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Three-dimensional Interstitial Space Mediates Predator Foraging Success in Different Spatial Arrangements

Stephen Gregory Hesterberg

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Three-dimensional Interstitial Space Mediates Predator Foraging Success in Different Spatial
Arrangements

by

Stephen Gregory Hesterberg

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
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College of Arts and Sciences
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3D printing

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DEDICATION

To my wife, Rebecca, my parents, Greg and Sally, and to all who have helped me get to this point in my life. I am forever grateful.

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TABLE OF CONTENTS

List of Tables	ii
List of Figures	iii
Abstract	iv
Introduction	1
Methods	5
Structural Components	5
Mesocosm Experimental Setup	8
Field Tethering Experimental Setup	11
Statistical Analyses	13
Results	15
Mesocosm Experiments	15
Field Tethering Experiments	17
Discussion	19
References	25
Appendix A: <i>Eurypanopeus depressus</i> Size Distribution From Tampa Bay, Florida	31
Appendix B: Uncorrected Survivorship Data and Analyses From Mesocosm Experiments	33
Appendix C: Relationship Between Predator Size and Prey Survivorship in Mesocosm Experiments	35

LIST OF TABLES

Table 1: Mean ($\pm$ SD) three-dimensional interstitial space size (cm^3) and shape (i.e., Length, Width, Height, cm) of the oyster shell mimics used in both mesocosm and field tethering experiments.....	8
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LIST OF FIGURES

Figure 1: 3D printed oyster shell mimics, with white outlines identifying each component's interstitial space	7
Figure 2: Mean proportional survivorship ($\pm$ SE) of <i>Eurypanopesus depressus</i> prey after 24 h in mesocosms with a decapod predator and 3D printed oyster shell mimics of different (A) orientation [0° ($n = 10$) and 45° ($n = 11$)] or (B) shape [Shape 1 ($n = 16$) and Shape 2 ($n = 10$)]	16
Figure 3: Proportional survivorship of tethered <i>Eurypanopesus depressus</i> placed on an intertidal oyster reef in Tampa Bay, FL after 24 h with a 3D printed oyster shell mimic of different (A) orientation [0° ($n = 33$), 22.5° ($n = 32$), 45° ($n = 27$)] or (B) shape [Shape 1 ($n = 26$) and Shape 2 ($n = 28$)]	18
Figure A1: Carapace width (CW) of <i>Eurypanopeus depressus</i> (i.e., mud crabs) sampled from oyster reefs in Tampa Bay, Florida ($n = 900$)	32
Figure A2: Mean proportional uncorrected survivorship ($\pm$ SE) of <i>Eurypanopesus depressus</i> prey after 24 h in mesocosms with a decapod predator and 3D printed oyster shell mimics of different (A) orientation [0° ($n = 10$) and 45° ($n = 11$)] or (B) shape [Shape 1 ($n = 16$) and Shape 2 ($n = 10$)]	34
Figure A3: Correlation between proportional survivorship of <i>Eurypanopesus depressus</i> and predator size as measured by carapace width in mesocosms with 3D printed oyster shell mimics of different (A) orientation or (B) shape	35

ABSTRACT

Habitat structure modifies the strength of predator-prey interactions, but it remains unclear how to describe the three-dimensional spatial arrangement of structural components in a way that consistently predicts outcomes. Interstitial space may provide a useful target for measurement, but most studies use only two-dimensional methods to describe 3D space, limiting their predictive power. Using a novel technology to produce identical components, this study tests whether the 3D interstitial space of oyster shell mimics modifies the ability of blue crabs (*Callinectes sapidus*) to capture their mud crab prey (*Eurypanopeus depressus*) in mesocosms and a variety of reef-associated predators to capture tethered mud crabs in the field. To accomplish this, individual interstices were manipulated by changing either the orientation or internal shape of 3D printed shell mimics, representing possible ways natural oyster shells differ spatially on a reef. In mesocosms, 3D interstitial space strongly affected prey survivorship in both spatial arrangements, but striking variation in the ability of individual blue crabs to consume their prey in the Shape 1 structures was notable. Field tethering experiments mostly corroborated mesocosm findings, except in the shell shape treatment. These unexpected results were likely an artifact of differences in predation between field experiments and highlight the specificity of predator-prey interactions in structured habitats. Together, these results demonstrate that the 3D interstitial space created from the spatial arrangement of structural components can mediate predator foraging success independent of the widely studied density attribute, but these outcomes are further dependent on both predator and prey identity as well as

individual variation. This study also identifies a potential target for quantifying the spatial arrangement of structural components and proposes that such a measure should be three-dimensional, capture both the size and shape of an interstice, and scaled to the specific predator-prey interaction in question.

INTRODUCTION

Predator-prey interactions alter species abundance and diversity through the direct removal of prey and non-consumptive pathways (e.g., Paine 1966, Estes and Palmisano 1974, Preisser et al. 2005). Habitat structure, or the physical arrangement of structural components in space, is a universal property of all ecological systems (Bell et al. 1991) that modifies these trophic interactions to influence communities (Crowder and Cooper 1982, Diehl 1992). Numerous studies across freshwater, marine, and terrestrial systems have examined how various structural attributes of physical habitat mediate prey encounter rates (Anderson 1984, Ryer 1988, Brodmann et al. 1997, Gibb and Par 2010), predator and prey detection (Devereux et al. 2004, Ferner et al. 2009, McCormick and Lönnstedt 2013), the ability of predators to access prey (Anderson 1984, Toscano and Griffen 2013), and ultimately prey consumption (Coen et al. 1981, Gotceitas and Colgan 1989, Longland and Price 1991, Beukers and Jones 1997, Grabowski 2004, Warfe and Barmuta 2004, Andruskiw et al. 2008). Furthermore, habitat structure alters the strength of cascading effects across multiple trophic levels through both consumptive and non-consumptive pathways (Finke and Denno 2006, Grabowski et al. 2008, Kalinkat et al. 2013).

