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Enhanced Blue Crab Predation on Rangia Clams after Exposure to Hypoxia

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Enhanced Blue Crab Predation on Rangia Clams after Exposure to Hypoxia

A Thesis

Submitted to the Graduate Faculty of the
University of New Orleans
in partial fulfillment of the
requirements of the degree of

Master of Science
in
Biological Sciences

By

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Acknowledgments

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Abstract

Hypoxia or dissolved oxygen concentrations < 2 mg/L is a problem in estuaries worldwide. In Lake Pontchartrain, a 250 km^2 de-faunated zone exists as a result of salinity stratification and episodic hypoxia. Mature common rangia clams (*Rangia cuneata)* are not found within this zone. Blue crabs (*Callinectes sapidus)* are important estuarine predators and may move in and out of the hypoxic zone to feed on hypoxia-stressed rangia clams. To test the effects of hypoxia on predation, rangia clams were exposed experimentally to severe hypoxic conditions (< 0.75 mg/l) for 72-hours and then presented to blue crabs. One hypoxic and one normoxic clam were added to each aquarium containing a blue crab for each trial, and crab feeding choices were observed and recorded. I found prey choice varied among crabs, but in general, the experimental data demonstrates that crabs chose to feed on hypoxia-stressed clams over clams kept under normoxic conditions.

Introduction

Hypoxia (low dissolved oxygen concentrations <2 mg/L) occurs in estuaries, lakes, and coastal areas worldwide (Diaz & Rosenberg 1995). The effect of hypoxia on an ecosystem varies with the severity and duration of the hypoxic event. Differences in wind mixing, tidal circulation, water quality, gravity circulation, and density stratification can lead to spatial variation in severity, duration, and frequency of hypoxic conditions (Diaz et al. 1992). Hypoxia can cause mass mortality in fish and other marine organisms, as well as a decline in fisheries and benthic populations (Diaz & Rosenberg 1995). Even if hypoxia does not result in mortalities, relationships among organisms in the ecosystem are certainly altered as organisms try to adapt to low dissolved oxygen concentrations. Hypoxia can also alter community structure by decreasing species diversity and richness of fish and benthic populations. In general, large individuals and long-lived species are replaced by smaller and short-lived opportunistic species (Long & Seitz 2008).

Benthic organisms tolerate hypoxia with a variety of behavioral and physiological responses. Most immobile and sedentary organisms have a higher tolerance to hypoxia than mobile organisms, partly because they can reduce energy levels by changing their activity and metabolism (Stickle et al. 1989, Wu 2002). As dissolved oxygen concentrations decrease from 1.5 mg/L towards 0 mg/L, sedentary invertebrates, burrowing invertebrates and other benthic macrofauna display evidence of stress or die (Rabalais et al. 2001). Some infaunal bivalves migrate vertically, moving closer to the surface of the sediment and extending their siphons in an attempt to reach better-oxygenated waters (Seitz et al. 2003, Taylor & Eggleston 2000). Diaz et al. (1992) found that burrowing behavior of infaunal species changed even under mild hypoxic conditions. Several infaunal species were even observed laying on the sediment surface. Mobile

species move into shallower waters with higher dissolved oxygen concentrations (Pihl et al. 1991). Hypoxia disrupts normal behavior in most aquatic organisms and can remain altered for days after an event (Sagasti et al. 2001). Behavioral changes are usually not lethal, but can cause short-lived organisms to be less likely to reproduce. Behavioral changes caused by hypoxia may also increase the vulnerability of a prey species to predators (Taylor & Eggleston 2000, Pihl et al. 1992).   During episodic hypoxia, predators may take advantage of weakened and exposed prey. During long periods of hypoxia, prey organisms may simply die, and therefore not provide a beneficial food source (Nestlerode & Diaz 1998).

There are two models that predict predation scenarios associated with hypoxia.   Some prey organisms may experience a predation refuge during hypoxic events because predation rates may be decreased. This occurs in situations where prey organisms are more tolerant of hypoxia than their predators, and therefore experience less mortality (Sagasti et al. 2001). These models are called consumer stress models (Menge & Sutherland 1987). The other model is called prey stress model, in which prey species are more vulnerable than predators during hypoxic events, so predators can take advantage of weakened prey and predation is increased (Menge & Olson 1990). Periodic hypoxic events may stress the prey enough to make them more vulnerable but have no long-term effect on the predator (Sagasti et al. 2001). Mobile predators might move into hypoxic zones after the dissolved oxygen levels have increased in order to prey on organisms before they recover. Alternatively, chronic hypoxia may provide refuges for prey because predators may experience reduced feeding levels or increased mortality, leading to a reduction in predation. Most studies show reduced predation rates under hypoxic conditions due to reduced predator activity (Breitburg et al. 1994, Bell et al. 2003, Sagasti et al. 2001). However, some studies have suggested that periodic hypoxia is beneficial to predators and may result in

increased predation on benthic species. Taylor and Eggleston (2000) showed that the infaunal

bivalve *Mya arenaria* moved closer to the surface and increased siphon extension, resulting in

increased vulnerability to the blue crab. Stomach contents of predators in the York River

revealed an increase in large and deep burrowing prey species after hypoxic events (Pihl 1992).

Long and Seitz (2008) found that hypoxia increased the vulnerability of benthic prey to

predators, thus increasing the availability of infaunal prey to predators and reducing the stability

of the benthic community in the York River.

      This study was designed to determine if predation by blue crabs associated with episodic

low-oxygen events can help explain the lack of mature rangia clams in the hypoxic zone of Lake

Pontchartrain. Lake Pontchartrain, located north of New Orleans, Louisiana, is an estuarine

system of great economic importance. It has an average salinity of 4.0 parts per thousand, mean

depth of 3.7 meters, and surface area of 1620 km^2 (Sikora & Kjerfve 1985). High salinity water

from the Gulf of Mexico enters the lake through the Inner Harbor Navigation Canal (IHNC) via

the Mississippi River Gulf Outlet (MRGO). The resulting stratification causes episodic summer

hypoxia and gives rise to an approximately 250 km^2 zone where hypoxic events are frequent and

produce a severe impact on benthic organisms (Poirrier 1978, Junot et al. 1983, Abadie &

Poirrier 2001). Salinity stratification prevents mixing in the water column and causes bottom-

water hypoxia (Poirrier 1978). Mature rangia clams (>20 mm) are absent from this zone, and

although smaller Rangia clams are present, they die before they reach reproductive maturity

