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DRILLING PREDATION INTENSITY AND FEEDING PREFERENCES BY *NUCELLA* (MURICIDAE) ON LIMPETS INFERRED FROM A DEAD-SHELL ASSEMBLAGE

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ABSTRACT

Although limpets are common in rocky intertidal shores, little is known about drilling predation on them. Drilling intensity and preferences by *Nucella* (Muricidae) on three Lottiidae species (*Lottia pelta*, *L. digitalis*, and *Tectura scutum*) were explored in a modern limpet death assemblage from False Bay (San Juan Island, Washington, USA). Of the 1,531 shells, only 61 (4%) were drilled, with drilling frequencies of 5.9% (*L. digitalis*), 2.4% (*L. pelta*) and 0.5% (*T. scutum*). The higher drilling frequency observed for *L. digitalis* may reflect spatial differences in prey distribution within the intertidal zone. Hole diameter correlated positively with limpet size, suggesting that larger predators drill larger prey. No differences in drilling frequency were observed due to prey ornamentation or size; however, drill holes were never observed on the largest and thickest *L. pelta* shells, suggesting a possible size refugium. The majority of holes occurred near the apex, indicating stereotypic attack behavior. Uniform frequency distributions across taphonomic grades and similar central tendencies between drilled and undrilled shells suggest that holes were not affected by taphonomic bias. The preservation of drilled and undrilled shells differed significantly, however; thus, drill holes may have negatively affected the preservation potential of shells, possibly by weakening the shell. Poor shell preservation indicates that biostratinomic effects may play a larger role in preservational biases and underestimation of predation frequencies than previously thought. Studies using drilling frequencies demand careful identification of predatory traces when shells are poorly preserved. In addition, careful evaluation of predation frequency is needed when predatory strategies that may not leave visible traces are possible.

INTRODUCTION

Limpets are common grazing organisms in modern intertidal rocky shores, and they play an important role in marine ecosystems around the world. Individuals belonging to the clade Patellogastropoda are of particular evolutionary interest, since this is considered to be the most basal branch of the extant Gastropoda, as revealed by cladistic analysis of morphological characters (e.g., Nakano and Ozawa, 2004). They have a long fossil record (the oldest shells are found in the Middle Ordovician), and they are sister to all other gastropods (Nakano and Ozawa, 2007 and references therein). In addition, recent studies have shed light on the adaptive evolution of Patellogastropoda and their historical biogeography (e.g., Nakano and Ozawa, 2004), exemplifying the broad interest of further studies on these organisms for both biologists and paleontologists. Despite the evolutionary and ecological importance of limpets in marine ecosystems, however, little is known about predator-prey interactions between drilling gastropods and limpets or their coevolution, mainly due to the assumption that such interactions are rare and limited to isolated field observations and laboratory experiments (Bank, 1978; Lamb, 1978; West, 1986; Palmer, 1988; Yamamoto, 2004; Schiffbauer et al., 2008). In the present study we calculate, for the first time, drilling predation intensities and predator preferences by quantifying predatory drill holes recognized on limpets collected from a modern dead-shell assemblage.

Evidence of drilling predation on mollusk shells is commonly used to study predator-prey interactions in both modern (Bank, 1978; Palmer, 1988; Ishida, 2004; Kowalewski, 2004; Yamamoto, 2004; Schiffbauer et al., 2008) and fossil communities (Sheehan and Lesperance, 1978; Ausich and Gurrola, 1979; Kowalewski, 1993; Kowalewski et al., 1998; Kowalewski and Kelley, 2002; Leighton, 2002, 2003; Kelley and Hansen, 2006; Schiffbauer et al., 2008). This is especially true in paleontological studies where direct observations are impossible, and drill holes (Kowalewski, 2004) and repair scars (Alexander, 1986; Alexander and Dietl, 2001) are used as proxies for predation pressure. Studies that have used drill holes to estimate predation frequencies in the fossil record make several assumptions about their quality and significance (Leighton, 2002): (1) drill-hole abundance represents predation intensity, (2) all complete drill holes are considered successful attacks, and (3) incomplete drill holes are considered failed attacks. These assumptions can be tested and explored in modern communities and modern death assemblages (actualistic paleontology). When identifying drill holes, two major diagnostic errors can occur: (1) misidentification of traces that are not predatory in origin as drill holes, such as substrate borings, dissolution traces, or punctures (Lescinsky and Benninger, 1994), and (2) the misidentification of true drill holes as non-predatory in origin (e.g., Nebelsick and Kowalewski, 1999). Since recently dead shells are generally well preserved and direct observations are possible, studies of modern shell assemblages can yield valuable information that can be applied to paleocommunities, possibly minimizing the ambiguity of some of the interpretations of prey-predator interactions in the fossil record (Vermeij, 1980; Kowalewski, 2004 and references therein).

The muricid genus *Nucella* Röding (Muricidae) is one of the most abundant drilling, carnivorous mollusks living in the intertidal rocky substrate of the Pacific Northwest coast today. A common predatory strategy used by *Nucella* is to drill through the shell of the prey using the radula. Once a hole has been drilled, the snail injects a digestive enzyme into the body of the prey and sucks out the dissolved tissue (e.g., Navarrete, 1996). Barnacles and mussels are common prey for *Nucella* (Berlow and Navarrete, 1997; Sanford et al., 2003; Kowalewski, 2004), but only a few species—including *N. ostrina* (Gould), *N. canaliculata* (Duclos), and *N. lima* (Gmelin)—include limpets in their diet (Lamb, 1978; West, 1986; Palmer, 1988).

Lottiidae limpets are among the most common invertebrates in the rocky intertidal zone of the Pacific Northwest and occupy the same habitat as *Nucella*. The dominant organisms that prey upon these limpets include crabs, fish, sea stars and birds (Chapin, 1968; Lowell, 1986). Despite the accessibility of limpets as prey, they are unusual in the diet of *Nucella* (Lamb, 1978; West, 1986; Palmer, 1988). During field observations made by Palmer (1988), only four out of 2,082 limpets were drilled by *N. ostrina*, 14 of 518 by *N. lima*, and one of 2,001 by *N. canaliculata*. West (1986) reported no observations of drilling predation

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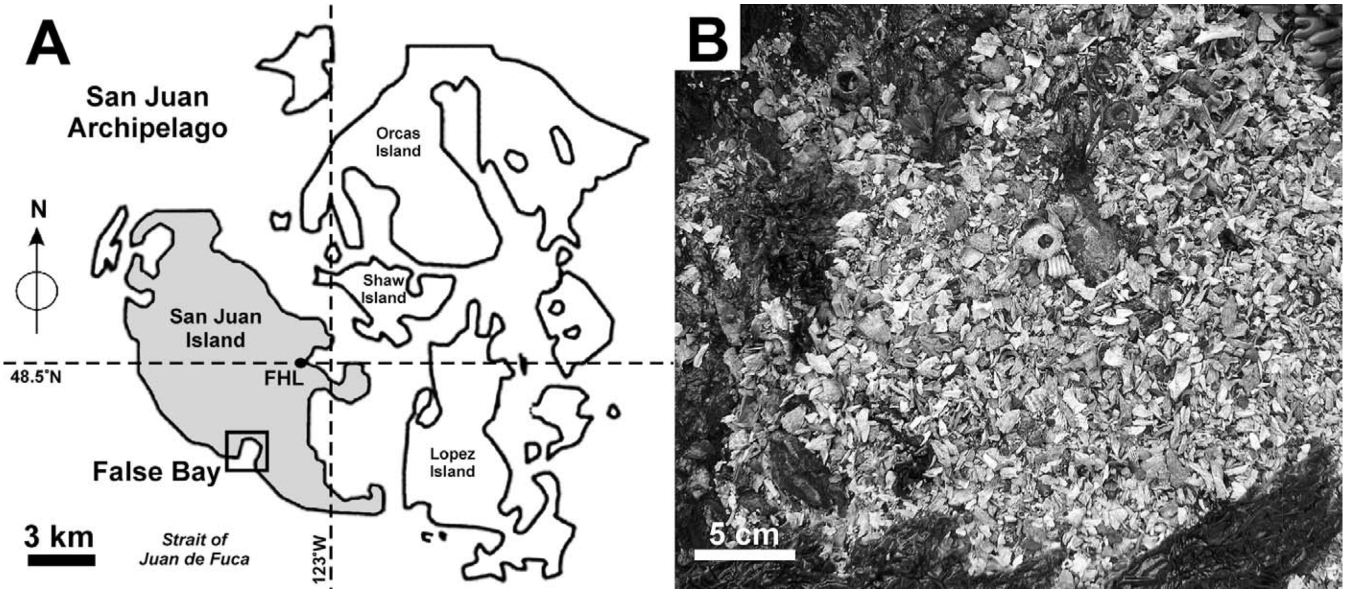

