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Erica Valdez  
*DePaul University, Evaldez4@mail.depaul.edu*

Danielle N. Araiza  
*DePaul University, daraiza1@mail.depaul.edu*

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Size-, Side- and Site-Related Predation of Naticid Gastropods on Dwarf Surf Clams (*Mulinia lateralis*) and Incongruous Ark Clams (*Anadara brasiliana*) on The Atlantic Coast

Erica Valdez* and Danielle N. Araiza*
Department of Biological Sciences

ABSTRACT Naticid gastropods are common predatory mollusks in marine systems where they feed on bivalve mollusks. Predation involves boring a hole through the shell of the prey, which provides the opportunity for beach collections of shells to be used to determine feeding preferences of predators in nature. We examined whether naticids exhibited preferences for prey size, valve side (left vs. right) and valve site (location on the shell) and whether these preferences differed between prey species (*Mulinia lateralis*, dwarf surf clam; *Anadara brasiliana*, incongruous ark clam). Random samples of *A. brasiliana* and *M. lateralis* were collected from Otter Island, South Carolina and preferences for body size, valve site, and valve side determined. We found that predators feeding on *M. lateralis* exhibited preferences for body size, valve site and valve side. In contrast, predators feeding on *A. brasiliana* exhibited preferences for body size and valve site but not valve side. These results indicate that predators appear to adopt species-specific feeding strategies, which are likely shaped by variation in the benefits and costs associated with feeding on the different prey types.

INTRODUCTION

Naticid gastropods are aquatic mollusks that regulate community dynamics in marine systems by feeding on multiple species of bivalve prey (Chiba & Šato, 2011; Figure 1). These predators feed by boring through the shell, using a radula, which results in a characteristic borehole on the shell of predated bivalves (Kelley, 1991).

This radula grows proportionally with the body size of the predator and as a result can be used to gain insights into the size-related feeding preference of naticids in their natural environment (Dietl & Alexander, 1995, Grey et al., 2005, Clements et al., 2013).

The presence of boreholes on naturally-predated shells has provided insights into a variety of topics including co-evolution, cannibalism, and selective predation based on prey size, valve side (left vs. right) and valve site (borehole location on the shell) (Kitchell et al. 1981; Kelley, 1991, 1992; Dietl & Alexander, 1995; Hasegawa & Šato, 2009).
Several previous studies have demonstrated feeding preferences of naticid gastropods in experiments with a single prey species (Dietl & Kelley, 2006). The research presented here builds on this information by examining the feeding preferences of naticid gastropods in a natural community containing multiple prey species. We focused on the two most common prey species to examine these relationships, which were the dwarf surf clam (*Mulinia lateralis*) and the incongruous ark clam (*Anadara brasiliana*). The following questions were examined in this study: Do naticid gastropods exhibit size-, side- (left or right valve) and site-selectivity (location on the shell) on *A. brasiliana* and *M. lateralis* and do these preferences differ between the prey species? Predatory preferences for size have been proposed as a strategy to maximize the benefits obtained from feeding on larger prey with the costs associated with boring through thicker shells (Kitchell et al., 1981). Preferences for both the site on the shell and the side of the shell have been proposed to be associated with the likelihood that predation is successful (Hasegawa & Sato, 2009).

First, it was predicted that there would be high site-selectivity near the umbo based on previous studies. Therefore, we wanted to determine if our data aligned with the results of other studies to determine the generality of this relationship. Secondly, based on optimal foraging theory larger predators are expected to exhibit preferences for larger prey. Thirdly, predated valve side was explored to investigate if predators exhibited side-selectivity on different prey species. Overall, we wanted to determine if there was species-specific difference to understand the dynamics of naticid gastropods in their natural environment.

**METHODS**

Random samples of bivalves were collected from Otter Island, South Carolina during December 2013 and December 2014. The shells were identified to species-level and separated based on the presence of successful boreholes. Weathered and cracked shells were removed, to increase accuracy of the measurements. For each shell that possessed a borehole, length and outer borehole diameter were recorded from a random sub-sample of 100 *M. lateralis* and 100 *A. brasiliana*.

*Mulinia lateralis* (dwarf surf clam)

Dwarf surf clams (n=469) were sorted, identified (Abbott, 1974), and placed into labeled vials. A random sub-sample of 100 shells was then obtained from the larger sample. Each shell was observed under a dissecting microscope (Leica MZ12) and length was recorded. The side of the clam that contained the borehole was determined by categorizing the shell as either the left or right valve. Side preference was assessed by comparing the frequency of attacks on each side to the values expected if there was no preference using a $\chi^2$ goodness-of-fit test.

Site-selectivity was investigated using a method outlined in Chiba & Sato (2011, Figure 2a). For the procedure, the shell was divided into nine zones that are relatively equal in size. Site-selectivity was analyzed by observing the location of the boreholes on the shell and comparing it to the expected values if feeding was random ($\chi^2$ goodness of fit test).

To determine whether a size preference occurred that was associated with the size of the predator, we measured the outer borehole diameter of each shell using a Leica MZ12 microscope. Due to the slight non-circularity of the boreholes, two measurements were obtained per borehole (one horizontal, one vertical). The average value was calculated obtained from these two measurements. A linear regression analysis was used to determine if borehole size (a measure of predator size) was a predictor of prey size (shell length).