In aquatic environments, benthic invertebrates (e.g., corals, oysters, mussels), macroalgae, macrophyte vegetation, rock, and woody debris are structural components that can provide potential refuge from predation (Kovalenko et al. 2012). Most studies investigating trophic interactions and habitat structure in aquatic systems have focused on the relationship between predator foraging success, or the ability of predators to remove their prey through

consumption, and the density of structural components in some manner. These studies either purposely manipulate component density (Heck and Thoman 1981, Crowder and Cooper 1982, Gotecitas and Colgan 1989, Ferner et al. 2009, Lannin and Hovel 2011, Hill and Weissburg 2013, Carroll et al. 2014) or inadvertently alter the number of structural components to manipulate other spatial attributes, but neglect to separate their effects (e.g., Vince et al. 1976, Stoner 1982, Bartholomew et al. 2000, Grabowski and Powers 2004, Humphries et al. 2011, Toscano and Griffen 2013). However, other aspects of habitat structure, such as the position of structural components (i.e., orientation) (Bartholomew et al. 2000, Horinouchi et al. 2009) or their external form (i.e., shape) (Coull and Wells 1983, Ryer 1988, Dionne and Folt 1991, Beukers and Jones 1997, Warfe and Barmuta 2004), might further influence predator-prey outcomes independent of density. Thus, these findings question whether density is the only spatial attribute that mediates predator foraging success and propose that the three-dimensional (3D) arrangement of components in space may also influence prey capture.

Although it remains unclear how to describe the 3D arrangement of objects in a way that predicts predator foraging success, the space within or between objects (i.e., interstitial space) may provide a useful target for measurement. For example, several studies have proposed that the space created by structural components (e.g., algal fronds, corals, macrophyte blades, rocks in a streambed) are strong predictors of habitat selection or abundance of both marine and freshwater fauna, and these patterns are likely due to refuge effects (Hacker and Steneck 1990, Gratwicke and Speight 2005, Finstad et al. 2007, Horinouchi et al. 2009, Warfe et al. 2008, Martin et al. 2012). However, the few manipulative studies that use space-focused measures to assess predator-prey interactions in structured habitats have been mixed at consistently predicting prey consumption, likely due to the 2D methods used to describe the total 3D

interstitial space available for prey to exploit within a structure (Bartholomew et al. 2000, Wong 2013, but see Humphries et al. 2011). Viewing interstitial space in a 3D perspective might offer a more complete insight into predator-prey interactions by fully describing areas where prey hide and predators must access. For example, the location of prey within an angled “crevice” was shown to strongly affect predator handling time and prey capture across a suite of predator sizes, presumably a result of the 3D aspects of the interstitial space utilized by the prey (Toscano and Griffen 2013). Thus, expanding discussions beyond density of structure and its impact on the strength of predator-prey interactions will benefit from a rigorous evaluation of whether three-dimensional interstitial space may also affect predator foraging successes, but such a study is currently lacking.

Within the estuarine landscape, oyster reefs are patches of bivalve hard-structure (Guitérrez et al. 2003), composed of live and dead shells that vary widely in both their three-dimensional shape and orientation to other oysters. The spatial arrangement of these shells create interstices of differing size and shape that are utilized by numerous benthic fauna (Bartol et al. 1999), thereby providing a useful model to investigate whether interstitial space mediates interactions between space-dwelling prey and reef-associated predators. The flatback mud crab (*Eurypanopeus depressus*, hereafter ‘mud crab’) is an abundant macroinvertebrate on oyster reefs that directly use the spaces between and within oyster shells as a refuge (McDonald 1982, Tolley and Volety 2005), presumably from predators such as the Atlantic blue crab (*Callinectes sapidus*) (e.g., Grabowski et al. 2008, Hill and Weissburg 2013). Predator-prey interactions between space-dwelling mud crabs and their predators have been widely studied in the oyster reef system (Grabowski 2004, Grabowski et al. 2008, O’Conner et al. 2008, Hill and Weissburg 2013, Geraldi et al. 2015), but consideration of the 3D reef structure has yet to be explored.

This study tests whether the 3D interstitial space within structural components (i.e., oyster shell mimics) modifies the ability of blue crabs to consume their mud crab prey in mesocosms. Additionally, this study tests whether the 3D interstitial space of these oyster shell mimics modifies the ability of various reef-associated predators to consume tethered mud crabs in the field. To accomplish this, individual interstices were altered by manipulating either the orientation or shape of structural components, representing two aspects by which natural oyster shells can differ spatially in three-dimensions on a reef. In a first set of mesocosm and field tethering experiments, interstitial space was manipulated by changing only the orientation of identically sized shells. In a second set of experiments, interstitial space was manipulated by modifying internal shell shape, but keeping shells at the same orientation. By testing the effects of interstitial space on predator foraging success separately in two different spatial arrangements (i.e., orientation and shape), this study provides a rigorous assessment of whether measures of 3D interstitial space should be considered when evaluating the influence of habitat structure on predator-prey outcomes.

