Journal of Experimental Marine Biology and Ecology 547 (2022) 151679

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Short Communication

Habitat selection by post-settlement juvenile stone crabs (*Menippe mercenaria*) and predation risk in shallow near-shore habitats

Linae Boehme-Terrana [a,*,1], Michelle Roux-Osovitz [a,b,1], Erin Goergen [a,1], Harrison Mancke [e,d], Samantha Fisher [d,a], Philip M. Gravinese [c,d]

[a] St. Petersburg College, Baccalaureate Biology, Clearwater, FL 33675, USA
[b] The University of Tampa, Department of Biology, College of Natural and Health Sciences, Tampa, FL 33606, USA
[c] Florida Southern College, Department of Biological Sciences, 111 Lake Hollingsworth Drive, Lakeland, FL 33801, USA
[d] Mote Marine Laboratory and Aquarium, Fisheries Ecology and Enhancement Program, Sarasota, FL 34236, USA
[e] Florida International University, Department of Biological Sciences, College of Arts, Sciences and Education, Miami, FL 33199, USA

ARTICLE INFO

Keywords:
Stone crabs
Habitat selection
Fishery
Juveniles

ABSTRACT

Characterizing habitat selection of the stone crab *Menippe mercenaria* (Say) provides crucial information for the successful management of this commercially important fishery in Florida. The post-settlement juvenile stage of the stone crab lifecycle faces unique environmental, physiological, and survival challenges prior to becoming sexually mature, yet little is known about their preferred habitat. Our study focuses on post-settlement juvenile (< 1 year, 2–20 mm carapace width) habitat selection between structured artificial seagrass, structured oyster shell rubble, and non-structured sand habitats in the laboratory. Our laboratory experiments provided a unique opportunity to uncouple chemical and environmental cues from the structure of habitats, allowing the study to focus predominantly on the effect of structure on habitat selection. In the controlled laboratory environments, post-settlement juvenile stone crabs preferred structured habitats (artificial seagrass and oyster shell rubble) over non-structured habitats (sand). Survivorship across all trials was high (97%). The laboratory experimental results were complemented with a field predation risk experiment in comparable shallow, near-shore habitats. During the field experiments, predation risk was highest in structured oyster shell rubble and lowest in structured vegetated seagrass. In the seagrass habitat, post-settlement juvenile stone crabs experienced 33% mortality. The sand and oyster shell rubble habitats experienced 69.3% and 83.3% mortality respectively. The data presented here indicate that stone crab juveniles prefer structurally complex habitats and have higher survival in comparable natural habitats. Our results suggest that structurally complex habitats (i.e., seagrass beds) may provide better nurseries for post-settlement juvenile stone crabs and that seagrass restoration or preservation efforts may improve stone crab post-settlement survivorship possibly allowing new recruits to enter the stone crab fishery.

1. Introduction

The larvae of many brachyuran crustaceans return from the plankton to settle as juveniles in near-shore nursery habitats of varying complexity. Structured, vegetated (e.g., algal or seagrass) and structured, non-vegetated habitats (e.g. oyster reefs, coral reefs) significantly reduce post-settlement juvenile mortality by providing refuge for crustaceans and reducing inter- and intraspecific competition, predation, cannibalism, and physiological stress (Andrews et al., 2001; Fernandez et al., 1993; Moksnes et al., 1998; Moksnes, 2002; Stoner et al., 2010; Wahle and Steneck, 1992). Studies to determine if varying habitat complexity influence habitat choice and contribute to post-settlement juvenile survival can therefore help characterize potential source habitats that may supply new recruits into a fishery. For example, Lecchini et al. (2010) investigated habitat preference for nine crustacean species and found that in the post-larval stage, 67% actively chose settlement habitat. In the Lecchini et al. (2010) study, habitat type choice differed by species and was not influenced by the presence or absence of conspecifics. Similarly, Pallas et al. (2006) found that substrate type, more than depth or wave action, influenced juvenile settlement in a variety of

* Corresponding author.
E-mail address: boehme.linae@spcollege.edu (L. Boehme-Terrana).
[1] Authors contributed equally.

https://doi.org/10.1016/j.jembe.2021.151679
Received 23 August 2021; Received in revised form 5 December 2021; Accepted 7 December 2021
Available online 17 December 2021
0022-0981/

decapod crustaceans. Although our understanding of post-settlement crustacean habitat selection is based on a wide variety of species, few studies have investigated habitat choice by commercially important stone crabs. The study presented here addresses the need for post-settlement juvenile habitat selection data for the Florida stone crab using two independent experimental approaches. The first tests the influence of structure on habitat choice in a controlled laboratory experiment using artificial structure and exclusion of environmental and chemical cues associated with those specific habitats. The second experimental approach uses comparable shallow, near-shore field sites to assess survival in relation to habitat type in three non-manipulated natural stone crab environments.

