. Asterisks denote events when Sondes were either deployed or retrieved while an event was in progress. NA indicates dates when the shallow site was not sampled.

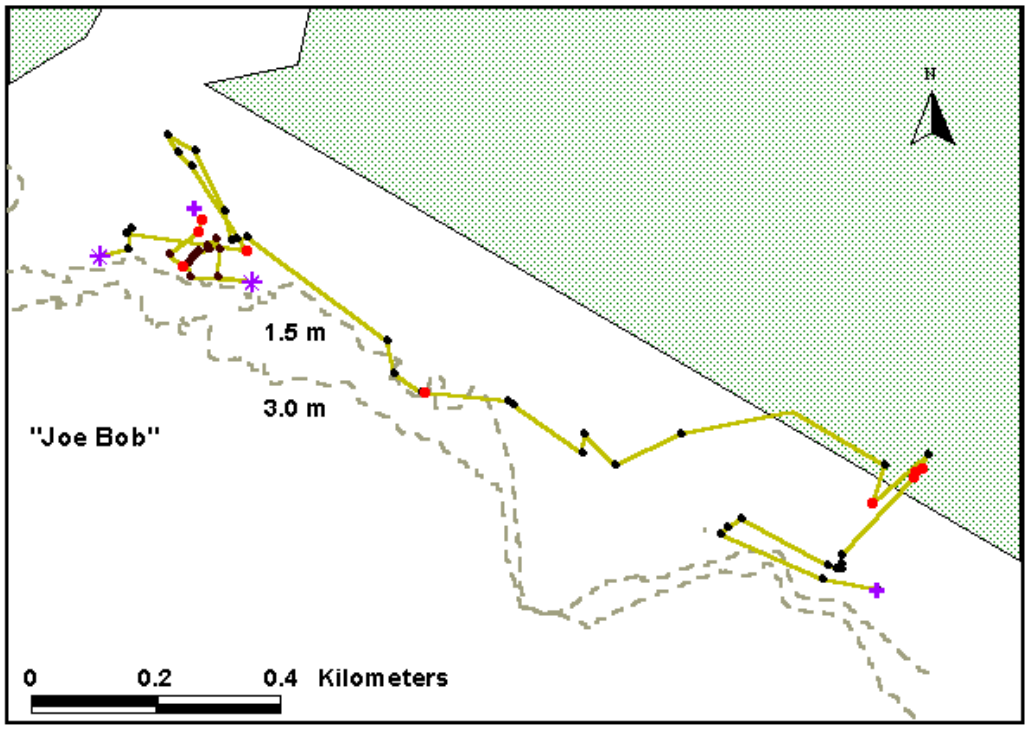
Deployment Date	Date + Time of Event	Duration of Event (hrs)	Mid-depth Sonde		Shallow Sonde	
			Low DO (mg/l)	Avg DO ±SE	Low DO (mg/l)	Avg DO ±SE
7/22/01 (3)	None	—	—	—	—	—
7/27/01 (5)	7/28/01 0700	5	1.37	1.71 ± 0.11	4.00	4.15 ± 0.09
	7/30/01 0700	3	1.30	1.45 ± 0.12	5.34	5.46 ± 0.07
8/8/01 (5)	8/8/01 1030	5*	0.90	1.15 ± 0.23	7.14	8.27 ± 0.32
	8/9/01 0330	12	0.32	0.47 ± 0.06	5.20	6.85 ± 0.42
	8/10/01 0230	1	1.02		6.20	
	8/10/01 0730	6	0.25	0.32 ± 0.04	5.71	6.98 ± 0.45
	8/11/01 0130	4	0.29	0.81 ± 0.31	5.77	6.06 ± 0.12
	8/11/01 0930	1	0.28		5.84	
	8/12/01 0230	8	0.16	0.27 ± 0.08	4.81	5.72 ± 0.19
8/17/01 (5)	8/18/01 0800	1	1.32		NA	NA
	8/19/01 0300	1	0.71		NA	NA
	8/19/01 1000	6	0.46	0.78 ± 0.16	NA	NA
	8/20/01 0700	3	0.37	0.75 ± 0.38	NA	NA
	8/21/01 0000	5	0.36	0.42 ± 0.05	NA	NA
	8/21/01 1000	5	0.54	1.29 ± 0.25	NA	NA
	8/21/01 2300	5	0.62	0.93 ± 0.15	NA	NA
	8/22/01 0700	4*	0.60	1.47 ± 0.28	NA	NA
9/5/01 (5)	9/5/01 1000	6*	0.12	0.81 ± 0.22	4.56	6.82 ± 0.80
	9/5/01 2200	1	0.96		7.92	
	9/6/01 0700	11	0.00	0.31 ± 0.13	1.87	4.36 ± 0.65
	9/7/01 0800	4	1.34	1.72 ± 0.14	5.76	6.24 ± 0.30
	9/8/01 0700	3	0.30	0.84 ± 0.41	4.73	5.12 ± 0.20
	9/9/01 0300	2	1.77	1.87 ± 0.08	5.81	5.93 ± 0.10
	9/10/01 0200	4	0.09	0.48 ± 0.27	5.55	5.68 ± 0.08
9/10/01 (5)	9/11/01 0600	30	1.15	1.80 ± 0.07	1.75	2.99 ± 0.14
	9/13/01 0800	5	0.38	0.77 ± 0.27	4.73	5.23 ± 0.17
	9/14/01 1700	2	1.87	1.88 ± 0.01	4.91	4.98 ± 0.07
	9/14/01 2200	1	1.96		4.93	
9/23/01 (5)	9/23/01 1430	2	1.83	1.94 ± 0.11	8.33	8.57 ± 0.24
	9/25/01 0530	28	0.23	1.55 ± 0.11	3.84	5.38 ± 0.21
	9/27/01 0930	1	1.96		5.76	
	9/28/01 0330	4*	1.37	1.76 ± 0.14	6.74	7.25 ± 0.18

Appendix 2. Map of study site including telemetry tracks for 4 crabs (Billy Bob, Jethro, Clawed, and Joe Bob). Each point is a single tracking location along a crab's track that is classified based on whether DO measurements were normoxic (small black circles) or hypoxic (larger red circles). Purple asterisk indicates release location, and purple plus sign shows last relocation point for each crab. Dashed gray lines denote depth contour lines that separate the shallow from mid-depth stratum (1.5 m depth), and mid-depth from deep stratum (3.0 m depth) (see Fig. 1).


"Billy Bob"
N
1.5 m
3.0 m
0
0.3 Kilometers


"Jethro"
N
1.5 m
3.0 m
0
0.3 Kilometers


1.5 m
3.0 m
"Clawed"
N
0
0.6 Kilometers


1.5 m
3.0 m
"Joe Bob"
N
0
0.2
0.4 Kilometers