Journal of
Molluscan Studies

The Malacological Society of London

Journal of Molluscan Studies (2013) **79**: 310–322. doi:10.1093/mollus/eyt023
Advance Access publication date: 16 July 2013

TESTING THE INFLUENCE OF SEDIMENT DEPTH ON DRILLING BEHAVIOUR OF *NEVERITA DUPLICATA* (GASTROPODA: NATICIDAE), WITH A REVIEW OF ALTERNATIVE MODES OF PREDATION BY NATICIDS

CHRISTY C. VISAGGI[1,2], GREGORY P. DIETL[3,4] AND PATRICIA H. KELLEY[5]

[1]*Department of Biology and Marine Biology, University of North Carolina Wilmington, 601 S. College Road, Wilmington, NC 28403, USA;*
[2]*Department of Geosciences, Georgia State University, PO Box 4105, Atlanta, GA 30302, USA;*
[3]*Paleontological Research Institution, 1259 Trumansburg Road, Ithaca, NY 14850, USA;*
[4]*Department of Earth and Atmospheric Sciences, Cornell University, Ithaca, NY 14853, USA; and*
[5]*Department of Geography and Geology, University of North Carolina Wilmington, 601 S. College Road, Wilmington, NC 28403, USA*

Correspondence: C.C. Visaggi; e-mail cvisaggi@gsu.edu

(Received 12 January 2013; accepted 12 May 2013)

ABSTRACT

Predatory naticid gastropods typically attack other infaunal molluscs by drilling holes that record their activities in the shells of their prey. Other modes of naticid predation, which need not leave complete boreholes, have been noted in the literature and may complicate interpretation of the record of naticid predation in fossil and modern assemblages. ‘Smothering’ is an alternative form of predation that has never been defined clearly with respect to naticid gastropods. Feeding occurs in the absence of a completed drillhole; in most cases suffocation is implied, but reported deaths may be linked to an array of mechanisms (e.g. direct feeding, anaesthetizing mucus). We examine the pervasiveness of alternative modes of predation employed by naticids reported in the literature and offer recommendations regarding the terminology used in referring to such mechanisms. Because it is unclear if predatory behaviours such as suffocation are common in natural settings or are mostly artefacts of laboratory conditions such as insufficient substrate, we examined experimentally the influence of different sediment depths on drilling *vs* suffocation of *Mercenaria mercenaria* prey by *Neverita duplicata*. More than 99% ($n = 404$) of the clams recorded as consumed in our experiments were drilled, regardless of sediment depth, with $<1\%$ ($n = 3$) noted as cases of potential suffocation. Our results indicate that shallower sediment depths do not affect drilling in this species. Analysis of previous studies indicates that prey health and other laboratory effects are likely responsible for many instances of suffocation reported in the literature. Thus concerns regarding use of drillholes as an indicator of predation by naticids in modern and fossil deposits should be alleviated. Future work on other alternative modes of predation by naticids, in both laboratory and field experiments, should focus on validating reported occurrences of such predation and identifying different mechanisms that may be involved.

INTRODUCTION

The Naticidae are a cosmopolitan family of predatory marine gastropods (Kabat, 1990; Kelley & Hansen, 2003). Commonly referred to as moon snails, naticids are widely recognized for their shell-drilling (boring) behaviour that results in characteristically countersunk drillholes in the shells of their prey, comprised mostly of other infaunal molluscs. Naticid drillholes preserved as trace fossils provide a record of ancient predator-prey interactions and are commonly utilized by palaeontologists in studying evolution (e.g. Kitchell, 1986; Vermeij, 1987; Kowalewski & Kelley, 2002; Kelley & Hansen, 2003; Harper & Kelley, 2012). Although drilling is the dominant predatory behaviour employed by moon snails, nondrilling mechanisms by naticids have been reported in the literature. Over the last decade, increased awareness of alternative modes of predation (sometimes referred to as ‘atypical’, ‘anomalous’ or ‘aberrant’ behaviours) has raised uncertainty about the interpretation of data provided by bevelled drillholes attributed to naticids (e.g. Leighton, 2002; Harries & Schopf, 2007; Kelley & Hansen, 2007); however, no report has yet addressed specifically how pervasive alternative forms of predation are among the Naticidae and how these predatory behaviours are executed. In this study we review literature accounts of alternative forms of naticid predation and employ laboratory experiments to examine how factors in artificial settings, specifically insufficient sediment depth, may influence reported occurrences of alternative modes of predation. In particular, we focus on predation commonly referred to as 'suffocation' by biologists and 'smothering' by palaeontologists.

Alternative modes of predation

Naticid gastropods are often regarded as models of stereotypy in their predatory behaviour (Kitchell, 1986; Kabat, 1990). Burrowing through soft substrates, most naticids forage at or below the sediment surface and remain submerged while in pursuit of their prey. Prey manipulation begins as a victim is captured, secured in the large muscular foot of the naticid and enveloped in a film of mucus. Although foraging may occur near the sediment surface, an immobilized prey is usually dragged down into the substrate before drilling is initiated (see summaries in Kitchell, 1986; Kabat, 1990; Reyment, 1999; Kelley & Hansen, 2003). Shell penetration is achieved by alternation of chemical etching and physical abrasion (Ziegelmeier, 1954; Fretter & Graham, 1962; Carriker, 1981; Kabat, 1990), after which the proboscis is inserted through the hole for consumption of prey. Alternative modes of naticid predation do not require completed drillholes for feeding to commence.

To facilitate discussion, we categorize modes of naticid predation (Table 1) first by the primary attack (drilling or nondrilling) and then according to the outcome of each death scenario (preservation of a complete drillhole, incomplete drillhole, or no drillhole, which would affect interpretation of predation in the fossil record). Nondrilling predation includes operculum wedging and direct feeding via a natural opening. Suffocation is an alternative mode of naticid predation that may either accompany or occur without drilling of prey.

Alternative modes of naticid predation have been recorded in both field (Table 2) and laboratory (Table 3) settings. Field reports of alternative predatory behaviours are based mostly on gaping prey or rely on indirect observations, such as incompletely drilled or undamaged shells from experimental plots. Documentation of suffocation in bivalves capable of tightly closing their margin is restricted usually to laboratory observations. This situation is not surprising given that the infaunal mode of naticids prevents study of their behaviour in the field without interruption.

The present work focuses on deaths due to suffocation in which entry through the commissure is permitted via forced gaping before or during the drilling process, rather than through an existing permanent gape, which may allow feeding without prior suffocation of prey. Suffocation, whether intentional or not, may be advantageous if it reduces prey handling time before feeding begins (Hughes, 1985; Ansell & Morton, 1987). It also may be less expensive energetically than is drilling (Ansell & Morton, 1987; Kabat, 1990) and should limit periods of rest needed for repair of the radula due to wear (Reyment, 1999). Such suffocation has sometimes been referred to as 'smothering'. However, this term is not defined clearly in the literature and smothering has not been addressed explicitly as a form of naticid predation. Therefore, we begin by tracing the evolution of the word 'smothering' as used by authors in studies of drilling predation. A thorough investigation of the term's nuanced history and semantic connotations requires a wide diversity of information sources, including primary literature (e.g. peer-reviewed journal articles) and grey literature (e.g. technical reports, dissertations, government documents and conference proceedings). An integration of the qualitative and quantitative information from these sources allows for a richer understanding of what 'smothering' means.

Table 1. Types of naticid predation as summarized from the literature and categorized based on initial attack, cause of mortality, entry for feeding and whether any form of a drillhole (DH) results from the predation event.

Mode of attack	Cause of mortality	Entry for feeding	End product
Drilling	Drilling	Drillhole	Complete DH
	Suffocation*	Aperture/existing gape/ opened valves	Incomplete DH
Nondrilling	Suffocation*	Aperture/existing gape/ opened valves	No DH
	Operculum wedging	Aperture	No DH
	Direct entry	Existing gape	No DH

Only live attacks are addressed; scavenging is not included.

*The precise role of the mucus in this process is unclear; anaesthetizing substances are proposed in the literature.

What is smothering?

Part of the confusion concerning the definition of 'smothering' in studies of drilling predation is caused by a division in the language used by different disciplines. 'Smothering' is an alternative form of naticid predation usually cited by palaeontologists, whereas 'suffocation' is utilized more frequently by biologists (Appendix 1), although Aronowsky (2003) incorporated both words in discussing alternative naticid predation. Further complicating matters, the etymology of the word 'smothering' indicates multiple meanings (e.g. to suffocate or to cover thickly, with some substance). To our knowledge, smothering, as an attack behaviour executed by gastropods, was used first by Morton (1958) to describe predation by members of the Cassididae, Harpidae, Olividae, Tonnidae and Volutidae. Suffocation was not stated explicitly as the cause of death but was implied by the phrase "smothering with the foot" (Morton, 1958: 95). Nondrilling predation by moon snails has been linked to suffocation for nearly a century (Agersborg, 1920). Ricketts & Calvin (1962) used 'smothering' alongside suffocation in the third edition of their book *Between Pacific tides*. Leighton (2001, 2002) applied 'smothering' when citing alternative predation modes described by Vermeij (1980) and Ansell & Morton (1987). Leighton, as well as subsequent palaeontologists (e.g. Harries & Schopf, 2007; Kelley & Hansen, 2007), apparently employed this term as a synonym for nondrilling predation by suffocation, although this use was never stated clearly and perhaps led to misinterpretation of the term as a catch-all phrase for any instance of naticid feeding in the absence of drilling. More recently, Hasegawa & Sato (2009) used 'smothering' to denote merely the encasement of mucus that immobilizes naticid prey for days, even though eventual death is due to drilling and not suffocation, adding further confusion to the meaning of smothering as a predatory behaviour exhibited by moon snails.

Even in cases of mortality attributed specifically to suffocation by naticids, relatively little is known about the actual cause of death. Agersborg (1920) described suffocation first as an outcome of siphon plugging (e.g. in *Mya*) or as a result of being held in the naticid foot until adductor muscles relaxed or the prey died (e.g. in *Protothaca* and *Clinocardium*). However, many bivalves are noted for their capacity to remain closed for long periods, suggesting that such questionable deaths may not be attributable entirely to suffocation; consequently, copious mucus secretions that aid in prey capture and handling are often considered (Ansell & Morton, 1987).

