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RESEARCH NOTE

A NOTE ON EDGE DRILLING PREDATION BY NATICID GASTROPODS

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Edge drilling is a strategy used by some gastropod predators when feeding on bivalve or brachiopod prey in which the borehole is positioned at the valve margin. This strategy can potentially reduce drilling times by a factor of two to three as compared with wall drilling (i.e. drilling near the thicker centre of the valve), the typical default drilling behaviour (Dietl & Herbert, 2005). Dietl, Herbert & Vermeij (2004) showed that, at least for muricid predators, edge drilling is expressed more frequently when drillers are exposed to intense competition risk. They speculated that the reduction in drilling time achieved by edge-drilling snails may be advantageous, allowing a predator to achieve either a higher net energy gain per unit time or reduced exposure to their own predators. There are few reports of edge-drilling behaviour by species of the gastropod family Naticidae, however, and the extent of its use across the family has never been investigated systematically, either in field studies or in experimental settings.

A review of the literature on drilling studies indicates that gastropods of the family Naticidae employ multiple modes of predation when attacking bivalve prey (Table 1; Vermeij, 1980; Ansell & Morton, 1985, 1987). Drilling is most prevalent, but other methods include feeding through the open gape of bivalves that cannot tightly shut their valves (Edwards, 1974) or suffocating prey by enveloping them within the foot (Vermeij, 1980; Hutchings & Herbert, 2013; Visaggi, Dietl & Kelley, 2013). Wall drills are the most common type of drilling employed, particularly by naticid species outside the tropics (Kitchell *et al*., 1986; Ansell & Morton, 1987). Wall drills are typically placed near the umbonal region of the shell (Kelley & Hansen, 2003 and references therein; Morton, 2008) or directly over the centre of the valve (Cata, 1992; Kingsley-Smith, Richardson, & Seed, 2003).

The first confirmed observations of edge drilling by naticids were made in an experimental study of *Polinices tumidus* in Guam, where edge drilling was used against soft-bottom bivalves, with frequencies ranging from 50 to 100%, depending on the prey species (Vermeij, 1980; see also Ansell & Morton, 1985, 1987). Although edge drilling in the laboratory is potentially a behavioural artefact, edge-drilling traces attributed to various naticids have also been reported in field samples collected from localities in and around Guam (Vermeij, 1980) and Hong Kong (Taylor, 1980; Ansell & Morton, 1985). Examples of edge drilling by naticids are mostly restricted to Pacific species of the genus *Polinices*, as defined by Torigoe & Inaba (2011), the sole exception being Morton & Knapp's (2004) report of edge drilling by the western Atlantic *Naticarius canrena*, which was based on field samples from the Florida Keys. However, no direct observations of edge drilling by *N. canrena* were made by Morton & Knapp (2004) in their limited experimental trials; other confirmed edge drillers co-occurred at their field sites (e.g. muricids *Chicoreus dilectus* and *Phyllonotus pomum*: Dietl, Herbert & Vermeij, 2004; Dietl & Herbert, 2005; *Stramonita rustica*: G.S. Herbert, unpublished) and could account for the edge-drilled bivalves found in their field samples. Therefore, there are no confirmed examples of edge drilling naticids in the Atlantic.

