CSIRO PUBLISHING

www.publish.csiro.au/journals/mr *Molluscan Research*, 2003, **23**, 239–249

Observations on the feeding behaviour of *Nassarius clarus* (Gastropoda : Nassariidae) in Shark Bay, Western Australia

Brian Morton

The Western Australian Museum, Francis Street, Perth, Western Australia.
Email: prof_bsmorton@hotmail.com

Abstract

On a pristine sandflat at Monkey Mia in the World Heritage Site of Shark Bay, Western Australia, lives a single species of nassariid, *Nassarius clarus*. The inner reaches of Shark Bay are hypersaline, i.e. salinity > 60, but at Monkey Mia, waters are metahaline, salinity ranging from 40 to 45. At Monkey Mia, *Nassarius clarus* is attracted to, and feeds on, both autochthonous (bivalves) and allochthonous (fish) carrion. A few records of the species attacking other beach inhabitants, including hermit crabs, which it interacts with at carrion, were also obtained. *Nassarius clarus* is attracted to carrion from a maximum recorded distance of 26 m, reflecting the large scale of such Australian shores. An experiment of disturbing, by scraping, plots of beach sand revealed that *N. clarus* investigates such areas where it feeds on organic detritus and, presumably, damaged meio- and macrofauna. These feeding observations highlight new facets of nassariid behaviour. That is, first, on such pristine beaches, *Nassarius clarus* exploits a range of feeding options, from detritivory, to scavenging and the hunting down of damaged 'prey'. On other shores impacted by pollution and dead fish from fishery by-catches, this opportunism has been masked leading to nassariids being considered near-obligate scavengers. Second, the well-known phenomenon of nassariids departing carrion tainted by damaged conspecifics because, it was thought, of a potential threat of predation upon themselves, is here also seen to occur as soon as the bait was touched by the returning tide. Fish predation on such pristine beaches appears to be a real threat but this aspect of nassariid behaviour has again been masked on polluted and (over-) fished beaches by the near absence of significant predators.

Introduction

Species of the caenogastropod Nassariidae have a virtual global distribution on soft shores and the sea bed (Britton and Morton 1994*a*) and, as more studies are made, the many representatives of the family are revealing a wider than hitherto appreciated adaptive radiation in terms of their behaviours, particularly in relation to feeding.

One of the most well-known nassariids is *Bullia digitalis* (Dillwyn, 1817), which, on exposed South African shores, surfs breaking waves to feed on moribund carrion deposited by the tide (Brown 1971). On north-eastern American shores, *Ilyanassa obsoleta* (Say, 1822) forages on carrion and algae over long expanses of shore, following the tide (Crisp 1969). Other intertidal nassariids, e.g. *Nassarius festivus* (Powys, 1835) in Hong Kong, however, lie buried, awaiting the scent of fresh carrion before they emerge from the sediment to move towards it (Britton and Morton 1992). When *Nassarius reticulatus* (Linnaeus, 1758) was either fed or exposed to food odours, oxygen uptake increased dramatically (Crisp *et al.* 1978), suggesting immediate recognition of carrion. In Queensland, Australia, McKillup and McKillup (1997) reported a nassariid which they identified as *Nassarius dorsatus* (Röding, 1798), ranging widely over the surface of tidally exposed sandflats and foraging actively. Morton and Britton (2003) showed that on a pristine beach in north-western Western Australia, *N. dorsatus* forages actively but only during a narrow window of opportunity at low tide. On the same beach, the sympatric

 10.1071/MR03008 1323-5818/03/030239

Nassarius albinus (Thiele, 1930) behaves in the same manner, as do three other non-nassariid gastropod scavengers. All do so, however, at subtly different states of the tide, i.e. there was a temporal separation in terms of foraging behaviour.

A reconnaisance visit in 2000 to a large intertidal sandflat at Monkey Mia in the World Heritage Site of Shark Bay, Western Australia, showed that only one scavenger (apart from a few hermit crabs), *Nassarius clarus* (Marrat, 1877), was present on the beach and, like *N. dorsatus* at Watering Cove, Burrup Peninsula, Western Australia (Morton and Britton 2003), was only active for a brief period of time over the tidal cycle.

Nassariids occurring in Western Australia have been illustrated by Wells and Bryce (2000). The Australian Nassariidae have also been identified by Wilson (1994) and this author (p. 86–87) stated that *N. clarus* occurs from around Shark Bay, Western Australia, across the northern coastline of Australia and down to Townsville, Queensland, in the east. It is thus tropical and has been recorded from elsewhere in the Indo-West Pacific, e.g. Thailand (Cernohorsky 1984). Nothing of any consequence has, however, been written about the species and Morton and Britton (2003) did not record it from the shores of the Burrup Peninsula in north-western Western Australia.

