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Edge-drilling behavior in the predatory gastropod *Notocochlis unifasciata* (Lamarck, 1822) (Caenogastropoda, Naticidae) from the Pacific coast of Panama: taxonomic and biogeographical implications

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ABSTRACT

We conducted a laboratory study to determine drillhole site-selectivity patterns in the predatory behavior of *Notocochlis unifasciata* (Lamarck, 1822), which is a common naticid gastropod on the eastern Pacific coast of Central America, preying on two infaunal venerid bivalves – the thin-shelled and weakly ornamented *Leukoma grata* (Say, 1831) and the thick-shelled and strongly ornamented *Iliochione subrugosa* (Wood, 1828). Spatial patterns of drillhole distribution indicate strong preferences for drilling the umbonal region and the ventral edge of the shell, with the proportion of edge- to wall-drilling attacks increasing in thicker, strongly ornamented prey that were larger than their predator's own size. Drilling patterns from museum and beach samples of *I. subrugosa* collected across the geographic range of *N. unifasciata* (Panama to Costa Rica) were consistent with laboratory findings. Review of the confirmed cases of edge-drilling behavior by other naticids indicates that this study is the first confirmed report of the behavior in the naticid subfamily Naticinae. In light of these findings, we discuss hypotheses on the geography and ecology of edge-drilling predation by subtropical and tropical naticids to guide future research.

INTRODUCTION

Naticid gastropods are important infaunal predators of mollusks in marine soft-bottom communities worldwide that drill a circular hole through their prey's shell in order to feed (Kabat, 1990; Kelley & Hansen, 2003). Numerous studies on fossil and extant naticid predation have taken advantage of these highly quantifiable drilling traces in molluscan death assemblages to study the ecology and evolution of naticids and their prey (Kitchell, 1986; Kowaleswki, 2002; Kelley & Hansen, 2003). We still know very little, however, about how prey-capture behavior varies within and among naticid species in large part because research has focused on the traces of predation preserved on prey shells more than the behavior of the living organisms that produced them (Gonor, 1965; Kowalewski, 2002; Kelley & Hansen, 2003).

By far the most common mode of naticid predation is drilling a hole through the wall of the prey's shell, typically near the umbo or center of the shell of bivalved prey (Negus, 1975; Rosewater, 1980; Vignali & Galleni, 1986; Ansell & Morton, 1987; Dietl & Alexander, 1997; Alexander & Dietl, 2001; Kingsley-Smith et al., 2003). A less well-known mode of naticid predation is edge drilling, in which a predator drills a hole at a point on the commissure between the closed valves of a bivalved prey (Vermeij, 1980; Taylor, 1980; Ansell & Morton, 1985; Vermeij & Roopnarine, 2001). Edge drilling takes less time than wall drilling because the prey's shell is typically thinnest at its margin, and is hypothesized to be advantageous in biologically hazardous environments where naticids face risks from enemies during the slow process of drilling prey (Vermeij & Roopnarine, 2001; Dietl et al., 2004; Dietl & Herbert, 2005).

Here we report on the drilling behavior of the naticid *Notocochlis unifasciata* (Lamarck, 1822) – formerly "*Natica unifasciata*"; see Appendix 1 – from Panama feeding on the venerid bivalves *Leukoma grata* (Say, 1831) and *Iliochione*

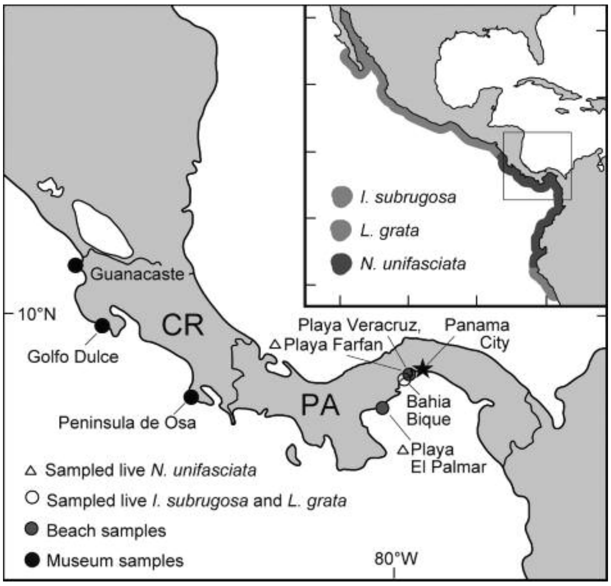

Figure 1. Map of southern Central America showing collecting localities. Geographic ranges of *Iliochione subrugosa, Leukoma grata* and *Notocochlis unifasciata* are shown in inset. CR = Costa Rica, PA = Panama.

subrugosa (Wood, 1828) under laboratory conditions. This geographically wide-ranging naticid species occurs on intertidal mud- and sand-flats from Costa Rica to northern Peru (Keen, 1971), where it preys on a diversity of gastropod and bivalve prey (Gonor, 1965; Hughes, 1985). Our laboratory observations with *N. unifasciata* provide the first unequivocal evidence of edge-drilling behavior in the genus *Notocochlis*. We also discuss the role of prey morphology (shell thickness, ornamentation and size) on edge-drilling behavior by *N. unifasciata*, provide evidence of edge drilling from beach-collected and museum samples of *I. subrugosa* across the geographic range of *N. unifasciata*, and outline hypotheses on the geography and ecology of edge-drilling predation by subtropical and tropical naticids to guide future research.