FIGURE 1—Location of the study area and shell assemblage. A) Geographic location of False Bay in San Juan Island, Washington. Black dot shows the sampling site. B) Detail view of the death shell assemblage in the field that was subsequently collected and studied.

on limpets by *N. ostrina*. Additionally, species of *Nucella* from the San Juan Archipelago, Washington, USA have been observed employing other predatory strategies (rather than drilling) when preying upon limpets, such as flipping the prey over and extending the proboscides under the margin of the shell (West, 1986). Consequently, predation intensity by *Nucella* upon limpets is not completely understood, and a thorough testing of the assumptions made by drilling frequency estimations is needed, using modern field and laboratory experiments.

The main goal of this study is to estimate *Nucella* drilling intensities on Lottiidae limpets by analyzing a modern dead-shell assemblage from San Juan Island, Washington, USA. The following questions are addressed: (1) How frequently are drill holes observed on limpet shells; (2) are there any differences in drill-hole morphology or frequency based on prey size, morphology, or species; and (3) are there any differences in the preservation potential between drilled and undrilled shells?

METHODS

Geographical Location and Sample Collection

Limpet shells were collected by both authors during the Summer of 2006 in False Bay, a wave-protected, intertidal habitat consisting of extremely shallow bottom sand and mud on the southwest shore of San Juan Island, Washington, USA (Fig. 1A). The bay experiences diurnal tides with a maximum range of −0.8 m to +2.6 m (Dent and Uhen, 1993 and references therein). Consequently, organisms of the rocky intertidal community experience several hours per day of subaerial exposure (personal observations by both authors, 2006). The Strait of Juan de Fuca (Fig. 1A) provides the dominant source of physical energy in the bay (Dent and Uhen, 1993).

Abundant populations of many species of limpets, as well as muricids of the genus *Nucella*, inhabit rocky patches and isolated boulders. Several species of *Nucella* are found in False Bay, including *N. lamellosa* (Gmelin), *N. ostrina* (Fig. 2A–C), *N. lima*, and *N. canaliculata*. Although the muricid *Ocenebra lurida* (Middendorff) does include limpets in its regular diet (Palmer, 1988) and has been found in the San Juan Archipelago, this species was never observed during our field work in False Bay. As this is a study of modern shells, it was possible to make direct observations to determine which drilling predators were living in False Bay. Since *Nucella* is the only muricid genus that is found in False Bay, and seeing that naticids prefer to burrow in softer substrates, focusing on infaunal prey (Kelley and Hansen, 2003), it seems most likely that the drill holes found on the analyzed limpets were all made by *Nucella* individuals.

After an exhaustive search of False Bay, only a single modern dead-shell assemblage was found. The assemblage was located between several isolated boulders and a patch of rocky shoreline in the southeast part of the bay (Fig. 1A–B). Such a dead-shell assemblage would be expected to be influenced by taphonomic effects to varying degrees. The shell assemblage had an approximate maximum length of 4 m and a maximum width of 3 m. Due to the large size of the shell assemblage, it was logistically unfeasible to exhaustively examine the entire assemblage. Therefore, in order to obtain a representative sample, 12 sample replicates were collected along a linear transect of the long axis of the assemblage. Replicates were located ~20 cm apart and each one consisted of ~0.5 kg of wet shells. The 12 replicate samples were then transported to Friday Harbor Laboratories (FHL) for analysis (Fig. 1A).

Laboratory Analyses

Sample Preparation and Species Identification.—Samples were washed with fresh water and dried at room temperature. Remains of limpets, barnacles, mussels, bivalves, gastropods, and crabs were present, so limpet shells were picked by hand from each sample replicate. A total of 2,285 limpet shells were found in the whole assemblage (12 replicates pooled); however, only 1,531 of these were whole specimens (>80% of the shell intact). While one shell does represent one individual, with shell fragments or partial shells, it is possible to overestimate the number of individuals, as several fragments could belong to the same individual. In addition, if part of the shell is missing, shells could be incorrectly classified as undrilled if the missing portion of the shell contained a drill hole. Thus, to eliminate overestimation of total individuals and underestimation of drilling frequency, only whole specimens were included in the drilling frequency analyses (n = 1,531). In contrast, the taphonomic analysis (explained below), included all shells, i.e., both shell fragments and whole shells (n = 2,285).

Each limpet was identified to the species level. Of the more than six species of limpets found in False Bay (VanDuzer, 1978), only three (Patellogastropoda: Lottiidae) occurred in the assemblage: *Lottia digitalis* (Rathke) (n = 817), *L. pelta* (Rathke) (n = 494), and *Tectura scutum* (Rathke) (n = 220). These species vary in size, shape, and ornamentation

