

The marine biodiversity of the western Indian Ocean and its biogeography: How much do we know?

M. D. Richmond

Marine Education, Awareness and Biodiversity (MEAB) Programme
Western Indian Ocean Marine Science Association (WIOMSA), P.O. Box 3298, Zanzibar, Tanzania

ABSTRACT

Prior to the 1960s the biota of the western Indian Ocean inshore marine habitats received scant attention from taxonomists resulting in a poorly known flora and fauna. Fortunately, over the last 40 years there have been considerable developments in the study of marine biodiversity in this region, both from regional scientists and by those based at institutions in Europe and elsewhere. This paper reviews the current status of taxonomic knowledge of the marine biodiversity of the western Indian Ocean, focusing on the macroflora and macrofauna of the intertidal and shallow subtidal environments. The taxonomy of many of the smaller and particularly the softer-bodied invertebrate taxa remains a challenge to specialists, and as a result these taxa continue to be inadequately known from this region. Such groups include sponges, ctenophores, octocorals, polychaetes and tunicates. There is however, considerably greater knowledge on the taxonomy and diversity of groups such as coastal plants, mangroves, seagrasses, macroalgae, scleractinian corals, most crustacean taxa, molluscs, echinoderms, fishes, reptiles and marine mammals. For some of these groups this paper provides an examination of their possible origins, the levels of regional endemism and compares their diversity with that of other provinces of the Indo-Pacific for which similar knowledge is available. Finally, the importance of continued taxonomic research in the region is discussed, in light of the current threats to marine biodiversity, and the need to make the information which is currently available on the western Indian Ocean marine diversity more accessible to decision makers and to the public in general.

INTRODUCTION

At the turn of the century Gardiner (1907) stated that "... of all oceanic areas none seems so little known in 1905 as that between India and Madagascar". He then led the Percy Sladen Trust Expedition with H.M.S. *Sealark* for 6 months, visiting mainly the western Indian Ocean islands, including Madagascar, from which numerous reports were produced.

Despite these reports and those of later expeditions, in his landmark treatise of marine zoogeography of the world, Ekman (1953) acknowledged that the “northern and western parts of the Indian Ocean are on the whole not so systematically investigated that their zoogeographical position can be determined”. More poignantly Salm (1995) recently stated that “not only are we unaware of the extent of our biological wealth, but also of the rate at which we are losing it”.

Fortunately, in the last 40 years various taxonomic groups have received attention, resulting in a considerable growth of information (see Macnae and Kalk, 1958; Branch et al., 1994; Kalk, 1995). *A Guide to the Seashores of Eastern Africa and the Western Indian Ocean Islands* (Richmond, 1997) provides a recent, brief and concise summary of the many taxa which contribute to the diversity of flora and fauna of the shores and shallow seas of the region. In this text over 1600 species are described and illustrated, and the many confusing synonyms which plague some of the taxa (e.g. molluscs and echinoderms) are revised. Though this work is by no means complete, it provides for most taxa, for the first time, a brief examination of marine species diversity as well as a basis for continued documentation of marine taxa for the region.

The purpose of this paper is to compile the information from Richmond (1997), extending further the discussion for the various taxonomic groups and highlighting groups where more research is required. The focus is on the taxa present in the intertidal and shallow subtidal waters of the western Indian Ocean. The diversity and biogeography of the Polychaeta, Mollusca and Echinodermata were also examined in more detail by Richmond (1999) and a summary of those findings is incorporated.

MEASURING BIODIVERSITY

The definition of and methods used to measure biodiversity have been an area of considerable controversy. The definition employed by the Convention on Biodiversity (Article 2), UNCED 1992 is as follows: *Biological diversity means the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are a part; this includes diversity within species, between species and of ecosystems*. Unfortunately, the Convention does not assist in defining how to measure biodiversity. Nevertheless, there is a need to quantify biodiversity in some way, so that changes over time can be monitored, locations of change determined and ways of maintaining it considered.

