

Proceedings of the 13th International Marine Biological Workshop

The Marine Fauna and Flora of Moreton Bay, Queensland

Volume 54, Part 1

Editors: Peter J.F. Davie & Julie A. Phillips

Memoirs of the Queensland Museum | **Nature
54(1)**

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National Library of Australia card number

ISSN 0079-8835

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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

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Citation: Morton, B. 2008 12 01. 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, Davie, P.J.F. & Phillips, J.A. (Eds), Proceedings of the Thirteenth International Marine Biological Workshop, The Marine Fauna and Flora of Moreton Bay, Queensland. *Memoirs of the Queensland Museum — Nature* 54(1): 303–322. Brisbane. ISSN 0079–8835.

ABSTRACT

On the highly exposed sandy shores of the eastern coast of North Stradbroke Island, Queensland, and on One Mile Beach, further south at Port Stephens, New South Wales, the naticid moon shell *Polinices incei* surfs up the beach to attack juvenile surf clams, or pipsis, (*Donax deltoides*). It moves shallowly within the sand, its presence indicated by a raised trail. Apparently, the surf clams recognise *P. incei* in their vicinity as they, unusually, emerge from the sand and attempt to escape from the predator by leaping. If captured, however, surf clam juveniles (up to three individuals) are held by *P. incei* beneath the posterior margin of its foot. *Polinices incei* was also recorded drilling *D. deltoides* lower down the shore.

To move up shore and return down shore, *Polinices incei* ‘surfs’ the swash and backwash, respectively. Surfing involves rapid inflation of the foot and propodium such that the predator floats shell down but is carried by the waves either up or down. Surfing downshore, *P. incei* was often observed holding bivalve prey. Downward migrating *P. incei* individuals also ‘roll’ in the backwash, but brake by digging in the anterior end of the foot and resume burrowing rapidly. Other identified behaviours include hunting and galloping — the latter to chase potential prey.

The nassariid *Bullia digitata* surfs similar exposed beaches in South Africa, but to access carrion. As far as is known, therefore, *Polinices incei* is the only known naticid predator which has evolved a surfing behaviour that enables it to attack its prey, the tidally migrating surf clam *Donax deltoides*. The evolution of naticid drilling predation is part of the Mesozoic Marine Revolution. As predicted by escalation theory, the dangers to infaunal bivalve residents from naticid predation seem to have increased over time but since shallow water benthic assemblages are thought to be particularly susceptible to mass extinction events it seems probable that the *Polinices incei* (predator)/*Donax deltoides* (prey) relationship is relatively modern. Hitherto, surf clams have always been regarded as occupying a ‘safe refuge’ niche, at least from marine predators. The relationship identified herein, therefore, is a remarkable example of predatory adaptive radiation. □
exposed sand beaches, eastern Australia, Polinices incei, Naticidae, Donax deltoides, Donacidae, surf clams, swash riding, predation.

Virtually worldwide on beaches of sand and mud, and offshore on similar sediments, species of the mesogastropod Naticidae are predators of resident bivalves. This has been reviewed most recently by Kelley & Hansen (2003), especially with regard to the fossil record of drilling predation. Naticids can be traced back to the early Jurassic, some 200 million years ago (Taylor 1981), and representative species thus constitute some of the earliest drilling molluscan predators. Prey can include foraminiferans, and other gastropods but, more usually, bivalves. Naticids typically drill a characteristic counter-sunk borehole through the bivalve shell, using a combination of mechanical drilling using the radula, and chemical etching by secretions from an accessory boring organ (ABO) in the mouth to penetrate the shell of the prey (Carriker 1981). Drill holes are made usually on the dorsal valve surface, often above the nutritious visceral mass (Negus 1975), or, in the case of the tropical *Polinices* species, at the valve margin (Vermeij 1980; Ansell & Morton 1985, 1987).

Intertidal naticids are typically inhabitants of relatively sheltered beaches, and attack their prey underground. In subtropical Hong Kong such sheltered beaches often possess a suite of naticids that partition the bivalve resources of their habitat (Ansell & Morton 1985), typically in relation to shell thickness. Similarly, Morton & Knapp (2004) have shown that in the warm, shallow waters off Florida, *Naticarius canrena* (Linnaeus, 1758) feeds on a wide variety of bivalve prey but notably *Chione elevata* (Say, 1822). In more temperate waters, resident naticids have a more conservative diet. Wiltse (1980) demonstrated that the larvae of *Polinices duplicatus* (Say, 1822) settle in close proximity to populations of its sole bivalve prey *Gemma gemma* (Totten, 1834). There is a large literature on naticids and the biology of their predatory behaviours (Kabat 1990).

Because they are thought to track their prey underground using olfactory cues, naticids are typically absent from high-energy, wave disturbed, beaches although, as this study will demonstrate, one species of naticid in eastern Australia is an exception to this generalisation.

Ansell & Trevallion (1969) point out that macrobenthic species that live in constantly disturbed

high-energy sandy substrata, have evolved specific morphological and, equally important behavioural features to allow them to flourish. Some species that can exploit such habitats are called 'swash riders', because of their ability to exploit the force of waves racing up the shore. Such species must also exploit the backwash, typically on the falling tide, to escape the dangers of desiccation. Species of the tropical Donacidae surf clams (*Bivalvia*) are well known to exploit the swash and the backwash to keep within the zone of breaking waves in order to feed on the sparse nutrients held briefly in suspension by them (Ansell 1981). Similarly, there are several swash-riding species of *Bullia* that occur in South America, south and west Africa, and the Indian Ocean (Brown 1982). Most notably, *Bullia digitalis* (Dillwyn, 1817) periodically expands its foot and uses it like a sail to be propelled upwards by the swash (Brown 1961, 1971, 1979; Ansell & Trevallion 1969). *Bullia* species, including *B. digitalis*, have been reported to ride the swash on South African surf beaches (Odendaal *et al.* 1992) although this is to seek carrion food rather than live prey (Hodgson & Brown 1987). Brown *et al.* (1989) have reviewed the similarities and differences between bivalves (*Donax serra* (Röding, 1798)) and gastropods (*B. digitalis*) that occupy wave-exposed sandy beaches in South Africa.

On West Malaysian shores, the highly active, filter feeding trochid *Umbonium vestiarium* (Linnaeus, 1758) is the sole prey of *Natica maculosa* Lamarck, 1822 (Berry 1982). In the Azores, huge numbers of drilled tellinids, *Ervilia castanea* (Montagu, 1803), wash up on wave-exposed beaches, where it was once believed they had been attacked by the naticid *Natica cf. intricata* (Donovan, 1804). However, Morton (1990a) has shown that *E. castanea* actually lives subtidally (to depths of ~50m), and neither it nor its predator occurs intertidally.

Polinices incei (Philippi, 1853) is known from Queensland, New South Wales and southern Australia, though absent from Tasmania (Wilson & Gillett 1971) and Western Australia (Wells & Bryce 1985). *Polinices incei* was reported by Wilson & Gillett (1971) and Ludbrook & Gowlett-Holmes (1989) to live in the mid-littoral zone of high-energy surf beaches although, curiously, Wilson

(1993: 220; 2002: 120) reported it as living on 'muddy substrates' and 'muddy flats', respectively, a habitat more typical of *Polinices sordidus* (Swainson, 1821) and *P. melanostomus* (Gmelin, 1791), at least in the Moreton Bay region. The present study confirms that *P. incei* really is a specialised inhabitant of wave-exposed beaches, and thus a highly unusual naticid. *Polinices incei* has been surprisingly little studied, except for an examination of its burying and crawling behaviour in response to diesel oil contamination (Chapman *et al.* 1988), and a report that it responds positively to sound (Kitching & Pearson 1981). The former authors showed that diesel oil produced a significant response in terms of burial and crawling activity, whereas the latter authors speculated that the response of *P. incei* to sound may assist in capturing prey. Surprisingly, however, no one has commented upon the uniqueness of such a high energy habitat for a naticid and, consequently, the different behaviours that *P. incei* must have developed for such an unusual mode of life. This forms the subject of the present paper.

MATERIALS AND METHODS

From 9–22 February 2005 a number of exposed surf beaches on North Stradbroke Island were regularly visited on falling tides. These included Frenchman's Bay, Main Beach, Home Beach, Cylinder Beach and Blue Lake Beach. It became apparent, that *Polinices incei* was most abundant on the most exposed Blue Lake Beach, and its resident population thus became the object of more detailed study. Captured individuals of *P. incei* from the other beaches were also kept and used in laboratory experiments to examine behaviour in more detail.

In addition, field observations of *Polinices incei* from One Mile Beach, Port Stephens, New South Wales, were also made.

