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First evidence of drilling predation by *Conuber sordidus* (Swainson, 1821) (Gastropoda: Naticidae) on soldier crabs (Crustacea: Mictyridae)

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Abstract

Moonsnails (Naticidae) are major predators in marine soft substrates worldwide and are thought to prey almost exclusively on shelled molluscs by drilling predation. However, reports on single individuals of various naticid species showing unusual feeding behaviour indicate that naticids possibly also feed on other prey which have an external skeleton. The present study provides the first evidence for size selective feeding of an Australian moonsnail (*Conuber sordidus*) on crustaceans. *C. sordidus* preys on soldier crabs (*Mictyris longicarpus* and *Mictyris platycheles*) on intertidal sand/muddy tidal flats, representing the first well-documented example of a naticid preying on large non-molluscan invertebrates in addition to shelled molluscs. This indicates that prey choice in *C. sordidus* is less stereotyped than predicted for naticid species, although the feeding mode documented here is similar to that used to capture their main diet of shelled molluscs. The results strongly support some contested earlier studies that have also indicated that naticids will eat non-molluscan prey with an external skeleton, highlighting a need to re-examine generally accepted models concerning naticid feeding ecology.

Key words: *Mictyris*, hermit crab, size-related feeding, behaviour, intertidal, Caenogastropoda, Naticoidea

Introduction

Shell drilling molluscs are major invertebrate predators in Modern and Early seas (Vermeij 1987; Harper 2003). Such drilling predation is known in several groups of caenogastropods, particularly Muricidae and Naticidae (Carriker 1981) but also some species of Buccinidae, Marginellidae, Fasciolariidae, Ranellidae and Tonnidae (see reviews by Taylor and Taylor 1977 and Harper 2003). The Naticidae are one of the largest and earliest groups of shell drillers with strong influences on community structure and species diversity (Sohl 1969; Wiltse 1980; Popenoe *et al.* 1987; Kabat 1990).

Naticids are reported to select prey specifically in sand or sandy-mud substrata and to feed almost exclusively on shelled molluscs (Yochelson *et al.* 1983; Kelley and Hansen 1993; Huelsken *et al.* 2008). Naticids access prey tissue by drilling distinct circular, bevelled-edged holes. These drill holes are different from those of other drilling predators (Dietl 2001) making them identifiable and traceable in fossil mollusc shells through time (Kelley and Hansen 1993). Predatory interactions between naticids and other shelled molluscs have therefore contributed to the development of models for predator-prey systems (e.g., ‘arms race’ effect, co-evolution, cost-benefit maximization, escalation) (e.g., Edwards 1974; Kitchell *et al.* 1981; DeAngelis *et al.* 1985; Vermeij 1987; Kelley and Hansen 1993). Among others (e.g., Kingsley-Smith *et al.* 2003; Grey *et al.* 2007), these studies have assumed a strong or immutable association of predator (naticid) to prey (shelled molluscs) based on the supposed stereotyped, predictable, and apparently specialized feeding behaviour of naticids on a range of shelled molluscs. Possible other prey species have not been taken into account, in large part because of a general paucity of direct observations of naticid feeding.

Some naticids have been reported as showing ‘unusual’ predatory behaviour and possible feeding on non-molluscan prey (Table 1). For example, some are assumed to feed on dead fish and other carrion (Gould 1841; Perry 1940) and may occasionally feed on polychaetes (Paine 1963), crustaceans (Livan 1937; Cameron 1966; Reyment 1966; Maddocks 1988; Bhatia *et al.* 1989), brachiopods (Witman and Cooper 1983) and even egg capsules from various marine species (both invertebrate and vertebrate) (Thorson 1935; Jensen 1951; Ansell 1961) (see Table 1). As many of these reports were based on indirect evidence (drilled holes) or by observations of single specimens, the observations have usually been dismissed as aberrant behaviour of starved specimens rather than normal events of naticid feeding (Boettger 1930; Kabat 1990).

Thus, it remains unclear if naticids exclusively prey on shelled molluscs or select other animals as regular prey as well. The present study gives the first well-documented example of a naticid species, *Conuber sordidus* (Swainson, 1821), preying on comparatively large crustaceans using the same stereotypic feeding behaviour used on shelled molluscan prey. In this case *C. sordidus* is shown to prey on the brachyuran crabs, *Mictyris longicarpus* (Latreille, 1806) (Fig. 1A) and *Mictyris platycheles* (H. Milne-Edwards, 1852), and an unidentified hermit crab on intertidal muddy or muddy-sand localities in eastern and southern Australia.