(Abadie & Poirrier 2001) (Figure 1). The density of mature rangia clams increased lake wide

after the cessation of shell dredging in 1990 except in this zone north of the IHNC, suggesting

that an increase in salinity, as well as low dissolved oxygen concentrations affect the

establishment of older and larger rangia clams (Abadie & Poirrier 2000). In addition, the area is

characterized by low species diversity and prevalence of annelids, indicating that the hypoxic events have altered community structure. The interaction between fluctuating salinity, low dissolved oxygen concentrations, and blue crab predation may contribute to the lack of mature clams in the hypoxic zone.
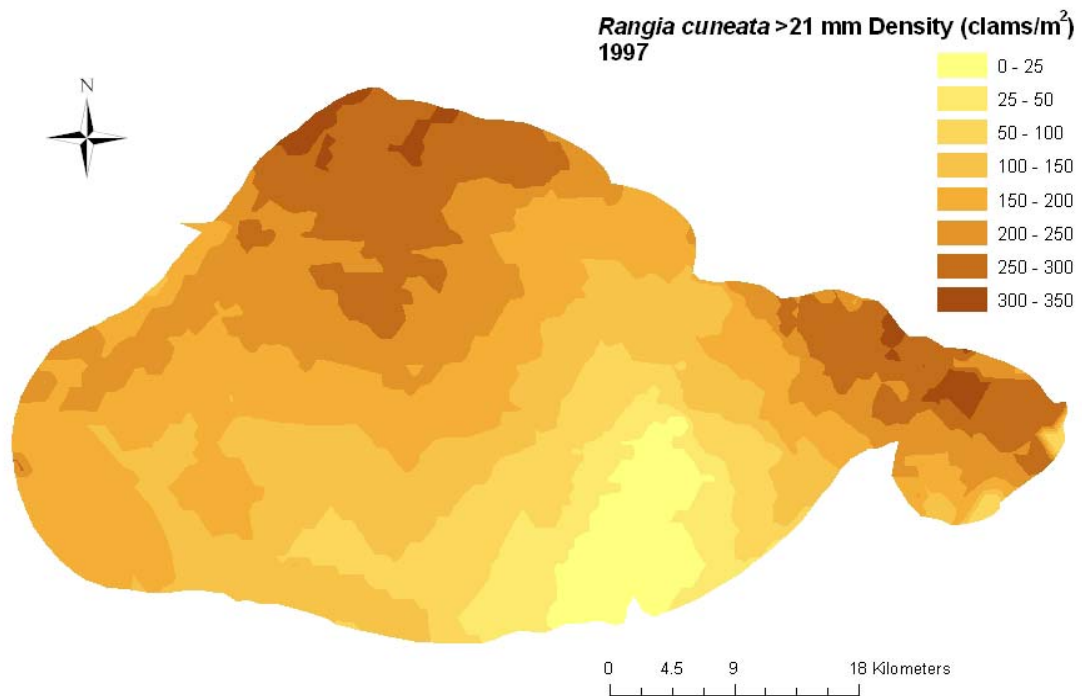
Figure 1: Distribution of rangia clam > 21 mm density (1997) in Lake Pontchartrain

Two recent events may have also impacted the establishment of mature rangia clams in Lake Pontchartrain. In 2005, Hurricane Katrina wiped out rangia clams from 50% of the lake bottom, likely due to abrupt changes in salinity and dissolved oxygen concentrations (Poirrier et al. 2008).   Further, the area affected by hypoxia may have expanded to 815 km^2 after Katrina (Poirrier et al. 2008).   Another problem was the opening of the Bonnet Carre Spillway in April 2008. The Bonnet Carre spillway is a man-made structure that connects the Mississippi River to Lake Pontchartrain that can be opened if the river reaches flood stage to protect the city from

flooding. When the spillway was opened in 1997, species diversity, abundance, and number of taxa decreased and appeared to have a deleterious impact on the benthic community in Lake Pontchartrain (Brammer et al. 2007).

Rangia cuneata (Mollusca: Bivalvia: Matridae) is the dominant bivalve species in Lake Pontchartrain (Darnell 1961). They are found along the Gulf Coast in low salinity environments of usually less than 19 parts per thousand (La Salle & De La Cruz 1985). Rangia shells are thick, heavy, and globose (Linton et al. 2007). Unlike some soft-shelled clams, rangia can fully retract their siphons into their shells and close up tightly (Linton et al. 2007). Although they have a relatively large functional foot, they move very little once they mature. Rangia clams are important in the food web of Lake Pontchartrain; ducks, fish, and blue crabs frequently prey upon them (Darnell 1961, La Salle & De La Cruz 1985) and the clams provide important trophic links between phytoplankton and nekton. Rangia clams are also important filter feeders that cover most of the lake bottom. Filter feeders improve water quality, contribute to habitat diversity and stability of the ecosystem, and accelerate nutrient regeneration (Ostroumav 2005). Clams can improve water quality by reducing turbidity, phytoplankton, and the impact of fecal pollution (Spalding et al. 2007). Bivalves have also been shown to increase seagrass productivity by nutrient enrichment and reduction of epiphytic biomass (Peterson and Heck 1999).

Callinectes sapidus (Arthropoda: Crustacea: Portunidae) are important predators and scavengers in estuarine environments and can control diversity, structure, distribution, and abundance of local populations of benthic organisms (Micheli 1995). They are classified as "opportunistic benthic omnivores," eating a variety of prey including fish, bivalves, gastropods, crustaceans, plant material, and other blue crabs (Stickle et al. 1989, Laughlin 1982). Bivalves,

however, constitute one-third to one-half of their diet (Laughlin 1982).   Blue crabs can exhibit behavioral plasticity in other prey choice parameters including size of clams (Micheli 1995) and energy profitability between prey species (Ebersole & Kennedy 1995, Micheli 1995). For example, Juanes (1992) determined that decapod predators chose small-sized bivalve prey because the possibility of claw damage. The size of a bivalve may serve as an indicator of higher profitability and lower risk to the crabs, resulting in an individual preying more heavily on a certain size of bivalve because of increased efficiency (Micheli 1995). In a study by Ebersole & Kennedy (1995), blue crabs chose bivalve prey species based on sediment depth, foraging time, prey availability and shell strength. Although blue crabs are classified as opportunistic feeders, individuals may concentrate on a particular abundant or profitable prey source (Seed & Hughes 1997).

Blue crabs employ different opening techniques on hard-shelled rangia clams versus soft-shelled clams. The shape of the shell makes the rangia clam difficult to handle and causes the chelipeds to slip off (Linton et al. 2007). Rangia clamshells can withstand blue crab claw crushing power in the 30-35 mm size class (Blundon & Kennedy 1982), and this results in alterative techniques, usually a combination of chipping/biting and wedging methods, used by the crabs to successfully open the rangia clam (Linton et al. 2007). Chipping/biting is a technique in which crabs break the shell edges with their mandibles to create an opening that allows the chelae to enter and pull the valves apart. Wedging occurs when crabs insert appendages in between the valves and push until the gap between the valves is widened, resulting in the adductor muscle being cut. Blue crabs can also pull apart rangia clams by using their chelae.

