

Aspects of the distribution, population structure and reproduction of the gastropod *Tibia delicatula* (Nevill, 1881) inhabiting the oxygen minimum zone of the Oman and Pakistan continental margins

Eva Ramirez-Llodra ^{a,*}, Celia Olabarria ^b

^aNational Oceanography Centre, Southampton, European Way, SO14 3ZH, Southampton, UK

^bDepartamento de Ecología e Bioloxía Animal, Universidad de Vigo, Campus Lagoas-Marcosende, 36200 Vigo (Pontevedra), Spain

Received 27 October 2004; accepted 13 June 2005

Available online 2 August 2005

Abstract

The present study describes some aspects of the distribution and biology of *Tibia delicatula* (Nevill), a gastropod belonging to the family Strombidae. This species has been found in large numbers in the upper oxygen minimum zone (OMZ) of the Oman margin, and has also been collected from the OMZ of the Pakistan margin. The highest abundance of adult specimens in the Oman OMZ was found between 300 and 450 m. Numbers dropped rapidly below 450 m, to zero below 500 m depth. Similarly dense populations were not observed in the Pakistan OMZ. Multiple regression with oxygen concentration and depth indicates that depth (and its related variables) is the main factor explaining the variation in abundance of *T. delicatula*. The populations from the Oman and Pakistan OMZs were dominated by juveniles. This suggests a unimodal size structure with evidence of a marked recruitment event. Basic reproductive aspects were analysed. All specimens had a penis and sperm groove. The gonad wall consisted of reticular tissue that might be used for nutrient storage or as an irrigation system. Only vitellogenic oocytes were present. The large oocyte sizes observed (200–300 µm) suggest a lecithotrophic larval development. © 2005 Elsevier B.V. All rights reserved.

Keywords: *Tibia delicatula*; Distribution; Population structure; Reproduction; Oxygen minimum zone; Hypoxia; Arabian Sea

1. Introduction

Tibia delicatula (Nevill, 1881) is a gastropod species that belongs to the family Strombidae. The shell is varicose and has five processes on the outer lip. Young specimens have thinner shells than adults and lack these processes (Fig. 1). Although this species

* Corresponding author. Present address: Institut de Ciències del Mar, CMIMA-CSIC Psg. Marítim de la Barceloneta 37-49 E-08003 Barcelona, Spain.

E-mail address: eazr@icm.csic.es (E. Ramirez-Llodra).



Fig. 1. *Tibia delicatula*. (top) External shell morphology of an adult specimen showing denticles on the outer lip, and (bottom) a juvenile specimen with a thin outer lip lacking the denticles.

has been reported previously throughout the northern Indian Ocean at depths ranging from ~180 to 320 m (e.g. Woodmason and Alcock, 1891; Melvill and Standen, 1905; Subba Rao, 1977), the basic aspects of its ecology and biology are unknown. Recent studies in this area have either not reported the presence of this species (Levin et al., 2000), or have found very few individuals at shallower locations (150 m) (Oliver, 2001).

Oliver (2001) indicated the unusual presence of this species at 150 m in the oxygen minimum zone (OMZ) of the Oman Margin in the Arabian Sea. OMZs are characterised by oxygen concentrations below 0.5 ml l^{-1} and usually occur from near the surface to 1500 m depth. OMZs are formed in areas where there is a high primary productivity in the surface layers and poor water circulation (Rogers, 2000; Levin, 2003). In such areas, the biological degradation of sinking organic matter results in oxygen depletion. Such areas of oxygen minima develop in the eastern Pacific, NW Pacific margin, Philippines area, Bay of Bengal, Arabian Sea and SW Africa beneath the Benguela current (Rogers, 2000; Levin, 2003). In the northern Arabian Sea, there is a persistent OMZ between 50 and 1000 m (Pfannkuche and Lochte, 2000). This OMZ extends from the Oman margin to southern India (Levin et al., 2000) and has been considered to play an important role in the global carbon and biogeochemical fluxes (Owens et al., 1991; Gage et al., 2000).

