AÇOREANA, Suplemento 6, Setembro 2009: 157-165

DRILLING PREDATION UPON *DITRUPA ARIETINA* (POLYCHAETA: SERPULIDAE) FROM THE MID-ATLANTIC AÇORES, PORTUGAL

Brian Morton & E.M. Harper

Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK. E-mail: prof_bmorton@hotmail.co.uk
Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, UK. E-mail: emh21@cam.ac.uk

ABSTRACT

A small, but significant proportion of the empty tubes of the free-living serpulid *Ditrupa arietina* dredged from the seabed off São Miguel, Açores, were punctured by small round holes. Analysis of these holes shows that they are typically single, made from the outside of the tube and located preferentially, suggesting that they represent the work of a predator. The likely identity of the predator is discussed but based on the co-occurrence in the dredges and the fact that most of the holes have a distinctive countersunk morphology, it is suggested that they were made by the small naticid *Natica prietoi*. If so, this study is the first record of such a predator/prey relationship.

RESUMO

Uma pequena mas significativa porção de tubos do serpulídeo livre *Ditrupa arietina* dragados do fundo marinho ao largo de São Miguel, Açores, estavam perfurados por pequenos orifícios redondos. Análise desses orifícios mostra que eles são tipicamente singulares, feito a partir do exterior do tubo e localizados preferencialmente, sugerindo que representam o trabalho de um predador. Discute-se a identidade provável do predador mas, com base na co-ocorrência nas dragagens e no facto de que a maioria dos orifícios possui uma distinta morfologia chanfrada, sugere-se que foram feitos pelo pequeno naticídeo *Natica prietoi*. Assim sendo, este estudo é o primeiro registo de tal relação predador/presa.

INTRODUCTION

Although polychaete worms are a major source of food for a number of predatory taxa including fish, gastropods and birds, most of our knowledge is focused on predation of the larger errant taxa. For example, amongst the predatory gastropods, representatives of the Muricidae, Columbellidae, Fasciolariidae, Vasidae and Buccinidae as well as many conoideans are specialist worm predators (Pearce & Thorson, 1967; Taylor, 1978a, b, 1980; Taylor *et al*., 1980; Shimek, 1984; Taylor & Lewis, 1995). Similarly, many wading birds are specialist predators upon intertidal endobenthic polychaetes (Goss-Custard, 1975).

In contrast, little appears to be known about predatory activities upon the tube-dwelling Serpulidae (Polychaeta) despite their cosmopolitan occurrence and frequently high abundance. There is, however, observational evidence that gastropods (Taylor & Morton, 1996; Tan & Morton, 1998), fish (Bosence, 1979; Witman & Cooper, 1983) and crustaceans (Bosence, 1979) feed on serpulids and, in the case of the buccinid gastropod *Engina armillata* (Reeve, 1846) in Hong Kong, they are its prey of choice (Tan & Morton, 1998). Additionally, the development of calcareous tubes, a well-developed "fright response" (Poloczanska *et al*., 2004) and, in the case of encrusting species, an often cryptic habit suggest that the evolution of the Serpulidae may have been influenced by predation pressure. Part of the problem in recognising predatory activity on serpulid worms undoubtedly results from their typically cryptic lifestyles that make direct observations difficult. Indirect methods to detect predatory activity on serpulids must rely on analyses of the predator's gut contents to recognise setae (Taylor & Morton, 1996) or the identification of any characteristic damage to the tube caused by a predator, although for many predators, for example *E. armillata,* which was recorded feeding *via* the prey's aperture (Tan & Morton, 1998), no such characteristic damage results.

In this paper we describe drill holes made in the tube of the endobenthic serpulid *Ditrupa arietina* (Müller, 1776) from the subtidal seabed off the island of São Miguel in the Açores (Portugal). We present evidence that these are the result of predation and further discuss evidence as to the likely culprit(s).