MATERIAL AND METHODS

LABORATORY OBSERVATIONS

Thirty live specimens of *N. unifasciata* (13.2-40.0 mm in shell height (H)) were collected from intertidal habitats at Playa Farfan and Playa El Palmar near Panama City, Panama (Fig. 1). Live prey specimens of both *L. grata* (~9-34 mm length (L)) and *I. subrugosa* (~12-30 mm L) were periodically collected from Bahia Bique (Fig. 1) throughout the duration of the 2-month long study, which ran between April and May 2010 at the Smithsonian Tropical Research Institute's Naos Island Laboratory in Panama City, Panama. These bivalve taxa were selected because of their contrasting shell morphology, which has been reported to influence the selection of a drilling site by other tropical naticid species (Ansell & Morton, 1985). *Leukoma grata* typically has a large, thin, relatively flat, and weakly sculptured (cancellate) shell (Fig. 2B), whereas the shell of *I. subrugosa* is relatively smaller, thicker, more inflated, and often strongly ornamented with rounded, commarginal folds (Fig. 2A) (Coan & Valentich-Scott, 2012).

Each *N. unifasciata* specimen was kept separately in a 20 l tank with flow-through seawater maintained at 23.3˚-29.7˚C and 28.9-34.8 ppt. Each tank contained 5 cm of fine sand, which was sufficient for prey to maintain a shallow burrowing depth within 1 cm of the sediment surface as is typical for other venerids in life position (Stanley, 1970). Approximately 50 *L. grata* and *I. subrugosa* specimens were stored together in two separate 20 l holding tanks with 5 cm of fine sand and restocked periodically as prey were consumed by *N. unifasciata* predators. Potential prey fed on naturally occurring algae in the flow-through seawater system. After a 3-day acclimation period, three *I. subrugosa* and *L. grata* prey from the holding tanks were randomly selected from the range of sizes available and added to each *N. unifasciata* tank. The drilling activity of *N. unifasciata* predators was monitored daily, with consumed prey in each tank replaced by a specimen of the same species and approximate size.

SITE SELECTIVITY OF BIVALVE PREY BY *NOTOCOCHLIS UNIFASCIATA*

Drillhole site-selectivity by *N. unifasciata* on its bivalve prey was quantified using a landmark approach (Roopnarine & Beussink, 1999). All drilled specimens removed from the laboratory tanks were digitally imaged using a standard photogrammetric protocol (Perea et al., 2008; Kolbe et al., 2011). Four pseudolandmarks were selected on the exterior surface of the valve to capture drillhole position: (1) the point of maximum curvature of the ventral margin; (2) the point of maximum curvature of the anterior margin; (3) the tip of the beak of the valve; and (4) the point of maximum curvature of the posterior margin. A fifth point corresponded with the drillhole itself. The selected points reflect the general external shape of the valve, which is an important factor for naticid predators when manipulating their prey (Kabat, 1990). The two-dimensional landmark coordinates obtained for left valves were inverted to compare directly with the right valves (Kowalewski, 2004). The partial Procrustes superimposition method was used to remove effects of shell size from the analysis using landmarks 2 and 4 as a reference baseline. The R function for landmark-based morphometrics developed by Claude (2008) was used to undertake this analysis.

EFFECT OF BODY SIZE ON DRILLHOLE SITE SELECTIVITY OF *NOTOCOCHLIS UNIFASCIATA*

To explore the effect of relative predator and prey size on the drillhole site selectivity of *N. unifasciata*, both predator H and L of *L. grata* and *I. subrugosa* prey were measured to the nearest 0.1 mm after each predation event observed in the laboratory tanks. Predators and prey were binned into "small" < 20 mm and "large" ≥ 20 mm size classes to form four predator / prey size ratio combinations: small predator / small prey; small predator / large prey; large predator / small prey; and large predator / large prey.

Sample source	Locality name	Locality ID	Species	Sample ID	# valves	# wall-drilled	# edge-drilled
Museum	Golfo Dulce	31174	*I. subrugosa*	INB001479934	54	5	-
		30265		INB001480878	11	1	4
		31941		INB001483904	72	-	1
		31934		INB001484152	52	3	7
		31985		INB001484506	45	-	1
		32604		INB001486309	57	-	1
Museum	Peninsula de Osa	31627	*I. subrugosa*	INB001481419	8	-	1
		31170		INB001481918	59	5	2
		31935		INB001484084	4	1	-
		31942		INB001484313	3	1	-
		32113		INB001484483	10	2	-
		32439		INB001486114	1	-	1
		31170		INB003303326	4	-	4
Museum	Guanacaste	31850	*I. subrugosa*	INB001485606	2	2	-
		NA		INB001463585	52	6	3
Beach*	Veracruz	-	*I. subrugosa*	-	574	30	12
			L. grata	-	46	2	-
Beach*	Palmar	-	*I. subrugosa*	-	235	24	23
			L. grata	-	29	2	-

*Beach samples represent combined tallies from three bulk replicates per locality.