Commonly used measures of biodiversity include: (a) higher taxonomic levels, such as order or family, which have been shown to increase with species richness (Gaston and Williams, 1993); (b) phylogenetic diversity, which reflects the closeness of species in evolutionary terms, capturing the degree of relationship and the degree of difference in many other characteristics; (c) species richness referring simply to the total number of species, and (d) species richness combined with numbers of each species (occurrence) thus giving a more balanced measure of the overall diversity. In

practice it is the measure of species richness which is used most often to reflect biodiversity. Reasons for using this simple measure include the fact that species richness is positively correlated with number of higher taxa and character richness (Roy et al., 1996; Williams and Humphries, 1996) and it is therefore a good 'surrogate measure' (Gaston and Spicer, 1998). Species richness is also frequently measurable with ease and significant information already exists in the literature, in museums and other documentation agencies.

APPROACH AND METHODS

Between January 1992 and October 1997 work on the preparation of *A Guide to the Seashores of Eastern Africa and the Western Indian Ocean Islands* was conducted primarily from a base at the Institute of Marine Sciences, (University of Dar es Salaam) on Zanzibar. The area considered as the western Indian Ocean extends from southern Somalia to the Natal coast of South Africa, embracing the islands of Madagascar, Comoros, Réunion, Mauritius and the Seychelles. Visits were made to most parts of the region to conduct brief field surveys, liaise with regional specialists and examine taxonomic collections. Sites visited included: Watamu and Mombasa (Kenya), Mafia and Pemba islands (Tanzania), Inhaca Island (Mozambique), northern Natal (South Africa), Tulear (SW Madagascar), Nose Be (NW Madagascar), Moroni (Comoros) and the La Digue and Mahe islands (Seychelles). In addition, quantitative sampling of soft substratum benthic surveys were conducted in Zanzibar (Tanzania). For comparison purposes detailed ecological surveys were also conducted in eastern Saudi Arabia (Arabian Gulf) and brief field surveys were conducted in western Saudi Arabia (Red Sea) and more recently SE Papua New Guinea (Solomon Sea/Coral Sea).

Material for each taxonomic group was collected and catalogued in Zanzibar. Where necessary specimens were deposited or exchanged with specialists from other institutions, many of which provided assistance with collection and identification. Of these, 48 specialists contributed directly to the guide book with chapters on their specialty.

The phyla Polychaeta, Mollusca and Echinodermata were subsequently examined in greater detail by Richmond (1999). A collection of polychaetes from Zanzibar and Mafia were identified and their wider distribution established from the literature. A preliminary species checklist of molluscs was prepared based on material collected, records from 72 publications and reports dating from 1932 to 1997, unpublished collection lists and the species list of the material held by the National Museum of Wales. The latter museum holds the Melvill-Tomlin collection which includes many species from Mauritius as well as other parts of the western Indian Ocean. An echinoderm faunal checklist was compiled for the western Indian Ocean using data from 53 sources. Records were included only for species which were reported from depths shallower than 100m. The checklist also includes species records from numerous provinces within the entire Indo-Pacific region as well as the eastern Pacific and Atlantic Ocean, thus allowing for a biogeographical analysis of the western Indian Ocean echinoderm fauna.

STATUS OF KNOWLEDGE

A summary from the various taxonomic sections in Richmond (1997, 1999) allows an estimate of the overall species richness of the taxa in the region to be ascertained (see Table 1). The figures from Table 1 when represented graphically permit the contribution of each taxon to be visualised with ease (Figure 1). A cautionary note is that, as with all taxonomic studies, continuous progress is underway to elucidate confusing species, synonyms and describe new species, thus any findings are automatically outdated the moment they are put to paper.

