

## **Abstract**

Yip-Hoi, Trevor Andrew. An investigation of effects of dissolved oxygen level, sediment type, stocking density and predation on the growth rate, survivorship, and burrowing behavior of juvenile brown and white shrimp. (Under the direction of James A. Rice and James F. Gilliam.)

Brown shrimp (*Farfantepenaeus aztecus*) and white shrimp (*Litopenaeus setiferus*) are important components of estuarine food webs and support valuable aquaculture and commercial fishing enterprises. Both species exhibit clumped distributions correlated with sediment type. Escalating cultural eutrophication in estuaries has increased the frequency, spatial scale and duration of concurrent hypoxia (dissolved oxygen, DO,  $\leq 2.0$  ppm), which is often associated with specific regions of estuarine bottom, where shrimp may have higher risks of exposure with negative impacts. Shrimp densities may increase in unimpacted habitats due to avoidance of hypoxia, where increased predation rates, density-dependent mortality and growth attrition may result. I used laboratory and field experiments to investigate effects of DO level, sediment type, density and predation on the growth rate, survivorship, burrowing behavior and sediment preference of juvenile brown and white shrimp.

In the laboratory, white shrimp growth rate was positively related to DO level from 2-6 ppm, but brown shrimp growth rate was not. Fluctuating (super-saturated/hypoxic) DO reduced growth rate relative to constant high DO in white shrimp only. White shrimp appeared to display an acclimation response whereas brown shrimp did not.

In the laboratory, brown shrimp emergence was examined under different DO (high or low) and predation threat (caged predator, uncaged predator or no predator) treatments. DO level had a significant effect in all cases. With an uncaged predator, emergence at low DO was significantly less than with no predator, suggesting a trade-off between emergence at low DO and the probability of a lethal encounter.

In the laboratory, burrowing preferences of both brown and white shrimp among five sediment types (sand, peat, sandy mud, muddy sand, and shell sand) were significantly different from the expected null ratio (1:1:1:1:1). Brown shrimp frequencies were higher than expected in sand and peat, as expected in muddy sand, and lower than expected in sandy mud and shell sand. White shrimp frequencies were higher than expected in sand, as expected in sandy mud and peat, and lower than expected in muddy sand and shell sand.

Field mesocosm experiments revealed a significant negative relationship between shrimp density and growth from 5-20 shrimp·m<sup>-2</sup>, but there was no effect on survivorship. Sediment type (sand, peat, muddy sand) had no effect on growth rate or survivorship. Predator presence (1 or 2 predators·m<sup>-2</sup>) resulted in significantly lower survivorship than in the absence of a predator and demonstrated the efficiency of pinfish as shrimp predators.

Results indicate that there may be different consequences of sublethal low DO, even at levels that are not considered hypoxic, for the growth rates of these two closely related species, with white shrimp being more vulnerable. Hypoxia increases the vulnerability of shrimp to predators by increasing exposure time, but predation threat can dampen the emergence response, emphasizing behavioral considerations when examining the net effect of biotic and abiotic factors. Both species preferred sand substrate, suggesting that observed field distributions may be based less on foraging considerations than on other factors (substrate penetrability, ease of respiration when burrowed, habitat recognition, predator-avoidance tradeoffs, and on proficiency at locating preferred substrate). Substrate type did not affect shrimp growth rate, whereas shrimp density appears to be critical. Outside hypoxic zones, density-mediated growth attrition and predation mortality may be important factors affecting shrimp populations. This highlights the necessity for future research using larger-scale studies to more precisely characterize and quantify the extent of such impacts.

**AN INVESTIGATION OF EFFECTS OF DISSOLVED OXYGEN LEVEL,  
SEDIMENT TYPE, STOCKING DENSITY AND PREDATION  
ON THE GROWTH RATE, SURVIVORSHIP, AND BURROWING BEHAVIOR OF  
JUVENILE BROWN AND WHITE SHRIMP**

by

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**A dissertation submitted to the Graduate Faculty of  
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in partial fulfilment of the  
requirements for the Degree of  
Doctor of Philosophy**

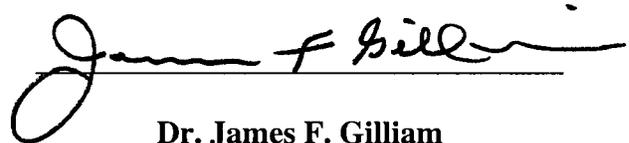
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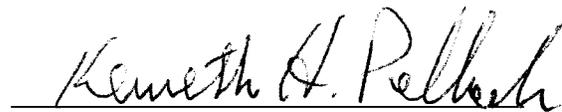
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**Dedication**

To mother and father - a small and inadequate token in acknowledgement of the countless gifts of love, patience and guidance that you bestowed on your children, that we believed we could achieve these things. With love.

## **Biography**

I am currently on my 37th circumnavigation of the sun. My mother is Irish and my father Trinidadian. I was born in Aylesbury, England, about 35 miles NW of London and was raised between England, Ireland and Trinidad, mostly in the latter. After obtaining my BS in Zoology from the University of the West Indies and working for three years as an ornithological tour guide, I was awarded a scholarship to pursue my MS at King's College, University of London, England. I then worked for four years as an environmental consultant in Trinidad before moving back to London to settle there, hoping to reinvent myself. It was there that I was offered a scholarship to pursue my Ph.D. here at NCSU. Leaving London again was the most difficult decision of my life, with its shelter of anonymity and its bright city lights. And a salary!

I came to NCSU intending to study birds but, for some vague reason, I ended up studying shrimp. That's probably a typical story for a graduate student. I am thinking, more and more, that it is not really important what one studies as much as it is learning to think, and then applying that thought process to solving relevant issues. I look forward to the upcoming years, hoping to effect some sort of positive change, first in Trinidad and Tobago, then who knows where...

## **Acknowledgements**

I'd like to express my gratitude to Jim Gilliam and Doug Fraser for their friendship and inspiration, and for planting and nurturing the seeds of science in my barren mind, all those years ago, in the hills and valleys of the mighty Northern Range of Trinidad. Without Jim Gilliam's persistence I could not be here today. I am indebted to Jim Rice for taking in an orphaned bird and giving him a second chance to fly. Thanks to my aunt, Eudora Chay, for her generosity. Finally, I thank the Organization of American States for funding to begin my Ph.D. program and the Government and people of the Republic of Trinidad and Tobago, for the good faith they have placed in this citizen, that it may come to fulfillment in our common future.

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## Chapter 1. General Introduction.

The Crustacea, a successful and diverse group that dates back at least 500 million years to the Cambrian era, currently contains some 50,000 species. Within the order Decapoda (shrimp, lobsters and crabs), suborder Dendrobranchiata includes about 450 species of penaeid and sergestid shrimps that can grow up to 30 centimeters (Tudge 2000). Penaeid shrimp are widely distributed among the world's tropical and subtropical waters, from about 40°N to 40°S latitude. Adults inhabit offshore waters, seldom below 60 m depth, whereas postlarvae and juveniles are generally found in protected coastal habitats (Bailey-Brock and Moss 1992). Penaeids are high-fecundity broadcast spawners that migrate over relatively large distances, e.g., Dall et al. (1990) made estimates of  $> 800,000$  eggs·female<sup>-1</sup> for large white shrimp (*Litopenaeus setiferus*) and tagged individuals have been known to migrate as much as 600 km (Lindner and Anderson 1956). These traits suggest demographically open, panmictic metapopulations, with local recruitment uncoupled from local reproduction by a dispersive larval phase (Caley et al. 1996), a process that may function as a means of ensuring genetic exchange (Scheltema 1971, 1986).

During spring and summer months, larval stages are transported into estuaries by wind-driven surface currents and shoreward-moving convergence zones, facilitated by diel vertical migrations from within the water column during the daylight hours to surface waters at night (Shanks 1998). Postlarvae eventually settle out in lower-salinity regions of estuaries, such as the creeks and tributaries that house intertidal salt marshes, oyster beds and adjacent muddy bottoms, with brown and white shrimp arriving from February to March and May to

September, respectively (Williams 1964, Williams 1984, NCDENR 1999). Within nurseries, postlarvae grow to the juvenile stage in four to six weeks (Pérez Farfante 1969). Both species are known to display substrate associations (Williams 1958) and exhibit a pattern of daytime burrowing and nighttime locomotor activity (Williams 1958, Wickham and Minkler 1975, Matthews et al. 1991). Burrowing may be an important energy-conservation and predator-avoidance mechanism (Williams 1958, Wickham and Minkler 1975, Rulifson 1981, Minello and Zimmerman 1984, Larson et al. 1989). As juveniles mature, they migrate downstream toward higher salinity, deeper waters of the lower estuary (secondary nurseries). Intra-estuarine movement continues through summer until populations have migrated from the upper estuary to the sound, and finally to the open ocean to spawn, thus repeating the cycle (McCoy 1968). It is generally acknowledged that nursery environmental parameters such as temperature and salinity play a major role in determining distribution patterns and yearly abundance levels (Hunt et al. 1980, Cohen and Fishman 1983, NCDENR 1999).

Pérez-Farfante and Kensley (1997) suggested several new names for farmed penaeids of the genus *Penaeus*. The species formerly known as *Penaeus aztecus* (brown shrimp) and *P. setiferus* (white shrimp) were designated *Farfantepeneaeus aztecus* and *Litopenaeus setiferus* respectively. These names were first endorsed in a review by Bauer (1998) who cited differences in reproductive biology as additional evidence. More recent mtDNA analyses (Maggioni et al. 2001) have added even further support to the adoption of these proposed genera, and I have thus chosen to use them here.

*Ecological and commercial importance*

Among estuarine-dependent invertebrates and fishes, penaeid shrimp are of particular ecological and commercial importance. They are opportunistic omnivores, scavenging among marsh grasses and on the surface of estuarine sediments on a diverse spectrum of food types. This includes polychaetes, oligochaetes, harpacticoid copepods, pericarideans, ostracods, small molluscs, benthic diatoms, bacteria, phytoplankton, filamentous green and blue-green algae, and vascular plant detritus (Darnell 1958, Eldred et al. 1961, Williams 1965, Dall 1968, Condrey et al. 1972, Odum and Heald 1972, McTigue and Zimmerman 1991, McTigue and Zimmerman 1998, Nunes and Parsons 2000, Riera et al. 2000) and thus play an important role linking benthic producers with pelagic consumers in estuarine communities. Penaeids are higher in energy content than polychaetes, gastropods, bivalves or echinoderms (Thayer et al. 1973) and are thus an important food source for a large number of finfish predators, the major source of their mortality (Gunter 1956, Pérez-Farfante 1969, Lindner and Cook 1970, McKenzie 1981, Benson 1982, Minello et al. 1987).

Penaeid shrimp support single year-class fisheries. In 2001, the total estimated value and weight of all commercially landed shrimp species in U.S. waters were  $\$5.8 \times 10^8$  and  $1.6 \times 10^5$  t (personal communication, David Sutherland, National Marine Fisheries Service, Fisheries Statistics and Economics Division, Silver Spring, MD), of which brown and white shrimp were worth  $\$2.9 \times 10^8$  ( $6.9 \times 10^4$  t), and  $\$1.9 \times 10^8$  ( $4.1 \times 10^4$  t) respectively, accounting for 83.3% by dollar value, and 70.2% of the total shrimp landings. Gracia (1996) demonstrated recruitment overfishing in Gulf of Mexico white shrimp, and a spawning stock recruitment relationship has been clearly demonstrated in other species (Penn and Caputi

1986, Penn et al. 1995). Ye (2000) performed a meta-analysis of 13 sets of time series data from published sources in an explicit test of the null hypothesis that recruitment is independent of spawning stock in penaeid shrimp fisheries and determined that recruitment is related to spawner abundance. It was concluded that shrimp populations should be managed so as to maintain sufficient spawning stock abundance to yield high recruitment (Ye 2000).

Since the collection of wild seed in the 1970s and the supply of hatchery-reared postlarvae in the 1980s, marine shrimp farming has become one of the most outstanding success stories in the modern history of aquaculture (Czavas, 1993). Although U.S. shrimp culturists currently prefer *Litopenaeus vannamei*, an eastern Pacific species, the inherent potential for escapement has raised concerns of displacement and genetic- and disease-related threats to Atlantic penaeid populations. This has encouraged the adoption of the indigenous white shrimp (*L. setiferus*) instead, which can yield as much as 6400 kg·ha·crop<sup>-1</sup>. It should still be kept in mind that, despite their value, both the commercial harvest and aquaculture of penaeid shrimp remain controversial issues because of the associated problems of excessive finfish bycatch (Hendrickson and Griffin 1993, Griffin et al. 1993, Samonte-Tan and Griffin 2001) and nutrient overloading (Moss 2002), respectively.

### *Eutrophication and hypoxia*

Cultural eutrophication is one of the most severe and widespread forms of disturbance affecting coastal marine systems (Gray 2002). The increasing spatial extent and duration of associated hypoxia (generally, dissolved oxygen levels  $\leq 2$  ppm) in many U.S. estuaries in recent decades is cause for serious concern because it can disrupt benthic community

structure and trophic dynamics (Officer et al. 1984, Renaud 1985, Dauer et al. 1992, Stanley and Nixon 1992, Valiela et al. 1992, Winn and Knott 1992, Breitburg et al. 1997, Paerl et al. 1998, Diaz and Solow 1999, Ritter and Montagna 1999, Goolsby 2000, Selberg et al. 2001, Buzzelli et al. 2002). Apart from proximal impacts of low DO on organisms within hypoxic zones, behavioral insights from laboratory and field studies clearly indicate that many estuarine organisms can detect and successfully avoid hypoxic regions (Leming and Stuntz 1984, Renaud 1986a, Stickle et al. 1989, Pihl et al. 1991, Howell and Simpson 1994, Wannamaker and Rice 2000, Lenihan et al. 2001, Eby and Crowder 2002), yet population dynamics and fitness can still be indirectly affected via the energetic and lost opportunity costs of risk avoidance (Frid and Dill 2002). Optimal foraging and competition theories further suggest that increased predation rates, density-dependent effects, and interactions between the two may affect the survivorship and growth of displaced and congested populations (Hardin 1960, Emlen 1966, MacArthur and Pianka 1966, Schoener 1971, Pulliam 1974, Charnov 1976, Pyke 1984, Stephens and Krebs 1986, Schoener 1987, Mangel and Clark 1988, Gurevitch et al. 2000, Schoener et al. 2001, Chase et al. 2002).

### *Hypoxia and penaeid shrimp*

There is a growing literature on the effects of DO availability on various aspects of penaeid biology (Table 1). Although the current pool of information is substantial, a lack of standardization of experimental protocols complicates making direct comparisons between studies, which is essential to broaden the scope of relevance of data, e.g., use of dry weight vs. wet weight to describe size, use of different salinities and temperatures, use of hatchery-

reared vs. wild stock, use of varying feed types, and a lack of reporting of other parameters that may interact with DO to bias results and complicate drawing correct conclusions. In addition, some of the information may be unreliable, e.g., the unrealistically high LC50s (approaching normoxia) reported by Stickle et al. (1989), which suggests that great care should be taken to isolate test organisms from other factors that might affect the response variable(s) of interest, such as different handling procedures and/or maintenance of organisms before and during experiments. After careful consideration of the literature in Table 1, the following key points emerge:

- (i) Levels of DO that cause significant mortality (as measured by standard LC50 tests) generally occur  $< 1.5$  ppm DO, and interactions with other physicochemical parameters (notably ammonia, salinity and temperature) can raise LC50 values;
- (ii) Low-DO induced mortality may be positively correlated with size;
- (iii) DO levels that are not considered hypoxic (2-3 ppm) can still negatively affect metabolism and growth rate;
- (iv) Shrimp can distinguish between low levels of DO (e.g., 2 vs. 1 ppm), and avoidance behaviors are elicited in the laboratory at DO levels  $\leq 2$  ppm DO. Field distributions indicate that shrimp will vacate areas where DO falls to between 2 and 3 ppm;
- (v) Short-term hypoxia (1 ppm) can have deleterious effects on hematological and immune parameters and increase disease susceptibility.

### *Rationale for investigations*

Many pieces of the hypoxia puzzle still remain to be solved in terms of the precise mechanisms whereby hypoxia can impact estuarine organisms. Specifically, it remains unknown how hypoxia, its severity, or temporal and spatial differences in its process of formation, can affect the responses of penaeid shrimp and their eventual distribution. Neal and Maris (1985) have already noted that the entire area of penaeid behavior in general has received little scientific attention. It is also unknown whether redistribution to more oxygenated habitat will necessarily lead to negative effects in outlying habitat when it does occur. Thus, there remains a basic and urgent need for additional research to identify and quantify these potential impacts of hypoxia on penaeid shrimp. My dissertation addresses some of these cause-and-effect information gaps via investigations into effects of dissolved oxygen level, sediment type, density and predation on the growth rate, survivorship, and burrowing behavior of juvenile brown and white shrimp. These investigations are summarized below by chapter.

## **Chapter 2**

*Question:* Do juvenile brown and white shrimp exhibit differences in growth rates when exposed to various levels of sublethal dissolved oxygen?

*Importance:* It is currently unknown how the growth rates of juvenile brown and white shrimp respond to levels of DO above hypoxia. This knowledge is important to more accurately delineate the range of DO values over which negative growth effects may occur. If coupled with field measurements and modeling efforts, this information can lead to more

precise estimates of the spatial scale of DO-induced growth attrition, provide more reliable predictions about repercussions for population biomasses, and improve the meaningfulness of management decisions.

*Investigation:* In a laboratory experiment, juvenile brown and white shrimp growth rates were measured under three constant DO treatments (2, 4, 6 ppm) and a fluctuating (2-12 ppm) treatment over a 20-day period. My findings, potential impacts and implications for management are discussed in light of current published information.

### **Chapter 3**

*Question:* Is the duration of daytime emergence of juvenile brown shrimp affected by hypoxia, and is that response modified by the presence of a predation threat?

*Importance:* Daytime burrowing is an important predator defense and energy conservation mechanism for brown shrimp. If that behavior is disrupted by large-scale hypoxia, a significant proportion of shrimp populations may become vulnerable to opportunistic or hypoxia-tolerant predators. Information on penaeid behavior is scarce or has been largely ignored, but nonetheless must be directly integrated with other traditional response parameters to accurately assess the overall impacts of hypoxia.

*Investigation:* In a laboratory experiment, I examined the emergence behavior of juvenile brown shrimp under normoxia and hypoxia (6 vs. 1.5 ppm DO) and three predator-threat scenarios (caged predator, free-ranging predator, no predator). Results are discussed in the context of a trade-off between negative effects of low DO versus increased vulnerability

to predators, and the importance of behavioral considerations when examining the net effect of biotic and abiotic factors.

## **Chapter 4**

*Question:* Do juvenile brown and white shrimp exhibit sediment preferences?

*Importance:* Because of tight redox coupling between organic-rich sediments and overlying water, hypoxic episodes are often associated with specific regions of estuarine bottom and, consequently, epibenthic species with specific substrate affinities may have higher risks of exposure and consequent negative impacts.

*Investigation:* A laboratory experiment tested for sediment burrowing preferences of individual juvenile brown and white shrimp for five common sediment types (sand, peat, sandy mud, muddy sand, and shell sand). I compare my findings with those of previous studies, noting differences in scale and design, and discuss the factors that may ultimately explain burrowing preferences.

## **Chapter 5:**

*Question:* How are the growth rate and survivorship of juvenile white shrimp affected by shrimp density, sediment type and predator density?

*Importance:* Because shrimp are known to detect and avoid hypoxia, it is possible that resulting habitat compression may increase densities of shrimp in outlying habitats, where

theory suggests that increased predation rates, density-dependent mortality and growth effects are likely consequences.

*Investigation:* I used three field mesocosm experiments to examine the impacts of shrimp density (5, 10 or 20 m<sup>-2</sup>) and sediment type (sandy mud, sand, peat) on shrimp growth rate, and predator density (0, 1 or 2 m<sup>-2</sup>) and shrimp density (5, 10 or 20 m<sup>-2</sup>) on shrimp survivorship. The relative importance of sediment type, shrimp density and predation to growth and survivorship in displaced shrimp populations are discussed.

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Table 1. Summary of representative published information on the effects of DO level on penaeid shrimp in laboratory and field studies. Size (length/weight) or stage of life cycle is given where possible.

Penaeid species	Parameter(s) investigated	Information	Source
<i>Farfantepenaeus aztecus</i>	Mortality	Across various salinity (10, 20, 30 ppt) and temperature (20, 30°C) combinations, juveniles (21-32 mm) were very sensitive to hypoxia with 28-d LC50 values > 4.5 ppm.	Stickle et al. 1989
	Mortality	Effects of salinity (2.5, 5, 10 and 36 ppt), size (51 and 91 mm juveniles and subadults), sex, and rate of reduction in DO (0.7, 1.4 and 2.6 ppm·hr <sup>-1</sup> ) on lethal DO level (LDO) were examined. LDOs were generally < 2ppm. Salinity affected LDOs of juveniles only. Size had a positive and direct relation to LDOs. Sex had no effect on LDOs. Rates of reduction of DO as high as 2.6 ppm·hr <sup>-1</sup> had little or no effect on LDOs.	Kramer 1975
	Avoidance behavior	Subadults (118 mm) avoided 1 ppm DO in two choice trials (2 vs. 1 ppm and 4 vs. 1 ppm).	Wannamaker and Rice 2000
	Field distribution	CPUE declined exponentially with increasing distance away from the edge of the hypoxic zone, suggesting aggregations on flanks.	Craig 2001
<i>Litopenaeus setiferus</i>	Diet, metabolism	Juveniles (0.5 g wet weight) change their energy substrate from lipids-proteins (at 4 and 5 ppm DO) to proteins (at 2 and 3 ppm).	Rosas et al. 1999
	Mortality	At 15 ppt and pH 8, 48-h LC50 for postlarvae (18 mg wet weight) was 1.27 ppm and 72-h LC50 for juveniles (720 mg wet weight) was 1.16 ppm. More acidic and/or saline water resulted in higher LC50s.	Martínez et al. 1998
	Growth, mortality, metabolism	2, 3, 4 and 5.8 ppm DO were used. For postlarvae (35 mg dry weight), survival was not affected by DO levels between 2 and 5.8 ppm. Growth was constant between 4 and 5.8 ppm, but decreased at lower DO levels. Routine metabolism decreased with decreasing DO level. Apparent heat increase decreased with increasing DO level. Assimilation of ingested food was constant between 4 and 5.8 ppm, but decreased at lower levels.	Rosas et al. 1998

Table 1 (continued)

<i>Farfantepenaeus aztecus</i> , <i>Litopenaeus setiferus</i>	Avoidance behavior, field distribution	There were decreases in field abundances at DO levels < 3 ppm.	Trent et al. 1976
	Avoidance behavior	It was concluded that pelagic species avoid low DO and that waters that average < 1.0 ppm DO will result in a mass avoidance response.	May 1973
	Avoidance behavior	Bottom-water DO level varied with distance from shore and there was mass avoidance of waters measured at 0.5 ppm DO.	Loesch 1960
	Field distribution, CPUE	Some evidence of a negative relationship between shrimp catch and hypoxia; effects of hypoxia on distribution, and adjustment of fishing effort to maintain CPUE.	Zimmerman et al. 1997
	Avoidance behavior	Juvenile (65-101 mm) shrimp avoided water $\leq$ 1.5 ppm (white shrimp) and $\leq$ 2.0 ppm (brown shrimp).	Renaud 1986a
	Field distribution	Offshore bottom water DO was significantly correlated with combined catches of brown and white shrimp.	Renaud 1986b
	Avoidance behavior, field distribution	Trawl data indicated subadults/adults had an avoidance threshold of 2.2 ppm.	Eby and Crowder 2002
	Field distribution	Above 2.5 ppm DO, trawl catch rates were independent of DO level.	Leming and Stuntz 1984
Field distribution	Trawl catches rapidly declined to zero whenever DO approached 3 ppm, suggesting that hypoxia can cause redistribution over hundreds of kilometers, or delayed arrival at spawning or feeding grounds, and possible greater negative effect on <i>F. aztecus</i> .	Diaz and Solow 1999	
<i>Penaeus monodon</i>	Immune system	Phagocytic activity of hemocytes was less efficient in oxygen-depleted shrimp.	Direkbusarakom and Danayadol 1998
	Mortality, growth	The 96-h DO LC50 for 2.6 g juveniles was 0.9 ppm. There was no change in growth after short-term (4, 8 or 12 h) low DO at 0.5-0.6 ppm or 1.0-1.1 ppm.	Allan and Maguire 1991
	Mortality, interactions with ammonia	Reduced DO (2.1 ppm) significantly increased the toxicity of ammonia.	Allan et al. 1990

Table 1 (continued)

<i>Litopenaeus vannamei</i>	Disease susceptibility, immune system, mortality	Hypercapnic hypoxia caused higher mortality following bacterial challenge by <i>Vibrio</i> and reduced total hemocyte count.	Mikulski et al. 2000
<i>Litopenaeus vannamei</i> , <i>Penaeus monodon</i>	Growth	Growth was constant for juveniles (60.2 and 55.5 mg WW) of both species between 2 and 4 ppm.	Seidman and Lawrence 1985
<i>Litopenaeus vannamei</i> , <i>Litopenaeus stylirostris</i>	Growth, mortality, metabolism	Growth, survival and molting frequency were significantly depressed under a diurnally fluctuating regime (6:18 h; 1.5 ppm DO and saturation).	Aquacop et al. 1988
<i>Litopenaeus stylirostris</i>	Disease susceptibility, immune system	Hypoxia (1 ppm for 24 h) induced alteration of haematological and immune parameters and increased sensitivity to vibriosis in adults (15 g).	Le Moullac et al. 1998
<i>Litopenaeus schmitti</i>	Behavioral response	Juveniles (60-100 mm) became lethargic at 0.9 ppm.	MacKay
<i>Marsupenaeus japonicus</i>	Burrowing behavior	Emerge from substratum when DO drops to around 10% saturation.	Egusa and Yamamoto 1961
<i>Penaeus semisulcatus</i>	Mortality, metabolism	Mortality and inhibition of moulting when kept at 2 ppm for 17 days.	Clark 1986
<i>Farfantepenaeus californiensis</i>	Growth	Juveniles grew significantly less at 2.6 ppm than at 5.8 ppm, although starting weights were substantially less than in my experiment.	Ocampo et al. 2000

## **Chapter 2. Effect of various dissolved oxygen regimes on the growth rates of juvenile brown and white shrimp.**

### **ABSTRACT**

The goal of this research was to elucidate whether juvenile brown shrimp (*Farfantepenaeus aztecus*) and white shrimp (*Litopenaeus setiferus*) exhibit differences in growth rates or any evidence of an acclimation response when exposed to various levels of sublethal dissolved oxygen (DO). Previously published papers report that these species will not begin avoidance behavior under laboratory conditions until DO levels drop to  $\leq 2.0$  and  $\leq 1.5$  ppm, respectively, and field work indicates that some individuals remain in hypoxic ( $\leq 2$  ppm) waters. It was thus decided to expose shrimp to three constant dissolved oxygen treatments (2, 4, 6 ppm) representing hypoxic to normoxic conditions, and a fluctuating treatment (2/12 ppm), chosen to represent the night/day cycling of DO expected in a hypereutrophic estuary, for a period of 20 days. Three growth rates were measured: from day 0 to day 10, from day 10 to day 20, and from day 0 to day 20.