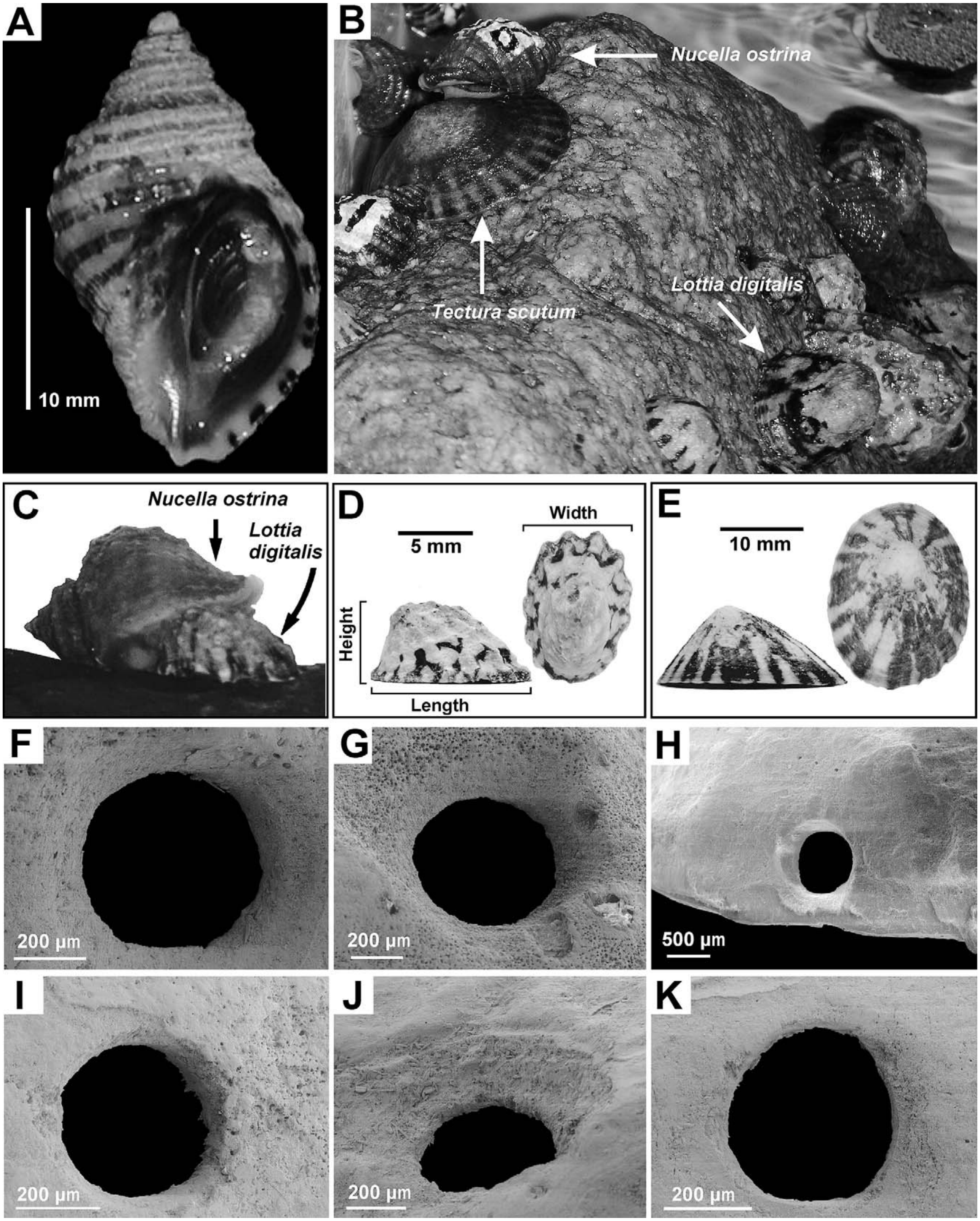

FIGURE 2—Photographs of the drilling gastropod, limpet prey, and field-emission SEM (FE-SEM) of the observed drill holes. A) *Nucella ostrina*. B) *Nucella ostrina* upon *Tectura scutum* in living communities. C) Higher magnification of *Nucella ostrina* drilling *Lottia digitalis*. D) *Lottia digitalis* showing maximum body-size measurements made on limpet shells (length, width, and height). E) *Lottia pelta*. F–K) FE-SEM micrographs of drill holes observed on *Lottia digitalis* (F–H) and *Lottia pelta* (I–K) specimens.

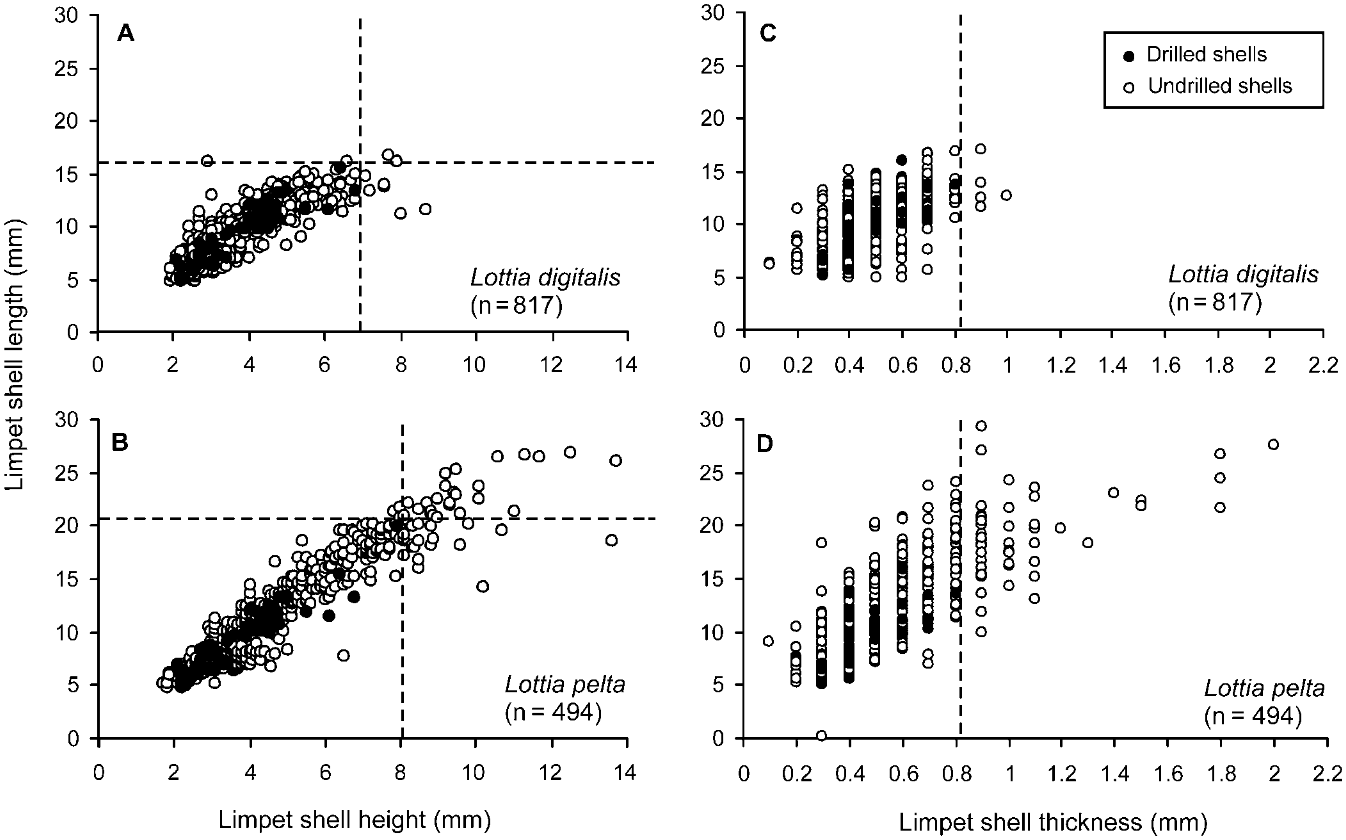

FIGURE 3—Bivariate plots of drilled and undrilled limpet shell size. A–B) Bivariate plots of body size of limpet shells (length versus height) of the species *Lottia digitalis* (A) and *L. pelta* (B). Discontinuous lines indicate the greatest height and length of identified drilled shells. C–D) Size of limpet shells (length versus thickness) of *L. digitalis* (C) and *L. pelta* (D). The dashed line shows the greatest thickness founded on drilled shells. Black dots = drilled shells; white dots = undrilled shells.

and can be easily identified (VanDuzer, 1978) even when poorly preserved. The shell of *L. digitalis* has heavy ribs extending from the apex to the scalloped margin, with a maximum length of ~25 mm (Fig. 2D). *Tectura scutum* has a very flat, smooth shell with a regular margin and a maximum length of ~55 mm. *Lottia pelta* is polymorphic, with radial ribs and scalloped edges that may or may not be present and has a maximum length ~40 mm (Fig. 2E).

The sampled material is reposited in the Department of Geosciences at Virginia Polytechnic Institute and State University (Virginia Tech.), USA.

Identification and Study of Predatory Drill Holes.—Shells were examined for muricid predatory traces (presence or absence of drill holes), and size and position of drill holes were recorded (Fig. 2F–K). Linear morphometric measurements of size (maximum shell length, width, and height) were obtained to the nearest 0.02 mm using digital calipers (Fig. 2). Shell length and height were plotted per species, relative to the presence or absence of drill holes (Fig. 3A–B). Shell thickness (also calculated using digital calipers to the nearest 0.02 mm) was measured on the anterior margin of the shell between ribs, for those shells with ribbed ornamentation. Only drilled specimens of *L. pelta* were used to explore predator preferences based on shell morphology, because it is the only polymorphic species (i.e., radial ribs and scalloped edges may or may not be present).

Predatory drill holes were identified under a binocular microscope based on the following criteria: (1) distinct circular shape, (2) regularity of the hole outline, and (3) holes do not go through the opposite side of the shell (Kowalewski, 1993; Kowalewski and Kelly, 2002; Kowalewski, 2004; Grey et al., 2005; Dietl and Kelley, 2006) (see examples in Fig. 2F–K). Drill holes were photographed parallel to the plane of the camera lens, and the maximum diameter of the drill-hole outline was measured using ImageJ software (Rasband, 1997–2007). Drill-hole diameter is commonly used as a proxy for predator size because it is directly related to the size of the accessory boring organ (ABO) (Kingsley-Smith et al., 2003; Kowalewski, 2004 and references therein); thus, holes with larger diameters typically belong to larger predators. Therefore, drill-hole diameter was used as a proxy for predator size to determine potential correlation between hole diameter (i.e., predator size) and prey size.