Here, we report the first laboratory studies of the predatory behaviours of *Polinices lacteus*, which include the first direct observation of edge drilling by an Atlantic naticid. Our results are limited in scope due to the opportunistic nature of our collections and the small number of naticid individuals available. Dead shells of *P. lacteus* are not uncommon throughout the Florida Keys, but live animals are nocturnal and difficult to find. Five specimens of *P. lacteus* were collected at night from Ohio Key, Florida, in March 2011. Predators were housed separately in recirculating seawater aquaria ($50 \times 26 \times 30$ cm^3, salinity: 34 ± 2, temperature: 22 ± 2°C) with well-sorted siliciclastic sand as a substrate and were offered three *Chione elevata* prey at a time, replenished *ad libitum*. Prey ranged in length from 16.0 to 30.1 mm (mean prey shell length: 22.8 ± 2.6 mm). *Chione elevata* was chosen as the prey as it is one of the most common bivalves in habitats where *P. lacteus* is found and is frequently drilled with 'naticid-like' bevelled holes over the umbo, valve centre and valve margins. Aquaria were monitored daily. Observations included checking for dead prey and whether or not the drillers were feeding. Over the 4-month trial, all predators were active, but three eventually died of unknown causes without feeding. Only two of the snails, with shell lengths of 22.8 and 24.8 mm, drilled and consumed prey. Every attack by these two predators resulted in an edge drill located at the valve margins, with semicircular, countersunk traces on both valves (Fig. 1). Predation success frequencies—as measured by presence of a complete drill hole and dead, consumed prey—were 60% (3 of 5 prey successfully consumed) and 92% (12 of 13 prey successfully consumed), respectively, for these two snails. Edge drilling occurred over the entire range of prey sizes offered.

Experiments with other species of *Polinices* have found that edge-drilling behaviour may be a response to shell traits of the prey (Ansell & Morton, 1985) rather than the threat of

Table 1. Experimental, field (**) and indirect (inferred; marked *) observations on different types of attack modes employed by species of Naticidae.

Predator	Bivalve prey	Prey attack mode			Study area	References
		E	W	O		
Neverita didyma (Röding, 1798)	*Anomalodiscus squamosus* (Linnaeus, 1758)		+	+	Hong Kong	Ansell & Morton (1985, 1987)
	Atactodea striata (Gmelin, 1791)		+	+	Hong Kong	Ansell & Morton (1987)
	Placamen lamellatum (Röding, 1798)		+		Hong Kong	Ansell & Morton (1985)
	Coecella chinensis (Deshayes, 1855)		+	+	Hong Kong	Ansell & Morton (1985, 1987)
	Glauconome chinensis Gray, 1828		+	+	Hong Kong	Ansell & Morton (1987)