FIELD STUDIES

Habitat sediment analyses. At each 10 m interval down shore from the approximate position of mean high water tide at Blue Lake Beach, samples of sand were taken and sediment analysis undertaken using a series of graded sieves (16,000, 8,000, 4,000, 2,000 and 1,000 μ m). Sediment particle size distributions < 1,000 μ m were determined using a Malvern

Mastersizer 2000 particle sizer. Such data have previously been validated by comparison with wet sieving (Hart 1996) and such Mastersizer output describes particle size distributions in terms of mean phi (f), fraction percentages (coarse sediments, sands and fines), sorting (mixture of sediment sizes) and skewness (weighting of sediment fractions > and < the mean sediment size) (Folk & Ward 1957). Also analysed were total organic contents of the sediment samples calculated as percentage losses on ignition (LOI).

Parameters which had different values among samples, including mean mm, mean f, and total organic content (% LOI), were subjected to non-parametric multivariate analysis using PRIMER Version 5 (Clark & Gorley 2001), to identify differences in them among shore levels. A similarity matrix was constructed using the Bray-Curtis similarity measure, and multi-dimensional scaling (MDS) was performed to visualise the parameters which varied among samples, that is, mean mm, mean f and organic content.

Distributions and population structures of *Donax deltoides* and *Polinices incei*. At each 10 m interval down the shore of Blue Lake Beach, the occurrence of dominant macrofaunal species were identified. In addition, 1 m x 1 m quadrats were laid out from the approximate position of mean high water mark and scraped to a depth of 5 cm to determine numbers of infauna, that is, largely, the bivalves *Donax deltoides* Lamarck, 1818, and *Polinices incei*.

Empty *Donax deltoides* shells and *Polinices incei* individuals. For five days, the sands of Blue Lake Beach were searched for living individuals of *Donax deltoides* and *Polinices incei* (in particular, the trails of foraging individuals) and the empty shells of *D. deltoides*. Each living and empty shell (or single valves) of *D. deltoides* was measured along its greatest length to the nearest 1 mm, and the latter examined for the presence of drill holes. In the case of *P. incei*, each captured individual was measured in the field along its greatest shell width to the nearest 0.1 mm using vernier calipers. It was then examined to see if it was feeding or holding prey items in its foot. If so, the numbers and shell lengths of the captured *D. deltoides* individuals were recorded and the positions of any drill

holes (and attempts) recorded on a master diagram of the species.

These observations on *Donax deltoides* and *Polinices iniei* individuals were repeated over a lesser period of three days at One Mile Beach, Port Stephens, New South Wales.

BEHAVIOURAL STUDIES (FIELD AND LABORATORY)

Blue Lake Beach and One Mile Beach were watched to determine aspects of the behaviour of *Polinices iniei*. This also resulted in some aspects of the behaviour of *Donax deltoides* being recorded.

In the laboratory, *Polinices iniei* individuals collected from Frenchman's Bay, Main Beach, Home Beach and Cylinder Beach were kept in trays of aerated seawater changed daily. Aspects of the locomotion of *P. iniei* were examined using lines drawn 10 mm apart on the bottom of the trays and a stopwatch. When the water in the trays was agitated, *P. iniei* individuals turned on their backs, as will be described. Ten *Polinices iniei* individuals were also kept for a period of 10 days in trays with 20 small (<10 mm shell length) individuals of *Donax deltoides*, but none were attacked and this trial is not reported upon further.

As will be described, five *Polinices iniei* individuals were found drilling *Donax deltoides* in the field. The drilled shells were cleaned in an ultrasonic shaker, sputter coated with gold, and examined using scanning electron microscopy (Jeol 820) at the University of Cambridge, England.

RESULTS

FIELD STUDIES

Habitat sediment analyses. Results of the downshore sediment analysis (0–80) at Blue Lake Beach are given in Table 1. Mean particle size ranged from 282–397 μ m with the highest values > ~300 μ m being recorded from the lower half of the shore. All sediments were, however, classified as well sorted (units ranging from >1.70 to <1.70 at the upper and lower levels of the beach, respectively), medium sand with a very low total organic content (< 0.3% Loss on Ignition). Statistical analysis of the dataset identified differences in sediment composition down the shore at Blue Lake Beach and MDS results (Fig. 1) show that sand from shore levels 0–10 m, 10–20 m, 20–30

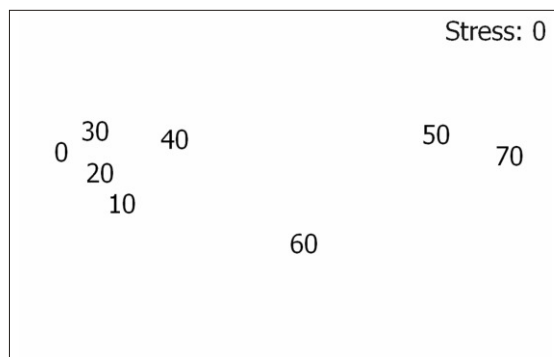


FIG. 1. Multivariate analysis of the particle size dataset for the sands of Blue Lake Beach, North Stradbroke I., Queensland, using the Bray-Curtis similarity matrix and non-metric multidimensional scaling (MDS) ordination in two dimensions.

m, 30–40 m and 40–50 m were similar, and different from shore levels 50–60 m, 60–70 m and 70–80 m. That is, mean particle size at the former levels were all <300 μ m and >1.75 respectively, whereas the latter were all >300 μ m and <1.75 respectively.

Population structure of *Donax deltoides*. Table 2 shows the ranges and means of living shells and drilled valves (by an unknown predator) of *Donax deltoides* on Blue Lake Beach (plus Main Beach for comparison), and One Mile Beach, NSW. Mean shell lengths for undrilled and drilled shells for Blue Lake Beach and One Mile Beach were 44.2 mm and 31.2 mm (43.6 mm and 34.2 mm for Main Beach) and 38.3 mm and 28.4 mm, respectively. Generally, therefore, *D. deltoides* individuals (both undrilled and drilled) from One Mile Beach were smaller than conspecifics from North Stradbroke Island.

Length frequency histograms of the population of *Donax deltoides* on Blue Lake Beach are illustrated in Fig. 2. This composite figure shows that living individuals collected during all surveys ranged in shell length from a minimum of 3.2 mm to a maximum of 56.9 mm. There appear to be peaks at shell lengths of 0–10 mm, 35–40 mm and 50–55 mm. These may represent age cohorts, but in the absence of data from other months this cannot be confirmed. However, it is clear that <10 mm individuals are juveniles.

The incidence of drilling predation by *Polinices iniei* on *Donax deltoides*. Table 3

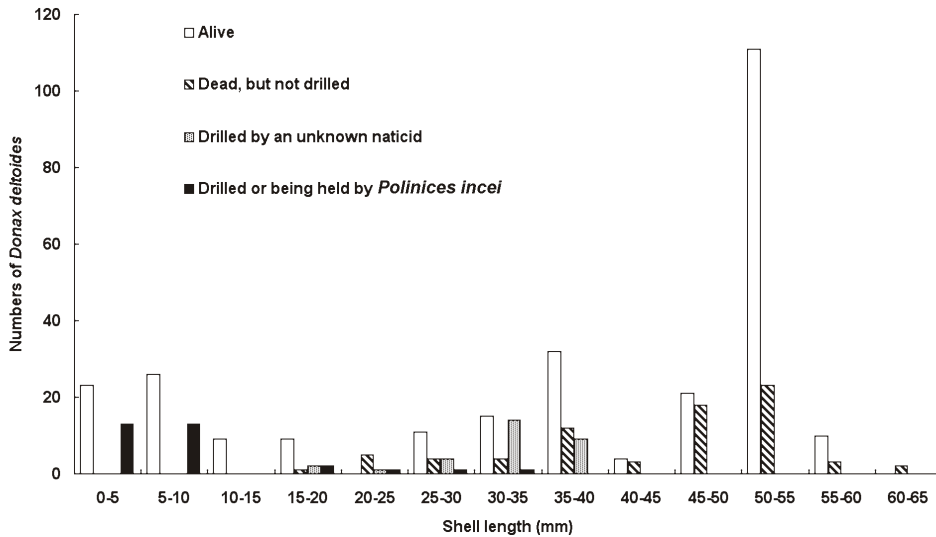


FIG. 2. *Donax deltooides*. The shell length frequencies of living individuals, empty (undrilled) shells, valves drilled by an unknown naticid and individuals observed to be either being drilled or held by *Polinices incei* on Blue Lake Beach, North Stradbroke Island, Queensland.

shows the size distribution of *Donax deltooides* individuals from Blue Lake Beach and One Mile Beach that were known to be either drilled or being held by *Polinices incei*. The bivalves ranged in shell length from 3.1–29.5 mm (mean = 7.6) with a peak in 0–10 mm individuals in the case of Blue Lake Beach, and 2.2–18.7 mm (mean = 5.0) with a peak also in 0–10 mm individuals in the case of One Mile Beach. Results of a

t-test show that the populations of *D. deltooides* on Blue Lake Beach and One Mile Beach were not significantly different in terms of shell size ($p < 0.02$).

