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Exposure of rangia clams to hypoxia enhances blue crab predation

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ABSTRACT

This experimental study questions whether exposure of non-mobile prey to episodic hypoxia might enhance predation by a mobile predator, which moves into the former hypoxic area immediately after a shift back to normoxic conditions. We used *Rangia cuneata* (common rangia clam) and *Callinectes sapidus* (blue crab) from an oligohaline estuary where mature clams are rare in areas subject to episodic anoxia and hypoxia. Clams were exposed to severe laboratory hypoxia for 72 h. One clam stressed by hypoxia and another clam maintained under aeration (normoxia) were placed in aerated aquaria containing a crab. Feeding choice of hypoxic *vs.* normoxic clams was then monitored for 12 h. We used 20 different crabs for two experimental replicates each for a total of 40 replicates. To test for homogeneity of the feeding response, we used a 1-tail binomial test with 0.5 expected probabilities. Eleven of the 20 crabs fed (55%), and 16 out of 18 hypoxia-stressed clams were eaten first compared to two out of 18 clams kept under normoxic conditions ($p = 0.001$). The significant frequency choice of stressed clams indicates that in this experimental study, exposure of clams to hypoxia enhanced crab predation.

1. Introduction

Hypoxia is generally regarded as dissolved oxygen lower than 2 mg l^{-1}, and is known to cause stress and mortality in benthic organisms (Diaz and Rosenberg, 1995). However, adverse effects at concentration higher than 2 mg l^{-1} may also occur (Vaquer-Sunyer and Duarte, 2008). After hypoxic episodes, mobile predators can take advantage of weakened, sedentary prey (Pihl et al., 1992; Long and Seitz, 2008; Powers et al., 2005; Riedel et al., 2014). This study questions whether exposure of a clam to episodic hypoxia might enhance predation by a crab, which moves into the former hypoxic area immediately after a shift back to normoxic conditions.

Rangia cuneata (Sowerby, 1831), the common rangia (also called Atlantic rangia or wedge clam), occurs in Atlantic and Gulf of Mexico estuaries at salinities below 19 (LaSalle and de la Cruz, 1985) and dominates the benthos of Lake Pontchartrain (Darnell, 1961). This study was prompted by long-term field studies of the decline in *R. cuneata* density in Lake Pontchartrain, an oligohaline estuary located north of New Orleans, Louisiana (Poirrier and Caputo, 2015).

Through predation, *Callinectes sapidus* (Rathbun 1895), the blue crab, can influence the community structure of bivalves (Laughlin, 1982) and other biota (Micheli, 1995). *Callinectes sapidus* feeds on small *R. cuneata* by crushing shells, but larger clams can withstand cheliped crushing power (Blundon and Kennedy, 1982) so crabs use a combination of chipping and wedging to open large clams (Linton et al., 2007). Since *C. sapidus* is sensitive to hypoxia (Hines, 2007) and *R. cuneata* can withstand persistent levels of moderate hypoxia, under some conditions hypoxia might provide a refuge from predation, similar to that described for the quahog, *Mercenaria mercenaria* (Altieri, 2008). Although blue crabs avoid hypoxic areas (Bell et al., 2003), they are abundant and active foragers (Clark et al., 1999). Therefore, blue crabs may be adapted to move into areas after severe episodic hypoxia to take advantage of stressed clams as potential prey before the clams have a chance to recover from hypoxia. This is similar to the hypoxia-enhanced foraging described by Long and Seitz (2008) and Broszeit et al. (2013) for several prey species. This study differs from other studies of blue crab predation on bivalves because it uses a laboratory experiment to test the possibility that crabs recognize and select hypoxia stressed clams over non-stressed clams as a preferred prey item.

Lake Pontchartrain has a surface area of 1631 km^2, a mean depth of 3.7 m, and a mean salinity of 4 (Sikora and Kjerfve, 1985). It is an urban, subtropical estuary where summer bottom temperatures up to 30 °C, coupled with salinity stratification and eutrophication, can produce the rapid development of bottom water hypoxia. Algal nutrients are introduced into Lake Pontchartrain with runoff from metropolitan New Orleans and agriculture (Turner et al., 2002). In the past, saltwater intrusion from navigation canals occurred (Poirrier, 1978; Abadie and Poirrier, 2000, 2001; Poirrier et al., 2009), but this was stopped in 2009 (Poirrier, 2013). However, saltwater intrusion has recently increased due to hurricane and tropical storm surges from high rates of relative sea level rise, wetland loss and barrier island erosion (Poirrier and Caputo, 2015). These surges of higher salinity water

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produce salinity stratification and bottom water hypoxia (Poirrier et al., 2013). Stratification and hypoxia sets up after late summer and fall storms and usually remain for weeks to a month until stratified waters are mixed by strong winds associated with weather events. Wind driven circulation gyres (Signell and List, 2001) also move cells of hypoxic bottom water from areas near the tidal passes to other areas of the estuary. These episodes are often persistent enough to cause anoxic sediment, death of crabs in traps and death of clams in the sediment, as evidenced by articulated valves.

This experimental study was conducted to determine if predation by *C. sapidus* on *R. cuneata* is enhanced by clam exposure to hypoxic stress. The specific goal was to determine whether *C. sapidus* would have a significant feeding preference for *R. cuneata* exposed to hypoxia over clams kept under normoxic conditions.

2. Materials and methods

2.1. Experimental design

We conducted a preliminary experiment to obtain baseline data on the frequency of crabs feeding on clams under normoxic conditions. Two marked clams were added to five tanks each containing a crab, and tanks were checked after 12 h to see if crabs fed. The same crabs were used, but the clams were replaced after each experimental replicate. The experiment was run twice for a total of 10 replications.