The marine macro-taxa occurring in the intertidal and shallow seas of the western Indian Ocean comprise an estimated minimum of 10,627 species. The Mollusca and the Pisces represent about half of the entire marine biodiversity of the region, with a clear domination by molluscs. Within the Mollusca the class Prosobranchia is the most

Table 1. Summary of the minimum estimated species number for major macroflora and macrofauna taxa from littoral and shallow sublittoral waters of the western Indian Ocean. Data from Richmond (1997) unless indicated

Taxa	Minimum no. of species	Taxa	Minimum no. of species
Mangroves	10	Caridea	150
Seagrasses	12	Palinura	20
Macroalgae ¹	1011	Thalassinidea	20
Porifera ²	200	Anomura	50
Ctenophora	20	Brachyura	100
Scyphozoa ³	30	Scaphopoda	10
Hydrozoa	100	Polyplacophora ⁴	39
Octocorallia	300	Prosobranchia ⁴	2550
Ceriantharia	20	Opisthobranchia ⁵	400
Actiniaria	30	Pulmonata	20
Corallimorpharia	10	Bivalvia ⁴	667
Zoanthidea	5	Cephalopoda	20
Scleractinia	200	Echinoidea ⁴	62
Antipatharia	10	Holothuroidea ⁴	148
Platyhelminthes	100	Asterioidea ⁴	58
Echiura	22	Ophiuroidea ⁴	132
Sipuncula	50	Crinoidea ⁴	19
Polychaeta ⁴	300	Phoronida	5
Oligochaeta	10	Brachiopoda	5
Cirripedia	30	Bryozoa	500
Nemertea	59	Hemichordata	20
Amphipoda	300	Chaetognatha	50
Isopoda	100	Thaliacea	30
Stomatopoda	30	Ascidiacea ⁶	100
Dendrobranchiata	10	Pisces	2000
Total			10,627

¹Silva et al. (1996) (excluding South Africa); ²Van Soest, 1994 (including Red Sea and Arabian Sea); ³Cornelius (pers. commun.); ⁴Richmond (1999); ⁵Yonow (pers. commun.); ⁶ Monniot (pers. commun. estimate for Mozambique).

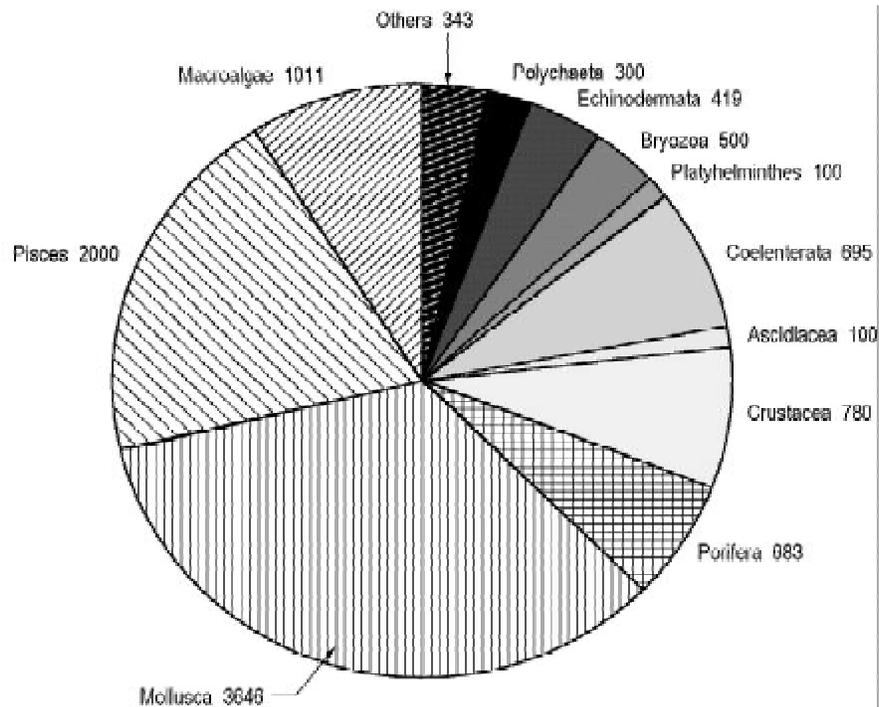


Figure 1. Conservative estimates of the number of species of the major marine taxa of the western Indian Ocean (data from Table 1)

species-rich taxon. For many taxa the figures can be largely regarded as conservative estimates of the true diversity of species for the region, as will be discussed below for the major taxonomic groups. In a study of the Hawaiian marine diversity Paulay (1997) found similar proportions among the taxa, with a total of over 7000 species recorded from those islands. Molluscs comprised about 20% of the total species number, though Paulay's study excluded fish and macroalgae, but included such groups as Nematoda and Protista which are excluded from the present study.