Table 3 also shows the size distribution of *Polinices incei* individuals from Blue Lake Beach and One Mile Beach. The species had mean shell lengths of 12.2 mm on Blue Lake Beach and 9.5 mm on One Mile Beach. That is, the mean size

Table 1. Particle size analysis of the sands of Blue Lake Beach, North Stradbroke Island, Queensland and the approximate pattern of zonation of characterising macrofaunal species and estimates of the numbers of *Donax deltooides* and *Polinices incei* • m². Otherwise, all samples comprised well-sorted medium sand with 0% fine (<63 μ m) and coarse (>2 mm) sand and 100% medium sand.

Metres down shore from MHTL	Mean particle size (mm)	Mean phi	Total organic content (% LOI)	Characterising species	Numbers <i>D. deltooides</i> / <i>P. incei</i> per m ²
0 – 10	289	1.79	0.3	Adult <i>Ocypode ceratophthalma</i>	
10 – 20	294	1.77	0.2	Juvenile <i>Ocypode ceratophthalma</i> + <i>Scopimera inflata</i>	
20 – 30	289	1.79	0.2		
30 – 40	282	1.82	0.2	Adult <i>Donax deltooides</i>	96
40 – 50	298	1.75	0.1	Adult + juvenile <i>D. deltooides</i>	96 + 48/16
	368	1.44	0.1	Juvenile <i>D. deltooides</i>	0 + 16/32
60 – 70	337	1.57	0.2	Juvenile <i>D. deltooides</i>	0 + 16/16
70 – 80	397	1.33	0.1	Occasional <i>D. deltooides</i>	

Table 2. Ranges and means of shell lengths of undrilled and drilled *Donax deltoides* individuals on Blue Lake Beach, North Stradbroke Island and One Mile Beach, Port Stephens. *Data for drilled and undrilled shells collected from Main Beach, North Stradbroke Island, are also given for comparison with Blue Lake Beach.

Beach	Mean shell length undrilled (mm)	Range shell length undrilled (mm)	Mean shell length drilled (mm)	Range shell length drilled (mm)
Blue Lake Beach	44.2	17.3 – 60.7	31.2	15.0 – 38.2
*Main Beach	43.6	21.3 – 62.8	34.2	31.4 – 38.6
One Mile Beach	38.3	15.3 – 61.2	28.4	14.6 – 35.2

Table 3. Results of a *t*-test to determine differences in the shell width (mm) of *Polinices incei* and the shell lengths (mm) of *Donax deltoides* individuals being either drilled or held between A, Blue Lake Beach, North Stradbroke Island, Queensland, and B, One Mile Beach, Port Stephens, New South Wales. The null hypothesis is rejected when $p < 0.05$.

Taxon	Site	<i>t</i> -test, <i>p</i>	<i>t</i> -test, df	N	Mean $\pm$ S.E. (mm)	Range (mm)
<i>Polinices incei</i>	A	0.002	66	34	12.19 $\pm$ 0.74	1.6–22.3
	B			34	9.53 $\pm$ 0.39	5.9–15.5
<i>Donax deltoides</i>	A	0.02	73	38	7.61 $\pm$ 0.99	3.1–29.5
	B			37	5.01 $\pm$ 0.42	2.2–18.7

of *P. incei* was significantly larger ($p=0.002$) on Blue Lake Beach, possibly explaining why larger *Donax deltoides* prey were attacked on the former beach (see above).

The sizes of empty undrilled shells of *Donax deltoides* (intact and right valves only) on Blue Lake Beach (Fig. 2) ranged from 10.7–62.8 mm, with peaks again of 35–40 mm and 50–55 mm shell lengths matching those values, save for the juveniles, identified for the resident living *Donax deltoides* population (also Fig. 2). The shell lengths of drilled (by an unknown naticid predator) *D. deltoides* collected from Blue Lake Beach ranged from 15.0–38.6 mm with a peak in the 30–35 mm size class (Fig. 2). The shell lengths of *D. deltoides* individuals from One Mile Beach observed to be either being held or drilled by the predator *Polinices incei* ranged from the 0–5 mm to 30–35 mm size classes (Fig. 2). That is, there is considerable overlap between the *D. deltoides* shells drilled by an unknown naticid and those individuals observed being attacked by *P. incei*.

Population structure of *Polinices incei*. The population structures of *Polinices incei* individ-

uals inhabiting Blue Lake Beach and One Mile Beach are illustrated in Fig. 3. At both localities there is a peak of individuals ~10 mm in shell width. A greater range in shell widths was obtained from Blue Lake Beach, that is, from 16–22.3 mm, whereas on One Mile Beach the range was from 5.9–15.5 mm (Table 3). It seems clear therefore that in both locations, the intertidal components of the two populations mainly comprise juvenile individuals. On the basis of growth rings present in its statoliths, Richardson *et al.* (2005) showed that *Polinices pulchellus* (Risso, 1826) lives for a maximum of two to three years.

MORPHOLOGY AND BEHAVIOUR OF *POLINICES INCEI*

Morphological characteristics. The shells of *P. incei* are rounded with a very depressed, low spire. Size ranges up to 19 mm in height and 28 mm in width (Ludbrook & Gowlett-Holmes 1989). Individuals collected in this study ranged in shell width from 5.7–29.3 mm. A button-like callus within the umbilicus, surrounded by a groove, characterises the ventral surface of the shell. The most distinguishing feature of the shell dorsally, however, is its colour polymorphism (Fig. 4). Colours range from cream, pale

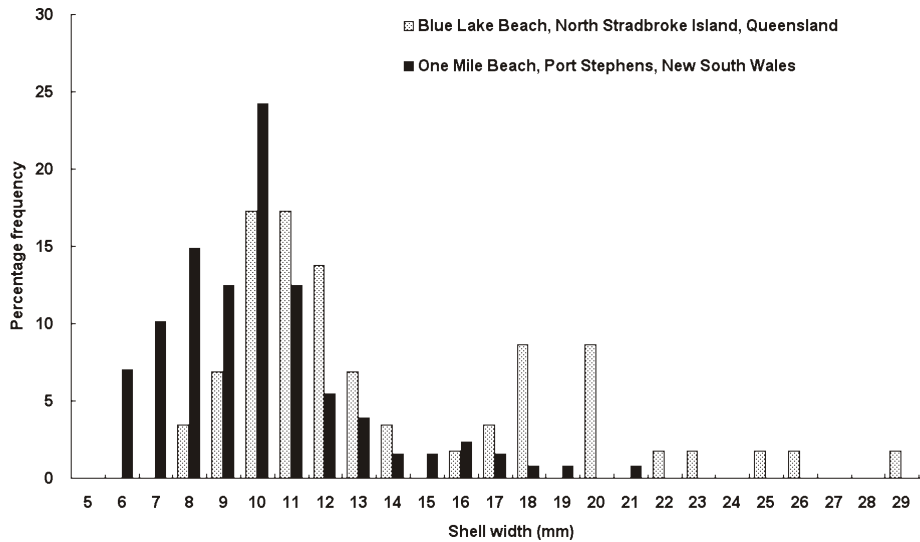


FIG. 3. The size (shell length) frequencies of the populations of *Polinices incei* on Blue Lake Beach, North Stradbroke Island, Queensland, and One Mile Beach, Port Stephens, New South Wales.

yellow, grey, brown, purple and near black, although the spire is often patterned variably. Figure 5 illustrates shells representing the full spectrum of colours. There seems to be a progressive loss of the purple/black coloration towards cream, but then an increase, or replacement, with brown. Clearly the blacks morphs stand

out most clearly on the clean beaches of eastern Australia, whereas the other colour morphs are more cryptic in such sands that contain fragments of shells, stones and other marine debris.