Materials and methods

Specimens of *Conuber sordidus* (Fig. 1B) were observed feeding on *Mictyris* spp. at North Stradbroke Island (Moreton Bay, Queensland, Australia) and Port Welshpool (Victoria, Australia) during low tide periods when the substrate was exposed and semi-dried, with occasional tidal pools.

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TABLE 1: Reports of naticids preying on non-molluscan prey, sorted by publication date.

Naticid species	**Prey (species, group)**	**Observation/identification of predation**	**Reference**
Euspira lewisii (Gould, 1847)	Dead fish (Pisces, carrion)	Live observation	Gould 1841
Naticidae	Egg capsules of buccinids (Gastropoda)	Drill hole investigation	Thorson 1935
Naticidae	Ostracoda (Crustacea)	Drill hole investigation	Livan 1937
Naticarius canrena (Linnaeus, 1758)	Dead fish (Pisces, carrion)	Live observation	Perry 1940
Naticidae	Egg capsules of rays (*Raia* sp.)	Drill hole investigation	Jensen 1951
Naticidae	Egg capsules of dogfish *Scyliorhinus canicula* (Linnaeus 1758)	Drill hole investigation	Ansell 1961
Neverita duplicata (Say, 1822)	*Owenia fusiformis* delle Chiaje, 1841 (Polychaeta)	Live observation	Paine 1963
Conuber sordidus	Juvenile Blue Soldier Crab *M. longicarpus*	Live observation(?)	Cameron 1966 (pers. comm. F.C. Vohra)
Naticidae	*Cytheropteron* sp. (Ostracoda, Crustacea)	Drill hole investigation	Reyment 1966
Naticidae	Brachiopoda	Drill hole investigation	Whitman & Cooper 1983
Naticidae	Ostracoda (Crustacea)	Drill hole investigation	Reyment & Reyment 1987
Naticidae	Ostracoda (Crustacea)	Drill hole investigation	Maddocks 1988
Naticidae	Ostracoda (Crustacea)	Drill hole investigation	Bhatia *et al.* 1989
Conuber sordidus	Blue soldier crab (*M. longicarpus, M. pachyeles*)	Live observation in the field and in aquaria	This study
Conuber sordidus	Hermit crab	Live observation	This study

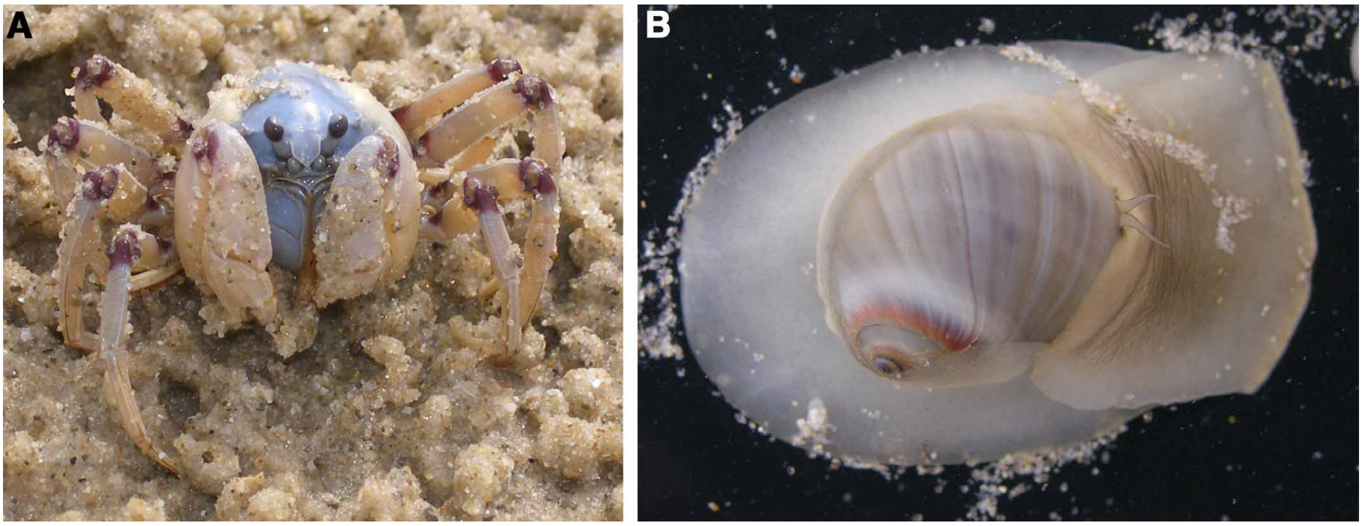

FIGURE 1. **A**. *Mictyris longicarpus* (Latreille, 1806), North Stradbroke Island, Queensland, Australia. Approximate carapace length 15 mm; **B**. *Conuber sordidus* (Swainson, 1821), North Stradbroke Island, Queensland, Australia. Approximate shell length 15–20 mm.