Table 1. Drilling data on beach and museum samples of *Iliochione subrugosa* and *Leukoma grata*.

BEACH AND MUSEUM SAMPLES

We used beach-collected and museum samples to assess the occurrence of edge-drilling relative to wall-drilling by naticid gastropods under natural conditions across the geographic range of *N. unifasciata*. Beach samples were bulk sampled by collecting all mollusk specimens within a defined area (usually less than a square meter) from the strand line on Playa Veracruz and Playa El Palmar on the eastern Pacific coastline of Panama (Fig. 1). These sites are both relatively low- to moderate wave energy settings with tidal flats generally composed of sandy sediments. Three replicate samples collected at each beach were wet sieved through a 5 mm screen, and valves of *L. grata* and *I. subrugosa* sorted out. In addition, we examined collections of *I. subrugosa* from several localities on the Pacific coast of Costa Rica housed at the Museo de Zoología of the Universidad de Costa Rica for evidence of predatory drillholes. We focused on beach-collected specimen lots that were associated with large collections resulting from survey efforts to document the molluscan diversity of the region. Specimen lots were grouped into three broad localities based on their spatial proximity (Fig. 1): Guanacaste, Golfo Dulce and Peninsula de Osa (Table 1).

Valves of *I. subrugosa* and *L. grata* were measured to the nearest 0.1 mm L and examined for evidence of predatory drillholes. Only complete or nearly complete valves – i.e., valves that were sufficiently complete to describe their original dimensions (Kowalewski, 2002) – bearing a complete naticid-like (Kelley & Hansen, 2003) drillhole were included in the analysis. [Because the position of an incomplete drillhole may "migrate" with subsequent shell growth following an unsuccessful attack we did not include incomplete drillholes found in the beach or museum samples in our site-selectivity analysis.]

The site selectivity of naticid predators and the effect of relative predator and prey size on drillhole placement for beach and museum samples were analyzed using similar methods as the laboratory observations (see above), with the following modification: for body size analysis, maximum outer drillhole diameter was used as a proxy for the size of predators because such information was unknown (Kitchell et al., 1981; Kitchell, 1986). We validated this assumption by using a subsample of *N. unifasciata* specimens and the drillhole sizes they produced from our laboratory observations to estimate the relationship between body size and drillhole size. This approach resulted in the following function: outer drillhole diameter = 0.106 *(predator shell height) + 0.084; $r^2 = 0.65$, $p < 0.001$. Because *N. unifasciata* coexists with other similarly sized naticid species – such as *Polinices uber* (Valenciennes, 1832) – throughout its geographic range, which likely increases observed variation in the relationship between body size and drillhole size due to different species-specific prey-handling behaviors, this estimate was used only as a coarse filter of size. Accordingly, predators were binned into "small" < 20 mm and "large" ≥ 20 mm body size classes, corresponding roughly with an outer drillhole diameter of < 2.2 mm and ≥ 2.2 mm for small and large predator size classes, respectively.