The north Arabian Sea OMZ impinges on the continental margin, resulting in benthic areas of very low oxygen concentrations. The ecosystems that develop on these OMZs are subjected to strong vertical gradients in physical and biological parameters, but are still poorly understood. However, they play an important role in global biogeochemical fluxes through coupling of the deep-sea benthos with the upper ocean (Gage et al., 2000; Levin et al., 2000), as well as in the generation of deep-sea biodiversity, speciation and gene flow (Rogers, 2000). In general, species diversity, richness and evenness in the macrobenthic communities are lower within the OMZ than beneath it, while dominance is higher in the OMZ (Levin et al., 2000). Annelids account for 90% or more of macrofauna in muddy OMZ sediments, whereas echinoderms, crustaceans and molluscs are less abundant (Levin, 2003).

The deep Arabian Sea has been the focus of a number of programmes that investigated several aspects of the biogeochemical, geophysical and biological processes and interactions in the area, from the upper ocean to the abyssal benthos. These studies have mainly concentrated in the Oman margin (Gage et al., 2000; Pfannkuche and Lochte, 2000; Jacobs, 2003) and the Pakistan margin (Cowie et al., 1999; Bett, 2004a,b; Cowie, 2004a,b). The present study describes some aspects of the distribution and biology of the gastropod *T. delicatula* collected in the OMZ of the Oman and Pakistan margins.

2. Material and methods

The samples and photographic data analysed in this paper were collected during a series of cruises to the Oman and Pakistan margins. The Oman margin was surveyed during November–December 2002 as part of the Scheherezade II project (Jacobs, 2003). The Pakistan margin was surveyed between March and October 2003 during four cruises as part of a large research programme focusing on the benthic biogeochemistry of the margin (Bett, 2004a,b; Cowie, 2004a,b).

Tibia delicatula was collected with an Agassiz trawl within the OMZ of the Oman margin (400–500 m depth) and the Pakistan margin (132–134 m depth) (Table 1). Samples were fixed in 5% borax-buffered formaldehyde in seawater and stored in 80%

Table 1

Cruise and station data for samples of *Tibia delicatula* collected with Agassiz trawls in the Oman and Pakistan margins

Cruise	Station	Date	Latitude (start-end)	Longitude (start-end)	Depth	<i>Tibia delicatula</i> sampled
CD143	55760#1	03/11/2002	23° 23.47 N	58° 59.40 E	400–500 m	Large catch
Oman			23° 23.86 N	58° 59.27 E		
CD150	56075#1	12/09/2003	23° 17.10 N	66° 43.98 E	133–134 m	1 adult and 1 young (dead)
Pakistan			23° 16.91 N	66° 43.22 E		
CD151	56101#25	23/09/2003	23° 16.32 N	66° 44.37 E	133–134 m	16 juveniles (4 dead)
Pakistan						

methyated spirit. Trawling was complemented with video footage obtained during SHRIMP (Seafloor High Resolution Imaging Platform) deployments in the Oman margin and WASP (Wide Angle Survey Photography) deployments in the Pakistan margin.

Population structure diagrams were constructed for samples collected with the Agassiz trawl. For each specimen, the body length (from apex to aperture) and body width (maximum width) were measured to the nearest 0.01 mm. Body length data was grouped in 13 mm size classes (following criteria from Sokal and Rohlf, 1995) and the size distribution for each population (Oman and Pakistan) was plotted.

SHRIMP images were analysed to calculate the abundance of both live and dead specimens of *T. delicatula* in the Oman margin. During the SHRIMP deployment, a photographic image was taken every 12 s, starting at 300 m depth and finishing at 530 m. A second SHRIMP deployment was conducted down to 880 m depth. The number of live and dead *T. delicatula* was recorded from each image (7 m²), and the abundance calculated as number of specimens per 10 m². The abundance data obtained from the SHRIMP run were grouped every 50 frames, equivalent to 6 m depth increments and analysed in relation to oxygen concentration (mean values from CTD data grouped into 6 m classes) and depth. Forward stepwise regression analysis was performed to test the variation of this species abundance with oxygen concentration and depth. Oxygen concentration and depth data were log₁₀ (x + 1)-transformed to meet requirements for parametric tests (homogeneity of variances, normal distribution). *F*-to-enter was set at 0.10, and *F*-to-remove was set at 0.00.

For reproductive studies, specimens were processed for histology. Sections were cut at 7 µm and stained with haematoxylin and eosin. Gonads were analysed by image analysis using the Rainbow Runner and SigmaScan Pro 4 software.

