PATTERNS OF GASTROPOD MOLLUSK PREDATION ON BIVALVE MOLLUSKS ALONG THE UPPER TEXAS GULF COAST

Serena J. Randolph* and Alan D. Maccarone
Department of Biology, Friends University
Wichita, Kansas 67213
**Corresponding author; Email: serena_randolph@student.friends.edu*

Abstract.–Predation on bivalve mollusks by gastropod mollusks is common in coastal regions of the United States; however, few previous studies have examined whether drilling gastropods exhibit prey selection. In 2016, shells with small holes drilled by as many as two gastropod predators were collected at three sites separated by 30 km along the Texas Upper Gulf Coast on the Bolivar Peninsula (29° 40'N, 94° 90'W). The likeliest predators in these waters are the southern oyster drill (*Stramonita haemastoma* Linnaeus 1767) and the moon snail (*Neverita duplicate* Say 1822). Collected shells were identified to species and measurements were taken to examine statistical relationships between predators and prey species. These measurements included drill-hole diameter, shell thickness, drill-hole completeness, number of drill attempts, and collection site. Across the three locations, 17 different species of shells with drill holes were collected; of these, we focused on the ten most abundant species ($n = 277$ shells). The sample showed high variation in drill-hole diameter, shell thickness, and drill-hole completeness. Both the total number of holes and mean drill-hole diameter differed significantly among prey species (ANOVA, both $P < 0.0001$). In addition, drill-hole diameter correlated directly with prey shell thickness ($P < 0.0001$). Shells whose drill holes were complete were significantly thinner than shells with incomplete holes ($P < 0.0001$). Mean prey shell thickness, mean drill-hole diameter, and mean number of drill holes all differed significantly by collection site (all $P < 0.0001$). Ecological and morphological implications related to gastropod predation on mollusks are discussed.

Key words: bivalve, gastropod, predation patterns, Bolivar Peninsula, Texas

---

Phylum Mollusca comprises one of the most diverse of all animal groups. Their soft unsegmented bodies have allowed mollusks to evolve into an array of forms, which has enabled them to exploit many different habitats and food resources (Gilpin 2006). Predation on bivalve mollusks by gastropod mollusks is common in coastal regions; however, few studies have examined whether predatory gastropod mollusks exhibit prey selection. Despite limited previous research into the feeding patterns of predatory mollusks, their anatomical features have provided insight into how these predators select their prey. For

Recommended citation:
Randolph, S.J. & A.D. Maccarone. 2018. Patterns of gastropod mollusk predation on bivalve mollusks along the upper Texas Gulf Coast. Texas J. Sci. 70: Article 5.
https://doi.org/10.32011/txjsci_70_1_Article5.

example, Tunnel et al. (2010) showed that the Southern oyster drill (*Stramonita haemastoma* Linnaeus 1767) is an important predator of oysters and other bivalves in coastal habitats. Similarly, the moon snail (*Neverita duplicate* Say 1822) is an abundant generalist that inhabits shallow intertidal to subtidal habitats and feeds primarily on infaunal bivalves. The presence of drilling mollusks in an area is confirmed by small holes created mechanically by the radula and chemically by secretions that soften the shell. Once the hole has been bored all the way through, the snail slides its extensible proboscis through the hole to ingest the prey's soft tissue.

The mechanisms that allow molluscan predators to function dictate how these predators select their prey. Brown and Richardson (1988) examined the effect of shell size and the spatial density of bivalves (mussels and oysters) on the foraging behavior of *S. haemastoma,* and found a direct relationship between size of predator and preferred prey species. Foraging efficiency, as measured by handling time and profitability, was higher for some prey species than for others. Therefore, they suggested that prey selection by *S. haemastoma* is constrained by the size of the oyster drill as well as predator density.

To better understand molluscan prey selection, 277 shells were collected and examined from three collection sites along the Texas Upper Gulf Coast on the Bolivar Peninsula (29º 40'N, 94º 90'W) to test the hypothesis that drilling gastropods exhibit prey selection. If this is true, it is predicted that some prey species would be overrepresented in the random sample, while other common species would be underrepresented. In addition, it was predicted that the number and diameter of drill holes would correlate with other measures of prey species, such as size and shell thickness. Key to this assumption was that the diameter of a drill hole is correlated with predator radula diameter and therefore with the size of the predator.