Table 2. Alternative modes of naticid predation reported in the literature based on field investigations.

Naticid taxon	Localities	Prey taxon	Prey family	Gape	Un/Inc	Obs/shells	Reference
Glossaulax reclusiana	CA and OR, USA	*Olivella biplicata*	Olivellidae	n/a	Inc	Both*	Edwards (1969)
Lunatia heros	NB, Canada	*Mya arenaria*	Myidae	Y	Un and Inc	Shells	Thurber (1949) and Medcof & Thurber (1958)
	NS, Canada	*Mya arenaria*	Myidae	Y	Un	Both	Wheatley (1947)
	PE, Canada	*Spisula solidissima*	Mactridae	S	Un	Obs	Wheatley (1947) and Medcof & Thurber (1958)
	ME, USA	*Mya arenaria*	Myidae	Y	Un	Shells	Vencile (1997)
Lunatia triseriata	NS, Canada	*Mya arenaria*	Myidae	Y	Un	Both	Wheatley (1947)
	ME, USA	*Mya arenaria*	Myidae	Y	Un	Shells	Vencile (1997)
Lunatia lewisii	BC, Canada	*Tresus nuttallii*	Mactridae	Y	Un	Obs	Grey (2001)
	BC, Canada	*Saxidomus giganteus*	Veneridae	S	Un and Inc	Both*	Bernard (1967)
	WA, USA	*Tresus nuttallii*	Mactridae	Y	Un	Obs	Reid & Friesen (1980)
	WA, USA	*Mya arenaria*	Myidae	Y	Un	Obs	Agersborg (1920)
		Protothaca staminea	Veneridae	N	Un	Obs	
		Clinocardium nuttallii	Cardiidae	N	Un	Obs	
Neverita duplicata	MA, USA	*Ensis directus*	Pharidae	Y	Un	Shells	Edwards (1974)
	MA, USA	*Ensis directus*	Pharidae	Y	Un	Obs	Schneider (1982)
	n/p	*Ensis directus*	Pharidae	Y	Un	Both	Turner (1955)
Tectonatica tecta	South Africa	n/p	n/p	n/p	Un	Obs	Ansell & Morton (1985)

Taxon names for naticids are updated as per Torigoe & Inaba (2011). Author interpretations are noted as based on observations, shells or both; items marked by an asterisk indicate that laboratory accounts of alternative predation were additionally discussed (see Table 3 for further details). Only live attacks are incorporated here; scavenging is not reviewed. Abbreviations: n/a, not applicable; n/p, not provided; Y, yes; N, no; S, slight; Un, undrilled; Inc, incompletely drilled; Obs, observations. Standard postal abbreviations for states (USA) and provinces (Canada) are employed.

The role of mucus secretions in naticid predation, particularly by suffocation, is controversial. Mucus may: (1) serve in subduing prey by keeping valves or the operculum closed and thus limiting escape (Richter, 1962), (2) produce suffocation by obstructing access to oxygen (Reid & Gustafson, 1989) or (3) have anaesthetizing properties that facilitate prey subjugation as hypothesized by many authors (e.g. Wheatley, 1947; Turner, 1955; Carriker, 1981; Hughes, 1985; Ansell & Morton, 1987). Such a narcotic effect might yield relaxation of the muscles keeping the valves closed, leading to apparent suffocation by permitting an entry for feeding through the margin. Savazzi & Reyment (1989) suggested that mucus from *Natica gualteriana* affected *Umbonium vestiarium* prey even after removal of the predator. Control specimens free of mucus burrowed rapidly (perhaps a flight response), whereas prey with apertures plugged by mucus remained stationary and retracted for several hours. Removal of mucus yielded an active response from *U. vestiarium* within 30 min, however, indicating that any numbing effect was not permanent. Reid & Gustafson (1989) stated that bivalve prey were limp and unresponsive after being drilled, leading them to investigate pharmacological properties of oesophageal gland secretions of *Lunatia lewisii*. They found no paralysing effect in placing these secretions on the heart of *Tresus nuttallii* and concluded that prey must be suffocated as suggested by others.

Nondrilling attacks on bivalves with a permanent gape, or by forced entry through the aperture of gastropods, are not usually considered by palaeontologists to represent deaths by smothering, due to the availability of direct access for feeding. This view is supported by Morton & Morton (1983: 285) in discussions of predation by nonnaticid gastropods as "either smothering them with the foot, or plunging the proboscis into the soft parts". Unfortunately, it is often not clear from the literature if feeding occurs directly through the natural opening or if it is only feasible after first suffocating or anaesthetizing prey, particularly as Agersborg (1920) initially described suffocation by naticids in part based on the gaping prey *Mya*. Thus it remains uncertain if a single agent or a combination of factors may be responsible for several so-called smothering deaths in the literature; resolving such accounts is beyond the scope of our work.

Our review of the literature generates several recommendations concerning terminology applied to alternative modes of naticid predation: (1) avoid using the phrase 'nondrilling predation' if death of prey occurs as a byproduct of the drilling process (e.g. due to suffocation); (2) restrict use of 'suffocation' to situations in which mortality is attributed to respiratory distress; (3) promote the more appropriate phrase 'alternative modes of predation' as encompassing all feeding by naticids that is not accomplished using a completed drillhole and (4) abandon the term 'smothering' as it is not employed consistently or clearly in the literature, in part because multiple mechanisms may be executed by naticids in achieving apparent suffocation. This problematic usage extends to descriptions of 'smothering' predation by other gastropods. Our literature review also highlights that different causal mechanisms may allow moon snails to feed in the absence of a completed drillhole; research is needed on alternative naticid predation modes that may be a concern for studying predator-prey interactions using drillholes. The experiments conducted in this study are a first step in such research.

Sediment depth

Alternative modes of predation such as suffocation may result from unnatural laboratory environments, and in particular a lack of sufficient sediment for burrowing with captured prey. Most aquaria contain only a few centimetres of sand, in contrast to the greater depths naticids might inhabit in the wild. Maximum depths reported from field observations range

Table 3. Alternative modes of naticid predation reported in the literature based on laboratory investigations.

Naticid Taxon	Size, no.	Collected (Exp)	Prey Taxon	Prey Size	Prey Family	%	no./Total	Gape	Un/ Inc	Sed Depth	Monitored	Reference
Conuber melastoma	~27.5, Mu	Hong Kong	*Venerupis philippinarum*	20–40	Veneridae	13%	3/23	N	Un	SL	Daily	Ansell & Morton (1985)
Glossaulax didyma	47–52, Si	Hong Kong	*Venerupis philippinarum*	30–39	Veneridae	50%	8/16	N	Un and Inc	SL	Daily	Ansell & Morton (1987)
			Anomalocardia squamosa	n/p	Veneridae	78%	7/9	N	Un			
			Atactodea striata		Mesodesmatidae	25%	1/4	N	Un			
			Coecella chinensis		Mesodesmatidae	13%	3/23	N	Un			
			Glauconome chinensis		Glauconomidae	57%	4/7	Y	Un			
Glossaulax reclusiana	~29.5, Mu	CA and OR, USA	*Olivella biplicata*	18–28	Olivellidae	81%	17/21	n/a	Un and Inc	SL	n/p	Edwards (1969)
Lunatia heros	24.5–47.5, Si	NJ (NC), USA	*Mercenaria mercenaria*	25–43	Veneridae	27%	13/48	N	Inc	3 cm	1–2 days	Friend (2011)
	Large, B	MA (CA), USA	*Venerupis philippinarum*	20–40	Veneridae	38% (Un),	42/111 (Un),	N	Un and Inc	10–15 cm	Daily	Aronowsky (2003)
			Mercenaria mercenaria	~40	Veneridae	16% (Inc)^	18/111 (Inc)^	N	Un and Inc			
			Macoma spp.	8–45	Tellinidae			S-N	Un and Inc			
	n/p, Mu	NJ, USA	*Spisula solidissima*	larger	Mactridae	n/p	n/p	S	Un	n/p	n/p	Weissberger & Grassle (2003)
	30–60, Si	NB (ON), Canada	*Protothaca staminea*	20–60	Veneridae	9% (Un),	n/p	N	Un and Inc	10 cm	n/p	Grey (2001)
Lunatia lewisii	50–100, Si	BC (ON), Canada	*Protothaca staminea*	20–60	Veneridae	21% (Inc)^		N	Un and Inc	10 cm	n/p	Grey (2001)
	n/p, Mu	BC, Canada	*Saxidomus giganteus*	n/p	Veneridae	≥25%	n/p	S	Un	7.6 cm	daily	Bernard (1967)
	n/p, B	BC (AB), Canada	*Venerupis philippinarum*	37–57	Veneridae	54%	917/1687	N	Un and Inc	SL	n/p	Newel & Bourne (2012)
Natica gualteriana	20.9, Si	Guam	*Tellina robusta*	n/p	Tellinidae	11%	2/19	N	Un	1.4–3.5 cm	n/p	Vermeij (1980)
Natica unifasciata	25–34 (H), Mu	Panama	*Olivella volutella*	15–20	Olivellidae	100%	3/3	n/a	Un	5 cm	Hourly–daily	Hughes (1985)
Neverita duplicata	15–26, B	NC, USA	*Mercenaria mercenaria*	7–23	Veneridae	10%	81/807	N	Un	7.6 cm	2–3 days	Gould (2010)
	Medium–small, B		*Macoma* spp.	~25	Tellinidae	4% (Un),	11/265 (Un),	S-N	Un and Inc	10–15 cm	Daily	Aronowsky (2003)
		MA (CA), USA	*Venerupis philippinarum*	~37	Veneridae	12% (Inc)^	32/265 (Inc)^	N	Un and Inc			
			Neverita duplicata	smaller	Naticidae	100%	1/1	n/a	Inc			
Polinices mammilla	~28, Mu	Hong Kong	*Venerupis philippinarum*	10–40	Veneridae	36%	44/114	N	Un	SL	Daily	Ansell & Morton (1985)
	Larger, B	Hong Kong	*Venerupis philippinarum*	n/p	Veneridae	55%	78/142	N	Un	SL	Daily	Ansell & Morton (1987)
			Anomalocardia squamosa		Veneridae	44%	10/23	N	Un			
			Atactodea striata		Mesodesmatidae	14%	4/28	N	Un			
			Coecella chinensis		Mesodesmatidae	20%	10/49	N	Un			
			Donax faba		Donacidae	16%	3/19	N	Un			
			Glauconome chinensis		Glauconomidae	15%	5/34	Y	Un			
	25.7–35.4, Si	Guam	*Gafrarium pectinatum*	n/p	Veneridae	13%	1/8	N	Un	1.4–3.5 cm	n/p	Vermeij (1980)
			Timoclea marica		Veneridae	100%	4/4	N	Un			
			Tellina robusta		Tellinidae	21%	4/19	N	Un			
			Quidnipagus palatam		Tellinidae	60%	6/10	S	Un			

Taxon names for naticids are updated as per Torigoe & Inaba (2011).