3. Results

3.1. Distribution and population structure

The SHRIMP survey conducted off the coast of Muscat (Oman margin) in 2002 indicated large numbers of the gastropod *Tibia delicatula* between 300 and 450 m of depth. The distribution of *T. delicatula* was very patchy, with specimens present between 300 and 500 m depth. The mean abundance of adult specimens between 300 and 450 m depth was 3.3 ± 0.3 individuals per 10 m². From 450 to 500 m depth, abundances dropped to almost zero, and below 500 m *T. delicatula* disappeared. The distribution of dead specimens followed a similar patchy pattern, with an important accumulation of dead adults between 410 and 420 m. However, note that the results obtained from the SHRIMP survey underestimated the abundances of *T. delicatula*, since only adult individuals could be identified on the images.

The regression analysis showed that depth and oxygen explained 77.5% of variance in abundance of *T. delicatula* adults ($r^2=0.774$; $F_{2,79}=135.52$; $P<0.001$). Depth explained most of the variance ($r^2=0.67$; $t(79)=-7.38$; $P<0.001$), whereas oxygen concentration only explained 10.5% ($r^2=0.104$; $t(79)=6.04$; $P<0.001$). Abundance was negatively correlated with depth, but positively with oxygen concentration (Fig. 2A, B). Number of individuals decreased with increasing depth with peaks of abundance at 318 and 390 m (Fig. 2A). Although the relationship between oxygen concentration and number of individuals was not strong, oxygen concentrations higher than 0.19 ml l⁻¹ led to increasing abundance with peaks at ~0.22 ml l⁻¹ O₂ (Fig. 2B).

The Agassiz deployment between 400 and 500 m depth (O₂ levels ranging from 0.20 ml l⁻¹ at 400 m to

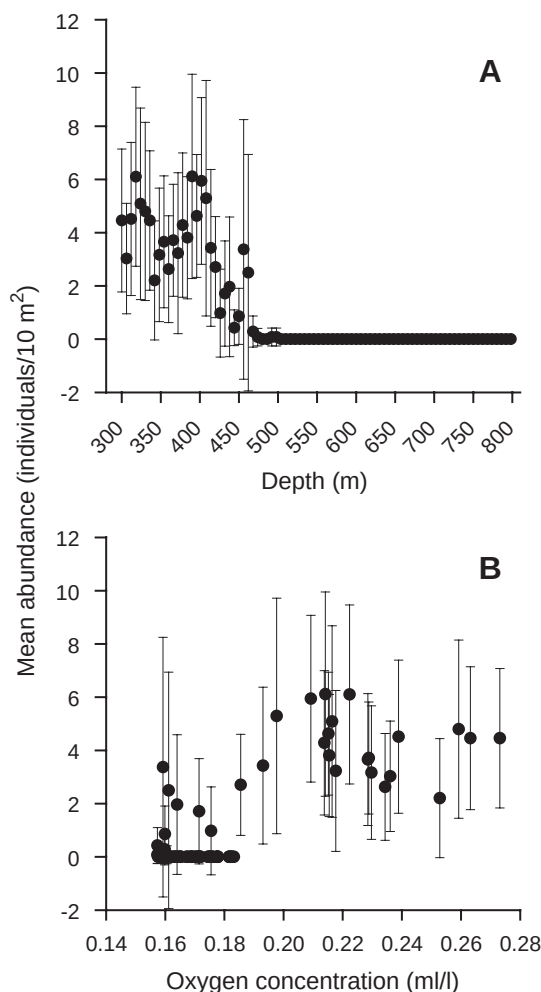


Fig. 2. Mean abundance ($\pm$ SD) of adult *Tibia delicatula* from the Oman OMZ. (A) Variation with depth. (B) variation with oxygen concentration.

0.15 ml l⁻¹ at 500 m) targeted the population of abundant gastropods observed on SHRIMP footage. In the catch, most large specimens were empty shells, while the live animals were of a smaller size. A total of 1043 live individuals (~ 1.15 ind m⁻²) collected with the Agassiz trawl in the Oman margin were counted and measured. Body length varied between 10 and 73 mm. The size distribution of the population was unimodal, with most of the specimens (67%) in the 10–23 mm size class. These small specimens had no denticles in their outer lip and their shells were thin, which defines them as juveniles (Woodmason

and Alcock, 1891). The high proportion of juveniles indicates a marked recruitment of juveniles (Fig. 3).