The stone crab *Menippe mercenaria* (Say) is an epibenthic species with a biogeographical range from North Carolina, throughout the Gulf of Mexico to Belize. Stone crabs form the basis of a valuable commercial industry, however, the annual statewide harvest has declined for several years, with 2019–2020 reporting a 11.4% decrease in landings from the previous 5-year average (Florida Fish and Wildlife Conservation Commission, 2021). This decline is likely due to a combination of overharvesting (Muller et al., 2006; Muller et al., 2011), shelter limitation (Shervette et al., 2004), and influences of seasonal trends on recruitment in early life stages (Bert et al., 2021). The stone crab's early life stages occur predominantly in subtidal locations with larval release and post-larval recruitment occurring in shallow near-shore habitats (Gravinese et al., 2018; Krimsky and Epifanio, 2008; Lindberg and Marshall, 1984). Stone crab larvae actively respond to specific exogenous cues (gravity, light intensity, hydrostatic pressure) that result in newly hatched larvae being positioned near the surface where currents can facilitate transport away from coastal areas (Gravinese, 2018). After developing in the plankton, later larval stages are heavier, less buoyant, and alter their response to the aforementioned exogenous stimuli resulting in a relatively deeper distribution where bottom currents facilitate transport back to potential settlement sites where they settle as megalopae and eventually metamorphose into juveniles (Gravinese, 2018). During settlement, the time to metamorphose into stone crab megalopae is influenced by a variety of cues associated with nursery habitats including the brown alga *Sargassum fluitans*, rock/rubble substratum, and *Crassostrea virginica* oyster shell rubble associated biofilms (Krimsky and Epifanio, 2008), suggesting that megalopae have a preferred habitat. Therefore, characterizing post-settlement juvenile stone crab habitat selection could yield crucial information for the successful management of potential landings for this commercially important fishery.

Despite these studies, no work has characterized the influence of structured artificial seagrass and oyster shell rubble on post-settlement juvenile stone crabs (< 1 year old, 2–20 mm carapace width (CW)). This is surprising given previous studies using commercially and ecologically important crustaceans as models for post-settlement habitat selection (Wahle and Steneck, 1992), predation risk (Fernandez et al., 1993; Orth and van Montfrans, 1987), and the role of habitat in molting and recruitment success (Krimsky and Epifanio, 2008; Moksnes, 2002). Here we tested if post-settlement juvenile stone crabs select structurally complex habitats including artificial seagrass, oyster shell rubble, or non-structured sand in an environmentally controlled laboratory study. We also tested if post-settlement juvenile survival differed among comparable habitats within shallow, near-shore field sites that mimicked the laboratory habitats without manipulation of exogenous influences. Characterizing post-settlement juvenile stone crab habitat selection and describing the factors that may affect survival of these stone crabs could help managers quantify which habitats contribute to the survival of new recruits and thereby help sustain the stone crab fishery.

2. Materials and methods

2.1. Animal collection and maintenance

Post-settlement juvenile *M. mercenaria* (CW ranging from 2.57 to 20.5 mm for all experiments) were collected by hand from sandy oyster shell rubble habitats at Bird Key and Overlook Park in Sarasota, Florida and from Florida Fish and Wildlife Conservation Commission Stone Crab Independent Monitoring Programs Tampa Bay site. Collected post-settlement juveniles were transported to Mote Marine Laboratory in Sarasota, Florida for acclimation to laboratory conditions over 24 h. Post-settlement juvenile crabs were maintained in individual clear acrylic boxes (80 ml) and fed a diet of enriched *Artemia* (Brine Shrimp Direct, enriched with Selco, 1 ml^{-1}). Larger post-settlement juveniles (15–20.5 mm CW) were fed small pieces of shrimp every other day.