MATERIALS AND METHODS

Structural Components

As the morphology of natural oyster shell is highly variable, we utilized 3D printing to produce identical oyster shell mimics for use in both mesocosm and field tethering experiments. The consistent replication of structural components provided by 3D printing allowed for the control of external spatial properties in trials while manipulating interstitial space. All shell mimics were created from the 3D image of a 60 mm long, left oyster valve that was digitized using a Konica-Minolta vivid 9i short-range laser scanner at the University of South Florida's Alliance for Integrated Spatial Technologies. While keeping shell dimensions constant, the valve was resized to create different shell sizes when necessary. A MakerBot 3D printer with polylactic (PLA) or acrylonitrile butadiene styrene (ABS) plastic was used to produce individual shells at the University of South Florida's Advanced Visualization Center and X-Laboratory.

Methods of assessing 3D interstitial space are not well developed and a single measure that simultaneously describes an interstice's size and shape does not currently exist. Thus, interstitial space size, or the volume created between the shell mimic and the base to which it was attached, and interstitial space shape, or the form of the interstice created by the shell mimic and its base, were measured using two independent methods to describe the 3D nature of each interstitial space. To determine interstitial space size, oil-based modeling clay was inserted into an interstitial space, removed, and then its volume (cm^3) determined using water displacement. For interstitial space shape, the length, width, and height of an interstice were assessed to provide

a relative measure of its form. Five replicate shells for each orientation and two shape level were measured and the mean of those observations was used to describe a specific component's interstitial space size or shape.

To manipulate the 3D interstitial space of shell mimics, components were attached to flat surfaces and either the orientation or internal shape of shell mimics were varied, producing different levels of interstitial space (Table 1). Specifically, to change interstitial space via orientation, shell mimics of the same shape (Fig. 1A) were attached at angles varying of 0, 22.5, and 45° (Fig. 1B), representing a similar range of angles used in other studies to manipulate shell orientation (e.g., Soniat et al. 2004) and observed from oyster clumps in the study area (E. Salewski, *personal communication*). To change interstitial space via shape, shell mimics were modified internally by inserting ~13.8 cm³ of oil-based modeling clay (Fig. 1C) and then attached to the base at the same angle (0°) (Fig. 1D). Shell mimics with added clay approximated both differences in oyster shell shape as well as the additional occupancy of space by attached epifauna, which commonly attach to live and dead shells, such as mussels, barnacles, and oyster spat (Boudreaux et al. 2006). Together, shell mimics and the flat surfaces to which they were attached simulated shells adjacent to either an articulated right valve or another oyster shell. Initial observations indicated that *E. depressus* did not utilize shell mimics differently than natural shells and colonized both mimic and natural shell in aquaria (S. Hesterberg, *personal observation*).

Figure 1. 3D printed oyster shell mimics, with white outlines identifying each component's interstitial space. (A) Underside of oyster shell mimic [60 mm shell height (SH)] used to manipulate interstitial space by changing shell orientation. (B) Oyster shell mimics (60 mm SH) oriented sequentially at angles of 0°, 22.5°, and 45°. (C) Underside of oyster shell mimics (80 mm SH) modified with modeling clay to manipulate interstitial space by changing shell shape. (D) Shapes 1 and 2 were fixed at the same orientation (0°), thereby differing in only their interstice shape.

Table 1. Mean ($\pm$ SD) three-dimensional interstitial space size (cm^3) and shape (i.e., Length, Width, Height, cm) of the oyster shell mimics used in both mesocosm and field tethering experiments. The interstitial space of shell mimics was manipulated by either changing their orientation or shape, representing two possible ways natural oyster shells differ in spatial arrangement.

Spatial Arrangement	Space Size (cm^3)	Space Shape (L, W, H, cm)
Shell Orientation		
0°	9.5 ± 0.2	4.76, 3.04, 1.31
22.5°	17.4 ± 0.6	4.42, 3.06, 2.91
45°	20.4 ± 0.8	3.02, 3.05, 4.68
Shell Shape		
Shape 1	9.5 ± 1.3	2.60, 4.23, 1.91
Shape 2	9.6 ± 0.7	6.25, 1.51, 1.55

Mesocosm Experimental Setup

Two separate experiments were conducted between July and October 2015 at the University of Tampa's Marine Science Center, Tampa, Florida to test whether the 3D interstitial space of shell mimics modifies the ability of blue crabs to consume their mud crab prey. In the first mesocosm experiment, 3D interstitial space was manipulated by changing the orientation of shell mimics (Table 1). To accomplish this, 60 mm shell mimics of the same shape were arranged into one of two orientations (0° or 45°) (Fig. 1A and B). In the second mesocosm experiment, 3D interstitial space was manipulated by changing only the internal shape of shell mimics (Table 1). To do this, 80 mm shell mimics with contrasting internal shapes (Shape 1 or Shape 2) were kept at the same orientation (0°) (Fig. 1C and D). Shape 1 contained clay added to the base of the left valve near the hinge, simulating a mussel that creates a shallow interstice

close to the ventral edge. Shape 2 had clay added along the sides of each shell to simulate fouling, thereby creating a narrow interstice.