Abbreviations: as in Table 2; SL, sand layer provided but precise depth not given. Locations for specimen collection *vs* experimentation are noted separately, with the latter enclosed in parentheses. Percentages and numbers listed represent the proportion of prey consumed by alternative means. Both predator and prey size are recorded in mm; sizes are based on lengths unless otherwise defined as height (H). The number of predators confined to the same aquarium setup is denoted as single (Si), multiple (Mu) or both (B). Only live attacks are incorporated here; scavenging is not reviewed. ^Available data listed here for prey consumed by alternative means were not divided by prey species by Aronowsky (2003) or by predator species by Grey (2001).

upwards of 15–25 cm (Stinson, 1946; Medcof & Thurber, 1958; Bernard, 1967; Kenchington, Duggan & Riddell, 1998). Mismatches between field and experimental conditions could lead to altered behaviours in laboratory settings, as normal burrowing activities may be restricted (Kabat, 1990). For example, Bayliss (1986) found that *Euspira pulchella* was unable to drill prey in aquaria containing only a few millimetres of sand; although victims could be captured, moon snails were unable to burrow and merely moved in circles, dragging their prey with them. Drilling captive prey commenced only upon relocation to a setup containing 9 cm of sand, in which they immediately burrowed. Hasegawa & Sato (2009) capitalized on modified behaviours exhibited by *Laguncula pulchella* in varying sediment depths to demonstrate how altered life-positions of prey led to differences in drilling of right *vs* left valves. Depth of sediment is often not considered in setting up laboratory experiments; whether or not insufficient depths of sand may lead to predation via suffocation has yet to be explored. Here we address this concern by investigating changes in predatory mode with sediment depth using a naticid species that is studied intensely in both modern communities and palaeontological assemblages.

Neverita duplicata (Say, 1822) is an abundant moon snail inhabiting shallow intertidal to subtidal environments along the eastern coast of the United States. It is a generalist predator that feeds primarily on infaunal bivalves (Belding, 1930; Edwards, 1974). This species is often utilized in laboratory settings (e.g. Kitchell *et al*., 1981; Kardon, 1998; Dietl & Kelley, 2006), and has been reported to suffocate its bivalve prey (Table 3). Fregeau (1991) found that *N. duplicata* preyed on clams at a mean depth of 12.7 cm in laboratory experiments and that it did not attack prey deeper than 16 cm, even when surface clams were removed. Carriker (1951) also reported feeding by *N. duplicata* at 12.7 cm depth in a field setting in New Jersey.

To determine whether insufficient substrate for burying with prey is related to laboratory reports of alternative predation modes, our experiments examined changes in frequency of different forms of predation (drilling *vs* suffocation) by *N. duplicata* when exposed to various substrate levels, ranging from no sand to a maximum depth of 20 cm. We hypothesize that suffocation should be more common than drilling at shallower sediment depths due to extensive prey carrying during prolonged searching for a preferred location to burrow with prey. By varying only sediment depth, we focus on suffocation rather than other alternative modes of predation. For instance, any influence from potentially paralysing mucus secretions should not vary predictably with the amount of substrate provided.

MATERIAL AND METHODS

Sediment depth

The hypothesis that decreasing substrate depths yield increasing deaths by suffocation was tested in a laboratory setting through five treatments: 0 (i.e. no sediment), 1, 2, 6 and 20 cm. The sediment consisted of fine sand collected from nearby Wrightsville Beach, NC, similar to the natural habitat of *Neverita duplicata*. Three replicate trials of 48 days each were conducted at the University of North Carolina Wilmington's Center for Marine Science during September–October 2010, October–December 2010 and June–July 2011, in part due to limited availability of specimens during the winter and concerns regarding suppressed feeding rates in cooler months. Multiple pairwise Fisher exact tests showed that there were no differences across trials in clams consumed by drilling *vs* other deaths ($P > 0.05$ in all cases); thus, only pooled data are reported in subsequent analyses. Variation in the frequency of clams consumed by drilling in different sediment depths was assessed using a chi-square goodness-of-fit test with an alpha level of 0.05.

Each experimental setup contained only a single predator and six prey, which were replaced every 6 d as consumed. *Neverita duplicata* were collected locally from an intertidal flat near Masonboro Inlet, NC (UNCW Research Lease: 34°10′46″N, 77°50′30″W); all moon snails were initially sized at 25–26 mm in length. Height (maximum dimension parallel to the coiling axis) and length (perpendicular to height) were recorded every 6 d for each naticid to evaluate growth rates during the experimental period. *Mercenaria mercenaria* (18–21 mm in anteroposterior length) were used as prey. Predator-prey size ratios for these species are appropriate based on the work of Kitchell *et al*. (1981). Bivalves were obtained from Virginia and North Carolina hatcheries and held in aquaria with access to flowing seawater to permit natural filter feeding prior to use in experiments.

The decision to use *M. mercenaria* as prey was based on several factors. Alternative modes of predation on this species are attributed to naticids in multiple laboratory experiments; other members of the Veneridae are additionally noted as suffocated by naticids in the literature (Table 3). This species is a common prey item of *N. duplicata* in the field (Edwards, 1974) and in experimental research in laboratory settings (e.g. Kitchell *et al*., 1981), in part because it is readily available as a commercial species.

Experiments were conducted in a closed system; each 37.85-l aquarium included an air pump for oxygen circulation. Tanks were monitored every 72 h and seawater was partially changed in each setup during the interval halfway between experimental checks. To minimize the impact of external factors on feeding behaviour, only seawater controlled to room temperature was used (19.4–23.4°C). Surface observations were noted at this midpoint between 6 d experimental checks, but moon snails within the substrate were not disturbed if possible. Salinity and pH also were monitored every 6 d. Salinity fluctuated between 19.2 and 37 ppt; pH ranged between 6.2 and 9.2.

Monitoring of prey health

To test the hypothesis that suffocation is more common at shallower sediment depths due to prolonged prey carrying, it is essential that prey used in laboratory experiments are healthy. Otherwise, decay or scavenging following natural mortality of weak prey could leave empty shells that might be misinterpreted as deaths due to suffocation. To minimize concerns regarding prey health in our study, we eliminated unhealthy prey from our study, i.e. individuals unable to maintain tight valve closure and/or that did not exhibit normal burrowing behaviour (Flimlin, 2004).

Several measures were employed to assess the condition of *Mercenaria mercenaria* prey before, during and after being incorporated in our experiments. First, strength of valve closure was tested before placing prey in experimental setups as well as during experimental checks by trying to insert a fingernail in the ventral margin. The few bivalves exhibiting signs of questionable health, as indicated by successful wedging, were discarded prior to experiments. This process also removed any empty shells that were held together by surface tension (Flimlin, 2004). Ability to wedge a fingernail between valves during the course of experiments was noted as a potential sign of deteriorating health and used as an indicator to replace bivalves as discovered. Secondly, dates of entry into aquaria were recorded on all prey as a way to monitor how long individuals remained in experiments; average duration of occupancy in aquaria was quantified. Thirdly, every 72 h surface observations were noted for signs of decay or weak clams that had gaped or could not bury themselves in the sand (Flimlin, 2004). Finally, following Visaggi (2012), empty shells recovered every 6 d were analysed for signs of decay following natural mortality, including odour and whether any soft parts remained, as naticids typically consume the entire soft tissues of prey (Kitchell *et al.*, 1981).

Incomplete drilling

Incomplete drillholes in several laboratory studies have been linked to abandonment of drilling during suffocation (Table 3). In our study, incomplete drilling, typically due to interruption during experimental checks, was monitored carefully. *Mercenaria mercenaria* containing incomplete drillholes were returned to the same setup upon experimental checks if exhibiting signs of good health. Drillholes were tallied as complete, incomplete or near complete (perforating the shell, but with the opening too small to permit entry by the proboscis), in order to track whether incomplete or nearly complete drillholes were redrilled during subsequent attacks.

RESULTS

Sediment depth

Differences in sediment depth did not impact frequency of prey consumed by drilling *vs* suffocation for *Neverita duplicata* (Fig. 1).

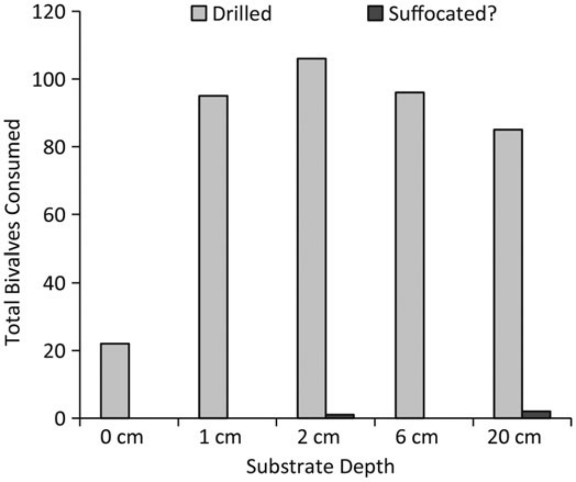

Figure 1. Number of *Mercenaria mercenaria* consumed by *Neverita duplicata* for different sediment depths based on pooled data from all replicates. Mode of death was categorized as either drilled or potentially suffocated.