The waters of Inner Shark Bay (Fig. 1*a*) are hypersaline, especially within Lharidon Bight and Hamelin Pool demarcated by the Faure Sill (Logan and Cebulski 1970), and *Nassarius clarus* does not occur there (personal observations). Outside the sill, however, salinities are metahaline, i.e. salinity between 40 and 56, and, thus, still high in comparison with the oceanic water outside the bay. On the shores at Monkey Mia (Fig. 1*b*), *N. clarus* is the only scavenging gastropod and the first aim of this study was to determine if, like *N. dorsatus*, it is an active forager and if so over what period of the tidal cycle. Coincidentally, any observations of *N. clarus* feeding on other elements of the resident macrobenthic community at Monkey Mia were also recorded as part of this survey (and on a repeat visit in August 2002). One of the problems of putting carrion bait out on some beaches is that gulls become attracted to it quickly and make such field experiments difficult. This was particularly true at Monkey Mia and constrained the second aim of the study, which was to determine over what state of the tide feeding occurs. A third aim of the study, was to attempt to determine over what distance *N. clarus* could travel to arrive at bait and how long individuals fed on it. Finally, a fourth aim was, following on from the observations of Morton and Britton (2002) on *N. dorsatus* feeding on exhumed holothurians following a storm perturbation, to determine if *N. clarus* would investigate any disturbance to its sand habitat.

This is, therefore, a study of a single nassariid occupying a metasaline, pristine beach in Shark Bay and attempts to elucidate aspects of the behaviour that facilitates its colonisation of and singular success on this shore.

Materials and methods

Following the reconnaissance visit in 2000, a research trip was made to the intertidal sandflat south of Monkey Mia within the Shark Bay World Heritage Site in November and December 2001. Over a ten-day period of low tides, visits were made to the beach and a number of observations made and experiments undertaken. First, on four occasions, the beach was visited on a falling tide and the numbers of individuals of *Nassarius clarus* actively foraging was estimated by counting them in 50 randomly thrown 1-m^2 quadrats. This was repeated six hours later on the rising tide, just as the shore was about to be flooded. Thus, a total of 400 one-metre-square quadrats were investigated. During these surveys too, the occasional occurrences of small clusters of *N. clarus* at putative 'prey' were recorded. Second, on five occasions, five haphazardly arranged 25 cm × 25 cm areas of the shore were scraped (with a scraper) to a depth of 2–3 cm to imitate a beach disturbance. Five other, also haphazard, 25× 25 cm^2 areas were outlined on the beach, but

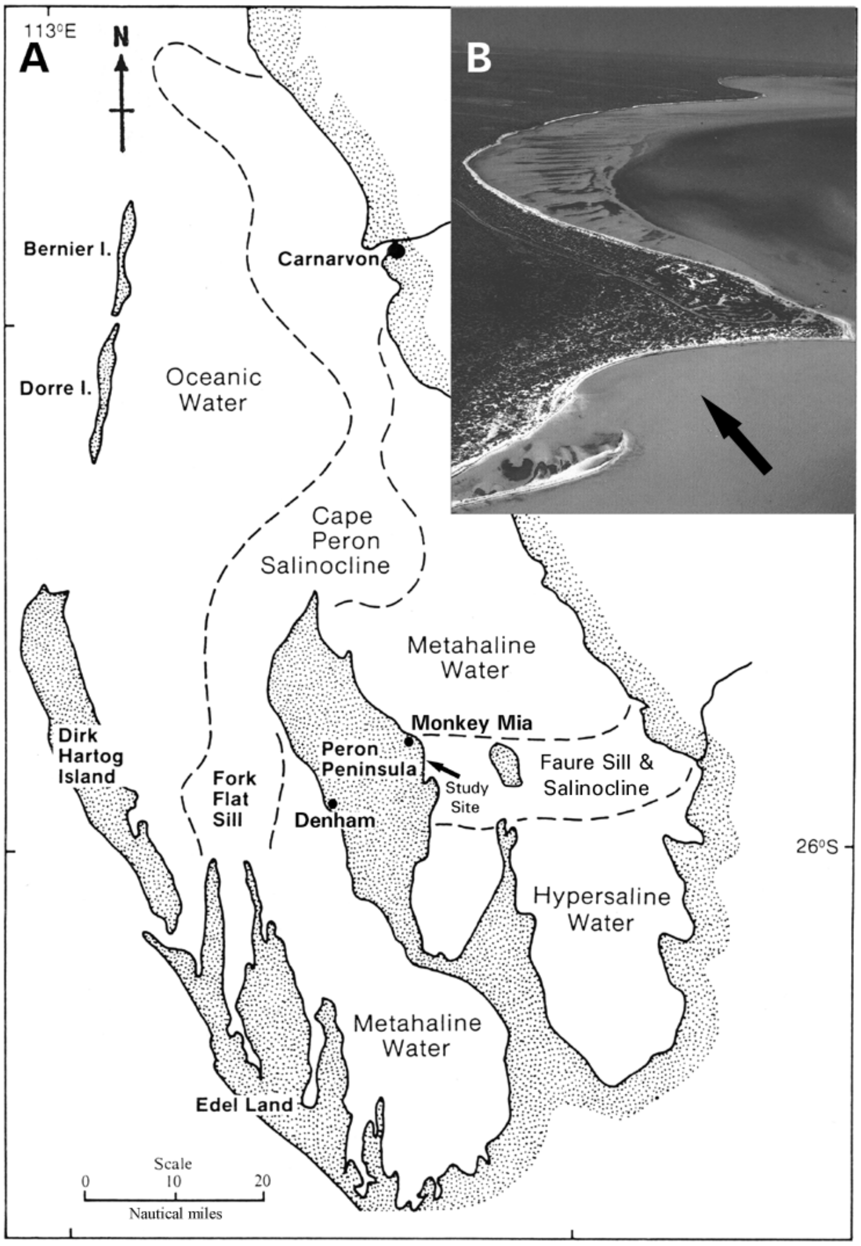

Fig. 1. (*a*) Map of Shark Bay, Western Australia, showing the approximate extents of the various salinity regimes; (*b*) view of the study beach at Monkey Mia, Shark Bay, Western Australia (after Slack-Smith 1990).