All experiments were conducted outdoors in covered mesocosms [151.4 L; 0.9 x 0.5 x 0.4 m (L x W x H)], the sides of which were surrounded by a black plastic tarp to reduce visual disturbance. Wire mesh (6.45 cm² opening) was placed on top of each mesocosm to prevent predator escape and large aerators were hung from the wire top to provide oxygen and water circulation. Mesocosms were filled with unfiltered seawater pumped directly from Tampa Bay and held at a constant depth of roughly 35 cm to simulate the shallow conditions where oysters can be found in the study area.

As only five mesocosms were available, each experiment was conducted in a block design to minimize potential effects of temporal heterogeneity. Treatments were randomly assigned to one mesocosm and the position of each mesocosm haphazardly rearranged at the start of each trial. “No-predator” controls ($n = 16$) were also conducted during trials to estimate background mortality and verify predator consumption of prey. All mesocosms received 15 shell mimics of the appropriate spatial arrangement treatment and level [i.e., orientation (0/45°) or shape (Shape1/Shape2)], which were attached to a plexiglass insert using epoxy putty, and the plexiglass sheet then attached to the bottom of a mesocosm using non-toxic silicone. Shell mimics were spaced at least 5 cm apart to ensure equal predator access and the position of shells relative to one another was constant across all experiments. A fine layer of filtered sand was added over each plexiglass base to a depth of approximately 0.25 cm.

Mud crabs (10-16 mm CW) were collected by hand before each experiment from an intertidal oyster reef in Tampa Bay, Florida (27°89.296 N, -82°54.076 W), held in 37.9 L aquaria, and fed shrimp pellets until use in trials. The range in prey size selected for these

experiments fell within the regional (McDonald 1982) and local size distribution of *E. depressus* (Fig. A1, Appendix A). Twelve mud crabs were haphazardly selected and placed in each mesocosm approximately 15 minutes prior to the start of a trial, allowing prey to access shelter before being exposed to predators. The density of prey used in these mesocosm experiments is consistent with estimates of mud crab abundance on oyster reefs in Southwest Florida (~ 20-40 crabs/m²; Tolley and Volety 2005).

Predators were obtained from hauls made by commercial fisherman caught in baited traps in the Tampa Bay vicinity. Since blue crab size influences the number of prey items consumed in a given trial (Hill and Weissburg 2013), only adult blue crabs >100 mm carapace width (CW) were used. Blue crabs were stored in 18.9 L plastic buckets with an aerator and starved for 72 h before each trial. The carapace width (cm) of each predator was recorded and only one blue crab was placed in each mesocosm. Once introduced to mesocosms, predators were allowed to forage for 24 h, encompassing the full diurnal period. Individual predators and prey were only used once across all experimental trials.

At the conclusion of each trial, two people independently counted the remaining prey in each mesocosm by thoroughly checking both structure and sand for mud crabs among the replicates (0°: $n = 10$, 45°: $n = 13$, Shape 1: $n = 16$, Shape 2: $n = 10$). If predators died, molted, or refused to eat, the replicate was excluded from analysis. The ability of blue crabs to consume their mud crab prey (i.e., predator foraging success) was measured using prey survivorship, or the number of surviving mud crabs after 24 h divided by the initial number of mud crabs present in each mesocosm ($n = 12$). However, mud crabs were able to access the corners of each mesocosm, presumably reducing predator access to prey items. Thus, prey survivorship is reported as a corrected proportion in this study by removing any mud crabs found above the

mesocosm base at the end of a trial from both the total number of mud crabs recovered and initially present. No differences existed between the uncorrected and corrected statistical analyses (Appendix B).

Field Tethering Experimental Setup

Two tethering experiments were conducted to test whether the 3D interstitial space of shell mimics effects the ability of reef-associated predators to consume tethered mud crabs in the field. Using a similar design to that of the mesocosm experiments, 3D interstitial space was modified by changing either the orientation or internal shape of shell mimics in separate field experiments (Table 1). In the first tethering experiment, 60 mm shell mimics of the same shape were arranged into one of three orientations (0° , 22.5° , or 45°) (Fig. 1A and B), thereby representing three different levels of interstitial space. In the second tethering experiment, 80 mm shell mimics with contrasting internal shapes (Shape 1 or Shape 2) were kept at the same orientation (0°) (Fig. 1C and D), producing structures of different interstitial space.

Both field experiments were conducted using mud crabs tethered to ceramic tiles (0.103 m^2) with a single shell mimic of the appropriate treatment and level attached by the umbo to the corner of ceramic tiles with epoxy putty. Each tether consisted of a 7.6 cm long section of monofilament line (2.79 kg test) attached to the top of each prey item's carapace using super glue. All tethers were attached to mud crab prey in the laboratory at least one day prior to experimentation and individual mud crabs were maintained in separate plastic containers until use. A metal stake and hollow, plastic bead were used to secure the free end of the monofilament line to the center of each square ceramic tile, preventing prey items from using any structure other than the artificial shell provided. Mud crabs (10-16 mm CW) were collected by hand 3 d

before each experiment from the same intertidal oyster reef from which *E. depressus* was collected for use in the mesocosm experiments.