In the Pakistan margin, the WASP video footage did not show evidence of populations of *T. delicatula* (B. Bett, pers. comm., 2004) and only 18 specimens were collected with the Agassiz trawl at ~ 134 m ($O_2 = 0.11$ ml l⁻¹), including 1 recently dead adult (according to the shell), 12 live juveniles and 5 recently dead juveniles (Table 1). Although this sample was too small for population structure analysis, the general trend was similar to that found in the Oman sample, with 17 small specimens (10–23 mm) out of 18 (Fig. 3).

3.2. Reproductive patterns

All specimens analysed had a penis and sperm groove. Microscopic studies showed that none of the specimens in the small size classes (size <49 mm) had mature gonads. Of the 7 large specimens (62–75 mm) available, only 3 had developed ovaries and no testes were found in any of the animals studied, allowing only for a preliminary description of the oogenesis and egg size.

The ovary wall consists of reticular tissue that might be used for nutrients storage or as an irrigation system adapted to low environmental oxygen conditions. In the three females with mature gonads,

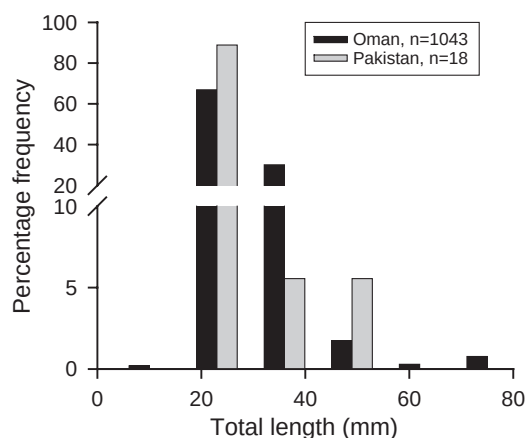


Fig. 3. Population structure (calculated from Agassiz trawl catches) of *Tibia delicatula* from the Oman OMZ at ~ 500 m depth (black bars) and the Pakistan OMZ at ~ 134 m depth (grey bars). n, number of specimens measured.

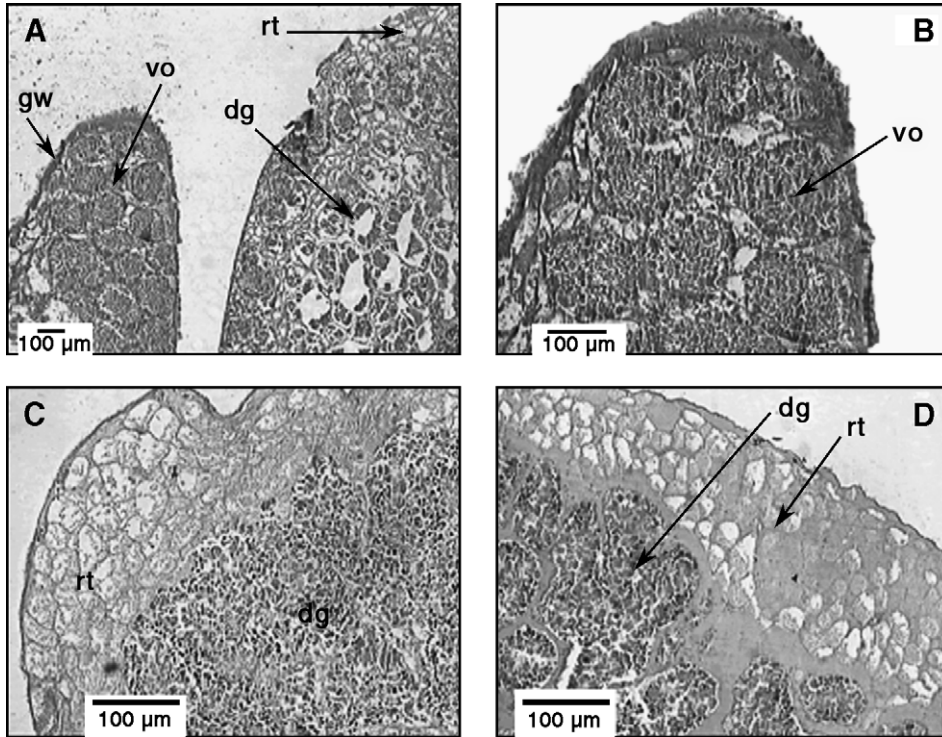


Fig. 4. Light histology of apical body end of *Tibia delicatula* from the Oman OMZ. (A, B) Mature female with developed ovary. (C, D) Specimen with no gonad development; dg, digestive gland; gw, gonad wall; rt, reticular tissue; vo, vitellogenic oocytes.

only vitellogenic oocytes were present (Fig. 4). In one of the females, 82% of the oocytes measured between 150–250 µm (Fig. 5A). In the other two females, over 90% of the oocytes measured between 50–150 µm (Fig. 5B, C). The maximum oocyte sizes were 296 µm, 182.0 µm and 169.2 µm for each female.