not scraped, and these served as 'disturbance' controls. Every individual of *N. clarus* within each plot was recorded at five-minute intervals until no more visits were identified. Third, on two days, five pieces of fresh fish bait, i.e. the pilchard, *Sardinops neopilchardus* (Steindachner, 1879), were staked out at three-metre intervals on the beach at about mid-tide level and at the time of low tide. A stake with no bait was used as a control on each day. The numbers of *Nassarius clarus* individuals arriving at each bait were recorded at five-minute intervals until no more arrived and they had all departed. Finally on five other

Table 1. Records of *Nassarius clarus* attracted to natural prey and fish carrion taken on five separate occasions (*including additional records made in August 2002)

Prey/carrion	Number of *Nassarius clarus*
Fragum unedo (juvenile)	5
Nereis sp.	4
Fragum unedo (juvenile)	5
Fighting hermit crabs	3
**Fragum unedo*	3
**Fragum unedo* (juvenile)	4
**Fragum unedo* (juvenile)	2
**Fragum unedo*	4
**Gnathanodon speciosus* (dead fish)	45

occasions, at the time of approximately low tide, five crushed bivalves *Callista chinensis* (Holten, 1803), were placed in a row, one metre apart facing into a draining area of the shore under the influence of strong offshore winds. Every five minutes, downwind and downflow from the bait, the distance of the furthest individual of *Nassarius clarus* that could be identified moving upstream towards it was measured. The numbers of individuals feeding on the bait were also recorded every five minutes. Checks were also made upwind and upstream from the baits to identify any individuals moving towards them from this direction.

Voucher specimens of *Nassarius clarus* have been lodged at the Natural History Museum, London (NHM 2001–0753) and the Western Australian Museum, Perth (WAM S10823).

Results

Numbers of individuals foraging

On a falling tide, the numbers of individuals of *Nassarius clarus* actively foraging was a mean of 0.89 ± 0.95 m^2. On a rising tide, this was 0.06 ± 0.24 m^2. A *t*-test (d.f. = 199) identified a significant difference ($P < 001$) between receding and rising tides in terms of the numbers of *N. clarus* visible on the beach. At the time of 'just awash' by the rising tide, no individuals could be seen. All had buried themselves and at the times of high tide wading inspections of the beach shallows similarly could not identify any foraging *N. clarus*.

Numbers at natural 'prey'

On four occasions, small groups of *Nassarius clarus* were observed clustered around possible 'prey' (Table 1). On two occasions these were small, exposed *Fragum unedo* (Linnaeus, 1758). On another occasion, four individuals were observed attacking (with proboscis extended) a species of *Nereis*. On a fourth occasion, three individuals were clustered around a pair of fighting hermit crabs. (The beach was visited again briefly in August 2002: at that time four more records of *N. clarus* clustered around exposed *F. unedo* were obtained and some 45 individuals were found consuming a dead fish, golden trevally *Gnathanodon speciosus* (Forsskål, 1775), and arriving at it from downwind and downstream in a line (Fig. 2).

Numbers attracted to 'disturbed' sand

Figure 3 shows the numbers of *Nassarius clarus* attracted to five plots disturbed by scraping and their five controls. Although this experiment was repeated four more times, the results were all comparable. That is, *N. clarus* arrived at the five disturbed plots after 5 min to peak at ~2 individuals·plot^{-1} after 30 min and then to decline to zero after 95 min. In contrast,