All moon snails fed during the course of the experiment except for two of the individuals in aquaria lacking sand. Of 411 dead clams recovered, 404 were consumed by drilling. Frequency of prey consumed by drilling is consistent across aquaria regardless of substrate depth (1, 2, 6, 20 cm) using a chi-square goodness-of-fit test ($\chi^2 = 2.31$, df $= 3$, $P = 0.51$).

Three clams were drilled to completion, but were not consumed due to interruption during an experimental check. Two of these individuals (in the 2- and 6-cm aquaria) were not subsequently redrilled; observations 3 d later revealed decay instead. The third clam showed no indication of decay afterward or weakness, yet was discovered in the 20-cm setup within the substrate and completely empty at the next experimental check. Three additional clams were recovered completely empty, but without a drillhole (one each in the 2-, 6- and 20-cm aquaria). One final clam without a drillhole was found gaping atop the sediment surface in the 1-cm setup, but decaying flesh accompanied by an unpleasant odour indicated death by natural causes.

Prey health

Most prey (75%) were consumed within 6 d of entry into aquaria and thus did not linger in experiments long enough for health to deteriorate (Fig. 2). Only eight live individuals were removed and consequently replaced during the course of experiments due to health concerns; four or fewer were replaced per trial. Four of these individuals contained incomplete drillholes. Of the three clams found empty but undrilled, previous signs of poor health followed by evidence suggestive of decay were recorded for the clam in the 6-cm setup, but not for the individuals in the 2- or 20-cm aquaria. Shells of drilled prey were void of soft tissue upon recovery from aquaria; only one individual was documented as partially consumed with the remaining residue left to decay.

Incomplete drilling

Incomplete drillholes resulted from interruptions in drilling during experimental checks and possibly during water changes. Interruptions were most common at the shallowest depths of 1 cm and decreased in frequency as depth of sand increased. Nearly all prey with incomplete drillholes were redrilled successfully regardless of the amount of substrate provided (including the 0-cm setup). Tracking of incomplete boreholes revealed that subsequent drilling occurred in both valves, with 22 instances in the opposite valve *vs* 24 occurrences in the same valve (21 of

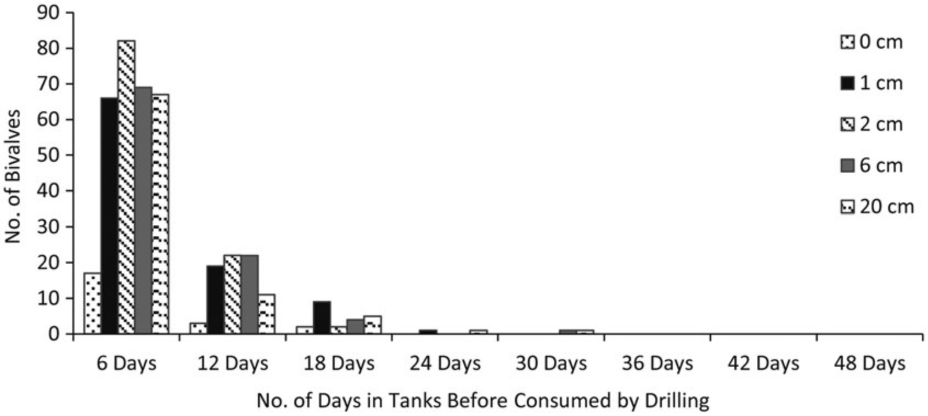

Figure 2. Residency of *Mercenaria mercenaria* in experimental aquaria before being consumed by *Neverita duplicata* by drilling for all substrate depths (all replicates combined).

which coincided completely with earlier incomplete drillings such that incipient attempts were no longer visible). In addition, four holes that were complete but not yet sufficiently widened for feeding were subsequently redrilled, as later observations revealed expanded inner diameters.

DISCUSSION

Our experiments indicate a lack of deaths by suffocation in *Neverita duplicata* consuming *Mercenaria mercenaria*. As discussed below, shallow sediment depths did not impact successful drilling predation. Moon snails were mostly engaged in drilling upon being disturbed during experimental checks in all aquaria containing sand, and nearly all bivalves were drilled regardless of the depth of available substrate. Only three specimens (<1%) were found empty without drillholes.

Possible suffocation events

One of the three individuals found empty without drillholes showed clear evidence of decomposition, indicating decay following natural mortality rather than suffocation or scavenging. The latter interpretation is further supported by the observation that a naticid repeatedly ignored a decaying *Mercenaria mercenaria* on the sediment surface in a 6-cm setup. The other two nondrilled clams lacked signs of decay and may have been suffocated. One specimen, in a 20-cm aquarium, was discovered empty on the sediment surface after only 3 d. The other, in a 2-cm tank, was found on the surface at 3 d but with signs of gaping, perhaps indicating that weakness prevented it from burrowing. Three days after these observations suggesting questionable health, this specimen was discovered empty with no drillhole. Although our experiment was not designed specifically to test the effect of prey health on suffocation, it appears that poor prey health may have made these two individuals susceptible to suffocation.

The only other indication of potential suffocation is represented by a prey item that had lingered in a 20-cm aquarium for 24 days before being drilled to completion, but then was not eaten due to interruption by an experimental check. Although the clam appeared healthy and was returned to the tank, a week later it was found empty within the sediment yet with no signs of decay. If the bivalve was in fact injured by the previous drilling attempt and gaped shortly after being enveloped by the naticid at the onset of a second attack, it may have been suffocated, eliminating the need for further drilling. Alternatively, the naticid may have been able to feed using the former drillhole.

Influence of sediment depth on suffocation

Overall, our experiments indicate that suffocation by *Neverita duplicata* is not linked to insufficient sediment. Two of the three possible instances of suffocation occurred in aquaria with 20 cm of sand, which exceeds the burrowing depth of *N. duplicata* in the field as well as in this experiment; naticids were always found in the upper half of the sediment (usually in 8 cm of sand or less). The results demonstrate that shallower sediment depths do not impede the capacity of *N. duplicata* to drill prey as long as at least 1 cm of sand is provided. Predators often attempted to bury themselves at least partially in the sediment, however, indicating that more substrate is preferred. Drilling occurred beneath the sediment, on the sediment (Fig. 3A), and in the absence of it (Fig. 3B). Prey were held underneath the snail in the 6- and 20-cm aquaria; less substrate forced naticids to drill while lying sideways or upside down with prey wrapped in the foot. However, as long as some sediment was present, regardless of depth, variation in drilling position did not impact predation mode, frequency of feeding or stereotypy of drillholes, as nearly all penetrated in the vicinity of the umbo (Fig. 3C). Drillholes were evenly distributed among right and left valves in each setup (51.2% R: 48.8% L for all depths combined).

Although shallower sediment depths did not seem to impact outcome of predation by *N. duplicata* significantly, absence of sediment greatly affected predatory behaviour. Two of the naticids in our 0-cm setup did not feed over the 48 d and mostly remained upside down on the apex of their shell with their foot extended (Fig. 3D). This behaviour is not commonly observed if sand is provided; Bernard (1967) noted that such behaviour by naticids likely reflects undesirable conditions. These moon snails were stressed in the absence of sediment and showed no interest in available prey. Both naticids immediately reverted to infaunal behaviours, however, when placed in aquaria with sand at the conclusion of experiments. They burrowed promptly and drilled prey despite a nearly seven week hiatus from exposure to infaunal surroundings.

Insufficient sediment hindered feeding by naticids in other laboratory experiments (Bayliss, 1986); nevertheless, some moon snails are capable of foraging in the absence of sand or if given an artificial substrate instead. For example, several authors used clear beads instead of sediment to facilitate viewing of infaunal behaviours (Bernard, 1967; Rodrigues, 1986; Hasegawa & Sato, 2009); apparently naticids were not deterred by this altered substrate. Kingsley-Smith, Richardson & Seed (2003) did not provide any substrate in aquaria for *Euspira pulchella*, but this unnatural state did not impact drilling on cardiid prey (*contra* Bayliss, 1986). Although sediment likely offers greater stability in handling of prey items, one of our *N. duplicata* regularly pursued and drilled clams in the absence of supportive sediment; however, fewer prey were consumed relative to most moon snails in aquaria with sand (22 prey compared with an average of 32 prey per predator in tanks with sediment). Upon conclusion of our sediment depth experiments, four additional *N. duplicata* were placed in aquaria lacking sand for further observation. One individual quickly drilled several *Mercenaria mercenaria* prey without difficulty; all others appeared fixated in the upside-down position with their foot extended.

Our results provide insight as to appropriate sediment depths for laboratory work on *N. duplicata*, alleviating prior concerns that minimal sediment leads to suffocation of prey. However, other species may have different depth requirements (e.g. Huelsken *et al*., 2008) and may not respond in the same way if exposed to varying sediment levels in laboratory settings. In addition, predator size may influence the depth of sediment required for normal feeding behaviour; Kabat (1990) noted that most experiments offer only slightly more sand than the size of the predators or prey under observation. Appropriate substrate depths for prey species should be considered as well, especially for any that exhibit escape behaviours such as leaping or are large and have long siphons for deep burrowing within the sediment, as discussed by Bayliss (1986); extrapolation of laboratory observations to field settings may not be appropriate if artificial conditions do not reflect natural habitats. Rodrigues (1986) specifically commented on this matter, stating that reduced sediment likely altered normal foraging behaviours of *Glossaulax didyma* on *Venerupis philippinarum*. Due to shallow depths of the laboratory setup, moon snails were limited in their capacity to attack prey from below as may occur under natural circumstances.