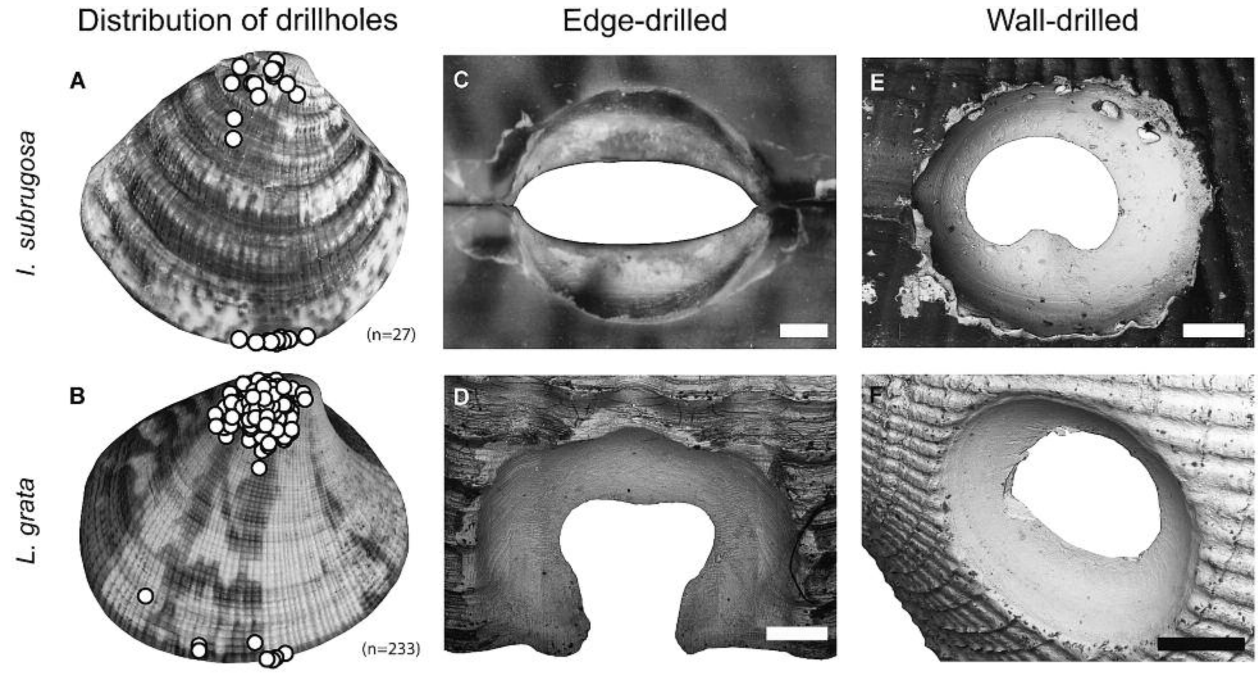

Figure 2. Drilling of bivalve prey by *Notocochlis unifasciata* under laboratory conditions. **2A**. Spatial distribution of *N. unifasciata* drillholes on *Iliochione subrugosa*. **2B**. Spatial distribution of *N. unifasciata* drillholes on *Leukoma grata*. **2C**. SEM image of an edge-drilled *I. subrugosa*; drillhole circular in outline, parallel and highly symmetric relative to the commissural plane between valves. **2D**. SEM image of an edge-drilled *L. grata*; drillhole outline following the shell's commarginal lamellae and oriented nearly perpendicular relative to the commissural plane between valves. **2E**. SEM image of a wall-drilled *I. subrugosa*; drill hole outline circular with irregular margin. Note ragged appearance of the periostracum along the outer margin of the drillhole. **2F**. SEM image of a wall-drilled *L. grata*; oblique view of a drillhole circular in outline and parabolic in cross-section. Scale bars 2C-F = 0.5 mm.

RESULTS

DRILLHOLE SITE SELECTIVITY BY *N. UNIFASCIATA*

A total of 233 individuals of *L. grata* (9.6-34.0 mm L; x̄ = 18.4 mm L) was drilled by *N. unifasciata* in the laboratory tanks. The spatial distribution of *N. unifasciata* drillholes on *L. grata* was non-uniform across the shell surface – 96% (n= 227) of drillholes was located around the umbo (wall drilling), and 3% (n = 6) placed on or near the edge of the prey's shell (i.e., edge drilling; Fig. 2B). Drillholes made by *N. unifasciata* on the wall of its prey were typically circular-ovate in outline and parabolic in cross section (Fig. 2F). In contrast, drillholes on the edge of the prey's shell were more variable in shape and were consistently placed with the vertical axis of the drillhole oriented perpendicular (sensu Dietl & Herbert, 2005) to the commissural plane between the valves of the shell (Fig. 2D).

A total of 27 individuals of *I. subrugosa* (12.7-29.7 L; x̄ = 20.8 mm L) was also preyed upon by *N. unifasciata* in the laboratory. Similar to *L. grata* prey, the spatial distribution of drillholes on the shell of *I. subrugosa* was non-uniform across the shell surface (Fig. 2A). Two areas of the shell were nearly equally drilled – the umbo (56%; n =15) and the ventral edge (44%; n =12). Drillholes located on the wall were typically circular in outline; their borders, however, often appear ragged (or irregularly shaped) under the microscope due to damage to the shell's periostracum (Fig. 2E). In contrast with *L. grata* prey, all drillholes placed on the edge of *I. subrugosa* had the vertical axis of the drillhole oriented parallel (sensu Dietl & Herbert, 2005) to the commissural plane between the valves of the shell (Fig. 2C).

EFFECT OF BODY SIZE ON PATTERNS OF DRILLHOLE SITE SELECTIVITY

Under laboratory conditions, *N. unifasciata* predators drilled *I. subrugosa* prey that matched their own size (Fig. 3A-D). Small (< 20 mm) *N. unifasciata* also tended to drill selectively on or around the umbo of small (< 20 mm) *I. subrugosa* prey (Fig. 3C) and large (≥ 20 mm) *N. unifasciata* preferred to drill on or near the point of maximum curvature of the ventral edge of large (≥ 20 mm) prey (Fig. 3B). This pattern was less evident for *L. grata* prey (Fig. 3I-L); although predators tended to select prey close to their own size (e.g., small (< 20 mm) predators drilled small (< 20 mm) prey in 72.4% of 116 attacks), rare occurrences of edge drilling in *L. grata* prey were not related to prey size.

BEACH AND MUSEUM SAMPLES

Naticid predators wall-or edge-drilled 89 of the 809 (7.8-34.7 mm L; x̄ = 16.0 mm L) and 51 of the 234 (7.0-33.7 mm L; x̄ = 16.9 mm L) valves of *I. subrugosa* that were found in