Predators may gain an advantage by staying in hypoxic zones rather than migrating to areas of higher dissolved oxygen concentrations (Taylor & Eggleston 2000, Seitz et al. 2003). Some predators even switch prey as dissolved oxygen concentrations decrease to take advantage of the less tolerant organisms during a hypoxic event (Sandberg 1994). Blue crabs are sensitive to hypoxia, but because of their mobility, they may be able to find the transitional zones between normoxic and hypoxic waters to prey on vulnerable clams that have been weakened by episodes of severe hypoxia (Das & Stickle 1993). Another possible explanation is that the blue crabs within the hypoxic zone become stressed and migrate out of the area, but unstressed crabs from outside the hypoxic zone move in and feed directly after the dissolved oxygen concentrations increase (Long & Seitz 2008). Pihl et al. (1992) suggested that predators reach maximum prey exploitation during or immediately after hypoxic events as a result of increased prey availability. Bivalve species can take hours to days to recover from a hypoxic event. Blue crabs can avoid low oxygen concentrations and therefore reduce or eliminate recovery time, which may allow them to move into an area directly after a hypoxic event and take advantage of vulnerable prey (Taylor & Eggleston 2000, Nestlerode & Diaz 1998). However, studies have shown that blue crabs are very sensitive to hypoxia, and that blue crabs reduce feeding during hypoxic conditions (Seitz et al. 2003) and do not increase predation during relaxation events between periodic hypoxia (Bell et al. 2003).

Blue crabs may be able to utilize the hypoxic zone and stressed rangia clams as a source of easy prey by traveling in and out of the zone to feed, thereby creating a feeding halo around the hypoxic zone. Although the salinity stratification north of the IHNC remains fairly constant, the hypoxic conditions in Lake Pontchartrain are episodic and patchy (Figure 2). The entire area is probably seldom affected at the same time. Areas within the 250 km^2 are differentially

affected due to differences in tides, wind direction and speed, and circulation within the lake. The 250 km^2 zone where mature rangia clams are not found is a result of these periodic fluctuations of hypoxia interacting with salinity shifts.
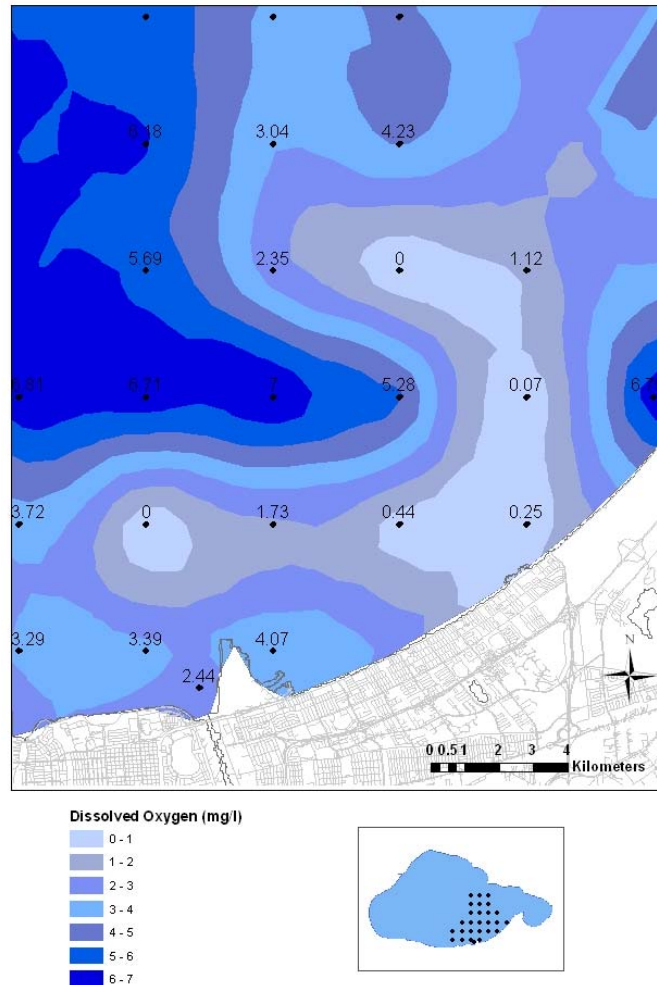
Figure 2: Hypoxic zone fluctuations north of the Inner Harbor Navigation Canal

Predation density and pressure may be especially elevated along the outside of the hypoxic zone during hypoxic events and most intense on the inside edge directly after the hypoxia has relaxed and predators re-invade (Lenihan et al. 2001, Clark et al. 1999b). If clams exposed to hypoxia are a profitable prey source for the blue crab, differential predation may help explain the lack of mature rangia clams. The purpose of this study was to determine if blue crabs

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can recognize hypoxia-stressed clams, if they chose to feed on clams exposed to severe hypoxia (<0.75 mg/L) or clams kept under normoxic conditions, and how this interaction may help explain the relationship between the hypoxic zone and lack of mature rangia clams in Lake Pontchartrain.

Materials and Methods

Study Organisms, Study Area, and Collection Sites

This study was conducted from October 2007 through January 2009 using animals collected from Lake Pontchartrain, north of New Orleans, Louisiana, USA. Experiments were carried out in the Estuarine Research Laboratory at the University of New Orleans.

Rangia clams (30 to 35 mm) were collected by hand from sites in Lake Pontchartrain including Fontainebleau State Park in Mandeville, Louisiana and the southern shoreline in New Orleans East every two weeks to a month in an effort to use the freshest clams for each experiment. Rangia clams 30-35 mm were chosen because they are an abundant potential prey source, and clams larger than 20 mm are not found within the hypoxic zone in the lake. Prior research has shown crabs larger than 115 mm will eat rangia clams up to 46 mm (Linton et al. 2007, Ebersole & Kennedy 1995).

Blue crabs were collected in traps from Pirate's Bayou, in the Pirates Harbor Subdivision south of Slidell, Louisiana. Medium sized, (130 mm to 160 mm point to point carapace width) male crabs with both a cutter and crusher claw were used to avoid feeding preferences differences based on sex or physiological characteristics. Male crabs were used because they are common in oligohaline waters, where rangia clams occur, while females are relatively rare. Darnell (1958) demonstrated that crabs larger than 124 mm carapace width had mollusc dominated diets in Lake Pontchartrain. The number of days that the crabs were kept in captivity ranged from 15 days to 78 days.