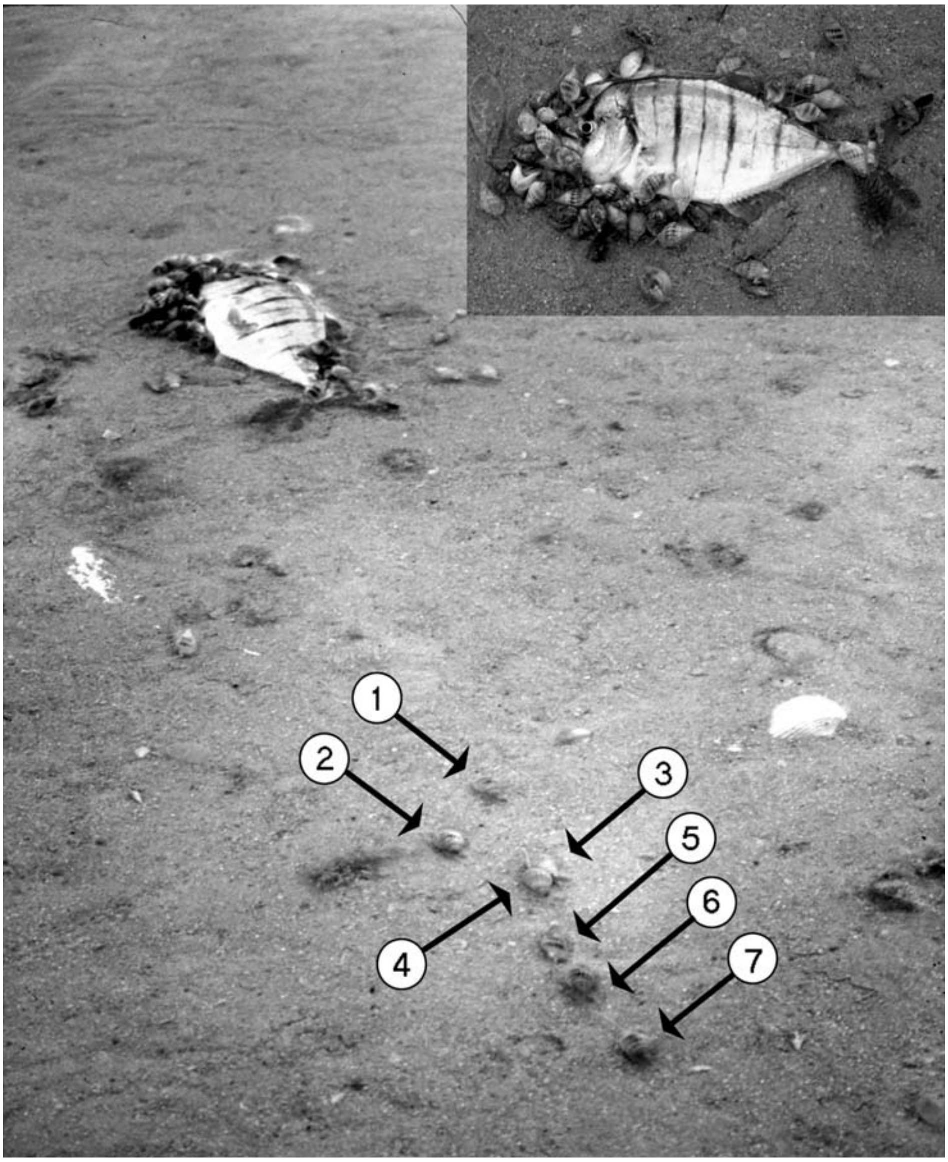

Fig. 2. Individuals of *Nassarius clarus* feeding on (top right) and advancing towards (arrows 1–7) in a line from downward and downstream of a dead fish, *Gnathanodon speciosus*, deposited on the beach at Monkey Mia, August 2002.

only occasionally was *N. clarus* recorded from the control plots. At such times they were either moving across or inspecting the marked perimeters of the plots.

Attraction to staked-out fish bait

The numbers of *Nassarius clarus* attracted to staked-out fish bait on the beach at Monkey Mia, on two occasions, are shown in Fig. 4. No individuals came to control unbaited stakes. On the first occasion, the total numbers of arriving *N. clarus* rose rapidly to 58 within 55 minutes and remained high until >85 min. Thereafter, numbers declined to 22 after

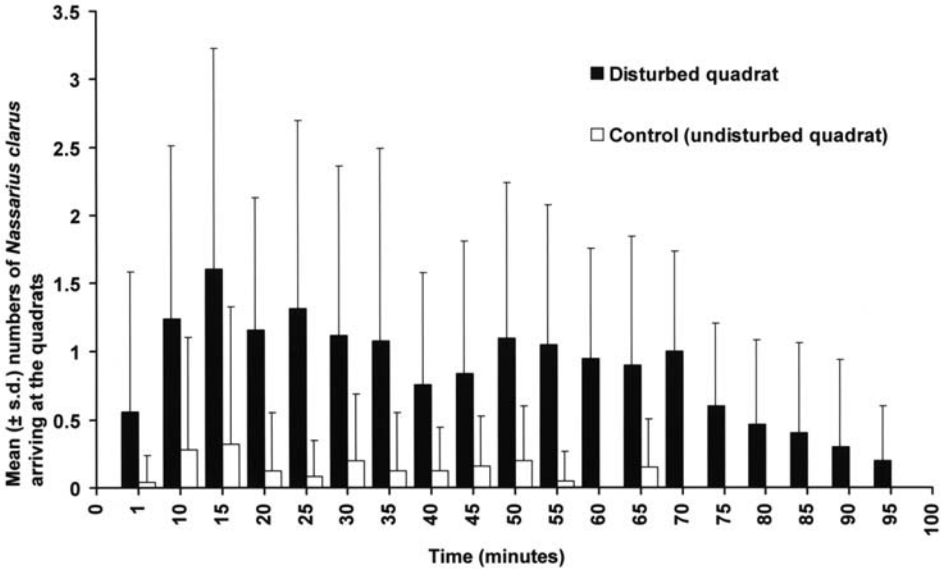

Fig. 3. Mean numbers of individuals (± s.d.) of *Nassarius clarus* arriving at five replicates of 25 × 25 cm quadrats of disturbed sand and an equal number of controls (perimeter-marked only quadrats).