The unusually dorso-ventrally flattened form of *Polinices incei* is best illustrated by comparison with *Polinices sordidus* (Swainson, 1821)

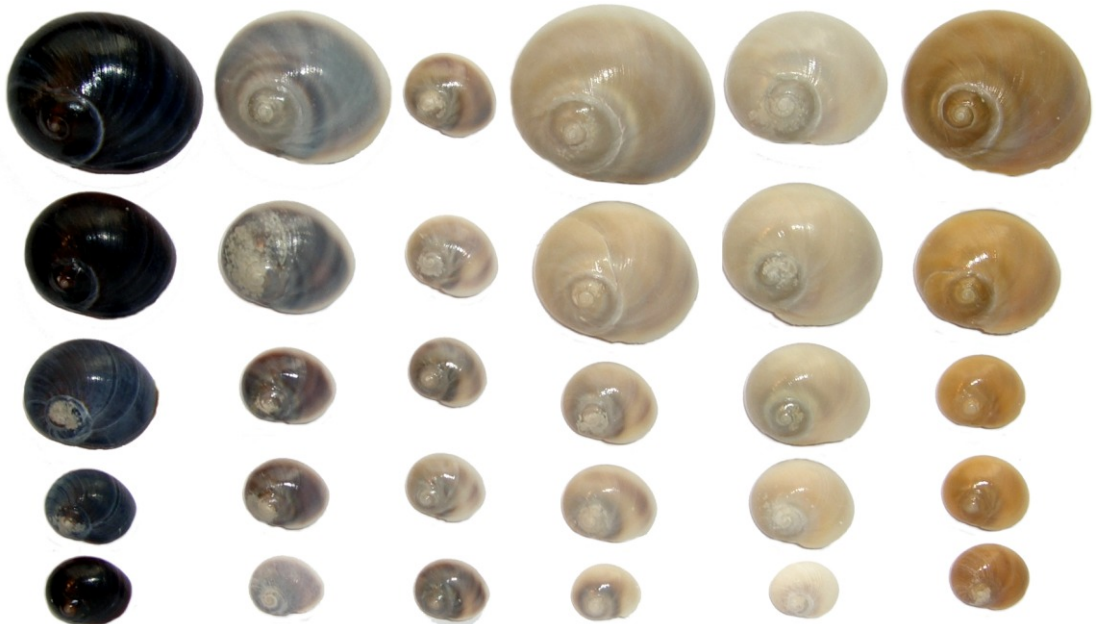


FIG. 4. *Polinices incei*. The range of colour polymorphism expressed on the dorsal surface of the shell.

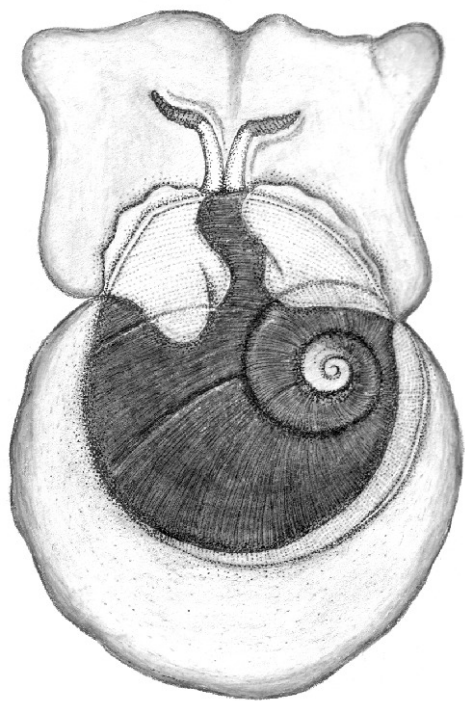


FIG. 5. *Polinices incei*. A black-shelled individual as seen from the dorsal aspect.

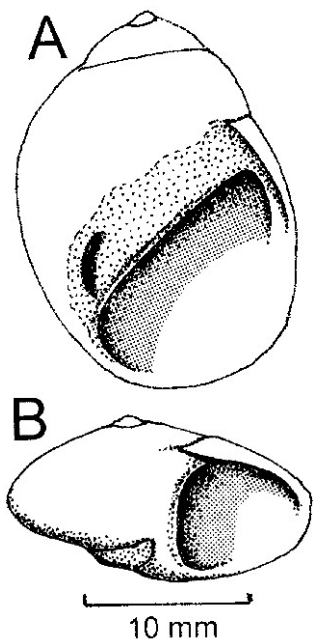


FIG. 6. Ventral views of A, *Polinices sordidus*, and B, *Polinices incei*, both drawn to the same scale.

from the sheltered, muddy shores of Moreton Bay on the west side of North Stradbroke Island (Fig. 6). The latter species (Fig. 6A) is conically ovate, with a moderately high spire, and has a maximum shell height and width of 49 mm and 45 mm, respectively. That is, a height to width ratio of $\sim 1:0.98$. In comparison, the height to width ratio of *P. incei* is $\sim 1:1.37$ (Fig. 6B).

Behaviour of *Donax deltoides*. On both Blue Lake Beach and One Mile Beach, *Donax deltoides* is tidally migratory. Most obviously, large individuals emerge from the sand and are tumbled down the beach in the backwash during periods of falling tides. Smaller individuals were rarely observed doing this, but this might simply be a reflection of the observer's inability to see them migrating. Notwithstanding, *Polinices incei* does migrate up the shore during rising tides and remains there to hunt resident small *D. deltoides* individuals.

Behaviour of *Polinices incei*. As the tide recedes on the exposed beaches of North Stradbroke Island and One Mile Beach, individuals of *P. incei* are exposed. Densities are, however, low (<1 individual 10 m^2). Typically, individuals are solitary, burrow to a shallow depth (Fig. 7A) and leave meandering trails at the sand surface as the tide falls. Such trails are obliterated by the swashes of the periodically larger waves, but in intervals between such surges, the trails can lead to the capture of the individuals making them. This is especially true towards the top of the beach, but lower down the regular swash obliterates the trails making individuals harder to find. Several behaviours of *P. incei* were identified. These included:

Surfing. An unusual behaviour is here termed surfing. In aquarium trays, most *P. incei* moved across the bottom, however when small imitation waves were created by lifting the trays up and down at one end, individuals turned onto their backs, and the foot and propodium became hugely inflated (Fig. 7B & C) such that the animals became buoyant and were washed to and fro. This behaviour is interpreted as a way for *P. incei* to quickly reach higher levels of the shore to hunt for small *Donax deltoides*. Clearly, to crawl up a beach that may be over one hundred metres wide, over each tidal cycle, would be impossible.

Surfing by *P. incei* was observed in the field only on a falling tide and in the backwash, at

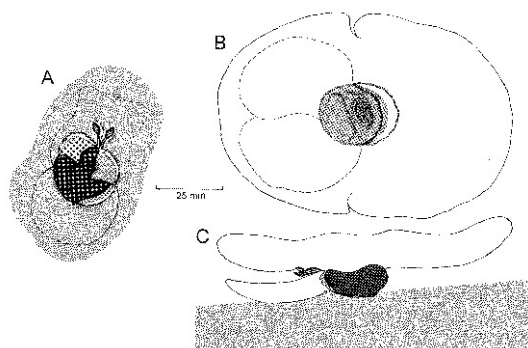


FIG. 7. *Polinices inaei*. A, dorsal view of a burrowing individual; B, C, ventral and lateral views of an inflated, surfing individual (all drawn to the same scale).

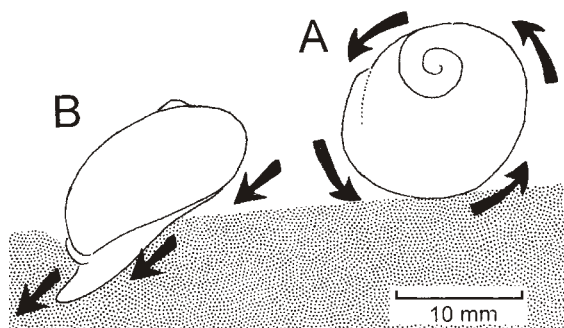


FIG. 8. *Polinices inaei*. Illustrations of A, a retracted individual rolling down the beach, and B, a braking individual with only slightly extended propodium and foot.

both Blue Lake Beach and One Mile Beach. It was impossible to observe on the rising tide as the breaking waves put too much sand into suspension for clear observations. This inability to observe migrating or surfing animals at this critical time has also been commented upon by Odendaal *et al.* (1992). Notwithstanding, as the tide and wave backwashes recede, *P. inaei* individuals are observable emerging instantaneously from the sand and inflating the foot and propodium so as to be rapidly carried down-shore. Many such individuals were determined also to be carrying prey in the foot (Table 4).