To test whether this is typical behaviour in *C. sordidus* or an 'incidental' occurrence, experimental manipulations (North Stradbroke Island) of snails and soldier crabs (*M. longicarpus*) were conducted in the field (n = 85) and in aquaria (n = 11) (n = number of *C. sordidus* tested). In field experiments, captured *M. longicarpus* of variable size (6–21 mm) were placed directly in the path of crawling *C. sordidus*. To avoid repeated analysis of the same specimens, experimental manipulations were performed along independent transects of 64.0–268.8 m lengths and 2 m width (n = 12) at low tide at two different localities on North Stradbroke Island (Amity Point (AP): 27°24.2548'S 153°26.1130'E [8 transects, n = 59], Dunwich (DW): 27°29.4329'S 153°24.143'E [4 transects, n = 27]) (Table 2).

TABLE 2: Data obtained from transects performed at Amity Point (AP) and Dunwich (DW), North Stradbroke Island, Australia.

Transect	Length (m)	Surface area (m^2)	No. of *C. sordidus* tested	No. of successful attacks	No. of unsuccessful attacks	% attacks per transect	*C. sordidus* per m^2
AP1	110.0	220.0	5	3	0	0.80	0.02
AP2	64.0	128.0	6	4	1	0.67	0.05
AP3	138.6	277.2	14	3	2	0.29	0.05
AP4	118.3	236.6	9	4	1	0.33	0.04
AP5	148.1	296.2	6	2	1	0.33	0.02
AP6	204.3	408.6	6	2	1	0.83	0.02
AP7	268.8	537.2	10	1	1	0.30	0.02
AP8	70.5	141.0	3	3	2	1.00	0.02
Average	140.3	280.6	-	-	-	0.57	0.03
Sum	-	-	59	22	9	-	-
DW1	85.6	171.2	8	1	0	0.13	0.05
DW2	65.9	131.8	11	1	1	0.09	0.08
DW3	97.0	197.0	5	1	0	0.20	0.03
DW4	76.8	153.6	3	0	0	0.33	0.02
Average	81.3	163.4	-	-	-	0.19	0.05
Sum	-	-	26	3	1	-	-

To analyze whether *C. sordidus* is size selective in its predation, 3–5 *M. longicarpus* of different sizes [small (5–9 mm): 7.9 mm ± 1.2 mm (n = 11); medium (10–14 mm): 12.2 mm ± 1.2mm (n = 14); large (≥ 15 mm): 16.8 mm ± 2.8mm (n = 11)] were placed together with one *C. sordidus* in aquaria. Aquaria (30 x 15 cm) were filled with 20–30 mm of sand and 25–35 mm filtered seawater to simulate an intertidal ecosystem.

In field experiments, behaviour was classified as 'successful attack' when a snail attacked a soldier crab and wrapped it into its large foot and as 'unsuccessful attack' when a crab escaped the attack. In aquaria experiments, feeding behaviour was classified as 'preyed' when a snail has chosen and consumed a soldier crab and as 'not preyed' for any other crabs that have not been eaten. After a few hours, caught soldier crabs were manually released from the snail's foot to identify the mode of feeding.

Sizes of crab carapaces and snail shells were measured with callipers in each experiment. To test whether *C. sordidus* shows size related predation, ratios of crab size (carapace length) to snail size (shell length) (c/s) were calculated. Data sets were analyzed using the non-parametric Mann-Whitney test implemented in PRISM 5.0 (Motulsky 2007). Observations were digitally recorded with an Olympus 7070WZ digital camera. Remains of consumed soldier crabs were sampled and photographed.

Results

Predation on *M. longicarpus* and *M. platycheles* by *C. sordidus* was observed on sand flats on North Stradbroke Island (Queensland, Australia) and in Port Welshpool (Victoria, Australia), respectively (Figs 2A–D). During field work several other individuals of *C. sordidus* were observed to feed on 'typical' prey such as bivalves (e.g., Veneridae) and gastropods (e.g., Naticidae, Nassaridae). At Amity Point, we furthermore observed a specimen of *C. sordidus* preying on a hermit crab in a *Nassarius* shell (Figs 2E–F). A video showing feeding behaviour is available as supplementary material at http://www.mapress.com/mr/content/v31/data/v.mp4.