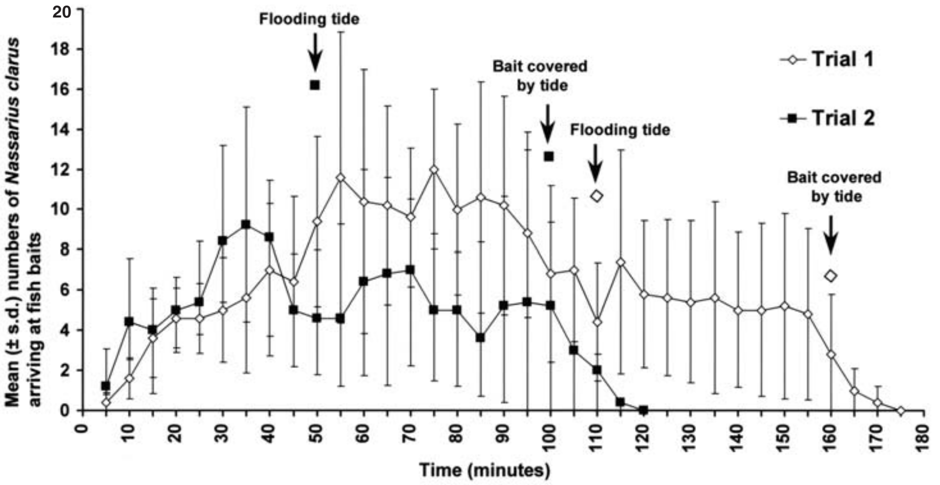

Fig. 4. Mean numbers of individuals (± s.d.) of *Nassarius clarus* arriving at and remaining with five pieces of fish bait staked out on two days on the beach at Monkey Mia, Shark Bay, Western Australia, and at approximately two hours before the return of the tide.

>110 min, this fall coinciding with the rising tide. *Nassarius clarus* remained at the bait (in numbers of ~25), however, until >155 min when the tide covered the bait. At >175 min, no individuals were present. This rapid decline was not accounted for, as described earlier, by individuals arriving at, feeding and then departing the bait, but by *in situ* burial.

On the second occasion, the pattern was repeated. Total numbers of *Nassarius clarus* arriving at the baits rose rapidly to 48 after 35 min and then declined to 23 at >50 minutes. The above decline once again coincided with the advancing tide. Subsequently, however, numbers rose again to 48 at >35 minutes and remained high until >100 min. At this

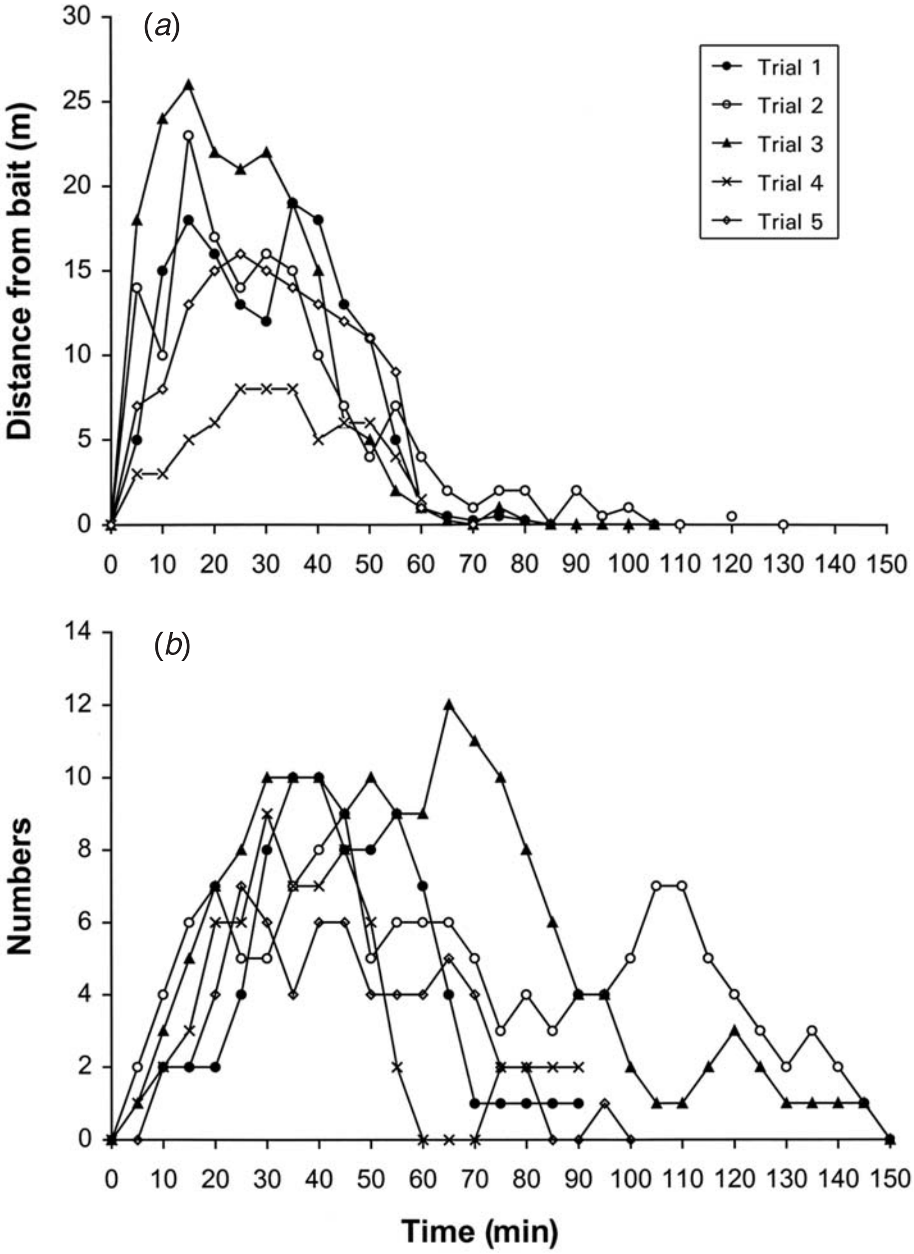

Fig. 5. (*a*) Mean maximum distance from which individuals of *Nassarius clarus* were identified moving towards five pieces of bivalve bait set out on the beach at Monkey Mia, Shark Bay, Western Australia; (*b*) mean numbers of individuals of *N. clarus* arriving at and remaining on the above baits to feed.

moment, the incoming tide covered the baits and within 10 min the numbers of *N. clarus* had fallen from 26 to 0. These individuals had also buried themselves *in situ.*

Attempts were made to repeat the above experiments on three more occasions. On the third, the baits were detected by silver gulls (*Larus novaehollandiae*) and they foiled any further attempt.