Braking. One aspect of the behaviour of *P. inaei* often observed on Blue Lake Beach and One Mile Beach was braking. When individuals higher on the shore were exhumed from the sand by a breaking wave, or were attempting to

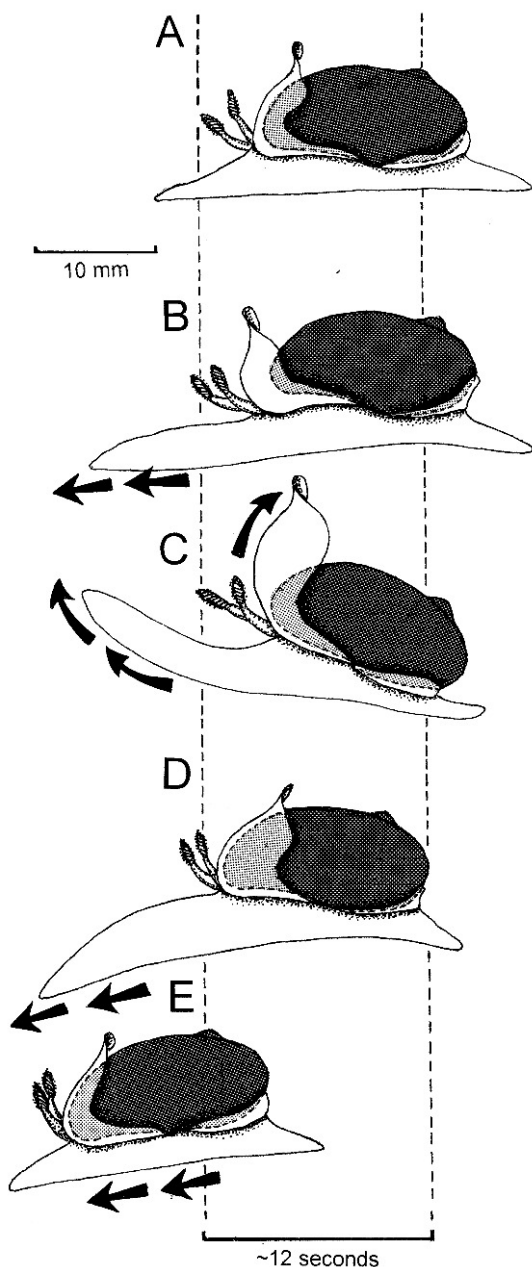


FIG. 9. *Polinices inaei*. A-E, Stages in the sequence of galloping locomotion.

relocate downshore (sometimes with captive prey held by the foot), they retracted the body into the shell and rolled down the beach in the backwash (Fig 8A). At some point, however, the anterior region of the foot and the propod-

Table 4. The numbers of cases of drilling predation, prey holding (1, 2 or 3 prey items) and prey chasing by *Polinices incei* on *Donax deltooides* on A, Blue Lake Beach, North Stradbroke Island, Queensland, and B, One Mile Beach, Port Stephens, New South Wales. (* indicates *P. incei* individuals actively surfing down shore with captured prey individuals).

Site	Predator/prey interaction	Number of cases	Mean shell width/ length of predator/prey (mm)
Blue Lake Beach	Drilling	4	18.2 / 23.4
	Prey holding	22 (19 x 1; 2 x 2; 1 x 3 prey items)	11.3 / 5.9
	Prey nearby	9	12.4 / 5.3
	Prey chasing/ escaping	1 (11.3 / 5.0)	
One Mile Beach	Drilling	1	15.5 / 22.4
	Prey holding	27 (22 x 1*; 5 x 2 prey items**)	9.3 / 4.6
	Prey nearby	4	8.4 / 4.6
	Prey chasing/ escaping	None observed	

Table 5. Predator shell width, prey shell length and outer borehole diameter data for the five examples of *Polinices incei* attacking *Donax deltooides* on Blue Lake Beach, North Stradbroke Island, Queensland, and *One Mile Beach, Port Stephens, New South Wales.

	<i>Polinices incei</i> shell width (mm)	<i>Donax deltooides</i> shell length (mm)	Valve drilled / attempt	Outer drill hole / attempt diameter (mm)
	22.3	29.5 + attempt	Left / Left	1.5 / 1.1
	20.3	25.6 + attempt	Left / Left	1.3 / 1.1
	19.8	23.1	Right	1.2
	10.5	15.2	Left	0.6
	15.5*	18.7*	Left*	1.1*
Mean	17.7	22.4	4 Left x 1 right	1.1 / 1.1

ium was extended a short distance causing, on succeeding rolls, the animal to halt its down-shore progress and end up in a position enabling it to instantly resume locomotion (Fig. 8B).

Hunting. *P. incei* hunts within the sand, typically at depths of 5–10 mm such that no part of the shell or body is visible at the surface. Only a meandering surface trail marks the progress of an individual. In laboratory aquarium trays, measured normal locomotory speeds of *P. incei* ranged from 9–17 seconds · cm⁻¹ (n=20), with a mean of 12 seconds · cm⁻¹.

Galloping. On the surface of the sand, it was occasionally observed that *P. incei* engages in a second form of locomotion to the usual slow crawling. This may be related to more active prey pursuit. The speedier locomotion is termed

galloping and is illustrated in Fig. 9. When seen from the side, the posterior part of the foot that is normally extended posteriorly (A), is sharply retracted (B). The cephalic lobes and anterior region of the foot are then extended upwards, the latter being extended dramatically (C). The greatly anteriorly elongate foot is then extended forwards where it grips the sand (D). It then contracts rapidly pulling the body forwards (E), such that the original position in (A) is obtained but ~ half a shell length further forward. Speeds obtained during galloping (in aquarium trays) ranged from 5–11 seconds · cm (n = 20), with a mean of 8 seconds · cm.

Prey holding. *Polinices incei* actively forages on the surf beaches of North Stradbroke Island, most notably Blue Lake Beach, and on One Mile

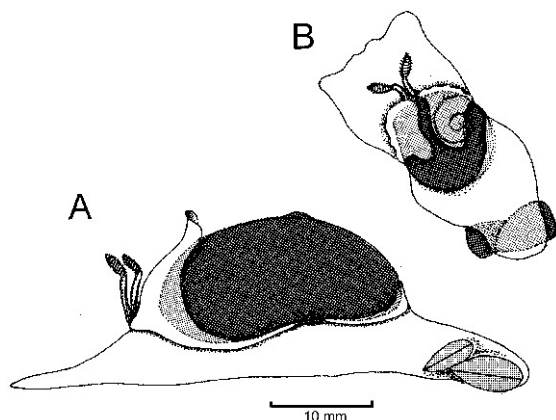


FIG. 10. *Polinices incei*. A, dorsal, and B, lateral views of an individual holding a captured prey item of *Donax deltoides* under the posterior end of the foot.

Beach, NSW. Table 4 identifies the numbers of cases of a) prey drilling; b) prey holding (including the numbers of cases of 1, 2 or 3 prey items being held); c) incidences of prey and predator near to each on the sand surface; and d) incidence of a prey actively trying to escape a pursuing predator, on both beaches. In all cases, the captured *Donax deltoides* individuals were held in place by mucus under the posterior edge of the foot, as illustrated in Fig. 10. Altogether, 22 individuals of *P. incei* (mean shell width = 11.3 mm) were identified holding their prey (mean shell length = 5.9 mm) in such a manner on Blue Lake Beach. Of these, 19 were holding 1, two were holding two, and one was holding three prey items. On One Mile Beach, 27 cases of prey holding by *P. incei* (mean shell width = 9.3 mm) were identified. Of these 22 were holding one, and five were holding two prey items. Mean shell length of the *D. deltoides* prey was 4.6 mm. On Blue Lake Beach and One Mile Beach there were nine and four cases of predator (mean shell widths of 12.4 mm and 8.4 mm, respectively) and prey (mean shell lengths of 5.3 mm and 4.6 mm, respectively) items close together on the sand surface, respectively, whereas on the former beach one case of a *D. deltoides* (shell length = 5.0) prey actively trying to escape a *P. incei* individual (shell width = 11.3 mm) was observed (Fig. 11). In addition, on One Mile Beach (Table 5*), there were three observed cases of *P. incei* surfing downshore each holding either one (x 1) or two (x 2) *D. deltoides* prey items.

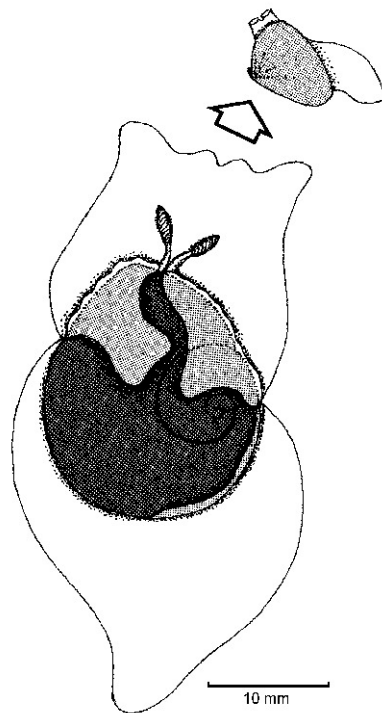


FIG. 11. *Polinices incei*. An individual high on the shore chasing a juvenile *Donax deltoides* that is attempting to escape by leaping.

The relationships between predator *Polinices incei* shell width and either drilled or captured prey (*Donax deltoides*) shell length for Blue Lake Beach and One Mile Beach are illustrated in Fig. 12 (● and ○, respectively). The slopes of the data plots are generally similar. Generally too, the shell lengths and widths of the *D. deltoides* and *P. incei* populations (in both cases including actual prey and predator sizes) on One Mile Beach, New South Wales are smaller than their conspecifics on Blue Lake Beach, Queensland (Tables 2, 3 & 4).