The first and second tethering experiments were conducted on the same oyster reef in upper Tampa Bay, Florida (28°00.100 N, -82°37.310 W) but on two different dates: 19 September 2014 and 7 December 2015, respectively. Located at the mouth of a tidal creek, this site is characterized by a mosaic of oyster reefs and mangrove islands, interspersed with a loose shell and mud bottom. Tidal exchange is relatively high and salinity typically varies between 10-25 ppt. The faunal community is representative of other oyster reefs described in Southwest Florida (Tolley and Volety 2005), with *E. depressus* as one of the most abundant organisms at this site (S. Hesterberg, *personal observation*). Numerous mud crab predators, primarily sheephead (*Archosargus probatocephalus*) and *C. sapidus*, have also been observed foraging on oyster reefs in the area (S. Hesterberg, *personal observation*). All replicate tiles (0-45°: $n = 35$, Shape 1 and 2: $n = 30$) were haphazardly placed around mean low water (MLW) and separated by at least 0.5 meters to ensure independence.

Additionally, as the composition and abundance of predators may differ seasonally on oyster reefs (Stunz et al. 2010), an additional set of tethered mud crabs with shell mimics at the 45° orientation ($n = 18$) was included in the December experiment. By doing so, these tiles provide a relative comparison of whether predation intensity (i.e., rate of predation, Menge 1978) differed between experiments, representing one potential artifact of tethering designs (Peterson and Black 1994). Since predation intensity is a rate and experiments lasted for the same duration (24 h), differences in prey survivorship between tiles were assumed to be a result of variation in the predator guilds present.

The ability of various reef associated predators to capture the mud crab prey (i.e., predator foraging success) was measured by recording prey survivorship, or the presence or absence of mud crabs on ceramic tiles after 24 h. Observations on whether surviving mud crabs upon recapture were utilizing the shell mimic or tangled around the central stake after 24 h were also recorded. Replicates were excluded from analysis if tiles were missing or overturned, mud crabs molted, or loose oyster shell moved onto the tile providing unintentional refuge. Additionally, the assumption that loss of mud crabs was a result of predation was examined by placing tethered mud crabs in 37.9 L laboratory aquaria without a predator and recording the number of detached and surviving mud crabs after 24 hours. No mud crabs were found dead or detached ($n = 12$).

Statistical Analyses

For all experiments, prey survivorship was identified as a binomial response in the form of x successes (i.e., lived) out of number of initial prey (Warton and Hui 2011). Thus, the effect of 3D interstitial space on prey survivorship in different spatial arrangements was analyzed using generalized linear models (GLM) with either a binomial or a beta-binomial error distribution and subsequent likelihood ratio tests. The beta-binomial error distribution is typically used to model overdispersed counts or proportions (Lensoff and Lancelot 2012). To select the appropriate error distribution, each response variable was fitted using both distributions and the resulting models were compared using corrected Akaike Information Criterion (AICc) scores. The model with the lowest AICc score was then selected.

For mesocosm experiment 1 and both tethering experiments, a binomial error distribution was used to model prey survivorship as a function of either shell orientation or shell shape,

depending upon the experiment. In the second mesocosm experiment, a large reduction in the AICc score was observed when the data were fit with a beta-binomial error distribution ($\Delta\text{AICc} = 108.6$), and thus this distribution was selected to model prey survivorship as a function of shell shape. In both mesocosm experiments, trial was initially included as a predictor in each model, but the blocking factor was removed after being insignificant and the analyses re-run. As predator size is well understood to influence predator foraging success in structured habitats (e.g., Ryer 1988, Hill and Weissburg 2013, Toscano and Griffen 2012, Toscano and Griffen 2013), this study included blue crab size (i.e., carapace width) as an additional predictor in both mesocosm experimental models to assess whether body size influenced the ability of predators to consume mud crab prey. Furthermore, the interaction between spatial arrangement and predator size was also included in both mesocosm experimental models. All analyses were conducted in the R statistical computing environment (R Development Core Team 2015, ver. 3.1.3).

RESULTS

Mesocosm Experiments

The interstitial space of 3D printed shell mimics affected the ability of blue crab predators to consume their mud crab prey in both spatial arrangements (Fig. 2). A significant effect of shell orientation on mud crab survivorship was observed in the first mesocosm experiment (Fig. 2A; $df = 1$, $\chi^2 = 79.29$, $P < 0.001$). Mean ($\pm$ SE) proportional survivorship was highest for mud crabs in shell mimics of 0° orientation, with 86.0% (± 4.0) of prey surviving, compared to only 27.0% (± 6.0) of prey surviving in shell mimics with 45° orientation. A significant effect of shell shape on mud crab survivorship was also observed in the second mesocosm experiment (Fig. 2B; $df = 1$, $\chi^2 = 17.81$, $P < 0.001$), as mean proportional survivorship of mud crabs was lower in Shape 1 than Shape 2 (54.0% $\pm$ 11.0 and 95.0% $\pm$ 2.0, respectively). Survivorship outcomes were highly variable in the Shape 1 treatment, with the majority of data points clustering either near 0 or 100% survivorship (Fig. 2B). Only one mud crab died during the “No-predator” control trials ($n = 16$), suggesting that the loss of prey items in mesocosm experiments was due to blue crab consumption.

Neither predator size nor the interaction between spatial arrangement and predator size influenced the ability of blue crabs to consume their mud crab prey in either mesocosm experiment (Appendix C). Width of blue crab carapaces ranged between 114.6 and 197.1 and 126.4 and 164.5 mm for the first and second mesocosm experiment, respectively, but was not a significant predictor of predator foraging success in either model ($df = 1$, $\chi^2 = 0.16$, $P = 0.690$

and $df = 1$, $\chi^2 = 2.63$, $P = 0.1049$, respectively). Furthermore, the interaction terms were insignificant in the first and second mesocosm experiments as well ($df = 1$, $\chi^2 = 3.13$, $P = 0.077$ and $df = 1$, $\chi^2 = 0.006$, $P = 0.981$, respectively).