Distances and numbers attracted to bivalve bait

It was noted that the silver gulls did not recognise crushed bivalve bait. Thus, five sets of this bait were set out and the numbers of arriving *Nassarius clarus* counted. The greatest distance at which *N. clarus* was seen moving to the bait in the five trials (Fig. 5*a*) rose progressively to between 8 and 26 m after between 25 and 15 min respectively. Numbers declined slowly thereafter and no more arrivals were detected after >80 min. In one trial, this time was extended to 140 min by one or two *N. clarus* intermittently departing and leaving the bait usually into *in situ* buried repose. Beyond the maximum 26-m downstream distance from the bait, other individuals of *N. clarus* were oriented haphazardly, as they were upwind and upstream of the baits.

The numbers of *Nassarius clarus* arriving at the bivalve baits in the five trials is shown in Fig. 5*b*. Numbers peaked at 7 and 12 individuals, respectively, between 20 and 65 min after establishment. Subsequently, numbers generally declined so that by >140 min all had either departed the bait or were buried *in situ*. This burial was again associated with the arrival of the tide but was less obvious because the baits were placed downwind of a flow of draining water. All individuals in all replicates of all five trials had, however, reburied themselves *in situ* before the tide covered them.

Discussion

Britton and Morton (1994*a*) described the Nassariidae as the closest gastropod group in the sea to obligate scavengers. For example, *Bullia digitalis* in South Africa surfs up beaches using a specially modified foot to access stranded carrion (Brown 1971). In the shallow subtidal zone, nassariids are also attracted to carrion (Britton and Morton 1994*b*; Morton and Chan 2001). Both intertidally and subtidally, moreover, the numbers of nassariid individuals and their dominance in the benthic community hierarchy reflect the availability of carrion. On the seabed of Hong Kong, a series of papers (Liu and Morton 1994; Morton 1995; Leung and Morton 1997) showed how the gastropod community has, over time, become dominated mostly by *Nassarius siquijorensis* (A. Adams, 1852) which is also highly tolerant of anoxia (Chan and Morton 1997). Similarly, Hong Kong's soft intertidal shores are dominated by the scavenging *Nassarius festivus* (Britton and Morton 1992; Morton *et al.* 1995). This is also true of shores in southern Australia, so that the degree of hunger expressed by *Nassarius pauperatus* (Lamarck, 1822) on different beaches is related to the availability of food, which also affects egg and egg capsule production and regulates population size (McKillup 1983; McKillup and Butler 1979, 1983).

Most of the above studies have been conducted on beaches that are more (Hong Kong) or less (South Australia) polluted. In these locations, the nassariids identified are lie-in-buried-repose scavengers, which emerge in large numbers when any washed-up carrion is detected. A 'proboscis search reaction' (Kohn 1961) is initiated when carrion is encountered and feeding commences rapidly thereafter. Sometimes, as on the shore of Princess Royal Harbour, Albany, and subtidally at Rottnest Island, both in Western Australia, a number of scavenging species are present and interact with each other to spatially partition the available resources (Morton and Britton 1991; Britton and Britton 1999; Morton and Jones 2003). Most recently, Morton and Britton (2003) reported upon a scavenging gastropod community on a near-pristine beach, Watering Cove, on the Burrup Peninsula, Western Australia. Here, the most surprising observation was that the species involved did not lie in buried repose, but all emerged at some point during the low-tide period to forage for food and demonstrated a temporal partitioning of the available resources. *Nassarius dorsatus*, in particular, actively pursued, overwhelmed and consumed any damaged animal on the beach.

A final point of interest regarding the above study was that all the gastropod scavengers retreated actively into the sand with the approaching tide presumably because, as was observed, with it came shoals of teleost fishes, bottom feeding rays and small sharks. Morton and Britton (2003) called this beach 'near-pristine', because even in this remote locality, there were some impacts from recreational fishermen. At the World Heritage Site of Shark Bay, the beach at Monkey Mia must be considered 'pristine', or as close to it as is possible today.