Prey consumption. Four cases of *Polinices incei* successfully attacking *Donax deltoides* were identified on Blue Lake Beach and one on One Mile Beach (Tables 4 & 5). In these cases, the attack was as described for other naticids with the bivalve being held by the foot, and with the proboscis, mostly obscured by the propodium, involved in drilling the prey shell. Four attacks (plus two initial attempts) were on the left valve and one on the right. There is not only a positive

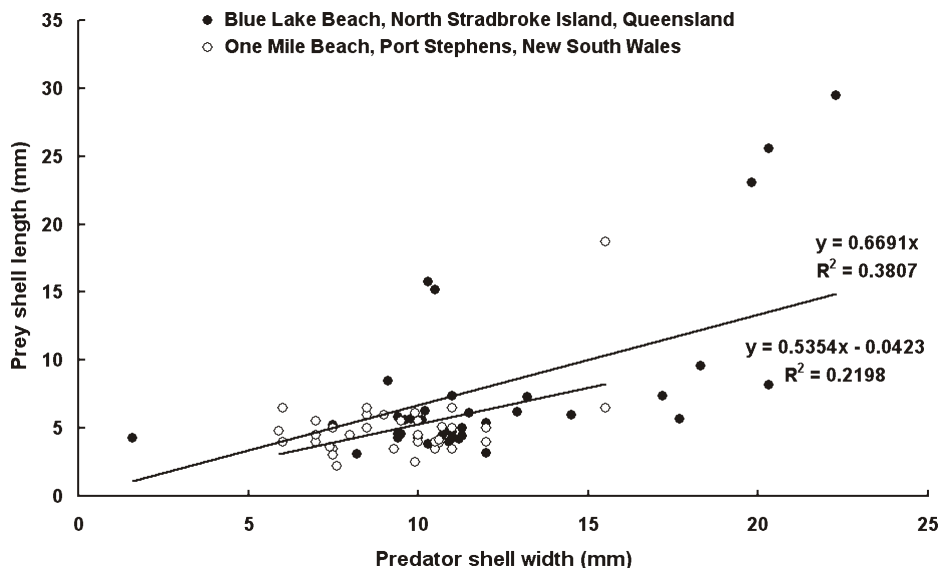


FIG. 12. The relationships between predator (*Polinices incai*) shell width and prey (*Donax deltooides*) shell length of individuals collected from (●) Blue Lake Beach, North Stradbroke Island, Queensland and (○) One Mile Beach, Port Stephens, New South Wales.

relationship between predator shell width and prey shell length but also a relationship between predator shell width and drill hole diameter, larger individuals making larger drill holes (Table 5).

The positions of the five identified drill holes made in the shells of its *Donax deltooides* prey by *Polinices incai* are illustrated in Fig. 13. Four attacks were identified from Blue Lake Beach,

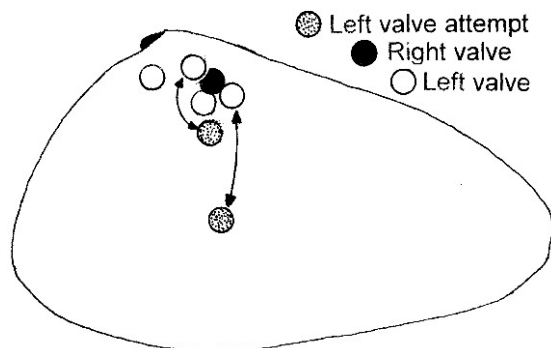


FIG. 13. The positions of drill holes made in the shells of five individuals (plus two abandoned attempts) of *Donax deltooides* by *Polinices incai* from Blue Lake Beach, North Stradbroke Island, Queensland, and One Mile Beach, Port Stephens, New South Wales.

three on the left valves and one on the right, plus two abandoned attempts on left valves below two of the above identified attacks. Only one attack on the left valve was identified for One Mile Beach. All attacks were close to the umbones of *D. deltooides*, that is, at a position above the digestive diverticula. The two initial attempts were more ventral to the final adopted attack site, suggesting that the predator chose to finalise its attack more dorsally.

Four drill holes and the one abandoned attempt are illustrated as SEM photomicrographs in Figs 14 and 15. Figure 14A shows the abandoned attempt wherein only the periostracum has been removed but interestingly by etching not radula scraping. In Fig. 14B, the drill hole is deeper showing evidence again of chemical etching. Fig. 14C shows how a central 'boss' has been created in the centre of the drill hole, while Fig. 14D illustrates a completed, countersunk drill hole characteristic of naticids (Ziegelmeier 1954; Carriker 1981). Fig. 15 shows another early drill hole (~ equivalent to Fig. 15B) with a near circular countersunk hole and Fig. 15B is a higher magnification of the periostracum around this hole showing clear evidence of chemical etching.

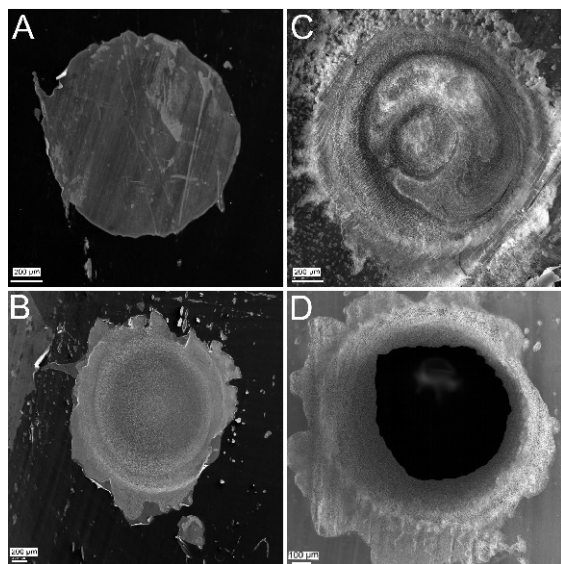


FIG. 14. *Donax deltooides*. Scanning electron micrographs (Jeol 820) of four drill holes made by *Polinices incei*. **A**, An abandoned attempt showing that the periostracum has been removed by etching; **B**, drilling has commenced creating a characteristic near circular, countersunk drill hole; **C**, drilling nearly complete with a characteristic central boss to the drill hole; and **D**, a completed drill hole.

DISCUSSION

The earliest holes resembling those of naticids are Triassic between ~195–225 mya (Newton 1983; Fursich & Jablonski 1984), although the group diversified, alongside the Muricidae, in the Cretaceous between 65–136 mya (Sohl 1969; Kabat 1990). Today, this diverse group of predators is dominant on soft substrata virtually worldwide, while representatives of the Muricidae are more common on hard substrata. Both, however, largely but not exclusively, drill their prey. Ziegelmeier (1954), Carriker (1981), Kitchell (1986), Kabat (1990) and Reyment (1999) have reviewed naticid predation.

Temperate shore predators such as the muricids *Nucella lapillus* (Linnaeus, 1758) and *Urosalpinx cinerea* (Say, 1822) attack shells both mechanically by rasping with the radula, and chemically using the secretion of the accessory-boring organ (ABO) (Gabriel 1981). *Urosalpinx cinerea* largely uses its radula to scrape holes in the shells of *Mytilus edulis* Linnaeus, 1758, and

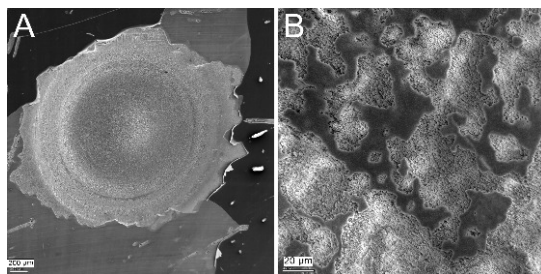


FIG. 15. *Donax deltooides*. Scanning electron micrographs (Jeol 820) of **A**, an initially etched shell and periostracum approximately equivalent to Fig. 14B, and **B**, a higher magnification micrograph of the chemically etched periostracum and dissolved shell material.

Mya arenaria Linnaeus, 1758 (Carriker *et al.* 1974). Radula scrape marks were also identified from the holes drilled by *Lepsiella paivae* (Crosse, 1864) in its bivalve prey, the venerid *Katelysia scalarina* (Lamarck, 1818) (Morton 2005). Notwithstanding, the accessory boring organ is considered to be an essential component of the shell penetrating mechanism of drilling gastropods (Carriker 1981). It is located in the foot of Muricidae and is responsible for producing acidic secretions, chelating agents and enzymes (Carriker & Williams 1978; Carriker 1981). Carriker & Williams (1978) hypothesised that drilling by muricid gastropods employs a combination of enzymes, an inorganic acid, chelating agents in a hypertonic medium to facilitate shell dissolution, and intracellular transport of calcium during the chemical phase of valve penetration.