Ditrupa arietina (Müller, 1776)

Ditrupa arietina is a widespread endobenthic serpulid worm, common in the Mediterranean where it achieves high densities and there is evidence in some areas that its abundance is increasing (Gremare *et al*., 1998a, b; Bolam & Fernandes, 2002; Labrune *et al*., 2007). The worm secretes a curved, tusk-shaped, calcareous tube up to 23 mm long and about 3 mm across at its widest point. It lives within the sediment, the narrowest posterior end down, with an anterior bulge (about 10% of the tube) exposed above the substratum. This anterior bulge houses the circlet of twenty feeding tentacles when they are retracted and the anterior aperture is sealed by a further tentacle bearing an operculum. Morton & Salvador (2009, figure 4) illustrate a living *D. arietina* in its life position in the sediment.

The species has been recorded as a dominant member of soft-bottom communities at depths of 100–250 metres in the Açores where the tubes of dead individuals also provide domiciles for the sipunculan worm *Aspidopsiphon muelleri* Diesing, 1851 (Morton & Britton, 1995; Morton & Salvador, 2009).

MATERIALS AND METHODS

During July 2006, large numbers of the serpulid polychaete *Ditrupa arietina* were collected from depths of between 50-200 metres off Vila Franca do Campo, São Miguel, Açores. The samples were collected and processed as reported in Morton & Salvador (2009). Following initial observations that some tubes were perforated by drill holes, the tubes of dead individuals were separated and inspected for evidence of such drilling. For each holed tube, the following data were collected: tube length to the nearest 1 mm using vernier callipers, number of drillholes per tube and the morphology of the drillhole. Further observations were made on the morphology of the drillholes of a small number of specimens by scanning electron microscopy (SEM). These specimens were prepared by cleaning in an ultrasonic bath prior to mounting them, coated in gold, for SEM (JEOL 820 – University of Cambridge).

Finally, the mean tube lengths plus standard deviations of intact living individuals of *Ditrupa arientina* and those with drill holes were compared using a t-test.

RESULTS

Holed individuals of *Ditrupa arietina* were identified from each of the six sampling stations, described by Martins *et al.*

(2009), but no significant differences in numbers were obtained between them with regard to the incidence of drilled tubes (see Morton & Salvador, 2009 for details). In total 5,453 tubes of *D. arietina* were retrieved and examined and from which we identified 104 fragments and intact empty tubes with holes in them, that is, approximately 1.9% of all empty tubes examined. The vast majority of the tubes were perforated by a single drill-hole but a few had two or even three complete holes. No incomplete holes were observed nor any that showed signs of repair or healing by the occupant. All were drilled perpendicular to the surface of the tube and were clearly produced from the outside, as evidenced by a wider outer diameter.

All holes in the tubes of *Ditrupa arietina* were small, with an outer diameter of less than 700 μm. In outline, the perforations were mostly circular (Figure 1A, B) but a few were more elliptical (Figure 1C). The outer edges of the drillholes were clearly defined, and SEM observations of the surface of the tube adjacent to the hole show no obvious signs of either dissolution or rasping. The inner perforations were rather more ragged and smaller than the outer diameter. Most of the holes we have examined had curved walls leading to a countersunk morphology, although some (Figure 1D) were more straight-sided.

The positions of drill holes in the tubes of *Ditrupa arietina* are shown in Figure 2. It is clear that most are located in the mid portion of the tube, below the anterior bulge. Although they occur all around the circumference of the tube, the distribution of the holes is not uniform, there being a clear preference for the concave aspect.

The length distributions of a sub-sample (n = 376) of living *Ditrupa arietina* recorded by Morton & Salvador (2009) are plotted together with the same data for drilled individuals in Figure 3. Although virtually all sizes of *D. arietina* tubes were drilled (from 5-21 mm tube lengths), the mean length of the drilled *D. arietina*

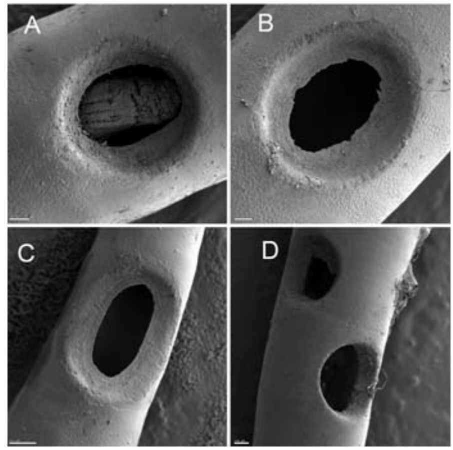

FIGURE 1. Scanning electron micrographs of a variety of drill holes in the tubes of *Ditrupa arietina* collected from the seabed offshore from Vila Franca do Campo, São Miguel, Açores, in 2006. Scale bars represent 100 μm for A and B and 200 μm C and D.