On this beach, *Nassarius clarus* behaved much like *N. dorsatus* at Watering Cove on the Burrup Peninsula. That is, on beaches of such large scale, carrion could be detected from long distances, i.e. ~26 m in both of the above cases. Shark Bay is, moreover, especially windy with hot, dry trade winds blowing north-westerly over it, keeping water off the beach and 'streaming' the draining pools. This does, however, assist *N. clarus* to find carrion quickly. On the rising tide, however, the situation changes and because the beach is so flat, water flows up it rapidly, as at Watering Cove. Thus, at both places, although the two species remained feeding at food until satiated, both would retreat into buried repose once the tide began to cover them. Like *N. dorsatus* too (Morton and Britton 2002, 2003), *N. clarus* would investigate any exposed, or damaged possible 'prey' and attack it. *Nassarius clarus* also interacts with hermit crabs, as has been demonstrated for *N. festivus* in Hong Kong (Morton and Yuen 2000), and consumes natural carrion (the present study). This study, however, reveals another aspect of nassariid biology. *Nassarius clarus* will investigate any disturbed area of the beach, presumably because in the sediment there must be particles of detritus and damaged meiofauna. In this situation, *N. clarus* does not evert its proboscis to feed. It does this only with carrion, which may be why experimenters (Britton and Morton 1992) have thought that nassariids feed solely on this material. *Nassarius clarus* appears to feed on detritus without everting its proboscis, as seen in *N. festivus* in Hong Kong (Morton and Chan 2003).

It is not known if *Nassarius clarus*, like other nassariids such as *N. pauperatus* (McKillup and McKillup 1994, 1995), *N. siquijorensis* (Morton and Chan 1999) and *N. festivus* (Morton *et al.* 1995), responds to the presence of damaged conspecifics by fleeing. This behaviour is more understandable now, however, because on pristine beaches such as at Monkey Mia and Watering Cove, any nassariid feeding on carrion at the surface when covered by the tide would be at a great risk of predation from incursing fish. At low tide, when it can be active, *Nassarius clarus* examined disturbed areas, investigated and tackled small exposed components of the normally buried meio- and macrofaunal community and actively sought out allochthonous (fish) and autochonous (bivalve) carrion. From facultative scavenging, therefore, the picture of the nassariid life style may be likened more to opportunism.

Acknowledgments

This research was undertaken during the tenure of a research associateship awarded by the Western Australian Museum, Perth, Western Australia. I am grateful to the Director of the Museum for the provision of facilities and to D. S. Jones for logistical assistance and hospitality. I am grateful to the Department of Conservation and Land Management (CALM) of the Western Australian Government for permission to undertake this research and to S. Slack-Smith of the Western Australian Museum for facilitating the application.

References

Britton, D. K., and Britton, J. C. (1999). A second example of resource partitioning by two subtidal scavenging gastropods (*Nassarius glans particeps*: Nassariidae and *Cominella tasmanica*: Buccinidae) from Rottnest Island, Western Australia? In 'The Seagrass Flora and Fauna of Rottnest Island, Western Australia'. (Eds D. I. Walker and F. E. Wells.) pp. 163–175. (Western Australian Museum: Perth.)

Britton, J. C., and Morton, B. (1992). The ecology and feeding behaviour of *Nassarius festivus* (Prosobranchia: Nassariidae) from two Hong Kong bays. In 'The Marine Flora and Fauna of Hong Kong and Southern China III. Proceedings of the Fourth International Marine Biological Workshop: the Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong 1989'. (Ed. B. Morton.) pp. 395–416. (Hong Kong University Press: Hong Kong.)

Britton, J. C., and Morton, B. (1994*a*). Marine carrion and scavengers. *Oceanography and Marine Biology: an Annual Review* **32**, 369–434.

Britton, J. C., and Morton, B. (1994*b*). Food choice, detection, time spent feeding and consumption by two species of subtidal Nassariidae from Monterey Bay, California. *Veliger* **37**, 81–92.

Brown, A. C. (1971). The ecology of the sandy beaches of the Cape Peninsula, South Africa. Part 2: the mode of life of *Bullia digitalis* Meuschen and *Bullia laevissima* (Gmelin). *Zeitschrift für Morphologie und Ökologie der Tiere* **49**, 629–657.

Cernohorsky, W. O. (1984). Systematics of the family Nassariidae. *Bulletin of the Auckland Institute and Museum* **14**, i–iv + 1–356.

Chan, K., and Morton, B. (1997). The tolerance of Hong Kong species of Nassariidae (Mollusca: Gastropoda) to anoxia and starvation. In 'The Marine Flora and Fauna of Hong Kong and Southern China IV. Proceedings of the Eighth International Marine Biological Workshop: the Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong 1995'. (Ed. B. Morton.) pp. 489–502. (Hong Kong University Press: Hong Kong.)

Crisp, M. (1969). Studies on the behaviour of *Nassarius obsoletus* (Say) (Mollusca, Gastropoda). *Biological Bulletin* **136**, 355–373.

Crisp, M., Davenport, J., and Shumway, S. E. (1978). Effects of feeding and of chemical stimulation on the oxygen uptake of *Nassarius reticulatus* (Gastropoda: Prosobranchia). *Journal of the Marine Biological Association of the United Kingdom* **58**, 387–399.

Kohn, A. (1961). Chemoreception in gastropod molluscs. *American Zoologist* **1**, 291–308.

Leung, K. F., and Morton, B. (1997). The impacts of dredging on the epibenthic molluscan community of the southern waters of Hong Kong: a comparison of the 1992 and 1995 trawl programmes. In 'The Marine Flora and Fauna of Hong Kong and Southern China IV. Proceedings of the Fourth International Marine Biological Workshop: the Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong 1995'. (Ed. B. Morton.) pp. 246–261. (Hong Kong University Press: Hong Kong.)

Liu, J. H., and Morton, B. (1994). Scavenging by the subtidal Nassarius siquijorensis (Gastropoda: Nassariidae) in Hong Kong. In 'Proceedings of the Third International Workshop on the Malacofauna of Hong Kong and Southern China, Hong Kong 1992'. (Ed. B. Morton.) pp. 357–375. (Hong Kong University Press: Hong Kong.)