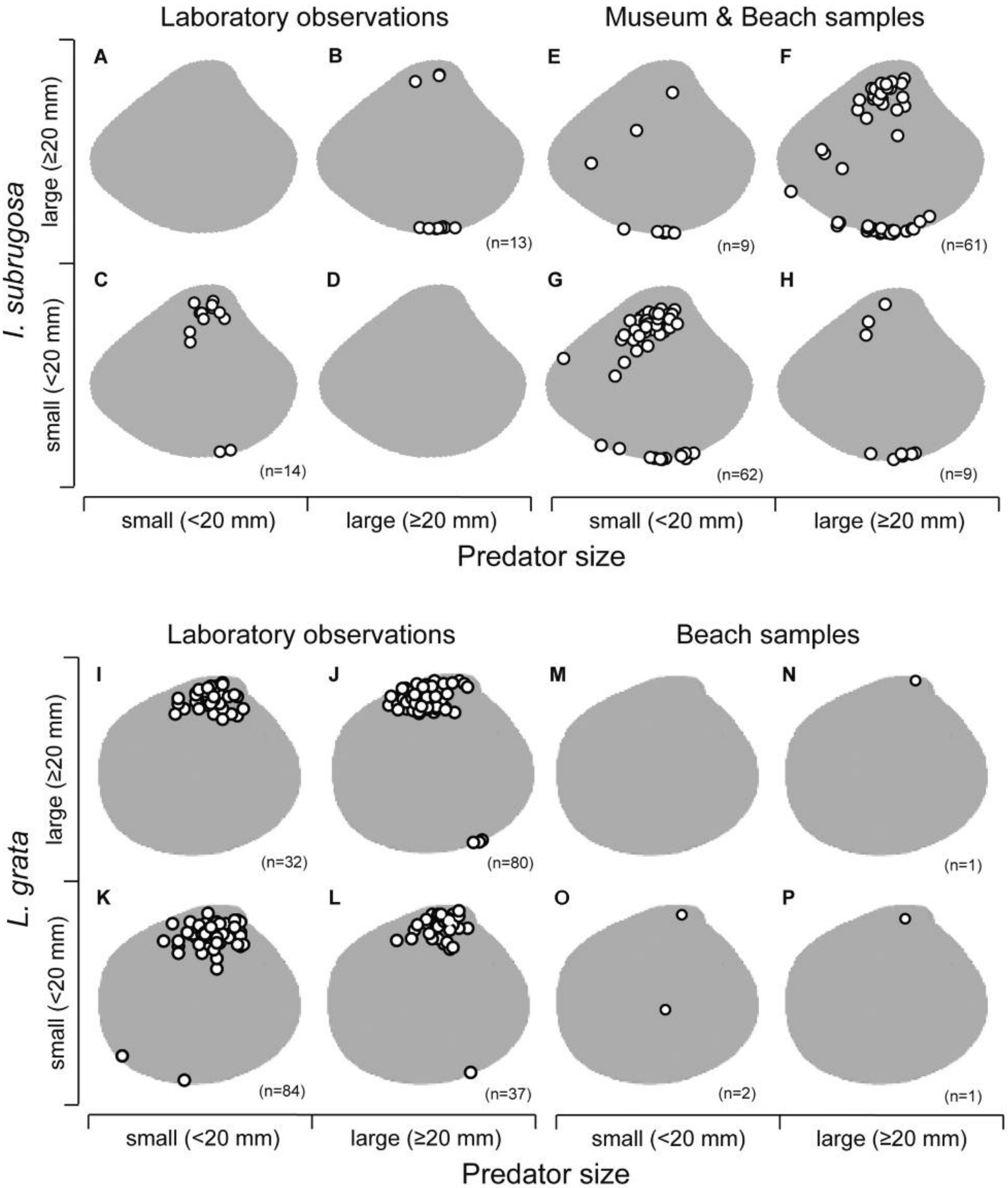

Figure 3. Spatial distribution of naticid drillholes for subsets of predator and prey size classes. **3A-D**. *Iliochione subrugosa* (laboratory). **3E-H**. *I. subrugosa* (combined museum and beach samples). **3I-L**. *Leukoma grata* (laboratory). **3M-P**. *L. grata* (beach samples).

the beach and museum samples, respectively (see Table 1 for breakdown by locality). The spatial distribution of naticid-like drillholes on *I. subrugosa* in both beach and museum samples was non-uniform across the shell surface (Figs 4-5, respectively). As with our laboratory observations with *N. unifasciata*, drillholes were clustered mainly around the umbo and the ventral edge of prey shells. The spatial distribution of drillholes also was consistent among localities (Figs 4-5); however, the proportion of edge- relative to wall-drilled shells varied slightly. The percentage of edge-drilled shells (~40%) relative to wall-drilled shells (~60%) was similar at Golfo Dulce (Table 1; Fig. 5B), Peninsula de Osa (Table 1; Fig. 5C), Playa

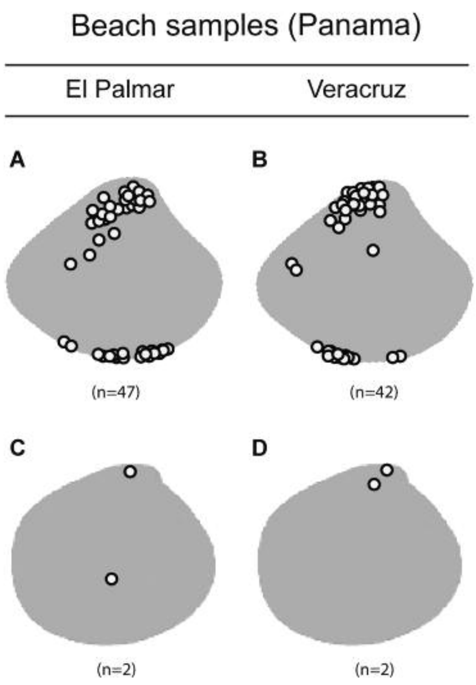

Figure 4. Spatial distribution of naticid drillholes in beach samples from Panama. **4A-B**. *Iliochione subrugosa*. **4C-D**. *Leukoma grata.*