2.2. Habitat selection: laboratory experimental design

Experimental trials were conducted in a clear acrylic circular chamber (49.5 cm inside diameter, 50.8 cm outside diameter, 30.5 cm height) with a 0.19 m^2 area (see Fig. S1) filled with filtered natural seawater (500 μ mesh). For each replicate trial, the experimental chamber was evenly split into two sections, with each section housing one of the three artificial habitats tested: non-structured sand (control), structured, artificial seagrass, or structured, oyster shell rubble. The oyster shell rubble and sand were separately sterilized by heating in an oven at 450 °C for 12 h. The artificial seagrass was made using green polypropylene ribbon, which was then adhered to a mesh screen whose base was submerged beneath the sandy substrate (Chavanich et al., 2004; Layman, 1992). Artificial habitats were systematically alternated to hemisphere A and hemisphere B in each independent trial (Fig. S1). This study only examined structural preference, therefore the use of sterilized oyster shell rubble and artificial seagrass minimized the presence of any habitat specific chemical cues that may influence habitat selection. Any potential chemical cues from the natural seawater were mitigated by constant circulation of water during the 24-h. trial.

Experimental trials consisted of simultaneously adding experimentally naive post-settlement juvenile stone crabs ($n = 6$) into the experimental chamber (Fig. S1). Density of crabs in each trial was chosen based on availability of appropriately sized crabs, but also to limit high density-induced cannibalism that could alter habitat choice (Sinclair, 1977). Other methods to reduce cannibalism included feeding crabs prior to trials. All juvenile crabs were introduced via PVC pipe positioned in the center of the experimental chamber. Once introduced, juvenile crabs were free to move about the chamber for 24 h. without manipulation. After the 24 h. period, a fitted acrylic divider was inserted into the experimental chamber, bisecting the habitat types into A and B hemispheres, avoiding movement of crabs while sorting. Post-settlement juvenile crabs in each habitat type were then sorted and quantified as to selected habitat and their CW was measured. Each habitat type comparison was replicated with each experiment using independent post-settlement juvenile crabs (artificial seagrass vs. sand: $n = 6$; oyster shell rubble vs. sand: $n = 7$; artificial seagrass vs. oyster shell rubble: $n = 8$).

The experimental chamber was equipped with two pumps and aerators that were positioned opposite each other to create a continuous flow (Fig. S1). Salinity, temperature (°C), and dissolved oxygen (mg L^{-1}) were measured at the beginning and end of each replicate trial using a handheld YSI (ProPlus series). All trials used a 14 h. light:10 h. dark summer light regime and were conducted in the summers of 2018 and 2019.

2.3. Field predation study

To determine if predation risk was influenced by habitat structure, post-settlement juvenile stone crabs were tethered into one of three