Potential role of prey health

The rarity of suffocation in our experiments contrasts with accounts of more frequent suffocation by *Neverita duplicata* in other laboratory studies (Table 3); explanations other than insufficient sediment are needed for reports of alleged suffocation. Because suffocation is not easily observed, empty shells that lack completed boreholes typically serve as evidence that suffocation has occurred (and specimens covered in mucus at least are

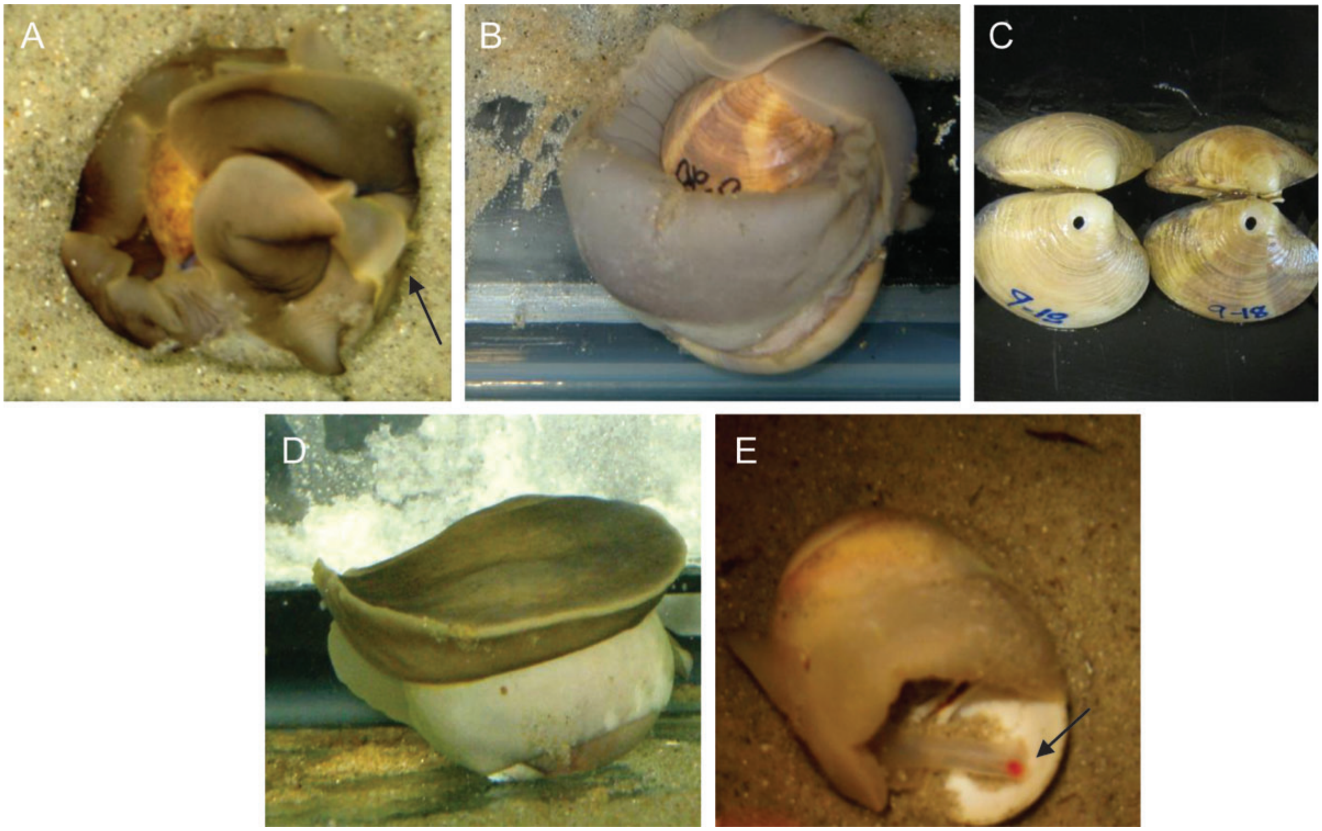

Figure 3. Specimens of predatory *Neverita duplicata* (*c.* 25 mm in length) and *Mercenaria mercenaria* prey (*c.* 20 mm in length). **A.** *N. duplicata* drilling on the surface of the sand in a 1-cm setup. The bivalve prey is visibly wrapped in foot of the naticid; proboscis is engaged as shown by arrow. **B.** *N. duplicata* preying on a *M. mercenaria* in a 0-cm aquarium. Position of prey reflects stereotypical drilling of umbonal region. **C.** Two drilled prey from experiments conducted in autumn. Note date of entry used to monitor duration of prey in experiments. Nearly all drillholes in this investigation were located at umbo, as seen in these specimens. **D.** The recurrent behavioural display characterized as upside-down and foot extended by a naticid in a 0-cm setup. This behaviour was very rarely observed in moon snails exposed to aquaria containing substrate ≥1 cm. **E.** Evidence of scavenging by *N. duplicata* in a laboratory setting. This freshly killed *M. mercenaria* was offered as prey independent of the sediment depth experiments. Note the proboscis indicated by arrow. The naticid wrapped its foot around the prey and attempted to drag and bury with the specimen, although the latter was open and recently dead.

suggestive of handling by naticids; e.g. Ansell & Morton, 1987). However, the condition of prey used in experiments is often not mentioned, so it is unclear in many cases if deaths attributed to suffocation are accidental byproducts of poor prey health. Quality control and monitoring of prey are crucial to identify cases of natural mortality (as recognized by Ansell & Morton, 1985, 1987) or inadvertent suffocation of stressed prey.

Studies that control explicitly for prey health seem to show low frequencies of suffocation. We were able to minimize prey health as a concern by assessing the condition of prey before, during and after experimentation and monitoring the duration of prey used in aquaria. Because 75% of clams consumed by drilling were preyed upon within 6 d, most individuals did not survive long enough to merit concerns regarding gradual deterioration of health. In addition, prior to use in experiments, *Mercenaria mercenaria* had access to food in flow-through holding tanks. Seawater changes offered a new source of food every six days, which should have been adequate to maintain prey that likely fed less actively in the presence of predators. Similarly, Edwards & Huebner (1977), Fregeau (1991) and Vencile (1997) used prey collected locally in their laboratory experiments, offering control in quality and health, and did not report nondrilling mortality. Furthermore, Kardon (1998) did not observe any alternative modes of predation by *N. duplicata* on *M. mercenaria* in long-term experiments that carefully monitored the prey offered.

Nevertheless, recurrent documentation of suffocation has been noted for venerid bivalves, including *Mercenaria*, which are often used as experimental prey (Table 3). Such commercially important taxa are easier to obtain in large batches for use in experiments and bulk purchases are more likely to include empty shells and individuals weakened by parasites or stressful holding conditions, perhaps leading to more instances of perceived suffocation. Experiments conducted using prey purchased at fish markets (e.g. Aronowsky, 2003) or during stressful warm summer temperatures (e.g. Gould, 2010) could have led to gaping, allowing for feeding via the margin, or natural mortality followed by scavenging, which could have been perceived as suffocation. *Neverita duplicata* typically avoids carrion (Kitchell *et al.*, 1986; Fregeau, 1991), but consumes freshly injured (Edwards & Huebner, 1977) or, albeit rarely, recently killed prey (Fig. 3E). However, carrion consumption has been reported for several other species that are also thought to suffocate prey, including *Lunatia heros* (Gould, 1841; Ganong, 1889; Kenchington *et al.*, 1998). In addition, prey health issues could be accentuated in laboratory studies with multiple predators in a tank, if extensive carrying of prey occurred due to a perceived threat from other naticids. Presence of multiple predators could be a factor influencing suffocation in some previous studies (Table 3); decreased incidence of suffocation in our experiments may be related also to the fact that only single predators were utilized in each tank.

Kitchell *et al*. (1986) recognized the issue of prey health in laboratory studies and proposed that Medcof & Thurber (1958) incorrectly ascribed *Mya arenaria* deaths without drillholes to naticid predation instead of considering background mortality of experimental prey after being placed in the field. Although some authors have attributed undamaged shells to naticid predation in field settings (e.g. Wheatley, 1947), others have regarded natural mortality or disease as the destructive agents (e.g. Turner, 1950; Edwards & Huebner, 1977). Most field experiments are conducted in the summer months; heat stress may be a contributing factor that allows naticids to feed on weakened prey without drilling in nature. These examples highlight the challenges in assessing how undrilled prey perish in the field; concerns regarding prey health are not limited to laboratory experiments in attempting to recognize alternative modes of predation by naticids.

Susceptible prey

We found suffocation of *Mercenaria* prey to be extremely infrequent in our experiments. *Mercenaria mercenaria* has tightly closing valves and a moderate metabolic rate and may be able to withstand lower oxygen conditions (Savage, 1976), perhaps contributing to the low incidence of suffocation observed here. We recognize, however, that other prey species may be more susceptible to suffocation.

Studies of drilling predation often consider the antipredatory role of morphological traits such as shell thickness, sculpture and tightness of valve closure (e.g. Vermeij, 1980). The extent to which such morphological characteristics affect susceptibility of prey to suffocation is unknown. For instance, Ansell & Morton (1987) found certain prey (*Venerupis philippinarum* and *Anomalocardia squamosa*) were more frequently consumed by *Polinices mammilla* in the absence of drilling. Yet no clear pattern existed between the percentage of prey attacked through supposed suffocation and characteristics such as surface ornamentation or shell thickness. Tightness of valve closure, however, is likely to be more closely related to suffocation susceptibility. Christensen (1970), for instance, reported that there is an inverse correlation between size of the gape and oxygen tolerance in bivalves, suggesting that widely gaping bivalves are likely more susceptible to suffocation. Although it is often unclear from the literature whether such bivalve prey are suffocated or attacked directly via a natural opening, reports of prey consumed despite incomplete boreholes imply that suffocation may have led to abandonment of a drillhole for easier feeding through the gaped valve margin. Gastropods that can be attacked through the aperture may also be suffocated more easily. For example, Edwards (1969) noted that, of 21 *Olivella biplicata* consumed in laboratory experiments, only 19% were completely drilled; 67% had incomplete drillholes and 14% remained undrilled. Deaths were mostly attributed to suffocation as opposed to operculum wedging, due to the presence of incomplete drillholes.

Because the capacity to endure lower oxygen concentrations is most often inversely correlated with metabolic rate (Christensen, 1970), taxa with faster metabolisms may be more prone to suffocation. For instance, highly active prey such as *Spisula* may be particularly vulnerable. In contrast, species able to remain sealed for very long periods should be drilled exclusively. Vermeij (1980) noted, in experiments on bivalves in Guam, that lucinids were always drilled as opposed to other species apparently expiring from suffocation. Although his comments are based on only 11 observations, he cited high anaerobic capacities of the Lucinidae (e.g. Jackson, 1973) in support of his speculation. Drilling on lucinids is pervasive in modern and fossil assemblages globally (see compilation by Kabat, 1990); suffocation has not been reported in laboratory studies of naticid predation on lucinids (Vermeij, 1980; Ishikawa & Kase, 2007). However, lucinids are not frequently used in predation experiments, likely influenced by the fact that other bivalves of commercial importance are more readily available to use as prey.