The growth responses of the two species were remarkably different. For constant DO treatments, white shrimp growth rate was positively related to DO level across all three time periods (growth at 2 ppm was  $\approx 26\%$  less than at 6 ppm), but brown shrimp did not exhibit any significant relationship to DO. For white shrimp, mean growth rate in the 2/12 ppm treatment was also significantly less than at 6 ppm (by 23%), but this also was not evident in brown shrimp. White shrimp also appeared to display an acclimation response to low DO whereas brown shrimp did not. These findings suggest that white shrimp are vulnerable to

negative growth effects if subjected to constant hypoxia (2 ppm DO), DO levels above hypoxia (4 ppm), or sporadic hypoxia (2/12 ppm). My findings suggest that there may be different consequences of sublethal low dissolved oxygen for the population biomasses of these two species, underscoring the necessity for caution when extrapolating growth and biomass predictions across even closely-related species, as well the need for more specific data for species that may potentially be affected by hypoxia.

*Key words:* Juvenile shrimp, hypoxia, eutrophication, growth rate, white shrimp, brown shrimp, *Litopenaeus setiferus*, *Farfantepenaeus aztecus*, *Penaeus aztecus*, *Penaeus setiferus*.

## INTRODUCTION

Estuaries progress towards natural eutrophication as they evolve over geological time, but increasing anthropogenic inputs to aquatic environments in recent decades has greatly accelerated this process, leading to widespread symptoms of degradation. Increased nutrient loading associated with urban expansion, coastal development, atmospheric deposition, and large-scale agricultural runoff have been implicated as primary causative factors. The impacts of eutrophication can be severe and far-reaching: shifts in community composition, reductions in species diversity, fish kills, algal and bacterial blooms, unstable oxygen levels, hypoxia (the deoxygenation of water to low levels  $\leq 2$ ), anoxia, human health problems and disruption of commercial and recreational usage have all been widely reported (Pearson and Rosenberg 1978, Burkholder et al. 1992, Burkholder et al. 1995, Diaz and Rosenberg 1995, Nixon 1995, Richardson and Jørgensen 1996, Breitburg et al. 1997, Paerl 1997, Paerl et al. 1998, Burkholder et al. 1999, Chorus and Bartram 1999, Diaz and Solow 1999, Paerl et al. 1999, Smith et al. 1999, Luttenberg et al. 2000, Nilsson and Rosenberg 2000, Pinckney et al. 2000, Diaz 2001, Selberg et al. 2001, Breitburg 2002, Gray et al. 2002, Trainer 2002).

Hypoxia is believed to be one of the most important stress factors influencing habitat quality and ecosystem health. The Harmful Algal Bloom and Hypoxia Research and Control Act of 1998 (Public Law 105-383) mandated the submission of an assessment of hypoxia that examined the ecological and economic consequences of hypoxia in United States coastal waters, alternatives for reducing, mitigating, and controlling hypoxia, and the social and economic costs and benefits of such alternatives. The resulting report (NOAA 1999) identified 44 estuaries nationally that exhibited “high expressions of eutrophic conditions”

and 77 estuaries that were affected by hypoxia (defined in that report as DO between 0 and 2 mg·L<sup>-1</sup>). Ritter and Montagna (1999) found < 2 mg·L<sup>-1</sup> DO to be the most common definition for hypoxia, but that definitions of < 2 ml·L<sup>-1</sup> and < 2 ppm were also common (2.0 mL·L<sup>-1</sup> is approximately 2.8 mg·L<sup>-1</sup> at 20 ppt salinity and stp; ppm and mg·L<sup>-1</sup> are interchangeable) and chose 3 mg·L<sup>-1</sup> to define hypoxia for Corpus Christi Bay, Texas. They suggested that mg·L<sup>-1</sup> (ppm) should be used to express oxygen concentration because mass is not temperature or pressure sensitive.

A precise definition of hypoxia has proven elusive for several reasons, most important of which are the lack of agreement on exactly what DO level causes stress and because stress responses vary with the tier of biological organization under investigation, e.g., Tyson and Pearson (1991) recognized the complexity of determining exactly what critical level of oxygenation should apply to a whole biological community. The sensitivity of organisms, communities, or ecosystems to hypoxia also varies with other factors such as temperature, activity level, mode of life (infaunal, epifaunal, pelagic, etc.), ability to emigrate, stage of life cycle, substrate association, rate of oxygen decline, and sulphide tolerance (Tyson and Pearson 1991). To avoid confusion, I will refer to specific levels of low DO whenever possible and, when using the term hypoxia, will quote the precise level cited by the author(s) in question.

Despite the problems associated with environmental degradation, estuaries must play a fundamental role as nurseries for a suite of marine euryhaline species including penaeid shrimp, which have a complex life cycle spanning several habitats. Penaeid shrimp provide important links between primary producers and secondary consumers and are also

tremendously valuable to industrial fishing and mariculture enterprises. In 2001, the estimated value and weight of all commercially landed species in the United States were  $\$3.2 \times 10^9$  and  $4.3 \times 10^6$  t, of which shrimp (all species) comprised  $\$5.8 \times 10^8$  and  $1.6 \times 10^5$  t (personal communication, David Sutherland, National Marine Fisheries Service, Fisheries Statistics and Economics Division, Silver Spring, MD). Thus, although shrimp were only 3.6% by weight of the total domestic catch, they represented 17.8% of its dollar value, ranking them as the most valuable commercial fishery in the United States. In 2001, the values and weights of brown and white shrimp (*Farfantepenaeus aztecus* and *Litopenaeus setiferus* respectively), were  $\$2.9 \times 10^8$  and  $6.9 \times 10^4$  t, and  $\$1.9 \times 10^8$  and  $4.1 \times 10^4$  t respectively, accounting for 83.3% by dollar value, and 70.2% by weight, of all commercially-landed shrimp. The species occur over large overlapping geographical ranges: brown shrimp from Massachusetts to the Florida Keys and through the Gulf of Mexico to the northwest coast of the Yucatan Peninsula (Lassuy 1983, Larson et al. 1989), and white shrimp from New York to Saint Lucie Inlet, Florida, and along the Gulf of Mexico coast from Apalachee Bay, Florida, to Ciudad, Mexico (Muncy 1984a, 1984b).

The occurrence of low DO in many of the estuaries in these regions is well documented (Officer et al. 1984, Renaud 1985, Dauer et al. 1992, Stanley and Nixon 1992, Valiela et al. 1992, Winn and Knott 1992, Breitburg et al. 1997, Paerl et al. 1998, Diaz and Solow 1999, Ritter and Montagna 1999, Goolsby 2000, Selberg et al. 2001, Buzzelli et al. 2002). Field data indicate that the majority of shrimp are caught in areas where bottom DO levels are above about 2 ppm (Leming and Stuntz 1984, Zimmerman et al. 1997, Diaz and Solow 1999, Eby and Crowder 2002). However, some shrimp are also found where DO is

substantially less than 2 ppm. Although before- and after-hypoxia studies are lacking, the evidence suggests that the majority of shrimp successfully avoid waters below 2 ppm DO but that individuals that do not are somewhat resilient to hypoxia (since dead shrimp are not recovered in trawls from these areas of low DO). This may mean that shrimp exhibit different phenotypes, some that avoid low DO and others that do not, and/or that some fraction of shrimp populations is unable to escape from hypoxic zones. The distribution of shrimp relative to hypoxia may also be a function of the spatial scale of the event and its speed of formation.

With respect to penaeid shrimp, previous authors have documented the effects of low DO on several biological parameters including mortality, disease susceptibility, growth, foraging, distribution, physiology and metabolism and behavior (see Chapter 1, Table 1). However, there remain substantial information gaps, and recently heightened interest and debate over the negative impacts of hypoxia and other eutrophication-linked factors on ecosystems (Paerl et al. 1998, Burkholder et al. 1999, Paerl et al. 1999) stress the need for continued research on the effects of low DO on estuarine species. This paper examines the effect of DO concentrations, including hypoxia, on the growth rate of juvenile brown and white shrimp.

## **MATERIALS AND METHODS**

During August, 2000, and July, 2001, juvenile white and brown shrimp (respectively) were collected from Calico Creek, Morehead City, North Carolina using a 2.3-m cast net (0.63-cm mesh), and transported to 7500-L outdoor flow-through tanks ( $1000 \text{ L}\cdot\text{hr}^{-1}$ ) at the

National Marine Fisheries Service Laboratory, Pivers Island, North Carolina. Before the commencement of experiments, shrimp were fed daily an excess of aquaculture-grade feed (55% crude protein; Corey Feed Mills Limited, New Brunswick, Canada; Table 1), in addition to any organic matter settling out of the unfiltered seawater supply.

The experiment employed a closed-system, recirculating design modified after Taylor (1999), in which seawater at 15 ppt salinity was gravity-fed from a 600-L header tank into a series of three countercurrent oxygen stripping columns that used a nitrogen displacement technique (nitrogen bubbled against the direction of flow) to sequentially strip oxygen from the seawater. Degassing within these columns was independently controlled using valves, and seawater was bled off at four points corresponding to four dissolved oxygen (DO) treatment levels. Three of these DO treatments were kept constant (6 ppm, 4 ppm and 2 ppm) and the fourth was a fluctuating treatment (2/12 ppm night/day). My choice to use a 2 ppm low DO threshold was based on evidence from three published studies: Renaud (1986a) found that brown and white shrimp begin to avoid low DO water at  $\leq 2.0$  ppm and  $\leq 1.5$  ppm, respectively. In a laboratory study, Wannamaker and Rice (2000) found that brown shrimp could differentiate between 1 ppm and 2 ppm, spending more time in the latter in avoidance/choice trials. Eby and Crowder (2002) found in a field study that shrimp (cited as *Penaeus* spp.) avoided a threshold of 2.2 ppm. Collectively, these results indicate that an avoidance threshold for shrimp exists in the vicinity of 2 ppm DO. The 6 ppm DO level was chosen to represent normoxia. The fluctuating treatment was chosen to represent diel fluctuations known to occur in hypereutrophic waters.

DO levels were attained by adjusting the nitrogen perfusion rate (also oxygen, in the fluctuating treatment) in each column while carefully monitoring DO levels with a DO meter (YSI Model 52, YSI Incorporated, Yellow Spring, OH). Seawater flows at these four treatment levels were then routed into four 19-L secondary header tanks, each of which served as a distribution manifold for three 62-L receiving glass aquaria where shrimp were kept. The distribution of seawater into the aquaria at the various DO levels was completely randomized. Thus, seawater was fed through a total of 12 62-L aquaria that overflowed into sumps where the water was reaerated before being pumped back into the main header tank via a sand filtration unit. Flow rates into the aquaria were equalized using valves and set to  $72 \text{ L}\cdot\text{hr}^{-1}$  (~52 minutes flushing time). Secondary reaeration was accomplished in the main header tank by bubbling air. Temperature was maintained at  $25^{\circ}\text{C}$  and a 14:10 LD photoperiod established with lighting from overhead fluorescent lights. To prevent shrimp from accessing the air-water interface, and to reduce the opportunity for partial re-oxygenation of seawater, all secondary header tanks and aquaria were covered with Styrofoam sheeting (Dow Chemical Company, Midland, MI). A single 5-cm hole was bored into the center of each cover to facilitate feeding and DO/temperature measurements.

Aquaria were stocked with 20 shrimp, each uniquely marked by injecting permutations of three colors of an elastomer (Northwest Marine Technology Incorporated, Shaw Island, WA) into three positions on the 6<sup>th</sup> abdominal segment. This marking procedure permitted the tracking of individual growth rates. Both species were fed to excess, ~10% bodyweight per day, at the beginning of the night cycle (when shrimp typically begin foraging) and surplus food was siphoned from aquaria each morning. Experiments lasted 20

days (after an initial 72-hr acclimation period) and shrimp were individually measured for weight and length at day 0, day 10 and day 20 using a digital scale and calipers. Water quality was monitored using a saltwater test kit (Aquarium Pharmaceuticals, Incorporated, Chalfont, PA) that tested for ammonia, nitrate, nitrite and pH. Shrimp wet weight was used for growth rate calculations, as is common practice (Seidman and Lawrence 1985, Allan and Maguire 1991, Hopkins et al. 1993, Davis and Arnold 1994, Williams et al. 1996). Growth rate (GR) was expressed as percent body weight per day and scaled to an individual's average weight during the growth period using the equation:

$$GR = \{(\text{end wt.} - \text{start wt.}) \div [\# \text{ days} \times (\text{end wt.} + \text{start wt.}) / 2]\} \times 100.$$

I calculated three growth rates for each individual: growth rate from day 0 to day 10, from day 10 to day 20, and from day 0 to day 20. For each of these growth periods, mean growth rate from each tank was regressed linearly on DO level for the three constant DO levels (2, 4, 6 ppm). Growth rate in the fluctuating (2-12 ppm) treatment was then included in an overall ANOVA analysis followed by Tukey's HSD tests for pairwise comparisons (it was not included in the regression because it was not a constant DO treatment like the others). In these contrasts, a comparison of particular interest was the 6 ppm constant DO treatment vs. the 2-12 ppm fluctuating DO treatment because the 6 ppm DO level was closest to the mean DO level in the fluctuating treatment (about 7.2 ppm DO). There were 3 replicates (N=3 aquaria for each of the four DO treatments) and 20 shrimp (subsamples) per DO treatment. Linear regressions, ANOVAs and Tukey's tests were performed using SAS software (version 8.2, SAS Institute Incorporated, Cary, NC). Mean wet weights and lengths

were  $2.82 \pm 0.05$  g and  $70.4 \pm 0.4$  mm (mean  $\pm$  1 SE) for brown shrimp and  $2.16 \pm 0.04$  g and  $65.4 \pm 0.4$  mm for white shrimp.

## RESULTS

### *Physicochemical conditions in the tanks*

Target and realized DO values for constant DO treatments were very close, differing by averages of only 2.3, 1.5 and 6.4% for brown shrimp in the low, medium and high DO treatments, and by 3.3, 0.2 and 1.9% for white shrimp. Realized DO levels were also of low variability. For example, the SEs of low, medium, high and fluctuating DO levels were all considerably less than 0.1 ppm (Table 2). Ammonia, nitrate and nitrite levels were  $< 0.6$ ,  $< 3.9$  and  $< 1.4$  ppm in both experiments, salinity was between 14.7 and 15.7 ppt and pH was virtually constant at 8.2 (Table 2).

### *Growth Rates*

Growth rate of white shrimp responded positively to increased DO level, but growth rate of brown shrimp did not (Figs. 1 and 2). For white shrimp, there were statistically significant linear relationships between growth rate and DO level over the 2 to 6 ppm range for all three time periods (Fig. 1). Over the first and second 10-day periods, growth rate at 2 ppm was less than at 6 ppm by 26% and 18%, respectively. The overall 20-day growth rate reflected this decline with a mean difference of 24%. Tukey's HSD tests revealed that growth rate in the fluctuating DO treatment was significantly lower than in the constant high DO treatment over both the first 10-day and the full 20-day periods (values in fluctuating DO

were lower than at constant high DO by about 23% in both instances), but there was no difference over the second 10-day period. Growth rate in the fluctuating DO treatment was indistinguishable from those at 4 ppm and 2 ppm for all growth periods.

The results of the brown shrimp growth rate regressions contrasted sharply with those of white shrimp. For all three time periods, there were no statistically significant linear relationships between growth rate and DO level over the 2 to 6 ppm range with all P-values > 0.32 (Fig. 2). Tukey's HSD tests found growth rates in the fluctuating treatment to be indistinguishable from any of the other DO treatments for all three growth periods.

There was a notable decrease in growth rate in all DO treatments from the first 10-day period to the second, by about 35% for white shrimp and 70% for brown shrimp. The decline was also less pronounced for white shrimp at the lowest DO level, compared to brown shrimp or to white shrimp at higher DO levels (Figs. 1 and 2). The cause of this is uncertain. However, there was some suggestion of physiological adjustment by white shrimp to low DO level in the second half of the experiment (see section on acclimation in discussion).

## **DISCUSSION**

### *White shrimp*

DO level was a good predictor of juvenile white shrimp growth in the range 2-6 ppm, especially over the first 10-day period (first 10-day growth rate regression  $P = 0.0001$  and  $R^2 = 0.89$ ), with reductions in growth rate of about 9% and 22% at the 4 and 2 ppm levels, respectively, relative to the 6 ppm normoxic treatment. This pattern demonstrates that direct

effects of lowered DO on growth are apparent at levels approaching normoxia, and indicates that the spatial scale over which negative DO effects on white shrimp growth rate occur can extend beyond the margins of hypoxic zones (defined as  $\leq 2$  ppm DO).

The fluctuating DO treatment, which averaged  $\approx 7.2$  ppm, resulted in lower white shrimp growth rates than the high DO (6 ppm) treatment. The most likely explanation for this result is that the changeover from daytime high DO to nighttime low DO coincided with the beginning of the shrimp activity cycle: many penaeids exhibit such a pattern of daytime quiescence and nighttime locomotor and foraging activity (Williams 1958, Wickham and Minkler 1975, Matthews et al. 1991). Thus, normal foraging may have been suppressed by the presence of low DO during the night cycle. These data suggest that if shrimp remain in hypereutrophic waters, the nighttime low-DO sometimes observed in these systems may still have negative impacts on growth rate despite several hours of daylight hyperoxia.

### *Brown shrimp*

Brown shrimp were slower growers than white shrimp at all DO treatment levels. In contrast with white shrimp, there was no correlation between DO level and brown shrimp growth rate in the range 2-6 ppm (first ten-day growth rate regression P-value = 0.45 and  $R^2$  was 0.083). This finding was somewhat unexpected, as Ocampo et al. (2000) found that juveniles of another member of the genus (*F. californiensis*) grew significantly less at 2.6 ppm than at 5.8 ppm, although starting weights were substantially less than in my experiment. Renaud (1986a) found that juvenile brown shrimp (65-101 mm) were more sensitive than white shrimp to low DO, with the two species initiating avoidance responses at

$\leq 2.0$  ppm and  $\leq 1.5$  ppm, respectively, suggesting that negative effects of low DO might commence at higher DO levels for brown than for white shrimp. However, Renaud (1986a) also found that white but not brown shrimp would perform abdominal flexures (a typical emergency avoidance response) till exhaustion when exposed to water  $\leq 2.0$  ppm and that brown shrimp had quicker avoidance response times, shorter residence times, and less frequent returns to low DO test water than white shrimp. Thus, it is possible that brown shrimp may simply be better at avoiding low DO than white shrimp and that possession of this phenotype is unrelated to subsequent growth effects of low-DO exposure.

#### *Acclimation*

In crustaceans, acclimation to low DO can occur via several mechanisms, e.g., enhancing oxygen conductance by increasing ventilation rate and/or circulation, increasing hemocyanin oxygen efficiency (Hagerman and Vismann 1995) or concentration (Engel et al. 1993) in conjunction with lactate metabolism (Truchot 1980), or by switching to anaerobic biochemical pathways (Herreid 1980, Burnett 1997). It is possible that once compensatory physiological mechanisms come into effect, energy can be reallocated to growth. The expected net result would be a gradual increase in growth rates with exposure time to low DO. However, in my experiments, the opposite occurred: there were negative shifts in growth rate from the first to the second 10 days of the experiment in all instances and for both species. The fact that these growth rate reductions were also observed at normoxia suggests that DO availability could not have been a significant causative factor. It is possible that a micronutrient deficiency in the feed (which was not specially formulated) could have

had a cumulative effect over time, eventually causing growth decline, or it may have been a delayed manifestation of the extremely high shrimp density of 80 shrimp·m<sup>-2</sup> (deliberately chosen to improve the number of subsamples). Despite the universal decreases in growth rates, it was felt that comparisons between the first and second 10 day periods might still yield some qualitative evidence of acclimation, provided that the above “system effect” was discounted first. This was done multiplying 10-day growth rates by a correction factor, calculated as:

$$\text{Correction factor} = [(\text{GR at normoxia, 2}^{\text{nd}} \text{ ten days)} \div (\text{GR at normoxia, 1}^{\text{st}} \text{ ten days})]$$

Values were 0.62 and 0.26 for white and brown shrimp, respectively. These correction factors were then used to adjust second 10-day growth rates in the 4 ppm and 2 ppm DO treatments, permitting a comparison with their corresponding first 10-day values to test for acclimatization (Table 3).

The results were different for the two species. For white shrimp, both corrected second 10-day growth rates were higher than first 10-day growth rates (by 5% and 11% in the 4 ppm and 2 ppm treatments, respectively). This supports the notion that there is a small degree of growth compensation in this species, a finding that agrees with Rosas et al. (1998) who found evidence of compensatory mechanisms to preserve growth, regardless of DO concentration. For brown shrimp, corrected second 10-day growth rate was 46% higher than first 10-day growth rate at 4 ppm, but 19% lower at 2 ppm, suggesting strong compensatory growth at 4 ppm but depensatory growth at 2 ppm.