Maintenance of Study Organisms

Crab Maintenance

Crabs were kept in five 10-gallon aquaria connected to a 50-gallon filtration tank layered

with rangia clamshells and filter floss (Figure 3). Each aquarium had a mesh crab-wire top with a vertical section from the top to the bottom of the aquarium to protect thermometers and other equipment from the crabs. A network of PVC pipes drilled with small holes was placed on the bottom of the filtration tank to keep water flowing throughout the entire tank and prevent organic material from accumulating in one area. Water was supplied to the aquaria using a submersible pump and was returned via gravity flow. Tap water was de-chlorinated with Aquarium Pharmaceuticals Tap Water Conditioner, which detoxifies heavy metals and removes chlorine and chlorinated compounds from the water. Instant Ocean commercial sea salt was used to maintain salinity in the system at 5 parts per thousand (ppt). One crab was added to each of the ten-gallon aquaria and allowed to acclimate for at least a week prior to the start of the experiment. This allowed for the conditioning of the system to provide appropriate nitrifying bacteria levels to be present to process toxic ammonia from the crab excretion to relatively non-toxic nitrate. Percent saturation of dissolved oxygen (% DO) was maintained between 90% and 100%. Ammonia levels were also monitored twice a week using a Hach DR/890 data logging colorimeter. In the first twelve experiments, water temperatures of all aquaria were kept at room temperature (22-25º C). In the thirteenth to twenty-first experiments, tank heaters were added to increase the temperature to 30ºC to simulate summer water temperatures in Lake Pontchartrain.

Crabs received natural light through the laboratory windows, and a florescent light was installed approximately one meter above the five tanks to provide supplementary light. The florescent light remained on for seven hours per day to help prevent the development of bacterial infections. Longer light periods resulted in heavy growth of algae. Between experiments, crabs were fed Wardley's shrimp pellet formula by Hartz and opened live clams collected from Lake

Pontchartrain. Broken shells, uneaten organic material, and fecal matter were removed daily.

The crabs were returned to Lake Pontchartrain after they were finished with laboratory trials.

Figure 3: Aquarium system used for blue crab maintenance during trials

Clam Maintenance

Clams were kept under normoxic conditions in 10-gallon aquaria or shallow grey plastic

tubs. Instant-Ocean commercial sea salt was added to de-chlorinated tap water to produce a

salinity of 5 ppt. The aquaria and tubs were aerated with an electric air pump with air stone.

Salinity was maintained in the aquaria by adding more commercial sea salt if the salinity

dropped or adding more de-chlorinated water if the salinity rose. Percent DO saturation was

monitored using the YSI 85 and maintained between 90-100%. Ammonia was monitored once a

week by using a colorimeter. The temperature of the clam tanks for the first twelve experiments

was 22-25ºC. Tank heaters were added at the thirteenths to twenty-first experiment to increase the water temperature to 30ºC.

Experimental Design

Reference experiment: blue crab predation on rangia clams kept under normoxic conditions

To obtain base line values for blue crab predation on rangia clams under normoxic conditions, two normoxic clams from holding aquaria were placed in each crab tank. Two vertical lines were etched into one clam's shell, and two horizontal lines were etched into the second clam's shell. Crabs were given 12 hours to feed, and clams that were not eaten after 12 hours were removed. The reference experiment was run 8 times, resulting in 40 replications. Eighty rangia clams kept under normoxic conditions and 5 blue crabs were used.

Choice Experiments: blue crab predation on hypoxia-stressed rangia clams vs clams kept under normoxic conditions

A total of 21 experiments were conducted, with each experiment including five trials. A trial is defined as a tank containing a single crab that was given the choice between one hypoxia-stressed clam and one clam kept under normoxic conditions. I conducted 105 paired trials that used 105 hypoxia-stressed clams and 105 normoxic clams and the pairs were presented to 37 crabs.   All clams were measured with calipers before experimental use to confirm that they measured between 30 and 35 mm.

For each experiment, five rangia clams were subjected to a 72-hour exposure period of severe hypoxia. Hypoxic conditions (DO < 0.75 mg/L) were created by bubbling nitrogen into a covered 10-gallon aquaria covered with plastic wrap to avoid evaporation and gas exchange. Dissolved oxygen levels were checked twice a day. Percent saturation, salinity, and temperature were monitored using an YSI 85 oxygen, conductivity, salinity, and temperature meter.

After 72 hours, one hypoxia-stressed clam and one normoxic clam were placed randomly

in each of the five 10-gallon aquaria containing one crab. Crabs were starved for 48 hours prior to each experiment to standardize hunger levels. Clams were differentiated by etching two horizontal lines on hypoxia-stressed clam's shell and two vertical lines on normoxic clam's shell. Markings were alternated between trials to eliminate potential bias due to scratch area and handling time differences.   Each experimental trial was monitored regularly to observe which clams were eaten and note if the hypoxia-stressed or the normoxic clam was eaten first. Clams that were not eaten after 12 hours were removed.

Statistical analysis

To test for homogeneity of feeding response of each crab presented with hypoxic or normoxic clams, I employed a 1-tail binomial test with 0.5 probabilities (Moore & McCabe 1998). This test is appropriate because in each trial there were two possible outcomes in feeding response: a crab either chose a hypoxia-stressed clams or normoxic clams to eat first. A binomial test determines if the number or proportion of successes observed in a data set are significant based on a theoretical expected distribution of the two possible outcomes. A 2 x 2 chi square Fisher's exact test was also performed to determine if there was a difference between experiments carried out at 22-25º C and those carried out at 30º C.

Results

Reference experiment (test trial): blue crab predation on rangia clams kept under normoxic conditions

Two normoxic clams were introduced to each crab aquarium to obtain base line values

for the ability of crabs to feed on normoxic clams (Table 1). The experiment was run 8 times,

using a total of 80 normoxic clams. Three individuals fed, opening a total of three clams out of

eighty. Seventy-seven clams were left uneaten. Five crabs were used in the reference

experiment, and although 3 crabs ate initially, none of the crabs ate again.

Table 1: Test trial using only rangia clams kept under normoxic conditions to determine the ability of blue crabs to feed on normoxic clams. N= Normoxic clam eaten

Reference Experiment	Tank 1	Tanks 2	Tank 3	Tank 4	Tank 5	# of Normoxic Eaten	# Left Uneaten
1	0	N	0	N	0	2	8
2	N	0	0	0	0	1	9
3	0	0	0	0	0	0	10
4	0	0	0	0	0	0	10
5	0	0	0	0	0	0	10
6	0	0	0	0	0	0	10
7	0	0	0	0	0	0	10
8	0	0	0	0	0	0	10
					TOTAL	*3*	*77*

Choice Experiment

The choice experiment was run a total of 21 times (Table 2). Each experiment had five

trials, resulting in a total of 105 repetitions. Thirty-seven crabs and 210 rangia clams (105

hypoxia-stressed clams and 105 clams kept under normoxic conditions) were used.

Table 2: Summary table of choice experiments: N= normoxic clam eaten, H= hypoxic clam eaten, H,N= both clams eaten (<u>hypoxic first</u>), N,H= both clams eaten (<u>normoxic first</u>), 0= neither hypoxic nor normoxic clam eaten.