Figure 2. Mean proportional survivorship ($\pm$ SE) of *Eurypanopesus depressus* prey after 24 h in mesocosms with a decapod predator and 3D printed oyster shell mimics of different (A) orientation [0° ($n = 10$) and 45° ($n = 11$)] or (B) shape [Shape 1 ($n = 16$) and Shape 2 ($n = 10$)]. See Table 1 for information on relationship between spatial arrangement and 3D interstitial space.

Field Tethering Experiments

The interstitial space of shell mimics influenced the survivorship of tethered mud crabs only when shell orientation varied (Fig. 3). Specifically, survivorship of tethered prey was significantly affected by shell orientation in the field, with approximately 75.8, 12.5, and 0% proportional survivorship in the 0°, 22.5°, and 45° levels of the orientation treatment, respectively (Fig. 3A; $df = 2$, $\chi^2 = 54.00$, $P < 0.001$). All deployed tethers in this first field tethering experiment were recovered after 24 h, and one mud crab was found tangled upon recapture. While no crabs were recovered from the 45° shell mimics, 96.0% were using the shell structure upon recapture in the 0° orientation and 25.0% in the 22.5° orientation. In the second tethering experiment, survivorship of tethered prey was not significantly affected by shell shape, with approximately 88.5 and 96.4% proportional survivorship of mud crabs in shell mimics of Shape 1 and 2, respectively (Fig. 3B; $df = 1$, $\chi^2 = 1.29$, $P = 0.255$). All deployed tethers were recovered after 24 h, and three mud crabs were found tangled upon recapture. Of the mud crabs recovered, 91.3% were using the shell structure upon recapture in Shape 1 and 88.9% in the Shape 2 level.

The inclusion of shell mimics with 45° orientation in the second tethering experiment provided evidence of predators consuming tethered prey, but not to the same intensity that was observed in the first tethering experiment, in which no mud crabs survived (Fig. 3A). A total of 26.7% of mud crabs initially tethered onto tiles with 45° shell orientation ($n = 15$) were recovered after 24 h. No deployed tethers were lost and three mud crabs were found tangled upon recapture. Of the mud crabs recovered ($n = 5$), none were using the shell structure in this control treatment.

Figure 3. Proportional survivorship of tethered *Eurypanopesus depressus* placed on an intertidal oyster reef in Tampa Bay, FL after 24 h with a 3D printed oyster shell mimic of different (A) orientation [0° ($n = 33$), 22.5° ($n = 32$), 45° ($n = 27$)] or (B) shape [Shape 1 ($n = 26$) and Shape 2 ($n = 28$)]. See Table 1 for information on relationship between spatial arrangement and 3D interstitial space.

DISCUSSION

Identifying which properties of a structure mediate the ability of predators to consume their prey has the potential to expand discussion of predator-prey interactions and help develop a habitat structure metric that captures the 3D arrangement of structural components in space for which predator-prey outcomes are often dependent. A number of studies investigating trophic interactions in structured habitats have alluded to the importance of crevices, holes, or space as refugia from predation (e.g., Bartholomew et al. 2000, Almany 2009, Horinouchi et al. 2009, Toscano and Griffen 2013), but these investigations almost exclusively view interstitial space as a 2D attribute, measuring only the linear space within or between structural components (e.g., Bartholomew et al. 2000, Almany 2009, Horinouchi et al. 2009, Humphries et al. 2011, Wong 2013). Despite the recognized limitations of using a 2D perspective to predict predator-prey outcomes (Humphries et al. 2011), and the suggested potential value of viewing these interactions in a 3D context (Toscano and Griffen 2013), a rigorous three-dimensional evaluation of whether interstitial space mediates predator-prey outcomes independent of other spatial properties, specifically density, had not been conducted to date. Using a novel technology (i.e., 3D printing mimics) this study demonstrated that altering the 3D interstitial space of identical structural components in two possible ways natural oyster shells can vary spatially (i.e., orientation and shape) strongly influences the ability of certain reef-associated predators to consume their space-utilizing prey.

Evidence to support the importance of 3D interstitial space as refugia from predators was generally consistent across the experimental trials. When the 3D interstitial space of structural components were manipulated in mesocosms, blue crab foraging success was significantly modified in both spatial arrangements (Fig. 2). Blue crabs consumed more mud crab prey in trials with shell mimics oriented at 45° compared to those at 0° (Fig. 2A) and these findings were consistent with the changes in 3D interstitial space observed between orientation levels. Although interstices became larger in size with increasing angle, they also became more shallow (i.e., length decreased) and open (i.e., height increased) (Table 1), suggesting a greater ability of blue crabs to detect and access mud crabs utilizing the interstices of the 45° shell mimics. Predator foraging success was also altered when the 3D interstitial space of structural components varied by shell shape. Interestingly, the Shape 1 and 2 interstices did not differ in their size, only their interstitial space shape (Table 1). Shape 1 possessed a more shallow and wider space than Shape 2, which corroborated the reduction in predator foraging success observed in the Shape 2 interstice (Fig. 2B). Together, these mesocosm experiments not only demonstrate that interstitial space mediates the ability of blue crabs to consume their mud crab prey, but also that the three-dimensional nature of this spatial attribute is a critical aspect for predicting the outcome of interactions between this particular predator and prey. Interestingly, if a 2D measurement of space opening (i.e., width or height) had been used instead of a three-dimensional perspective (e.g., Bartholomew et al. 2000), little to no difference in the interstitial space of these components would have been observed (Table 1), resulting in a significant reduction of such a measure's predictive power.