*Implications for management*

Overall, these results demonstrate that there are negative effects on growth for juvenile white shrimp well above the DO levels that elicit an avoidance response. Consequently, if white shrimp populations are subjected to low DO for prolonged periods, they will exhibit reduced growth rates compared with populations in normoxic waters. The increasing occurrence of stable, large-scale hypoxic events within U.S. Atlantic estuaries is thus a reason for serious concern for this species. In addition, there may be likely competitive effects on growth due to overcrowding when hypoxia does drop to avoidance thresholds, as shrimp are crowded into more confined spaces (the subject of Chapter 5). There is a robust body of evidence documenting the occurrence of shrimp and other estuarine organisms in proximity to, and undertaking movements away from, waters that range in DO level from 1 to 3 ppm (Loesch 1960, Huddart and Arthur 1971, May 1973, Pihl et al. 1991, Howell and Simpson 1994, Zimmerman et al. 1997, Diaz and Solow 1999, Downing et al. 1999, Wannamaker and Rice 2000, Eby and Crowder 2002).

Chronic seasonal low DO has been well documented in many areas occupied by brown and white shrimp (Rabalais 1998, Paerl et al. 1998, Downing et al. 1999, Ritter and Montagna 1999, Glasgow and Burkholder 2000, Joyce 2000, Boesch et al. 2001, Diaz 2001, Rowe 2001, Rabalais et al. 2001, Selberg et al. 2001, Buzzelli et al. 2002). The findings of previous studies (Leming and Stuntz 1984, Renaud 1986a, Wannamaker and Rice 2000, Eby and Crowder 2002) indicate that brown and white shrimp avoid DO levels in the vicinity of 1.5-2.5 ppm, and suggest that mortality thresholds would begin below these levels as well. Further evidence in the form of positive correlations between DO level and shrimp

abundance is provided by Diaz and Solow (1999), Zimmerman et al. (1997), Renaud (1986b) and Trent et al. (1976). A study by Martínez et al. (1998) found a 72-h DO LC50 of 1.16 ppm for white shrimp early juveniles (720 mg wet weight) at pH 8 and 15 ppt salinity, with higher LC50s found at higher salinities. Kramer (1975) found in a laboratory study that DO was not lethal to brown shrimp juveniles or subadults until it fell below 1.0 ppm.

The fact that low DO events can increase vulnerability to predators (see Chapter 3) and/or compress shrimp populations into smaller areas means that there is a potential for overharvesting as fleets adjust fishing patterns to maintain catch per unit effort (Zimmerman et al. 1997). For example, in a study of a crustacean fishery in the southern Kattegat, catch per unit effort (CPUE) of Norway lobster more than doubled when DO levels dropped below 40% saturation (Baden et al. 1990). After prolonged periods of overharvesting, initially-realized increases in harvests can actually reverse themselves as stocks border on collapse. In the Gulf of Mexico, there is evidence of continuous declines in decadal CPUEs of both brown and white shrimp since the 1960s, yet no evidence of recruitment failure and, although declines may be linked to changes other than hypoxia, these trends are consistent with the hypothesis of environmental impact (Caillouet et al. 1981, Downing et al. 1999). Habitat restriction can also lead to indirect negative effects via increased metabolic costs, intra- and interspecific competition in suboptimal habitats, promoting compensatory growth, disease, cannibalism and predation (Mittelbach 1988, Turner and Mittelbach 1990, Breitburg 1992, Persson and Eklöv 1995). In an economic analysis of Gulf of Mexico shrimp data, Diaz and Solow (1999) had equivocal results when looking for a relationship between CPUE and hypoxia, primarily because of the difficulty of disentangling effects due to covarying factors

besides hypoxia (such as climatic factors) that can also affect shrimp populations. Nonetheless, Diaz and Solow (1999) noted that the possibility of a relationship between CPUE and hypoxia could not be dismissed, after finding evidence of a hypoxic effect on brown shrimp CPUE by examining the correlation between a detrended hypoxia index and detrended log CPUE. Another important finding of Diaz and Solow (1999) was an overall tendency for mean size of harvested brown and white shrimp to decrease over the 40-year study period 1957-1997, suggesting a decline in shrimp growth rates. Craig (2001) used fishery-independent bottom trawl surveys from the northwestern Gulf of Mexico to examine the displacement effects from hypoxic bottom waters on brown shrimp, and found high local aggregations on the offshore edge of hypoxic zones diminishing rapidly with distance away from the edge. Low DO also has the potential to block or alter migration routes, rendering habitats that are necessary for certain life stages inaccessible (Renaud 1986b, Zimmerman et al. 1997, Diaz and Solow 1999, Downing et al. 1999).

In addition to the evidence of such mass movements to avoid hypoxia, my results show that statistically significant reductions in growth can be expected for white shrimp at levels as high as 4 ppm DO down to 2 ppm in as little as ten days. This finding is important because even though shrimp catch rates become independent of DO concentration above 2.5 ppm (Leming and Stuntz 1984), there may still be negative effects on white shrimp growth in higher DO regions that flank hypoxic (< 2 ppm DO) zones. Although brown shrimp did not display such a growth response, it should be noted that there was some suggestion of reduced growth at lower DO that my sample size may have been inadequate to detect. It is also possible that statistically significant differences in brown shrimp growth rates would begin to

be observed at lower DO levels than I tested, in the range 1.5-2.0 ppm. McNatt (2002) found precisely such a trend with Atlantic menhaden (*Brevoortia tyrannus*) and spot (*Leiostomus xanthurus*), which experienced significant reductions in growth rate at 1.5 ppm DO compared with growth at 2.0 ppm DO. It is not currently known whether shrimp can recover from the negative effects of exposure to low DO on growth via post-event compensatory mechanisms but it is reasonable to posit that reduced growth can have serious implications for ensuing fecundity, which is a linear function of body weight in both species (Velázquez and Gracia 2000) and may enhance size-dependent predation mortality (Post and Evans 1989, Lundvall et al. 1999). My findings add further weight to the body of evidence suggesting that DO levels between 2 and 5 ppm are biologically stressful (NOAA 1999). This phenomenon argues for continued emphasis on the need for reduced nutrient inputs into estuaries.

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Table 1. Composition of commercial feed used to maintain juvenile brown shrimp (*Farfantepenaeus aztecus*) and white shrimp (*Litopenaeus setiferus*) in outdoor tanks.

Composition (%) of Corey "Hi-Pro" Starter Feed*	
Feed Size	0.7 gr
Crude Protein (min)	55
Crude Fat (min)	16
Crude Fiber (max)	2
Moisture (max)	9
Ash (max)	9
Phosphorus (actual)	1.2
Nitrogen-free extract (NFE, actual)	9.4
Protein: Energy Ratio (grams DP/MJ DE)	30.5
Digestible Energy (MJ/Kg)	16

\*Ingredients: Fish Meal (LT), Fish Oil, Wheat, Krill, Salt, Vitamins, Minerals, Pigment, Methionine

Table 2. Summary of physicochemical measurements (mean  $\pm$  1 SE ) taken during growth experiments on juvenile brown shrimp (*Farfantepenaeus aztecus*) and white shrimp (*Litopenaeus setiferus*).

Parameter	Brown Shrimp (2001)	White Shrimp (2000)
Ammonia (ppm)	0.59 $\pm$ 0.10	0.37 $\pm$ 0.12
Nitrite (ppm)	1.33 $\pm$ 0.13	1.42 $\pm$ 0.22
Nitrate (ppm)	3.85 $\pm$ 0.40	2.95 $\pm$ 0.50
pH	8.20 $\pm$ 0.01	8.20 $\pm$ 0.01
Alkalinity (meq/L)	3.04 $\pm$ 0.05	3.10 $\pm$ 0.05
Salinity (ppt)	15.0 $\pm$ 0.3	15.2 $\pm$ 0.5
DO, low trt.	2.11 $\pm$ 0.04	2.06 $\pm$ 0.01
DO, med trt.	4.06 $\pm$ 0.04	4.00 $\pm$ 0.02
DO, high trt.	5.61 $\pm$ 0.05	5.88 $\pm$ 0.02
DO, fluc. trt.	7.34 $\pm$ 0.08	7.17 $\pm$ 0.01

Table 3. Correction factors applied to second 10-day GRs to test for acclimatization to low DO.

Species	DO level (ppm)	First 10-day GR	Second 10-day GR	Correction Factor	Corrected Second 10-day GR
White Shrimp (2000)	6	2.32	1.43	0.62	
	4	2.06	1.33		2.17
	2	1.72	1.17		1.91
Brown Shrimp (2001)	6	1.11	0.29	0.26	
	4	1.11	0.43		1.62
	2	0.95	0.20		0.77

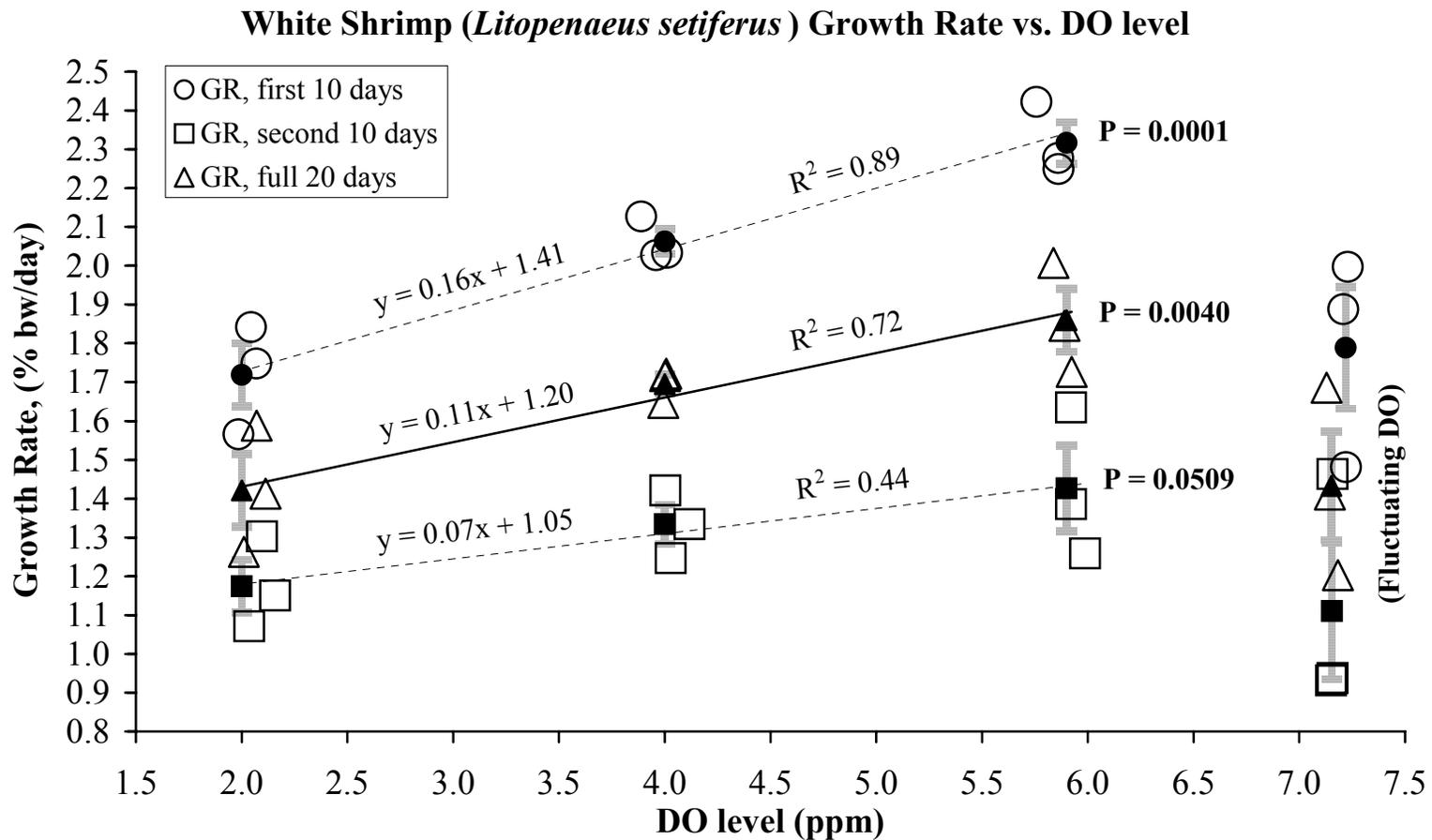


Fig. 1. Regression of growth rate (% bodyweight per day) against constant dissolved oxygen (DO) level for juvenile white shrimp (*Litopenaeus setiferus*). Fluctuating DO levels (data points on the right > 7 ppm) was not included in the regression analysis. Solid shapes represent means. Error bars represent 1 SE.

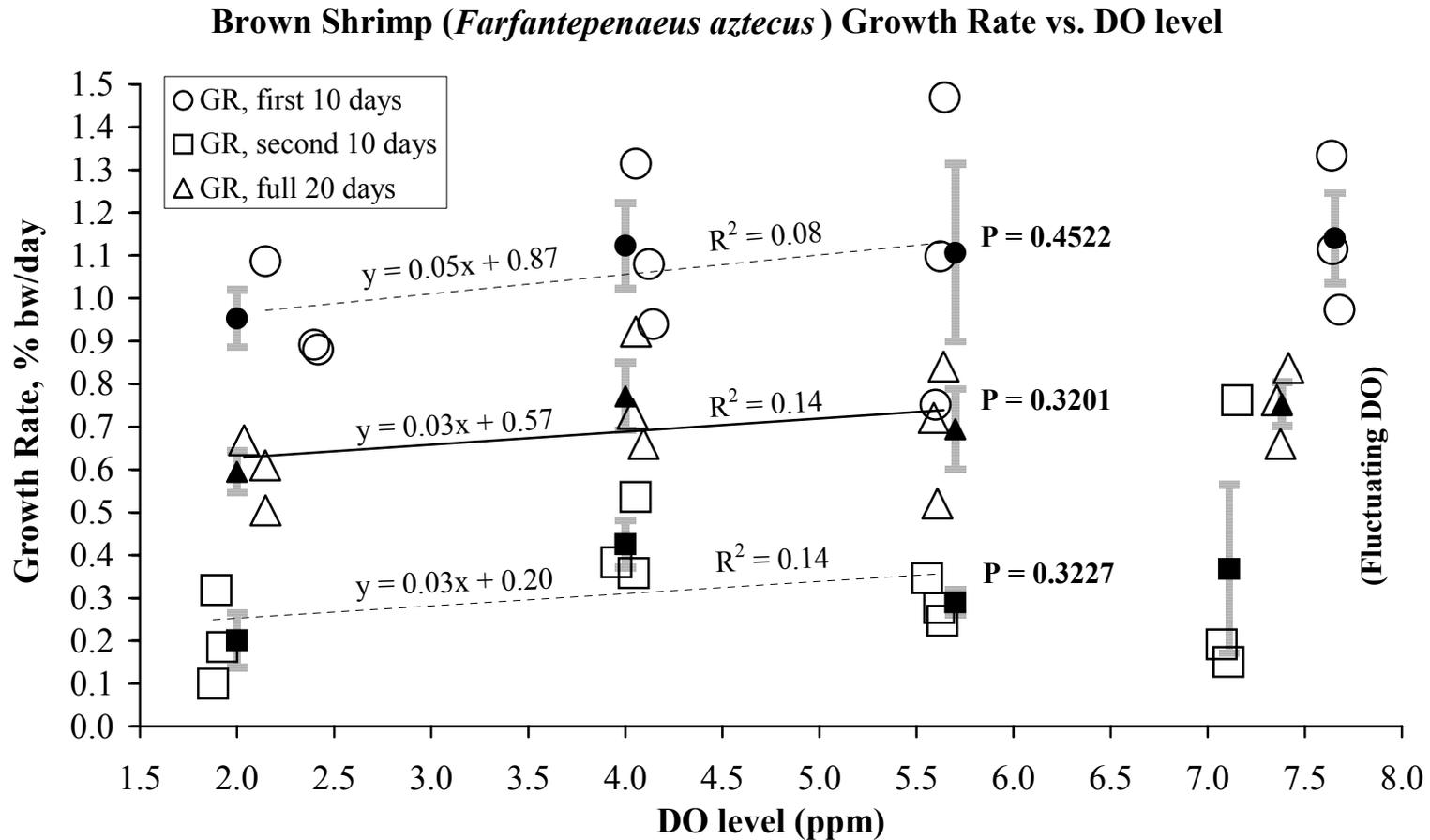


Fig. 2. Regression of growth rate (% bodyweight per day) against constant dissolved oxygen (DO) level for juvenile brown shrimp (*Farfantepenaeus aztecus*). Fluctuating DO levels (data points on the right > 7 ppm) were not included in the regression analysis. Solid shapes represent means. Error bars represent 1 SE.

### **Chapter 3. Effect of dissolved oxygen level and predation threat on the emergence behavior of juvenile brown shrimp.**

#### **ABSTRACT**

Brown shrimp (*Farfantepenaeus aztecus*) typically burrow into estuarine sediments during daylight to conserve energy and avoid fish predation, their major source of mortality. There is evidence that hypoxia, the decline of dissolved oxygen (DO) below 2.0 ppm, reduces burrowing by stimulating shrimp to emerge from their refugia to seek higher-DO water. At the onset of hypoxia there thus exists a trade-off between negative effects of low DO versus increased vulnerability to predators. Here, two experiments examined this trade-off between biotic and abiotic factors by: (1) asking whether juvenile brown shrimp altered the duration of their daytime emergence when exposed to different combinations of DO level (6.0 ppm vs. 1.5 ppm) and perceived predation threat (a fish caged behind a screen vs. screen only); and (2) asking whether shrimp mortality or emergence duration depended on DO level when a free-ranging (uncaged) predator was present.

Time-lapse video cameras recorded the emergence durations of individual shrimp from a substrate during daylight hours. In the first experiment, the proportion of time emerged was significantly greater in the low DO treatment than at high DO, regardless of predator treatment (DO level was a significant main effect, but predator treatment was non-significant, with no interaction). In the second experiment, attack and predation events were rare. However, although the mean proportion of time emergent in the low DO treatment was again higher than in the high DO treatment, it was about 50% less than in the first experiment at low DO. This suggests that when a free-ranging predator is present, shrimp show a trade-

off between the urge to emerge from cover that hypoxia elicits and the probability of a lethal encounter with a predator, and reduce their exposure time accordingly. These results indicate that low DO can increase the vulnerability of shrimp by increasing their exposure time, but that predation threat can modify the magnitude of response, emphasizing the importance of behavioral considerations when examining the net effect of biotic and abiotic factors.

*Key words:* Predator, predation, prey, emergence, burrowing, juvenile shrimp, hypoxia, brown shrimp, *Farfantepenaeus aztecus*, *Penaeus aztecus*, pinfish, *Lagodon rhomboides*.

## INTRODUCTION

The brown shrimp (*Farfantepenaeus aztecus*) is a key component of estuarine ecosystems that, via differential selection of prey/food items from sediments, may affect infaunal community structure (McTigue and Zimmerman 1998), as has been shown for other shrimp species (Bell and Coull 1978). Brown shrimp are also a significant dietary component for a suite of estuarine finfish species (Knapp 1949, Lindner and Cook 1970, Minello and Zimmerman 1983, Minello and Zimmerman 1984, Minello et al. 1987), thus providing an important link between primary producers and secondary consumers. The species is also a major contributor to commercial harvests over a large portion of the Atlantic seaboard of the United States and into the Gulf of Mexico: in 2001, the estimated value and weight of all commercially landed shrimp species in the United States were  $\$576 \times 10^6$  and  $157 \times 10^3$  t, of which brown shrimp contributed  $\$289 \times 10^6$  and  $69 \times 10^3$  t, accounting for 50.2% and 44.0% of the total shrimp values respectively (personal communication, David

Sutherland, National Marine Fisheries Service, Fisheries Statistics and Economics Division, Silver Spring, MD).

Many penaeids, including brown shrimp (*Farfantepenaeus aztecus*), exhibit a pattern of daytime burrowing and nighttime locomotor activity and feeding (Williams 1958, Wickham and Minkler 1975, Matthews et al. 1991). Burrowing has been suggested as an important energy-conservation and predator avoidance mechanism (Williams 1958, Wickham and Minkler 1975, Rulifson 1981, Minello and Zimmerman 1984, Larson et al. 1989). Eutrophication has been escalating in many Atlantic estuaries in recent decades, and with it has come the problem of large-scale seasonal hypoxia (Diaz and Rosenberg 1995, Nixon 1995, Richardson and Jørgensen 1996, Breitburg et al. 1997, Paerl et al. 1998, Diaz and Solow 1999, Smith et al. 1999, Luttenberg 2000, Diaz 2001, Breitburg 2002, Gray et al. 2002). Because estuaries house the nursery habitats that are crucial to the success of earlier shrimp life stages, hypoxia ( $DO \leq 2.0$  ppm) has the potential to cause serious disruption of their normal patterns of behavior, including the burrowing behavior described above.

Moving objects create visual, mechanical and olfactory stimuli, while immobility is often required for crypsis in both predators and prey (Edmunds, 1974). Movement is thus frequently associated with an increased probability of detection or attack of prey by predators, and with an increased probability of detection or flight from predators by prey (Kramer and McLaughlin 2001). Brown shrimp begin to avoid low DO water at 2.0 ppm (Renaud 1986) and are not capable of swimming above hypoxic bottom waters for extended periods of time (Lowery 1983). Thus, hypoxic events have the potential to disrupt normal patterns of shrimp burrowing behavior and lead to periods of increased availability to

predators as they seek higher-DO waters. Large aggregations of demersal species, including shrimp, have been documented evading low DO waters (Loesch 1960, May 1973) but direct mortalities were low probably due to the animals' avoidance responses.

Some studies have considered the trade-offs in behavioral responses of organisms in the face of potentially negative biotic and abiotic factors (Poulin et al. 1987, Rahel and Kolar 1990) and specifically the effects of hypoxia on predator-prey and other trophic interactions and community structure (Kersten et al. 1991, Rosenberg et al. 1992, Pihl et al. 1992, Kolar and Rahel 1993, Breitburg et al. 1994, Pihl 1994, Sandberg 1994, Breitburg et al. 1997, Johansson 1997, Taylor and Eggleston 2000, Tallqvist 2001). At the threshold of hypoxia, shrimp will be faced with a trade-off between the negative effects of low DO on sedentary individuals versus the increased vulnerability of those that emerge from cover. Possible disruption of behavioral responses due to oxygen deficiency can have serious consequences for organisms because many behaviors have important survival value, thus detailed investigations are needed to understand changes in the relationship between predator and prey mediated by hypoxia (Sandberg 1994). Here, I examined the trade-off between predator avoidance and emergence from cover under hypoxia in juvenile brown shrimp with two experiments assaying the emergence duration of brown shrimp under various combinations of DO level and predation threat.

## **MATERIALS AND METHODS**

Juvenile brown shrimp and age-1 pinfish (*Lagodon rhomboides*) predators were collected from Calico Creek, Morehead City, and Pivers Island, Beaufort, North Carolina,

respectively, using a 2.3 m cast net (0.63-cm mesh), and transported in a 500-L truck-mounted tank to 7500-L outdoor flow-through ( $1000 \text{ L}\cdot\text{hr}^{-1}$ ) tanks at the National Marine Fisheries Service Laboratory, Pivers Island, North Carolina. To reduce shrimp mortality in transit, seawater was saturated with pure oxygen. Shrimp and pinfish were fed daily an excess of aquaculture-grade feed (55% crude protein; Corey Feed Mills Limited, New Brunswick, Canada), in addition to any organic matter settling out of the unfiltered seawater supply. The feed composition is summarized in Chapter 2 (Table 1). A pinfish predator was chosen for these experiments because its consumption of shrimp is well documented (Hansen 1969, Carr and Adams 1973, Brook 1977, Stoner 1980, Minello and Zimmerman 1983) during daylight hours (Minello and Zimmerman 1983), and also because it is resilient to low DO levels. During July 24 - September 15, 2002, shrimp and/or pinfish were taken daily from these outdoor tanks and transported in 45-L coolers to the NCSU Center for Marine Sciences and Technology/Carteret Community College (CMAST/CCC) Laboratory in Morehead City, where the experiments were conducted.

The experimental apparatus consisted of two identical and independent recirculating closed-systems, each of which gravity-fed seawater at 35 ppt salinity from a 550-L header tank into a custom-built 40-L ( $30 \text{ cm} \times 30 \text{ cm} \times 45 \text{ cm}$ ) Plexiglas aquarium. The two aquaria lay side-by-side (left/right) with an opaque screen between them to prevent any visual interaction. Seawater overflowed from each of these aquaria into a 300-L sump before being pumped back to each header tank. The system was mounted on scaffolding and covered in heavy-duty black plastic sheeting to preclude visual disturbance to test animals, and to ensure

darkness at night to prevent light phase resynchronization, i.e., to ensure normal diurnal patterns of activity (Wickham and Minkler 1975).