A choice experiment was conducted to determine if crabs under normoxic conditions fed on hypoxic-stressed over normoxic clams. In each experimental replicate, one crab was held in an aerated 42 l glass tank with filtration, but without sediment. Crabs were not fed for 48 h prior to introducing the clams. One hypoxic and one normoxic clam were added at the same time equidistant to the crab already in the aquarium to begin each experimental replicate. Five replicate experiments using five tanks were run on eight different dates to give a total of 40 replicates (Table 1). The same five crabs were used for two replicate runs on four successive dates (runs 2, 4, 6, and 8). Crabs were designated *a*, for the first and *b* for the second replicate in Table 1. Crabs were held six or seven days (Table 1) between the replicate runs to reduce possible pseudoreplication. Experiments were run for 12 h to determine whether a hypoxic or a normoxic clam was eaten and if both were eaten, which one was eaten first. The first clam eaten was considered the choice.

Clam hypoxia exposures and crab choice experiments were conducted at room temperature (22–25 °C). Hypoxic stress was produced by exposing clams to dissolved oxygen concentrations between 0.3 and 0.8 mg l^{-1} for 72 h by continuous nitrogen sparging in a covered 42 l aquarium. We wanted to use a time period near *R. cuneata*'s sub-lethal limit because of the low frequency of crabs feeding on clams (15%) in the preliminary experiment. In our unpublished studies, some clam mortality occurred after 96 h. Dissolved oxygen and temperature were measured daily using a YSI-85-SCT meter to ensure that aeration maintained normoxic conditions while holding crabs and during the feeding experiments.

2.2. Clam and crab collection sites

Experiments were conducted from October 2007 through April 2008 (Table 1). Clams (30–35 mm long) were collected by hand while wading in southeastern Lake Pontchartrain and survivors returned to the Lake after each experiment. Crabs were captured using crab traps from Pirate's Bayou, a canal connected to Lake Pontchartrain south of Slidell, LA. Male crabs (130–160 mm carapace width) with all appendages including cutter and crusher chelae were used.

2.3. Maintenance of clams and crabs

Crabs were held separately in the five 42 l experimental aquaria connected to a 189 l closed recirculating, biological filtration tank and experiments were conducted in these tanks. Ammonia levels were monitored twice a week to ensure safe levels of biological filtration. Clams were kept in aerated 42 l aquaria and held for a week to a month before each experiment. Both crabs and clams were held in de-chlorinated, aged New Orleans tap water with synthetic sea salts added to maintain the salinity at 5, the mean salinity of eastern Lake Pontchartrain. Between experiments, crabs were fed Wardley shrimp pellets supplemented with shucked rangia clams.

2.4. Observational methods

Hypoxic clams were distinguished from normoxic clams by etching two horizontal or vertical lines in the periostraca depending on the treatment. Markings were alternated among experiments to eliminate any potential effect of the markings on feeding. Thirty of the forty replicates were visually monitored for the first hour of the 12 h experiment to determine whether crabs handled normoxic or hypoxic clams first. Random, detailed observations of methods that crabs used to feed on clams were made as time and opportunity permitted during the 12 h experiment. At the end of the replications, the valves were examined for chipped areas characteristic of crab feeding behavior. Which clam a crab handled or fed upon first was determined by observing the large marking on the periostracum on the clam being handled and/or the marking of the opposite choice not being handling by the crab. In most cases, crabs opened and fed on a single clam, so this determination was simple. In rare cases when both clams were eaten, the hypoxic clam was eaten much earlier in the 12 h replication than the normoxic clam.

2.5. Statistical analysis

To test for homogeneity of feeding response, we employed a 1-tail binomial test with 0.5 expected probabilities (Moore and McCabe, 1998). We used the twenty one replicates (Table 1) in which crabs

Table 1
Results of the choice experiment: N = normoxic clam eaten, H = hypoxic clam eaten, H,N = hypoxic clam eaten first, then normoxic clam eaten, – = no clam eaten. The total number of hypoxic or normoxic clams eaten are for the 5 experimental replicates run in 5 separate tanks on different dates, 1–8. Numbers (1) through (20) denote the 20 crabs used, and *a*, *b* indicate replicates in which the same crab was used in another run on a succeeding date. When two clams were eaten in a replicate, the first clam eaten was the choice and when a second clam was eaten it was not included in the totals.

Date	Tank 1	Tank 2	Tank 3	Tank 4	Tank 5	Total hypoxic	Total normoxic
1 (10/09/07)	(1*a*) H	(2*a*) N	(3*a*) --	(4*a*) --	(5*a*) --	1	1
2 (10/16/07)	(1*b*) --	(2*b*) H	(3*b*) --	(4*b*) --	(5*b*) --	1	0
3 (10/29/07)	(6*a*) H	(7*a*) H	(8*a*) --	(9*a*) H	(10*a*) H	4	0
4 (11/06/07)	(6*b*) H	(7*b*) H	(8*b*) --	(9*b*) N	(10*b*) H	3	1
5 (02/05/08)	(11*a*) --	(12*a*) H,N	(13*a*) --	(14*a*) H	(15*a*) H,N	3	0
6 (02/21/08)	(11*b*) --	(12*b*) H	(13*b*) H	(14*b*) --	(15*b*) H,N	3	0
7 (04/08/08)	(16*a*) --	(17*a*) --	(18*a*) --	(19*a*) --	(20*a*) --	0	0
8 (04/14/08)	(16*b*) --	(17*b*) H	(18*b*) --	(19*b*) --	(20*b*) --	1	0
Totals						16	2