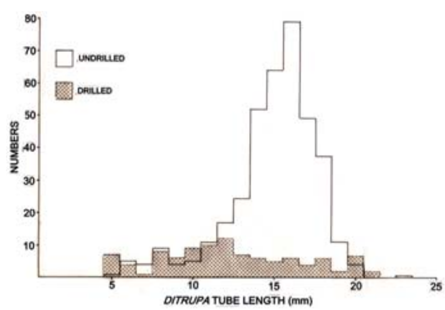

FIGURE 2. Histograms showing the size distributions (tube lengths) of living (white) and drilled (black) individuals of *Ditrupa arietina* collected from the seabed offshore from Vila Franca do Campo, São Miguel, Açores, in 2006.

tubes (n = 102) was 12.7 (S.D. 4.3) whereas that of the tubes occupied by living *D. arietina* (n = 378) was 14.9 (S.D. 2.8). The result of the t-test showed that the means of the two samples were significantly different (p = <0.05), suggesting that drilled individuals were smaller.

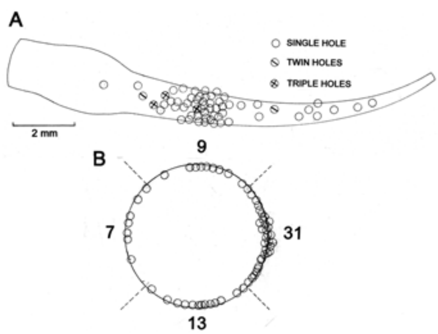

FIGURE 3. Master drawings of the tube of *Ditrupa arietina* showing the pattern of distribution of drill holes (possibly) made by *Natica prietoi*. Above, seen from the side and, below, in section.

DISCUSSION

The holes described in the tubes of *Ditrupa arietina* fulfil all the criteria used to differentiate either predatory or parasitic drillholes (Baumiller, 1990; Kowalewski 2002; Harper, 2003) from those caused by either endolithic organisms or non-biological processes. That is, the holes are typically single perforations, aligned perpendicular to the surface of the tube, drilled from the outside, show stereotypical positioning in the mid-region on the tube's concave surface, and are not of widely-ranging size or shape. From this we conclude that in the Açores, *Ditrupa arietina* is, albeit infrequently, attacked (successfully) by a drilling predator.

An obvious question to try and address is the identity of the drilling predator(s). A wide array of predatory taxa, including several species of gastropods, cephalopods, and worms, are known to be able to drill holes in the skeletons of their prey items (Kabat, 1990). However, as noted by Bromley (1981), it is notoriously difficult to assign drillholes, with any degree of certainty, to a particular creator. Nevertheless we do feel that it is possible to make a number of deductions that, in this case, indicate a likely culprit.

The majority of the holes we have examined are circular in plan but a small number were more elliptical. We suggest that this is an artefact caused on the smaller diameter tubes where the boring organ is forced to wrap around the curved walls causing distortion of the typical shape. The majority of holes have bevelled sides and conform to the ichnospecies *Oichnus paraboloides* Bromley, 1981 that is commonly associated with naticid gastropods (Carriker, 1981). The sizes of the holes (< 700 μm) studied here, moreover, indicate a small predatory taxon. They are, for example, much smaller than the majority of naticid gastropod drill holes that have been reported upon (Carriker, 1981; Kabat, 1990). Similar low diameter drillholes have, however, also been shown to be drilled by marginellid gastropods (Ponder & Taylor, 1992) and by the dorid nudibranch *Okadaia elegans* Baba, 1930 (Young, 1969; Kabat, 1990). A representative of the Nudibranchia, is thus a possible candidate for the *Ditrupa arientina* drill holes. However, the only nudibranchs reported to drill holes in serpulid prey are species of the genus *Okadaia* that are restricted to the Pacific (Young 1969).