I chose to use a 1.5 ppm low DO threshold in these experiments based on evidence from earlier studies indicating avoidance behavior by penaeid shrimp at levels around 2 ppm (Renaud 1986, Wannamaker and Rice 2000, Eby and Crowder 2002) although there were some field observations of shrimp even in extremely hypoxic waters close to anoxia. DO treatments were applied to each system by bubbling either nitrogen or air (via a custom-made diffuser incorporating several airstones) at carefully controlled rates in the header tanks. Header and sump tanks were covered with Styrofoam sheeting (Dow Chemical Company, Midland, MI), which effectively minimized oxygen diffusion rates into or out of the system, allowing the attainment of stable DO levels. A single 5-cm hole was bored into the center of each header tank lid to facilitate DO and temperature measurements, using a YSI Model 57 digital DO meter (Yellow Springs Instruments, Yellow Springs, Ohio). Every two days a water sample was taken from each system to test for pH, nitrate, nitrite, ammonia and salinity.

Each aquarium was lined to a 10-cm depth with an artificial substrate, consisting of 250  $\mu\text{m}$  glass beads (Potters' Ballotini glass impact beads, Potters Industries Inc., Apex, NC). Artificial substrate was used because bacterial decomposition of organic matter in naturally-occurring sediments can alter their redox potential and produce hydrogen sulphide, which could have confounded the interpretation of the main factors of interest. In the first ("caged-predator") experiment, a 30 cm  $\times$  30 cm monofilament mesh screen (0.63-cm mesh) was positioned 8 cm above the sediment surface, partitioning each aquarium into two sub-

compartments. During each 24-hr trial, the smaller, lower sub-compartment housed an individual juvenile brown shrimp, and the larger, upper sub-compartment housed either a single mature (age 1) pinfish, or no pinfish. New individuals were used for each trial and the application of predator treatments was randomized. High and low DO treatments were applied to a specific left or right tank during the first half of trials and were then switched when both systems were drained and replenished with fresh seawater. The screens were placed at an 8-cm height above the sediment to permit enough volume for shrimp to move freely across the sediment surface, while still enabling both pinfish and shrimp to be within each others' reactive distance. Shrimp and pinfish were placed in the aquaria at the beginning of the night cycle to acclimate to ambient DO levels for about ten hours. In the second ("free-predator") experiment, no screen was present, and it was important to acclimate shrimp and fish without the possibility of a predation event before the commencement of the daylight cycle the following morning. Pinfish were thus acclimated separately overnight in the sump tanks using 19-L perforated buckets and were subsequently transferred to the aquaria at the beginning of the following daylight cycle using a dip net, loading from above via a 6 cm × 20 cm slit in each aquarium lid to minimize disturbance.

Ambient air temperature was used (generally 27-28 °C), as stricter temperature control was not possible in the building, equipped only with exhaust fans. Each aquarium was exposed to an ambient diel light cycle (14:10 LD photoperiod) using a single overhead fluorescent light (General Electric "Gro & Sho Light Stik", 33 Watts) placed 40 cm above the aquaria. Shrimp emergence behavior was monitored and recorded using a pair of infrared cameras (Panasonic model WV-BL204 CCTV security camera) placed 40 cm in front of each

aquarium. Nighttime observations were facilitated by the use of infrared lights (SONY HVL-IRC Infrared Video Light) which were left on continuously, positioned 1 m behind and 20 cm above each aquarium. Video feed was recorded by a time-lapse video recorder (Eversecure Time Lapse VCR) which switched back and forth between the two aquaria (Eversecure Quad Switching Unit). In the caged-predator experiment, four predation threat  $\times$  DO level combinations were used: predator  $\times$  high DO, predator  $\times$  low DO, no predator  $\times$  high DO, and no predator  $\times$  low DO. There were ten replicates of each predation threat  $\times$  DO level treatment, using a different individual shrimp/pinfish each time. In the free-predator experiment, two predation threat  $\times$  DO level combinations were used: predator  $\times$  high DO, and predator  $\times$  low DO, with 14 replicates of each treatment.

At the end of experiments, videotapes were carefully reviewed and the time that each shrimp spent emergent during the day cycle was recorded. Emergence was defined as any point in time when  $> 50\%$  of the thorax was exposed above the surface of the substrate, including sedentary periods in open excavated trenches. This protocol was adopted because burrowed shrimp occasionally leave the tips of their rostra, antennal scales and antennae visible when burrowed. Emergence time was converted to a proportion by dividing by the total time of the day period. Data were analyzed using SAS Proc GLM (version 8.2, SAS Institute Incorporated, Cary, NC) with proportion of time emergent as the response variable. An ANOVA model for the caged-predator experiment incorporated predation threat, DO level, and tank (left/right) as fixed main effects, with DO level  $\times$  predation threat as an interaction term. For the free-predator experiment, I used a Mann-Whitney U-Test (Wilcoxon two-sample rank test) and a t-test to look for differences between the proportions

of time spent emergent. A second ANOVA using combined data from both experiments incorporated predation threat (free-predator or no predator) and DO level (high/low) as fixed main effects, with threat  $\times$  DO level as an interaction term. Shrimp weights and lengths were  $6.5 \pm 0.2$  g and  $94.5 \pm 1.3$  mm, and  $7.9 \pm 0.3$  g and  $100.6 \pm 1.3$  mm (mean  $\pm$  1 S.E.) for caged- and free-predator experiments respectively. Corresponding mean pinfish weights and lengths were  $48.5 \pm 3.3$  g and  $146.0 \pm 3.4$  mm, and  $49.2 \pm 1.9$  g and  $150.8 \pm 2.0$  mm (Table 1).

## RESULTS

In both experiments, ammonia and nitrite levels were below 0.3 ppm and nitrate did not exceed 0.5 ppm, pH was virtually constant at 8.2 and salinity ranged between 34 and 35 ppt (Table 2). At 1.5 ppm DO, shrimp burrowed for a substantial proportion of daylight (about 42% and 70% of daylight time in caged- and free-predator experiments, respectively). In the caged-predator experiment there was a strong effect of DO on emergence time, with the proportion of time emerged increasing from about 0.2 at high DO to about 0.6 at low DO (Fig. 1). This effect was highly significant statistically ( $P = 0.0002$ , Table 3). However, none of the other model components (predation threat, tank side, DO level  $\times$  predation threat interaction) was significant (Table 3).

In the free-predator experiment, there was again a significant effect of DO on emergence time (Mann-Whitney  $P = 0.02$ ; t-test  $P = 0.089$ ), but predation events (one of three attacks successful in high DO; one unsuccessful attack in low DO) were too low to permit any evaluation of DO effects on predation mortality. While I did not initially plan to

compare emergence time of shrimp with free-predator vs. no predator (i.e., across experiments), I noted that the emergence time under low DO in the free-predator experiment was depressed relative to the caged-predator experiment. Analyzing this contrast as a  $2 \times 2$  ANOVA (free/no predator, high/low DO) yielded a significant DO effect ( $P = 0.0007$ ), with a marginally non-significant predator effect ( $P = 0.08$ ) and interaction ( $P = 0.11$ ).

## DISCUSSION

The use of a caged predator to simulate predation threat is a common practice (e.g., Weetman et al. 1998, Brown and Godin 1999, Weetman et al. 1999, Chivers et al. 2001, Peacor 2002). The most prominent trend in the data of both experiments is the greater shrimp emergence at low DO compared to high DO (Fig. 1). In the caged-predator experiment, low DO more than doubled emergence time both in the presence of the screened predator as well as when no predator was present, but predator presence/absence had no discernable effect on emergence (Table 3; Fig. 1). It is possible that this lack of a predator effect on emergence arose because the height of the screen above the substrate exceeded brown shrimp reactive distance. Although shrimp have the ability to visually detect mobile predators and can reduce predation rates in clear, normoxic water by burrowing (Minello et al. 1987), the acuity of the crustacean compound eye is much lower than that of the vertebrate eye (Waterman 1961, Goldsmith 1973) so that alterations in shrimp behavior may not occur until interactions are more proximal, i.e., in the particular instance of the caged-predator experiment, predator recognition and the subsequent urge to burrow might have only occurred over shorter distances than the screen height of 8 cm. Shrimp may have

evolved this phenotype because of the inherent turbidity of the estuaries in which they evolved. This demonstrates the possibility of inaccuracies when using a captive predator as a substitute for a real predation threat, and the need for careful scaling considerations.

In the free-predator experiment, the strong effect of DO on emergence was again evident and, although the combined ANOVA (free/no predator, high/low DO) revealed only a marginally non-significant predator effect, the reduction in emergence durations in the free-predator experiment relative to the caged-predator experiment was quite striking (Fig. 1). It appears that the presence of a free-ranging predator changes the nature of the trade-off between the urge to emerge from cover (that hypoxia evokes), and the likelihood of a possible lethal encounter with a predator, resulting in a reduction in exposure time. This also suggests that predator stimuli must somehow still play into escape response decisions even at DO levels as low as 1.5 ppm. The contrast in shrimp emergence responses between caged and free-ranging predator treatments also suggests that olfactory stimuli from pinfish were not an important factor in shrimp burrowing decisions (since these cues were present in both experiments).

The fact that shrimp burrowed for substantial periods of daylight while under low DO underscores some important points: (1) Brown shrimp will not necessarily initiate an avoidance response even as low as 1.5 ppm DO, which contradicts previous evidence suggesting an avoidance threshold beginning at 2.0 ppm (Renaud 1986). However, the design of the Renaud (1986) study did not incorporate substrate, which may be an important consideration in shrimp response to low DO; (2) The critical level for complete emergence of juvenile brown shrimp must be at some level lower than 1.5 ppm DO; and (3) Shrimp may

seek to minimize the cost of obtaining oxygen by remaining quiescent, i.e., burrowed, until some critical oxygen level is reached. The latter point is corroborated by Kramer (1975) who concluded that shrimp can tolerate low levels of DO by becoming inactive.

Based on evidence from studies on shrimp and other benthic organisms, there are two particularly interesting behavioral scenarios that may occur as DO level declines beneath the hypoxia threshold. Under a “stress-compromised” scenario, physiological stress and resultant abnormal behavior that may result from unavoidable exposure to hypoxia (emergence from burrowing, morbidity) may render shrimp more vulnerable to waiting predators or predators tolerant of low DO that are making temporary incursions into hypoxic zones (Renaud 1986, Pihl et al 1991, Pihl et al. 1992, Rahel and Nutzman 1994, Diaz and Rosenberg 1995). Under an “opportunistic predator” scenario, predators may forage within large aggregations of emigrating shrimp now known to occur at the periphery of recent hypoxic events (Craig 2001), or otherwise benefit from the overall increase in shrimp densities that may occur in the reduced area of suitable high DO habitat (a delayed, indirect hypoxia effect).

Several published studies offer insight regarding the likelihood of these scenarios in natural systems. Kramer (1975) found that for brown shrimp (91 mm) mean lethal dissolved oxygen levels were 0.8 and 0.5 ppm at DO reduction rates of 1.4 and 2.8 ppm/hr respectively, an important finding that implies that the speed of formation of hypoxia can determine when and at what level of DO shrimp mortality begins. Kramer (1975) also found that shrimp maintained normal patterns of swimming and burrowing until a critical level of DO was reached, 2-4 times the lethal dissolved oxygen concentration, suggesting values of

1.6-3.2 and 1.0-2.0 ppm for the above DO reduction rates, respectively. In an experimental design that did not incorporate the use of sediment, Renaud (1986) found that brown shrimp (65-101 mm) avoided  $DO \leq 2.0$  ppm. In preference trials using sand substrate too shallow (5-7 mm) to permit burrowing, Wannamaker and Rice (2000) similarly found that brown shrimp spent more time at 2 ppm DO (80%) when given a choice between 1 and 2 ppm DO. Many estuarine finfish species display a graded response to declining oxygen concentrations, and typically larger nekton will vacate hypoxic zones before crustaceans, annelids and bivalves (Reish 1970, Rosenberg et al. 1992, Nilsson and Rosenberg 1994, Diaz and Rosenberg 1995). Although there is a dearth of information about critical levels of DO for known major predators of brown shrimp, there is some information on other species: Wannamaker and Rice (2000) found that juvenile pinfish, mullet (*Mugil curema*), croaker (*Micropogonias undulatus*), spot (*Leiostomus xanthurus*) and menhaden (*Brevoortia tyrannus*) all preferred 2 ppm over 1 ppm DO. Breitburg (2002) found that most fish avoid not only lethal DO concentrations but those that reduce growth, which were typically 2-3 times higher than those that lead to 50% mortality in 24- to 96-hour exposures. McNatt (2002) reported that growth rates of juvenile spot (*Leiostomus xanthurus*) and menhaden (*Brevoortia tyrannus*) were significantly reduced (30-90%) at 1.5 ppm DO compared to 2.0 ppm. Eby and Crowder (2002) examined behavioral avoidance thresholds of ten fish species in the Neuse River Estuary, North Carolina: shrimp (cited as *Penaeus* spp.), pinfish, spot, menhaden, croaker, hogchoker (*Trinectes maculatus*), blue crab (*Callinectes sapidus*), silver perch (*Bairdiella chrysoura*), southern flounder (*Paralichthys lethostima*) and weakfish (*Cynoscion regalis*). Their data clearly indicated that all ten species avoided waters with DO

levels < 2.0 ppm. The study of Rahel and Nutzman (1994) gave clear indication that mudminnows (*Umbra limi*) in a Wisconsin lake readily forage in hypoxic water (spending up to 12 minutes there) but, as an important caveat, mudminnows can use aquatic surface respiration and a lung-like gas bladder as an oxygen reservoir during forays into hypoxic conditions (Magnuson et al. 1983, Magnuson et al. 1985), and most fish lack such behavioral/morphological adaptations. Pihl et al. (1991, 1992) found that some predator species (spot; hogchoker; mantis shrimp, *Squilla empusa*) exhibited optimal exploitation of moribund or slowly recovering large-sized macrobenthic infauna affected by hypoxia, although most of the prey items identified were sedentary species (there were no penaeid shrimp).

This collective body of evidence suggests that shrimp are likely to choose higher DO water if there is a choice and if they are already active on the sediment surface. When burrowed during daylight hours, however, brown shrimp will likely remain quiescent until some critical threshold is reached. My laboratory findings suggest that this threshold may be < 1.5 ppm, although the use of an artificial glass-bead substrate free of organic matter may have made it more hospitable to burrowing than in natural sediments where a redox potential discontinuity lying closer to the sediment surface and the evolution of hydrogen sulfide and mobilization of other harmful substances might stimulate shrimp emergence at higher levels of DO. It is unlikely that most vertebrate predators will actually remain in waters when DO drops to levels < 2 ppm. The stress-compromised scenario, if it does occur, is thus likely to involve complex trade-off decisions until DO levels drop to the critical levels (< 2.0 ppm) that trigger a shrimp flight response and may be the exception rather than the rule. The

opportunistic-predator scenario remains the most viable. Direct evidence for the higher shrimp densities necessary for an opportunistic-predator scenario is provided by Craig (2001) who used fishery independent bottom trawl surveys from the northwestern Gulf of Mexico to examine the displacement effects from hypoxic bottom waters on brown shrimp, and found high local aggregations on the offshore edge of hypoxic zones, diminishing rapidly with distance away from this edge. Additional support comes from Eby and Crowder (2002) who clearly demonstrated via CPUE analyses that the majority of shrimp and finfish populations inhabit regions above 2 ppm DO and, interestingly, that avoidance thresholds are affected by the spatial extent of hypoxia.

## **CONCLUSIONS**

Although behavior is an extremely important determinant of survival, the investigation of behavior and the application of behavioral insights to aquatic conservation has been largely neglected (Shumway 1999). Hypoxia and anoxia in estuaries are phenomena associated with natural eutrophication and have thus existed through geological time (Diaz 2001) sufficient for shrimp and their predators to have evolved behaviors that minimize their effect, or exploit them (Meffe 1984). However, with the recent acceleration of cultural eutrophication, Pihl et al. (1991) noted that many estuaries may become characteristically stressed, i.e., experience longer durations and greater spatial scales of hypoxia as they are driven closer to anoxia. It is likely that there will be serious and widespread ramifications of such an expansion of hypoxia within estuarine ecosystems due to altered normal behavior resulting in population- and community-level effects. My research

has shown that brown shrimp will often remain burrowed for substantial periods during daylight hours even at hypoxic DO levels of 1.5 ppm, despite the proximity of such DO levels to their threshold of physiological tolerance.

A predation threat in the form of a free-ranging fish has a suppression effect on shrimp emergence at DO levels as low as 1.5 ppm. These results, when considered with other information about the responses of shrimp to low DO, suggest that they are somewhat adapted to biotic and abiotic stresses and that some variation in responses exists. Such heterogeneity in behavioral responses, which may also exist at the individual level, needs to be more clearly understood if we are to successfully scale up to ecosystem-level effects via modeling efforts (Morales and Ellner 2002). The evidence points in the direction of increased shrimp mortality outside zones of hypoxia/anoxia, as opposed to concurrent mortality within them. In keeping with optimal foraging theory, predators (including humans) may capitalize on large aggregations of emigrating shrimp at the periphery of recent hypoxic events or in outlying high-DO areas where shrimp densities may presumably increase. Additionally, there are many density-dependent sub-lethal effects to shrimp that can occur due to population overcrowding and the simultaneous compression of suitable habitat. Further basic field and laboratory research efforts are needed, particularly across larger scales, to more fully understand the dynamics between juvenile shrimp and their predators in the face of large-scale hypoxia.

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Table 1. Summary of means  $\pm$  1 SE for predator threat  $\times$  DO level treatment combinations, proportion of time emergent, DO level, temperature, weights and lengths of juvenile shrimp and age-1 pinfish used in Experiment 1 and Experiment 2.

	Treatment combination	n	Proportion of time emergent	DO level (ppm)	Temperature (°C)	Shrimp Weight (g)	Shrimp Length (mm)	Pinfish Weight (g)	Pinfish Length (mm)
<b>Experiment 1</b>	Screen, predator, high DO	10	0.23 $\pm$ 0.08	6.01 $\pm$ 0.05	28.41 $\pm$ 0.43	6.20 $\pm$ 0.44	94.1 $\pm$ 2.7	48.83 $\pm$ 4.75	144.8 $\pm$ 4.0
	Screen, predator, low DO	10	0.58 $\pm$ 0.13	1.54 $\pm$ 0.05	28.72 $\pm$ 0.43	6.59 $\pm$ 0.41	97.0 $\pm$ 2.6	48.10 $\pm$ 4.82	147.2 $\pm$ 5.7
	Screen, no predator, high DO	10	0.14 $\pm$ 0.06	5.98 $\pm$ 0.06	28.32 $\pm$ 0.49	7.54 $\pm$ 0.51	98.4 $\pm$ 2.3	n/a	n/a
	Screen, no predator, low DO	10	0.57 $\pm$ 0.08	1.52 $\pm$ 0.04	28.69 $\pm$ 0.51	5.76 $\pm$ 0.45	88.6 $\pm$ 1.9	n/a	n/a
<b>Experiment 2</b>	No screen, predator, high DO	14	0.13 $\pm$ 0.08	6.12 $\pm$ 0.03	27.12 $\pm$ 0.13	8.40 $\pm$ 0.44	102.7 $\pm$ 1.7	47.22 $\pm$ 2.03	148.2 $\pm$ 2.6
	No screen, predator, low DO	14	0.29 $\pm$ 0.09	1.50 $\pm$ 0.03	27.43 $\pm$ 0.17	7.41 $\pm$ 0.46	98.4 $\pm$ 2.0	51.15 $\pm$ 3.25	153.3 $\pm$ 2.9

Table 2. Summary of physicochemical measurements (means  $\pm$  1 SE) in Experiment 1 and Experiment 2.

Test	Experiment 1		Experiment 2	
	Aquarium 1	Aquarium 2	Aquarium 1	Aquarium 2
Ammonia (ppm)	0.24 $\pm$ 0.09	0.29 $\pm$ 0.12	0.18 $\pm$ 0.07	0.22 $\pm$ 0.10
Nitrite (ppm)	0.21 $\pm$ 0.09	0.19 $\pm$ 0.07	0.16 $\pm$ 0.08	0.27 $\pm$ 0.11
Nitrate (ppm)	0.49 $\pm$ 0.11	0.40 $\pm$ 0.16	0.43 $\pm$ 0.13	0.50 $\pm$ 0.09
pH	8.20 $\pm$ 0.01	8.20 $\pm$ 0.01	8.20 $\pm$ 0.01	8.20 $\pm$ 0.01
Salinity (ppt)	34.7 $\pm$ 0.6	34.4 $\pm$ 0.3	34.5 $\pm$ 0.5	34.8 $\pm$ 0.4

Table 3. Summary of ANOVA used to analyze shrimp emergence duration in Experiment 1 (Proc GLM, SAS software version 8.2). The model incorporated DO level (high/low), predation threat (fish/no fish) and tank (left/right) as main effects, with DO level  $\times$  predation threat as the interaction term.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	4	1.5636	0.3909	4.37	0.0057
Error	35	3.1295	0.0894		
Corrected Total	39	4.6931			
Breakdown of main effects and interaction term of the model:					
DO	1	1.5057	1.5057	16.84	0.0002
Predation	1	0.0266	0.0266	0.30	0.5891
Tank	1	0.0124	0.0124	0.14	0.7122
DO * Predation	1	0.0189	0.0190	0.21	0.6481

Table 4. Summary of ANOVA used to compare the data of Experiments 1 and 2 (Proc GLM, SAS software version 8.2). The model incorporated predation threat (free-predator or no predator) and DO level (high/low) as main effects, with predation threat  $\times$  DO level as the interaction term.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	1.3603	0.4534	5.80	0.0020
Error	44	3.4420	0.0782		
Corrected Total	47	4.8023			
Breakdown of main effects and interaction term of the model:					
DO	1	1.0306	1.0306	13.17	0.0007
Predation	1	0.2433	0.2433	3.11	0.0847
Predation * DO	1	0.2106	0.2106	2.69	0.1080

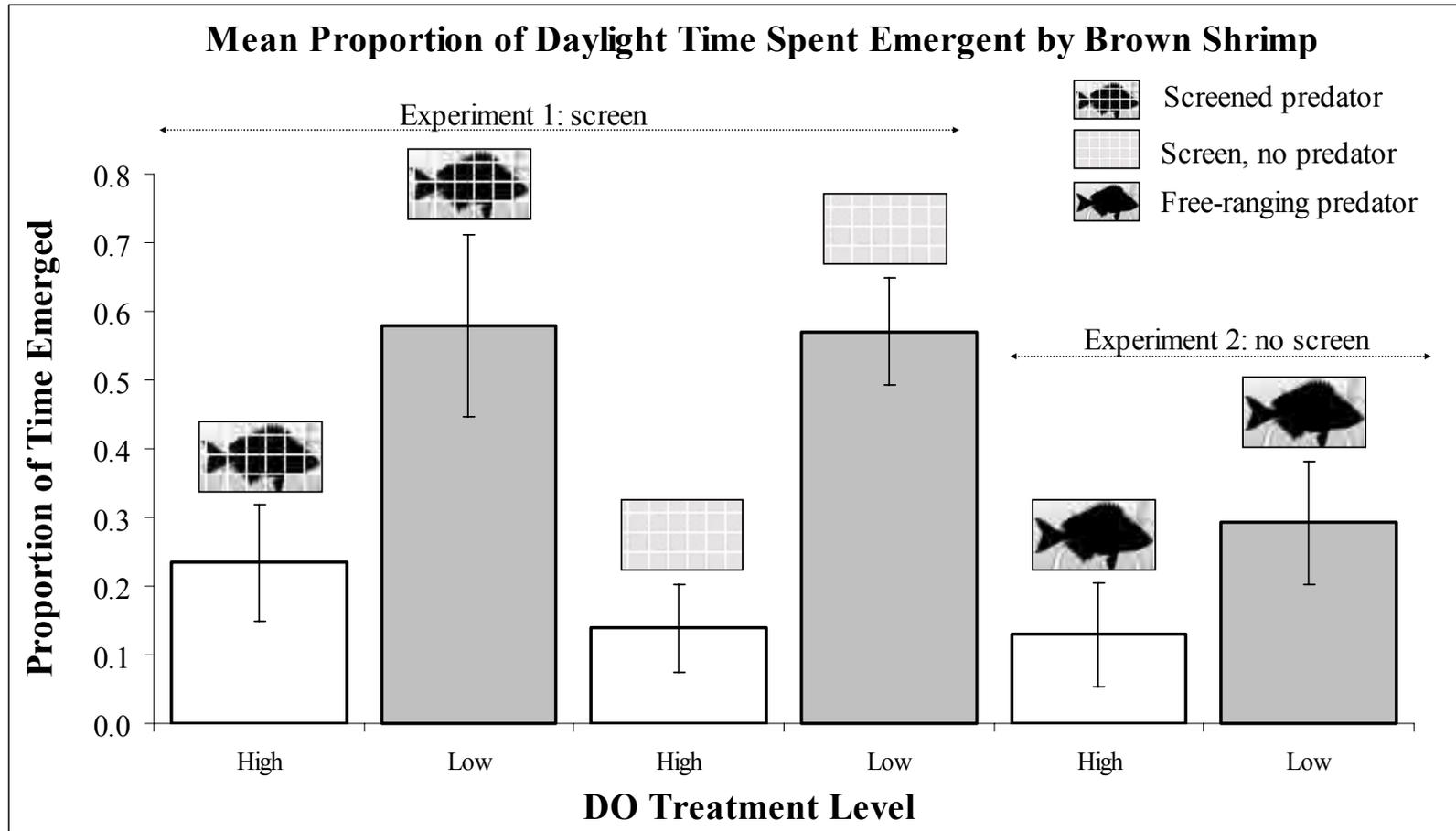


Fig. 1. Proportion of daylight time spent emergent by brown shrimp (*Farfantepenaeus aztecus*) under various DO level and two predation threat treatments. Results of two experiments are shown: Experiment 1 involved use of a screen (left four bars) and Experiment 2 used a free-ranging predator (right two bars). Values are means  $\pm 1$  standard error.