Description of behaviour

Conuber sordidus was observed to attack *M. longicarpus* of any size (6–21 mm) at both study sites on North Stradbroke Island. Once a snail came close to a soldier crab, the snail started to reach for it with its large propodium (Fig. 2A) and then rapidly wrapped the crab in its foot (Fig. 2B). With the soldier crab secured, the snail fell back onto its shell and started to cover and gradually immobilise the soldier crab with thick mucus (Fig. 2C). Capturing and seizing a soldier crab took only a few seconds, whereas it took several minutes to coat the soldier crab with mucus. Once coated in mucus, the soldier crab became attached to the snail's mesopodium, after which the snail re-buried itself in the sand (Fig. 2D) (see video http://www.mapress.com/mr/content/v31/data/v.mp4).

Mostly, attacks were successful when soldier crabs had not yet started burrowing into the sand. Attacks were unsuccessful when soldier crabs dug themselves out of the sand and scurried away, or started to defend themselves by using their chelipeds. In these cases *C. sordidus* was not able to envelop the soldier crab with its propodium.

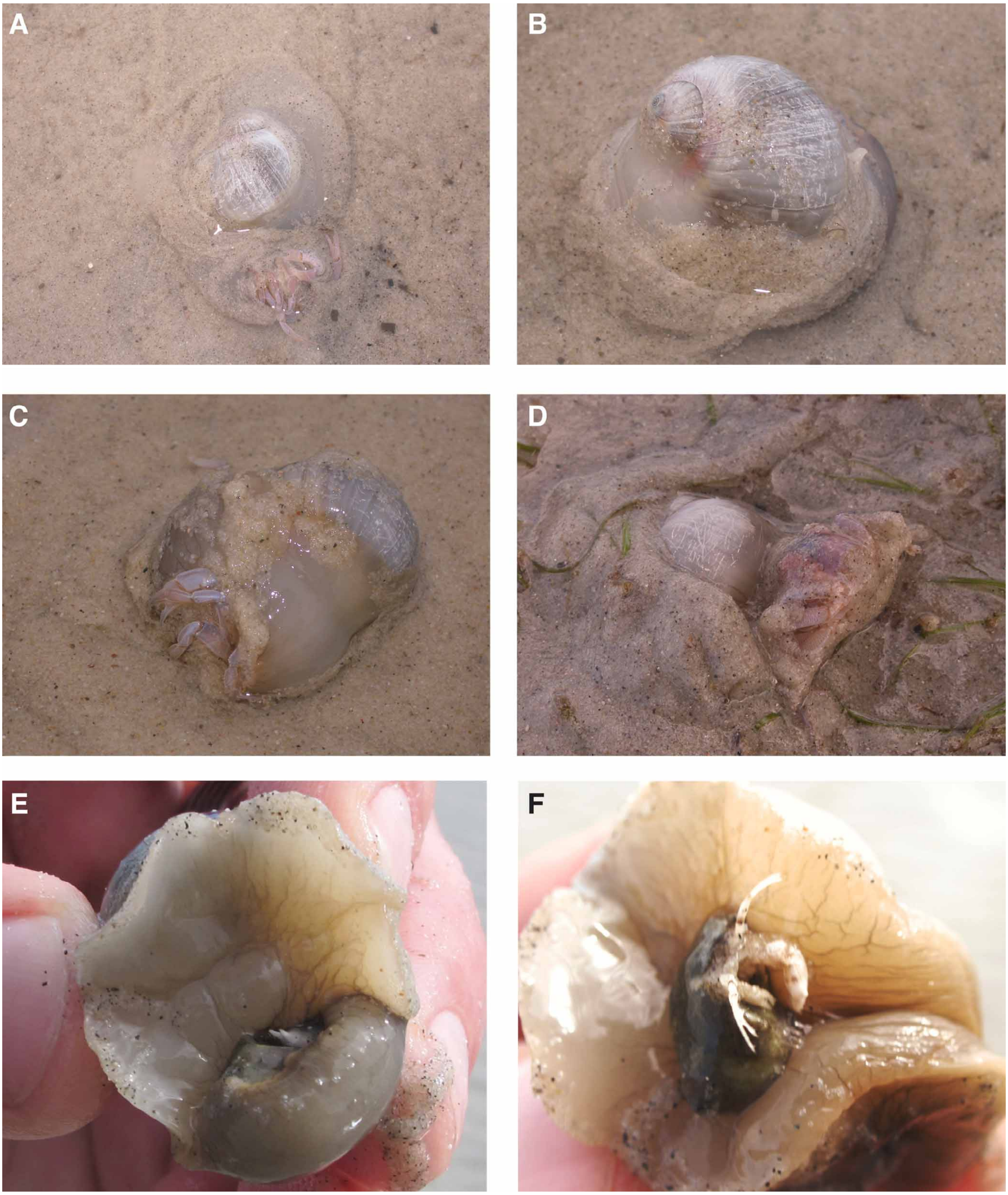

FIGURE 2 A–D. Sequential hunting behaviour of *C. sordidus* (shell size ca. 30 mm) on *M. longicarpus* (carapace length ca. 15 mm). **E–F.** *C. sordidus* (ca. 25 mm) preying on a hermit crab in a *Nassarius* shell (Amity Point, North Stradbroke Island, Australia).

Results of field and aquaria experiments

On average, density of crawling *C. sordidus* was 0.05 m^{-2} for transects at Dunwich (DW) and 0.03 m^{-2} for transects at Amity Point (AP) (Table 2). Average size of tested *C. sordidus* was 19.2 mm ± 6.3 for Amity Point and 15.1 ± 3.7 for Dunwich. Soldier crabs provided were 11.4 mm ± 3.3 in Amity Point and 11.7 mm ± 1.8 in Dunwich. Whereas the soldier crabs are of identical size in both localities ($p = 0.313$), *C. sordidus* was significantly smaller at Dunwich ($p = 0.007$).