The striking variation in blue crab foraging success in the second mesocosm experiment is notable, as predators consumed either nearly all mud crabs in the Shape 1 level or none at all

(Fig. 2B). Given that predator size and the interaction term were not significant predictors in this study (Appendix C), predators were used only once, starved for the same amount of time, and blue crabs consistently consumed mud crabs in other mesocosm treatments (see Fig 2A), the observed dichotomy of response is likely due to some unmeasured individual variation within blue crab predators that caused intraspecific differences in foraging success. Although not quantified, some blue crabs were observed to be more aggressive or active than others (S. Hesterberg, *personal observation*). Behavioral syndromes, or “personality types,” refer to suites of correlated behaviors (e.g., aggression) across populations or species (Sih et al. 2004). These personality differences amongst individuals have been suggested to influence predator-prey interactions through consumptive and non-consumptive pathways (Griffen et al. 2012, Toscano and Griffen 2014) and even alter community structure in mesocosms (Royauté and Pruitt 2015). It is possible that an interaction between predator personality and 3D interstitial space was observed, with more aggressive and/or active blue crabs having an increased chance of encountering and/or detecting mud crab prey utilizing the interstices provided by the Shape 1 structures. Irrespective of the mechanism, these results are noteworthy because they suggest that even the same interstice (e.g., Shape 1) may result in different predator-prey outcomes depending on the traits of an individual predator or prey.

The relationship between 3D interstitial space and prey survivorship of tethered mud crabs in the field mostly corroborated the mesocosm experimental findings, except in the second tethering experiment. Although a strong effect of interstitial space was observed on mud crab survivorship when shell orientation varied (Fig. 3A), no significant effect of the interstitial space provided by shell shape on prey survivorship was detected in the December field experiment (Fig. 3B). These unexpected findings may have been an artifact of generalizing an interstice’s

refuge potential across a range of different predator-prey interactions in the field. Numerous studies have shown that prey consumption in structured habitats depends on predator identity and the body size of both predator and prey, with some species or sizes performing better in the same structure than others (Ryer 1988, O’Conner et al. 2008, Horinouchi et al. 2009, Toscano and Griffen 2012, Hill and Weissburg 2013, Toscano and Griffen 2013, Carroll et al. 2014, Klecka and Boukal 2014). Although predators were known to be present based upon field evidence, the results from shell mimics at the 45° orientation in the second tethering experiment provided evidence that predation on mud crabs was proportionally unequal between the September and December experiments, suggesting differences in the abundance, size, and/or composition of reef-associated predators (i.e., comparison of 26.7% [45°, exp.2] to 0% [45°, Fig. 3A] survivorship). Given the specificity of predator-prey interactions in structured habitats, it is possible that the Shape 1 and 2 interstices were not sufficiently different with respect to prey detection or access for any of the predator species or sizes present on that particular day.

One challenge of this study was to describe the 3D interstitial space of the structural components. To date, a single three-dimensional measurement of interstitial space for predator-prey interactions has not been developed, presumably due to the limited techniques available to model 3D components rapidly in the field. Although this study does not provide a new metric, these findings can help inform method development. Specifically, this study suggests that when assessing the refuge potential of a 3D interstitial space a measure must simultaneously capture both an interstice’s size and shape. This follows from the finding that the interstitial space shape of shell mimics alone was sufficient to influence the ability of blue crab predators to consume their mud crab prey in the second mesocosm experiment independent of interstitial space size (Table 1, Fig. 2B). Studies have proposed measuring the variation in a spatial attribute, such as

interstitial space size, to predict faunal distribution patterns (e.g., St. Pierre and Kovalenko 2014), but this approach may fail if species abundance and richness are strongly determined by predation, especially if interstitial space shape is ignored.

Instead, a single metric that can capture some aspect of interstitial space size (i.e., whether a space is habitable) along with the 3D shape of an interstice (i.e., whether a space is accessible given the identities of both predator and prey) would be a valuable assessment of refuge potential. For example, Finsted et al. (2007) used flexible PVC tubes of different diameters to count the number and size of interstitial spaces available to juvenile Atlantic salmon in streambeds. Only spaces deeper than 3 cm (fish body length) were counted, representing a 3D scale for the organism in question. Expansion of this measurement could relate the various PVC sizes to different predator morphologies, providing a rough estimate of the number of interstices locally abundant predators could access. Furthermore, 3D modeling of structural components using X-ray computed tomography (CT) and subsequent image reconstruction might assist with method development. Non-destructive CT scanning of corals and kelp holdfasts has already been utilized to calculate spatial properties, including volume (Laforsch et al. 2008, Orland et al. 2016). Use of novel techniques, such as 3D modeling, combined with a species-specific measurement approach as described above (e.g., Finsted et al. 2007) could help advance efforts to quantify 3D interstitial space and assess refuge potential. While this study worked with a relatively simple arrangement of structural components, use of CT technology should allow similar efforts in more complex settings.