## **Chapter 4. Sediment burrowing preferences of individual juvenile brown and white shrimp.**

### **ABSTRACT**

Juvenile brown shrimp (*Farfantepenaeus aztecus*) and white shrimp (*Litopenaeus setiferus*) exhibit clumped distributions within estuaries that are correlated with sediment type. Hypoxia (dissolved oxygen  $\leq 2$  ppm) is often associated with specific underlying sediments and, consequently, epibenthic species with biased substrate affinities may have higher risks of exposure to it and consequent negative impacts. A laboratory experiment tested for sediment burrowing preferences of juvenile brown and white shrimp among five common sediment types (sand, peat, sandy mud, muddy sand, and shell sand). The preferences of the two species were different from each other (contingency table P-values  $< 0.001$ ) and both species' observed burrowing frequencies among the five sediment types were different from the unbiased null ratio of 0.2 (chi-square  $P < 0.001$  for both species). For brown shrimp, frequencies were higher than expected in sand and peat, as expected in muddy sand, and lower than expected in sandy mud and shell sand. For white shrimp, frequencies were higher than expected in sand, as expected in sandy mud and peat, and lower than expected in muddy sand and shell sand. I compare my findings with those of previous studies, noting differences in scale and design. Burrowing preferences of these penaeids may be based on sediment characteristics, including the ease with which substrate can be penetrated, on foraging and predator-avoidance tradeoffs, and on shrimp proficiency at locating preferred substrate, which is scale-dependent.

*Key words:* Sediment, preference, burrowing, hypoxia, juvenile shrimp, brown shrimp, *Farfantepenaeus aztecus*, *Penaeus aztecus*, white shrimp, *Litopenaeus setiferus*, *Penaeus setiferus*.

## INTRODUCTION

All estuaries receive inorganic and organic sediment from upland rivers, the adjacent ocean, peripheral marshes, and autochthonous production (Matson et al. 1983). Estuaries thus exhibit characteristic distributions and accumulations of benthic sediments that possess various scales of spatial and temporal heterogeneity. Discharge volume, velocity, turbulence and tidal motion displace complex mixtures of dead phytoplankton, nekton, particulate organic matter, sand, peat, silt and clay across distances and directions that depend on sediment properties such as grain size and cohesiveness. The Neuse River Estuary, North Carolina, and its tributaries, are typical examples (Fig. 1). Bottom sediment type is clearly related to bathymetry, dominated by organic-rich mud (silt and clay) in the middle of the basin, with greater contributions of sand and peat deposits towards the shorelines (Riggs et al. 1991, Benninger and Wells 1993). Variations in sediment size show sharp transitions and can change from 90% sand to 90% mud across distances < 1 km (Benninger and Wells 1993). The deposition of allochthonous and autochthonous organic matter sustains benthic macrofaunal and microbial communities that, via degradation of this organic matter, can in turn have a profound effect on the redox and nutrient conditions of the overlying water. Sediment zonation is an important habitat parameter for estuarine ecosystems because it determines which areas collect nutrients and pollutants and, ultimately, which areas form

optimal habitat for estuarine benthos, e.g., Riggs (1996) concluded that the sedimentological characteristics of the organic-rich mud that dominates the Albemarle estuarine system, North Carolina, were primarily determinants of its benthic habitats and resulting benthic community structure.

An increase in cultural eutrophication over recent decades has resulted in a greater incidence of low dissolved oxygen (DO) in many estuaries along the east coast of the United States (Officer et al. 1984, Renaud 1985, Dauer et al. 1992, Stanley and Nixon 1992, Valiela et al. 1992, Winn and Knott 1992, Breitburg et al. 1997, Paerl et al. 1998, Diaz and Solow 1999, Ritter and Montagna 1999, Goolsby 2000, Selberg et al. 2001, Buzzelli et al. 2002). Although decomposition of organic matter in the water column can account for a substantial fraction of oxygen consumption (Stanley and Nixon 1992, Hopkinson et al. 1999), sediment oxygen demand can account for more than 50% of the total respiration in shallow estuaries (Rizzo and Christian 1996, Buzzelli et al. 2002). The subsequent bottom-water hypoxia (DO  $\leq$  2 ppm) is exacerbated by low discharge, density stratification and warm temperatures which inhibit vertical mixing of the water column and enhance biological oxygen demand (Stanley and Nixon 1992, Buzzelli et al. 2002). This means that low DO waters often reside in clearly demarcated spatial zones above estuarine bottoms, often in deeper central parts. The net result is a correlation between certain sediment types and the occurrence of hypoxia in overlying waters.

Brown shrimp (*Farfantepenaeus aztecus*) and white shrimp (*Litopenaeus setiferus*) are key estuarine species, providing important links between primary producers and secondary consumers. Finfish predation appears to be a major source of mortality for both

species (Cook and Lindner 1970, Lindner and Cook 1970, Minello et al. 1987) particularly when they are at peak biomass between June and August (Knapp 1949). These two species are also tremendously valuable to industrial fishing and mariculture enterprises. In 2001, the estimated total value and weight of all commercially landed species in the United States were  $\$3.2 \times 10^9$  and  $4.3 \times 10^6$  t, of which shrimp (all species) comprised  $\$5.8 \times 10^8$  and  $1.6 \times 10^5$  t (personal communication, David Sutherland, National Marine Fisheries Service, Fisheries Statistics and Economics Division, Silver Spring, MD). Thus, although shrimp were only 3.6% by weight of the total domestic catch, they represented 17.8% of its dollar value, ranking them as the most valuable commercial fishery in the United States. In 2001, estimates for brown and white shrimp were  $\$2.9 \times 10^8$  ( $6.9 \times 10^4$  t) and  $\$1.9 \times 10^8$  ( $4.1 \times 10^4$  t) respectively, accounting for 83.3% by dollar value, and 70.2% by weight, of all commercially-landed shrimp.

The habitat associations of postlarval and juvenile brown and white shrimp have been well documented (Anderson et al. 1949, Giles and Zamora 1973, Trent et al. 1976, Zimmerman and Minello 1984, Zimmerman et al. 1984, Minello and Zimmerman 1985, Wenner and Beatty 1993, Rozas and Reed 1993, Rozas and Minello 1998, Howe et al. 1999). Fry et al. (2003) found that 10-20 mm immigrating postlarval and juvenile brown shrimp continued movement through sub-optimal habitats (deep channels and open bays), but exhibited much less movement once optimal habitats (marsh ponds or shallow channel margins) were reached. The primary factors affecting distribution appear to be larval ingress and settlement, food availability, substrate, and vegetative cover. These factors lead to higher densities in meso- and oligohaline areas that support intertidal salt marshes and

adjacent muddy bottoms, with white shrimp juveniles appearing to travel farther up estuaries than brown shrimp juveniles (Pérez-Farfante 1969). Densities of juvenile shrimp can vary considerably, reflecting habitat-specific larval recruitment dynamics and post-settlement mortality, e.g., Minello and Webb (1997) reported a density of 30.4 m<sup>-2</sup> for 24-mm juveniles and Clark et al. (1999) reported a value of about 7.5 m<sup>-2</sup> for 32 mm juveniles, both in Galveston Bay, Texas.

Toward the end of the growing season shrimp exhibit within-estuary ontogenetic shifts in habitat utilization as they begin moving toward outside waters (littoral waters beyond the outer beach line). Anderson (1966) reported that, as white shrimp juveniles grew, they moved from shallow marshes into deeper creeks, rivers, and bays when they were about 50-63 mm long. Movement rates of tagged subadult/adult shrimp suggest that populations may take as long as 4 to 5 months to complete the transition from inside to outside waters (Lindner and Anderson 1956). Emigration from estuaries eventually occurs at an approximate size of 100 mm (100 – 124 mm) for both species (Williams 1955, Joyce 1965, Parker 1970, Muncy 1984a, 1984b, Wicker et al. 1988), although estuarine environments with more of an oceanic influence may induce shrimp to remain for longer periods of time (Brusher and Ogren 1976).

Penaeids burrow via coordinated use of both pleopods and pereopods to penetrate forward and down into the substratum (described in detail by Dall et al. 1990). Burrowing may serve for purposes of predator avoidance, energy-conservation and avoidance of thermal stress (Williams 1958, Aldrich et al. 1967, Wickham and Minkler 1975, Rulifson 1981, Minello and Zimmerman 1984, Larson et al. 1989). Earlier work (Springer and Bullis 1954,

Hildebrand 1954, Williams 1955, Mock 1966, Jones 1973, Weinstein 1979, Geaghan 1980, Rulifson 1981, Dall et al. 1990) suggests that shrimp may display species-specific substrate preferences and are thus likely to aggregate in distinct spatial zones of estuaries. Penaeid shrimp are competent swimmers and tidal transport via diurnal vertical migration during ebbing tides has been suggested as an important emigration mechanism (Copeland 1965, Rulifson 1983). These en masse migrations towards the ocean mean that shrimp must traverse relatively large geographical areas where sediment characteristics are likely to exhibit high variability, precisely at a time when water conditions are becoming conducive to the buildup of severe large-scale hypoxia and anoxia.

Kramer (1987) proposed four categories of behavioral responses by organisms to reduced external availability of DO: increased use of air breathing, increased use of aquatic surface respiration, changes in activity and vertical/horizontal habitat changes, of which shrimp can perform the latter two. Published laboratory and field DO avoidance/preference data for shrimp indicate that they are likely to vacate hypoxic areas at threshold levels of about 2.0 ppm (Leming and Stuntz 1984, Renaud 1986, Stickle et al. 1989, Wannamaker and Rice 2000, Eby and Crowder 2002). Thus, apart from direct effects such as mortality and morbidity upon individuals that cannot escape hypoxic zones, forced spatial segregation can place populations under other significant indirect risks, such as reduced growth rates in suboptimal habitats, enhanced competition, predation (including human fishing pressure and cannibalism), and disease.

Such effects should hardly be unexpected: it is a well known fact that population dynamics and fitness can be indirectly affected by disturbance stimuli via the energetic and

lost opportunity costs of risk avoidance (Frid and Dill 2002). From an environmental management perspective, it is critical to understand how the behavior of penaeids and other benthic organisms may be altered by physical and chemical disturbance (Rulifson 1981). Knowing the strength of penaeid substrate associations is part of this management task, and the objective of my study.

## **MATERIALS AND METHODS**

Sediment preference experiments were conducted for juvenile brown and white shrimp in July and August, 1999, respectively. Shrimp were collected from a sandy-mud habitat adjacent to a *Spartina* marsh at Calico Creek, Morehead City, North Carolina using a 2.3 m cast net (0.63-cm mesh), and transported to 700-L indoor flow-through tanks (100 L·hr<sup>-1</sup>) at the National Marine Fisheries Service Laboratory, Pivers Island, North Carolina. Before the commencement of experiments, shrimp were fed each dusk with an excess of aquaculture-grade feed (55% crude protein; Corey Feed Mills Limited, New Brunswick, Canada), in addition to any organic matter settling out of the unfiltered seawater supply.

Sediment types were selected to represent the diversity of substrates that are widely but not uniformly distributed across North Carolina estuaries and were also the same categories chosen by Williams (1958) in an earlier preference experiment: sand, shell sand, sandy mud, muddy sand and peat. Sediments were retrieved using shovels to remove the upper 10 cm of subtidal bottom (to include the oxic layer, which varies by sediment type), and were immediately transported back to the laboratory in 500-L tanks. Sand was collected from the western shore of Radio Island, NC, sandy mud from a mudflat adjacent to a

*Spartina* marsh north of Radio Island, peat from Broad Creek, 20 km west of Morehead City, NC, and muddy sand and shell sand from two locations north and south of the intracoastal waterway west of Pivers Island, NC. These sediments were stored 15 cm deep in 500-L cylindrical tanks at the laboratory under 30 cm of aerated seawater at ambient temperature. Caches of sediments were replaced every 72 hours. Four of the five sediment types were sieved to characterize their particle size distributions (the physical composition of peat, largely a fibrous mat of partially-decomposed leaves, precluded such an analysis). A 500 g sample of each sediment type was split into two equal portions. One portion was dried and the other was sieved with mesh sizes 2 mm and 63  $\mu\text{m}$  to retain shell and sand respectively. These shell and sand sieve fractions were dried and weighed to determine their percentage contributions to the whole sample. The silt-clay fraction was calculated by subtracting the sum of the dried shell and sand fractions from the dry weight of the 250 g whole sample.

In order to simultaneously offer each shrimp the opportunity to make an unbiased choice between the five sediment types, a circular/radial wedge design was devised for the experimental units. In such an arrangement, with five sediment types and without repetition, there are 12 possible mirror-image pairs of permutations. Making the rational assumption that shrimp would be equally likely to move clockwise as counter-clockwise, one permutation of each pair was randomly chosen, and the resulting set of 12 sediment permutations was used throughout the experiments. Each of the twelve experimental units was made by first welding together a 33.5-cm diameter wire ring (9 gauge or 3.76 mm) with 5 equal ( $72^\circ$ ) sectors. Galvanized square mesh (6 mm) was bent into wedge-shaped trays that were stitched with monofilament onto each of these frames to create 6-cm deep

compartments beneath the sectors (Fig. 2). These wire-mesh baskets were sized to fit snugly into the bottom of 12 cylindrical tanks (radius 17 cm, depth 17 cm), so that sediments could then be loaded into each sector using the 12 permutations described above. Great care was taken to ensure that there was a uniform radial flow of water through each tank towards the circumference, to prevent any locomotory bias towards any of the underlying sediment types. To ensure this, a custom drain was built for each tank using a closed ring of Tygon tubing (1.9-cm ID), which was fused to the rim of each tank using silicone, and then perforated with 3 mm diameter holes at 2.5-cm intervals (Fig. 2). Tanks were leveled precisely using adjustable platforms (Fig. 3). Six tanks were equally spaced on each of two adjacent water tables, each 1.2 m × 2.4 m (Fig. 4). An overhead distribution system delivered ambient seawater via twin distribution manifolds mounted on wooden scaffoldings, one over each table (Figs. 3 & 4). From these manifolds a series of tubes fed seawater into full-circle spinner micro-sprinklers (Mister Landscaper, model MLM-05). Flow rates to micro-sprinklers (Fig. 5) were equalized using screw valves so that flushing time was 30 minutes (15 L·hr<sup>-1</sup>). Each of the twelve tanks was randomly assigned one of the twelve unique sediment permutations, and assignments were changed every day. The five sectors in each tank were carefully loaded with 1 L of each sediment type, tanks were leveled, and the seawater flow was turned on. This meticulous procedure of seawater delivery and leveling ensured that the ensuing water flow pattern in each experimental unit was always both uniform and radial towards the tank circumference.

Trials commenced at 2:00 pm each day when a single shrimp was introduced to the center of each tank with its rostrum pointing in a randomized direction (N, S, E or W). Each

trial ran for 20 hours, until 10:00 am the next morning, when shrimp would be located by visual search (usually the tip of the rostrum, eyes, or antennae were visible) or by lifting baskets to search compartments for deeply burrowed shrimp, at which point the substrate type chosen for burrowing was recorded for each shrimp. After dark during each trial, a visual inspection was made of tanks using a night scope, which confirmed that all shrimp were active and emerged from burrows. The majority of both species burrowed at the commencement (93% and 76% for brown and white shrimp respectively) as well as at the end (97% and 91%) of trials (Figs. 5 & 6; Table 3), so I decided to compare initial preferences (defined as the sediment first burrowed into after introduction, before nightfall) with final preferences (defined as the sediment burrowed into after 20 hrs., at the termination of the experiment) to see if there was any substrate fidelity in terms of individuals returning to their first-chosen sediment the subsequent morning, when there was no longer any influence of handling-related stress. 120 shrimp of each species were tested in this manner, thus data consisted of preference frequencies for each of the five sediment types. Sediments were changed daily, before the commencement of each trial. The experiments were conducted in an outdoor wet laboratory. The experimental area was shielded with heavy-duty black plastic sheeting to preclude visual disturbance to test animals, and to ensure darkness at night in order to prevent phase resynchronization, i.e., to ensure normal diurnal patterns of activity (Wickham and Minkler 1975). Lighting was natural, via a transparent corrugated ceiling.

If no substrate preferences were exhibited, then 1/5 of all observations would be expected for each sediment type. In order to test for deviation from the hypothesized ratio, a

5-category chi-square goodness of fit test was employed. Although a rejection of the null hypothesis may be satisfactory in some instances, further chi-square analyses were also performed to elucidate whether any significant disagreement between observed and expected frequencies were concentrated in certain of the sediment types, or whether the difference was due to effects of the data in all of the sediment types. This was done by subdividing chi-square analyses (Zar 1999) to compare one sediment type at a time versus the other four types, i.e., a 1:4 null ratio of the specified sediment type to the remaining four sediments combined.

Mean DO and temperature values were  $5.19 \pm 0.01$  ppm and  $30.37 \pm 0.04^{\circ}\text{C}$  for brown shrimp and  $4.75 \pm 0.03$  ppm and  $28.53 \pm 0.05^{\circ}\text{C}$  for white shrimp (mean  $\pm 1$  S.E.). Average sizes of brown and white shrimp used in these experiments were  $74.3 \pm 1.7$  mm and  $89.1 \pm 1.8$  mm respectively.

## RESULTS

As a consequence of the high flushing rate used, measurements for DO, temperature and salinity exhibited very low variability among tanks during the experiment (Table 1). Sieve analyses demonstrated that the sediment types had typical compositions, with highest silt-clay fractions (71% and 11%) in sandy mud and muddy sand, and highest sand fractions (94% and 65%) in sand and shell sand respectively (Table 2).

Chi-square analyses of contingency table data (Table 3) revealed that brown and white shrimp were different in their preferences across the five sediment types, for both initial and final burrowing positions (chi-square  $P < 0.001$  for both initial and final burrowing

positions). Similar within-species analyses of preferences revealed that initial and final burrowing preferences were also different for both species (chi-square  $P < 0.001$  for both brown and white shrimp).

Under the null hypothesis, the proportion of burrowers in each sediment type should equal 0.2. For both species, this null was rejected for final burrowing positions (Tables 3 & 4; Fig. 6). Chi-square values were highly significant for both species ( $P < 0.001$  for both brown and white shrimp). For brown shrimp, the chi-square analyses showed attraction for both sand and peat with repulsion from shell sand and sandy mud, while observed occurrences on muddy sand were not significantly different from the expected frequency (Table 4; Fig. 6). For white shrimp there was strong attraction for sand with repulsion from shell sand and muddy sand, while observed occurrences on sandy mud and peat were not significantly different from the expected frequencies (Table 4, Fig. 6).

Initial burrowing behavior at the start of experiments was also strongly biased, with chi-square  $P$  values of  $< 0.01$  and  $< 0.001$  for brown and white shrimp respectively (Table 4; Fig. 6). For brown shrimp, the main contributors to this difference were attraction to sand and repulsion from peat, while observed occurrences on shell sand, sandy mud and muddy sand were not significantly different from expected frequencies. For white shrimp, the difference was explained by attraction to sand and repulsion from shell sand and sandy mud, while observed occurrences on muddy sand and peat were not significantly different from expected frequencies (Table 4, Fig. 6).

Sediment fidelity (here defined as a return by an individual shrimp to burrow in the same sediment type that it chose at introduction) was low and consistent for both species:

across all sediment types, only 29% of brown shrimp and 30% of white shrimp had repeat burrows in the same sediment type. Despite the fact that there was so much movement between sediment types (the majority of individuals choosing different sediment types for initial and final burrows), the overall outcome remained the same: sand was the sediment of greatest preference for both species.

## **DISCUSSION**

For practical reasons, the present study and previous studies of sediment preferences of brown and white shrimp (Williams 1958, Rulifson 1981) have been of smaller spatial scales than those over which sediments vary in the field. Even so, I considered the design of my study robust for a number of reasons: individual shrimp were used in each experimental unit, which precluded the likelihood of group effects (interactions with other shrimp influencing preference); each shrimp had free and immediate access to a wide array of (five) different sediment types; fresh sediments were used for each shrimp in each trial, so there was no influence from preceding occupations (olfactory cues, altered sediment characteristics, etc.); ambient light was used, so that shrimp had a realistic light impulse at dawn to stimulate burrowing activity; and the high flushing rate, radial flow design and randomization of sediment arrays for each trial/shrimp ensured that DO, temperature and salinity were virtually identical across all experimental units and that there were no locomotory biases.

Although overall chi-square P-values were significant for both species, they were lower for final than for initial positions, primarily due to a stronger sand preference in the

former (Table 4). This greater bias occurred when handling-related stress was absent, a finding consistent with a hypothesis that the presence of stress makes shrimp less selective about where they burrow: under such circumstances, shrimp may have a stronger and more immediate urge to escape and find cover. Despite the fact that the majority of shrimp did not return to their initially-chosen sediment type for subsequent (final) burrowing, overall preference for sand by both species was clearly stated with peat as a significant contributor for final brown shrimp positions.

In laboratory preference experiments, Williams (1958) determined that white shrimp preferred peat over other substrate types, whereas brown shrimp showed a split preference for peat and sandy mud over muddy sand, sand and shell sand respectively. Rulifson (1981), in experiments that did not include peat or muddy sand, found that both species preferred sandy mud over sand and shell sand. Both of these studies used groups of shrimp: Williams (1958) used a density of 20 shrimp per  $2.3 \text{ m}^{-2}$  experimental unit, whereas Rulifson (1981) used 6 shrimp per  $4.7 \text{ m}^{-2}$  experimental unit (representing absolute densities of  $8.7 \text{ m}^{-2}$  and  $1.3 \text{ m}^{-2}$  respectively). At these experimental scales, burrowing preferences may be linked to the site of foraging activity. At Rulifson's (1981) scale, shrimp may have been more likely to burrow in patches of foraging activity because search radius at the onset of the burrowing stimulus may have been less than the average diameter of substrate patches. In the Williams (1958) design, difficulty in moving between subcompartments meant that, once shrimp found a foraging patch, they were more likely to remain there when it was time to burrow. At the smaller scale of my study (a single shrimp ranging across each  $908 \text{ cm}^2$  unit), burrowing decisions may have become effectively uncoupled from foraging decisions because shrimp

had an extremely high probability of locating preferred burrowing sediments. In further support of this point, Rulifson (1981) suggested that factors such as sediment grain size may affect distribution of shrimp (shrimp avoided shell sand in his experiments even though it had a similar organic content to the preferred sandy mud), and Williams (1958) stressed that respiratory requirements and the ease with which substrate can be entered could play some role in burrowing habits. If sand is indeed the preferred burrowing substrate, then a comparison of the scale of my experiment with that of Rulifson (1981) indicates that, at the onset of a burrowing stimulus, shrimp will range a search radius  $\geq 0.17$  m and  $\leq$  about 1.2 m when searching for the most preferred substrate (sand) to burrow into.