Previous studies have suggested that due to the stereotyped nature of drilling, predatory gastropods commonly prefer to drill on a particular site on the prey shell, typically located over the gonads or digestive tissues of the prey (Palmer, 1988; Harper and Morton, 1997; Kingsley-Smith et al, 2003). To determine whether drill holes occur more frequently at certain locations on the prey shell, two categories were assigned to each limpet shell (Table 1): (1) apical drill holes (those located within the top half of the shell height), and (2) edge drill holes (those located within the bottom half of the shell height) (Fig. 4), *sensu* Palmer (1988).

Taphonomic Study.—A taphonomic analysis was performed on both drilled and undrilled specimens to assess the potential effects of drill holes on shell preservation. This analysis included shell fragments and whole specimens (n = 2,285). Five taphonomic features were scored (fragmentation, color preservation, corrasion, bioerosion, and encrustation) for each shell under a binocular microscope. The taphonomic data were recorded as binomial variables, with (1) being poorly preserved and (0) being well preserved. Taphonomic features were graded as follows. Shells were considered fragmented if <80% of the shell was present and were scored as poorly preserved (1); complete shells (≥80% or more of the shell present) were classified as well preserved (0). Shells with no preservation of color were classified as poorly preserved (1) while shells with color were considered well preserved (0). Corrasion was measured as any internal or external sign of abrasion or dissolution on the shell (1); shells with no sign of corrasion were considered well preserved (0). Bioerosion was identified as any internal or external micro-perforation

TABLE 1—Sample size, drilling frequencies, and location of drill holes on shells for the three limpet species from False Bay.

	Total shells		Whole shells only		Undrilled		Drilled		Apical hole		Edge hole	
Limpet species	n	%	n	%	n	%	n	%	n	%	n	%
L. digitalis	1,092	47.8	817	53.4	769	94.1	48	5.9	42	76.4	6	100
L. pelta	878	38.4	494	32.2	482	97.6	12	2.4	12	21.8	0	0
T. scutum	315	13.8	220	14.4	219	99.5	1	0.5	1	1.8	0	0
Total	2,285	100	1,531	100	1,470	-	61	-	55	100	6	100

not caused by predation or parasitism (1); shells without bioerosion were classified as well preserved (0). Finally, encrustation (e.g., by serpulids, barnacles, or algae) on the internal and external part of the shell was surveyed (1); when no encrustation was present, shells were considered well preserved (0). The Total Taphonomic Grade (TTG) was recorded for each shell as the sum of all the taphonomic features listed above. The TTG in this study ranged from 0 (well preserved) to 7 (very poorly preserved).

Statistics.—All statistical analyses performed (chi-square test, Kruskal-Wallis test, and Pearson correlation) were computed using SAS 9.1/STAT software (SAS Institute, Cary, NC). Statistical significance was assumed at $\alpha = 0.05$.

RESULTS

Of the 1,531 complete shells, only 61 drill holes (4% of the bulk sample) were observed (Table 1). No significant differences were observed in regards to drill hole distribution between replicate samples (Kruskal-Wallis, $x^2 = 7.6$, $p = 0.75$, $n = 12$). Consequently, all replicates were pooled and subsequent analyses performed using the pooled data. No incomplete drill holes were observed and only four individuals of *L. digitalis* had multiple drill holes (two on each shell). Each drilled shell was considered a single, successful predatory encounter regardless of how many drill holes were on the shell—i.e., multiple holes on a single shell were only counted once.

Of the 61 drill holes, 48 were on *L. digitalis* (78.7%), 12 on *L. pelta* (19.7%), and only one (1.6%) on *T. scutum* (Table 1). Because only one hole was observed on *T. scutum*, this species was excluded from further statistical analyses. Drilling frequencies for each species were also calculated: *L. digitalis* 5.9%, *L. pelta* 2.4%, and *T. scutum* 0.5% (Table 1). Therefore, *Nucella* preyed on all three of the studied limpet species, although drill holes were most frequently observed on *L. digitalis* ($x^2 = 17.92$; $p = 0.0001$).

From a total of 12 drilled *L. pelta* shells, radial ribs and scalloped edges were only present on two. A chi-square test yielded a marginally significant result ($x^2 = 3.36$; $p = 0.067$). This result is obviously circumspect due to the small sample size ($n = 12$) and requires additional investigation to clarify.

Using length as a proxy for size, limpet species differed significantly in size (Kruskal-Wallis, $x^2 = 57.95$; $p < 0.0001$) (Table 2). While drill holes were found on specimens throughout the size range (Fig. 3A–B), total drilling frequency across species varies statistically by size (Kruskal-Wallis $x^2 = 12.55$; $p = 0.004$). Within each species, the drilling frequency in relation to the size of specimens was not significant for *L. digitalis* (Kruskal Wallis; $x^2 = 1.68$; $p = 0.19$), but was for *L. pelta* (Kruskal-Wallis; $x^2 = 9.03$; $p = 0.0027$). There appeared to be a maximum prey size above which no drill holes were found on *L. pelta* shells (Fig. 3B). Maximum prey size above which drill holes never occurred was not clear for *L. digitalis* (Fig. 3A).

There was no relationship between shell thickness and the presence of drill holes (Fig. 3C–D) for pooled limpet data (Kruskal Wallis; $x^2 = 0.79$, $p = 0.37$) or for individual species (Kruskal Wallis; *L. digitalis*: $x^2 = 3.5$, $p = 0.55$; *L. pelta*: $x^2 = 3.4$, $p = 0.07$). Although no significant differences were observed, it is worth noting that no drill holes were found in *L. pelta* shells with length >22 mm and height >8 mm (Fig. 3B) or with a thickness >0.8 mm (Fig. 3D).

When all drilled limpets were pooled together, drilling frequencies were significantly non-random relative to drill-hole location. There was a higher occurrence of drill holes located apically ($x^2 = 58.76$, $p < 0.0001$). In fact, 55 out of 61 drill holes occurred in the apical position

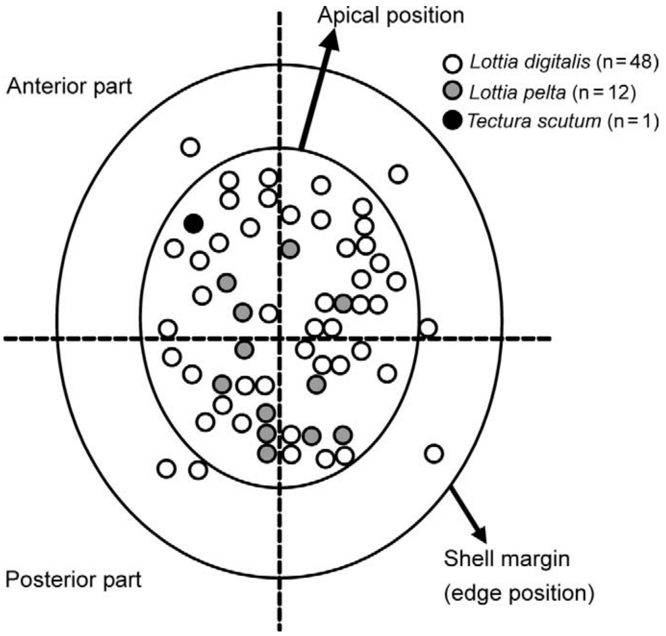

FIGURE 4—Dorsal view of a hypothetical limpet shell showing the drill-hole positions made by muricids from False Bay. For this study, the shell is divided into two parts: apical (upper half of the shell, closer to the apex) position and edge (bottom half of the shell, farther from the apex) position (adapted after Palmer, 1988).

TABLE 2—Body size and shell thickness of the analyzed limpet shells.

Limpet species (whole shells)	Mean	SD	Max	Min
Lottia digitalis (n = 817)				
Length (mm)	10.05	2.40	17.10	5.0
Width (mm)	7.11	1.59	12.70	3.50
Height (mm)	3.93	1.06	8.70	1.90
Thickness (mm)	0.38	0.16	1.20	0.10
Lottia pelta (n = 494)				
Length (mm)	12.21	5.11	27.6	0.10
Width (mm)	9.14	3.88	21.3	0.50
Height (mm)	4.82	2.12	13.70	1.60
Thickness (mm)	0.44	0.27	2.00	0.10
Tectura scutum (n = 220)				
Length (mm)	11.87	3.37	23.70	6.00
Width (mm)	9.14	2.94	20.10	4.80
Height (mm)	3.23	1.16	7.40	1.50
Thickness (mm)	0.26	0.15	0.90	0.10

TABLE 3—Diameter of drill holes in studied limpets.