STUDY AREA & METHODS

In May 2016, three collection sites along 30 km of beach were established along the Texas Gulf Coast on the Bolivar Peninsula (Fig.

https://doi.org/10.32011/txjsci_70_1_Article5

1). At each collection site, shells were selected randomly along the intertidal zone to determine relative species abundance. Collected shells with one or more drill holes were examined to determine patterns of prey selection. All sampled shells were identified to species (Morris 1975; Rothschild 2004; Wye 2014). For each shell with drill holes, the following measurements were taken: shell thickness (in mm), drill-hole diameter (in mm), number of drill holes, and whether the holes were complete or incomplete. Calipers were used to measure shell thickness. To measure drill-hole diameter, each shell was placed on a dissecting microscope stage and the hole was measured with a mm rule. Collected shells bore the holes of as many as two different species of drilling mollusks. The only species of boring sponge found in the study area is *Cliona celata*; however, the holes created by boring sponges can easily be distinguished from those created by the molluscan predators examined in our study.

The ten most abundant prey species ($n = 8$ or more individuals) were used for statistical analysis to examine patterns of prey selection. All measured variables met the conditions for normality, so ANOVA was used to compare shell thickness, the number of drill holes, and drill-hole diameter by prey species. ANOVA also compared drill-hole diameter and the number of drill holes by collection site, as well as shell thickness and drill-hole diameter in shells with complete versus incomplete holes. Pearson's correlation examined the relationship between shell thickness and drill-hole diameter, and Chi-square compared relative species abundance in a random sample of 300 shells and in the 288 predated shells. For this test, the number of individuals of each bivalve species collected randomly along the beach was compared to the number of individuals of those same species collected specifically with bore holes. Chi-square also compared (1) the relative abundance of prey species and drill-hole completeness by collection site and (2) drill-hole completeness by species. For these tests, each shell collected specifically with one or more holes was assigned to its collection site (Rollover Bay, Crystal Beach, or Bolivar Flats), and also to either the "complete hole" or "incomplete hole" category.