Experiment Number	Tank 1	Tank 2	Tank 3	Tank 4	Tank 5	Total # Hypoxic Clams Eaten	Total # Normoxic Clams Eaten	Total # Uneaten Clams
1	H	N	0	0	0	1	1	8
2	0	H	0	0	0	1	0	9
3	H	H	0	H	H	4	0	6
4	H	H	0	N	H	3	1	6
5	0	H	0	N	0	1	1	8
6	H	0	0	0	0	1	0	9
7	0	H,N	0	H	H,N	3	2	6
8	0	H	H	0	H,N	3	1	6
9	0	0	0	0	0	0	0	10
10	0	H	0	0	0	1	0	9
11	0	H	0	H	H	3	0	7
12	0	0	0	0	0	0	0	10
13	0	0	0	0	0	0	0	10
14	0	0	0	0	0	0	0	10
15	N	0	0	0	0	0	1	9
16	0	H	H	0	0	2	0	8
17	0	H	H,N	0	0	2	1	7
18	0	N,H	0	N	0	1	2	7
19	H	H	H	0	0	3	0	7
20	0	0	H	N	0	1	1	8
21	H	H	H	N	0	3	1	6
TOTALS						*33*	*12*	*165*

Nineteen crabs fed and 18 crabs did not feed. Forty-five clams were eaten and 165 clams were left uneaten. Out of the crabs that did feed, 33 out of 45 hypoxia-stressed clams were eaten compared to 12 out of 45 clams kept under normoxic conditions (p= 0.0012). The pooled data

include clams that were eaten second if the crab ate both the hypoxia-stressed clam and normoxic clam in a trial.

The pooled data were further restricted to determine if the first or only choice of the crabs was hypoxia-stressed clams. The total number of hypoxia-stressed clams eaten only or first was 32, and the total number of normoxic clams eaten only or first was 8. A binomial test determined that restricted data show hypoxia-stressed clams were significantly chosen over normoxic clams (p<0.0001). To summarize, the pooled data indicate that significantly more hypoxia-stressed clams were eaten than normoxic clams, and the restricted data demonstrate that blue crabs significantly chose hypoxia-stressed clams only or first over normoxic clams.

Overall Crab Feeding Preference

Y-axis: # of Blue Crabs (0 to 20)
X-axis: Treatment of Clam — Hypoxic (11), Normoxic (2), Both (6), None (18)
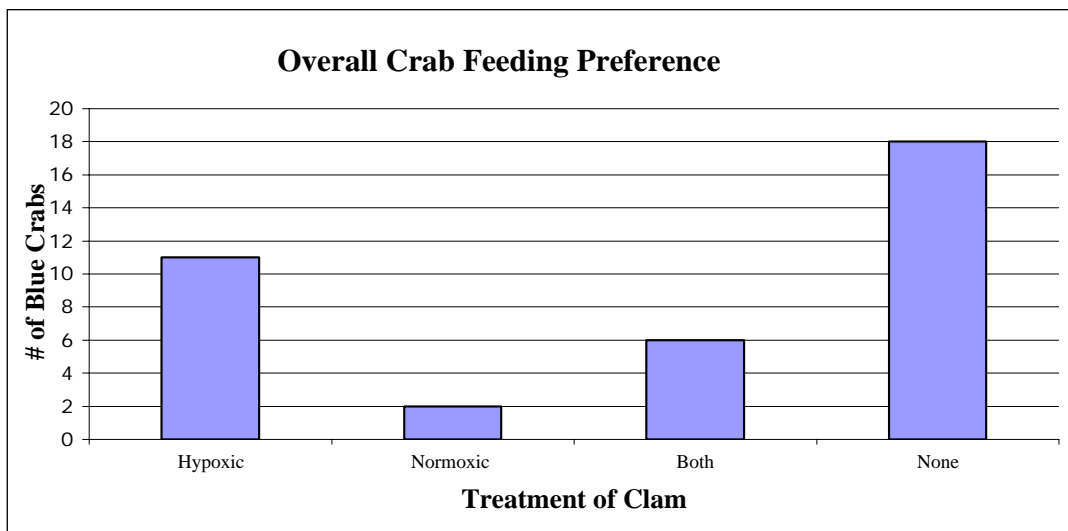
Figure 4: Blue crab feeding preference based on clam treatment (hypoxia-stressed, clams kept under normoxic conditions, both eaten, or none eaten).

There was a large amount of variation in individual crab feeding preferences (Figure 4). Some crabs ate both clams during an experiment, and some crabs never fed. Out of the 37 individual crabs used, 11 ate only hypoxia-stressed clams, 2 ate only normoxic clams, 6 ate both hypoxia-stressed and normoxic clams, and 18 ate neither hypoxia-stressed clams nor clams kept under normoxic conditions. Six ate both hypoxia-stressed and normoxic clams (Table 3). Crab

#15, used in two experiments, ate both clams in both experiments, but always ate hypoxic first.

Crab #32, used in 6 experiments, ate only the hypoxic-stressed clams in five trials, but ate the

normoxic clam followed by the hypoxic clam in another trial. Crab #33 ate only the hypoxic in

five trials but ate the hypoxic followed by the normoxic in one experiment. The remaining three

individuals ate either the hypoxic or normoxic in a single trial, but their preference differed

between experiments. The six crabs that ate both hypoxia-stressed clams and normoxic clams

ate a total of 24 clams out of the 45 eaten in the experiment (H=16, N=8). A binomial test

determined that these 6 individuals did not significantly chose hypoxia-stressed clams over

normoxic clams (p=.0758),

Table 3: Preference of crabs that ate both hypoxia-stressed clams and normoxic clams during the choice experiments and number of trials each crab eat each combination H,N= hypoxic clam and normoxic clam eaten (<u>hypoxic first)</u> N,H= hypoxic and normoxic eaten (<u>normoxic first</u>), H= only hypoxic eaten, N= only normoxic clam eaten.

Individual Crab Identification Number	# Experiments Used In	# Trials Individual ate H,N	# Trials Individual ate N, H	# of Trials Individual ate only H	# of Trials Individual ate only N
#2	2	0	0	1	1
#9	4	0	0	1	2
#12	2	1	0	1	0
#15	2	2	0	0	0
#32	6	0	1	5	0
#33	6	1	0	5	0

Statistics cannot be run on individual crab choice because of the small number of trials

for which each crab was used. Ideally, each individual crab should be run through more

experiments to increase the probability of exhibiting individual crab prey choice. A variety of

circumstances including molting, illness, unresponsiveness or death influenced the number of experiments in which individual crabs were used. Crabs were run two times (N=20), three times (N=9), four times (N=5) or six times (N=3) (Table 4).

Table 4: Numbers of crabs that fed in each category based on number of experimental trials

Number of Experiments Run Per Crab	# of Crabs that Only Ate Hypoxic Clams	# of Crabs that Only Ate Normoxic Clams	# of Crabs that Ate Both Hypoxic and Normoxic Clams	# of Crabs that Ate Neither Hypoxic nor Normoxic Clams	Total Number of Individual Crabs
2	4	1	3	12	20
3	4	1	0	4	9
4	2	0	1	2	5
6	0	0	2	1	3

Analysis of variation in crab feeding

There was variation among crab feeding preferences. Crabs may not have eaten during the experiments for many reasons including the number of days in held in captivity, the season of crab capture, the season of rangia clam collection and increase in temperature. Eighteen crabs of 37 did not eat and observations were analyzed to determine if any of these factors contributed to not feeding or variation in feeding preference.