Ponder & Taylor (1992, plates III & IV) provided SEM pictures of the drill holes made by *Austroginella johnstoni* in various bivalve prey while Ansell (2000: fig 2A–D) illustrates the structure of drill holes made by the New Zealand *Xymene plebeius*. Harper & Peck (2003, fig. 2A–D) illustrate the holes made by *Trophon longstaffi* in its bivalve prey, the Antarctic laternulid *Laternula elliptica*, and those made by *Lepsiella paivae* in the shells of *Katelysia scalarina* were illustrated by Morton (2005: figs 3, 4).

Ponder & Taylor (1992) could not identify radula scrape marks in the excavations made on the shells of bivalve prey by the marginellid *Austroginella muscaria* (Lamarck, 1822). Both the crossed-lamellar and homogeneous shell micro-

structures exposed in the excavations were all highly corroded with the aragonite crystals having rounded edges. This suggested a dominantly solutional, rather than mechanical, drilling mechanism. Similarly, an SEM study of the holes drilled by *Hexaplex trunculus* (Linnaeus, 1758) (Muricidae) in the shells of various species of bivalve prey by Peharda & Morton (2006) found no evidence of radula scrape marks. The scanning electron microscope images revealed etched shell surfaces indicating chemical shell penetration.

Unlike the mainly chemical method of pre shell access in representatives of the Muricidae and Marginellidae, however, drilling in the Naticidae is thought to involve mechanical radula rasping and secretions from an accessory boring organ (ABO) located in the proboscis (not the foot as in muricids). The secretions produced by the naticid ABO comprise hydrochloric acid, enzymes and chelating agents (Carriker & Gruber 1999). Prey is first detected by chemo- and/or mechano-reception, evaluated by handling and, if accepted, engulfed in a gelatinous mucous and finally enveloped and oriented by the propodium in preparation for drilling. Unlike straight-sided muricid drill holes, those made by naticids are beveled and parabolic in cross section such that the outer drill hole diameter is larger than the inner (Bromley 1981; Carriker 1981; Kowalewski 1993; Reyment 1999). Zeigelmeier (1954) described the drilling mechanism in *Lunatia nitida* (Donovan, 1800) — during prey shell penetration, the proboscis is rotated by 90° at a time and radula rasping is undertaken systematically, sector by sector, from the centre of the developing drill hole to the periphery. The centre of the hole where the least radular rasping occurs is thereby formed into a boss that is characteristic of naticid drill holes. Such a boss is also seen in the holes drilled by *Polinices incae* (Fig. 14C). According to Zeigelmeier (1954), radula rasping is followed by raising the proboscis from the incomplete drill hole and placing the ventral lip of the mouth containing the ABO in the hole. Secretions from the ABO dissolve the shell layers, and the weakened shell is further radula rasped to complete the drill hole. Zeigelmeier (1954) also noted that *L. nitida* swallowed the

shell material produced in the process of drilling. However, in the *Donax deltooides* shells herein examined using the SEM, there is no indication of radula rasping (Figs 14 & 15) at any stage of the shell penetration process.

Aquarium observations of naticid gastropods in Hong Kong showed that different species attack their bivalve prey in different ways (Ansell & Morton 1987). *Polinices tumidus* has been shown to adopt at least three different tactics in dealing with bivalve prey, that is, conventional side drilling, edge drilling, and non-drilling predation. None of these is used exclusively against any particular prey, at least not under aquarium conditions, but the frequency of occurrence of a particular method differs with different prey. No clear relationship between prey shell thickness and degree of shell ornamentation and the percentage of non-drilling attacks was identified (Ansell & Morton 1987).

Taylor *et al.* (1969) examined the shell microstructure and mineralogy of four species of *Donax*. In all cases, the aragonitic shell comprised three layers, that is, an outer composite prismatic, a middle crossed lamellar and inner complex crossed lamellar layers. The prismatic outer layer is believed to give the best protection against drilling gastropods, and possibly other shell-penetrators (Gabriel 1981). Although protection from shell drilling predators may have been a major factor in the evolution of shell types, it is clear that *Polinices incae* has overcome the inherent resistance to abrasion by the outer prismatic layer of the *Donax deltooides* shell and penetrates it chemically. Harper & Skelton (1993a) suggest that the inert bivalve periostracum confers a degree of protection against drilling predators by retarding penetration of the ABO secretion. The same authors (Harper & Skelton 1993b) demonstrated this for mytilid bivalves that with the periostracum stripped from the shells were more vulnerable to muricid drilling predation than those with the periostracum intact.

This is clearly not the case, however, for *P. incae* attacking *D. deltooides* using ABO secretions, and thus raises the question whether the periostracum does have any role in protecting the bivalve shell from penetration by either mechanical or chemical erosion.

Many predatory gastropods detect their prey by chemoreception (Kohn 1961). Nassariid gastropods, like naticids, do not generally occupy high energy, wave-exposed, beaches, chemical cues emanating from stranded carrion being better detected on long, gently sloping beaches under conditions of low exposure to wave action (Britton & Morton 1994). A remarkable exception to this generalisation is *Bullia digitalis* in South Africa that 'surfs' or swash-rides up wave-exposed shores in search of carrion, for example, stranded jellyfish (Odendaal *et al.* 1992). *Polinices incei* lacks eyes, as in other swash riders such as species of *Bullia*. Instead the latter has an acute sense of smell, responding rapidly to amino acids in the water (Hodgson & Brown 1987) although exactly how food can be located even by this means is unknown. Any chemical gradient that nassariids are thought to need to successfully arrive at carrion (or its prey in the case of *P. incei*) (Britton & Morton 1994) is likely destroyed by the turbulence created by wave action. In this context, however, *P. incei* is probably a more efficient predator than *B. digitalis* is a scavenger, because in the latter species its food, carrion, is randomly moved by waves whereas in the former, unless migrating, the *Donax deltooides* prey is internally resident. Further, since the *P. incei* examined in this study were actively hunting their prey up shore, at or just above the region of maximum wave reach, it seems possible that *D. deltooides* juveniles are not so readily migratory as their adult conspecifics. Kitching & Pearson (1981) make the interesting observation that *P. incei* may detect its prey by sound or, more likely, the sound vibrations made as the bivalve moves in the sand. This might explain why *P. incei* hunts high on the shore above wave reach as the swash and backwash would mask any such vibrations. That is, within the waves any such minute vibrations would be undetectable. Numerous cases of *P. incei* in close association with *D. deltooides* juveniles lying on the sand surface were recorded for both Blue Lake Beach and One Mile Beach (Table 4) and on one occasion a bivalve was seen leaping to escape from a pursuing predator. Laws & Laws (1972) record that the mesodesmatid *Donacilla angusta* [= *Paphies elongata* (Reeve, 1854)] emerges

from the sand in shallow subtidal water to avoid capture when *Polinices conicus* approaches it, and then reburrows once the predator has passed. Significantly, the five examples of *P. incei* drilling its captured prey were all identified lower down the shore, in the surf during low tide periods.

It thus appears that *Polinices incei* hunts *Donax deltooides* juveniles either close to, or at the sediment surface, high on the drying shore, and a captured prey (up to three individuals) is held at the rear of the foot and taken downshore where manipulation and drilling occurs within the substratum. The olive *Oliva tigris* Duclos, 1835, that occupies low intertidal sand flats in eastern Australia also carries its prey, typically bivalves and gastropods, on the rear of its foot before consuming them later (Taylor & Glover 2000). 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. A similar observation was made upon *P. tumidus* by Vermeij (1980), that is, ~30% of the bivalve prey consumed by this predator in the laboratory showed no signs of drilling activity. It is thus significant that the prey individuals of *Donax deltooides* being held orally and drilled by *P. incei*, ranged in shell length from 15.2–29.5 mm, whereas those being held in the foot ranged in shell length from 3.1–15.8 mm. That is, there was little overlap between the two categories of prey. Although as this study shows there is a positive correlation between prey shell length and predator shell width, it would be very difficult to identify drilled shells of the *D. deltooides* juveniles being captured and held by *P. incei* in the beach sands. The smallest empty drilled individual of *D. deltooides* collected from One Mile Beach had a shell length of 15.0 mm. Sieving the beach sands might reveal if small individuals of *D. deltooides* are drilled post capture by *P. incei*. Further, it is unknown at what size and age *P. incei* commences drilling, although Wiltse (1980) has demonstrated that the larvae of *Polinices duplicatus* settle in close proximity to populations of its bivalve prey *Gemma gemma* and commence feeding soon after metamorphosis into juveniles occurs. Morton &

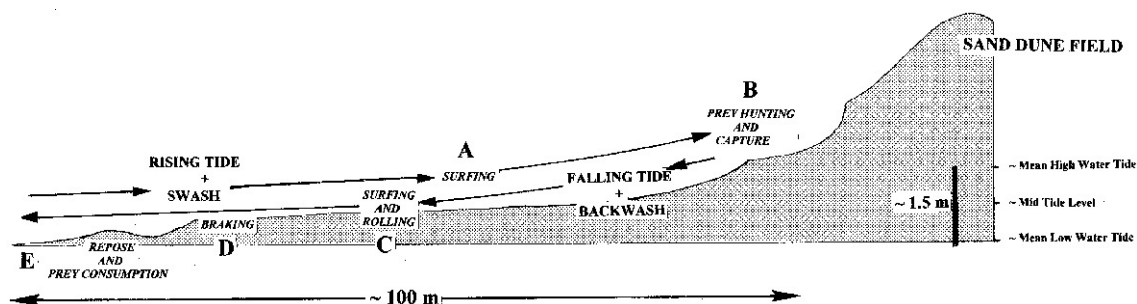


FIG. 16. A diagrammatic illustration of the profiles of the wave-exposed beaches on North Stradbroke Island and Port Stephens. The diagram also identifies aspects of the behaviour of *Polinices incae* that enable it to A, surf up the shore, and B, hunt and capture juvenile *Donax deltoides* in the swash of rising tides and return downshore by C, surfing and rolling, D, braking and burrowing to E, finally repose and consume its captured prey in the backwash of falling tides.