	Venerupis philippinarum (A. Adams & Reeve, 1850)		+	+	Hong Kong, Japan	Ansell & Morton (1985, 1987); Rodrigues (1986)
Neverita reclusiana (Deshayes, 1839)	*Chione undatella* (G.B. Sowerby I, 1835)		+		California*	Peterson (1982)
	Leukoma staminea (Conrad, 1837)		+		California*	Peterson (1982)
Neverita lewisii (Gould, 1847)	*Leukoma staminea* (Conrad, 1837)		+	+	Canada, Washington**	Agersborg (1920); Bernard (1967); Peitso *et al.* (1994); Grey (2001)
	Tresus nuttallii (Conrad, 1837)		+	+	Canada**, Washington*	Bernard (1967); Reid & Friesen (1980); Grey (2001)
	Macoma nasuta (Conrad, 1837)		+		Canada**	Reid & Gustafson (1989)
	Saxidomus gigantea (Deshayes, 1839)		+	+	Canada	Bernard (1967)
	Clinocardium nuttallii (Conrad, 1837)		+		Canada	Bernard (1967)
	Mya arenaria Linnaeus, 1758		?	+	Washington**	Agersborg (1920)
	Clinocardium nuttallii (Conrad, 1837)			+	Washington**	Agersborg (1920)
	Venerupis philippinarum (A. Adams & Reeve, 1850)		+	+	Canada	Bernard (1967); Newel & Bourne (2012)
Neverita delessertiana (Récluz, 1843)	*Chione elevata* (Say, 1822)		+	+	Florida	Hutchings & Herbert (2013)
Neverita duplicata (Say, 1822)	*Ensis directus* (Conrad, 1843)			+	?**, Massachusetts	Turner (1955); Edwards (1974); Schneider (1982)
	Mya arenaria Linnaeus, 1758		+		Massachusetts	Edwards (1974); Berg & Porter (1974); Edward & Huebner (1977); Kitchell *et al.* (1981)
	Mercenaria mercenaria (Linnaeus, 1758)		+	+	North Carolina, New Jersey, Florida	Carriker (1951); Edwards (1974); Berg & Porter (1974); Kitchell *et al.* (1981); Boggs *et al.* (1984); Gould (2010); Visaggi, Dietl & Kelley (2013)
	Geukensia demissa (Dillwyn, 1817)		+		North America	Carriker (1951)
	Mytilus edulis Linnaeus, 1758		+		North America	Edwards (1974); Kitchell *et al.* (1981)
	Chione cancellata (Linnaeus, 1767)		+		North America	Kitchell *et al.* (1981)
	Angulus agilis (Stimpson, 1857)		+		Massachusetts**	Edwards (1974)
	Lyonsia hyalina (Conrad, 1831)		+		Massachusetts**	Edwards (1974)
	Gemma gemma (Totten, 1834)		+		Massachusetts**	Edwards (1974); Wiltse (1980)
	Venerupis philippinarum (A. Adams & Reeve, 1850)		+	+	Massachusetts	Aronowsky (2003)
	Macoma sp.		+	+	Massachusetts	Aronowsky (2003)
	Divalinga quadrisulcata (d'Orbigny, 1846)		+		New Jersey*	Alexander & Dietl (2001)
	Lunarca ovalis (Bruguière, 1789)		+		New Jersey*	Alexander & Dietl (2001)
	Periploma margaritacea (Lamarck, 1801)		+		?*	Rosewater (1980)
	Spisula solidissima (Dillwyn, 1817)		+		Delaware	Edwards (1974); Dietl & Alexander (1997)
Notocochlis tigrina (Röding, 1798)	*Mactra luzonica* Reeve, 1854		+		India**	Mondal, Bardhan, & Sarkar (2010)
Notocochlis gualteriana (Récluz, 1844)	*Anomalodiscus squamosus* (Linnaeus, 1758)		+		Hong Kong	Ansell & Morton (1987)