From 85 field experiments, *C. sordidus* attacked soldier crabs in 35 experiments, of which 25 were successful and 10 were unsuccessful. Four of 27 experiments and 31 of 59 experiments were classified as attacks at Dunwich and Amity Point, respectively. *C. sordidus* avoided attacking soldier crabs in 50 experiments (22 conducted at Dunwich and 28 at Amity Point; Table 2). In aquaria, 11 (20.9 mm ± 3.4) *C. sordidus* preyed on soldier crabs (9.9 mm ± 2.9).

Size relationships of successfully attacked soldier crabs and attacking *C. sordidus* in the field and of preyed soldier crabs and preying *C. sordidus* in aquaria indicate that larger snails consume larger soldier crabs (Fig. 3A). Size ratio of crabs to snails (c/s) range from 0.4–0.8 for successful attacks in field (Fig. 3B), while *C. sordidus* have chosen soldier crabs with a ratio of 0.3–0.75 in aquaria experiments (Fig. 3C). Size relationships between successful and unsuccessful attacks conducted in the field are significantly different ($p < 0.001$) (Fig. 3B) as are size relationships between preyed and unmolested soldier crabs in aquaria ($p = 0.051$) (Fig. 3C). The soldier crabs attacked by snails were of all sizes in the field (c/s = 0.3–1.2). Most *C. sordidus* that avoided attacking showed less or no activity, while the most active *C. sordidus* started attacking immediately after recognition of the prey.

Interestingly, *C. sordidus* was observed attacking soldier crabs significantly more often at Amity Point than at Dunwich ($p = 0.0283$). The proportion of attacks to number of experiments range from 33%–100% in transects at Amity Point (average = 0.57) and from 9%–33% in transects at Dunwich (average = 19) (Table 2).