Rather, we favour the conclusion that the holes recorded in the Açorean *Ditrupa arietina* were made by small naticids. In support of this contention, no marginellids are reported from the Açorean fauna and the trawls in which the drilled *D. arietina* were collected contained a number of individuals of *Natica prietoi* Hidalgo, 1873, formerly identified as *Natica adansoni* de Blainville, 1825 (see Gubbioli & Nofroni, 1998), and no nudibranchs of any species. Further evidence to support a naticid origin for the drill holes is the preferred position in an area of the tube that would be embedded in the sediment and hence accessible only to an endobenthic predator. Naticids are, moreover, known to be highly specific with regard to the position on the prey's exoskeleton chosen for attack (Thomas, 1976; Kabat, 1990).

Martins *et al.* (2009), although recording one living specimen of *Natica dilwinii* Payraudeau, 1826, dredged at 300 m depth off Vila Franca do Campo, consider that *Natica prietoi* is definitively the most common naticid recorded alive from the Açores, as described in this study. Notwithstanding, Morton (1990) recorded living *Natica intricata* (Donovan, 1804) from Ilhéu de Vila Franca, São Miguel, and was reported by this author to feed, by drilling, on the tellinoidean bivalve *Ervilia castanea* Montagu, 1803. Other naticids have also been reported to occur in the Açores (Table 1), but these are generally records of empty shells. *Euspira pulchella* (Risso, 1826) has been recorded from the seabed at 2,000 metres depth in the Açores by Ávila *et al.* (1998). *Natica variabilis* Recluz in Reeve, 1855 was recorded from the offshore sea-bed of São Miguel by Morton & Britton (1995) and by Ávila *et al*. (1998). *Natica alderi* Forbes, 1838 was recorded from São Jorge by Morton (1967) and, finally, Ávila *et al*. (1998) records *Polinices lacteus* (Guilding, 1834).

One further point which may have some bearing on these disparate records (except for *Natica prietoi* that, as this study shows, is numerous on the offshore seabed at ~ 200 metres depth), is that the Caribbean species *Natica canrena* (Linnaeus, 1758) has been recorded from the Açores by Morton & Britton (1998), Morton *et al*. (1998) and Ávila *et al*. (1998), an occurrence explained by the former authors as a chance event resulting from this species having a teleplanic larva (Laursen, 1981). The same argument has been presented for the occasional recorded occurrence of the North African *Polinices lacteus* in the Açores (Laursen, 1981; Ávila *et al*., 1998; Morton *et al*., 1998).

Natica prietoi is a small species (~ 10 mm in shell diameter) and was the only naticid collected along with the samples, in the same trawls, of *Ditrupa arietina* reported upon by Morton & Salvador (2009) and herein. It seems, therefore, that *Natica prietoi* is a plausible candidate

TABLE 1. A species list of Naticidae recorded from the Açores

Species	**Location**	**References**
Natica prietoi Hidalgo, 1873	São Miguel	Martins *et al*., 2009; this study.
Natica dillwinii Payraudeau, 1826	São Miguel	Martins *et al*., 2009.
Natica adansoni de Blainville, 1825	São Miguel	Ávila *et al*., 1998.
Natica intricata (Donovan, 1804)	São Miguel	Morton, 1990; Ávila *et al*., 1998.
Euspira pulchella (Risso, 1826)	2,000 metres	Ávila *et al*., 1998
Natica variabilis Recluz *in* Reeve, 1855	São Miguel	Morton & Britton, 1995; Ávila *et al*., 1998.
Natica alderi (Forbes, 1838)	São Jorge	Morton, 1967.
Natica canrena (Linnaeus 1758)		Laursen, 1981; Morton *et al*., 1998; Ávila *et al*., 1998; Morton & Britton, 2000.
Polinices lacteus (Guilding, 1834)		Laursen, 1981; Ávila *et al*., 1998; Morton *et al*., 1998.

for the identity of the predator responsible for the holes in *D. arietina.*

If the above conclusion is correct, this is the first record of a naticid attacking a serpulid polychaete. We are aware of only one other report, by Paine (1963), who observed a single individual of *Neverita duplicata* (Say, 1822) attacking the sabellid *Owenia fusiformis* delle Chiaje, 1841.

