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Island-coastal and oceanic epipelagic zooplankton biodiversity in the southwestern Indian Ocean

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The oceanic Indian Ocean zooplankton species and their distributions have been well described, but the zooplankton of coastal regions, particularly around the oceanic islands, has not been well researched, either taxonomically or experimentally. The environment of the Mascarene region in the southwestern Indian Ocean and zooplankton research that has been carried out there is detailed, along with gaps in our knowledge. Suggestions are given for future research, particularly on the zooplankton species adapted to live in the fluctuating environment of inshore waters, including studies on taxonomy and biodiversity, life cycles, dispersion and genetics. Problems of carrying out taxonomic research are highlighted.

[**Key words**: Indian Ocean, Mascarene Plateau, islands, zooplankton, dispersal, taxonomy, genetics, biodiversity]

Introduction

The Indian Ocean has been well researched biologically and there have been many extensive national and international research cruises that have investigated zooplankton taxonomy, biodiversity and species distributions in the open ocean areas[1]. As a result, the species of a vast range of zooplankton taxa have been described, although sometimes poorly, and descriptions published in a vast array of taxonomic compilations and individual papers. Some useful bibliographies of research and taxonomic resources are available[2-4].

While the zooplankton of the open Indian Ocean has been well documented, the more accessible coastal areas of some of the Indian Ocean rim countries and particularly around the oceanic islands have been superficially researched. This is a crucial gap in our knowledge, as many islands are of different geological ages and experience a wide range of environmental influences. The islands are also randomly distributed over a considerable area, so the population diversity of the obligate inshore zooplankton is of particular interest, because of their variable isolation from other equivalent populations.

There have been zooplankton studies around some of the oceanic Indian Ocean islands, such as the Lakshadweep[5], Andaman-Nicobar[6] and Seychelles[7-9], but usually of short duration, or limited in scope. In the southwestern Indian Ocean, the most detailed, long-term inshore zooplankton biodiversity studies were carried out in Madagascar[10,11]. In response to commitments made by the world nations under the 1992 Rio de Janeiro, Earth Summit Biodiversity Convention, a long-term zooplankton biodiversity research programme was started around two islands, Mahé in the Seychelles group and the Mauritian island of Rodrigues[4,12] (Fig. 1). The islands of Madagascar, Mahé and Rodrigues contrast in their size, geology, coastal environments and climatic influences and are all situated in the region of the shallow Mascarene Plateau. The plateau itself has been poorly studied, apart from a pair of epipelagic zooplankton transects carried out between Mauritius and Mahé[13] (Fig. 1).

This paper, consistent with the goals of the Census of Marine Life, reviews the current status of zooplankton biodiversity data available for the southwestern Indian Ocean and considers where future research might be directed, as a framework to strengthen co-operative projects in the region. The whole marine food chain, and thus the economies of coastal nations, revolves round zooplankton, so available data on patterns of diversity, distribution and abundance must be expanded. By doing this, any future changes in biodiversity, whether due to climate or human-induced changes, can be recognised and appropriate policy and management decisions made.

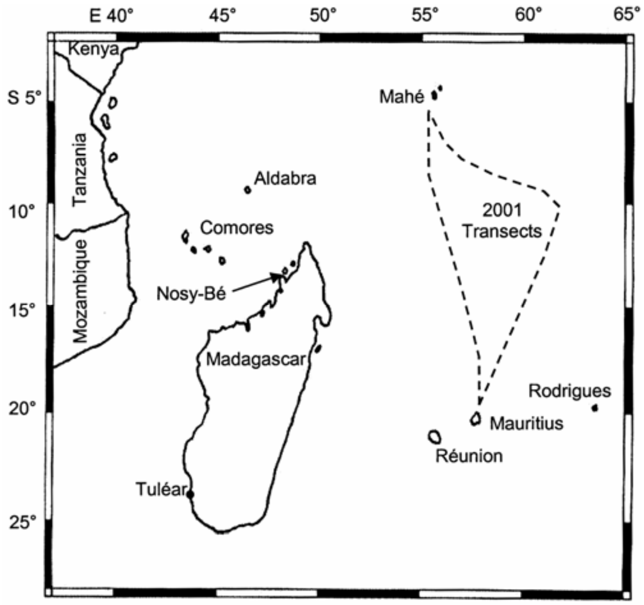

Fig. 1—The southwestern Indian Ocean, showing oceanic sites from where zooplankton biodiversity information is available; Nosy-Bé and Tuléar in Madagascar, Mahé and Rodrigues. The 2001 sampling transects are also shown.