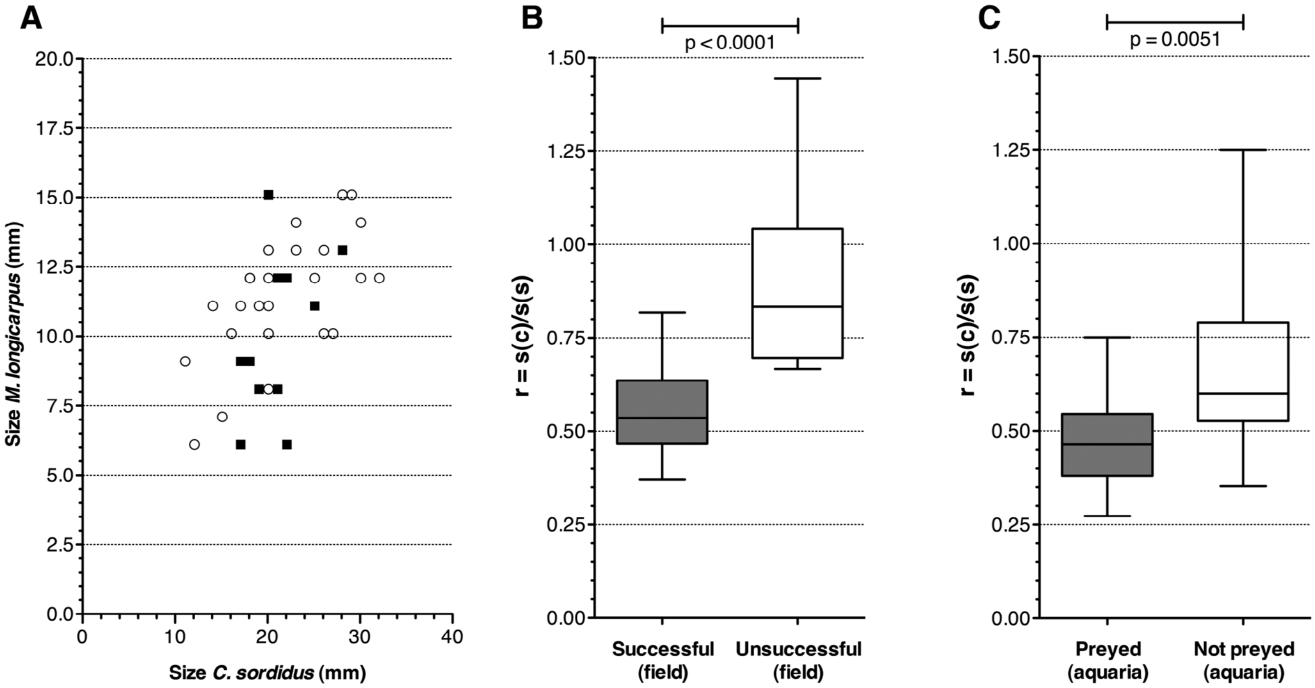

FIGURE 3 A. Predator size plotted against prey size for successful attacks in field experiments (open circles) and for proven predation in aquaria experiments (black squares). **B.** Ratio of crab size to snail size for successful (grey) and unsuccessful attacks (white) in the field. **C.** Ratio of crab size (c = carapace length) to snail size (s = shell length) for preyed (grey) and not preyed (white) soldier crabs in aquaria. r = s(c)/s(s) corresponds to the ratio of crab size (s(c)) to snail size (s(s)).

Mode of feeding

Carapaces (cephalon) of *M. longicarpus* were found drilled through the dorsal plate in aquaria and in the field within 2–4 hrs. Drilled holes show a variety of shapes from smooth (Figs 4A–B) to serrated edges (Fig. 4C). Alternatively, carapaces of the soldier crabs were ‘squeezed’ and consumed through the resulting opening at the front part of the soldier crab without drilling (Figs 4D–F). It is noteworthy that remains of consumed *M. longicarpus* were not always found in aquaria. In these cases only the remaining pereopods were found. Drilled carapaces readily break up and disintegrate as the result of constant movement of the animals in the sand.

Discussion

The present study demonstrates for the first time that a naticid species is capable of preying on, in addition to shelled molluscs, species of brachyuran crabs of the genus *Mictyris* Latreille, 1806, and possibly on hermit crabs, using both drilling and non-drilling predation. The present observation of predation on soldier crabs by *C. sordidus* is consistent with the statement by Cameron (1966: 231) that a *C. sordidus* specimen "preyed on juvenile soldier crabs" at North Stradbroke Island. Unfortunately Cameron did not elaborate on the details of *C. sordidus* predation on *M. longicarpus* and did not illustrate the phenomenon. The results presented here prove that the interaction between *C. sordidus* and *M. longicarpus* does occur.

Drilling predation and feeding on crustaceans (ostracods) by gastropods was proposed by Livan (1937) and inferred by the presence of drilled holes by Reyment (1966). Maddocks (1988) reviewed the occurrence of these holes in ostracod valves and concluded that ostracods may represent potentially important prey for juvenile naticids, a suggestion which was later adopted by Bhatia *et al.* (1989) to explain apparent drill holes in Early Lutetian ostracod valves of West India. However, due to the thin nature of ostracod valves and the wide variety of holes encountered, it is difficult to unequivocally infer naticid drilling predation. The holes drilled by C. *sordidus* into the carapaces of soldier crabs are indeed of different shape, presumably due to the softer, thinner shell, when compared to the bevelled holes drilled into shelled mollusc (Kabat 1990) and would probably not be assigned to naticid drilling predation on the basis of hole morphology alone (Fig. 4).