As previously mentioned, crabs were held for varying lengths of time in captivity (Figure 5). Three crabs that did not feed on experimental clams were held in captivity for 14 days, eight for 15 days, 2 for 22 days, 1 for 45 days, 2 for 55 days, 1 for 61 days and 1 for 78 days. Two crabs that fed were in captivity for 14 days, 4 for 45 days, 4 for 78 days, 2 for 15 days, 3 for 55

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days, 2 for 61 days and 2 for 39. There was no correlation between days in captivity and crabs

feeding (R^2=0.3133) or not feeding (R^2=0.3153)
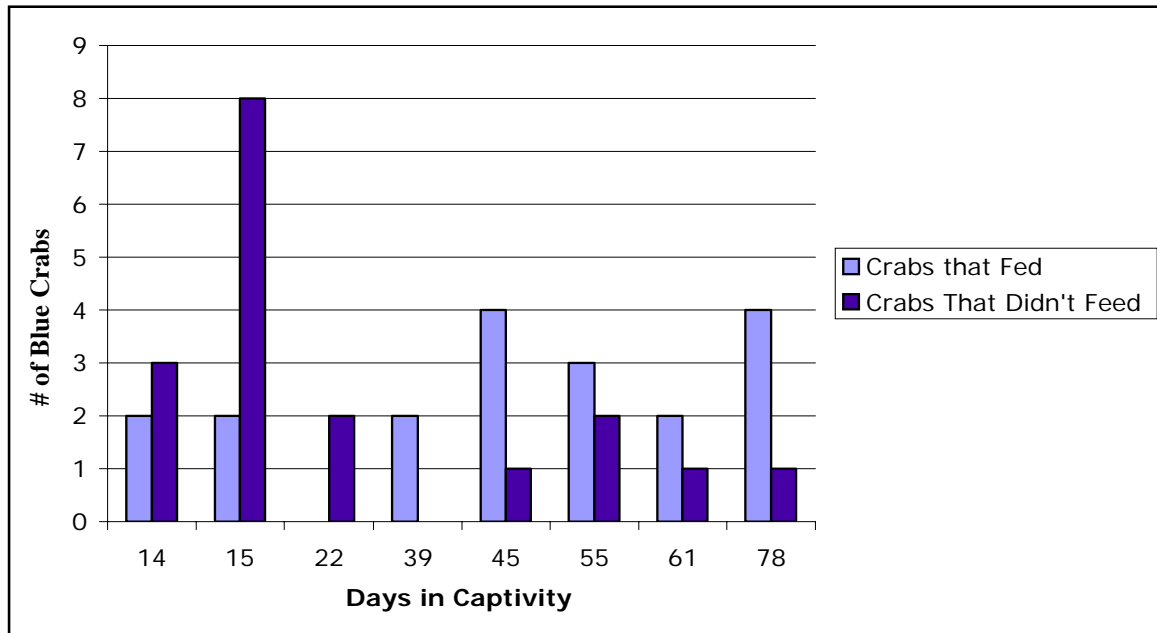
Figure 5: Number of crabs that fed or didn't feed compared to days in captivity.

This project was carried out year-round for two years. Crabs were collected as needed

for the experiment, so crabs were collected at all different times of the year (Figure 6). Seasons

were defined as fall (September through November), winter (December through February),

spring (March through May), and summer (June through August). Ten crabs were collected

during the fall months, 5 in the winter months, 10 in the spring months and 12 in the summer

months. The season of the year the crabs were captured did not affect the feeding preferences of

the crabs. The following are numbers of crabs that fed: 6 of 10 captured in fall, 4 of 5 captured

in winter, 4 of 10 captured in spring, and 5 of 12 captured in summer ($r^2 = 0.1636$).
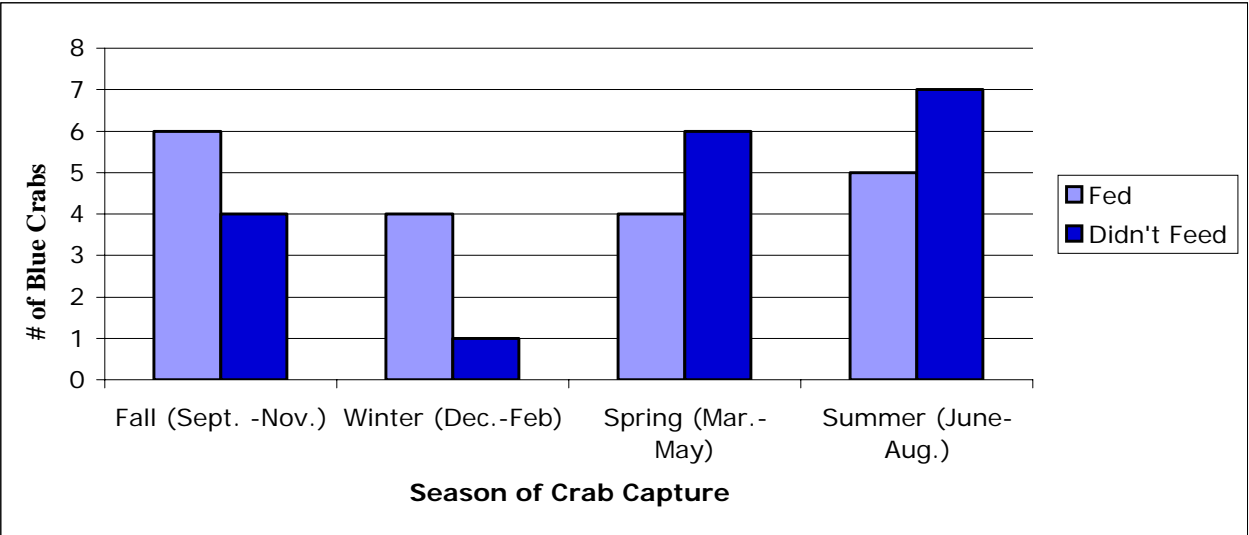
Figure 6: Crab feeding compared to season of capture