The marine environments of Madagascar, Mahé, Rodrigues and the Mascarene Plateau

Madagascar

Madagascar is one of the largest islands in the world, about 1580 km in length and 570 km wide. It extends from around 12°S-25°S, experiencing equatorial climatic influences in the north, to sub-tropical and temperate influences in the south. Because of its north south orientation, spanning almost 14° of latitude, open water sea-surface temperature ranges from 22-28 °C, with even greater extremes inshore (19-32 °C)[14]. It has a wide diversity of marine, coastal habitats, with coral reefs, particularly in the west, extensive tidal marshes and mangroves, sea grass beds, estuarine mud flats and rocky shores. Trade winds prevail from the east and monsoons from the northwest, so most of the precipitation is on the east and north. The wet season is from November to March and annual precipitation in the wettest regions can reach 360 cm. As a result of this, there are large river outflows, carrying exceptionally heavy sediment loads. Pollution impact is not great in most areas.

Mahé

The Seychelles comprises 115 widely dispersed islands, with Mahé the main and largest. It is a granitic island, 28 km in length and 5 km wide, situated on the shallow plateau of Seychelles Bank, which has a depth range of 44-65 m. It has heavily exploited fringing reefs that are intermittently under pressure from pollution, from sedimentation, from coastal reclamation schemes and agricultural practice, domestic and commercial effluents[15]. From May till October there are strong southeast trade winds and a period of low rainfall. Annual rainfall exceeds 800 mm, falling mainly from December till March during the northwest monsoon, swelling the few small rivers and streams. Annual sea-surface temperature usually ranges from 26-31 °C and salinity from 34.5-35.5 psu, but during the wet season these can fluctuate widely in the immediate coastal zone. The inshore regions are mainly sandy beaches, rocky shores, seagrass and algae beds and some marshy, mangrove areas.

Rodrigues

Rodrigues is a small isolated island situated 550 km northeast of Mauritius. It is of volcanic origin, 18 km long by 8 km wide, surrounded by a fringing coral reef[16]. Inside the reef are a few small basaltic and sandy islands. The reef flat is covered by sand and coral rubble with some small channels and is badly degraded due to trampling during constant octopus fishing activities. As a result of extensive deforestation over a long period and runoff from the land during the December till March wet season, some of the lagoons and embayments are silted, but support a rich benthic community. There are no distinct monsoons and from January till March there can be days of squally depressions from cyclones in the region. There are some seagrass beds and mangroves have been transplanted in three bays to stabilise the sediments. The population is low and relatively dispersed, so impact on the coastline is not evident.

The Mascarene Plateau

The Mascarene Plateau is around 2200 km in length and extends in a crescent shape ridge from Seychelles to Mauritius[13]. The islands, banks and shoals of the plateau form a barrier, continuous at depth, but with gaps above about 1500 m. It shallows to 20 m in many areas of the banks at the north and in places the 200 m isobath is more than 250 km wide. The banks and shoals of the ridge thus comprise a large shelf sea, but without a coastline.

The most northerly part of the plateau is under the influence of the northeast monsoon from December to February and during the remainder of the year the southeast trades and the south equatorial current.

Studies of physical data gathered during the Indian Ocean Expeditions and later[17,18], have indicated that the Mascarene Plateau affects the predominantly westward flow of the south equatorial current, causing divergence on the leeward side, especially during winter.