Penn (1984) categorized penaeids into three groups: clear water, nocturnally-active species that always burrowed in the day or when the moon was bright; slightly-turbid-water species that were mostly nocturnal; and turbid water species that seldom burrowed. However, such categorizations based on burrowing and turbidity characteristics do not explain the ultimate reasons why various species associate with specific substrata. Dall et al. (1990) made the additional important point that apparent preferences of penaeids cannot be gauged solely from field data in one area because a full range of substrata may not be available, e.g., three independent studies on *Penaeus latisulcatus* at different locations found this species over sediments with variable mud content of  $< 1.1\%$ ,  $31\%$  and  $< 50\%$  (Hall and Penn 1979, Branford 1981, and Somers 1987). This point becomes particularly important when the enormous geographical scales over which some penaeids are known to occur are considered. Somers (1987) found a significant correlation between depth and substratum but, after discounting the effect of depth on distribution, found that substratum only accounted for

11%, 16% and 25% of the variations in distributions of *P. esculentus*, *P. semisulcatus* and *P. latisulcatus* respectively, and concluded that organic carbon is a limiting factor for shrimp distributions only where its concentration is low. Likewise, Moller and Jones (1975) found that *P. semisulcatus* preferred areas with a high mud content in the field, but under experimental conditions the majority of them (> 90%) burrowed into substrata with no mud content. Penaeids thus seem to exhibit a great degree of flexibility and tolerance for the various types of substratum that they will burrow into.

Although preferences of shrimp for peat and/or sandy mud were in part explained as an attraction to food sources, there remain some important caveats. Penaeid shrimp are opportunistic omnivores, scavenging amidst marsh grasses and on the surface of estuarine sediments on a diverse spectrum of food types - polychaetes, oligochaetes, harpacticoid copepods, pericarideans, ostracods, small molluscs, benthic diatoms, bacteria, phytoplankton, filamentous green and blue-green algae, and vascular plant detritus (Darnell 1958, Eldred et al. 1961, Williams 1965, Dall 1968, Condrey et al. 1972, Odum and Heald 1972, McTigue and Zimmerman 1991, McTigue and Zimmerman 1998, Nunes and Parsons 2000, Riera et al. 2000). Although peat and sandy mud in natural settings would contain higher relative fractions of organic material, it must also be emphasized that virtually all areas within estuaries or the littoral zone of the ocean can afford such forage at concentrations that may not be limiting at natural shrimp densities. Consistent with this hypothesis, Williams (1958) noted that although substratum preference was species-specific, pink shrimp (*Penaeus duorarum*) preferred coarser substrates despite the relative absence of food there, implying that within-substrate food was not a limiting factor in their distribution. In fact, at the same

latitude, pink shrimp regularly attain sizes comparable with brown and white shrimp. Further corroboration comes from Ruello (1973) who found that sediment particle size was more important than food in affecting the distribution of *Metapenaeus macleayi*. Dall et al. (1990) noted that, because penaeids do not use permanent burrows, are not territorial, and choose a burrowing site at least once each 24-hr cycle, their choices are not final and are thus unlikely to be critical. In addition, he noted that migrating penaeids (from inshore to offshore areas) travel over substrata that may not be optimal for burrowing.

Dall et al. (1990) reported that most penaeids prefer sediments with a specific particle size range of 62  $\mu\text{m}$  to 1 mm and, in addition to food availability, suggested as reasons ease of burrowing, ease of respiratory activity when buried, and habitat selection. These properties reflect underlying sediment characteristics such as particle size distribution, pore space and porosity, water content, thixotropy (becoming more fluid when a shear stress is applied) and shear strength as well as organic content and the presence of other organisms (Dall et al. 1990). They concluded that choice of sediments suitable for burrowing is a function of the difficulty of burrowing into the coarse particles (in coarse sediments, particles interlock and are thus more difficult to push aside). For *Penaeus duorarum*, Fuss and Ogren (1966) found that the softer the bottom the more rapidly shrimp could burrow. The easiest substrata to erode are comprised of particles around 2 mm in diameter (Day 1981) and, because particle cohesion changes inversely with grain size, silts and clays are particularly difficult for shrimp to erode using a current generated by pleopods (Dall et al. 1990). Both brown and white shrimp were observed using this fanning technique in the present study and in other (unpublished) studies in my laboratory.

Extremely fine sediments may decrease foraging efficiency of penaeids or negatively affect respiratory activity by clogging gill chambers (Dall et al. 1990), and this may partly explain why white shrimp, although known to associate with very soft sediments, will seldom burrow into them (Penn 1984). Breathing when buried is less of a problem in coarser sediments because their high porosity obviates the need for a ventilation hole and respiratory siphon to reach the surface (Dall et al. 1990) although the significant presence of finer sediments amidst coarser grains may discourage burrowing. Habitat recognition may also offer another partial explanation: substratum may be one of several cues used by penaeids to locate nursery areas, migration corridors and spawning grounds. The use of substrate for habitat recognition, rather than being a limiting factor could explain the narrow preferences of penaeids despite their ability to burrow into a range of substrata (Dall et al. 1990). The strong selective force of predation pressure may thus have garnered penaeids the ability to either burrow into most sediment types encountered (Dall et al. 1990) or to avoid those that they cannot burrow into. Collectively, these facts help to explain the results of the present study: the sand substrate preferred by both species was comprised of 94% particles from 63  $\mu\text{m}$  to 2 mm, with only a 4% silt-clay fraction. As another caveat, many penaeids are morphologically similar yet still prefer different substrata in the field, and many juveniles (identical to adults except for size) often have distinct preferences as well.

It has been hypothesized that in certain low-energy estuarine habitats, turbid water together with suitable substrata for burrowing may enhance shrimp productivity by reducing predation. Minello et al. (1987) found that the effect of turbidity and burrowing by brown shrimp on predation by various fish species was complex and varied by species, with

potential interactions between turbidity and substratum. Sand substrate significantly reduced predation rates for visual feeders like pinfish (*Lagodon rhomboides*) and southern flounder (*Paralichthys lethostigma*), but had no effect on predation rates of Atlantic croaker (*Micropogonias undulatus*) or red drum (*Sciaenops ocellatus*). Turbidity decreased predation rates of pinfish and, to a lesser extent, Atlantic croaker, but increased predation rates of southern flounder, and had no effect on red drum predation rate. There was a significant interaction effect between predation and substratum for pinfish, but not for the other species. It must also be noted that, due to the high flushing rate in the present study, turbidity was extremely low. Not surprisingly, white shrimp, which seldom burrow in the field under turbid conditions, burrowed in the majority of trials (76% initial and 91% final). This was probably due to the clarity of the water and its shallowness (12 cm), which may have been perceived as increasing predation risk.

Under undisturbed field conditions, over the range of observed densities (Zimmerman et al. 1984, Zimmerman and Minello 1984, Minello and Zimmerman 1985, Rozas and Reed 1993, Wenner and Beatty 1993, Rozas and Minello 1998, Howe et al. 1999, Rozas and Zimmerman 2000) shrimp do not appear to be forage-limited (see Chapter 5), thus there must be other factors that more strongly influence their observed field distributions, of which competition and predation are the most likely candidates. Although the ghosts of competition past (Connell 1980) and predation past (Peckarsky and Penton 1988) may well prove elusive, character displacement, resource partitioning, and behavioral differences seen among sympatric penaeids may represent indirect evidence of such. Habitat selection can have significant repercussions for fitness, and its particular expression is often explained in

terms of a tradeoff between avoiding antagonists and acquiring resources (Decaestecker et al. 2002), for e.g., Aikins and Kikuchi (2002) demonstrated that amphipods will mostly select and inhabit substrate with enough available space to provide them with adequate protection but that availability of food also played an important role.

It is currently unknown if juvenile brown and white shrimp forage and/or travel only during specific periods of their active (nocturnal) cycle during migration, nor is it known what cues are used to detect optimal foraging patches. Rulifson (1983) suggested that shrimp may use selective tidal transport to select new patches during outmigration. Depending on water velocity, this mechanism may permit shrimp to move relatively large distances that may be on the order of hundreds of meters (Rulifson 1983). This activity might be an important aspect of penaeid shrimp ecology if preferred substrates are patchy (Rulifson 1981). If such activity is “hit or miss,” then outmigrating shrimp will have less likelihood of locating preferred habitats. Because large-scale hypoxic events are correlated with muddier sediment types, ousted shrimp are then more likely to exit the water column over other sediment types.

The question of whether shrimp will burrow into different sediment types has already been clearly answered. It is also clear that shrimp display preferences among different sediment types, and that preferences are influenced by several biotic and abiotic factors. The intriguing question of whether or not different sediment types affect growth remains to be answered and is particularly important because shrimp populations may be forced to occupy such sediment habitats as a consequence of anthropogenic disturbance. This question is addressed in Chapter 5. Scaling up from laboratory to field experiments in such a manner

will provide further information necessary to augment modeling efforts, with the ultimate goal of producing reliable guidelines for a more effective management of estuarine resources.

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Table 1. Dissolved oxygen (DO) and temperature readings for tanks used in the sediment preference experiment. Means and standard errors are reported.

		<b>Tank Number/Position</b>											
		<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>5</b>	<b>6</b>	<b>7</b>	<b>8</b>	<b>9</b>	<b>10</b>	<b>11</b>	<b>12</b>
<b>Brown shrimp, DO (ppm)</b>	Mean	5.18	5.20	5.21	5.23	5.16	5.17	5.14	5.19	5.22	5.19	5.19	5.21
	S.E.	0.12	0.12	0.12	0.11	0.11	0.11	0.11	0.11	0.10	0.11	0.11	0.10
<b>Brown shrimp, temp. (°C)</b>	Mean	30.23	30.18	30.28	30.27	30.27	30.28	30.47	30.47	30.50	30.45	30.47	30.52
	S.E.	0.20	0.19	0.21	0.18	0.18	0.19	0.19	0.19	0.19	0.18	0.19	0.19
<b>White shrimp, DO (ppm)</b>	Mean	4.97	4.97	4.73	4.74	4.74	4.53	4.65	4.74	4.75	4.72	4.73	4.74
	S.E.	0.25	0.22	0.12	0.13	0.12	0.28	0.13	0.12	0.12	0.12	0.12	0.12
<b>White shrimp, temp. (°C)</b>	Mean	28.39	28.39	28.47	28.46	28.44	28.16	28.66	28.64	28.69	28.69	28.69	28.70
	S.E.	0.46	0.44	0.45	0.44	0.45	0.71	0.44	0.44	0.43	0.43	0.43	0.43

Table 2. Sieve-analyses of substrate types. Weights and percentages of shell/debris, sand, and silt-clay fractions.

<b>Sediment Fraction</b>	<b>Particle Size (mm)</b>	<b>S U B S T R A T E T Y P E</b>									
		<b>Shell Sand</b>		<b>Sand</b>		<b>Muddy Sand</b>		<b>Sandy Mud</b>		<b>Peat</b>	
		Weight (g)	%	Weight (g)	%	Weight (g)	%	Weight (g)	%	Weight (g)	%
Shell/debris	> 2.0	80.2	32.1	5.2	2.1	2.3	0.9	4.8	1.9	N/A	N/A
Sand	> 0.0625 to < 2.0	162.3	64.9	234.8	93.9	220.2	88.1	67.5	27.0	N/A	N/A
Silt-clay	< 0.0625	7.5	3.0	10.0	4.0	27.5	11.0	177.7	71.1	N/A	N/A
<b>TOTAL</b>		250.0	100.0	250.0	100.0	250.0	100.0	250.0	100.0	N/A	N/A

Table 3. Contingency table of sediment preference data for brown shrimp (*Farfantepenaeus aztecus*) and white shrimp (*Litopenaeus setiferus*). The sediment chosen by each shrimp for burrowing was recorded at the beginning (initial position) and end (final position) of experiments. Total numbers of observations were lower for initial positions because fewer shrimp burrowed at the start of the experiment than the following morning.

		S U B S T R A T E T Y P E					
		Sand	Shell sand	Sandy mud	Muddy sand	Peat	Total
<b>Brown shrimp, final position</b>	Observed	40	3	11	25	37	<b>116</b>
	Expected	23.2	23.2	23.2	23.2	23.2	
<b>White shrimp, final position</b>	Observed	54	11	16	11	17	<b>109</b>
	Expected	21.8	21.8	21.8	21.8	21.8	
<b>Total (observed)</b>		<b>94</b>	<b>14</b>	<b>27</b>	<b>36</b>	<b>54</b>	<b>225</b>
<b>Brown shrimp, initial position</b>	Observed	32	22	20	29	9	<b>112</b>
	Expected	22.4	22.4	22.4	22.4	22.4	
<b>White shrimp, initial position</b>	Observed	38	7	8	22	16	<b>91</b>
	Expected	18.2	18.2	18.2	18.2	18.2	
<b>Total (observed)</b>		<b>70</b>	<b>29</b>	<b>28</b>	<b>51</b>	<b>25</b>	<b>203</b>

Table 4. Chi-square analyses of sediment preference data for brown shrimp (*Farfantepenaeus aztecus*) and white shrimp (*Litopenaeus setiferus*). Superscripted asterisks next to chi-square values refer to statistical significance (\*, \*\* and \*\*\* are  $\leq 0.05$ ,  $\leq 0.01$   $\leq 0.001$  respectively). Arrows indicate whether observed preference of the specified sediment type was higher or lower than expected based on a 1:4 ratio.

Species, preference	Chi-square Analyses					
	All Types Compared	Sand vs. Others	Shell Sand vs. Others	Sandy Mud vs. Others	Muddy Sand vs. Others	Peat vs. Others
Theoretical test ratio	1 : 1 : 1 : 1 : 1	1 : 4	1 : 4	1 : 4	1 : 4	1 : 4
<i>Farfantepenaeus aztecus</i> , initial	14.34**	5.14* ↑	0.01	0.32	2.43	10.02** ↓
<i>Farfantepenaeus aztecus</i> , final	44.52***	15.21*** ↑	21.98*** ↓	8.02** ↓	0.17	10.26** ↑
<i>Litopenaeus setiferus</i> , initial	35.21***	26.93*** ↑	8.62** ↓	7.15** ↓	0.99	0.33
<i>Litopenaeus setiferus</i> , final	60.86***	59.45*** ↑	6.69** ↓	1.93	6.69** ↓	1.32

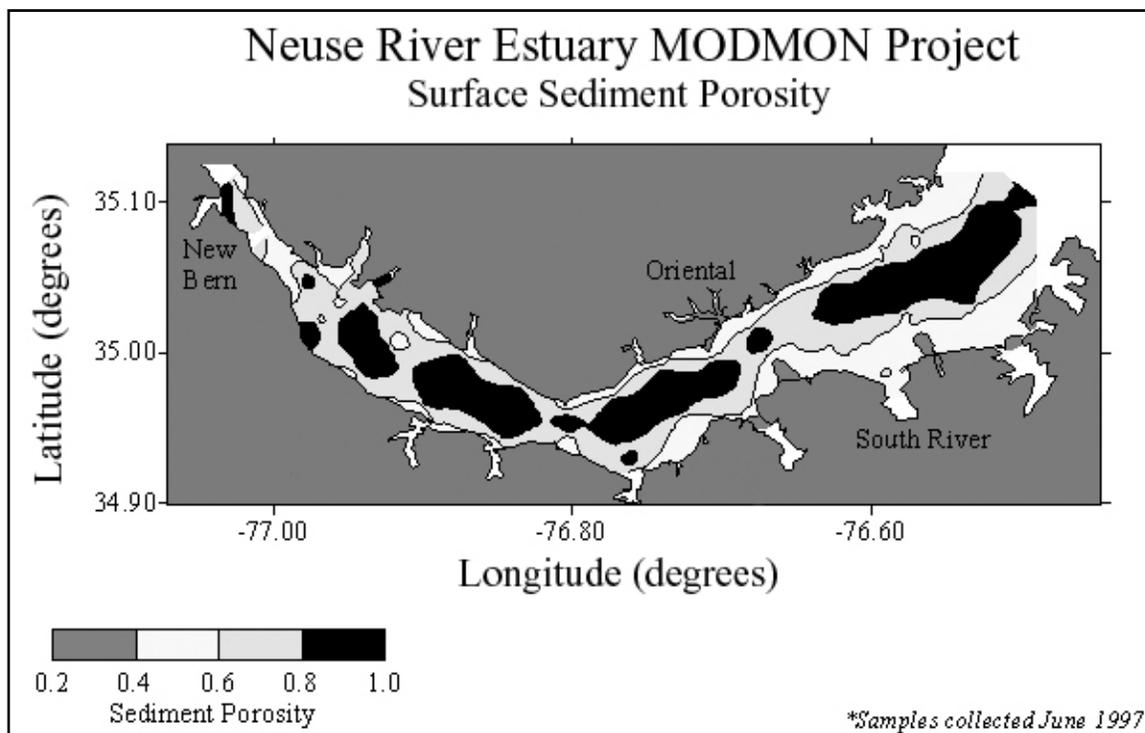


Fig. 1. Sediment porosity in the lower Neuse River Estuary, North Carolina. Muddier areas (predominantly silts and clays, darker areas towards the mid channel) have highest porosity. Sediments of lower porosity towards the shoreline have higher sand content. Used with permission.

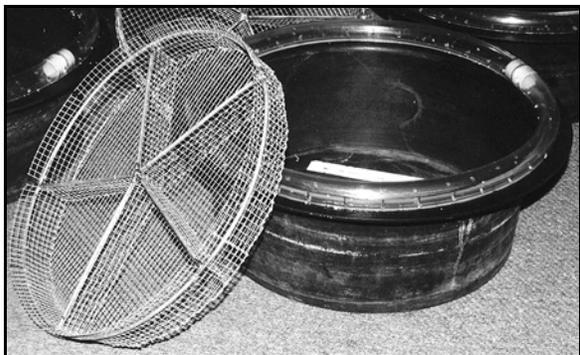


Fig. 2. Circular wire-mesh basket with wedges and cylindrical test tank (note Tygon tubing drain).

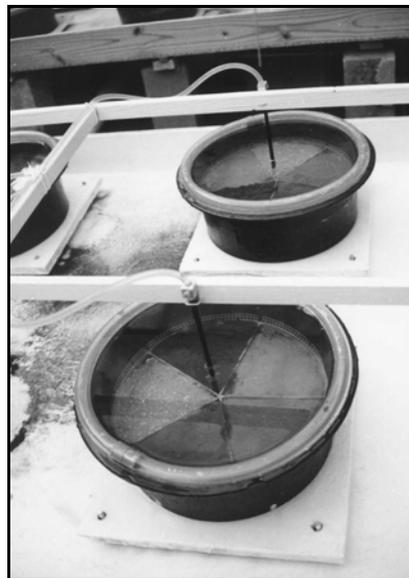


Fig. 3. Cylindrical tanks with wedges loaded with sediments, on leveling platforms (note overhead irrigation with flow valves).



Fig. 4. Arrangement of water tables with tanks on leveling boards.

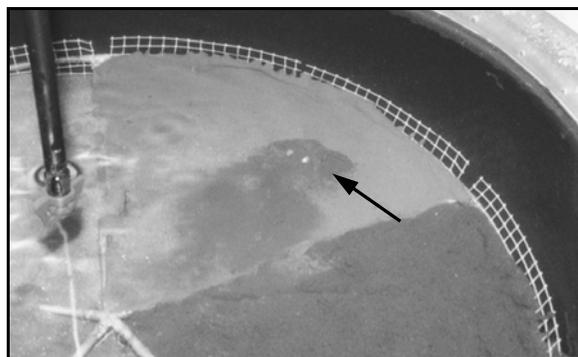


Fig. 5. Typical burrowed shrimp. Eyes are clearly visible at the sediment surface (note inverted 360° sprinkler).

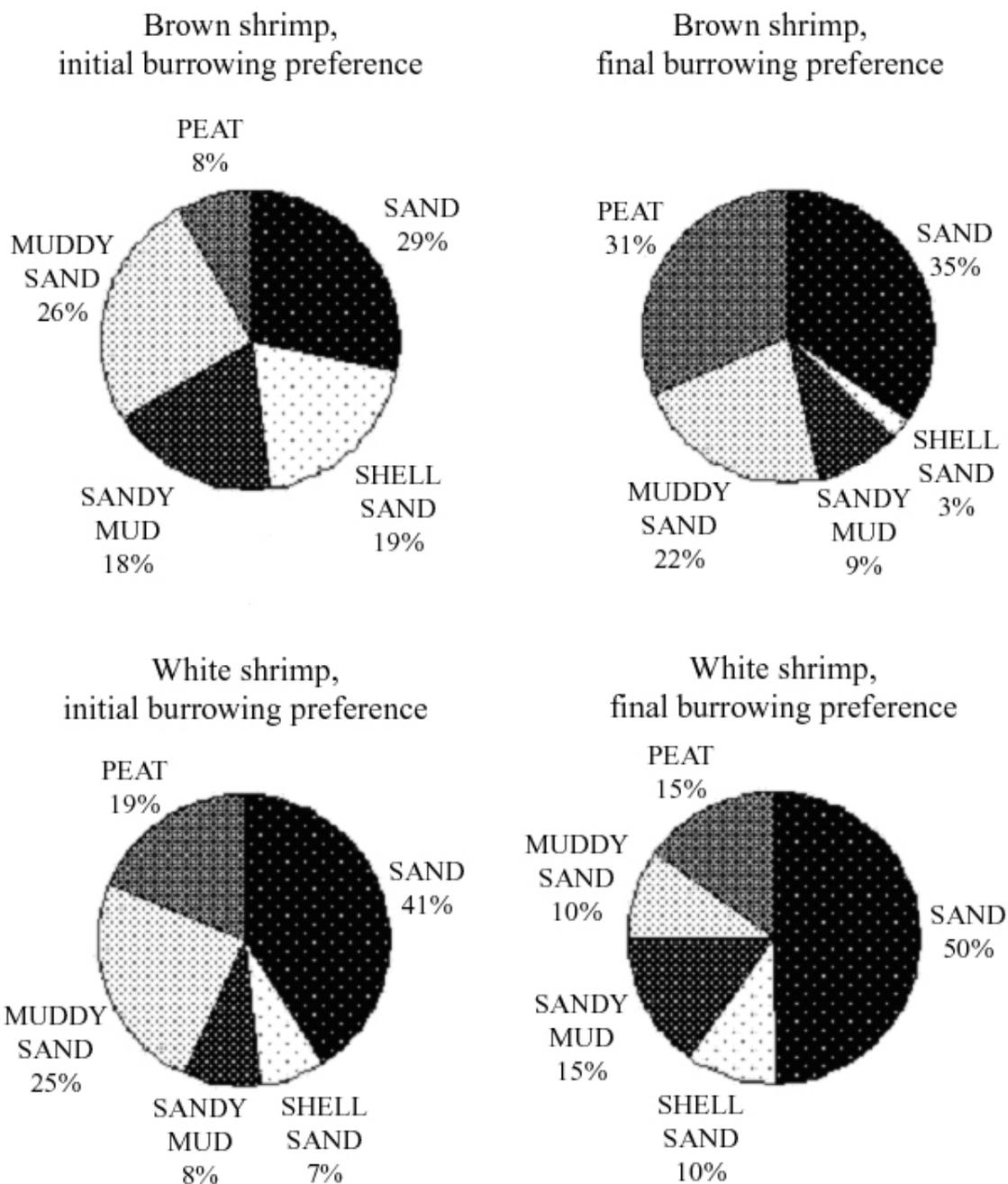


Fig. 6. Laboratory-determined sediment preferences of brown shrimp (*Farfantepenaeus aztecus*) and white shrimp (*Litopenaeus setiferus*). Preferences are reported as the percentage of individuals found burrowing on each sediment type.

## Chapter 5. Effects of density, sediment type and predation on the growth rate and survivorship of juvenile white shrimp.