The botanical groups

Although mangroves and seagrasses are the basis of entire habitats, of extremely high importance ecologically and economically, these groups are represented by few species which are well known and accurately described (see Macnae, 1968 and Phillips and Meñez, 1988). Consequently their geographical distribution is also reasonably established. Though macroalgae are far more numerous in terms of species numbers, they too benefit from a reasonably ample and accurate literature. Nevertheless, new species from the region continue to be described (e.g. Coppejans et al., this volume). Very little can be said at present for the distribution and species abundance of macroalgae, given the lack of comparative studies; however, research in this field is ongoing, a situation which applies equally to the tropical Pacific (see Abbott, 1995).

Porifera

Current accurate estimates for the diversity of the Porifera in the western Indian Ocean are not available, though Kelly-Borges (1997) estimates there could be 'several hundred' species but that further work is required to determine a closer approximation. Van Soest (1994) describes a total of 683 species (in this case including the Red Sea and Arabian Sea) and found 411 Demospongiae that the western Indian Ocean associates closely with the Malay-Indonesia area where a total of 965 species are reported. He suggests that for widespread genera (13% of the total examined) their distributions are probably determined by historical and large-scale geographic factors such as tectonic events and barriers associated with deep water, temperature and continental run-off. Kelly-Borges and DeFelice (in press) found that for sponge fauna in Hawaii, the presence of 'cosmopolitan' species (i.e. of worldwide distribution) has masked the true diversity of that fauna and following detailed examination some of the taxa have been shown to include more species. This likely applies for the western Indian Ocean where the taxa described in the early literature are in need of extensive revision (Kelly-Borges, 1997).

Coelenterata

There are only an estimated 150 species of scyphozoans (jellyfishes) in the world, with about 30 species reported and collected from the region (Cornelius, 1997). A new species for the region was added to the records this year (Cornelius, pers. commun.) from a specimen collected at Mafia Island, Tanzania, during a 5-day collecting visit. This demonstrates that as more scientists become aware of the paucity of information on the group, the reported diversity is likely to increase slightly.

In general, hydrozoans have not been well studied throughout the western Indian Ocean though a number of localised investigations have been conducted which serve to describe the scale of this group. Two studies from the Seychelles revealed 88 species (Millard and Bouillon, 1973, 1975). Comprehensive investigations in southern Africa report a total of about 286 species (Branch et al., 1994).

Within the class Anthozoa, the Octocorallia are a large and taxonomically complex group with only a few specialists qualified to determine many of the species. As a result, only very rough estimates on the diversity within the region can be made at present. Schleyer (1997a) estimates there could be a few hundred species in the region. The Hexacorallia are in general better known though the anemone orders Ceriantharia and Actiniaria do require further research to elucidate many taxonomic uncertainties which continue to exist (see den Hartog, 1997). The order Scleractinia has received perhaps the greatest attention within the phylum, with numerous papers from various parts of the western Indian Ocean describing the taxa and the ecology of this important reef-building group. Sheppard (1987) reports 439 species of scleractinian corals from the entire Indian Ocean with 47 species (approx. 11%) endemic to the region. Schleyer (1997b) reports on approximately 200 species from the western Indian Ocean alone. It appears that these are relatively homogeneously distributed in the region and that unlike the Pacific Ocean,

the Indian Ocean does not reveal a pattern of decreasing concentric coral diversity levels radiating from the Malay-Indonesian region (Sheppard, 1998). What is found instead is a band of high diversity stretching across the Indian Ocean, as proposed by Rosen (1971), with about half of the corals widespread (from and including the Red Sea to South Africa and the western coasts of Australia and Malaysia), with only a few genera limited to the western extremes. New species do however continue to be described (e.g. Riegl, 1995).