In addition to metabolic differences among species, metabolic rates vary during the ontogeny of a species. Several authors have noted that only larger prey were suffocated in their experiments (e.g. Weissberger & Grassle, 2003, for *Spisula* and Ansell & Morton, 1987, for *Venerupis*). These results seem counterintuitive because larger members of a species have reduced metabolic requirements (Bayne, 1976), though perhaps larger shells take longer to drill and put the individual, especially if it is weak, at greater risk of suffocation. Thus prolonged handling of oversized prey merits further consideration in susceptibility to suffocation.

Potential suffocation by other naticid species

Although we found little evidence for suffocation by *Neverita duplicata* in our experiments, suffocation may be more common for other naticid species. Information on feeding behaviours in modern naticids is limited, however, and data are lacking for the majority of extant species. Nevertheless, it is useful to hypothesize the circumstances under which suffocation might be employed by naticid species, as a starting point for future research.

Natural selection would be unlikely to favour suffocation if it is slower or more expensive energetically than drilling. If suffocation is faster than drilling, it could be favoured by natural selection in highly competitive settings (see Dietl, Herbert & Vermeij, 2004, for an analogous argument concerning edge drilling). However, a predator exerts less control over predation success in suffocation, in which success depends more on prey respiration rates, than in drilling. All else being equal, natural selection should favour active behaviours that are predictable (e.g. drilling time-prey shell thickness relationships are predictable), instead of those in which outcomes are less certain (e.g. suffocation). An exception may be suffocation that is aided by toxicity, as drilling is likely more expensive and slower than use of paralysing secretions.

Neurotoxins have been reported in several naticids from the Indo-Pacific, as a result of research on shellfish poisonings in humans (Hwang *et al*., 2007). Tetrodotoxin (TTX), produced by marine bacteria, is documented in a variety of organisms and is accumulated as ingested through diet at multiple trophic levels in the marine realm. Because TTX-bearing gastropods are strongly attracted to concentrations of TTX, Hwang, Noguchi & Hwang (2004) suggested that this neurotoxin may serve as a defence or attack behaviour for such species. Although TTX is found mostly in the muscle or digestive glands of naticids, *Natica lineata* demonstrated a capacity to release seawater yielding acute paralytic toxicity in response to external stimulation, i.e. removal from aquaria (Hwang, Chueh & Deng, 1990). It is interesting to note that TTX is found in *Polinices mammilla* and *Glossalaux didyma*, both reported to suffocate prey; use of TTX in alternative modes of predation by these naticids warrants investigation.

Biogeographical implications

Palaeontologists have focused recently on analysing latitudinal trends in drilling by naticids. No consensus yet exists regarding latitudinal variation in drilling frequency; peaks in drilling are reported poleward, equatorward or at mid-latitudes based on modern and fossil shell deposits (for a review, see Kelley & Hansen, 2007; Visaggi, 2012). Anecdotal suffocation by *Lunatia* under laboratory conditions initially guided Kelley & Hansen (2007) to propose that this behaviour may account for decreased drilling at higher latitudes; based on the present study, it is unclear whether such reports can be substantiated in light of concerns regarding prey health and extrapolated to natural settings. Furthermore, suffocation of prey noted in laboratory experiments is widespread latitudinally (Tables 2 and 3), perhaps indicating that alternative predation modes may contribute to lower drilling at warmer latitudes instead, especially if toxins are involved. Confirmation of alternative modes of predation in other naticid species is needed before a lack of drilling can be attributed to such behaviours based on laboratory observations.

Palaeontological implications

Most palaeontologists have not considered alternative modes of predation in studies of evolutionary patterns of naticid predation, such as tests of the hypotheses of escalation and coevolution based primarily on drillholes (e.g. Vermeij, 1987; Kelley, 1989, 1991, 1992; Dietl & Alexander, 2000; Kelley & Hansen, 2001, 2003). Such studies typically define predation intensity as percent of prey individuals with complete drillholes. However, if alternative modes of predation are regularly employed by moon snails, using only drillholes to infer frequency of successful naticid predation could lead to underestimation of mortality by predatory moon snails in both modern and fossil deposits (Vermeij, 1980; Ansell & Morton, 1987; Leighton, 2002). In addition, incomplete drillholes have been interpreted to signify failed attempts at drilling (e.g. Vermeij, 1987; Kelley & Hansen, 2003), yet this interpretation would be incorrect if suffocation commonly produces incomplete drillholes (Ansell & Morton, 1987; Kowalewski, 2004), as would estimates of prey effectiveness, i.e. the adaptive gap between predator and prey (Vermeij, 1987). Our experiments, however, show that most modern accounts of suffocation in tightly closing bivalves can be discounted as a result of weak prey in laboratory settings, alleviating concerns regarding the interpretation of the frequency of complete and incomplete drillholes.

CONCLUSIONS

Despite exhibiting stereotypic behaviours useful for studying ecological and evolutionary aspects of predator-prey interactions, naticid gastropods have been reported as utilizing alternative modes of predation, such as suffocation. Our study indicated a lack of suffocation by *Neverita duplicata* on *Mercenaria mercenaria*; 99% of consumed prey were drilled. Different sediment depths did not impact predation by drilling or frequency of feeding except in the absence of any sediment; reports of suffocation in the literature may largely be a result of poor prey health or other effects of laboratory settings.

Although our data indicate that shallower substrates do not impact predation by drilling, we recognize that only a single predator and prey species are examined here. We offer the following recommendations for future work on alternative modes of naticid predation in laboratory settings. (1) Tank space and substrate depths should be considered with respect to predator and prey sizes, life habits, and any attack, burrowing or escape behaviours. (2) Prey abundance should be controlled and monitored, and naticid predators should be isolated from one another unless testing for effects of multiple predators. (3) Prey health must be assessed initially and throughout experimental work to minimize incorrect attribution of deaths to scavenging or suffocation.

Although careful control of laboratory conditions may minimize false reports of suffocation by naticids, in some cases alternative modes of predation may be real. To understand better the extent and execution of alternative predatory modes, research in the following areas is needed: oxygen limits of prey, feeding behaviours for naticids not yet studied including scavenging, emergent effects due to multiple predators and especially other Naticidae, and the role of mucus secretions, particularly in regards to neurotoxins such as TTX. Understanding alternative modes of predation by naticids requires enhanced collaboration among malacologists, ecologists, physiologists, biochemists and palaeontologists.

Lastly, we advise caution in documenting alternative modes of naticid predation and applying terminology to mortality of the prey. Terms such as ‘smothering’ are ambiguous and should be abandoned; ‘nondrilling predation’ is not inclusive of all alternative predatory behaviours. Examining literature accounts of alternative modes of naticid predation is challenging, because potential confounding variables have often not been reported (e.g. predator-prey sizes, frequency of monitoring, density of predator and prey individuals and prey health). Validation of alternative predatory modes is needed in light of these concerns for several species of moon snails before questioning the quality of data provided by bevelled drillholes in modern and fossil shell assemblages.

ACKNOWLEDGEMENTS

This project resulted from work started as part of the National Science Foundation Research Experience for Undergraduates program awarded to P. Kelley and G. Dietl (Grant No. EAR-0755109). This research was completed in partial fulfilment of PhD requirements for C. Visaggi at the University of North Carolina Wilmington. Funding for writing of the dissertation was provided by a Ford Foundation Fellowship and Association for Women Geoscientists Chrysalis Scholarship. B. Parnell and D. Friend are valued for support in both the lab and field. E. Gould, M. Grey, M. Newel, G. Bourne, and E. Weissberger graciously shared data from their work. Thanks to G. Vermeij for input on valve closure. Translation guidance provided by C. Janot and J. Nagel-Myers is greatly appreciated. We also thank Melissa Grey and an anonymous reviewer for their comments on the manuscript.

REFERENCES

AGERSBORG, H.P.K. 1920. The utilization of echinoderms and of gasteropod molluscs. *American Naturalist*, **54**: 414–426.

ANSELL, A.D. & MORTON, B. 1985. Aspects of naticid predation in Hong Kong with special reference to the defensive adaptations of *Bassina (Callanaitis) Calophylla* (Bivalvia). In: *Proceedings of the second international workshop on the malacofauna of Hong Kong and southern China, Hong Kong* (B. Morton & D. Dudgeon, eds), pp. 635–660. Hong Kong University Press, Hong Kong.

ANSELL, A.D. & MORTON, B. 1987. Alternative predation tactics of a tropical naticid gastropod. *Journal of Experimental Marine Biology and Ecology*, **111**: 109–119.

ARONOWSKY, A. 2003. *Evolutionary biology of naticid gastropods*. PhD thesis, University of California, Berkeley.

BAUMILLER, T.K., MARINOVIC, J.C., TUURA, M.E., DAMSTRA, E.S. & MILLER, D.J. 2010. Signs of boring predation on Middle Devonian hyolithids from the Michigan Basin. *Palaios*, **25**: 636–641.

BAYLISS, D.E. 1986. Selective feeding on bivalves by *Polinices alderi* (Forbes) (Gastropoda). *Ophelia*, **25**: 33–47.

BAYNE, B.L. 1976. *Marine mussels, their ecology and physiology*. Cambridge University Press, Cambridge.

BELDING, D.L. 1930. The soft-shelled clam fishery of Massachusetts. Massachusetts Department of Conservation. Marine Fisheries Series No. 1: 1–65.

BERNARD, F.R. 1967. Studies of the biology of the naticid clam drill *Polinices lewisi* (Gould) (Gastropoda Prosobranchiata). *Fisheries Research Board of Canada, Technical Report*, **42**: 1–41.

CALVET I CATÀ, C. 1992. Borehole site-selection in *Naticarius hebraeus* (Chemnitz in Karsten, 1769) (Naticidae: Gastropoda)? *Orsis*, **7**: 57–64.