The incidence of multiple, complete, drillholes in a small number of tubes is curious (Fig. 1D). Simultaneous drilling by multiple individuals, although reported upon for muricids (Brown & Alexander, 1994; Taylor & Morton, 1996), is unlikely in naticids because of the manner in which such predators handle their prey that is (albeit in other species) enveloped by the foot of the attacker which would preclude access by another would-be predator. It is possible, however, that they represent sequential attacks, the first two of which were failures although they were evidently complete, in the sense that they perforate the full thickness of the tube, they may have been non-functional (Kitchell *et al.*, 1986). Another possibility is that they were caused by another predatory taxon and we do note that the multiple holes illustrated in Figure 1D are more straight-sided than are most of the others and thus more like muricid drill holes (Carriker, 1981). Moreover, muricids are known to feed in clusters of conspecifics and sympatric species (Abe, 1980; Tong, 1986; Taylor & Morton, 1996). This raises the possibility of there being a muricid predator on the offshore seabed that also feeds on *Ditrupa arietina*.

Notwithstanding, this study appears to be the first to record significant drilling predation upon *Ditrupa arietina* although Tan & Morton (1998) record the buccinid *Engina armillata* aperturally (but never drilling) attacking cemented serpulids in Hong Kong. In the Açores, the only significant predator captured in the dredges with *D. arietina* was the naticid *Natica adansoni*. However, we conclude, in the light of this study, that further research is needed to establish the predator-prey relationship(s) on and in the Açorean offshore seabed.

ACKNOWLEDGEMENTS

The authors are grateful to Prof. A.M. de Frias Martins, University of the Açores, for organising the workshop at which this research was undertaken and for providing the boat facilities allowing collection of the samples herein reported upon. Ms. Andreia Salvador (The Natural History Museum, London) is thanked for assistance with the sorting of the samples.

LITERATURE CITED

ABE, N., 1980. Food and feeding habit of some carnivorous gastropods (preliminary report). *Benthos Research*, 19/20: 39-47.

ÁVILA, S.P., J.M.N. AZEVEDO, J.M. GONÇALVES, J. FONTES & F CARDIGOS, 1998. Checklist of the shallow-water marine molluscs of the Azores: 1 – Pico, Faial, Flores and Corvo islands. *Açoreana*, 8(4): 487-523.

BAUMILLER, T.K., 1990. Non-predatory drilling of Mississippian crinoids by platyceratid gastropods. *Palaeontology*, 33: 743-748.

BOLAM, S.G., & T.F. FERNANDES, 2002. Dense aggregations of tube-building polychaetes: response to small-scale disturbances. *Journal of Experimental Marine Biology and Ecology*, 269: 197-222.

BOSENCE, D.W.J., 1979. The factors leading to aggregation and reef formation in *Serpula vermicularis* L. *In*: LAR-

WOOD, G., & B.R. ROSEN (eds.), *Biology and Systematics of Colonial Organisms*, pp. 299–318. Systematics Association Special Volume No. 11, Academic Press, London and New York.

BROMLEY, R.G., 1981. Concepts in ichnotaxonomy illustrated by small round holes in shells. *Acta Geologica Hispanica*, 16: 55-64.

BROWN, K.M., & J.E. ALEXANDER, 1994. Group foraging in a marine gastropod predator: benefits and costs to individuals. *Marine Ecology Progress Series*, 112: 97-105.

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

GOSS-CUSTARD, J.D., 1975. Beach Feast. *Birds*, September/October: 23-26.