Polychaeta

A recent collection of polychaetes from intertidal soft-substrates on Zanzibar and Mafia islands revealed 91 species with 29% found to occur at localities as far as the western Pacific, reflecting the occurrence of a widespread Indo-Pacific fauna (Richmond, 1999). An additional 22% of the collection were regarded as 'cosmopolitan'. No accurate estimate of the overall diversity of polychaetes of this region has been achieved to date, though a tentative, minimum estimate can be attempted by incorporating other studies, in particular those of Hughes and Gamble (1977) and Hove (1994). Such an analysis results in an estimate of between 300 and 500 species from the intertidal to the shallow subtidal.

Unfortunately, polychaete taxonomy suffers from the lack of precise and thorough descriptions of the species in the early literature, combined with inadequately preserved and catalogued type specimens. Claparède (1867) for example, was firm in his belief that studies on preserved specimens were "positively useless, and that the Annelida can only be well studied at the seaside and by means of living individuals"! A further problem faced by taxonomists is the use of 'out of area' reference material. As Mackie (1996) explains, the use of taxonomic keys which were designed for one particular area (e.g. Day, 1967 for southern African taxa) when used in other areas, i.e. can result in erroneous identifications. For example, the use of Day (1967) to identify a specimen from Europe may result in a new record of that species outside of the southern Africa region. When the description of the southern African species is expanded to accommodate the European one, this then represents the first step to that species becoming 'cosmopolitan'.

Any study is likely to provide new species depending on the level of investigation. In the Arabian Gulf for example, a study by a single experienced polychaete taxonomist found 61 genera from 23 families with 23 new species records and 8 new genera records for that area (Fiege, 1992). He also found that of the total entities recorded, only 45 could be positively identified to species level, reflecting the widespread lack of a thorough knowledge of this taxon. The study by Fiege (1992) is an example of the 'grey literature', often derived from diverse studies (environmental, ecological or consultative reports) which include polychaete species records and taxonomic keys but which fail to become more widely available, despite contributing to the overall understanding of the diversity and zoogeography of this taxonomically difficult group.

Polychaetes comprise the greatest percentage of the community of soft substrata and are the most important taxon in these communities (e.g. Knox, 1977; Guerreiro et al., 1996). Yet, despite this importance, much taxonomic research is required, especially on

tropical species, before a complete appraisal of the diversity and biogeography of this taxon is achieved. Major revisions to families are long and laborious processes, but they must be undertaken for those families where needed. Furthermore, revisions of families must be based on material, not descriptions, since interpretation of descriptions frequently is dependent on poorly understood and used terminology, which has obscured species differentiation in the past (see Fauchald, 1977).

Crustacea

Species richness among the vast phylum Crustacea varies considerably with taxonomic class, as does the level of knowledge on each taxonomic group. In general, the smaller the size of the organisms, the less known is the taxon. For example, ostracods, tanaids, mysids, cumaceans and amphipods, most usually less than a centimetre in length, are very poorly known from the western Indian Ocean region as well as other tropical areas. Decapod groups such as those including the lobsters, shrimps and crabs by comparison are well known. The meagre information on the former groups in part reflects the absence of specialists, while the former taxa, which include many species of commercial interest, have attracted greater attention of taxonomists.

In general the Crustacea are widely distributed, with the bulk of species from the western Indian Ocean occurring at sites across the Pacific Ocean. This distribution is mainly attributable to the extended larval life of many Crustacea. There is thus very little evidence for regional endemism. Among the Grapsidae and Ocypodidae from Tanzania and Madagascar, Hartnoll (1975) found a very limited level of endemism, with the majority of species occurring in both these sites and in the Malay-Indonesia area. Myers (1997) reasons that crustaceans with planktonic larvae have the greatest potential for extending their distribution. Furthermore, for the development of endemism, colonisation of new areas must be followed by a cessation of gene flow from donor regions to the new area for a long enough period to allow genetic isolation mechanisms to act. If this is the case, and larvae of the widespread species are constantly being supplied, the lack of endemism among crabs and other crustaceans with long planktonic life periods (e.g. lobsters of the genus *Panulirus*) can be partly explained.