Zooplankton biodiversity studies in the southwestern Indian Ocean

There is limited information on the coastal zooplankton biodiversity of the islands and shallow water regions of the oceanic southwestern Indian Ocean. The coastal regions of the French island of Réunion appear to have no zooplankton information, while information from the island of Mauritius is very sparse[19]. Madagascar has a vast range of coastal habitats and environmental influences, but most zooplankton research of extended duration was carried out at two separate locations, approximately 1600 km apart. French researchers worked on the island of Nosy-Bé in the northwest, mainly between 1963 and 1969 on general zooplankton[10,20], siphonophores[21,22], copepods[23], cladocera[24], decapods[25], pteropods and heteropods[26-30], polychaete larvae[31,32] and chaetognaths[33-35]. The other location was Tuléar in southwest Madagascar, between 1963 and 1964, where copepods were studied[11].

Little zooplankton research was carried out around the Seychelles, except a limited study on copepods[8], a study on chaetognaths[7] and one on hydromedusae[9] and none had been carried out round the Mauritian island of Rodrigues. However in November 2000, long-term zooplankton monitoring projects were set up at both locations[12,13].

Only sporadic zooplankton information is available for the shallow Mascarene Plateau, a few surveys having superficially studied the plateau and basin to the west[1,36]. However, a study of the epipelagic zooplankton, from two transects was carried out[13] in 2001, one across the deep Mascarene Basin and the other mainly on the plateau (Fig. 1).

Zooplankton biodiversity

The number of zooplankton species recorded from the coastal regions of Mahé and Rodrigues is continuing to grow, as the studies continue there[4]. However, the biodiversity information is currently not yet equivalent to that available from the intense taxonomic research that was carried out from Madagascar[10,11,20-35]. An accurate comparison of relative biodiversity is thus not yet possible, but some preliminary information is presented in Table 1, along with information from the transects carried out[13] between Mauritius and Mahé in 2001. For ease of comparison, only total number of species of the three main orders of copepods (which can be around 70% of zooplankton, numerically) and of the other main zooplankton groups is presented.

The Mahé, Rodrigues and 2001 transect numbers are very similar, apart from the high numbers of Hydrozoa recorded from Mahé, which results from a comprehensive specialist study that was carried out there[9]. Higher numbers of cyclopoid copepods at Rodrigues reflects more effort being put into the identification of that order there, although the lower number of calanoid species at Rodrigues probably reflects a real difference. The considerably higher numbers of almost all of the categories sampled at

Table 1—Comparison of number of zooplankton groups recorded from Madagascar[10,11,20-35], Mahé[4,7-9], Rodrigues[4] and on the 2001 cruise transects[13]

Zooplankton groups	Madagascar	Mahé	Rodrigues	2001 transects
Calanoid copepods	88	46	39	50
Cyclopoid copepods	61	8	27	6
Harpacticoid copepods	7	6	10	7
Euphausiaceae	9	1	0	5
Decapoda	7	9	6	3
Other crustacea	2	7	9	10
Polychaeta	0	4	4	4
Mollusca	47	16	12	12
Chaetognatha	13	3	5	5
Siphonophora	41	7	8	12
Hydrozoa	1	79	3	4
Urochordata	17	4	4	4
Other organisms	3	9	7	11
Total	296	199	134	133

Madagascar are mainly because some specialist groups, such as cyclopoid copepods, Mollusca, Chaetognatha, Siphonophora and Urochordata, were worked on in great detail there, but also because some of the sampling was carried out over deeper, more oceanic water than at the other locations.

Copepods are one of the more useful groups for making biodiversity comparisons, because of the wide range of species. Examination of the data for calanoid copepods, showed that of the 105 different species recorded, 17 were sampled at all 4 locations, 13 at 3, 21 at 2 and 54 at only 1 location. This gives a preliminary indication of considerable variability in biodiversity over this region.

However, comparing biodiversity of zooplankton from fixed coastal stations can be problematical, as the species list can change dramatically by moving a short distance coastally or seawards. Hydrographic variability also makes it difficult to have equivalent sampling sites. Thus, knowing the zooplankton biodiversity at one site is crucial to be able to monitor changes, but care must be taken when making comparisons between sites.