Species	n	Mean (mm)	SD (mm)	Max (mm)	Min (mm)
Lottia digitalis	48	0.7	0.2	1.0	0.4
Lottia pelta	12	0.7	0.4	1.8	0.3
Tectura scutum	1	1.8	-	-	-

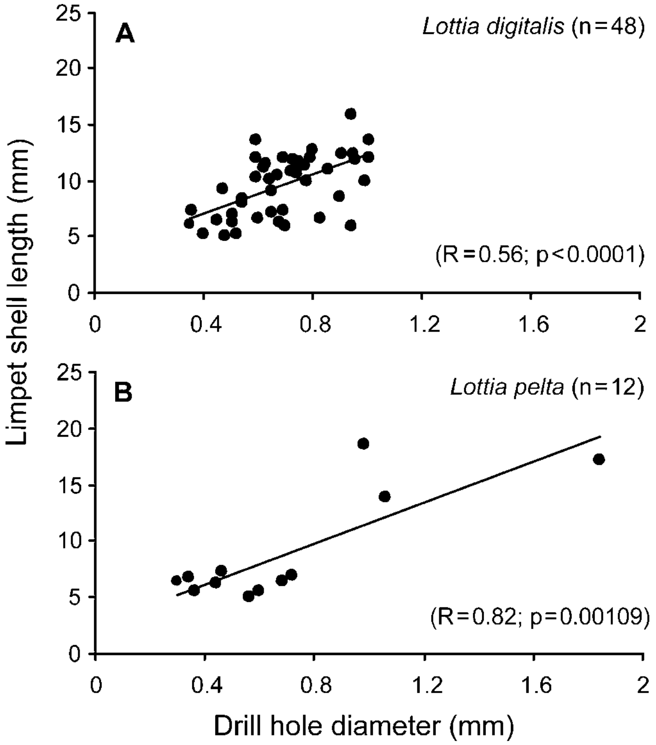

FIGURE 5—Correlation between drill-hole maximum diameter (mm) and maximum length (mm) of the two limpet shell species *Lottia digitalis* (A) and *L. pelta* (B).

(Table 1; Fig. 4). Similarly, analysis by species showed a significant preference for the apical location of drill holes ($x^2 = 42.35$, $p < 0.0001$ for *L. digitalis*, and $x^2 = 15.0$, $p < 0.0001$ for *L. pelta*).

The maximum drill-hole outer diameter ranged from 0.3 to 1.8 mm (Table 3), with an average of 0.7 ± 0.2 mm for both *Lottia* species (Table 3). There was a positive correlation ($r = 0.68$, $p < 0.0001$) between the outer maximum diameter of the drill hole (i.e., predator size) and the limpet shell length for pooled data. This correlation was also significant for both *L. pelta* ($r = 0.82$, $p = 0.0011$) and *L. digitalis* ($r = 0.56$, $p < 0.0001$) (Fig. 5) separately. Nonetheless, due to the small sample size for *L. pelta* ($n = 12$) and the presence of an outlier (Fig. 5B), this correlation should be viewed with caution and an increased sample size is required.

Both drilled and undrilled shells exhibited a wide uniform range of TTG, ranging from 1 to 7 for undrilled specimens (Fig. 6A) and 2–6 for drilled shells (Fig. 6B). The majority of shells (both drilled and undrilled) had a TTG of 3–4 (Fig. 6A–B). In addition, the frequency distribution of TTG for drilled individuals (Fig. 6B) did not differ from the central tendency of undrilled shells (Fig. 6A). While the TTG differed between drilled vs. undrilled pooled specimens (Kruskal Wallis; $x^2 = 61$, $p < 0.0001$), *L. digitalis* was the only species with sufficient sample size (48 drilled shells) to evaluate whether the presence of drill holes affected the preservation potential of shells. The TTG differed between drilled and undrilled specimens of *L. digitalis* (Kruskal Wallis; $x^2 = 27.85$, $p < 0.001$) and across species (Kruskal Wallis; $x^2 = 386$, $p < 0.001$).

Fragmentation was higher in undrilled shells (Table 4; Fig. 7), but drilled shells showed lower color preservation than undrilled specimens. Corrasion was elevated in drilled skeletons, although corrasion in all specimens was always >90% (Table 4; Fig. 7). Bioerosion was generally higher in drilled shells. Encrustation was consistently low for all samples, but higher in undrilled shells (Table 4; Fig. 7).

DISCUSSION

Drilling Frequency

The drill holes showed: (1) a single, cylindrical shape with regular outline (e.g., Fig. 2F–K); (2) a drill-hole axis perpendicular to the shell surface; and (3) an absence of multiple holes. This, in conjunction with the high abundance of *Nucella* species as well as the absence of naticids in the rocky substrate, indicates that drill holes were made by muricids of the genus *Nucella*. Here we demonstrate from the modern shell assemblage collected in False Bay that *Nucella* is clearly capable of utilizing limpets as potential prey items. In addition, species of *Nucella*, and almost certainly *N. ostrina* (G. J. Vermeij, personal communication, April 13, 2008), employ drilling to prey upon limpets, albeit in smaller quantities than their other main food sources, such as barnacles and mussels, where predation frequencies have been estimated at ~50% and 20%, respectively (West, 1986).

As far as we know, drill holes on fossil limpets have never been reported in the published literature. In this study, drilling predation was estimated at 4%. The predation pressure by *Nucella* on limpets may be higher than this and other estimations based on drilling frequencies (e.g., Palmer, 1988) because, as noted above, *Nucella* species have been reported using other strategies to attack prey (West, 1986; Kowalewski, 2004).

An in-depth inspection of fossil limpets from different geographic areas and time intervals is needed in order to estimate how long and how frequently this ecological interaction between drilling gastropods and limpets has occurred.

Studies made by Wieters and Navarrete (1998) show that the effects of the predator on prey populations often varies significantly in intensity, from relatively minor or no effect in some areas to very dramatic effects (local extinction) in others (Wieters and Navarrete, 1998). Likewise, predation intensity can determine the total effect of predators on prey assemblages. Here, a significantly higher drilling frequency was observed upon *L. digitalis*, which is of medium size and has a ribbed shell, compared to the other limpet species analyzed. This result may have ecological implications, as it is indicative of predation pressure on *L. digitalis* by *Nucella*. Even though the total percentage of predation frequency was low, a significant predation frequency for one species of limpet may affect the overall limpet population abundance and distribution (West, 1986). It is important to note, however, that this result must be viewed with caution, as muricids can prey upon limpets using other predatory strategies, which might not be recorded on the prey shells. Thus, the estimation of predation intensity based on the abundance of drill holes in fossil and modern shells is usually underestimated. Kowalewski (2004 and references therein) suggests that the predation intensity based on drill holes by predatory snails is generally underestimated by at least 10%–12%, depending on the studied organism.