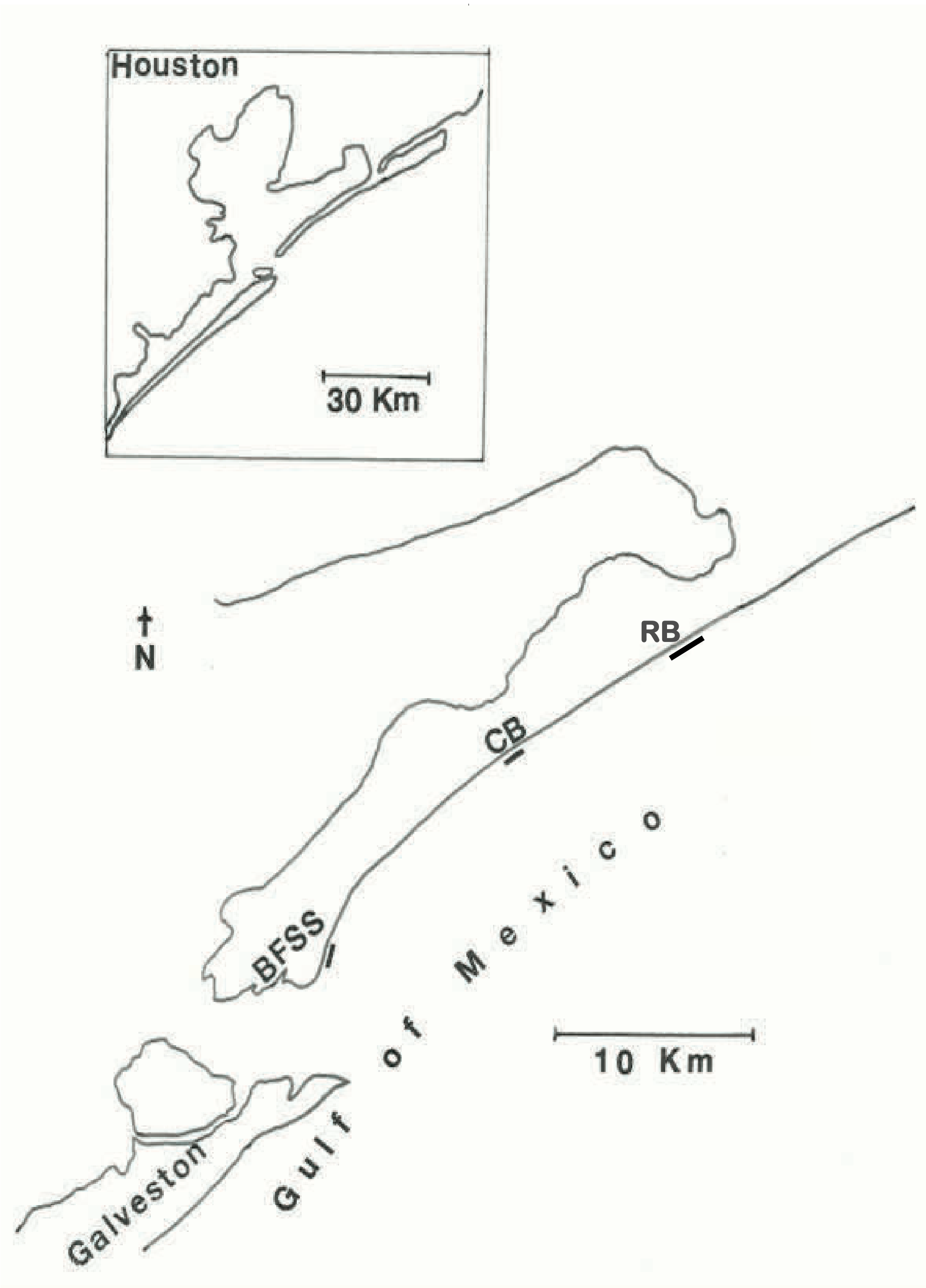

Figure 1. Study area (inset) and map of Bolivar Peninsula showing the three collection sites (separated by approximately 30 km) along the Upper Gulf Coast beach. RB = Rollover Bay, CB = Crystal Beach, and BFSS = Bolivar Flats Shorebird Sanctuary.

https://doi.org/10.32011/txjsci_70_1_Article5

RESULTS

A total of 572 shells of 17 different species were collected across the three sites, but only 10 species were abundant enough for statistical analysis. These species were Eastern oyster (*Crassostrea virginica*), Atlantic rangia (*Rangia cuneata*), ponderous ark (*Noetia ponderosa*), blood ark (*Anadara ovalis*), incongruous ark (*Anadara brasiliana*), unequal spoonclam (*Periploma margaritaceum*), channeled cuck clam (*Raeta plicatella*), moon snail (*Neverita duplicata*), Florida fighting conch (*Strombus alatus*), and dwarf surf clam (*Mulinia lateralis*). Sample sizes for seven other species were too small for statistical analysis. These were the lightning whelk (*Busycon perversum pulleyi*), disk dosinia (*Dosinia discus*), variable coquina (*Donax variabilis roemeri*), transverse ark (*Anadara transversa*), Texas quahog (*Mercenaria texana*), razor clam (*Tagelus plebeius*), and Florida cross-barred venus (*Chione elevata*) (Fig. 2).

In the random sample of 300 shells, 89 shells showed drill holes and 211 did not. However, there was a species-specific predation pattern ($\chi^2 = 64.6$, df = 15, $P < 0.001$; Fig 2). Three species (disk dosinia, moon snail, and dwarf surf clam) showed significantly higher than expected predation based on the number of shells collected for each species, whereas predation on Atlantic rangia was significantly lower than expected. For a different set of 272 shells collected specifically with drill holes, all species showed high variation in drill-hole diameter, shell thickness, number of drill holes, and drill-hole completeness (Fig. 3). Mean drill-hole diameter ranged from 1.10 mm in the dwarf surf clam to 2.85 mm in the Eastern oyster ($F = 15.2$, df = 9 & 263, $P < 0.0001$; Fig. 4). Mean shell thickness ranged from 1.80 mm to 3.90 mm in these same two species ($F = 55.7$, df = 9 & 263, $P < 0.0001$). The mean number of drill holes per shell ranged from 1.0 in three different species to a high of 4.6 in the Florida fighting conch ($F = 9.1$, df = 9 & 262, $P < 0.0001$). Drill-hole completeness ranged from 50% in the Florida fighting conch to 100% in six other species ($\chi^2 = 90.2$, df = 9, $P < 0.0001$). Drill-hole diameters correlated significantly with shell thickness ($r = 0.43$, df = 273, $P < 0.0001$), suggesting mollusks with larger drills selected larger prey.