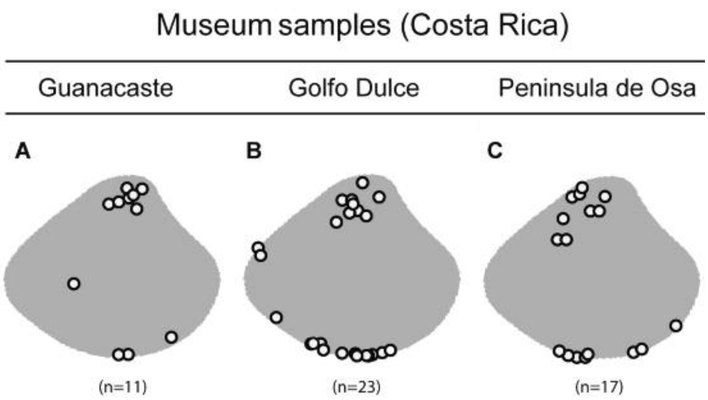

Figure 5. Spatial distribution of naticid drillholes in museum samples of *Iliochione subrugosa* from Costa Rica.

El Palmar (Table 1; Fig. 4A), and Playa Veracruz (Table 1; Fig. 4B). Drilled shells from Guanacaste, however, displayed a lower percentage (~27%) of edge attacks than the other sites (Table 1; Fig. 5A), although this locality also had the smallest number of valves (n =11). In the El Palmar and Veracruz beach samples, only four of the 75 *L. grata* valves (12.1-34.1 mm L; x̄ = 25.0 mm L) found had wall drillholes, which tended to be placed on the umbo by naticid predators (Fig. 4C-D); no edge drillholes were found (Table 1).

Given that the spatial distribution of naticid-like drillholes on the shell surface of *I. subrugosa* was consistent among localities (Figs 4-5), our body-size analysis will focus on combined beach and museum samples hereafter. Analysis resulted in a similar (albeit more variable) effect of predator and prey body size on drillhole site selectivity as we found in our laboratory observations with *N. unifasciata* (Fig. 3A-D vs. E-H). Edge- and wall-drilling were nearly equally employed (51%, n= 31 vs. 49%, n= 30, respectively) as a predatory behavior by large (≥ 20 mm) naticids when they attacked large (≥ 20 mm) *I. subrugosa* prey (Fig. 3F). Thirteen percent (n= 9) of attacks by small naticids (< 20 mm) occurred on large (≥ 20 mm) *I. subrugosa* prey; when this interaction occurred, predators tended to drill on the edge of the prey's shell (Fig. 3E). Small *I. subrugosa* prey (< 20 mm) were typically wall drilled (82% of 62 attacks) by small (< 20 mm) naticids (Fig. 3G). Attacks by large (≥ 20 mm) naticids on small (< 20 mm) *I. subrugosa* prey were uncommon (~ 13% of attacks; n= 9); when this interaction occurred, predators tended to drill on the prey's shell edge (Fig. 3H). Small sample size (n= 4) of *L. grata* prey in the beach samples from El Palmar and Veracruz precluded an assessment of the effect of predator and prey body size on drillhole placement for this species (Fig. 3M-P).

DISCUSSION

EDGE DRILLING OF BIVALVE PREY BY *N. UNIFASCIATA* AND OTHER NATICID GASTROPODS

Edge drilling by *N. unifasciata* was observed in predatory attacks on 42% and 3% of attacks on *I. subrugosa* and *L. grata*, respectively, under laboratory conditions. Previously, confirmed cases of edge drilling of bivalve prey by naticids were limited to two polinicine genera, *Polinices* and *Mammilla* in the Indo-West Pacific (IWP) region. Vermeij (1980) experimentally confirmed speculation of Taylor (1980) that *Polinices mammilla* (Linnaeus, 1758) – formerly *Polinices tumidus* (Swainson, 1840) – edge drilled its bivalve prey on reef-flats in Guam, and Ansell & Morton (1985, 1987) observed that *Mammilla melanostoma* (Gmelin, 1791) – formerly *Polinices melanostomus* – and *P. mammilla* edge drilled their bivalve prey in Hong Kong. Mondal et al. (2014) also recently showed that *Polinices lacteus* (Guilding, 1834) is capable of edge drilling bivalve prey in the Florida Keys, with the implication that the behavior is not restricted to the IWP region. Our observations with *N. unifasciata* provide the first confirmed case of edge-drilling behavior outside the Polinicinae as well as inside the eastern Pacific region.