Another possible source of variation is the season that the rangia clams were collected from Lake Pontchartrain. The season that the clams were collected may have affected the stress level of the clams in the laboratory, but because of the small and uneven number of experiments done in each season, the data could not be analyzed statistically. Six experiments were run in the fall, 2 experiments in the winter, 4 in the spring and 9 in the summer. The most hypoxia-stressed and normoxic clams were eaten in the summer, but the most clams were also collected in the summer (Figure 7). Clams were held for two to four weeks.
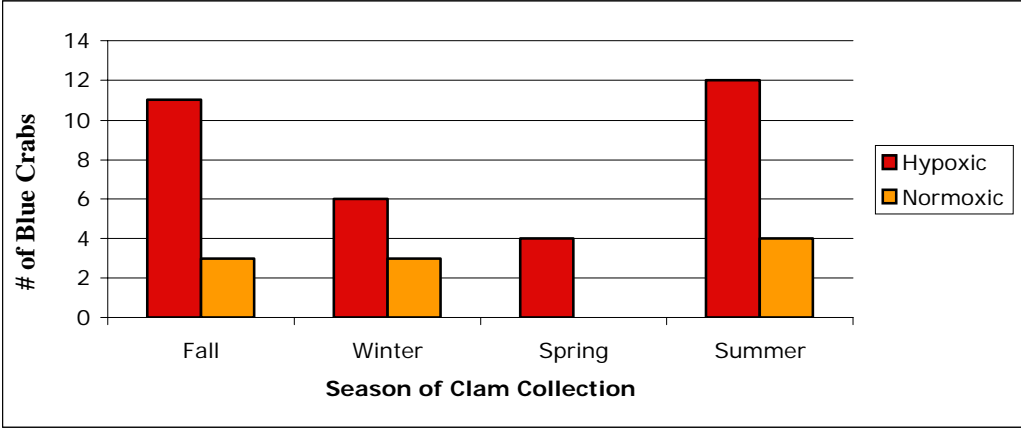
Figure 7: Numbers of clams eaten (N=33) compared to season of collection

In order to determine if there was a difference in feeding response between experiments carried out at 22-25º C and those carried out at 30º C, a 2 x 2 chi square Fisher's exact test was also performed (Table 5). The crabs ate 21 hypoxia-stressed clams and 6 normoxic clams at 22-25º C. The crabs ate 12 hypoxia-stressed clams and 6 normoxic clams during experiments carried out at 30º C. There was no significant difference in feeding between the two temperatures (p= 0.3126).

Temperature	Hypoxic	Normoxic
Room Temperature (22º C- 25º C)	21	6
30º C	12	6

Table 5: Fisher's exact test to determine significance between 22ºC-25ºC and 30ºC

Observational Data

Upon introducing two clams into a crab's tank, the crabs almost always handled the hypoxia-stressed clams first and held it tightly for several minutes. Unfortunately, handling data was not recorded for all 105 trials, but data was collected for 65 of the trials. Of the 65 trials, crabs handled a normoxic clam or a hypoxia-stressed clam 37 times. Thirty-four of the 37 times, the crabs handled the hypoxia-stressed clam first and 3 times the crabs handled the normoxic clam first (p<0.001).

The blue crabs used a standard technique for opening the clams. The rangia shells were chipped and bitten on the posterior edge of the shell, where the siphon extends. According to Linton et al. (2007) this creates a gap between the valves and allows for chelae to enter. Next, the crabs inserted chelae into the hole to widen the gap between the valves until the adductor muscle was cut. The combination of chipping/biting and wedging techniques was employed by the crabs in eating both the rangia clams kept under normoxic conditions, and hypoxia-stressed

clams. While being exposed to hypoxic conditions, the rangia clams remained tightly closed.

Once the hypoxia-stressed clams were placed into the crab tanks, however, most extended their

siphons in an attempt to re-oxygenate themselves. This gave the crab an opportunity to gain

access to the internal parts of the clams by chewing on the extended siphon. If the clams did not

extend their siphons, the crabs generally grabbed the hypoxic clam and held it for several

minutes, which maintained anoxic conditions inside the mantle cavity, forcing the clam to extend

its siphon for oxygen or die from anoxia or accumulation of excretory products (Heinonen et al.

1997). The shell remains of rangia clams that were eaten were whole, except for some chipping

on the edges, and separated at the valves (Figure 8). Often, clams that were alive at the end of 12

hours were still closed and had chipping on the edges, suggesting that the crab had tried to open

it, but failed. In fact, of the 34 times hypoxia-stressed clams were handled first, 18 were

successfully opened and eaten, and 16 were left unopened. The opening behaviors observed here

are consistent with observations of blue crabs from other studies (Linton et al. 2007, Ebersole &

Kennedy 1995).

Figure 8: Eaten rangia clam exhibiting chipping/biting

Discussion

Rangia clams are a major prey of the blue crabs in Lake Pontchartrain, and the reference experiment showed that some crabs can open normoxic clams. This study showed experimentally that blue crabs fed significantly more on hypoxia-stressed clams than clams kept under non-stressed conditions, and that clams' responses to hypoxia may make them more vulnerable to predators.

Blue crabs certainly feed on smaller rangia clams in Lake Pontchartrain, but once they reach a larger size (>21 mm), the clams become protected from predation (Abadie and Poirrier 2000). However, I found that larger clams become an available food source when they are exposed to hypoxia. Clarke et al. (1999a) suggested that blue crab forage primarily by using chemoreceptors and responding to chemical cues in their environments, along with touch and vision. Dead clam flesh releases amino acids into the water and draws blue crabs to an area (Clark et al. 1999a). Handling data from this experiment suggests that blue crabs can recognize a hypoxia-stressed clam from a non-stressed clam because they significantly handled hypoxic clams over normoxic clams, even if they were not able to open the clam. It is likely that the clams are releasing a chemical signal that allows the blue crab to recognize its weakened condition.

Behavioral adaptations to hypoxia, such as vertical migration and siphon extension, may also make the rangia clam more susceptible to blue crab predation. Such behaviors would allow blue crabs to reduce foraging time and provide easier access to the internal parts of the clam. Although migration in the sediment was not tested in this study, clams were observed to extend their siphons upon entering normoxic waters after 72 hours of exposure to hypoxia, and the blue crabs exploited this behavior by gnawing on the exposed area and gaining access to clam's flesh.

Rangia clams have been shown to tolerate both hypoxic and anoxic conditions. Rangia clams can tolerate temporary anoxic conditions with some individuals surviving 6.5 days in 0 ppm oxygen (Patillo et al. 1997), but Henry et al. (1980) reported 50% mortality of rangia clams after 5-7 days under hypoxic conditions in both 2 and 20 ppt salinities. Those that survived did not recover after being returned to normoxic conditions. These two studies contradict each other, but Henry et al. (1980) coupled hypoxia with salinity shifts and did not subject rangia clams to anoxia. Rangia survival decreased to 3 days when given a hypo- or hypersaline shock. A study in the Estuarine Research Lab has shown that at 5 ppt and 10 ppt salinity, clams survived 24, 48, and 72 hours of exposure to hypoxia at 1 mg/L, but died after 120 hours of exposure. The interactive effect of salinity shifts and hypoxia decreases survivorship. Experimental groups exposed to a downward salinity shift experienced less tolerance to the effects of hypoxia. Experimental groups that were shifted up from 5 ppt to 10, 15 or 20 ppt all tolerated longer exposure time to hypoxia before death. The combination of fluctuating salinity from the IHNC and episodic hypoxia and anoxia in Lake Pontchartrain may make rangia clams more susceptible to blue crab predation.