Among caridean shrimps Bruce (1984) reported that of the 133 carideans found on the Seychelles, 16.5% were endemic to the western Indian Ocean and the remainder extended to the Malay-Indonesia area and beyond. However, Bruce (1998) later concluded that for the many coral-associated pontonine shrimp species (which generally account for about half of the caridean fauna) the distributions are still not well known, due largely to the haphazard nature of collecting activities. For crustaceans with short larval stages, or none at all, the picture does appear to be somewhat different.

Of the Amphipoda (which brood their young), Madagascar supports 9% endemism of genera and 45% endemism among species (Ledoyer, 1982, 1986). The great species diversity among the amphipods, and other peracaridans (isopods, tanaids, cumaceans and mysids), which results from egg brooding as opposed to larval dispersal, results in large proportions of these taxa including as yet undescribed species.

Mollusca

The preliminary mollusc species checklist for the region provided by Richmond (1999) includes a minimum of 2550 species of gastropod prosobranchs from 75 families, 39 species of polyplacophorans representing 6 families and a minimum of 667 species of bivalves from 49 families. Among the gastropod prosobranchs, the most species-rich families were the Mitridae with 210 species, Conidae (198), Muricidae (187), Turridae (180) and Cypraeidae (97). Of the remainder, several families included in the checklist are considered little known. These tend to include members which are smaller than 10 mm, from deep water or from cryptic or parasitic habitats (e.g. living in sponges, or on echinoderms). The chitons, though few in number, are relatively well known, thus the diversity reported can be considered to be a reliable measure of the true diversity of this group.

The bivalve fauna has been less documented for the western Indian Ocean than the prosobranch fauna. Few detailed studies of bivalves exist and the checklist was compiled from only 30 sources compared to 72 used in preparing the prosobranch checklist. The most diverse families are the Veneridae with 101 species, Tellinidae (68) and Pectinidae (51).

The prosobranch molluscs described above have been studied intensively by numerous malacologists around the world over the last one hundred years. These studies, often in isolation, have resulted in confusing synonyms that plague a large proportion of the fauna, preventing regional comparisons from being made. Of those families that have been reviewed recently (e.g. Conidae, Cypraeidae, Cassidae, Littorinidae and Strombidae) the trend seems to be that most genera are widespread and smallscale endemism is apparent in areas of the Indo-Pacific.

For the western Indian Ocean, endemism varies between groups from 0–15%, some of which may be explained by larval dispersability and habitat. For example, Vermeij (1972, 1973a,b) found that many snails inhabiting the high intertidal zone have strikingly narrow geographical ranges compared to species lower down the shore. Citing examples from Kenya, Vermeij described how 6 of 13 species (46%) of snails found high on the limestone cliffs were restricted to the Indian Ocean while from the lower shore only one of 14 species was endemic to the Indian Ocean. A similar pattern was found in the northern Red Sea. Studies from Barbados, Hawaii and the Red Sea show that upper-shore gastropods exhibit a reduced planktonic phase or none at all and that the dispersal stage limits the spread of the species as a whole (Lewis, 1960; Kay, 1967). Vermeij (1978) also noted that the inshore gastropods adapted to harsh, sand-scoured shores in Brazil demonstrate more endemism than those of the less harsh lower shore or occurring under boulders. Whether a similar pattern exists in the western Indian Ocean remains to be determined.

Echinodermata

Echinoderm research in the Indo-Pacific region has benefited enormously from the comprehensive and invaluable monograph of Clark and Rowe (1971). Nevertheless, in a study of the fauna of the Seychelles, Clark (1984) found only 151 species and concluded

that "...it is clear that the echinoderm fauna of the western Indian Ocean is relatively limited in comparison to the rich fauna of the Malaysian/Indonesian area, having few characteristic species and only a small proportion of the widespread ones". Richmond (1999) demonstrated that this is no longer the case, reporting a total of 419 echinoderm species for the region, with over 100 species (25%) considered to be endemic and a large proportion of the fauna (53%) comprised of widespread Indo-Pacific species. Explanations for these observed patterns are associated with larval dispersal (across the Indian Ocean and along the northern shores), dispersal of adults on floating material and the presence of a widely distributed ancient fauna.