Unconfirmed reports of edge drilling of bivalve prey by subtropical to tropical naticids are limited to predation traces found in death assemblages of the following venerids: *Timoclea ovata* (Pennant, 1777) in the Azores, which, according to Morton (2009), was "likely" drilled by *Natica prietoi* Hidalgo, 1873; *Chione elevata* (Say, 1822) in the Florida Keys, which Morton & Knapp (2004) attributed to predation by *Naticarius canrena* (Linnaeus, 1758) (but see Mondal et al., 2014); and *Chionista fluctifraga* (Sowerby II, 1853) in the northern Gulf of California, which Smith & Dietl (in press) attributed to predation by *Notocochlis chemnitzii* (Pfeiffer, 1840). Vermeij (1993, fig. 5.6: p. 107) also illustrated an edge-drilled specimen of *I. subrugosa* from Playa Venado in Panama, implicating *P. uber* as the "likely culprit", although our results suggest that co-occurring *N. unifasciata* could also have been responsible (see below). These unconfirmed reports of edge drilling present promising targets for future research because they collectively suggest that the behavior may be taxonomically and geographically widespread within the Naticinae.

INFLUENCE OF SHELL MORPHOLOGY ON EDGE-DRILLING BEHAVIOR BY *N. UNIFASCIATA*

Edge-drilling behavior has been suggested as a means by which naticids overcome the defenses of thick-shelled prey (Ansell & Morton, 1987). Our results with *I. subrugosa* and *L. grata* confirm this interpretation: the proportion of edge- to wall-drilling attacks in our laboratory study increased in thicker-shelled *I. subrugosa* prey relative to *L. grata*; the latter thin-shelled species was overwhelmingly drilled in the umbonal area of the shell (Fig. 2B). *Notocochlis unifasciata* did not, however, employ edge-drilling behavior exclusively in attacking its thicker *I. subrugosa* prey, as is the case in other interactions between naticids and their bivalve prey. For instance, of the potential bivalve prey species from Hong Kong that Ansell & Morton (1985) offered *P. mammilla*, two thick-shelled *Anomaloardia* species elicited a 100% incidence of edge-drilling behavior by the predator. Vermeij (1980), excluding "questionable" non-drilling attacks on prey, also noted a 100% incidence of edge-drilling by *P. mammilla* on *Acropagia robusta* Womersley, 1964 and *Gafrarium pectinatum* (Linnaeus, 1758) bivalve prey from Guam. As with *N. unifasciata*, however, these species did not attack all bivalve prey species exclusively by edge-drilling, perhaps because the predator risks having its proboscis injured if the bivalve prey opens and closes its valves while the snail is in the process of drilling (Vermeij, 2001; Dietl & Herbert, 2005).

Ansell &Morton (1985) also suggested a potential role of ornamentation, particularly concentric lamellae located at the shell margin of venerid bivalves, in mitigating the occurrence of edge-drilling predation by *M. melanostoma* in Hong Kong. Several observations suggest that ornamentation may have played a role in the placement of both wall and edge drillholes by *N. unifasciata* on its *I. subrugosa* prey. Unlike other venerid bivalves (e.g., *Bassina*, *Chione*), *I. subrugosa* does not exhibit pronounced, sharp concentric lamellae that may "confuse" predators by offering false valve margins (sensu Ansell & Morton, 1985), but rather broad commarginal undulations (or rounded concentric folds). These folds are strong and regularly spaced on the umbo of the shell, but become weaker and irregularly spaced and often obsolete near the ventral margin of the shell. Wall drillholes of *N. unifasciata* placed in the umbo of *I. subrugosa* were typically positioned over the valley or space between folds (e.g., 67% of 15 (laboratory) and 89% of 54 (beach sample) wall-drilling traces). This preference is consistent with Klompmaker & Kelley's (2015) conclusion that siting of wall drillholes is influenced by the presence of pronounced concentric ornamentation in bivalves (perhaps decreasing prey-handling time for the predator because the prey's shell is thinner in this area). The irregular spacing and width of the folds towards the ventral margin of *I. subrugosa* (especially in large individuals), however, also may have influenced the selection of an edge-drilling site by attacking *N. unifasciata* predators. Edge drilling may have enabled the predator to avoid making potentially costly mistakes (in terms of increased drilling time) in areas of the shell where the location and space between folds is highly variable. Positioning of edge drillholes parallel (Fig. 2C) to the commissural plane of the prey's shell instead of perpendicular to the commissural plane – as is the stereotyped behavior for thin-shelled, weakly ornamented *L. grata* prey (Fig. 2D) – may also have decreased the likelihood of selecting a suboptimal (i.e., thicker) drilling site.

The body size of *I. subrugos*a prey was also an important aspect of prey morphology that influenced edge drilling of *I. subrugosa* prey by *N. unifasciata* in the laboratory. *Notocochlis unifasciata* predators tended to drill principally around the umbo of small *I. subrugosa* prey and on the ventral edge of large prey (Fig. 3B-C). Although beach-collected and museum samples may record the drilling activity of a wide range of drilling predators, including *N. unifasciata*, they confirm our laboratory findings (Fig. 3). These results suggest that edge drilling may not only speed up the predation process (sensu Vermeij & Roopnarine, 2001), but it may also expand the size range of available bivalve prey, allowing for more effective exploitation of thick-shelled, strongly ornamented prey resources in highly competitive environments.