Gaps in our knowledge of the southwestern Indian Ocean zooplankton

Taxonomy

Because there have been few zooplankton studies carried out round the oceanic islands, there are undoubtedly many undescribed and possibly endemic species still to be recorded. For example, when a study of the hydromedusae of the Seychelles was carried out[9], six species new to science were found. This was further evidenced during the sampling in Rodrigues, when a new species of calanoid copepod of the genus *Tortanu*s was disovered[37]. Further new copepod species have been found around other islands and are in the process of being described. From Mahé and Rodrigues, another interesting crustacean find were facetotectan nauplii, only previously recorded from the Atlantic and Pacific oceans and the Red Sea[38]. These are the first records for the Indian Ocean, but probably only because inshore samples taken with a reasonably fine net have not previously been carefully examined. The zooplankton groups that should yield most new species are those adapted to live in shallow coastal regions, particularly the demersal, epibenthic, brackish water and certain pelagic species.

Zooplankton biodiversity research, and probably biodiversity research in general, is currently hindered globally, due to a lack of taxonomic expertise in particular world regions. There is a requirement for training workshops, to spread sampling and taxonomic expertise and to intercalibrate techniques. Additionally, only scientists working in large, well-resourced institutes have access to adequate taxonomic literature. Literature that is available may be spread through diverse scientific journals, or monographs that are not accessible. There is a scarcity of taxonomic compilations on important topics, such as identification of the eggs and larvae of tropical marine fish, when most nations in the tropics depend heavily on fishing, and coastal areas are important spawning and nursery grounds. Lack of information makes it difficult to carry out research on topics such as location of the spawning stations utilised by some reef fishes and survival and recruitment studies, information which could be used in fisheries management and legislation.

To encourage zooplankton research in the southwestern Indian Ocean, a guide has been prepared to the coastal and surface zooplankton[4], [accessible free, from the Plymouth Marine Laboratory Website - http:/www.pml.ac.uk/pml/sharing/zooplankton.htm]. The species described make it useful for much of the shallow Indian Ocean. Computer based guides for all organisms, globally, are a necessity if we are to continue cataloguing the living world, so that amendments can be made, new species documented and rearrangement of groups made when necessary, so that the latest information is freely accessible to all.

Genetics

It is intriguing to consider how many undescribed, obligate inshore limited, zooplankton species there are still to be found around the oceanic islands and Indian Ocean rim coasts. These species may have been isolated for millennia and present an opportunity, through genetical studies, to examine population differences when they are distributed at separate locations, to assess how long they have been separated, and if there is still interchange between them. It should also be possible to examine how closely they are related to other members of the same genera at the same or separate locations, to assess how long since they diverged from their common ancestor. This information should provide information on whether they were recent introductions, as in ballast water, or how they were distributed in the ancient Indian Ocean current systems and clues to how, if currents are modified due to climate changes, their potential for future distribution. The type of genetical work required is already well established[39].

Biology

The biology of many inshore zooplankton species is poorly known, particularly their survival mechanisms in a fluctuating and stressful environment. For example, the coastal waters of the Indian Ocean contain large numbers of copepods of the families Acartiidae, Centropagidae, Pontellidae, Temoridae and Tortanidae, which have members known to lay resting eggs[40]. These eggs can remain dormant in bottom sediments for many years before hatching and may allow the population to be maintained over stressful periods, such as times of high precipitation or reduced production. However, few studies on the importance of this phenomenon on tropical plankton community structure have been conducted. The life cycles of the inshore zooplankton is also of interest, because it is these species that are potential invasive species[41], introduced to new locations in ballast water or by some other means. With increasing global concern about these introductions, more coastal research is required, both to understand their biology and to recognise and monitor any introductions.

Dispersion

While considerable research is currently being conducted into invasive species, little is known about the actual mechanisms of how inshore zooplankton are naturally dispersed between isolated locations, such as islands and the continental margins[42]. Because of the extensive system of ocean currents, and evidence from genetical studies that populations of some marine organisms are homogeneous over large areas[43], it can be inferred that they drift passively and regularly between locations. Meroplankton are specifically a dispersal phase and are considered to be more easily transported by currents than holoplankton[44,45]. However, the actual temporal and climatic situations under which inshore organisms are dispersed long distances have not been well studied.