CARRIKER, M.R. 1951. Observations on the penetration of tightly closing bivalves by *Busycon* and other predators. *Ecology*, **32**: 73–83.

CARRIKER, M.R. 1981. Shell penetration and feeding by naticacean and muricacean predatory gastropods: a synthesis. *Malacologia*, **20**: 403–422.

CHRISTENSEN, A.M. 1970. Feeding biology of the sea-star *Astropecten irregularis* Pennant. *Ophelia*, **8**: 1–134.

DIETL, G.P. & ALEXANDER, R.R. 2000. Post-Miocene shift in stereotypic naticid predation on confamilial prey from the mid-Atlantic shelf: coevolution with dangerous prey. *Palaios*, **15**: 414–429.

DIETL, G.P., HERBERT, G.S. & VERMEIJ, G.J. 2004. Reduced competition and altered feeding behavior among marine snails after a mass extinction. *Science*, **306**: 2229–2231.

DIETL, G.P. & KELLEY, P.H. 2006. Can naticid gastropod predators be discriminated by the holes they drill? *Ichnos*, **13**: 1–6.

EDWARDS, D.C. 1969. Predators on *Olivella biplicata*, including a species-specific predator avoidance response. *Veliger*, **11**: 326–333.

EDWARDS, D.C. 1974. Preferred prey of *Polinices duplicatus* in Cape Cod inlets. *Bulletin of the American Malacological Union*, **40**: 17–20.

EDWARDS, D.C. & HUEBNER, J.E. 1977. Feeding and growth rates of *Polinices duplicatus* preying on *Mya arenaria* at Barnstable Harbor, Massachusetts. *Ecology*, **58**: 1218–1236.

FLIMLIN, G. 2004. *How to buy clam seed… without getting shucked*. Rutgers Cooperative Research & Extension Fact Sheet FS452. Agricultural Experiment Station, NJ.

FREGEAU, M.R. 1991. *The trophic ecology of Lunatia heros and its competitive interactions with Polinices duplicatus*. PhD thesis, University of Massachusetts, Amherst.

FRETTER, V. & GRAHAM, A. 1962. *British prosobranch molluscs: their functional anatomy and ecology*. Ray Society, London.

FRIEND, D.S. 2011. *Foraging strategies and coevolutionary alternation in the modern naticid gastropod predator-prey system*. MSc thesis, University of North Carolina, Wilmington.

GANONG, W.F. 1889. *The economic Mollusca of Acadia*. Bulletin of the Natural History Society of New Brunswick, No. VIII.

GOULD, A.A. 1841. Report of the Invertebrata of Massachusetts, comprising the Mollusca, Crustacea, Annelida, and Radiata. Folsom, Wells and Thurston, Cambridge, MA.

GOULD, E.S. 2010. *Unexpected rates of cannibalism under competitive conditions by the naticid gastropod Neverita duplicata (Say)*. MSc thesis, University of North Carolina, Wilmington.

GREY, M. 2001. *Predator-prey relationships of naticid gastropods and their bivalve prey*. MSc thesis, University of Guelph.

HARPER, E.M. 2006. Dissecting post-Paleozoic arms races. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **232**: 322–343.

HARPER, E.M. & KELLEY, P.H. 2012. Predation of bivalves. Treatise on Invertebrate Paleontology, Part N, Revised, Volume 1. Treatise Online, **44**: 1–21.

HARRIES, P.J. & SCHOPF, K.M. 2007. Late Cretaceous gastropod drilling intensities: data from the Maastrichtian Fox Hills Formation, Western Interior Seaway, USA. *Palaios*, **22**: 35–46.

HASEGAWA, H. & SATO, H. 2009. Predatory behaviour of the naticid *Euspira fortunei*: Why does it drill the left shell valve of *Ruditapes philippinarum*? *Journal of Molluscan Studies*, **75**: 147–151.

HUELSKEN, T., MAREK, C., SCHREIBER, S., SCHMIDT, I. & HOLLMANN, M. 2008. The Naticidae (Mollusca: Gastropoda) of Giglio Island (Tuscany, Italy): Shell characters, live animals, and a molecular analysis of egg masses. *Zootaxa*, **1770**: 1–40.

HUGHES, R.N. 1985. Predatory behaviour of *Natica unifasciata* feeding intertidally on gastropods. *Journal of Molluscan Studies*, **51**: 331–335.

HWANG, D.-F., CHUEH, C.H. & DENG, S.S. 1990. Tetrodotoxin secretion from the lined moon shell *Natica lineata* in response to external stimulation. *Toxicon*, **28**: 1133–1136.

HWANG, P.-A., NOGUCHI, T. & HWANG, D.-F. 2004. Neurotoxin tetrodotoxin as attractant for toxic snails. *Fisheries Science*, **70**: 1106–1112.

HWANG, P.-A., TSAI, Y.-H., LIN, S.-J. & HWANG, D.-F. 2007. The gastropods possessing TTX and/or PSP. *Food Reviews International*, **23**: 321–340.

ISHIKAWA, M. & KASE, T. 2007. Multiple predatory drill holes in *Cardiolucina* (Bivalvia: Lucinidae): effect of conchiolin sheets in predation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **254**: 508–522.

JACKSON, J.B.C. 1973. The ecology of molluscs of *Thalassia* communities, Jamaica, West Indies. I. Distribution, environmental physiology, and ecology of common shallow-water species. *Bulletin of Marine Science*, **23**: 313–350.

KABAT, A.R. 1990. Predatory ecology of naticids gastropods with a review of shell boring predation. *Malacologia*, **32**: 155–193.

KARDON, G. 1998. Evidence from the fossil record of an antipredatory exaptation: conchiolin layers in corbulid bivalves. *Evolution*, **52**: 68–79.

KELLEY, P.H. 1989. Evolutionary trends within bivalve prey of Chesapeake Group naticid gastropods. *Historical Biology*, **2**: 139–156.

KELLEY, P.H. 1991. The effect of predation intensity on rate of evolution of five Miocene bivalves. *Historical Biology*, **5**: 65–78.

KELLEY, P.H. 1992. Evolutionary patterns within naticid gastropods of the Chesapeake Group: an example of coevolution? *Journal of Paleontology*, **66**: 794–800.

KELLEY, P.H. & HANSEN, T.A. 2001. The role of ecological interactions in the evolution of naticid gastropods and their molluscan prey. In: *Evolutionary paleoecology* (W. Allmon & D. Bottjer, eds), pp. 149–170. Columbia University Press, New York.

KELLEY, P.H. & HANSEN, T.A. 2003. The fossil record of drilling predation on bivalves and gastropods. In: *Predator-prey interactions in the fossil record* (P.H. Kelley, M. Kowalewski & T.A. Hansen, eds), pp. 113–139. Kluwer /Plenum Press, New York.

KELLEY, P.H. & HANSEN, T.A. 2007. Latitudinal patterns in naticid gastropod predation along the east coast of the United States: a modern baseline for interpreting temporal patterns in the fossil record. In: *Sediment-organism interactions: A multifaceted ichnology* (R.G. Bromley, L.A. Buatois, M.G. Mángano, J.F. Genise & R.N. Melchor, eds), pp. 284–299. SEPM Special Publications No. 88, Tulsa.

KENCHINGTON, E., DUGGAN, R. & RIDDELL, T. 1998. Early life history characteristics of the razor clam (*Ensis directus*) and the moonsnails (*Euspira* spp.) with applications to fisheries and aquaculture. Canadian Technical Report of Fisheries and Aquatic Sciences No. 2223.

KINGSLEY-SMITH, P.R., RICHARDSON, C.A. & SEED, R. 2003. Stereotypic and size-selective predation in *Polinices pulchellus* (Gastropoda: Naticidae) Risso 1826. *Journal of Experimental Marine Biology and Ecology*, **295**: 173–190.

KITCHELL, J.A. 1986. The evolution of predator-prey behavior: naticids gastropods and their molluscan prey. In: *Evolution of animal behavior: paleontological and field approaches* (M. Nitecki & J.A. Kitchell, eds), pp. 88–110. Oxford University Press, Oxford.

KITCHELL, J.A., BOGGS, C.H., KITCHELL, J.F. & RICE, J.A. 1981. Prey selection by naticid gastropods: experimental tests and application to the fossil record. *Paleobiology*, **7**: 533–552.

KITCHELL, J.A., BOGGS, C.H., RICE, J.A., KITCHELL, J.F., HOFFMAN, A. & MARTINELL, J. 1986. Anomalies in naticid predatory behavior: a critique and experimental observations. *Malacologia*, **27**: 291–298.

KLOMPMAKER, A.A. 2012. Drill hole predation on fossil serpulid polychaetes, with new data from the Pliocene of the Netherlands. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **321–322**: 113–120.

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

KOWALEWSKI, M. & KELLEY, P.H., eds 2002. *The fossil record of predation*. Paleontological Society Papers 8, Yale University Reprographics & Imaging Services, New Haven.

LEIGHTON, L.R. 2001. New example of Devonian predatory boreholes and the influence of brachiopod spines on predator success. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **165**: 53–69.

LEIGHTON, L.R. 2002. Inferring predation intensity in the marine fossil record. *Paleobiology*, **28**: 328–342.

MEDCOF, J.C. & THURBER, L.W. 1958. Trial control of the greater clam drill (*Lunatia heros*) by manual collection. *Journal of the Fisheries Research Board of Canada*, **15**: 1355–1369.

MORTON, B. 2008. Biology of the swash-riding Moon Snail *Polinices incei* (Gastropoda: Naticidae) predating the Pipi, *Donax deltoides* (Bivalvia: Donacidae), on wave-exposed sandy beaches of North Stradbroke Island, Queensland, Australia. In: *The marine fauna and flora of Moreton Bay, Queensland* (P.J.F. Davie & J.A. Phillips, eds), pp. 303–322. Memoirs of the Queensland Museum – Nature 54, Proceedings of the Thirteenth International Marine Biological Workshop, Brisbane.

MORTON, B. & MORTON, J. 1983. *The seashore ecology of Hong Kong*. Hong Kong University Press, Hong Kong.

MORTON, J.E. 1958. *Molluscs*. Hutchinson, London.