https://doi.org/10.32011/txjsci_70_1_Article5

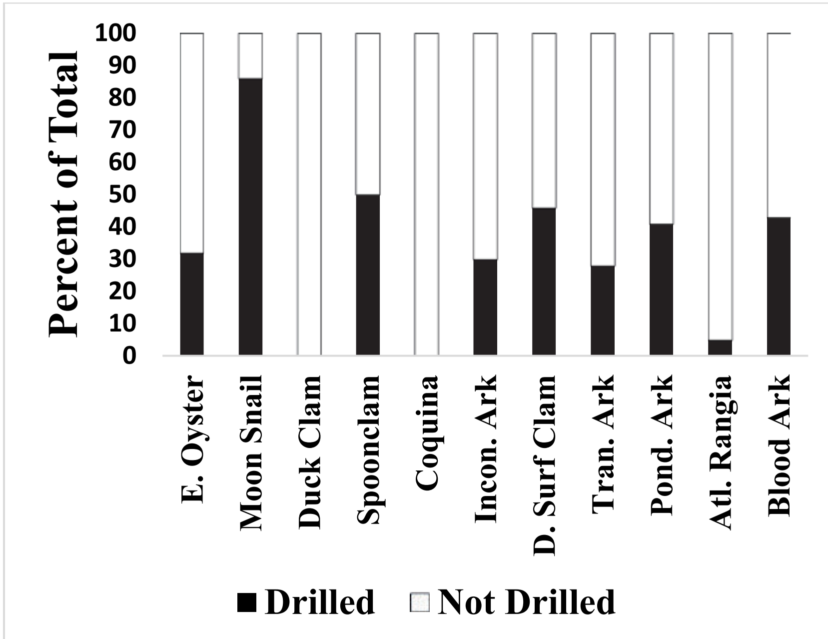

Figure 2. Species-specific predation patterns based on a sample of 11 species of bivalve mollusks collected in May 2016 on the Bolivar Peninsula, Texas. Figure based on 294 shells collected randomly at three different sites. Sample sizes for each species ranged from six to 77 individuals. There was a significant effect of predation by species (χ^2 = 52.9, df = 10, $P < 0.001$).

Figure 3. Photographs of representative predated bivalve mollusk shells. Clockwise from top left: unequal spoonclam (*Periploma margaritaceum*), incongruous ark (*Anadara brasiliana*), Atlantic rangia (*Rangia cuneata*), and moon snail (*Neverita duplicata*).