West (1986) also suggests that prey selection studies in nature should be tested using prey availability (accessibility) to the predator, which is difficult to define and measure. In False Bay, it was observed that *L. digitalis* is an upper intertidal species overlapping with barnacles, while *L. pelta* and *T. scutum* have a low to middle intertidal distribution (VanDuzer, 1978 and field observations by both authors, 2006). Even though *Nucella* species have a broad intertidal distribution, they may feed more frequently in the upper intertidal area, where barnacles and mussels (their main food source) are more abundant (West, 1986). Due to the greater abundance of *L. digitalis* in conjunction with other, more common *Nucella* prey (field observations by both authors, 2006), *L. digitalis* may be more frequently attacked simply due to higher encounter rates and

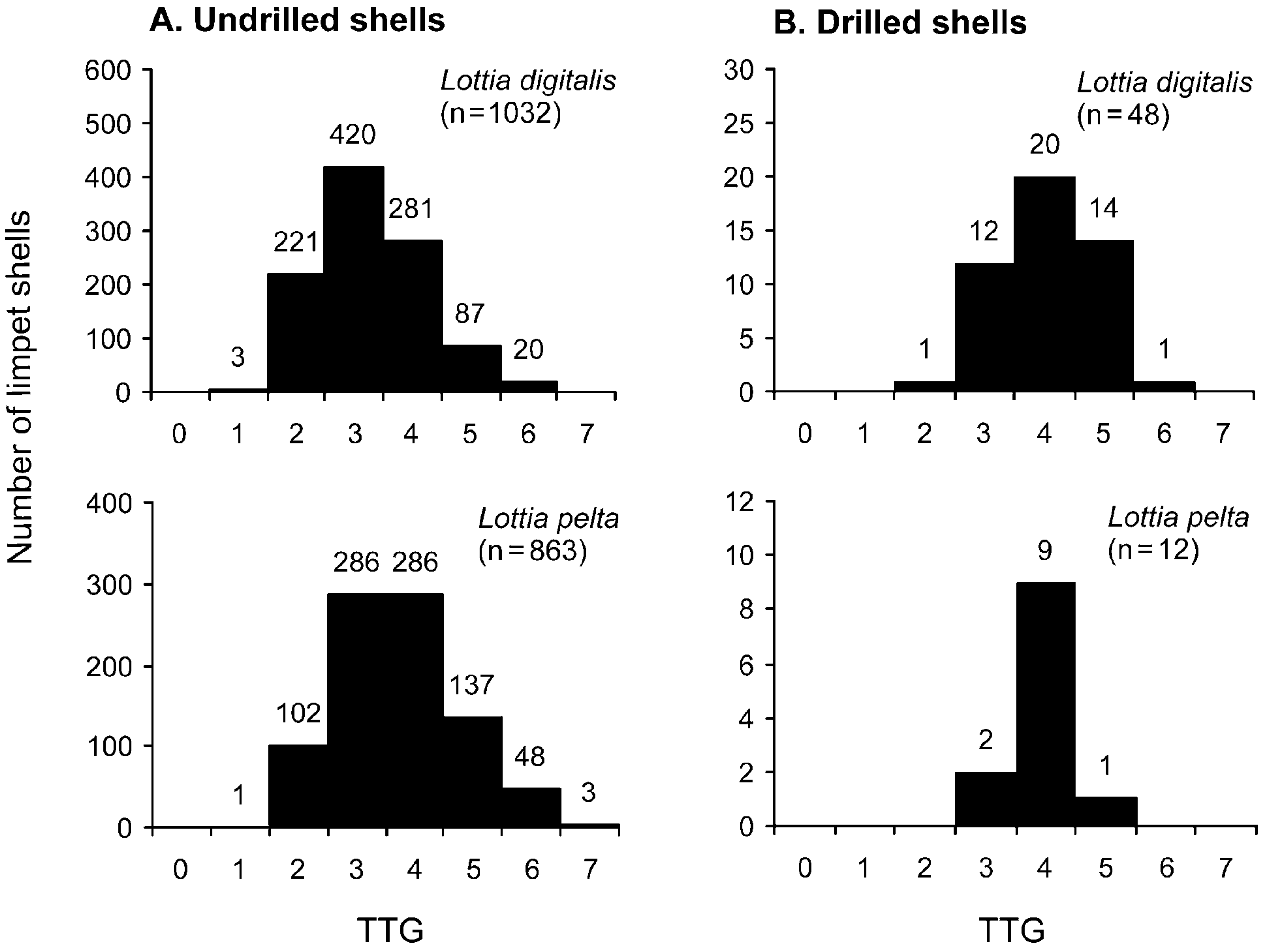

FIGURE 6—Frequency distribution of the total taphonomic grade (TTG) of undrilled (A) and drilled (B) shells of the two more abundant limpet species (*Lottia digitalis* and *L. pelta*). The TTG ranges from 0 (well preserved) to 7 (badly preserved).

distribution. Thus, the detected higher predation frequency by *Nucella* on *L. digitalis* is most likely due to opportunistic predation rather than nonrandom species-prey preference (Leighton, 2002).

Effect of Ornamentation

Shell ornamentation, such as spines, ribs, and other elaborate structures on the shell surface, is considered one of the most common evolutionary adaptations of shelly organisms as defense against gastropod drilling predators (Vermeij, 1978). Thus, several studies have shown preferences by drilling gastropods for smooth shells, as the energy and time required to drill smooth shells should be lower than that for heavily ribbed skeletons (e.g., Alexander and Dietl, 2003 and references therein). In the present study, the observed higher drilling frequency on smooth shells compared to ribbed shells of *L. pelta* suggests that there might be a tendency for the predator to prey more frequently on moderately ornamented shells than on heavily sculptured shells. As these three limpet species differ in ornamentation (presence or absence of radial ribs and scalloped edges), the differences in drill-hole frequency may be explained by differences in shell ornamentation of prey. Unfortunately, the available sample size to explore this potential relationship was insufficient ($n = 12$ drilled *L. pelta* shells) and consequently, a larger sample and further testing is required to corroborate this hypothesis.

Selection by Size

Drilling frequencies were not random across prey sizes. Above a certain size, *L. pelta* shells did not have drill holes (Fig. 3B). Laboratory experiments by Grey et al. (2007) demonstrated that naticid snails drilled bivalve prey that had thinner shells more often than those with thicker shells. In our study, however, there did not appear to be any significant relationship between shell thickness and drilling frequency, except that *L. pelta* limpet shells >0.8 mm thick were never drilled (Fig. 3D), suggesting a possible limit of prey shell thickness for *Nucella*.

Drill-Hole Location

Drill holes were found more frequently on the apical portion of the shell. This result agrees with previous studies that have examined other predatory muricid genera that employ drilling when preying upon shelly organisms. For example, *Ocenebra lurida*, *Morula musiva* (Kiener), *Thais clavigera* Küster, and *T. luteostoma* (Holten) drilled more frequently on the apical portion of the shell (Palmer, 1988; Harper and Morton, 1997). This site selectivity may result in additional underestimations of drilling frequencies. If drill holes are more frequently found on the apical portion of the shell and that portion is more frequently worn away, then drill holes will also be removed, leading to further possible underestimation of drilling frequencies.

Drill-Hole Diameter and Limpet Size

As noted above, drill-hole diameter is commonly used as a proxy for predator size (Kingsley-Smith et al., 2003; Kowalewski, 2004 and references therein), and predator size of drilling gastropods is often correlated with prey size (Palmer, 1988; Kingsley-Smith et al., 2003; Kowalewski, 2004). Hence, drill-hole size used as a proxy for predator size

TABLE 4—Summary of taphonomic features observed in drilled and undrilled shells.

		Fragmentation	No color preservation	Internal corrasion	External corrasion	Internal bioerosion	External bioerosion	Internal incrustation	External incrustation
Lottia digitalis									
Drilled shells (n = 48)	n	0	38	40	48	21	45	0	0
	%	0	79.2	83.3	100	43.8	93.8	0	0
Undrilled shells (n = 1,032)	n	286	687	452	1028	289	977	4	3
	%	27.7	66.6	43.8	99.6	28.0	94.7	0.4	0.3
Lottia pelta									
Drilled shells (n = 12)	n	0	8	11	12	4	10	0	1
	%	0	66.7	91.7	100	33.3	83.3	0	8.3
Undrilled shells (n = 863)	n	403	143	360	786	405	519	1	7
	%	46.7	16.6	41.7	91.1	46.9	60.1	0.1	0.8

should correlate with prey size. While the correlation between drill-hole size and predator size has generally been observed in naticid gastropods, it is not always the case for muricids. For example, Harper and Morton (1997) found no significant correlation between the size of the muricid predators *M. musiva*, *T. clavigera*, and *T. luteostoma*, and the size of their bivalve prey. In contrast, our results show a positive correlation between drill hole diameter and prey size, suggesting that at least *Nucella* may select prey depending on their body size. This hypothesis is consistent with Palmer (1988), who also found a positive correlation between *O. lurida* drill-hole diameter on limpet shells and the length of the drilling gastropod. Similarly, Kowalewski (2004) observed the same relationship when examining *N. lamellosa* and mussel prey under experimental control.