Many species of the inshore zooplankton are not adapted to survive in open sea conditions for long periods, whether for physiological reasons, or because of a requirement for shallow water and fine sediments during part of their reproductive cycle. These species, around oceanic islands, may be dispersed by currents to adjacent islands, but are limited in how far they can be carried and still survive to reproduce. One way in which coastal zooplankton can be carried long distances in the same body of water is as a result of eddy formation. Eddies from the coastal margins can transport entrained coastal zooplankton in their core[46], but this zooplankton gradually reduces in abundance and may not be carried into a favourable area while the organisms are still viable, or before the eddy dissipates.

Coastal zooplankton have behavioural mechanisms, such as swarming and vertical migration and predominately epibenthic and demersal life styles, which are considered to be adaptations to retain them at the same general location[47,48]. Successful retention mechanisms must operate, as evidenced by the number of endemic species around isolated islands, so marine populations may not be as open as they might seem[49].

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References

1 Rao T S S & Griffiths C, *Understanding the Indian Ocean—Perspectives on oceanography*, (UNESCO, Paris) 1998, pp. 187.

2 Prasad R R, *A bibliography of the plankton of the Indian Ocean*, Publication 3(INCOR [CSIR], New Delhi), 1964, pp. 87.

3 Zeitzschel B, *The Biology of the Indian Ocean*, (Springer-Verlag, Berlin) 1973, pp. 549.

4 Conway D V P, White R G, Hugues-Dit-Ciles J, Gallienne C P & Robins D B, *Guide to the coastal and surface zooplankton of the south-western Indian Ocean*, Occasional Publication No 15 (Marine Biological Association of the United Kingdom, Plymouth, UK) 2003, pp. 354.

5 Madhupratap M, Wafar M V M, Haridas P, Narayanan B, Gopala Menon P & Sivadas P, Comparative studies on the abundance of zooplankton in the surrounding sea and lagoons in the Lakshadweep, *Indian J. Mar. Sci*., 6 (1977) 138-141.

6 Madhupratap M, Nair S R S, Achuthan Kutty C T & Nair V R, Major crustacean groups and zooplankton diversity around Andaman-Nicobar islands, *Indian J. Mar. Sci*.,10(1981) 266-269.

7 Furnestin M L & Ducret F, Les Chaetognathes des Séchelles, *Rev. Zool. Afr*., 90(1976) 89-117.

8 Marques E, Copépodes marins des environs des Iles Séchelles, *Rev. Zool. Afr*., 90(1976) 984-1008.

9 Bouillon J, Hydromeduses de l'Archipel des Séchelles et du Mozambique, *Rev. Zool. Afr*., 92(1978) 117-172.

10 Frontier S, Zooplancton de la région de Nosy-Bé. I. Programme des récoltes et techniques d'études. II. Plancton de surface aux stations 5 et 10, *Cah. O.R.S.T.O.M., sér. Océanogr*., 4(1966) 3-36.

11 Gaudy R, Note préliminaire sur la systématique et la répartition annuelle des copepods des eaux superficielles de Tuléar (Madagascar), *Rec. Trav. Sta. Mar. End.*, Fasc. hors. série suppl. 6(1967) 71-99.

12 Burnett J C, Kavanagh J S & Spencer T, *Marine science, training and education in the western Indian Ocean: Shoals of Capricorn Programme Field Report 1998–2001*, (Royal Geographical Society [with The Institute of British Geographers], London) 2001, pp. 108.

13 Gallienne C P & Conway D V P, Epipelagic mesozooplankton distribution and abundance over the Mascarene Plateau and basin, southwestern Indian Ocean, *J. Mar. Biol. Ass. U.K*., 84(2004) 1-8.

14 Cooke A, Ratomahenia O, Ranaivoson E & Razafindrainibe H, Madagascar, in: *Seas at the millenium: An environmental evaluation*, edited by C R E Sheppard, (Elsevier Science, Amsterdam) 2000, pp. 113-131.