https://doi.org/10.32011/txjsci_70_1_Article5

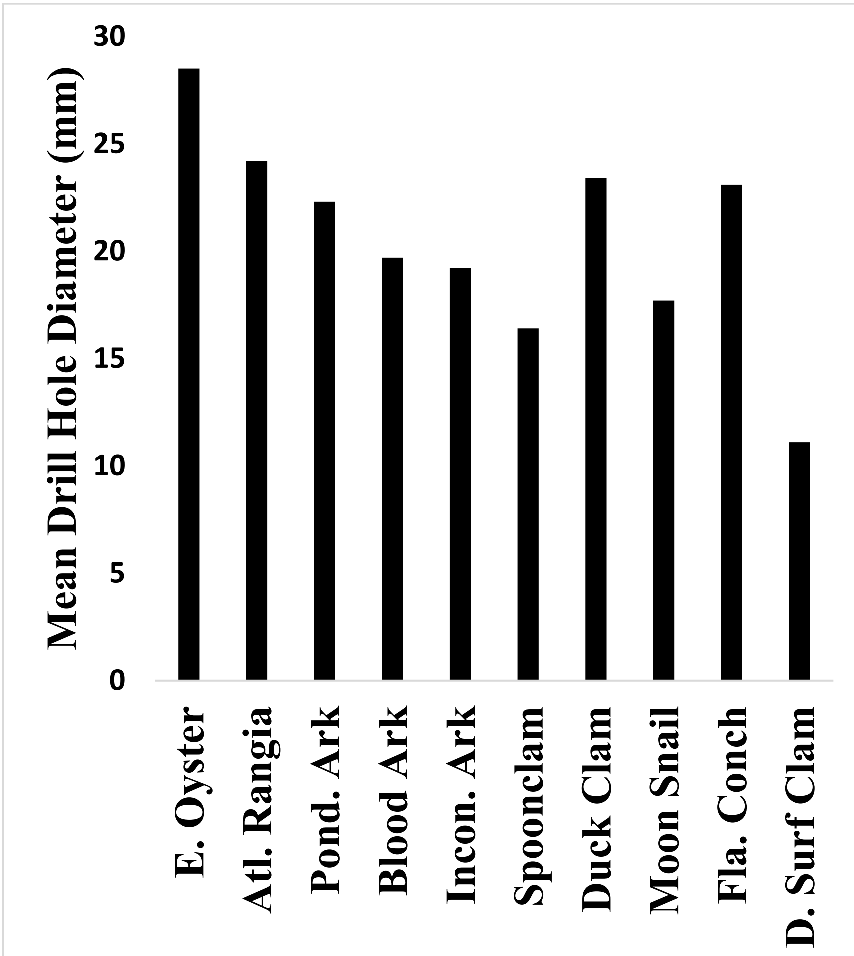

Figure 4. Mean drill-hole diameter (mm) for a sample of 273 mollusk shells collected in May 2016 on the Bolivar Peninsula, Texas. Sample sizes for each species ranged from eight to 57 individuals. There was a significant difference in mean drill-hole diameter by species ($F = 15.7$, df = 9 & 263, $P < 0.0001$).

Although all predated shells were collected along the same Gulf Coast beach at three sites separated by 30 km, these 272 shells showed patterns of predation that differed significantly by collection site ($\chi^2 = 218.7$, df = 18, P < 0.0001). Variables that differed by collection site included mean drill-hole diameter ($F = 22.0$, df = 2 & 270, $P < 0.0001$), mean shell thickness ($F = 94.2$, df = 2 & 270, $P < 0.0001$), the mean number of drill holes ($F = 22.7$, df = 2 & 269, $P < 0.0001$), and the proportion of shells with complete drill holes ($\chi^2 = 29.7$, df = 2, $P < 0.0001$) (Table 1).

https://doi.org/10.32011/txjsci_70_1_Article5

Table 1. Comparison of predation patterns by collection site. The three sites along the Bolivar Peninsula beach were separated by 30 km. Sample sizes are indicated in parentheses for each site.

	Bolivar Flats (n = 97)	Crystal Beach (n = 81)	Rollover Bay (n = 95)	Test	*P*
Mean Drill Hole Diameter (mm)	17.6	24.2	23.3	$F = 21.9$	0.0001
Shell Thickness (mm)	8.9	35.0	20.1	$F = 94.2$	0.0001
Number of Drill Holes	1.4	3.4	1.2	$F = 22.7$	0.0001
Drill Hole Completeness (%)	88	52	88	$\chi^2 = 29.7$	0.0001

Discussion & Conclusions

Significant differences occurred among collection sites in all measured variables; however, it is unlikely that the spatial distribution of shells at collection sites reflected a spatial pattern in prey selection. For example, large and heavy eastern oyster shells found along the beach likely had been washed out of nearby estuaries by tidal action or during high river flow. Marine species may have differentially settled along the beach as the result of wave action or current according to their weight, thickness, or shape. The Bolivar Flats collection site had many small and thin shells, whereas heavier shells were more abundant at the other sites with different current and wave patterns. It cannot be determined by the current methodology whether the spatial distribution of live mollusks or only their shells reflect the depositional effects of wave action, beach currents, and other physical forces. However, if mollusk shells with holes were not collected near where the predation actually occurred, prey availability for oyster drills and moon snails would be strongly skewed, and would include those species carried to different locations along the shore. As such, these two predators would not demonstrate preferences for prey species. Nor would the pattern of

https://doi.org/10.32011/txjsci_70_1_Article5

over- and underrepresentation of bivalve species at different collection sites support prey selection by oyster drills or moon snails.

Because sample shells were collected after the fact, predation could not be ascribed directly to either Southern oyster drills nor moon snails. Therefore, it was not possible to examine species-specific prey selection by these two predators. Similarly, Dietl and Kelley (2006) were unable to use slight differences in drill-hole morphology to distinguish between two predatory species of drills. It was assumed that drill hole diameter was related to radula diameter and therefore to the size of the predator. Although this relationship has been found in previous studies (Dietl & Alexander 1995), no measurements of radulas were made for this study.