*Anadara brasiliana* (incongruous ark clam)

Incongruous ark clams (n=134) were collected on December 2013 (n=78) and December 2014 (n=56). They were sorted and identified (Abbott, 1974). A random number generator was used to obtain a sub-sample of 100 shells from the larger sample (Urbiniak and Plous, 2008). Valve size and valve preference was analyzed as above. Borehole site was recorded using a modified zoning method, Figure 2b, created with narrower zones radiating from the valve hinge. It was necessary to design a zoning guide for the ark shells because they differ in morphology from *M.*
Lateralis. Site-selectivity was analyzed as above. Analyses of the borehole diameters were based on digital images obtained using a digital microscope (VT300). Borehole diameter was measured from each image using Image J software (two measurements per borehole), and shell length was recorded using calipers. Morphology difference between species, called for method difference, which provided more accurate borehole measurements.

RESULTS

Analysis of borehole site locations revealed that boreholes were not randomly distributed for either species (M. lateralis, \( \chi^2_s = 782, p < 0.05 \); A. brasiliana, \( \chi^2_s = 210, p < 0.05 \)). In both cases, the boreholes were located on the umbo, which is the curved region that is closest to the bivalves’ hinge. For M. lateralis 99% of boreholes were located on zone two (figure 1a). Similarly, for A. brasiliana, 81% of boreholes were located within zone one, two, and three, all of which are located on the umbo. Thus, there was a valve site preference by the naticid predators for each prey species.

Analysis of valve side preference revealed that there was a side preference for M. lateralis (\( \chi^2_1 = 13.0, p < 0.05 \)) but not for A. brasiliana (\( \chi^2_1 = 1.4, p > 0.05 \)). For M. lateralis, boreholes were more likely to be found on right valves (68%) than left valves (32%). For A. brasiliana, 56% of boreholes were on the right valve and 44% were on the left. Thus, there was species-specific preference for valve side by the naticid predators.

The relationships between prey size and borehole diameter are shown in Figure 3. For both prey species, borehole size (an indicator of predator size) was a predictor of prey size (M. lateralis: \( y = 0.18x + 1.15 \); A. brasiliana: \( y = 0.10x + 0.97 \)). This relationship was stronger for A. brasiliana than for M. lateralis.

DISCUSSION

The results indicated a relationship between prey size and borehole size, which revealed that larger predators preferentially feed on larger prey. This relationship has been explained as an energy-maximizing strategy that balances the energy payoff associated with large food items with the energy costs associated with capturing and boring through a large prey item (Kitchell et al., 1981). The results presented here also revealed that the strength of this relationship appeared to differ between prey types, which may indicate that the preferences are also somewhat specie-specific.

Preferences for valve site have been demonstrated in several naticid-bivalve interactions (Kitchell et al., 1981; Chiba & Sato, 2011). In general, it has been proposed that the valve site selectivity occurs because the predators exhibit a stereotypical method of handling and feeding on bivalve prey which results in an orientation that favors stereotypical feeding locations (Chiba & Sato, 2011). Exceptions to this site-specificity typically occur only when the predator to prey size ratio is mismatched. The results obtained here are consistent with this type of explanation, since the drilled holes were commonly observed around the umbo of each bivalve. In Figure 3 the size relationship between predator and prey could be observed as being correlated.

In contrast to preferences for valve side, preferences for valve sides are not common in naticid-bivalve interactions. When side preferences do occur they appear to be due to an interaction between the morphologies of the predators and prey, which favor feeding on a specific side of the prey to ensure that predation is successful (Hasegawa & Sato, 2009). The results obtained here showed that a side preference occurred for the dwarf surf clam but not for the incongruous ark clam. Comparison of the shell shape of the two species revealed that the shell of a dwarf surf clam has an asymmetry that is not present in the incongruous ark clam. This type of asymmetry could potentially favor a side preference. Future studies that incorporate behavioral analyses are necessary to determine the potential significance of this relationship.

Naticid predators feeding on different bivalve species exhibited consistent borehole site preferences but differed in their preferences for valve side and varied in the strength of the relationship between predator size (borehole size) and prey size. These results indicate that naticid predators appear to adopt species-specific feeding strategies. This type of species-specific effect is likely to be shaped by variation in the
benefits and costs associated with feeding on the different prey types.
Overall, our results show that patterns identified in previous studies on naticid-bivalve interactions are generally consistent with the relationships present in the Otter Island community. However, the results also reveal that the relationships differ between prey types. This type of variation can potentially influence both population and community dynamics in natural marine systems.

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REFERENCES


Figure 1. a) Common naticid gastropod found locally in South Carolina, (b, c) the focal prey species

a) Atlantic Moonsnail
   *Neverita duplicata*

b) Dwarf surf clam
   *Mulinia lateralis*

c) Incongruous ark
   *Anadara brasiliana*
Figure 2. Borehole zoning system for (a) *Mulinia lateralis* (dwarf surf clam) and (b) *Anadara brasiliana* (incongruous ark)
Figure 3. Relationship between prey length and predatory borehole size for (a) *M. lateralis* (n=100) and (b) *A. brasiliana* (n=100). Note that the axis scales are different on the panels for each species.