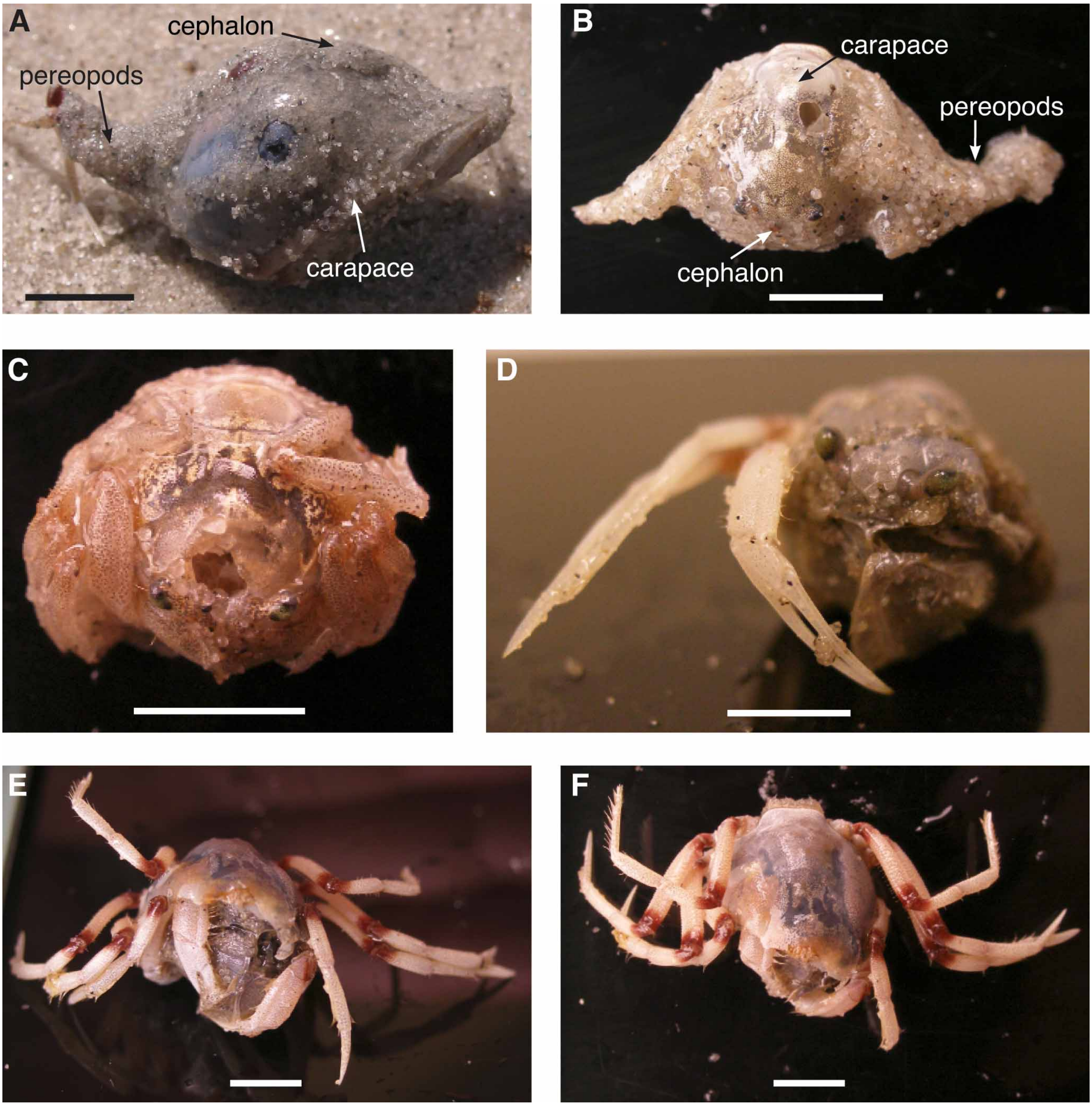

FIGURE 4 A–F. Remains of *M. longicarpus* specimens after being preyed by *C. sordidus*. Carapaces were either drilled (**A–C**) or preyed through the front of the crab (**D–F**). Scale bars 0.5 cm.