Continued

Table 1. *Continued*

Predator	Bivalve prey	Prey attack mode			Study area	References
		E	W	O		
	Atactodea striata (Gmelin, 1791)		+		Hong Kong	Ansell & Morton (1987)
	Arcopagia robusta (Hanley, 1844)		?	+	Guam	Vermeij (1980)
	Placamen lamellatum (Röding, 1798)		+		Hong Kong	Morton, Pers. Obs. (in Ansell & Morton, 1985)
	Venerupis philippinarum (A. Adams & Reeve, 1850)		+		Hong Kong	Ansell & Morton (1987)
Natica maculosa Lamarck, 1822	*Tegillarca granosa* (Linnaeus, 1758)		+		Malaysia	Broom (1982)
Natica prietoi Hidalgo, 1873	*Timoclea ovata* (Pennant, 1777)	? ^	+		UK*	Morton (2009)
Natica sp.?	*Dinocardium robustum* (Lightfoot, 1786)		+		Texas	Kornicker, Wise & Wise (1963)
Naticarius canrena (Linnaeus, 1758)	*Chione elevata* (Say, 1822)		+		Florida	Morton & Knapp (2004)
	Divalinga quadrisulcata (d'Orbigny, 1846)		+		Florida*	Alexander & Dietl (2001)
	Lunarca ovalis (Bruguière, 1789)		+		Florida*	Alexander & Dietl (2001)
Naticarius hebraeus (Martyn, 1786)	*Spisula subtruncata* (da Costa, 1778)		+		Spain	Cata (1992)
	Glycymeris glycymeris (Linnaeus, 1758)		+		Spain	Cata (1992)
Naticarius intricatoides (Hidalgo, 1873)	*Chamelea gallina* (Linnaeus, 1758)		+		Spain	Guerrero & Reyment (1988)
Euspira catena (da Costa, 1778)	*Donax vittatus* (da Costa, 1778)		+		South Wales	Negus (1975); Macé (1979)
Euspira nitida (Donovan, 1804)	*Spisula elliptica* (Brown, 1827)	? ^	+		Øresund	Bayliss (1986)
	Spisula subtruncata (da Costa, 1778)	? ^	+		Øresund	Bayliss (1986)
	Multiple species		+		UK*	Smith (1932)
	Cerastoderma edule (Linnaeus, 1758)		+		UK	Kingsley-Smith, Richardson, & Seed (2003)
	Chamelea striatula (da Costa, 1778)		+		UK*	Ansell (1960)
Polinices melanostomus (Gmelin, 1791)	*Placamen lamellatum* (Röding, 1798)	+	+		Hong Kong	Ansell & Morton (1985)
	Venerupis philippinarum (A. Adams & Reeve, 1850)	+	+	+	Hong Kong	Ansell & Morton (1985)
Polinices tumidus (Swainson, 1840)	*Anomalodiscus squamosus* (Linnaeus, 1758)	+	+	+	Hong Kong	Taylor (1980); Ansell & Morton (1985, 1987)
	Anomalocardia flexuosa (Linnaeus, 1767)	+	+		Hong Kong	Ansell & Morton (1985)
	Arcopagia robusta (Hanley, 1844)	+		+	Guam	Vermeij (1980)
	Atactodea striata (Gmelin, 1791)	+	+	+	Hong Kong	Ansell & Morton (1985, 1987)
	Coecella chinensis (Deshayes, 1855)	+	+	+	Hong Kong	Ansell & Morton (1985, 1987)
	Callista erycina (Linnaeus, 1758)	+	+		Oman*	Ansell, Pers. Obs. (in Ansell & Morton, 1985)
	Circe corrugata Chemnitz in Schröter, 1788	+	+		Oman*	Ansell, Pers. Obs. (in Ansell & Morton, 1985)
	Ctena bella (Conrad, 1837)	+	+		Guam	Vermeij (1980)
	Placamen lamellatum (Röding, 1798)	+	+		Hong Kong	Ansell & Morton (1985)
	Donax faba Gmelin, 1791	+	+	+	Hong Kong	Ansell & Morton (1985, 1987)
	Dosinia alta (Dunker, 1849)	+	+		Oman**	Ansell, Pers. Obs. (in Ansell & Morton, 1985)
	Gafrarium pectinatum (Linnaeus, 1758)	+		+	Guam	Vermeij (1980)
	Quidnipagus palatum (Iredale, 1929)	+	+	+	Guam	Vermeij (1980)
	Venerupis philippinarum (A. Adams & Reeve, 1850)	+	+	+	Hong Kong	Ansell & Morton, (1985, 1987)
	Glauconome chinensis Gray, 1828	+	+	+	Hong Kong	Ansell & Morton (1987)
	Timoclea marica (Linnaeus, 1758)			+	Guam	Vermeij (1980)
Polinices lacteus (Guilding, 1834)	*Chione elevata* (Say, 1822)	+			Florida	This study
	Divalinga quadrisulcata (d'Orbigny, 1846)		+		Florida*	Alexander & Dietl (2001)