15 Gabriel M, Marshall S & Jennings S, The Seychelles, in: *Seas at the millenium: An environmental evaluation*, edited by C R E Sheppard, (Elsevier Science, Amsterdam) 2000, pp 233-241.

16 Turner J, Jago C, Daby D & Klaus R, The Mascarene Region, in: *Seas at the millenium: An environmental evaluation*, edited by C R E Sheppard, (Elsevier Science, Amsterdam) 2000, pp. 243–258.

17 Ragoonaden S, Ramesh Babu V & Sastry J S, Physico-chemical characteristics and circulation of waters in the Mauritius-Seychelles ridge zone, Southwest Indian Ocean, *Indian J. Mar. Sci*., 16(1987) 184–191.

18 Sarma Y V B, Gopala Krishna V V, Rao D P & Sastry J S, Thermohaline circulation and water characteristics around Mauritius group of islands, *Indian J. Mar. Sci*., 19(1990) 196–200.

19 Grindley J R & Grice G D, A redescription of *Pseudodiaptomus marinus* Sato (Copepoda, Calanoida) and its occurrence at the island of Mauritius, *Crustaceana*, 16(1969) 125-134.

20 Frontier S, Zooplancton de la région de Nosy-Bé. IV. Plancton de surface stations 3, 4 et 11, *Cah. O.R.S.T.O.M., sér. Océanogr*., 8(1970) 3-17.

21 Patriti, G, Note sur deux nouvelles espèces du genre *Lensia*, recueilles dans les eaux du large de Tulear (S.W. de l'Océan Indien, Madagascar), *Rec. Trav. St. Mar. End. Fas. hors série*, suppl. No. 10 (1970) 103-106.

22 Patriti, G, Aperçu systématique de la faune de siphonophores des zones superficielles et subsuperficielles des eaux du large de Tulear (S.W. de l'Océan Indien, Madagascar). *Rec. Trav. St. Mar. End. Fas . hors série*, suppl. No. 10 (1970) 285-303.

23 Binet D & Dessier A, Zooplancton de la région de Nosy-Bé. III. Premières données sur les copépodes, *Cah. O.R.S.T.O.M., sér. Océanogr*., 6(1968) 3-26.

24 Frontier S, Zooplancton de la région de Nosy-Bé. V. Cladocères, *Cah. O.R.S.T.O.M., sér. Océanogr*., 11(1973) 259-272.

25 Petit D, Zooplancton de la région de Nosy-Bé. VIII: Répartition spatio-temporelle du genre *Lucifer* (Décapodes Sergestidae) dans la province néritique. *Cah. O.R.S.T.O.M., Sér. Océanogr*., 11(1973) 373-385.

26 Frontier S, Notes morphologiques sur les *Atlanta* récoltées dans le plancton de Nosy-Bé (Madagascar), *Cah. O.R.S.T.O.M., sér. Océanogr*., 4(1966) 131-139.

27 Frontier S, Liste complémentaire des ptéropodes du plancton de Nosy-Bé (Madagascar). *Cah. O.R.S.T.O.M., sér. Océanog*r., 4(1966) 141-146.

28 Frontier S, Deuxième liste complémentaire des ptéropodes du plancton de Nosy-Bé (Madagascar) et notes morphologiques, *Cah. O.R.S.T.O.M., sér. Océanogr*., 11(1973) 253-257.

29 Frontier S, Zooplancton de la région de Nosy-Bé. VI. Ptéropodes, Hétéropodes – première partie: espèces holonéritiques et néritiques-internes, *Cah. O.R.S.T.O.M., sér. Océanogr*., 11(1973) 273-289.

30 Frontier S, Zooplancton de la région de Nosy-Bé. VII. Ptéropodes, Hétéropodes – deuxième partie: espèces néritiques-externes et océaniques tolérantes, *Cah. O.R.S.T.O.M., sér. Océanogr*., 11(1973) 291-302.