4. Discussion

4.1. Distribution and population structure

The high abundance of *Tibia delicatula* observed and sampled in a region of low oxygen in the Oman margin was quite surprising. Molluscs are, in general,

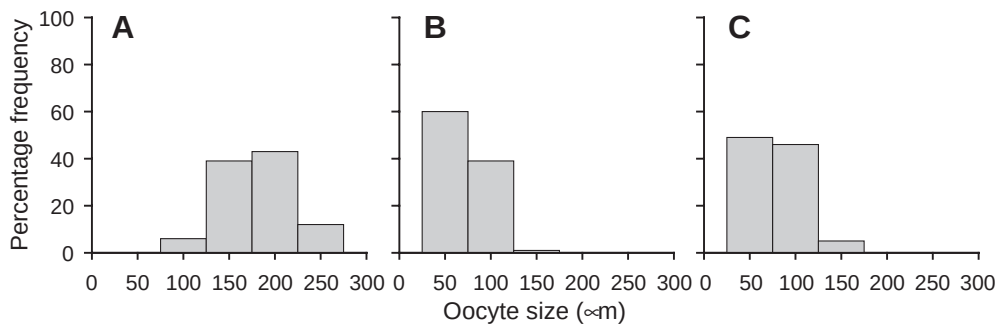


Fig. 5. Oocyte-size distribution of three mature females of *Tibia delicatula* from the Oman OMZ.

less sensitive than other invertebrates to low oxygen concentrations (Gray et al., 2002), but they are thought to be rare in low-oxygen environments because the associated low pH affects shell maintenance (Levin et al., 2000). Nevertheless, this species presented some features that can be interpreted as adaptations to low oxygen environments. For example, *T. delicatula* had a very bright pink colour that suggests the presence of haemoglobin with high affinity for oxygen. Morphological aspects such as presence of large gills (no endosymbionts were found in TEM microphotographs) or large body size could be related to a higher efficiency of oxygen uptake (Levin, 2003). For example, several polychaete species show increasing body size with decreasing oxygen within oxygen minimum zones. Also nematode body size can be exceptionally large within OMZs. However, it is unclear whether this trend is related to oxygen or to food availability, which varies inversely with oxygen (Levin, 2003). Moreover, the denticles on the outer lip could be interpreted as an effective adaptation to cope with sloppy OMZ mud (see Levin, 2003).

The bathymetric range of *T. delicatula* is difficult to assess, since specimens previously recorded came from shallower depths than the specimens observed in this study. In the present study, individuals collected or observed with photographic gear ranged from 132 to 474 m. In the Oman margin, *T. delicatula* was found at depths where oxygen concentrations ranged from $\sim 0.16 \text{ ml l}^{-1}$ to 0.26 ml l^{-1} , whereas in the Pakistan margin, where populations were scarce, oxygen concentration was only $\sim 0.11 \text{ ml l}^{-1}$. The multiple regression of abundance with depth and oxygen concentration indicated that the main factor explaining variation of adult abundance was depth. Therefore, we suggest that while *T. delicatula* seems to be well adapted to the low oxygen levels found in the upper OMZ, the lower limit to its distribution is dependent on depth. Moreover, its distribution within the OMZ might be conditioned, to a certain degree, by oxygen levels, with higher abundances in areas with oxygen concentration greater than 0.16 ml l^{-1} .

The spatial and temporal fluctuations of the OMZ (Creasey et al., 2000; Rogers, 2000) could result in variations in the population boundaries for *T. delicatula* in relation with changes in oxygen concentrations in the environment. Although oxygen-stressed communities seem to lack the structural heterogeneity of

oxygenated systems (Levin, 2003), variability in the vertical distribution of sediment biochemical properties can affect macrofaunal distributions within OMZs. Thus, the heterogeneity observed in the distribution of *T. delicatula* within the OMZ might be modulated by trophic processes as well as sulphide and oxygen concentrations (see Levin, 2003). If the OMZ fluctuates spatially and temporally, the populations of *T. delicatula* that are normally found where oxygen levels are greater than approximately 0.16 mg ml^{-1} might experience periods of more severe hypoxia (e.g. populations in the Pakistan margin), resulting in local extinctions. The potential local extinction of a population caused by variations in the severity and depth of the OMZ has been suggested also for the galatheid crab *Munidopsis scobina* from the Oman OMZ at 900 m and 1000 m depth (Creasey et al., 2000).