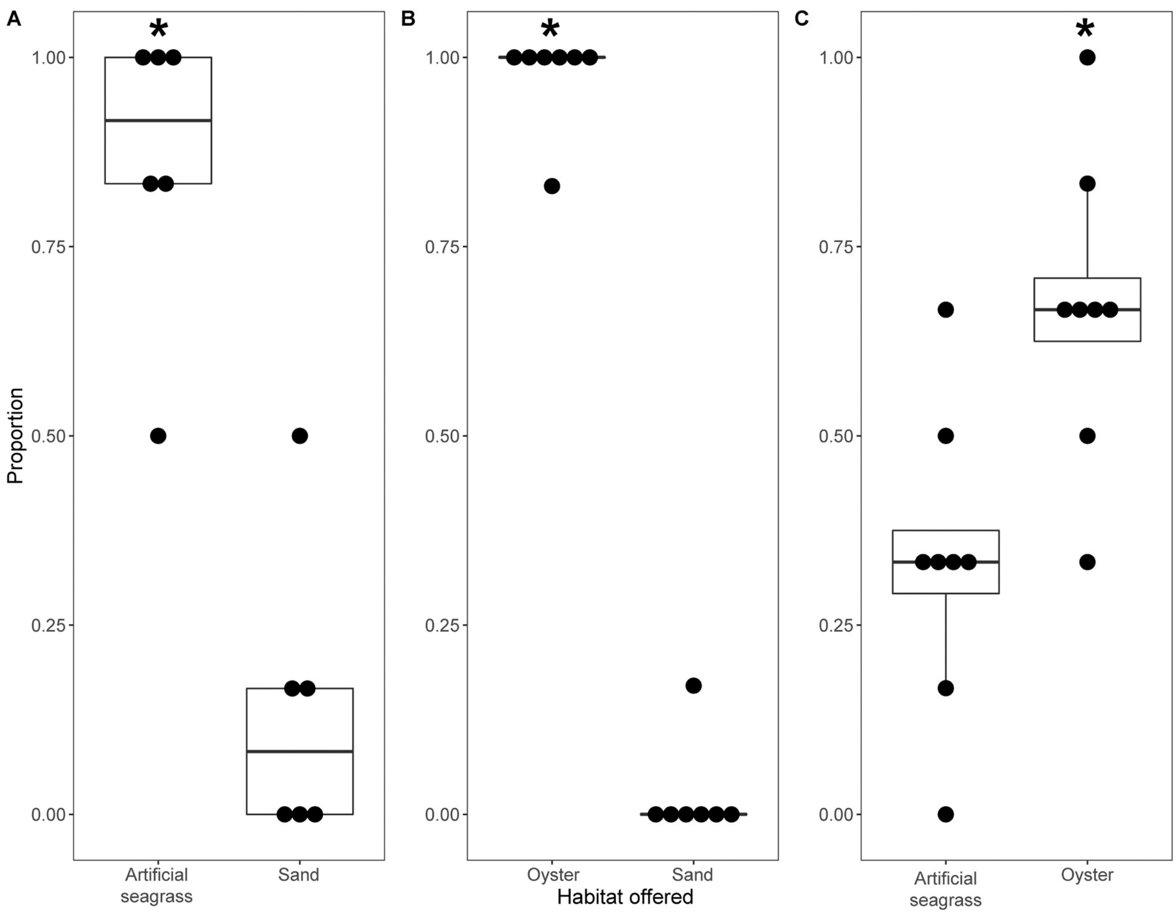

Fig. 1. Laboratory habitat selection by post-settlement juvenile stone crabs.
Box plot showing the median proportion of post-settlement juvenile stone crabs selecting A. structured artificial seagrass vs. non-structured sand, B. structured oyster shell rubble vs. non-structured sand, and C. structured artificial seagrass vs. structured oyster shell rubble. Asterisk above the boxes indicate significant differences at the α = 0.05 level. The dots represent the distribution within each replicate while the horizontal line represents the median.

different habitat types at a nearshore location in Pinellas County, Florida. The field sampling site was selected as comparable to the previously described laboratory trial habitats. The study area was 1.5 km long and consisted of sand habitat (non-structured control), seagrass habitat (structured, vegetated), and oyster shell rubble habitat (structured, non-vegetated). Due to the heterogeneous nature of Tampa Bay, each habitat type was clustered into patches within our field location (oyster shell rubble habitat: 27.916606, −82.828116, sand habitat: 27.917567, −82.839115, seagrass habitat: 27.917287, −82.824914), and temperature, salinity, and dissolved oxygen were similar among field sites during all trials (Table S1). All habitat patches were ~ 1.5 m in depth and greater than 2000 m^2 in size. During field predation trials, a different set of independent post-settlement juvenile stone crabs were randomly selected and tethered to monofilament (length 40 cm). The monofilament was glued to their carapace then secured to a 30 cm stainless steel rod. Deployment of the tethered crabs in the field consisted of submerging the entire rod into the benthic substrate. Within each habitat type, experimentally naive post-settlement juvenile stone crabs (n = 6) were individually tethered in a random location (more than 0.5 m apart) and left for 24 h., with all trials beginning between 8:00 and 10:00 am. After 24 h., tethered crabs were recovered and recorded as either dead (missing from tether and assumed to have suffered mortality), or alive (still on the tether). All 19 field trials were conducted between June and September of 2018 and 2019.

2.4. *Statistical analyses*

Habitat selection by post-settlement juvenile stone crabs during the laboratory trails were analyzed using a Wilcoxon sign rank test. To evaluate possible influence of crab size on the laboratory trials, we used a linear mixed effects model with CW as the dependent variable and habitat as a fixed factor. Trial number was included in the model as a random factor. The number of the crabs found dead or alive after 24 h. in the field experiment was analyzed for statistical difference using a general linear model (GLM) with crab status (alive vs. dead/missing) as the dependent variable, field habitat and CW as fixed factors. A post-hoc Tukey test was used to determine pairwise comparisons. All statistical analyses were performed using RStudio (3.6).