In this study, crabs exhibited variation in feeding activity and prey choice. Individual variation among crab prey preference has been found in other studies (Blundon & Kennedy 1982). One of the reasons crabs may not feed is molt status. Before crabs undergo ecydsis (molting), they stop feeding and hide to protect themselves from predators (Hartnoll 1982). After ecydsis, the shell does not fully harden again for a few days, probably decreasing the crab's ability to open hard-shelled clams.

Another possible explanation for variance in feeding behavior is the presence of bacterial or viral pathogens in the crabs. A bacterium, *Vibrio cholerae,* was common on the crabs and

detected by brown blotches disfiguring the exoskeleton. Although it did not seem to affect their behavior in the laboratory, crabs with *V. cholerae* present were avoided. The fluorescent grow light seems to prevent the development of *V. cholerae* in the laboratory.

In December 2007, the crabs exhibited strange symptoms including twitching, lack of buoyancy control, disorientation, loss of appetite, and eventually death. All specimens were disposed of and the tank system underwent an entire water change. After the initial outbreak, new crabs were monitored, and if any symptoms were exhibited, they were immediately replaced by another crab and released back into Lake Pontchartrain. Crabs may be captured with several viruses present, but may not show symptoms until stressed when their conditions are exacerbated in captivity (Messick and Sindermann 1992). Correspondence with Dr. Gretchen Messick suggested that this disease was viral because these symptoms were not consistent with high ammonia levels or water quality issues. Weakness and paralysis can be symptoms of viral pathogens in blue crabs (Johnson 1978). Water quality was constantly monitored and all parameters were normal at this time. In future studies, a flow-through aquarium set-up may be beneficial in maintaining water quality and reducing stress on the crabs.

Diet and nutrition may have affected crab feeding preference. The crabs were fed a diet of shrimp pellets and opened rangia clams when not being used in experiments. This is probably not a balanced diet and may have led to malnourished or weakened crabs. Poor nutrition could potentially have affected crab cheliped muscle stamina or mandible strength, both of which are important in opening of the hard-shelled rangia clam.

Two other possible sources of feeding variation are the number of days that the individuals were held in captivity and the season the specimens were collected. The number of days crabs remained in captivity did not strongly correlate with the ability to feed on the clams.

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The season of crab capture did not correlate with feeding choice, although more crabs captured in fall and winter fed. Fewer crabs captured in spring and summer fed. Crabs may have been less stressed in the wild during these months due to more consistent salinity and DO concentrations, than in the summer when lake is stratified by salinity and experiences bottom water hypoxia. Clams were held between two weeks and a month in an effort to use fresh clams in each experiment. Like the crabs, clams were collected year-round and may have experienced increased stress in the wild during certain months of the year.

Potential laboratory stress on the clams may have also led to variation in results. The salinity at the locations where the clams were collected was slightly higher (7.2-8.5 ppt) than the laboratory conditions (5 ppt). The clams were acclimated at least three days in the laboratory before being used in an experiment. Power outages occurred, leaving the clams without aeration for a few hours. Prolonged power outages resulted in death for most of the clams, and therefore new clams had to be collected. Stress from captivity or lack of proper nutrition may have led to weakened adductor muscles in the clams, making them less resistant to blue crab predation. Water temperatures also varied from the collection site to the laboratory depending on the season of collection.

Water temperatures in the laboratory did not affect crab feeding preference in this study. Hypoxic tolerance decreases with increased temperature in most bivalve species, presumably as a result of increased metabolic rate (Stickle et al. 1989). Lower temperatures correlate with increased survival rates during hypoxia (Diaz & Rosenberg 1995). The results here did not show significant differences between experiments done at 22-25ºC versus 30ºC ($p=0.3126$), but a higher number of replications may yield significant results. The higher temperatures coupled with hypoxic conditions certainly stress the benthic organisms of Lake Pontchartrain.

Another source of variation may be the experience an individual crab has handling bivalve prey. Conditioning blue crabs to certain prey types before an experiment has shown that blue crabs may be able to modify their prey choice based on experience (Micheli 1995). This would be advantageous for a mobile predator such as the blue crab that encounters variable conditions. Some crabs may simply have had more experience opening rangia clams than others. Some individuals may take advantage of other food sources in the lake because of the difficulty of opening hard-shelled rangia clams, which require longer handling times than other types of prey.

Despite the potential sources of variation among crab feeding preference, crabs in this study ate significantly more hypoxia-stressed clams than clams kept under normoxic conditions, suggesting that they can recognize and feed on weakened clams. The combination of salinity shifts and episodic hypoxia in Lake Pontchartrain makes the mature rangia clams an available food source for blue crabs.

Hypoxic zones are dynamic and the edges of the zone may fluctuate yearly, seasonally, daily, or even hourly depending on tides and wind direction and speed (Sagasti et al. 2001, Bell et al. 2003). In Lake Pontchartrain, there is a zone north of the IHNC that experiences hypoxia and anoxia caused by salinity stratification. Wind direction, circulation, and degree of mixing can cause the hypoxic and anoxic zones within the zone of salinity stratification to expand, contract, and change shape (Figure 2). The 250 km^2 zone in Lake Pontchartrain where mature rangia clams are not present is the cumulative effect of these shifting hypoxic and anoxic events, and the entire area is seldom affected at the same time. Clams located in areas frequently subjected to hypoxia and anoxia may simply die from stress and frequent exposure to hypoxia. Clams that do not die and are subjected to episodic hypoxia events are likely weakened and may

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become an available prey source to blue crabs. Fluctuations in dissolved oxygen concentrations may allow the blue crabs to exploit stressed rangia without exposing themselves to severe hypoxia. Blue crabs that remain in severely hypoxic waters migrate to normoxic waters to recover from the stress and are less likely to reinvade the hypoxic zone to forage on vulnerable prey (Bell et al. 2003). However, because of the uniqueness of Lake Pontchartrain's hypoxic events, blue crabs may wait in normoxic waters for conditions to improve and then move into an area before the rangia clams have a chance to recover.

Conclusion

In conclusion, although there was variability among individuals, experimental results showed that blue crabs significantly fed on hypoxic stressed clams over clams held under normoxic conditions. Data also show that blue crabs can recognize hypoxic clams and tend to handle them first. Although crabs tend to avoid hypoxic conditions, fluctuations of the hypoxic zone north of the IHNC may allow crabs to prey upon weakened clams when conditions improve. After a hypoxic event, it may take clams days to recover, whereas blue crabs can avoid hypoxia and move into an area before the clams have chance to recover. This study likely underestimates the predation on stressed clams because it did not explore anoxic conditions or osmotic stress on the clams. The interaction of salinity shifts from the high salinity waters entering Lake Pontchartrain from the IHNC, episodic hypoxic conditions during the summer, and blue crab predation could all contribute to the lack of mature rangia clams in Lake Pontchartrain's hypoxic zone.

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