Inter-annual variability in the strength of climatic events such as seasonal monsoons in the Arabian Sea (Barber et al., 2001; Reichart et al., 2002) might also play an important role in shaping the intensity of effects from year to year (Levin, 2003). For example, a previous cruise to the Oman area in October – November 1994 did not report high abundances of *T. delicatula* (Oliver, 2001). Also, there is evidence that inter-annual variability in the quantity and quality of organic matter supply can lead to longer-term and persistent changes in seafloor communities (Billett et al., 2001), affecting all aspects of community structure such as abundance, biomass and taxon composition.

The population structure of *T. delicatula* from Oman and Pakistan showed significant patterns, with juveniles dominating each population. Species inhabiting OMZ areas have been reported to exhibit population segregation (Creasey et al., 1997). For example, in populations of the spider crab *Encephaloides armstrongi* from the Arabian Sea the juveniles develop above the OMZ, while the adults are found within the area of oxygen minimum (Creasey et al., 1997). Moreover, this species shows sex-specific dispersal behaviour and it seems that the adults may need to move out of the OMZ for reproduction. Diverse species show vertical and/or ontogenetic migrations (Levin, 2003) inhabiting different oxygen zones during different developmental stages. For example, *Orchomene obtusus*, a scavenging amphipod, migrates into the anoxic zone to avoid predators and

exploit abundant food, while some species of crabs move out of the oxygen-minimum zone for reproduction (Rogers, 2000). Although the results from this study have to be interpreted with caution, the population structure of *T. delicatula* observed could respond to several factors such as seasonality in reproduction, periodic recruitment events (e.g. Nilsson and Sköld, 1996; Phil et al., 1991), population segregation (Creasey et al., 1997, 2000; Rogers, 2000) and/or reflect variations in food supply and interspecific competition with depth (Creasey et al., 2000; Rogers, 2000).

4.2. Reproductive patterns

In the three females available, the oocytes were all at the same stage of development and there were no previtellogenic oocytes, suggesting that a single cohort of oocytes grows, matures and is spawned at any single time. But because of the small sample size, these results are only preliminary and do not allow further interpretation.

The large oocyte sizes observed (200–300 µm) suggest a lecithotrophic larval development. Lecithotrophy is the dominant larval type exhibited by deep-sea invertebrates (Young, 2003) and is often associated with adaptations to stable, low-energy environments such as the deep sea or polar waters (Sanders, 1979; Clarke and Gorny, 1992; Eckelbarger and Walting, 1995; Ramirez-Llodra, 2002; Young, 2003). Although lecithotrophic development is commonly found in deep-sea molluscs (Scheltema, 1994), there is evidence now that planktotrophy might be the predominant larval development within deep-sea gastropods, in particular in species-rich families such as Turridae and Epitoniidae (see for review Colman et al., 1986; Rex and Warén, 1982; Scheltema, 1994; Bouchet and Warén, 1994). Bouchet and Warén (1994) reviewed the larval types and dispersal potential of deep-sea gastropods, concluding that mode of development in deep-sea snails reflects phylogenetically constraints.

The lack of males in the samples analysed is interesting. Warén and Bouchet (1990) studied the reproduction of laubierinid gastropods based on only six mature adults collected at abyssal depths from the Atlantic and Indian oceans. All six adults were female, but a recently settled larva that exhibited mature

testes and a male reproductive system was also found. These authors suggested that the Laubierinidae might be protandrous hermaphrodites with neotenic males reaching sexual maturity just before metamorphosis. *T. delicatula* could also be a protandric hermaphrodite, where the male stage develops in very early phases. Alternatively, the population could exhibit differential reproductive migration. This behavioural segregation has been observed in the spider crab *Encephaloides armstrongi* from the OMZ in the Oman margin (see above, Creasey et al., 1997) and in the hydrothermal vent crab *Bythograea thermydron* (Perovich et al., 2003). In the case of *Tibia delicatula*, however, results have to be interpreted with caution until further samples are available.