TWO HYPOTHESES ON THE GEOGRAPHY AND ECOLOGY OF EDGE DRILLING BY NATICIDS

Our study helps to refine specific hypotheses concerning the geography and ecology of edge drilling that can be tested in future research. For instance, if edge drilling is advantageous in biologically hazardous environments where naticids face risks from enemies (Vermeij & Roopnarine, 2001; Dietl & Herbert, 2005), the frequency of edge-drilling predation in the tropics should be greatest in the IWP region, which has been shown previously to be more ecologically rigorous relative to the Atlantic-eastern Pacific (AEP) region in terms of the expression of antipredatory traits of prey (see review of evidence in Vermeij, 1978, 1989, 2011). A rigorous test of this hypothesis would require a systematic survey of the geography and frequency of edge-drilling predation throughout the tropics.

Our observations on *N. unifasciata* have implications for testing this hypothesis. Because the proportion of edge- to wall-drilling attacks tends to increase in thick-shelled, strongly ornamented prey (Ansell & Morton, 1985; this study), and may be influenced by the predator-prey size ratio – as we have shown here for *N. unifasciata* – tests of this hypothesis should consider the effects of variability in adaptive prey types (e.g., modes of defense) within samples used to make comparisons (Vermeij, 2002; Alexander & Dietl, 2001). Our observation that edge attacks by *N. unifasciata* were oriented both parallel and perpendicular to the commissural plane between the valves of the shells of *I. subrugosa* and *L. grata* prey, respectively, adds a further complication to an assessment of the frequency of edge drilling that would have to be controlled for in any test of the hypothesis. An attack that is oriented at the edge (but perpendicular to the commissural plane) results in a drillhole penetrating only one of the valves of the shell, whereas an edge attack oriented parallel to the commissural plane results in a drilling trace on both valves of the shell – contra Chattopadhyay et al.'s (2013) assertion that edge-drilling attacks only affect one valve. This slight difference complicates standard corrections (see Kowalewski, 2002) to estimate drilling frequency for prey that have disarticulated elements, such as bivalves, which assume that evidence of predation is preserved by only one disarticulated element.

A related hypothesis articulated by Ansell & Morton (1985) predicts that interspecific competitive interactions between naticid species enable greater resource partitioning of bivalve prey. Ansell and Morton based this hypothesis on the observation that all edge-drilling naticid species (known to them at the time of their study) sympatrically occurred with one or more wall-drilling species (e.g., *P. mammilla* and *Notocochlis gualtieriana* (Récluz, 1844) in Guam, and *M. melanostoma* and *Glossaulax didyma* (Röding, 1798) in Hong Kong). This hypothesis can be restated in terms of the ecological concept of "species-for-species matching" (sensu Schulter, 1990, 2000), in which trait distributions repeat between ecologically equivalent sets of species evolving in physically similar environments.

In the context of the present study, given the consistency in the drilling patterns, it is tempting to consider *N. unifasciata* as the predator responsible for edge-drilling traces found in the beach-collected and museum samples of *I. subrugosa* shells that we examined (Figs 4-5). *Notocochlis unifasciata* coexists, however, with a diverse naticid fauna throughout its geographic range (Keen, 1971), including members of the same genus (*Polinices*) as confirmed IWP and AEP edge drillers, which undoubtedly led Vermeij (1993) to suspect *P. uber* as the "likely culprit" of edge-drilling traces he found in shells of *I. subrugosa* from Panama (and not the more abundant co-occurring *N. unifasciata*). Thus it is not possible at present to determine reliably how many naticid species edge drill *I. subrugosa* under natural conditions, given that a similar pattern of drillhole site-selectivity is commonly found for different naticid species drilling the same prey (Dietl & Alexander, 1997). For Ansell & Morton's (1984) pattern to be upheld in our study area, we would expect that *P. uber* (and other common sympatric species) should only drill through the wall of their prey's shell. Whether species-for-species matching is a general phenomenon of interspecific competition for prey resources of sympatric naticids in Panama (and the tropics more broadly), however, is an open question that can only begin to be addressed rigorously once species-specific and regionally constrained studies, such as we have conducted here with *N. unifasciata*, are done with other species to verify the pattern.

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APPENDIX 1

Notocochlis unifasciata is commonly known in the older literature as "*Natica unifasciata*" or "*Naticarius unifasciata*" (e.g., Keen, 1971; Marincovich, 1977). According to Kabat (2000), *Notocochlis* is the appropriate genus for a number of tropical and warm-temperate naticine species that had previously been lumped into *Natica* or *Naticarius*, including the eastern Pacific *N. chemnitzii*, which has close affinities with *N. unifasciata* (see Marincovich, 1977), and its "cognate" species, the amphi-Atlantic *N. marochiensis* (Gmelin, 1791) and the Indo-Pacific *N. gualtieriana*. Here we follow Kabat's taxonomic decision and provisionally accept *Notocochlis* – pending any further genetic or anatomical evidence – as the best fit for the eastern Pacific *N. unifasciata* (A. Kabat, in litt. 14 Oct. 2015).

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