Despite these limitations, there were detectable patterns of prey selection by one or both species of mollusk predators. For example, bivalve species with thicker shells were selected by larger predators, based on drill-hole diameter. Selection for prey size by drilling mollusks has been described by Grey et al. (2005), who did not report the mechanism that might enable a predator to determine shell thickness. Many shells in the current study sample bore incomplete holes, and the thickest shells often had multiple incomplete holes and one complete hole, possibly the final attempt. It is possible that predators use "test holes" as a way to determine shell thickness. An alternative explanation for incomplete holes might be an effective anti-predator defense or escape by prey species. If correct, then the species-specific pattern in this sample of shells with multiple holes and incomplete holes would suggest high variation in the ability to escape predation after an attack by an oyster drill or moon snail. Finally, incomplete drill holes may reflect prey suffocation, an alternative predation method used by drilling mollusks (Visaggi et al. 2013). A mollusk who bears one or more incomplete holes might not have escaped predation, but rather may have been killed in a different way.

This study could be extended in ways that would address two of our major findings. First, it is not certain whether the spatial patterns of predation reflect actual prey selection or whether the physical forces

https://doi.org/10.32011/txjsci_70_1_Article5

along the littoral zone carry different bivalve species to different locations, where they are then attacked by drilling gastropods. Because wave energy, current strength, and input from rivers varies throughout the year, it might be possible to undertake collections of predated shells under different such conditions. If patterns of shell spatial distributions differed in tandem with the strength of these physical forces, it would suggest that drilling gastropods were eating what was available. Second, because collections of bivalve shells along the beach were made after the fact, one cannot be certain whether an oyster drill or a moon snail was responsible for each act of predation. Prey selection in one or both gastropod species might be demonstrated in a large aquarium (Dietl & Alexander 1995; Dietl & Kelley 2006) by observing prey choice when predators are presented simultaneously with different bivalve species.

Acknowledgments

We are grateful to Patrick Mathews for his critical review of the manuscript. In addition, we thank the Bolivar Beachcomber's group for assistance in the identification of several mollusk species. Dr. Chris Hall at Texas A&M University-Galveston provided clarification for the species of drilling mollusks found around the Galveston study site.

Literature Cited

Brown, K. M. & T. D. Richardson. 1988. Foraging ecology of the southern oyster drill *Thais haemastoma* (Gray): constraints on prey choice. J. Exp. Marine Biol. and Ecol. 114:123-141.

Dietl, G. P. & P. H. Kelley. 2006. Can naticid gastropod predators be identified by the holes they drill? Ichnos 13:103-108.

Dietl, G. P. & R. Alexander. 1995. Bore hole size and prey size stereotypy in naticid predation of *Euspira (Lunatia) heros* say and *Neverita (Polinices) duplicata* say from the Southern New Jersey Coast. J. of Shellfish Res. 14:307-314.

Gilpin, D. 2006. Snails, shellfish & other mollusks. Compass Point Books, Minneapolis, MN, 30 pp.

Grey, M., P. G. Lelievre & E. G. Boulding. 2005. Selection for prey shell thickness by the naticid gastropod *Euspira lewisii* (Naticidae) on the bivalve *Protothaca staminea* (Veneridae). Veliger 48:317-322.

Morris, P. A. 2001. A field guide to shells: Atlantic and Gulf coasts and the West Indies, 3rd edition. Houghton Mifflin, Boston, MA, 350 pp.

https://doi.org/10.32011/txjsci_70_1_Article5

Rothschild, S. B. 2004. Beachcomber's Guide to Marine Life: Texas, Louisiana, Mississippi, Alabama and Florida, 3rd edition. Taylor Trade Publishing, Lanham, NY, 200 pp.

Tunnel, J. W., J. Andrews, N. C. Barrera & F. Moretzsohn. 2010. Encyclopedia of Texas seashells: identification, ecology, distribution, and history, 1st edition. Texas A&M Univ. Press, College Station, 512 pp.

Visaggi, C. C., G. P. Dietl & P. H. Kelley. 2013. Testing the influence of sediment depth on drilling behaviour of *Neverita duplicata* (Gastropoda: Naticidae), with a review of alternative modes of predation by naticids. J. Molluscan Stud. 79:310-322.

Wye, K. R. 2015. The Shell Collector's Handbook: The Essential Field Guide for Exploring the World of Shells. Wellfleet Press, Secaucus, NJ, 191 pp.

https://doi.org/10.32011/txjsci_70_1_Article5