Logan, B. W., and Cebulski, D. E. (1970). Sedimentary environments of Shark Bay, Western Australia. In 'Carbonate Sedimentation and Environments, Shark Bay, Western Australia.' *American Association of Petroleum Geologists, Memoirs* **13**, 1–37.

McKillup, S. C. (1983). A behavioral polymorphism in the marine snail *Nassarius pauperatus*: geographic variation correlated with food availability, and differences in competitive ability between morphs. *Oecologia* **56**, 58–66.

McKillup, S. C., and Butler, A. J. (1979). Modification of egg production and packaging in response to food availability by *Nassarius pauperatus*. *Oecologia* **43**, 222–231.

McKillup, S. C., and Butler, A. J. (1983). The measurement of hunger as a relative estimate of food available to populations of *Nassarius pauperatus*. *Oecologia* **56**, 16–22.

McKillup, S. C., and McKillup, R. V. (1994). The decision to feed by a scavenger in relation to the risks of predation and starvation. *Oecologia* **97**, 41–48.

McKillup, S. C., and McKillup, R. V. (1995). The responses of intertidal scavengers to damaged conspecifics in the field. *Marine and Freshwater Behaviour and Physiology* **27**, 49–57.

McKillup, S. C., and McKillup, R. V. (1997). Effect of food supplementation on the growth of an intertidal scavenger. *Marine Ecology Progress Series* **148**, 109–114.

Morton, B. (1995). Perturbated soft intertidal and subtidal marine communities in Hong Kong: the significance of scavenging gastropods. In 'The Marine Biology of the South China Sea II. Proceedings of the Second International Conference on the Marine Biology of the South China Sea, Guangzhou, China 1993'. (Eds B. Morton, Xu Gong Zhao, Zou Renlin, Pan Jinpei and Cai Guoxiong.) pp. 1–15. (World Publishing Corporation: Beijing.)

Morton, B., and Britton, J. C. (1991). Resource partitioning strategies of two sympatric scavenging snails on a sandy beach in Western Australia. In 'The Marine Flora and Fauna of Albany, Western Australia'. (Eds F. E. Wells, D. I. Walker, H. Kirkman and R. Lethbridge.) pp. 579–595. (Western Australian Museum: Perth.)

Morton, B., and Britton, J. C. (2002). Holothurian feeding by *Nassarius dorsatus* on a beach in Western Australia. *Journal of Molluscan Studies* **68**, 187–189.

Morton, B., and Britton, J. C. (2003). The behaviour and feeding ecology of a suite of gastropod scavengers at Watering Cove, Burrup Peninsula, Western Australia. In 'The Marine Flora and Fauna of Dampier, Western Australia'. (Eds F. E. Wells, D. Walker and D. S. Jones.) (Western Australian Museum: Perth.)

Morton, B., and Chan, K. (1999). Hunger rapidly overrides the risk of predation in the subtidal scavenger *Nassarius siquijorensis* (Gastropoda: Nassariidae): an energy budget and a comparison with the intertidal *Nasssarius festivus* in Hong Kong. *Journal of Experimental Marine Biology and Ecology* **240**, 213–228.

Morton, B., and Chan, K. (2001). Scavenging behaviour of *Nassarius pauperus* (Gastropoda: Nassariidae) from the dynamic subtidal sands of Lobster Bay, Cape d'Aguilar Marine Reserve, Hong Kong. In 'The Marine Flora and Fauna of Hong Kong and Southern China V. Proceedings of the Tenth International Marine Biological Workshop: the Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong 1998'. (Ed. B. Morton.) pp. 255–266. (Hong Kong University Press: Hong Kong.)

Morton, B., and Chan, K. (2003). The natural diet and degree of hunger of *Nassarius festivus* (Gastropoda: Nassariidae) on three beaches in Hong Kong. *Journal of Molluscan Studies*. **69**, 392–395.

Morton, B., and Jones, D. S. (2003). The dietary preferences of a suite of carrion-scavenging gastropods (Nassariidae, Buccinidae) in Princess Royal Harbour, Albany, Western Australia. *Journal of Molluscan Studies* **69**, 151–156.

Morton, B., and Yuen, Y. (2000). The feeding behaviour and competition for carrion between two sympatric scavengers on a sandy shore in Hong Kong: the gastropod *Nassarius festivus* (Powys) and the hermit crab *Diogenes edwardsii* (De Haan). *Journal of Experimental Marine Biology and Ecology* **246**, 1–29.

Morton, B., Chan, K., and Britton, J. C. (1995). Hunger overcomes fear in *Nassarius festivus*, a scavenging gastropod on Hong Kong shores. *Journal of Molluscan Studies* **61**, 55–63.

Slack-Smith, S. M. (1990). The bivalves of Shark Bay, Western Australia. In 'Research in Shark Bay'. (Eds P. F. Berry, S. D. Bradshaw and B. R. Wilson.) pp. 129–157. (Western Australian Museum: Perth.)

Wells, F. E., and Bryce, C. W. (2000). 'Seashells of Western Australia.' (Western Australian Museum: Perth.)

Wilson, B. (1994). 'Australian Marine Shells, Volume 2.' (Odyssey Publishing: Kallaroo, WA.)