3. Results

3.1. *Laboratory habitat selection*

Post-settlement juvenile stone crabs preferred structurally complex artificial habitats (structured, artificial seagrass and structured, oyster shell rubble) over non-structured sand. A significantly greater proportion of post-settlement juvenile stone crabs were found in artificial seagrass (n = 6 replicate trials; W = 35.5, $P < 0.001$; Fig. 1A) and oyster shell rubble (n = 7 replicate trials; W = 49, $P < 0.001$; Fig. 1B) relative to non-structured sand. When post-settlement juvenile stone crabs were offered the choice between two structured complex habitats, artificial seagrass and oyster shell rubble, a significantly greater proportion

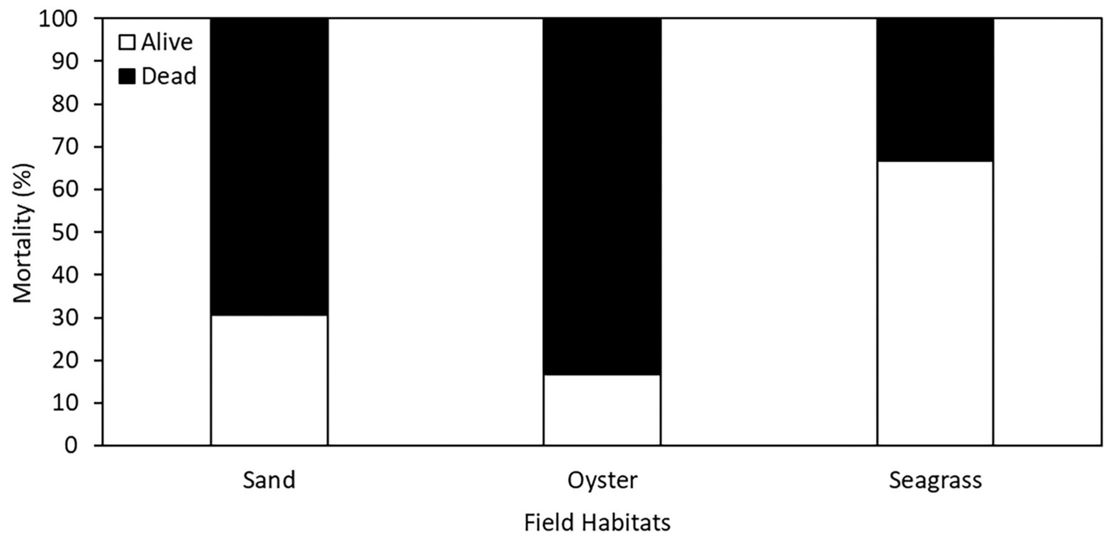

Fig. 2. Juvenile mortality in the field.
The percentage of post-settlement juvenile stone crabs that experienced mortality (black) or were alive (white) after being tethered for 24 h. in the field among the seagrass, oyster shell rubble, and sand habitats. Post-settlement juveniles in the seagrass habitat experienced significantly lower mortality than the oyster shell rubble and sand habitats.

selected oyster shell rubble ($n = 8$ replicate trials; W = 7.5, $P = 0.009$; Fig. 1C). Overall, only 4% of crabs chose non-structured sand, 37.6% chose artificial seagrass, and 58.4% were found in oyster shell rubble. Survivorship across all trials was high (97%). The linear mixed effects model showed there was no difference in the size of crabs (CW) choosing one habitat or another (artificial seagrass vs oyster shell rubble, $P = 0.16$; artificial seagrass vs non-structured sand $P = 0.77$; oyster shell rubble vs. artificial seagrass, $P = 0.91$). In only one case was a crab missing (potential cannibalism), indicating that mortality and cannibalism were not major influences in the laboratory trials.

3.2. Field predation

The GLM model showed a significant difference in mortality among field habitats (habitat: $X^2 = 12.0$, df = 2, $P < P = 0.002$). A Tukey test showed that mortality in the seagrass habitat was significantly lower than the oyster rubble habitat ($P < 0.0001$) and lower than the sand habitat ($P = 0.009$). There was no statistical difference in survival between the sand and oyster rubble habitat ($P = 0.35$). In the seagrass habitat, post-settlement juvenile stone crabs experienced 33% mortality. The sand and oyster shell rubble habitats experienced 69.3% and 83.3% mortality respectively (Fig. 2). The GLM also reported a negative relationship for CW indicating that individuals with larger CW were more likely to experience mortality than smaller individuals (carapace width: $X^2 = 14.6$, df = 1, $P < P = 0.0001$).