31 Bhaud M, Identification des larves d'amphinomidae (Annelides Polychaetes) recueillies près de Nosy-Bé (Madagascar) et problèmes biologiques connexes, *Cah. O.R.S.T.O.M., sér. Océanogr*., 10(1972) 203-216.

32 Day J H, Zooplancton de la région de Nosy-Bé. The biology of planktonic polychaeta near Nosy-Bé, Madagascar, *Cah. O.R.S.T.O.M., sér. Océanogr*., 13(1975) 197-216.

33 Furnestin M L & Radiguet J, Chaetognathes de Madagascar (sectuer de Nosy-Bé), *Cah. O.R.S.T.O.M., sér. Océanogr*., 2(1964) 55-98.

34 Bour W & Frontier S, Zooplancton de la région de Nosy-Bé. IX. Répartition spatio-temporelle des chaetognathes dans la province néritiques, *Cah. O.R.S.T.O.M,. sér. Océanog*r., 12(1974) 207-219.

35 Frontier S & Bour W, Note sur une collection de chaetognathes récoltee audessus du talus continental près de Nosy-Bé (Madagascar), *Cah. O.R.S.T.O.M., sér. Océanogr*., 14(1974) 267-272.

36 Piontkowski S A, Williams R & Melnik T A, Spatial heterogeneity, biomass and size structure of plankton of the Indian Ocean: some general trends, *Mar. Ecol. Prog. Ser.*, 117(1995) 219–227.

37 Ohtsuka S & Conway D V P, A new species of *Tortanus* (*Atorus*) (Copepoda: Calanoida: Tortanidae) from Rodrigues Island, Mauritius, *J. Mar. Biol. Ass. U.K*., 83(2003) 355-360.

38 Kolbasov G A & Høeg J T, Facetotectan larvae from the White Sea with the description of a new species (Crustacea: Thecostraca), *Sarsia*, 88(2003) 1-15.

39 Bucklin A, Frost B W, Bradford-Grieve J, Allen L D & Copley N J, Molecular systematics and phylogenetic assessment of 34 calanoid copepod species of the Calanidae and Clausocalanidae, *Mar. Biol*., 142(2003) 333-343.

40 Marcus N H, Ecological and evolutionary significance of resting eggs in marine copepods: past, present, and future studies, *Hydrobiologia*, 320(1996) 141-152.

41 Bollens S M, Cordell J R, Avent S & Hooff R, Zooplankton invasions: a brief review, plus two case studies from the northeast Pacific Ocean, *Hydrobiologia*, 480(2002) 87-110.

42 Barber P H, Moosa M K & Palumbi S R, Rapid recovery of genetic diversity of stomatopod populations on Krakatau: temporal and spatial scale of marine larval dispersal. *Proc. R.*

Soc. Lond. B, 269 (2002) 1591-1597.

43 Doherty P J, Planes S & Mather P, Gene flow and larval duration in 7 species of fish from the Great-Barrier-Reef, *Ecology*, 76(1995) 2373-2391.

44 Scheltema R S, Williams I P & Lobel P S, Retention around and long-distance dispersal between oceanic islands by planktonic larvae of benthic gastropod Mollusca, *Amer. Malcol. Bull.*, 12 (1996) 67-75.

45 Rios-Jara E, Spatial and temporal variations in the zooplankton community of Phosphorescent Bay, Puerto Rico, *Estuar. Coast. Mar. Sci*., 46(1998) 797-809.

46 Mackas D L & Galbraith M D, Zooplankton distribution and dynamics in a North Pacific eddy of coastal origin: 1. Transport and loss of continental margin species. *J. Oceanogr*., 58(2002) 725-738.

47 Qasim S Z, *Glimpses of the Indian Ocean*, (Universities Press, Hyderabad), 1998, pp. 224.

48 Ritz D A, Social aggregation in pelagic invertebrates, *Adv Mar. Biol*., 30(1994) 155-216.

49 Cowen R K, Lwiza K M M, Sponaugle S, Paris C B & Olsen D B, Connectivity of marine populations: open or closed?, *Science*, 287(2000) 857-859.