Acknowledgements

We would like to thank the officers and crew of RRS ‘Challenger’ for their valuable assistance at sea. This research has been partially supported by a Post-doctoral Marie Curie Fellowship of the European Community programme ‘Energy, Environment and Sustainable Development’ under contract EVK2-CT-2001-50010 to Celia Olabarria. We would also like to thank Dr Brian Bett and Dr David Billett for providing cruise information and advice throughout the preparation of this manuscript.

References

- Barber, R.T., Marra, J., Bidigare, R.C., Codispoti, L.A., Halpern, D., Johnson, Z., Latasa, M., Goericke, R., Smith, S.L., 2001. Primary productivity and its regulation in the Arabian Sea during 1995. *Deep-Sea Res.* II 48, 1127–1172.
- Bett, B., 2004a. RRS *Charles Darwin* cruise 145. Benthic processes in the Arabian Sea: mechanistic relationships between benthos, sediment biogeochemistry and organic matter cycling. Cruise Report. Southampton Oceanography Centre, Southampton. 37 pp.
- Bett, B., 2004b. RRS *Charles Darwin* cruise 150. Benthic processes in the Arabian Sea: mechanistic relationships between benthos, sediment biogeochemistry and organic matter cycling. Cruise Report. Southampton Oceanography Centre, Southampton. 40 pp.
- Billett, D.S.M., Bett, B.J., Rice, A.L., Thurston, M.H., Galéron, J., Sibuet, M., Wolff, G.A., 2001. Long-term change in the megabenthos of the Porcupine Abyssal Plain. *Progr. Ocean.* 50, 325–348.