### ABSTRACT

The white shrimp (*Litopenaeus setiferus*), a significant predator of infauna, plays an important role linking primary producers and secondary consumers in U.S. Atlantic and Gulf coast estuaries. In many of these estuaries, environmental disturbance, in the form of large-scale hypoxia, has been well documented. Because shrimp are known to detect and avoid hypoxia, resulting habitat compression may promote higher densities of shrimp in outlying habitats, where theory suggests that increased predation rates, density-dependent mortality and growth effects are likely consequences.

I used three field mesocosm experiments to examine the impacts of shrimp density (5, 10 or 20 m<sup>-2</sup>) and sediment type (sandy mud, sand, peat) on shrimp growth rate, and the effects of predator density (the pinfish, *Lagodon rhomboides*, at 0, 1 or 2 m<sup>-2</sup>) and shrimp density (5, 10 or 20 m<sup>-2</sup>) on shrimp survivorship. Sediment type had no effect on shrimp growth rate, but shrimp density had a strong effect. In the predation experiment, shrimp survivorship was significantly less at both 1 and 2 predators·m<sup>-2</sup> than in the absence of a predator, but unexpectedly high predation rates precluded a further planned analysis on shrimp growth rate effects due to very low survival. There was no effect of shrimp density on survivorship.

My results indicate that, across the range of densities and time intervals considered (7 or 20 days), substrate type is not an important determinant of juvenile shrimp growth or survivorship. The dominant effect on growth rate was shrimp density. The predation

experiments also demonstrated the high efficiency of pinfish as predators of white shrimp, suggesting that predation can be an important determinant of low field densities in non-vegetated habitats. My findings lend weight to the hypothesis that density-mediated growth reduction and predation mortality may be important factors affecting shrimp growth and survivorship in the face of large-scale environmental disturbance.

*Key words:* Predator, predation, prey, hypoxia, sediment, growth rate, survivorship, juvenile shrimp, white shrimp, *Litopenaeus setiferus*, pinfish, *Lagodon rhomboides*.

## INTRODUCTION

Temperate estuaries, among the most productive and diverse of all ecosystems, are continually subjected to threats from multiple anthropogenic stressors resulting primarily from human population expansion (Suchanek 1994). In U.S. Atlantic and Gulf coast estuaries, the incidence of eutrophication and subsequent summertime hypoxia (dissolved oxygen  $\leq 2.0$  ppm) has been well documented (Officer et al. 1984, Renaud 1985, Dauer et al. 1992, Stanley and Nixon 1992, Valiela et al. 1992, Winn and Knott 1992, Breitburg et al. 1997, Paerl et al. 1998, Diaz and Solow 1999, Ritter and Montagna 1999, Goolsby 2000, Selberg et al. 2001, Buzzelli et al. 2002). Although there is an obvious interest in the direct effects of hypoxia on organisms, behavioral insights from laboratory and field studies clearly indicate that many estuarine organisms can detect and successfully avoid hypoxic regions (Leming and Stuntz 1984, Renaud 1986, Stickle et al. 1989, Pihl et al. 1991, Howell and Simpson 1994, Wannamaker and Rice 2000, Lenihan et al. 2001, Eby and Crowder 2002). Despite this behavioral flexibility, it is possible that hypoxia-induced spatial compression of

remaining suitable habitat could still result in indirect negative effects on species, as optimal foraging and competition theories suggest that increased predation rates, density-dependent effects, and interactions between the two may affect the survivorship and growth of displaced and overcrowded organisms (Hardin 1960, Emlen 1966, MacArthur and Pianka 1966, Schoener 1971, Pulliam 1974, Charnov 1976, Pyke 1984, Stephens and Krebs 1986, Schoener 1987, Mangel and Clark 1988, Gurevitch et al. 2000, Schoener et al. 2001, Chase et al. 2002). It is also possible that eventually overcrowding in oxygenated refugia may force animals into waters with lower than preferred DO levels (Eby and Crowder 2002).

Among estuarine-dependent invertebrates and fishes, penaeid shrimp are of particular ecological and commercial importance. White shrimp are an important food source for a large number of finfish predators, which are a major source of their mortality (Gunter 1956, Pérez-Farfante 1969, Lindner and Cook 1970, McKenzie 1981, Benson 1982, Minello et al. 1987). Thayer et al. (1973) demonstrated that penaeids are higher in energy content than polychaetes, gastropods, bivalves or echinoderms and thus are more attractive prey items for finfish predators than small fish that, although higher in energy content, are more likely to flee from predators (Minello and Zimmerman 1984). In 2001, the estimated value and weight of all commercially landed species in the United States were  $\$3.2 \times 10^9$  and  $4.3 \times 10^6$  t, of which shrimp (all species) comprised  $\$5.8 \times 10^8$  and  $1.6 \times 10^5$  t (personal communication, David Sutherland, National Marine Fisheries Service, Fisheries Statistics and Economics Division, Silver Spring, MD). Thus, although shrimp were only 3.6% by weight of the total domestic catch, they represented 17.8% of its dollar value, ranking them as the most valuable commercial fishery in the United States. In 2001, white shrimp (*Litopenaeus setiferus*,

formerly *Penaeus setiferus*, Pérez-Farfante and Kensley 1997) estimates were  $\$1.9 \times 10^8$  and  $4.1 \times 10^4$  t, accounting for 32.8% by dollar value, and 25.6% by weight, of all commercially-landed shrimp.

Although reproduction and spawning take place in the relatively stable marine environment, ensuing in-migration and growth of postlarval and juvenile stages occur under the more unpredictable fluctuations of estuarine environments. Here, penaeids provide transtrophic links between primary producers and a suite of secondary and tertiary consumers, primarily finfish (Knapp 1949, Lindner and Cook 1970, Minello and Zimmerman 1983, Minello and Zimmerman 1984, Minello et al. 1987), many of which are commercially and recreationally important. White shrimp have also recently garnered keen interest from U.S. east coast growers because they are indigenous, which precludes the accidental release of an exotic, a factor making them attractive in the high-profit live bait market and to conservationists (Williams et al. 1996). White shrimp can also overwinter within estuaries (Sandifer et al. 1990), and there is experimental evidence that growth rate can approach that of *Penaeus vannamei* (Robertson et al. 1993), the most widely cultured shrimp in the western hemisphere (Wedner and Rosenberry 1992).

Shrimp are known to display species-specific substrate preferences (Springer and Bullis 1954, Hildebrand 1954, Williams 1955, Mock 1966, Jones 1973, Weinstein 1979, Geaghan 1980, Rulifson 1981) and are thus likely to aggregate in distinct spatial zones of estuaries. Although decomposition of organic matter in the water column can account for a substantial fraction of oxygen consumption in estuaries (Stanley and Nixon 1992, Hopkinson et al. 1999), sediment oxygen demand can account for more than 50% of the total respiration

in shallow estuaries (Rizzo and Christian 1996, Buzzelli et al. 2002). This means that low DO waters often reside in clearly demarcated spatial zones above estuarine bottoms, often in deeper central parts. The net result is a correlation between certain sediment types (muddier sediments containing a high fraction of organic matter) and the occurrence of hypoxia in overlying waters.

Towards the end of the growing season, white shrimp exhibit within-estuary ontogenetic shifts in habitat use as they out-migrate towards the ocean. Gaidry and White (1973) noted that under normal environmental conditions emigration of brown shrimp from nursery grounds occurred in two stages, the first at a size of 60-70 mm when juveniles left shallow marsh areas for “staging areas” in open bays where they continued to grow and feed until they began the second movement, migration to offshore waters, at a size of 90-110 mm. There was some variability in these events: some juvenile brown shrimp emigrated at smaller sizes (40-70 mm) on strong outgoing tides and others reentered estuaries. White and Boudreaux (1977) found that emigration at smaller than normal sizes was stimulated by adverse environmental conditions such as freshets or strong frontal passages.

The transition from inner-estuary nurseries to the open ocean can take up to 4-5 months to complete (Lindner and Anderson 1956). Bailey-Brock and Moss (1992) noted that penaeids may school during such emigration from estuaries. Leaving the relatively greater protection of inner estuarine nurseries, shrimp must traverse lower estuaries where they may encounter hypoxia that develops concurrently due to warmer water temperatures and salinity stratification. While hypoxia is a phenomenon of many naturally-eutrophied estuaries, the larger temporal and spatial scales of more recent anthropogenically-driven hypoxia mean that

there may be only a small fraction of the estuarine bottom suitable for occupation, with likely repercussions for penaeids and other estuarine organisms with preferences for specific substrate types. The purpose of my investigation was to quantify the magnitude of some of the possible negative effects on shrimp growth and survivorship that might occur on different sediments in outlying areas.

## **MATERIALS AND METHODS**

The pinfish (*Lagodon rhomboides*) was chosen because it has been documented preying on shrimp (Hansen 1969, Carr and Adams 1973, Brook 1977, Stoner 1980) during daylight hours (Minello and Zimmerman 1983). Over a 12-hr experimental period, Minello et al. (1987) found that 62-80 mm pinfish could eat between 20% (turbid water/sand substrate) and 57% (clear water/no substrate) of their body weight in 30-42 mm *Farfantepenaeus aztecus* (brown shrimp), and that predation rates may have been underestimated because all available shrimp were eaten before the end of some experiments. Minello and Zimmerman (1983) reported predation rates on juvenile brown shrimp (50-69 mm) of  $\approx 2-13 \text{ shrimp}\cdot\text{fish}^{-1}\cdot\text{day}^{-1}$ .

Densities of juvenile white shrimp vary widely, reflecting habitat-specific larval recruitment dynamics and post-settlement mortality, e.g., Minello and Webb (1997) reported a density of  $30.4 \text{ shrimp}\cdot\text{m}^{-2}$  for 24-mm juveniles and Clark et al. (1999) reported a value of about  $7.5 \text{ shrimp}\cdot\text{m}^{-2}$  for 32 mm juveniles, both in Galveston Bay, Texas. There are relatively fewer accurate density estimates for larger juveniles and subadults, primarily due to dispersion as a consequence of size-dependent out-migration (Joyce 1965) into areas of

expanding spatial scale and problems associated with converting trawl catch data to density estimates. The range of my experimental shrimp densities (5-20 shrimp·m<sup>-2</sup>) was based on a careful scrutiny of reported field densities of 20-90 mm white shrimp and, to a lesser extent, brown shrimp (Zimmerman et al. 1984, Zimmerman and Minello 1984, Minello and Zimmerman 1985, Rozas and Reed 1993, Wenner and Beatty 1993, Rozas and Minello 1998, Howe et al. 1999, Rozas and Zimmerman 2000) with the objective of encompassing normal field values as well as higher values that might be expected to occur if population crowding due to habitat compression occurred.

Three experiments were performed. The first, a 20-day experiment conducted in September of 2001, examined the effects of pinfish density (0, 2 m<sup>-2</sup>) and shrimp density (5, 10, 20 m<sup>-2</sup>) on the growth rate and survivorship of juvenile white shrimp, with three replicates of each predation × density treatment (i.e., 18 mesocosms). Because unexpectedly high predation mortality resulted in an insufficient number of replicates with surviving shrimp to do a growth rate analysis, I repeated this experiment the subsequent summer, in July 2002, after a study in outdoor concrete tanks suggested that reducing predation exposure by a factor of six (halving the predator treatment number and decreasing the duration of the experiment from 20 to 7 days) would be adequate to yield sufficient shrimp survival. However, this second experiment also resulted in extremely high predation losses, so the growth rate analysis was abandoned and I instead combined the data from these two experiments to analyze the effects of shrimp and pinfish density on shrimp survivorship only. Survivorship data (proportions) were arc-sine transformed and analyzed via an ANOVA, with each experiment/year as a random blocking factor, followed by multiple pairwise

contrasts (using a Tukey-Kramer adjustment). All analyses were performed in SAS (version 8.2, SAS Institute Incorporated, Cary, NC).

The third experiment, in August 2002, examined the effect of shrimp density (5, 10, 20 m<sup>-2</sup>) and sediment type (sandy mud, sand, peat) on shrimp growth rate, with three replicates of each density × sediment treatment (i.e., 27 mesocosms). These three sediment types were specifically chosen because they are common in many Atlantic and Gulf coast estuaries. Growth rate was expressed as percent body weight per day (bw·d<sup>-1</sup>) and scaled to an individual's average weight during the growth period using the equation:

$$\text{GR} = \{(\text{end wt.} - \text{start wt.}) \div [\# \text{ days} \times (\text{end wt.} + \text{start wt.}) / 2]\} \times 100$$

The presence of a strong positive relationship between initial shrimp weight and ensuing growth (regression  $P < 10^{-9}$ ) prompted us to analyze the data via an ANCOVA using shrimp initial weight as the covariate (after confirming homogeneity of the regression among treatments). Growth data were log<sub>10</sub> transformed prior to analysis. Because one of the three sediment types, sandy mud, was used in the two predation-density experiments, I decided to do a supplemental ANCOVA, again looking at the effect of density on growth rate on that substrate only, with each of the three experiments as a random blocking factor.

Apart from differences in predator treatment levels, sediment type, and the duration of experiments, the execution of each of these experiments was identical. White shrimp were collected from Calico Creek, Morehead City, North Carolina (2001 and 2002), and age-1 pinfish were collected from Calico Creek (2001) and Pivers Island (2002), North Carolina, using a 2.3-m cast net (0.63-cm mesh), and transported to 7500-L outdoor flow-through tanks (1000 L·hr<sup>-1</sup>) at the National Marine Fisheries Service Laboratory, Pivers Island, North

Carolina. Before the commencement of experiments, shrimp were fed daily an excess of aquaculture-grade feed (55% crude protein; Corey Feed Mills Limited, New Brunswick, Canada), in addition to any organic matter settling out of the unfiltered seawater supply.

Cylindrical cages were constructed (1.0 m<sup>2</sup> basal area, 1.2 m height) by stitching heavy-duty plastic mesh (Vexar, 0.63-cm mesh) with braided nylon twine onto cylindrical frames made of 2.5-cm (inside diameter, ID) plastic conduit pipe. A 40-cm aperture was made on the top panel of each cage through which sediment, shrimp and predators could be loaded. These apertures could be quickly sewn shut at the commencement of experiments. Cages were visually scrutinized before deployment to ensure there was no means of escape.

Cages were deployed in the intertidal zone on the north and south shores of Prytherch's Pond, Pivers Island, NC, by cable-tying each one to three PVC poles (3.3 m long, 2.5-cm ID) that were hammered into the substrate. This ensured that the bottom panel of each cage lay flush with the underlying substratum. As an added precaution, a 7-kg concrete block (30 cm square) was lowered by rope into the middle of each cage to ensure that there was no gap under any cage that might allow subsequently loaded sediment to escape.

Fresh sediment (sandy mud, sand or peat) was collected and stored in 600-L tanks in the intertidal zone of the pond two days before the commencement of experiments. Sand was collected from the western shore of Radio Island, NC, sandy mud from a mudflat adjacent to a *Spartina* marsh north of Radio Island, and peat from Broad Creek, 12 miles west of Morehead City, NC. Across the bottom of each cage, 40 kg of sediment was carefully distributed to  $\approx$  5 cm depth using a large PVC pipe (1.3 m long, 15-cm ID) as a trough to direct the placement of 1-kg scoops. The locations of the various density, sediment and

predator treatment combinations were randomized. Cages were then sewn shut for 48 hours, to permit acclimation.

Shrimp were uniquely marked by injecting permutations of three colors of an elastomer (Northwest Marine Technology Incorporated, Shaw Island, WA) into three positions on the 6<sup>th</sup> abdominal segment. This marking procedure permitted the tracking of individual growth rates. After blotting on paper towels to remove excess water, shrimp were measured for length and weight using calipers and a digital scale. Shrimp and pinfish were placed into fresh seawater in labeled 19-L buckets corresponding to cages of subsequent deployment. Buckets were bubbled with pure oxygen to minimize stress on shrimp, as the entire tagging procedure took several hours. Shrimp and /or pinfish were then transferred to the mesocosms, which were sewn shut, marking the commencement of the experiment. Daily readings of temperature and DO were taken beside each mesocosm  $\approx$  15 cm from the sediment surface to characterize any variability among mesocosms and within the pond. After the required time had elapsed, test animals were retrieved and measured again for length and weight. Shrimp wet weight was used for growth rate calculations, as is common practice (Seidman and Lawrence 1985, Allan and Maguire 1991, Hopkins et al. 1993, Davis and Arnold 1994, Williams et al. 1996).

For the 2001 predator-density experiment (20-d, 2 pinfish), mean wet weights and lengths were  $2.77 \pm 0.05$  g and  $71.5 \pm 0.4$  mm (mean  $\pm$  1 SE) for white shrimp and  $17.41 \pm 0.83$  g and  $103.1 \pm 1.6$  mm for pinfish. For the 2002 predator-density experiment (7-d, 1 pinfish), mean wet weights and lengths were  $2.67 \pm 0.05$  g and  $69.6 \pm 0.5$  mm for white shrimp and  $44.43 \pm 4.13$  g and  $125.4 \pm 15.9$  mm for pinfish. For the 2002 density-sediment

experiment mean white shrimp wet weight and length were  $4.77 \pm 0.06$  g and  $84.8 \pm 0.4$  mm (mean  $\pm$  1 SE) for white shrimp.

## RESULTS

DO and temperature were both stable, ranging from 6.0-6.3 ppm DO and 28.9-29.5°C (Table 1). The range of DO values was considered normoxic, and the range of water temperatures was typical for late summer. Across mesocosms there was no significant difference among values for either DO (ANOVA  $P = 0.16$ ) or temperature ( $P = 0.81$ ).

For the 2001 20-day density-predation experiment, mean white shrimp growth rates ranged between 1.2 and 2.3%  $\text{bw}\cdot\text{d}^{-1}$  (Table 2; Fig. 1) in the no-predator treatments where survivorship was high with 103 of the 105 shrimp recovered. However, there was high predation mortality in the predator treatments, with 100% loss of shrimp (subsamples) in five of nine replicates (Table 2) and 78% overall. For the 2002 7-day density-predation experiment, density-dependent patterns of mean growth rate were similar, ranging between 2.8 and 5.5%  $\text{bw}\cdot\text{d}^{-1}$  (Table 3; Fig. 1) in the no-predator treatments where survivorship was again high with 101 out of 105 recovered (Table 3), but among the predation treatments there was again high mortality, with 100% loss in eight of the nine replicates.

For the 2002 7-day sediment-density experiment, density-dependent patterns of mean growth rate were similar for sandy mud (range 0.3-1.4%  $\text{bw}\cdot\text{d}^{-1}$ ), peat (range 0.6-2.3%  $\text{bw}\cdot\text{d}^{-1}$ ) and sand (range 0.6-2.7%  $\text{bw}\cdot\text{d}^{-1}$ ) (Table 4, Fig. 2). Survivorship was very high, with 310 out of 315 shrimp recovered.

*Effects of shrimp density on the growth rate of juvenile white shrimp*

The ANCOVA on pooled growth rate data from all three experiments (the first three rows of Tables 2, 3 and 4) indicated a strong effect of shrimp density on growth rate (overall  $P < 0.0001$ ), and pairwise contrasts indicated significant differences in mean growth rates between all three levels of shrimp density ( $20 \text{ m}^{-2}$  vs.  $5 \text{ m}^{-2}$   $P < 0.0001$ ,  $20 \text{ m}^{-2}$  vs.  $10 \text{ m}^{-2}$   $P < 0.0001$  and  $10 \text{ m}^{-2}$  vs.  $5 \text{ m}^{-2}$   $P = 0.02$ ). There was a significant block effect ( $P < 0.0001$ ) on growth. This was expected, primarily because blocks corresponded to different experiments/years, meaning that these wild-caught shrimp were unlikely to have experienced identical conditions either before collection or during the experiments. This is reflected in the relatively high growth response in the 2002 density-predation experiment (Fig. 1). Despite the block effect, the effect of density was robust enough to be operative over a range of environmental conditions.

*Effects of sediment type and shrimp density on the growth rate of juvenile white shrimp*

The ANCOVA on growth rate data (Table 4) from the sediment-shrimp density experiment indicated that only shrimp density had a statistically significant effect on white shrimp growth rate ( $P < 0.0001$ ), with no effect of sediment type ( $P = 0.12$ ) and no sediment  $\times$  density interaction ( $P = 0.49$ ).

*Effects of pinfish predation and shrimp density on the survivorship of juvenile white shrimp*

The ANOVA on pooled survivorship data (last three rows of Tables 2 and 3) from the two predation-density experiments indicated a strong effect of predation on survivorship ( $P < 0.0001$ ) but no effect of density ( $P = 0.84$ ) and no density  $\times$  predation interaction ( $P = 0.98$ ).

**DISCUSSION***Effects of shrimp density on the growth rate of juvenile white shrimp*

The strongly density-dependent growth exhibited by juvenile white shrimp in the no-predator treatments of these experiments suggests that, at field levels of food abundance, intraspecific competition for food may have an important limiting effect on growth rate at shrimp densities  $\leq 20$  shrimp $\cdot$ m<sup>-2</sup>. Qualitative observations of white shrimp in holding tanks indicate a lack of aggressive interactions, which, in addition to the absence of cannibalism in my experiments, suggests that resource depletion and exploitative competition may be the primary cause of growth attrition, although interference competition cannot explicitly be ruled out. This is corroborated by evidence from intensive aquaculture projects where food is not a limiting factor: Williams et al. (1996) had 97.5% stocking-to-harvest survivorship of white shrimp in ponds that were initially stocked at 40 m<sup>-2</sup>, attaining a final biomass density of 526 g $\cdot$ m<sup>-2</sup>, and Hopkins et al. (1993) reported excellent growth and survivorship at 44 m<sup>-2</sup> with a strong linear correlation between mean shrimp weight and time ( $R^2 = 0.95$ ), indicating that higher densities and growth rates can be simultaneously attained without mortality, provided food inputs and water exchange are sufficient. For comparison, the biomass density of white shrimp in my 20-m<sup>-2</sup> mesocosms (where growth attrition was already evident) was

only  $\approx 95 \text{ g}\cdot\text{m}^{-2}$ . Further evidence comes from the higher growth rates attained in my laboratory experiments (Chapter 2; discussed below).

It should be noted that, apart from within-sediment food sources, my mesocosms were open to deposition of organic matter from the water column and there was also some algal growth on the mesocosm walls. Despite these extraneous food sources, the fact that my experimental field populations consistently displayed density-dependent growth between 5 and 20 shrimp $\cdot\text{m}^{-2}$  across all substrate types (Fig. 2) is instructive, implying that the combined total of within-substrate and outside food sources was still insufficient to support optimal growth at higher shrimp densities. Because aquatic environments of variable productivity exist that, in some cases, may be correlated with substrate type, the inputs of organic matter to sediments may display considerable inter-habitat variability. Thus repeating growth experiments in other habitats could result in a greater or lesser degree of density-dependent growth.

Interhabitat comparisons of animal densities have largely been between seagrass and non-vegetated bottom (Williams et al. 1990, Sheridan 1992, Valentine et al. 1994) with limited comparisons of nekton density between tidal marsh and nonvegetated bottom (Zimmerman and Minello 1984, Minello et al. 1991, 1994). Within shrimp cohorts there is a constant decline in numbers as shrimp progress from inside to outside waters: Dall (1990) reported high mortality of 10-25% $\cdot\text{week}^{-1}$  for juveniles over their 2-3 month stay in estuaries, vs. only moderate mortality of 2-10% $\cdot\text{week}^{-1}$  for adults during their 8-20 month offshore stay (mortality during larval phases,  $> 70\% \cdot \text{week}^{-1}$ , was the most severe), and attributed the lower mortality of adults to reduced predation. The question of why juvenile shrimp may not attain

densities where they become food limited in the field is particularly intriguing, and is at least partially answered by a consideration of size-selective predation factors. Knudsen et al. (1977) suggested that rapid growth rates ( $0.7\text{-}3.3\text{ mm}\cdot\text{d}^{-1}$ ) exhibited by brown shrimp might be an evolutionary response to such size-selective predation.

*Effects of sediment type and shrimp density on the growth rate of juvenile white shrimp*

The strong negative effect of density on growth rate discussed above was again evident in this experiment. However, the more striking result was the absence of an effect of sediment type on growth rate. In Chapter 4, it was pointed out that, although sediment preferences of white shrimp might be partially explained by food abundance, there was ample evidence in the literature that a number of other factors might also be equally or more important, such as particle size, problems associated with respiring when buried, turbidity, habitat recognition, competition and predation (Williams 1958, Fuss and Ogren 1966, Ruello 1973, Penn 1984, Minello et al. 1987, Dall et al. 1990). Additionally, spatial variations in habitat usage cannot be entirely attributed to preference when accessibility is restricted (Matthiopoulos 2003), which is likely to be the case in heterogeneous or disturbed environments, a fact that further complicates the interpretation of sediment preferences in the field.