Preservation of Limpet Shells

Comparing the drilled shell TTG frequency distributions against theoretically predicted taphonomic distributions proposed by Nebelsick and Kowalewski (1999) suggests that the identified drill holes were not of taphonomic origin and were unaffected by taphonomic bias, that is, drilled limpet shells show a uniform distribution across taphonomic grades and the central tendency does not differ from undrilled shells (Fig. 6A–B). Nonetheless, the preservation status between drilled and undrilled shells differed significantly; drilled shells showed relatively poorer preservation than undrilled shells (see Table 4; Figs. 7A–B). Undrilled shells were more fragmented and had higher encrustation than drilled shells; however, drilled skeletons had relatively lower color preservation and generally higher corrasion and bioerosion than undrilled shells (Fig. 7A–B). Hence, the presence of drill holes may have negatively affected the preservation potential of limpet shells, possibly by weakening the shells (relatively higher corrasion, bioerosion, and color loss than undrilled specimens) (Fig. 7A–B). Due to the disproportionate numbers of drilled and undrilled shells of all limpet species, however, further analyses are needed. As TTG varies statistically across species, possibly due to differences in shell strength or shape (Zuschin and Stanton, 2001), the large number of drilled specimens of *L. digitalis* could be driving the apparent difference in overall TTG between drilled and undrilled shells. Drill holes were never found on the edge of a shell fragment, indicating that drill holes were not the cause of shell breakage (Roy et al., 1994), so it is unclear how the presence of these holes could be contributing to differences in preservation potential of shells that have not been subjected to compaction or burial. It is possible that biostratinomic processes due to wave and current action (although both are minor in the study area, which is a wave-protected bay), such as fragmentation and corrasion, are exacerbated by the presence of drill holes. While the pooled results may be somewhat ambiguous, there seems to be a significant difference in preservation potential for *L. digitalis*. Higher TTG due to the presence of drill holes would result in the underrepresentation of drill holes in subfossil and fossil assemblages, and the inaccurate measurement of predation pressure. These results conflict with other studies (Kowalewski, 1993; Nebelsick and Kowalewski, 1999; but see Roy et al., 1994), which found no difference in the preservation of fossil assemblages due to the presence of drill holes. This apparent contradiction may be because this study examined a modern death assemblage where compaction had not yet occurred, and because the studied individuals here occur in a rocky intertidal shore where shell preservation is generally low, rather than on a soft substrate.

Poorly preserved shells (in this study those with high TTG) may increase the difficulty of drill-hole identification and can lead to two main types of diagnostic errors: (1) misidentification of traces other than drill holes (e.g., substrate borings, dissolution traces, punctures) as drillings of predatory origin (Lescinsky and Benninger, 1994); and (2) true drill holes misidentified as non-predatory in origin. These errors have noteworthy implications for the fossil record. The studied modern limpet shell assemblage is not likely to have been subjected to significant transportation, compaction, or reworking since False Bay has no strong, open-ocean circulation (Dent and Uhen, 1993). Yet the effects of taphonomic processes were already considerable (TTG up to 3–4 for the majority of

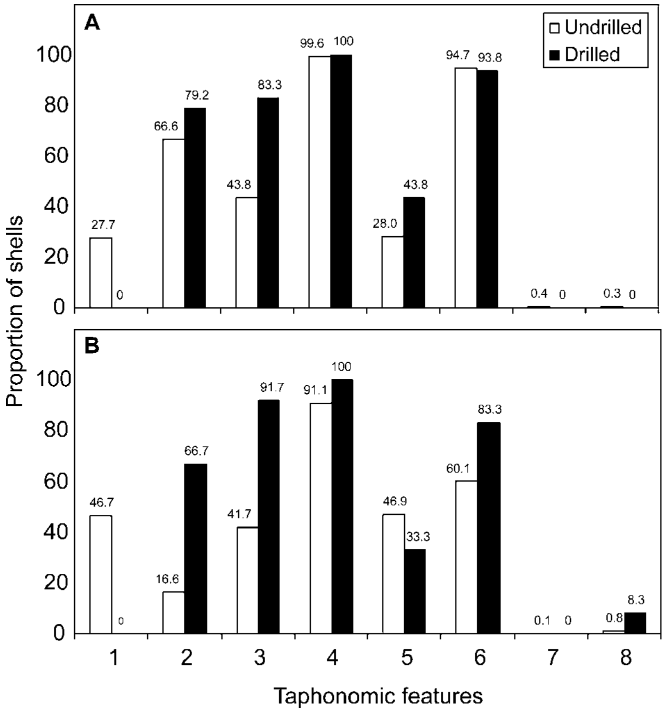

FIGURE 7—Taphonomic features measured on drilled and undrilled limpet shells of *Lottia digitalis* (A) and *L. pelta* (B). Taphonomic variables are as follows: 1 = fragmentation; 2 = non-color preservation; 3 = internal corrasion; 4 = external corrasion; 5 = internal bioerosion; 6 = external bioerosion; 7 = internal encrustation; 8 = external encrustation.

shells, both drilled and undrilled, suggesting a long residence time for this modern assemblage).

CONCLUSIONS

Predation by drilling gastropods on limpets is not commonly reported in the published literature, most likely due to the rarity of the preservation of this ecological interaction. This report is the first quantitative measure of drilling predation intensity and preferences by muricids (*Nucella*) on a modern Lottiidae limpet shell assemblage from False Bay (San Juan Island, Washington, USA). Our study shows that modern limpets (*Lottia digitalis*, *L. pelta*, and *Tectura scutum*) are indeed drilled by *Nucella* with a relatively low frequency (4%) and some non-random preferences with respect to prey species and drill-hole location. There was higher drilling predation intensity upon *L. digitalis*, probably explained by the upper-mid intertidal distribution of this species overlapping with barnacles and mussels (the main food sources of *Nucella*), suggesting opportunistic predation on *L. digitalis*. Drill holes were not found on the largest and thickest *L. pelta* shells, suggesting a size limit at which muricids either stop attacking this species, or employ other predatory strategies besides drilling. The majority of the drill holes (55 of 61) were found closer to the apex (within the top half of the shell) of the shell, although they did not show any specific distribution pattern within the limpet shell. No differences between drill-hole sizes among limpet species were detected. Additionally, there was a positive correlation between drill-hole size (i.e., predator size) and limpet size (maximum length), suggesting that larger predators may drill larger limpet prey.

Uniform frequency distributions across taphonomic grades (TTG) and similar central tendencies of drilled versus undrilled shells suggests that shells with drill holes were not seriously affected by taphonomic bias. The preservation status of drilled and undrilled shells was significantly different, however, suggesting that the presence of drill holes could have negatively affected the preservation potential of the shells. Drilled shells showed relatively higher corrasion, bioerosion, and color loss, and many drilled shells were fairly to poorly preserved. These findings suggest possible underestimation of predation pressure due to the loss of drill holes during biostratinomic processes or to the use of alternative predatory strategies that may not leave traces on the prey skeleton. In addition, these results indicate that pre-burial taphonomic effects may play a far larger role in preservational biases and underestimation of predation frequencies than previously thought. Hence, further studies of drilling-predation frequency and preferences by drilling gastropods on limpet shells is recommended in both modern and fossil assemblages.

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REFERENCES

Alexander, R.R., 1986, Resistance to and repair of shell breakage induced by durophages in Late Ordovician brachiopods: Journal of Paleontology, v. 60, p. 273–285.

Alexander, R.R., and Dietl, G.P., 2001, Shell repair frequencies in New Jersey bivalves: A recent baseline for tests of escalation with Tertiary, Mid-Atlantic congeners: PALAIOS, v. 16, p. 354–371.

Alexander, R.R., and Dietl, G.P., 2003, The fossil record of shell-breaking predation on marine bivalves and gastropods, *in* Kelley, P.H., Kowalewski, M., and Hansen T.A., eds., Predator-Prey Interactions in the Fossil Record: Kluwer Academic/Plenum Press, New York, p. 141–176.