Chan (1997) similarly showed that newly settled juveniles of the nassariid *Nassarius festivus* (Powys, 1835) could also drill. More significantly, however, Ansell (1982) was able to maintain cultures of *Polinices catena* (da Costa, 1778) and hence plot juvenile rates of predation and growth. Juvenile *P. catena* ate approximately one hatchery-provided juvenile *Venerupis decussata* (Linnaeus, 1758) each day, and it does not seem unreasonable to suggest that *P. incae* would have a similar predation rate. Ansell (1982) also showed that as *P. catena* grew, so the size of prey needed also increased. This is reflected in the observations recorded herein for *P. incae* that in the field larger predators attacked larger prey *D. deltoides*. The largest *D. deltoides* observed being drilled (by a *P. incae* of 22.3 mm shell width) had a shell length of 29.5 mm (Table 5). The largest drilled (by an unknown naticid) valve of *D. deltoides* collected from Blue Lake Beach had a length of 38.6 mm. The largest *P. incae* collected had a shell width of 29.3 mm and it would thus seem reasonable to suggest that this individual (extrapolating Fig. 11) could have preyed on a *D. deltoides* individual of 38.6 mm shell length. That is, *P. incae* seems to be the only naticid present on the eastern Australian wave exposed shores and that its principal prey is *D. deltoides* juveniles up to a shell of ~39.0 mm. It is presumably unable to catch, handle or penetrate larger *D. deltoides* individuals and, thus, at shell lengths > ~39.0 mm the bivalve enters a size refuge from predation. This may help explain the unusual *D. deltoides* population

histogram (Fig. 2) where the largest (oldest) individuals comprise the dominant cohort. Such a surprising situation is, however, made more remarkable by the conclusion that *P. incae* preys, possibly exclusively, on a surf clam living in a habitat which has hitherto been regarded as a haven from predation.

Figure 16 is a diagrammatic illustration of the profiles of the wave-exposed beaches on North Stradbroke Island and Port Stephens. The average tidal range on such beaches is but ~1.5 metres so that waves become the dominant factor effecting not just the structure of the shore, but also in extending the tidal zone much further upwards than the limits exposed by the tides. The shores are thus about 100 metres from top to bottom. Fig. 16 also identifies generalised aspects of the behaviour of *Polinices incae* that enable it to A) surf up the shores, and B) hunt and capture juvenile *Donax deltoides* residing at their highest. This is undertaken in the swash of rising tides. Return down shore by *P. incae* with captured *D. deltoides* held by the foot is by C) surfing and rolling, and D) braking, and is undertaken in the backwash of falling tides. Over low tide periods *P. incae* individuals burrow into the sediment to E) find repose and drill and consume their captured prey.

Although nothing is known of the physiology of *Polinices incae*, clues can be obtained from the comprehensive research undertaken on the similarly surfing *Bullia digitalis* in South Africa by A.C. Brown and his co-workers. Brown (1971) has studied the ecology of *B. digitalis* and

shown (Brown 1979) that transport in the surf is, surprisingly, similar energetically in terms of oxygen uptake (1250 g. hr^{-1}) to burrowing (1126 g. hr^{-1}), whereas crawling is much less (680 g. hr^{-1}). Thus, since once inflated, *P. incej* would (if it has a similar physiology to *B. digitalis*) not be spending any energy surfing, the increased energy required for such an activity must be related to the mechanism of inflation. Morris (1950) showed that inflation of the foot of the Australian naticid *Polinices strangei* (Reeve, 1855) was by a combination of muscular activity co-ordinated with the hydraulic pumping of blood into it. This creates a solid leading edge to the foot and a propodium shielding the front of the shell, as in all naticids, and which allows them to burrow in search of prey. In *Polinices incej*, however, such inflation, for the purposes of 'surfing' (or swash-riding) or crawling subsequent to 'braking', is extremely fast and must represent a possibly unique adaptation to the habitat it occupies and the prey it targets on such beaches. This is because the prey of naticids is not chosen randomly. Rather, there is a high degree of predator selectivity with respect to prey species and size — both absolute and relatively, according to predator size.

Such selective behaviour by naticids appears to be stereotypical, and has evolved over time, as evidenced by an inability to select novel prey under laboratory conditions (Boggs *et al.* 1984). Kitchell *et al.* (1981) have shown that prey selection by naticids is consistent with the concept and predictions of cost-benefit analysis, that is, optimal foraging theory (Hughes 1980) and its subsequent modification (Hughes & Dunkin 1984; Hughes & Drewett 1985). It is thus clear that *Polinices incej* has evolved to attack the surf clam *Donax deltoides* specifically. Donacids, it has been argued (Ansell 1981, 1983), have evolved to occupy highly dynamic surf beaches as, in part, a refuge from marine predators. As a result, donacids have generally escaped from naticid predation. The literature identifies only three examples of predation upon donacids. The first, by Ansell & Morton (1987) demonstrated that *Polinices tumidus* was able to feed on *Donax faba* (Gmelin, 1791) in laboratory experiments although the two do not naturally share

the same habitat. The second by Vignali & Galleni (1987) suggested that strandline shells of *Donax semistriata* Poli, 1795, and *Donax trunculus* Linnaeus 1758, had been drilled by a naticid but with no proof. The third, by Negus (1975) only showed that strandline collected *Donax vittatus* (da Costa, 1778) had been drilled by a naticid, presumably offshore. In the highly dynamic habitat of wave-exposed beaches in eastern Australia, however, *Polinices incej* has evolved a remarkable suite of adaptations to follow and attack its chosen prey in a perceived sanctuary. In so doing, this remarkable predator not only broadens our picture of naticid adaptive radiation but also provides a remarkable example of the evolutionary 'arms race' that must constitute the selective force that has forged such a predator-prey relationship.

In the arms race that exists between predator and prey (Vermeij 1978), *Corbula crassa* Hinds, 1843, successfully defends itself against naticid attack by developing proteinaceous layers in the usual calcite of its shell (Morton 1990b), although in the Miocene of Poland *Corbula gibba* (Olivi, 1792) was readily attacked by two naticids — *Natica tigrina* (Röding, 1798) and *Hinia restitutiana* Fontannes, 1879 (Zlotnik 2001). The evolution of naticid drilling predation is part of the Mesozoic Marine Revolution (Vermeij 1977) entailing, especially in the tropics, the diversification of infaunal bivalve and other prey resources. As predicted by escalation theory, the dangers to such infaunal residents from naticid predation (especially following the family's diversification in the Cenozoic) seems to have increased over time, albeit via a complex pathway mediated by abiotic events linked to mass extinctions (Kelley & Hansen 2003). Since shallow water benthic assemblages are believed to be particularly susceptible to mass extinction events (Jablonski & Valentine 1981), it seems probable that the *Polinices incej/Donax deltoides* relationship is relatively modern. Notwithstanding, the relationship identified herein is a remarkable, and hitherto unrealised, example of predatory adaptive radiation.

ACKNOWLEDGEMENTS

I am grateful to Peter Davie and the organising committee of the Australian Marine Sciences

Association (SE Queensland Branch), for organising the Thirteenth International Marine Biological Workshop and inviting me to participate. I am also grateful to Lisa Gershwin for allowing me to use her 4-wheel drive vehicle to access the beaches herein reported upon, and to Dr J.D. Taylor (The Natural History Museum, London) who acquainted me to the presence of *Polinices incei* on the surf beaches of North Stradbroke Island. Dr R. Bamber (The Natural History Museum, London) kindly arranged for the collected sediment samples to be analysed and Dr E.M. Harper (University of Cambridge) is thanked for taking the SEM photographs of the *Polinices incei* drill holes. Dr Katherine Lam (City University, Hong Kong) gave invaluable statistical advice.

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