GRÉMARE, A., J.-M. AMOUROUX & G. VÉTION, 1984a. Long term comparison of macrobenthos within the soft bottoms of the bay of Banyuls-sur-Mer (North-west Mediterranean Sea). *Netherlands Journal of Sea Research*, 40: 281-302.

GRÉMARE, A., R. SARDÁ, L. MEDERNACH, E. JORDANA, S. PINEDO, J.-M. AMOUROUX, D. MARTIN, C. NOZAIS & F. CHARLES, 1984b. On the dramatic increase of *Ditrupa arietina* (O.F. Müller) (Annelida: Polychaeta) along both the French and Spanish Catalan coasts. *Estuarine, Coastal and Shelf Science*, 47: 447-457.

GUBBIOLI, F., & I. NOFRONI, 1998. On the specific distinction between *Natica adansoni* Blainville, 1825 and *Natica prietoi* Hidalgo, 1873 (Discopoda: Naticidae). *La Conchiglia*, Roma, 30(289): 21-22.

HARPER, E.M., 2003. Assessing the importance of drilling predation over the Palaeozoic and Mesozoic. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 210: 185-198.

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

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

KOWALEWSKI, M., 2002. The fossil record of predation: an overview of analytical methods. *In*: KOWALEWSKI, M. & P.H. KELLEY (eds.), *The fossil record of predation. Paleontological Society Special Papers*. Volume 8, pp. 3-42. Yale Printing Services, New Haven, CT.

LABRUNE, C., A. GRÉMARE, J.-M. AMOUROUX, R SARDÁ, J. GIL & S. TABOADA, 2007. Assessment of soft-bottom polychaete assemblages in the Gulf of Lions (NW Mediterranean) based on a mesoscale survey. *Estuarine, Coastal and Shelf Science*, 71: 133-147.

LAURSEN, D., 1981. Taxonomy and distribution of teleplanic prosobranch larvae in the North Atlantic. *Dana Report*, 89: 1-43 + plates I-III.

MARTINS, A.M.F, S.P. ÁVILA, J.P. BORGES, A.C. COSTA, P. MADEIRA & B. MORTON, 2008. Illustrated checklist of the infralittoral molluscs off Vila Franca do Campo. *In:* MARTINS, A.M.F. (ed.), *The Marine Fauna and Flora of the Azores (Proceedings of the Third International Workshop of Malacology and Marine Biology, São Miguel, 2006). Açoreana*, Supplement 6: 15-103.

MORTON, B., 1967. Malacological Report. *In*: *Final Report, Chelsea College Azores Expedition, 1965*, pp. 30-39. Unversity of London, London

MORTON, B., 1990. The biology and functional morphology of *Ervilia castanea* (Bivalvia: Tellinacea) from the Azores.

In: MARTINS, A.M.F. (ed.), *The Marine Fauna and Flora of the Azores (Proceedings of the First International Workshop of Malacology, São Miguel, 1988). Açoreana*, Supplement 1990: 75-96.

MORTON, B., & J.C. BRITTON, 1995. Partitioning of shell resources by *Aspidosiphon muelleri* (Sipuncula) and *Anapagurus laevis* (Crustacea) in the Azores. *In*: MARTINS, A.M.F. (ed.), *The Marine Fauna and Flora of the Azores (Proceedings of the Second International Workshop of Malacology and Marine Biology, São Miguel, 1991). Açoreana*, Supplement 1995: 66-67.

MORTON, B., & J.C. BRITTON, 2000. Origins of the Açorean intertidal biota: the significance of introduced species, survivors of chance events. *Arquipélago* (Life and Marine Science), Supplement 2 (Part A): 29-51.

MORTON, B., & A. SALVADOR, 2008. The biology of the subtial polychate *Ditrupa arietina* (Serpulidae) in the Azores and a description of the life history of its tube. *In:* MARTINS, A.M.F. (ed.), *The Marine Fauna and Flora of the Azores (Proceedings of the Third International Workshop of Malacology and Marine Biology, São Miguel, 2006). Açoreana*, Supplement 6: 145-156.