Ausich, W.I., and Gurrola, R.A., 1979, Two boring organisms in a Lower Mississippian community of southern Indiana: Journal of Paleontology, v. 53, p. 335–344.

Bank, R., 1978, Tactics of whelks preying on limpets: Marine Biology, v. 46, p. 157–162.

Berlow, E.L., and Navarrete, S.A., 1997, Spatial and temporal variation in rocky intertidal community organization: Lessons from repeating field experiments: Journal of Experimental Marine Biology and Ecology, v. 214, p. 195–229.

Chapin, D., 1968, Some observations of predation on *Acmaea* species by the crab *Pachygrapsus*: The Veliger, v. 11(Supp.), p. 67–68.

Dent, S.R., and Uhen, M.D., 1993, Tidal reorientation and transport of recent bivalves on a temperate tidal flat, northwestern U.S.: PALAIOS, v. 8, p. 244–249.

Dietl, G.P., and Kelley, P.H., 2006, Can naticid gastropod predators be discriminated by the holes they drill?: Ichnos, v. 13, p. 1–6.

Grey, M., Boulding, E.G., and Brookfield, M.E., 2005, Shape differences among boreholes drilled by three species of naticid gastropods: Journal of Molluscan Studies, v. 71, p. 253–256.

Grey, M., Lelievre, P.G., and Boulding, E.G., 2007, Selection for prey shell thickness by the naticid gastropod *Euspira lewisii* (Naticidae) on the bivalve *Protothaca staminea* (Veneridae): The Veliger, v. 48, p. 317–322.

Harper, E., and Morton, B., 1997, Muricid predation upon an under-boulder community of epibyssate bivalves in the Cape D'Aguilar Marine Reserve, Hong Kong, *in* Morton, B., ed., The Marine Flora And Fauna of Hong Kong and Southern China IV, Hong Kong University Press, Hong Kong, p. 263–284.

Ishida, S., 2004, Initial predation and parasitism by muricid whelks demonstrated by the correspondence between drilled holes and their apparent enveloper: Journal of Experimental Marine Biology and Ecology, v. 305, p. 233–245.

Kelley, P.H., and Hansen, T.A., 2003, The fossil record of drilling predation on bivalves and gastropods, *in* Kelley, P.H., Kowalewski, M., and Hansen T.A., eds., Predator-Prey Interactions in the Fossil Record: Kluwer Academic/Plenum Press, New York, p. 113–139.

Kelley, P.H., and Hansen, T.A., 2006, Comparisons of class- and lower taxon-level patterns in naticid gastropod predation, Cretaceous to Pleistocene of the U.S. Coastal Plain: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 27, p. 302–320.

Kingsley-Smith, P.R., Richardson, C.A., and Seed, R, 2003, Stereotypic and size-selective predation in *Polinices puchellus* (Gastropoda: Naticidae) Risso 1826: Journal of Experimental Marine Biology and Ecology, v. 295, p. 173–190.

Kowalewski, M., 1993, Morphometric analysis of predatory drill holes: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 102, p. 69–88.

Kowalewski, M., 2004, Drill holes produced by the predatory gastropod *Nucella lamellosa* (Muricidae): Paleobiological and ecological implications: Journal of Molluscan Studies, v. 70, p. 359–370.

Kowalewski, M., Dulai, A., and Fursich, F.T., 1998, A fossil record full of holes: the Phanerozoic history of drilling predation: Geology, v. 26, p. 1091–1094.

Kowalewski, M., and Kelley, P.H., eds. 2002, The Fossil Record of Predation: Paleontological Society Special Papers, 8: Yale University, New Haven, Connecticut, 396 p.

Lamb, S., 1978, Snail-limpet interactions with emphasis on feeding and behavior responses in a ecological context, *in* Biological Studies on Limpets: Student Research Projects for Biology s32, Marine Ecology, Bates College, conducted at Friday Harbor Labs, Spring Quarter, 1978, University of Washington, p. 154–183.

Leighton, L.R., 2002, Inferring predation intensity in the marine fossil record: Paleobiology, v. 28, p. 328–342.

Leighton, L.R., 2003, Morphological response of prey to drilling predation in the Middle Devonian: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 201, p. 221–234.

Lescinsky, H.L., and Benninger, L., 1994, Pseudo-borings and predator traces: Artifacts of pressure-dissolution in fossiliferous shales: PALAIOS, v. 9, p. 599–604.

Lowell, R.B., 1986, Crab predation on limpets: Predator behavior and defense features of the shell morphology of prey: Biological Bulletin, v. 171, no. 3, p. 57–596.

Nakano, T., and Ozawa, T., 2004, Phylogeny and historical biogeography of limpets of the order Patellogastropoda based on mitochondrial DNA sequences: Journal of Molluscan Studies, v. 70, p. 31–41.

Nakano, T., and Ozawa, T., 2007, Worldwide phylogeography of limpets of the order Patellogastropoda: Molecular, morphological and palaeontological evidence: Journal of Molluscan Studies, v. 73, p. 79–99.

Navarrete, S.A., 1996, Variable predation: Effects of snails on a mid-intertidal succession community: Ecological Monographs, v. 66, p. 301–321.

Nebelsick, J.H., and Kowalewski, M., 1999, Drilling predation on Recent Clypeasteroid echinoids from the Red Sea: PALAIOS, v. 14, p. 127–144.

Palmer, A.R., 1988, Feeding biology of *Ocenebra lurida* (Prosobranchia: Muricacea): Diet, predator-prey, size relations, and attack behavior: The Veliger, v. 31, p. 192–203.

Rasband, W.S., 1997–2007, ImageJ: U. S. National Institutes of Health, Bethesda, Maryland, USA, http://rsb.info.nih.gov/ij/. Checked October 27, 2008.

Roy, K., Miller, D.J., and Labarbera, M., 1994, Taphonomic bias in analyses of drilling predation: Effects of gastropod drill holes on bivalve shell strength: PALAIOS, v. 9, p. 413–421.

Sanford, E., Roth, M.S., Johns, G.C., Wares, J.P., and Somero, G.N., 2003, Local selection and latitudinal variation in a marine predator-prey interaction: Science, v. 300, p. 1135–1137.

Schiffbauer, J.D., Yanes, Y., Tyler, C.L., Kowalewski, M., and Leighton, L.R., 2008, The microstructural record of predation: A new approach for identifying predatory drill holes: PALAIOS, v. 23, p. 810–820.

Sheehan, P.M., and Lesperance, P.J., 1978, Effect of predation on population-dynamics of a Devonian brachiopod: Journal of Paleontology, v. 52, p. 812–817.

Vanduzer, K., 1978, Identification guide to limpets of the Friday Harbor region, and a study of morphological variation in the limpet *Collisella peta*, *in* Biological Studies on Limpets: Student Research Projects for Biology s32, Marine Ecology, Bates College, conducted at Friday Harbor Labs, Spring Quarter, 1978, University of Washington, p. 1–20.

Vermeij, G.J., 1978, Biogeography and adaptation: Patterns of marine life: Harvard University Press, Cambridge, 332 p.

Vermeij, G.J., 1980, Drilling predation of bivalves in Guam: Some paleoecological implications: Malacologia, v. 19, p. 329–334.

West, L., 1986, Interindividual variation in prey selection by the snail *Nucella* (=*Thais*) *emarginata*: Ecology, v. 67, p. 798–809.

Wieters, E.A., and Navarrete, S.A., 1998, Spatial variability in prey preferences of the intertidal whelks *Nucella canaliculata* and *Nucella emarginata*: Journal of Experimental Marine Biology and Ecology, v. 222, p. 133–148.

Yamamoto, T., 2004, Prey composition and prey selectivity of an intertidal generalist predator, *Muricodrupa fusca* (Küster) (Muricidae): Marine Ecology, v. 25, p. 35–49.

Zuschin, M., and Stanton Jr., R.J., 2001, Experimental measurement of shell strength and its taphonomic interpretation: PALAIOS, v. 16, p. 161–170.

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