Since the publication of the monograph by Clark and Rowe (1971) to date, 156 new species records for the region—equivalent to an increase of 59%—have been documented. The increase in species diversity is not wholly surprising. A single study of Aldabra echinoderms (Sloan et al., 1979), only 10 years after the monograph data ceased to be collected, added 30 species to the records of the Seychelles. The increase of the known species over this period is also not exceptional to the western Indian Ocean. Pawson (1995) in a recent update of the echinoderm fauna of the Pacific islands found that the records of species diversity of that province had increased by 38%, largely attributed to the detailed work around the New Caledonia reefs by Guille et al. (1986). An increase in the known total number of species from southern China waters from 298 (Clark and Rowe, 1971) to 457 is shown by Liao and Clark (1995), resulting in an increase of 53%. Price (1982) demonstrated an increase in known species diversity for the Red Sea from the figure of 183 (Clark and Rowe, 1971) to 231, an increase of 26%.

In examining the overall diversity, direct comparisons of the western Indian Ocean fauna can be made with that of other provinces within or adjacent to the Indo-Pacific from where recent studies have been conducted. Table 2 shows that, as stated by Clark (1984), and many others, the Malay-Indonesia province is the richest as regards echinoderm diversity, though the western Indian Ocean fauna is by no means poor by comparison. Taxonomic uncertainties do exist with respect to the western Indian Ocean fauna, and further research is required to establish the true identity of a small component of the fauna.

Bryozoa

These small, often incrusting, colonial organisms have received scant attention from taxonomists in most parts of the world. The western Indian Ocean is no exception as Hayward and Yonow (1997) describe, despite these authors estimating that possibly 500 species occur in this region.

Asciadiacea

Ascidians, like bryozoans, contribute greatly to the marine diversity of shallow and deep seas, and similarly have been ignored by taxonomists. The widespread lack of ascidian taxonomic expertise is in part due to the difficulties associated with identification of a

Table 2. Echinoderm diversity for provinces within and adjacent to the Indo-Pacific

Families	Provinces							
	WIO ⁶	Southern Africa ¹	Arabian Sea ²	Red Sea ²	Malay-Indonesia ³	Northern Australia ³	China Japan ⁴	Pacific islands ⁵
Crinoidea	19	17	15	18	91	46	62	40
Asteroidea	58	99	51	29	108	102	78	105
Ophiuroidea	132	124	77	49	157	128	131	103
Echinoidea	62	59	45	48	89	70	85	90
Holothuroidea	148	108	45	80	161	114	101	114
Total	419	407	233	224	606	460	457	452

Sources: ¹Thandar (1989); ²Price (1982); ³Clark & Rowe (1971); ⁴Liao & Clark (1995); ⁵Pawson (1995); ⁶Richmond (1999).

large proportion of these organisms, and the absence of funding generally for a group considered, in the past, to be of little economic importance. Monniot (pers. commun.) noted that any estimates for this group are highly unreliable, as they are so little known from the western Indian Ocean.

Pisces

Fish, together with molluscs, are perhaps the best known marine taxa from the western Indian Ocean. Several comprehensive texts are dedicated to the taxonomy of this large and economically important group and the diversity present in the western Indian Ocean is well known. Most species are widely distributed throughout the Indo-Pacific, though the precise explanation for this pattern is not clear. Larval dispersal for example cannot account for the distribution of all species since the relationship between larval longevity is not supported by the observed distribution of adults (see Wellington and Victor, 1989; Thresher et al., 1989). For Hawaiian shorefish Randall (1995) reported 24.3% endemism and related the presence of some of the fauna to the geological history of the Pacific Plate rather than larval distribution.