4. Discussion

Post-settlement juvenile stone crabs have been observed in jetties, pilings, oyster shell rubble, gorgonians, sponges, *Sargassum* mats, and rocky riprap (Bender, 1971; Bert et al., 1978; Williams, 1965). This suggests that post-settlement juvenile stone crabs are largely dependent upon the presence of structurally complex habitats that likely minimize predation (Krimsky and Epifanio, 2008). Our results show that post-settlement juvenile stone crabs prefer habitats with complex structure (oyster shell rubble and artificial seagrass). A higher percentage of post-settlement juvenile stone crabs selected artificial seagrass and oyster shell rubble over non-structured sand, with a preference towards oyster shell rubble habitat during laboratory trials. These laboratory trials were free from predators (other than conspecifics) and free from known exogenous environmental cues that could impact habitat selection.

Our field trials provide evidence that structurally complex vegetated habitats reduce mortality in post-settlement juvenile stone crabs. We observed lower mortality in seagrass field sites, but higher mortality in both bare sand and oyster shell rubble sites (Fig. 2). One reason for the difference in survival between the field conditions could be the difference in physical structure impacting organism exposure (Daly and Long, 2014a; Daly and Long, 2014b; Pirtle et al., 2012). Observations during laboratory experiments noted stone crabs burying themselves in sand at the base of artificial seagrass where they were subsequently recovered at the end of the 24-h. trial. This supports increased ability to hide in seagrass which is a documented behavior in previously published field predation studies (Heck Jr and Wilson, 1987). Similarly, tests of the shelter bottleneck hypothesis indicated that post-settlement juvenile *Menippe* spp. (< 50 mm) were more likely to be found in the natural seagrass habitat as opposed to the supplemental shelters (Beck, 1995; Beck, 1997).

Field sites with oyster shell rubble, while structurally complex, had higher predation, similar to that seen in the bare sand. Stone crabs in oyster shell rubble face both increased competition for unoccupied shelter and risk of predation due to the desirability of oyster shell rubble habitats for other species (Daly and Long, 2014a; Daly and Long, 2014b). Predation by other crustaceans (Wahle and Steneck, 1992) and cannibalism by other post-settlement juvenile crabs (Moksnes, 2004) are well-documented sources of predation on settling crustaceans. Although our study does not include data on predator populations in the chosen field sites, we maintain that the risk of cannibalism in oyster shell rubble is predicted to be higher than in seagrass and could be seen as an important distinction when considering the success of post-settlement juveniles in these habitat types.

5. Conclusions

Our results suggest that the availability of complex structure, specifically seagrass, gives post-settlement juvenile stone crabs the ability to avoid predation (Caddy and Stamatopoulos, 1990). Given the declining harvest of the stone crab fishery, any means of increasing post-settlement juvenile crab survival could subsequently increase recruitment back into the fishery. Our field experiment suggests that seagrass beds reduce mortality; however, seagrasses are slow growing and subject to seasonal variation (Metz et al., 2020). The monitoring and preservation of seagrass habitat seems vital to reducing potential shelter bottlenecks, especially for post-settlement juveniles. Oysters remain an important habitat because, as stone crabs mature, their habitat preference may shift to oyster habitats due to prey availability. In fact, recent estimates suggest that increasing oyster shell reef habitat would enhance *Menippe* spp. populations in the Gulf of Mexico (zu Ermgassen et al., 2021). Future studies should investigate how artificial and restored habitats might enhance post-settlement juvenile stone crab recruitment, density, and post-settlement survival.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Funding for this project was supported by the Steinwachs Family Foundation and Mote Scientific Foundation awarded to P. Gravinese. Partial support was provided by the St. Petersburg College Foundation Titan Achievement Grant awarded to L. Boehme-Terrana, M. Roux-Osovitz, and E. Goergen. We thank our undergraduate students who assisted in laboratory trials and include H. Hollinger, E. Baker, J. Demarest, M. Mostrom, N. Hernandez, D. Hullett, S. Ingram, N. Schiller, and M. Beretta. We thank L. Toth for her assistance with figure preparation. We also thank the Florida Fish and Wildlife Stone Crab Independent Monitoring Program for assistance with animal collection. All animals were collected in compliance with Special Activity License #20-1868B-SR. Current research by P. Gravinese is supported by a National Science Foundation Biological Oceanography grant (award number OCE-2049047).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2021.151679.

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