Understanding how habitat structure modifies predator-prey interactions will improve our ability to decipher the mechanisms by which ecological communities are structured. This study adds to the current knowledge of how habitat structure modifies predator-prey interactions by

demonstrating that the three-dimensional interstitial space created from the spatial arrangement of structural components mediates the ability of a common reef-associated predator to consume its prey independent of the widely studied density attribute. By doing so, this study identifies a spatial attribute that bridges the gap between the common 3D spatial arrangements of oyster shells found in nature (i.e., orientation and shape) to measure habitat structure in a way that is relevant for predation. Moreover, these findings suggest that such a measure should be three-dimensional, capture both the size and shape of an interstice, and scaled to the specific predator-prey interaction in question. Inadvertently, these results also corroborate an increasing number of studies that highlight the importance of predator identity and individual variation for trophic interactions (O’Conner et al. 2008, Griffen et al. 2012, Carroll et al. 2014, Toscano and Griffen 2014, Royauté and Pruitt 2015) and suggest that knowledge of behavior is essential to interpreting the role of habitat structure in mediating predator-prey outcomes.

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APPENDIX A:

***EURYPANOPEUS DEPRESSUS* SIZE DISTRIBUTION FROM TAMPA BAY, FLORIDA**

Eurypanopeus depressus were obtained for size measurements by haphazardly collecting oyster clumps from three different field sites along the salinity gradient of Tampa Bay, FL (28.006668N, -82.618672W; 27.843938N, -82.61178W; 27.594312N, -82.596167W). Each site was sampled monthly for five oyster clumps between June and September 2014, for a total sample of 15 oyster clumps per site. Oyster clumps were immediately placed into plastic bags, returned to the laboratory, and frozen until further use. To obtain mud crabs, oyster clumps were disassembled and searched thoroughly for mud crabs. All xanthid species were identified and carapace width (CW) measured in mm using vernier calipers. Over the course of four months, a total of 900 *E. depressus* were measured with a mean ($\pm$ SD) carapace width of 6.71 ± 2.93 (Fig. A1). The sizes selected for our experiments (10-16 mm CW) is within the natural size range found in Tampa Bay, FL and represents approximately 15% of the total distribution. However, adult *E. depressus* are considered > 6 mm CW (McDonald 1982).

Figure A1. Carapace width (CW) of *Eurypanopeus depressus* (i.e., mud crabs) sampled from oyster reefs in Tampa Bay, Florida ($n = 900$). The dashed line represents the sample mean ($\pm$ SD) of the distribution (6.71 ± 2.93). The size range used in all experiments was between 10-16 mm CW.

APPENDIX B:
**UNCORRECTED SURVIVORSHIP DATA AND ANALYSES FROM MESOCOSM
EXPERIMENTS**

Similar to corrected analyses, comparison of model AICc values indicated that a binomial error distribution was most appropriate to model uncorrected prey survivorship as a function of shell orientation for the first mesocosm experiment and a beta-binomial was most appropriate to model uncorrected prey survivorship as a function of shell orientation for the second mesocosm experiment. It should be noted that AICc values were reduced when survivorship data were corrected (exp.1: $\Delta\text{AICc} = 15.43$, exp. 2: $\Delta\text{AICc} = 6.20$).

Statistical results were no different than analyses with corrected data. A significant effect of shell orientation on prey survivorship was observed for the first mesocosm experiment (Fig. A2A; $\text{df} = 1$, $\chi^2 = 33.14$, $P < 0.001$). Mean proportional survivorship ($\pm$ SE) was highest in the 0° orientation level, with $87.0\% \pm 4.0$ of prey surviving, compared to $54.0\% \pm 7.0$ of prey surviving at the 45° orientation (Fig. A2A). Furthermore, predator size and the interaction term were not significant predictors of survivorship in the first mesocosm experiment ($\text{df} = 1$, $\chi^2 = 0.02$, $P = 0.885$ and $\text{df} = 1$, $\chi^2 = 3.16$, $P = 0.075$, respectively). A change in results was most notable for the 45° orientation level in the first mesocosm experiment. The mean increased by 27% compared to the corrected mean due to a disproportionate number of prey items found on the side of the tank in this treatment (39%) compared to $< 8\%$ in all other treatments.

In the second mesocosm experiment, a significant effect of shell shape on prey survivorship was also observed (Fig. A2B; $\text{df} = 1$, $\chi^2 = 16.71$, $P < 0.001$). Mean proportional

survivorship ($\pm$ SE) was lower in Shape 1 than Shape 2 ($55.0\% \pm 10.0$ and $95.0\% \pm 2.0$, respectively), with the same variable pattern in the Shape 1 treatment (Fig. A2B). Also, predator size and the interaction term were not significant predictors of mud crab survivorship in the second mesocosm experiment ($df = 1, \chi^2 = 3.52, P = 0.061$ and $df = 1, \chi^2 = 0.005, P = 0.946$, respectively).

Figure A2. Mean proportional uncorrected survivorship ($\pm$ SE) of *Eurypanopesus depressus* prey after 24 h in mesocosms with a decapod predator and 3D printed oyster shell mimics of different (A) orientation [0° ($n = 10$) and 45° ($n = 11$)] or (B) shape [Shape 1 ($n = 16$) and Shape 2 ($n = 10$)]. See Table 1 for information on relationship between spatial arrangement and interstitial space.

APPENDIX C:

RELATIONSHIP BETWEEN PREDATOR SIZE AND PREY SURVIVORSHIP IN MESOCOSM EXPERIMENTS

Figure A3. Correlation between proportional survivorship of *Eurypanopesus depressus* and predator size as measured by carapace width in mesocosms with 3D printed oyster shell mimics of different shell (A) orientation or (B) shape.