	Lunarca ovalis (Bruguière, 1789)		+		Florida*	Alexander & Dietl (2001)
Polinices incei (Philippi, 1853)	*Donax deltoides* Lamarck, 1818		+	+	Australia**	Morton (2008)
Tectonatica tecta (Anton, 1838)	?			+	South Africa**	Ansell, Pers. Obs. (in Ansell & Morton (1985)
	Choromytilus meridionalis (Krauss, 1848)		+		South Africa	Griffiths (1981)
Laguncula pulchella Benson, 1842	*Venerupis philippinarum* (A. Adams & Reeve, 1850)		+		Japan	Hasegawa & Shinichi (2009); Chiba & Sato (2012)
	Solen strictus Gould, 1861		?	+	Korea	Frey, Howard & Hong (1986)
Lunatia heros (Say, 1822)	?			+	North America	Edward & Huebner (1977)
	Multiple species			+	Massachusetts	Fregeau (1991)
	Leukoma staminea (Conrad, 1837)		?	+	Canada	Grey (2001)
	Mya arenaria Linnaeus, 1758	?^	+	+	Canada*, Maine**, Connecticut	Wheatley (1947); Thurber (1949); Medcof & Thurber (1958); Berg & Porter (1974); Vencile (1997); Beal (2006); Dietl & Kelley (2006)
	Divalinga quadrisulcata (d'Orbigny, 1846)		+		New Jersey*	Alexander & Dietl (2001)
	Lunarca ovalis (Bruguière, 1789)		+		New Jersey*	Alexander & Dietl (2001)
	Spisula solidissima (Dillwyn, 1817)		+	+	Canada**, New York*	Wheatley (1947); Medcof & Thurber (1958); Franz (1977); Dietl & Alexander (1997); Weissberger & Grassle (2003)
	?		+		Canada	Beairsto (1965)
	Venerupis philippinarum (A. Adams & Reeve, 1850)		+	+	Massachusetts	Aronowsky (2003)
	Mercenaria mercenaria (Linnaeus, 1758)		+	+	Massachusetts	Berg & Porter (1974); Aronowsky (2003)
	Macoma sp.		+	+	Massachusetts	Aronowsky (2003)
Lunatia triseriata (Say, 1826)	*Mya arenaria* Linnaeus, 1758		+	+	Canada**, Maine*	Wheatley (1947), Berg & Porter (1974); Vencile (1997)
	Mercenaria mercenaria (Linnaeus, 1758)		+		?**	Berg & Porter (1974)
Sinum perspectivum (Say, 1831)	*Divalinga quadrisulcata* (d'Orbigny, 1846)		+		Florida*	Alexander & Dietl (2001)
	Lunarca ovalis (Bruguière, 1789)		+		Florida*	Alexander & Dietl (2001)
Naticid?^	?	?^			?	Macé (1979)

Taxonomic revisions have been made following the World Register of Marine Species (WoRMS) and Torigoe & Inaba (2011).

E, attack at valve commissure (i.e. edge drilling); W, attack at umbo or valve centre (i.e. wall drilling); O, other modes of attack (e.g. suffocation, feeding through gape, scavenging, etc.); ?, doubtful or incomplete observations; ^, ambiguous data (see text).

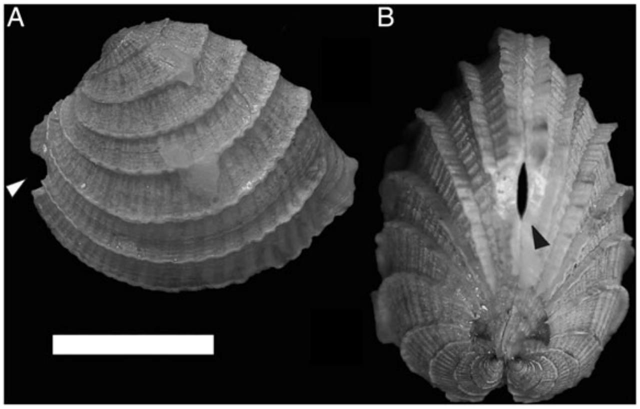

Figure 1. Edge-drilling predation traces on *Chione elevata* made by *Polinices lacteus* in present study (arrows). **A.** Edge drilling at the valve margin without concentric lamellae. **B.** Edge-drilled shells have freshly secreted concentric lamellae at the valve margin. Note that presence of newly secreted concentric lamellae at the ventral margin is not a deterrent against edge drilling on the studied species. Scale bar = 10 mm.