In the context of hypoxic events causing habitat loss and mass movements of shrimp to outlying areas of estuarine bottom, my data suggest that the primary factor of concern is growth rate attrition due to increased densities, and not due to forced emigration to non-preferred sediment types. On a more cautionary note, it should also be kept in mind that, as

eutrophication increases, water column primary productivity and the flux of organic matter to the bottom also increase, so that negative impacts may initially be counterbalanced by greater availability of organic carbon and fisheries production (Caddy 1993, Diaz and Rosenberg 1995). However, as eutrophication increases the temporal and spatial extent of hypoxia, the fisheries production base is affected and declines. This graded reaction to the combined problems of excess nutrients and hypoxia has been described in many systems around the globe (Diaz and Solow 1999).

In laboratory growth experiments without substrate (Chapter 2), at a density of  $\approx 80$  shrimp $\cdot$ m $^{-2}$ , 2.2 g white shrimp attained growth rates of 2.4% bw $\cdot$ d $^{-1}$  at normoxia (55% protein diet). This value is higher than growth rates attained at 20 m $^{-2}$  in my sediment experiment, although mean shrimp weights were more than double in the latter (4.8 g with growth rates of 0.55, 0.27 and 0.64% bw $\cdot$ d $^{-1}$  for peat, sandy mud and sand, respectively). Growth rates in my 2001 and 2002 density-predation experiments were of more comparable magnitude (2.8 g and 1.22% bw $\cdot$ d $^{-1}$  in 2001, and 2.7 g and 2.76% bw $\cdot$ d $^{-1}$  in 2002). Apart from presenting further evidence of food limitation at higher densities in the field, these comparisons suggest that white shrimp growth rate is somewhat independent of substrate, whether in the lab (glass aquaria without substrate) or on naturally-occurring sediments.

#### *Effects of pinfish predation and shrimp density on the survivorship of juvenile white shrimp*

Pinfish predation on juvenile white shrimp was severe on the bare sandy mud substrate used in both of my predation-density experiments in 2001 (2 pinfish $\cdot$ m $^{-2}$ ) and 2002 (1 pinfish $\cdot$ m $^{-2}$ ). The fact that predation was consistently high across all three shrimp density

treatments, with 100% depletion in most cases, suggests that pinfish are particularly efficient predators of white shrimp. As a caveat, it is possible that shrimp density may interact with predation to affect survivorship at lower values, but if this occurred in my experiments its effect was erased unobserved before the end of the trials due to near-complete shrimp mortality.

The use of vegetative cover for protection from fish predators by juvenile penaeids has been noted (Minello and Zimmerman 1983, 1985, Zimmerman and Minello 1984), but macrophyte cover varies across habitats and is often completely absent in many estuarine areas, especially those traversed by larger juvenile and subadult shrimp as they make the transition to the ocean. Pinfish exhibit several ontogenetic feeding stages, and Stoner (1980) reported that larger individuals > 100 mm were herbivorous on epiphytes and vascular plant material. These shifts in feeding behavior appear to be coupled with a change in dentition from conical- and canine-shaped teeth to chisel-shaped incisors in fish > 35 mm (Caldwell 1957). Oddly enough, cellulose activity is not found in the alimentary tract of pinfish (Stickney and Shumway 1974) and, as a further caveat, Carr and Adams (1973) found strict carnivory of pinfish on fish and shrimp > 80 mm. These findings suggest high variability in pinfish feeding preferences that may result from changes in absolute and relative abundances of suitable prey and/or plant items across habitats. My experiments corroborate these findings, clearly demonstrating that these 103-125 mm pinfish, in the absence of macrophytes, exhibit a marked degree of carnivory.

In my predation-density experiments, both shrimp and pinfish were larger than in the studies described earlier (Minello and Zimmerman 1983, Minello et al. 1987). The predator-

prey size ratio in my experiments was also notably larger: shrimp averaged only 16% and 6% of pinfish weight in 2001 and 2002 respectively (when pinfish were at 1 m<sup>-2</sup> and 2 m<sup>-2</sup>). Although mean pinfish length in 2002 was only 22% longer than in 2001, corresponding mean weight was 255% larger, perhaps reflecting the fact that pinfish were collected from different sites in each of these years. This unexpected upward shift in the predator-prey size ratio in my experiments from 2001 to 2002 explains why the reduction in predation exposure may have been unsuccessful in reducing predation mortality. However, it still appears that the functional response of pinfish to white shrimp is consistent across pinfish size classes. At the temporal and spatial scale of my experiment, pinfish were more than capable of depleting available shrimp. Interestingly, despite their voracious appetite for shrimp, pinfish did not always exhibit positive growth (13 of 27 pinfish exhibited declines in biomass over the experimental period), suggesting either that there were insufficient shrimp available to promote pinfish growth over the course of the experiment, that a pure-shrimp diet is suboptimal, or that pinfish may kill but not consume all available prey. The latter is likely because shrimp:pinfish body length ratios were relatively high (0.69 and 0.56 in 2001 and 2002 respectively) making it unlikely that shrimp were gulped whole.

The absence of density-related mortality was not entirely unexpected, as white shrimp can be grown in intensive aquaculture at densities as high as 44 m<sup>-2</sup> (Hopkins et al. 1993), albeit with large food inputs and enhanced water exchange. Although cannibalism was reported as common among juvenile and adult white shrimp (Pérez-Farfante 1969), McKenzie (1981) suggested that reports of cannibalism in the literature may be the result of crowding in experimental aquaria. Based on the high survivorship values in my no-predator

mesocosms, my experiments indicate that cannibalism among juveniles in the field does not occur at densities  $\leq 20 \text{ m}^{-2}$ .

## **CONCLUSIONS**

The premise that forced emigration to non-preferred sediment types may have direct consequences for growth and survivorship for white shrimp was not supported by my study. This does not exclude the possibility of negative effects during transitional phases. My study has also shown that there are strong density-dependent growth effects on juvenile white shrimp. There is evidence of continuous declines in CPUEs of both brown and white shrimp since the 1960s in the Gulf of Mexico (Caillouet 1981, Downing et al. 1999), yet no evidence of recruitment failure and, although such patterns may be linked to changes other than hypoxia-induced congestion, they are consistent with the hypothesis of environmental impact (Downing et al. 1999). Although somewhat problematic because of the difficulty of disentangling so many other confounding factors (e.g., fishing pressure, climatic variation, pollutants, etc.), further field research, and modeling efforts to support it, are necessary to better quantify risks to white shrimp and other species.

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Table 1. Dissolved oxygen (DO) and temperature readings for experimental mesocosms (mean  $\pm$  1 SE).

<b>Sediment Type</b>	<b>Shrimp Density</b>	<b>DO (ppm)</b>	<b>Temperature (°C)</b>
<b>Sandy Mud</b>	5	6.30 $\pm$ 0.35	28.88 $\pm$ 0.24
		6.10 $\pm$ 0.23	29.13 $\pm$ 0.25
		6.06 $\pm$ 0.25	29.08 $\pm$ 0.21
	10	6.25 $\pm$ 0.24	29.13 $\pm$ 0.21
		6.23 $\pm$ 0.23	29.08 $\pm$ 0.21
		6.20 $\pm$ 0.22	29.15 $\pm$ 0.19
	20	6.67 $\pm$ 0.59	29.40 $\pm$ 0.16
		6.27 $\pm$ 0.26	29.32 $\pm$ 0.17
		6.30 $\pm$ 0.25	29.30 $\pm$ 0.17
<b>Peat</b>	5	6.08 $\pm$ 0.26	29.05 $\pm$ 0.22
		6.27 $\pm$ 0.33	28.85 $\pm$ 0.20
		6.10 $\pm$ 0.29	29.08 $\pm$ 0.27
	10	6.05 $\pm$ 0.19	29.42 $\pm$ 0.23
		6.05 $\pm$ 0.26	29.12 $\pm$ 0.22
		6.26 $\pm$ 0.27	29.35 $\pm$ 0.17
	20	6.28 $\pm$ 0.21	29.28 $\pm$ 0.17
		6.16 $\pm$ 0.24	29.38 $\pm$ 0.16
		6.16 $\pm$ 0.17	29.25 $\pm$ 0.14
<b>Sand</b>	5	6.13 $\pm$ 0.25	29.05 $\pm$ 0.23
		6.14 $\pm$ 0.23	29.02 $\pm$ 0.23
		6.19 $\pm$ 0.32	28.98 $\pm$ 0.23
	10	6.28 $\pm$ 0.25	29.33 $\pm$ 0.15
		6.00 $\pm$ 0.17	29.50 $\pm$ 0.25
		6.13 $\pm$ 0.24	29.15 $\pm$ 0.25
	20	6.12 $\pm$ 0.18	29.22 $\pm$ 0.16
		6.32 $\pm$ 0.23	29.32 $\pm$ 0.17
		6.20 $\pm$ 0.28	29.38 $\pm$ 0.18

Table 2. Growth rates and survivorship of white shrimp (*Litopenaeus setiferus*) under various shrimp density and predator treatments. 20-day experiment (2001).

Pred #	Shrimp start #	Shrimp surv #	Shrimp surv %	Viable reps	GR (% bw·d <sup>-1</sup> )	Mean GR ± SE (% bw·d <sup>-1</sup> )	
0	20	20	100	3	1.14	1.22 ± 0.05	
		19	95		1.31		
		20	100		1.19		
	10	9	90	3	1.63	2.05 ± 0.28	
		10	100		1.94		
		10	100		2.57		
	5	5	100	3	2.53	2.32 ± 0.27	
		5	100		2.65		
		5	100		1.79		
	2	20	1	5	2	2.11	1.54 ± 0.57
			3	15		0.97	
			0	0		-	
10		8	80	1	1.5	1.5	
		0	0		-		
		0	0		-		
5		0	0	1	-	3.14	
		5	100		3.14		
		0	0		-		

Table 3. Growth rates and survivorship of white shrimp (*Litopenaeus setiferus*) under various shrimp density and predator treatments. 7-day experiment (2002).

Pred #	Shrimp start #	Shrimp surv #	Shrimp surv %	Viable reps	GR (% bw·d <sup>-1</sup> )	Mean GR ± SE (% bw·d <sup>-1</sup> )	
0	20	19	95	3	3.14	2.76 ± 0.26	
		20	100		2.88		
		20	100		2.26		
	10	9	90	3	5.42	4.69 ± 0.46	
		9	90		3.84		
		10	100		4.8		
	5	4	80	3	4.75	5.48 ± 0.84	
		5	100		7.15		
		5	100		4.53		
	1	20	0	0	1	-	1.83
			0	0		-	
			4	20		1.83	
10		0	0	0	-	N/A	
		0	0		-		
		0	0		-		
5	0	0	0	-	N/A		
	0	0		-			

Table 4. Growth rates of white shrimp (*Litopenaeus setiferus*) under various sediment and density treatments. 7-day experiment (2002).

Sediment Type	Shrimp start #	Shrimp surv #	Shrimp surv %	Viable reps	GR (% bw·d <sup>-1</sup> )	Mean GR ± SE (% bw·d <sup>-1</sup> )
Sandy Mud	20	20	100	3	0.55	0.27 ± 0.15
		20	100		0.04	
		20	100		0.22	
	10	10	100	3	1.37	1.29 ± 0.16
		10	100		1.51	
		10	100		0.98	
	5	5	100	3	1.39	1.42 ± 0.13
		5	100		1.21	
5		100	1.67			
Peat	20	17	85	3	1.06	0.55 ± 0.26
		20	100		0.34	
		20	100		0.25	
	10	10	100	3	1.47	1.33 ± 0.18
		10	100		1.54	
		10	100		0.98	
	5	5	100	3	1.59	2.29 ± 0.37
		4	80		2.84	
5		100	2.45			
Sand	20	19	95	3	0.71	0.64 ± 0.09
		20	100		0.75	
		20	100		0.47	
	10	10	100	3	0.53	1.08 ± 0.31
		10	100		1.1	
		10	100		1.6	
	5	5	100	3	2.6	2.70 ± 0.38
		5	100		3.41	
5		100	2.09			

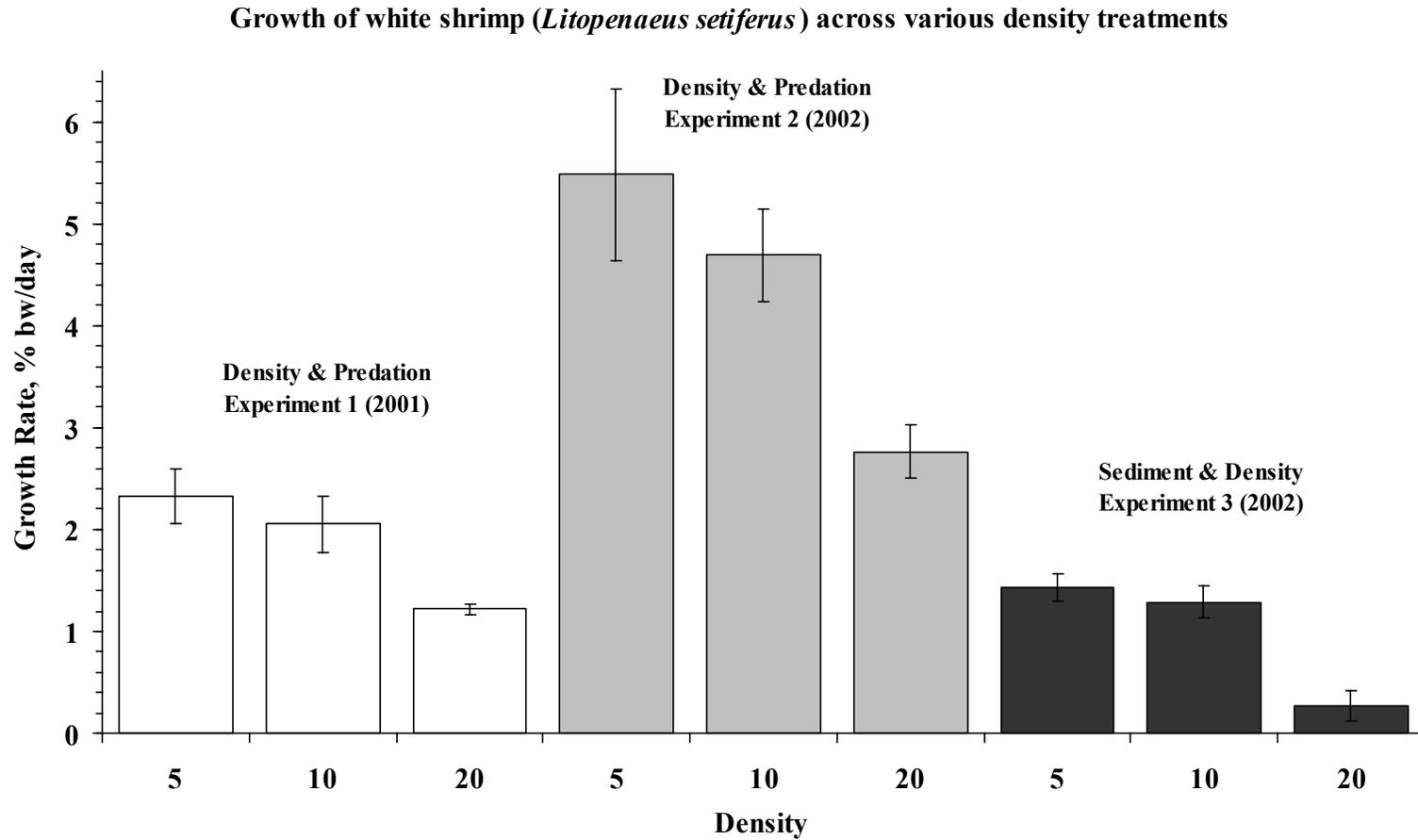


Fig. 1. Growth rates (% bodyweight per day) of white shrimp (*Litopenaeus setiferus*) at three densities (5, 10, 20 m<sup>-2</sup>), on the same substrate (sandy mud). Data are from three independent experiments: density-predation (2001), density-predation (2002) and sediment-density (2002). No-predator treatments only were used (means  $\pm$  1SE).

Growth of white shrimp (*Litopenaeus setiferus*) across various substrate/density treatments

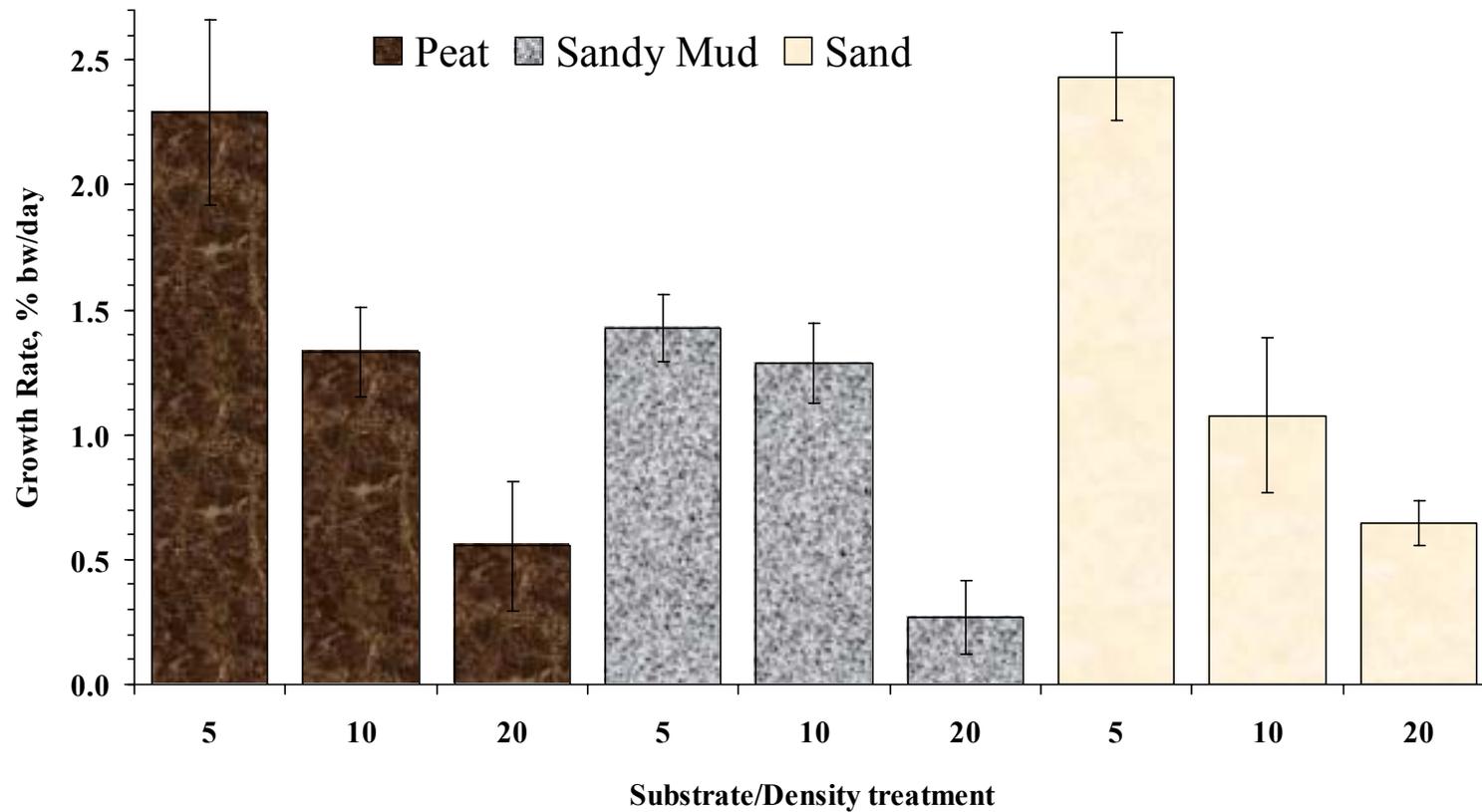


Fig. 2. Growth rates (% bodyweight per day) of white shrimp (*Litopenaeus setiferus*) across various density (5, 10, 20 m<sup>2</sup>) and substrate (peat, sandy mud, sand) treatment combinations (means  $\pm$  1 SE).

## Chapter 6. Summary.

My research has shown that DO levels above those that are normally considered to be hypoxic ( $\leq 2$  ppm), and DO regimes that fluctuate between high and low values, can both depress the growth rate of juvenile white shrimp. These responses were not observed in juvenile brown shrimp. Such asymmetries caution against extrapolation of data across even closely-related species. Hypoxia was shown to significantly increase the emergence behavior of brown shrimp, which has the potential to increase predation mortality to opportunistic predators. Despite this behavioral shift, brown shrimp tempered their willingness to flee somewhat when there was a predation threat present. This plasticity of response will need to be considered in any realistic modeling effort. My sediment preference and sediment-growth experiments indicated that both brown and white shrimp were not averse to burrowing into sediments that differ from those indicated by field distributions, and that white shrimp growth rate was unaffected by sediment type. Apart from demonstrating that there may be complex non-foraging reasons why these shrimp associate with specific sediment types, these results also imply that, under environmental disturbance, shrimp can occupy a wide range of substrates yet maintain their growth rates. However, if there is large-scale disturbance, density-dependent growth effects can manifest themselves in outlying refuge habitats across shrimp densities in the range 5-20  $m^{-2}$ . The pinfish, one of a suite of possible finfish predators, was shown to be a particularly voracious predator of juvenile white shrimp, a fact that highlights the potential importance of ensuing predator aggregative responses in such refuge habitats.

Based on current U.S. commercial landings, brown and white shrimp may be worth half a billion dollars over the next five years alone. From the perspective of human consumption, shrimp, as primary consumers, are a better alternative than fish higher up the food chain (that represent a comparatively enormous amount of primary production). There is increasing public awareness about the current vulnerability of many pelagic fisheries and overharvesting driven by overconsumption. With recent improvements in bycatch-reduction technology and reductions in the cost of implementation, it is likely that shrimp will become more and more important as a food source in the coming decades.

The threats facing estuaries around the globe are now well known, and many important mitigatory steps have already been taken to curb further damage. Even so, it is important to realize that a large degree of the confidence placed on such countermeasures can come only via relevant research and modeling efforts. For each question answered, there are many others that still need to be urgently addressed. Future research in the following areas will prove particularly useful:

For shrimp, there is a linear relationship between fecundity and length. Thus hypoxia-mediated depression of growth rates, if not countered by compensatory growth after migration from the estuary, can have large impacts on ensuing egg numbers. Experiments are thus needed to examine whether such compensatory growth is possible.

Basic research is also needed to identify mortality rates for specific stages of the shrimp life cycle. This will help us to identify the degree to which factors other than eutrophication and hypoxia can affect harvestable biomass, for e.g., egg predation; planktonic predation on nauplii, protozoa, mysids, or postlarvae; or adult mortality during

intracoastal migration (although it should be noted that some of these factors, even if proven to be important, are generally beyond anthropogenic control). Of particular interest are instantaneous rates of natural mortality and fishing mortality after shrimp reach a harvestable size.

In order to construct spatially explicit models of intra-estuarine movement and growth in response to changing regimes of hypoxia, basic information about the following parameters is essential: field densities as a function of habitat compression, movement patterns of penaeid shrimp, size-specific movement rates, environmental (and other) cues that elicit migration behavior, patch selection, size-specific growth rates, predation rates under different D.O. regimes and in different patch types, and the effect of competition on growth and mortality rates.

The fact that shrimp are comprised of panmictic metapopulations complicates analyses of environmental impacts because, without accurate means to estimate the magnitude of genetic exchange between metapopulations, sources and sinks cannot be distinguished, and thus the critical areas where conservation efforts are most needed may remain unidentified. This urgently needs to be addressed.

Instead of trying to maintain some specific level of diversity, our efforts should be focused on understanding the basic ecological processes that control populations, communities and ecosystems in order to better predict what kinds of stresses will cause the most serious impacts. Until we have a more comprehensive understanding of ecological processes and the ways that ecosystems respond to anthropogenic disturbance, it would be wise to be conservative about protecting them.