NEWEL, M.S. & BOURNE, G.B. 2012. Factors affecting the drilling and feeding behavior of Lewis' moon snail, *Euspira lewisii* (Gastropoda: Naticidae). *Integrative and Comparative Biology*, **52**: e303.

PEITSO, E., HUI, E., HARTWICK, B. & BOURNE, N. 1994. Predation by the naticid gastropod *Polinices lewisii* (Gould) on littleneck clams *Protothaca staminea* (Conrad) in British Columbia. *Canadian Journal of Zoology*, **72**: 319–325.

REID, R.G.B. & FRIESEN, J.A. 1980. The digestive system of the moon snail *Polinices lewisii* (Gould, 1847) with emphasis on the role of the oesophageal gland. *Veliger*, **23**: 25–34.

REID, R.G.B. & GUSTAFSON, B.D. 1989. Update on feeding and digestion in the moon snail *Polinices lewisii* (Gould, 1847). *Veliger*, **32**: 327.

REYMENT, R.A. 1999. Drilling gastropods. In: *Functional morphology of the invertebrate skeleton* (E. Savazzi, ed.), pp. 197–204. John Wiley & Sons, London.

RICHTER, G. 1962. Beobachtungen zum Beutefang der marinen Bohrschnecke *Lunatia nitida*. *Natur und Museum*, **18**: 185–192.

RICKETTS, E.F. & CALVIN, J. 1962. *Between Pacific tides*. Edn 3, revised by J.W. Hedgpeth. Stanford University Press, Stanford.

RODRIGUES, C.L. 1986. Predation of the naticid gastropod, *Neverita didyma* (Röding), on the bivalve *Ruditapes philippinarum* (Adams & Reeve): evidence for a preference linked functional response. *Publications from the Amakusa Marine Biological Laboratory, Kyushu University*, **8**: 125–141.

SAVAGE, N.B. 1976. Burrowing activity in *Mercenaria mercenaria* (L.) and *Spisula solidissima* (Dillwyn) as a function of temperature and dissolved oxygen. *Marine Behaviour & Physiology*, **3**: 221–234.

SAVAZZI, E. & REYMENT, R.A. 1989. Subaerial hunting behaviour in *Natica gualteriana* (naticid gastropod). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **74**: 355–364.

SAY, T. 1822. An account of some of the marine shells of the United States. *Journal of the Academy of Natural Sciences of Philadelphia*, **2**: 221–248, 257–276, 302–325.

SCHNEIDER, D. 1982. Escape response of an infaunal clam *Ensis directus* Conrad 1843, to a predatory snail, *Polinices duplicatus* Say 1822. *Veliger*, **24**: 371–372.

STINSON, R.H. 1946. Observations on the natural history of clam drills (*Polinices*). Fisheries Research Board of Canada. Manuscript Reports of the Biological Stations No. 383.

THURBER, L.W. 1949. Observations on and attempts to control the greater clam drill (*Polinices heros*). Fisheries Research Board of Canada. Manuscript Reports of the Biological Stations No. 408.

TORIGOE, K. & INABA, A. 2011. Revision on the classification of Recent Naticidae. *Bulletin of the Nishinomiya Shell Museum*, **7**: 1–133.

TURNER, H.J. 1950. Investigations on the soft-shell clam, *Mya arenaria*. Third Report on Investigations of Methods of Improving the Shellfish Resources of Massachusetts. Massachusetts Division of Marine Fisheries, WHOI Collection Reprints 1951, No. 564.

TURNER, H.J. 1955. How clam drills capture razor clams. *Nautilus*, **69**: 20–22.

VENCILE, K.W. 1997. *Interactions between naticid gastropods (Euspira spp.) and their bivalve prey Mya arenaria L.): effects of clam size, tidal height, and site*. M.Sc. thesis, University of Maine, Machias.

VERMEIJ, G.J. 1980. Drilling predation of bivalves in Guam: some paleoecological implications. *Malacologia*, **19**: 329–334.

VERMEIJ, G.J. 1987. *Evolution and escalation: an ecological history of life*. Princeton University Press, Princeton.

VERMEIJ, G.J., DUDLEY, E.C. & ZIPSER, E. 1989. Successful and unsuccessful drilling predation in Recent pelecypods. *Veliger*, **32**: 266–273.

VISAGGI, C.C. 2012. *Latitudinal variation in naticid gastropod predation on Western Atlantic mollusks: investigating evolutionary patterns in the fossil record through modern ecosystems*. Ph.D. thesis, University of North Carolina, Wilmington.

WEISSBERGER, E.J. & GRASSLE, J.P. 2003. Settlement, first-year growth, and mortality of surfclams, *Spisula solidissima*. *Estuarine, Coastal and Shelf Science*, **56**: 669–684.

WHEATLEY, J.M. 1947. Investigations of *Polinices* and clams at Belliveau Cove, N.S. Fisheries Research Board of Canada. Manuscript Reports of the Biological Stations No. 371.

ZIEGELMEIER, V.E. 1954. Beobachtungen über den Nahrungserwerb bei der Naticide *Lunatia nitida* Donovan (Gastropoda Prosobranchia). *Helgoländer Wissenschaftliche Meeresntersuchungen*, **5**: 1–33.

APPENDIX I

Use of ‘suffocation’ (SU) *vs* ‘smothering’ (SM) in the literature in reference to alternative predation by naticids. These examples do not include unpublished MSc or PhD work, abstracts, books, comments or replies to articles, or personal communication citations in publications.

Term	Reference	Text
SU	Agersborg (1920)	“In the case of *Mya*, the gasteropod sucks itself over the syphon down into the sand until its victim is dead from **suffocation**, and then when the clam has opened, *Polynices* simply sends its proboscis between the valves and devours the content.” p. 421
SU	Edwards (1969)	“Although *Polinices* may occasionally force its prey’s operculum, the incomplete bore holes suggest another explanation, viz., that *O. biplicata* **suffocates** while wrapped in the predator’s foot and relaxes.” p. 327
SU	Vermeij (1980)	“. . . *Arcopagia robusta* and *Quidnipagus palatam* which can be eaten by naticids without drilling. It is likely that these clams **suffocate** while being enveloped by the predator’s foot before drilling has proceeded very far.” p. 332
SU	Hughes (1985)	“Since in the present study, *N. unifasciata* consumed *O. volutella* within 12 h, a forceful entry through or round the edges of the flimsy operculum seems a more likely method than **suffocation**.” p. 334
SU	Ansell & Morton (1987)	“The immediate cause of gaping of the prey is interpreted here as **suffocation**, but it is also possible that the process is facilitated by the presence in the pedal mucus or other secretion of the predator of a narcotizing toxin.” p. 117
SU	Reid & Gustafson (1989)	“We explored the possibility... secretion might have a pharmacological effect [...] There was no such effect, and we conclude that the condition of prey is due to **suffocation** [. . .] An identical effect results from sealing clams in seawater in cooled plastic bags for 12 h.” p. 327
SU	Vermeij, Dudley & Zipser (1989)	“. . . but Ansell & Morton (1987) have shown in laboratory trials with *Venerupis japonica* eaten by various naticids that some incompletely drilled prey had nevertheless been consumed by the predator. In such cases, the prey was apparently **suffocated**. . .” p. 270
SU	Kabat (1990)	[used repeatedly in citing the work of others]
SU	Calvet i Catà (1992)	“Naticid gastropods use several strategies to feed on their prey <. . .> **suffocation** in snails with a large mesopodium (Ansell & Morton, 1987), and non-boring predation as observed in razor clams (Schneider, 1981).” p. 58
SU	Peitso et al. (1994)	“Large *Glossaulax didiyma* begin boring their prey, but consume it after the prey **suffocates**, before boring is complete (Ansell and Morton, 1987).” p. 323
SM	Leighton (2001)	“Vermeij (1980) noted that many of the smaller prey species in his study might have been killed by **smothering** before drilling was necessary.” p. 57
SM	Leighton (2002)	"Also, some naticids may be capable of **smothering**, rather than drilling, their prey (Ansell & Morton, 1987)." p. 333
SU	Weissberger & Grassle (2003)	"A naticid may kill a bivalve too large by **suffocating** it with its foot (Ansell & Morton, 1987; E. Weissberger personal observation), leaving no trace of predation on the bivalve’s shell." p. 680
SU	Kingsley-Smith *et al.* (2003)	"Shell valves cleaned of tissue that lacked evidence of drilling were not recovered from aquaria, such that *P. pulchellu*s did not appear to employ any non-drilling methods of subjugating prey, such as **suffocation**." p. 182
SU	Kowalewski (2004)	"Similarly, Ansell & Morton (1987) observed in aquarium experiments that the naticid *Glossaulax didyma* abandoned incomplete drill holes and consumed some of its prey, which **suffocated** during initial phases of drilling, without penetrating the shell." p. 365
SU	Harper (2006)	"Ansell and Morton (1987) observed that some individuals of the naticid *Glossaulax didyma* feeding on *Tapes philipinarum* started but failed to complete drillholes, but instead **suffocated** the prey and fed on it successfully." p. 326
SM	Kelley & Hansen (2007)	". . .alternative modes such as **smothering** may be more common at higher latitudes." p. 287
SM	Harries & Schopf (2007)	"Ansell and Morton (1987) have documented a range of feeding modes, such as **smothering** [. . .] Because **smothering** predation leaves no discernable signature in the fossil record. . ." pp. 42–43
SU	Morton (2008)	"Ansell & Morton (1987) also showed that *Polinices tumidus* Swainson, 1840, held its prey with the rear of its foot and, as a consequence, sometimes **suffocated** it such that there were no drill holes to identify the predation event." p. 317
SM	Hasegawa & Sato (2009)	". . .four successive phases of behaviour: (1) capture, (2) **smothering**, (3) rotation and (4) drilling. [. . .] pedal mucus, which enveloped and hardened around the prey, immobilizing it for a few days. . ." p.149
SU	Baumiller *et al.* (2010)	"It has been shown, however, that some extant boring predators can subdue their prey by **suffocating** them (Kowalewski, 2004). . ." p. 639
SM	Klompmaker (2012)	". . .how often **smothering** or rasping into the tube via the aperture to kill the organism was employed by naticids cannot be addressed." p. 117