competition, as in some muricids (Dietl, Herbert & Vermeij, 2004). Ansell & Morton (1985) found that *P. melanostomus* mostly preyed on the bivalve *Tapes philippinarum* by wall drilling, but the frequency with which it employed edge-drilling behaviour increased with increasing valve size and thickness of the prey. However, for other prey, such as the venerid *Bassina calophylla*, they showed that *P. melanostomus* employed edge drilling over a wide range of prey sizes, although use of this behaviour decreased when prey had a newly secreted, raised, concentric lamella at the shell margin. These authors proposed that raised lamellae at the shell margin are a deterrent to edge drilling. In our experiment, individuals both with and without freshly secreted concentric lamellae were edge-drilled by *P. lacteus* (Fig. 1) and edge drilling occurred while drilling snails were isolated from potential enemies.

Our experiment and literature review suggest that edge drilling is widespread within the genus *Polinices* (Table 1) and could be a behavioural synapomorphy of the genus, which was found to be a monophyletic clade by Aronowsky (2003). The literature on naticid drilling includes several other possible references to holes 'along the edge' produced by naticids of other genera (Table 1, see references marked ?^), but this language is ambiguous without photos or drawings of drill hole placement and could indicate holes near, but not over, the commissure. We consider these as unconfirmed and doubtful. If future research establishes that edge drilling within the Naticidae is indeed confined to *Polinices*, then the evolution of naticid predatory modes would contrast sharply with that of another drilling gastropod family, the Muricidae, in which edge-drilling behaviour is widespread (G.S. Herbert, unpubl.) and likely evolved multiple times (Vermeij & Carlson, 2000). Future work should also examine whether edge-drilling traces are associated with the earliest fossil *Polinices*, which would be predicted if the behaviour is a synapomorphy of the entire genus. However, we expect that the expression of edge drilling might have been delayed in ancestral *Polinices*, even if the capacity was present. The earliest examples of edge drilling are from the Late Paleozoic (Deline *et al.*, 2003), but the behaviour remained relatively uncommon before the Miocene and became an important mode of attack for tropical predators only in the Recent (Vermeij & Roopnarine, 2001; Vermeij, 2002). Vermeij & Roopnarine (2001) considered this recent increase in the expression of edge drilling to be an example of ongoing, evolutionary escalation at a global scale, in response to increasing risks faced by drilling gastropods from their own enemies.

Our data also have important implications for the interpretation of edge-drilling traces in the Late Neogene fossil record of Florida, where edge drilling was relatively widespread in *Chione* valves from the Pliocene and Early Pleistocene shell beds, but mostly disappeared in Late Pleistocene and Recent *Chione* (Dietl, Herbert & Vermeij, 2004). Pliocene edge drilling was attributed to muricid predators by Dietl, Herbert & Vermeij (2004), based on the absence of drill holes over the umbo (where naticid holes are typically placed) in samples where edge drilling was most common. If naticids had produced any of these edge drills, the authors reasoned, their samples from Pliocene shell beds would have contained a mix of holes over both the edge and the umbo. Our preliminary observations on drilling behaviour of *P. lacteus*, however, suggest that this species may edge drill exclusively in interactions with *Chione* prey. If these experimental observations are representative of the behaviour of *P. lacteus* or its Pliocene antecedents in Florida, then an absence of drill holes at the umbo would be insufficient to rule out changes in *Polinices* drilling activity as an explanation for changes in the distribution of edge drills in *Chione* over time.

However, it remains unlikely that *Polinices* contributed substantially to Late Neogene changes in edge-drilling frequency in Florida. This genus is absent or exceedingly rare in the Pliocene and Early Pleistocene shell beds where Dietl, Herbert & Vermeij (2004) reported edge drilling to be most common. These authors also reported an absence of edge-drilled *Chione* in Pleistocene units where *Polinices* is relatively abundant, which suggests that edge drilling by *P. lacteus* is a relatively recent (i.e. Holocene) phenomenon.

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