- Bouchet, P., Warén, A., 1994. Ontogenic migration and dispersal of deep-sea gastropod larvae. In: Young, C.M., Eckelbarger, K. (Eds.), *Reproduction, Larval Biology, and Recruitment of the Deep-Sea Benthos*. Columbia Univ. Press, New York, pp. 98–118.
- Clarke, A., Gorny, D.J., 1992. Egg size and composition in *Ceratoserolis* (Crustacea: Isopoda) from the Weddell Sea. *Polar Biol.* 12, 129–134.
- Colman, J.G., Tyler, P.A., Gage, J.D., 1986. Larval development of deep-sea gastropods (Prosobranchia: Neogastropoda) from the Rockall Trough. *J. Mar. Biol. Assoc. UK* 66, 951–965.
- Cowie, G.L., 2004a. RRS *Charles Darwin* cruise 146. Benthic processes in the Arabian Sea: mechanistic relationships between benthos, sediment biogeochemistry and organic matter cycling. Cruise Report. Edinburgh University, Edinburgh. 98 pp.
- Cowie, G.L., 2004b. RRS *Charles Darwin* cruise 151. Benthic processes in the Arabian Sea: mechanistic relationships between benthos, sediment biogeochemistry and organic matter cycling. Cruise Report. Edinburgh University, Edinburgh. 121 pp.
- Cowie, G.L., Calvert, S.E., Pedersen, T.F., Schulz, H., Von Rad, U., 1999. Organic content and preservational controls in superficial shelf and slope sediments from the Arabian Sea (Pakistan margin). *Mar. Geol.* 161, 23–38.
- Creasey, S., Rogers, A.D., Tyler, P.A., Young, C.M., Gage, J.D., 1997. The population biology and genetics of the deep-sea spider crab *Enchechaloides armstrongi* Wood-Mason 1891 (Decapoda: Majidae). *Philos. Trans. R Soc. Lond.* 352B, 365–379.
- Creasey, S., Rogers, A.D., Tyler, P.A., Gage, J.D., Jollivet, D., 2000. Genetic and morphometric comparisons of squat lobster, *Munidopsis scobina* (Decapoda: Anomura: Galatheidae) populations, with notes on the phylogeny of the genus *Munidopsis*. *Deep-Sea Res. II* 47, 87–118.
- Eckelbarger, K.J., Walting, L., 1995. Role of phylogenetic constraints in determining reproductive patterns in deep-sea invertebrates. *Invert. Biol.* 114, 256–269.
- Gage, J.D., Levin, L.A., Wolff, G.A., 2000. Benthic processes in the deep Arabian Sea: introduction and overview. *Deep-Sea Res. II* 47, 1–7.
- Gray, J.S., Wu, R.S., Or, Y.Y., 2002. Effects of hypoxia and organic enrichment on the coastal marine environment. *Mar. Ecol. Prog. Ser.* 238, 249–279.
- Jacobs, C.L., 2003. RRS *Charles Darwin* cruise 143. Scheherezade II: Geological and biological surveys of the Arabian Sea and the continental slope of Oman. Cruise Report, vol. 79. Southampton Oceanography Centre, Southampton. 70 pp.
- Levin, L.A., 2003. Oxygen minimum zone benthos: adaptation and community response to hypoxia. *Oceanogr. Mar. Biol. Annu. Rev.* 41, 1–45.
- Levin, L.A., Gage, J.D., Martin, C., Lamont, P.A., 2000. Macrobenthic community structure within and beneath the oxygen minimum zone, NW Arabian Sea. *Deep-Sea Res. II* 47, 189–226.
- Melville, J.C., Standen, R., 1905. *Rostellaria delicatula* Nevill. *J. Conchol.* 11, 161–164.
- Nilsson, H.C., Sköld, M., 1996. Arm regeneration and spawning in the brittle star *Amphiura filiformis* (O.F. Muller) during hypoxia. *J. Exp. Mar. Biol. Ecol.* 199, 193–206.
- Oliver, P.G., 2001. Functional morphology and description of a new species of *Amygdalum* (Mytiloidea) from the oxygen minimum zone of the Arabian Sea. *J. Moll. Stud.* 67, 225–241.
- Owens, N.J.P., Law, C.S., Mantoura, R.F.C., Burkill, P.H., Llewellyn, C.A., 1991. Methane flux to the atmosphere from the Arabian Sea. *Nature* 354, 293–296.
- Perovich, G.M., Epifanio, C.E., Dittel, A.I., Tyler, P.A., 2003. Spatial and temporal patterns in development of eggs in the vent crab *Bythograea thermydron*. *Mar. Ecol. Prog. Ser.* 251, 211–220.
- Pfannkuche, O., Lochte, K., 2000. The biogeochemistry of the deep Arabian Sea: overview. *Deep-Sea Res. II* 47, 2615–2628.
- Phil, L., Baden, S.P., Diaz, R.J., 1991. Effects of periodic hypoxia on distribution of demersal fish and crustaceans. *Mar. Biol.* 108, 349–360.
- Ramirez-Llodra, E., 2002. Fecundity and life-history strategies in marine invertebrates. *Adv. Mar. Biol.* 43, 88–170.
- Reichart, G.J., Schenau, S.J., De Lange, G.J., Zachariasse, W.J., 2002. Synchronicity of oxygen minimum zone intensity on the Oman and Pakistan Margins at sub-Milankovitch time scales. *Mar. Geol.* 185, 403–415.
- Rex, M.A., Warén, A., 1982. Planktotrophic development in deep-sea prosobranch snails from the western North Atlantic. *Deep-Sea Res. II* 29, 171–184.
- Rogers, A.D., 2000. The role of the oceanic oxygen minima in generating biodiversity in the deep sea. *Deep-Sea Res. II* 47, 119–148.
- Sanders, H.L., 1979. Evolutionary ecology and life-history patterns in the deep sea. *Sarsia* 64, 1–7.
- Scheltema, R., 1994. Adaptations for reproduction among deep-sea benthic molluscs: an appraisal of the existing evidence. In: Young, C.M., Eckelbarger, K. (Eds.), *Reproduction, Larval Biology, and Recruitment of the Deep-Sea Benthos*. Columbia Univ. Press, New York, pp. 44–75.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry. The Principles and Practices of Statistics in Biological Research*. W.H. Freeman & Company, New York. 887 pp.
- Subba Rao, N.V., 1977. On the collection of Strombidae (Mollusca: Gastropoda) from the Bay of Bengal, Arabian Sea and Western Indian Ocean, 2. Genera *Lambis*, *Terebellum*, *Tibia* and *Rimella*. *J. Mar. Biol. Assoc. UK* 19, 21–34.
- Warén, A., Bouchet, P., 1990. Laubierinidae and Pisanianurinae (Ranellidae), two new deep-sea taxa of the Tonnoidea. *Veliger* 33, 56–102.
- Woodmason, J., Alcock, A., 1891. On *Rostellaria delicatula*. *Ann. Mag. Nat. Hist. Lond.* 7, 16–17.
- Young, C.M., 2003. Reproduction, development and life history traits. In: Tyler, P.A. (Ed.), *Ecosystems of the World, Ecosystems of the Deep Ocean*, vol. 28. Elsevier, London, pp. 381–446.