MORTON, B., J.C. BRITTON & A.M. FRIAS MARTINS, 1998. *Coastal Ecology of the Açores*, i-viii + 249 pp. Sociedade Afonso Chaves, Ponta Delgada, São Miguel.

PAINE, R.T., 1963. Trophic relationships of 8 sympatric predatory gastropods. *Ecology,* 49: 63-73.

PEARCE, J.B., & G. THORSON, 1967. The feeding and reproductive biology of the red whelk, *Neptunea antiqua* (L.) (Gastropoda, Prosobranchia). *Ophelia,* 4: 277-314.

POLOCZANSKA, E.S., D.J. HUGHES & M.T. BURROWS, 2004. Underwater television observations of *Serpula vermicularis* (L.) reefs and associated mobile fauna in Loch Creran, Scotland. *Estuarine, Coastal and Shelf Science*, 61: 425-435.

PONDER, W.F., & J.D. TAYLOR, 1992. Predatory shell drilling by two species of *Austroginella* (Gastropoda: Marginellidae). *Journal of Zoology,* 228: 317-328.

SHIMEK, R.L., 1984. The diets of Alaskan *Neptunea. Veliger,* 26: 274-281.

TAN, K.S., & B. MORTON, 1998. The ecology of *Engina armillata* (Gastropoda: Buccinidae) in the Cape d'Aguilar Marine Reserve, Hong Kong, with particular reference to its preferred prey (Polychaeta: Serpulidae). *Journal of Zoology, London,* 244: 391-403.

TAYLOR, J.D., 1978a. Habitats and diets of predatory gastropods at Addu Atoll, Maldives. *Journal of Experimental Marine Biology and Ecology,* 31: 83-103.

TAYLOR, J.D., 1978b. The diet of *Buccinum undatum* and *Neptunea antiqua* (Gastropoda: Buccinidae). *Journal of Conchology.* 29: 309-318.

TAYLOR, J.D., 1980. Diets and habitats of shallow water predatory gastropods around Tolo Channel, Hong Kong. *In*: MORTON, B. (Ed.). *The Malacofauna of Hong Kong and Southern China. Proceedings of the First International Workshop on the Malacofauna of Hong Kong and Southern China: Hong Kong 1977*, pp. 163-180. Hong Kong University Press, Hong Kong.

TAYLOR, J.D., & A. LEWIS, 1995. Diet and radular morphology of *Peristernia* and *Latirolagena* (Gastropoda: Fasciolariidae) from Indo-Pacific coral reefs. *Journal of Natural History,* 29: 1143-1154.

TAYLOR, J.D., & B. MORTON, 1996. The diets of predatory gastropods in the

Cape d'Aguilar Marine Reserve, Hong Kong. *Asian Marine Biology*, 13: 141-165.

TAYLOR, J.D., N.J. MORRIS & C.N. TAYLOR, 1980. Food specialization and the evolution of predatory marine gastropods. *Palaeontology*, 23: 375-409.

THOMAS, R.D.K., 1976. Gastropod predation on sympatric Neogene species of *Glycymeris glycymeris* (Bivalvia) from the Eastern United States. *Journal of Paleontology*, 50: 488-499.

TONG, L.K.Y., 1986. The feeding ecology of *Thais clavigera* and *Morula musiva* (Gastropoda: Muricidae) in Hong Kong. *Asian Marine Biology*, 3: 163-178.

VERSTRAETEN, J., & F. NOLF, 2004. *Natica adansoni* de Blainville, 1825 and *Natica prietoi* Hidalgo, 1873: two similar but yet different species (Gastropoda: Naticoidea: Naticidae). *Neptunea*, 3: 13-28.

WITMAN, J.D., & R.A. COOPER, 1983. Disturbance and contrasting patterns of population structure in the brachiopod *Terebratulina septentrionalis* (Couthouy) from two subtidal habitats. *Journal of Experimental Marine Biology and Ecology*, 73: 57-79.

YOUNG, D.K., 1969. *Okadaia elegans*, a tube-boring nudibranch mollusc from the Central and West Pacific. *American Zoologist*, 9: 903-907.