The method used by *C. sordidus* to prey on *Mictyris* and possibly hermit crabs is identical to that used by all naticids when preying on shelled molluscs (Hughes 1985), indicating that the general mode of predation in *C. sordidus* is adaptable to prey species other than shelled molluscs. Essential anatomical key characters for predation on these fast-moving crustaceans seem to be the snail's large flexible foot to catch the prey, and tenacious mucus to enwrap and immobilise it (see video http://www.mapress.com/mr/content/v31/data/v.mp4). A reason for the successful predation on soldier crabs may also lie in the behavioural biology of the crabs themselves. *M. longicarpus* occur in large armies on sandy mud flats and during low tide spend a couple of hours burrowing just below the surface in a subterranean feeding phase (Cameron 1966). Hidden directly under the sand surface, the crabs are sightless and can apparently be easily detected by *C. sordidus* (possibly by chemoreception) hunting directly above them.

Field and aquaria experiments in this study demonstrate that *C. sordidus* show size-related predation on soldier crabs because of size-dependent escape success of *M. longicarpus.* While *C. sordidus* were observed to attack any size soldier crabs (Fig. 3B), the size of the majority of successfully attacked and preyed soldier crabs lies between 30–60% of the snails' shell size (Figs 3B–C). Larger *M. longicarpus* (c/s > 0.6) have greater ability to escape due to their size, faster movement and larger chelipeds and consequently, smaller sized individuals are more likely to be consumed. This confirms earlier results about feeding success and size selectivity in *C. sordidus* on the mud whelk *Pyrazus ebeninus* (Brugiere, 1972) (Bishop *et al.* 2008). The present data therefore suggests that *C. sordidus* is, in general, capable of eating *M. longicarpus* individuals of any size, but would consume large crabs only in cases of successful capture (Fig. 3A). Thus, the observed correlation between prey size and predator size confirms earlier predictions that smaller individuals within prey species suffer greater naticid mortality (Kabat 1990) as they are preyed on by a greater size range of predators.

Furthermore, *C. sordidus* shows site-related attacking rates on soldier crabs between two populations on North Stradbroke Island (10.1 km apart). The could indicate that *C. sordidus* may alter feeding behaviour or switch prey species from locality to locality depending on availability as has been demonstrated for other naticid species. *Natica maculosa* Lamarck, 1822 in Penang (Malaya) feeds predominantly on gastropods, whereas this same species preys on bivalves at Kuala Seiangor (Sumatra) (Broom 1982; Berry 1982). However, soldier crabs of the same size range were abundant at Amity Point and Dunwich while average sizes of *C. sordidus* are significantly smaller at the latter locality. Thus, further research is needed to investigate whether predator size or prey availability influence the site related differences in *C. sordidus* feeding behaviour.

Conuber sordidus preys on a wide range of prey species such as gastropods (Bishop *et al*. 2008), bivalves (Green 1968), soldier crabs (this study), and possibly hermit crabs (this study) and therefore accepts prey species featuring an external skeleton that can be caught with the snail's foot and that does not escape its mucus coating. Since *C. sordidus* uses the same predatory behaviour seen in other naticid species, the present observations support earlier suggestions that members of the Naticidae are apparently capable of feeding on prey other than shelled-molluscs by drilling predation (Table 1) and accept prey featuring an 'external skeleton' (Bandel 1999). This 'may indicate that the behaviour of *Natica* (n.b., Naticidae) in regard to recognition of food is less stereotyped than is supposed' (Ansell 1961: 249) and is consistent with observations of generalist predation in other caenogastropods that likewise employ drilling predation (see Introduction). Feeding on crustaceans by gastropods, however, seems to be uncommon, but has been reported for *Buccinum undatum* (Linnaeus, 1758), *Cantharus fumosus* (Dillwyn, 1817) and *C. undosus* (Linnaeus, 1758) (all Buccinidae), *Harpa* sp. (Harpidae) and *Drupa ricinus* (Linnaeus, 1758) (Muricidae) (Rehder 1973; Taylor and Taylor 1977; Taylor 1978; Taylor *et al.* 1983).

Whereas there is little doubt that predation on shelled gastropods and bivalves remains the main feeding mode among the Naticidae, at least some naticids may alter feeding behaviour and switch prey species depending on availability. The observations reported here on *C. sordidus*, and those of previous workers, indicating naticid predation on non-molluscs, shows the lack of understanding of the breadth of feeding strategies employed by naticids.

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