Analysis of the reef fishes of the entire Indo-Pacific confirms that the Indo-Australian Archipelago is a 'center' of diversity with over 3000 species of shorefish (Carcasson, 1977; Lieske and Myers, 1994). They also found that within the western Indian Ocean, the Mascarene islands are characterised by a significant endemic element, and that species diversity in this region, although high, is less than that of the central Indo-Pacific. For example, Allen (1991) found that of the 268 known damselfish species (family Pomacentridae), 24 are endemic to the western Indian Ocean.

BIOGEOGRAPHY AND ENDEMISM

Richmond's (1997) summary found that of the 1500 fully aquatic taxa for which reliable distribution information could be ascertained, the majority (70%) occur at sites extending to the western Pacific Ocean (half of which occur beyond and into the central Pacific). Of

the total, 15% were found to be endemic to the western Indian Ocean. These figures indicate only a broad pattern since they represent only the most common and typical coastal species. Notwithstanding, this serves as a general estimate which compares with the findings from the few well studied taxa described above. Gosliner and Draheim (1996) took a similar approach. In considering levels of endemism of Hawaiian opisthobranchs, they regard the figure of 43% (of all species known to occur only in Hawaiian waters) to be less reliable than the estimate of 4% endemism derived from figures only for the larger, more conspicuous and better known species. The latter they regard as less likely to be overlooked.

Three phenomena affect almost all aspects of biogeography: sampling, dispersal and evolution (Williamson, 1988). With regard to the origins and geographical distribution of the western Indian Ocean marine taxa, discrepancies arising from regionally unequal sampling indicates that any figures and observed patterns should be interpreted with caution (Veron, 1995; Gosliner et al., 1996; Paulay, 1997). The resulting paucity of reliable distribution records for many invertebrate taxa continues to be an intrinsic problem for the study of biodiversity (Myers, 1996) and is still applicable to most parts of the tropics. For many taxa, discussions on biogeography and origin cannot be undertaken since so little is known. For example, an analysis of the Indo-Pacific opisthobranch gastropod biogeography by Gosliner and Draheim (1996) entitled in part "... how do we know what we don't know?" points out the lack of baseline data even from localities that were believed to be well known (Hawaii) from which they claim the known diversity of opisthobranchs has increased by 75% in the last 3 years alone. Similarly, Sheppard (1998) recommends that with respect to Indian Ocean corals, the taxonomy still requires considerable revision despite the substantial improvements achieved recently, a condition which may also apply to many other groups in the Indian Ocean.

An overall estimate for regional endemism of about 15% (as noted above) may prove realistic although further taxonomic and biogeographical work is required, not only within this region but also throughout the Indo-Pacific. A well-known Coelocanth (*Latimeria chalumnae* Smith, 1938) was considered endemic to the southwestern Indian Ocean (Smith and Heemstra, 1995) until the discovery in July 1998 of this species from 100–150m depth off north Sulawesi (Indonesia), 10,000km from its known population around the Comoros Islands (see Erdmann et al., 1998). This discovery has major biogeographical and conservation implications for the fish, but also serves as a clear reminder to biogeographers of the continued need to give observed biogeographic patterns only as much confidence as a knowledge of the sampling efforts invested in providing the data on which patterns are based.

SPECIES RICHNESS AND AREA SIZE

The subject of whether the central Indo-Pacific, encompassing the coastal waters of the Philippines, Indonesia and Papua New Guinea, should be considered the 'center and focus' from which other sub-regions of the Indo-Pacific have recruited species, as Ekman (1953) suggested, has been examined by many (e.g. Ladd, 1960; Taylor, 1971; Briggs, 1974; Abele, 1982; Kay, 1984; Rowe, 1985; Donaldson, 1985). A summary of these and other studies suggests that this region, undoubtedly the richest in species diversity, has achieved this condition by maintaining a rich biodiversity derived from a widespread, warm, Tethyan Sea biota which was present up to the Late Eocene, about 45 million years ago (Vermeij, 1978). Speciation in some taxa would certainly have occurred while additional taxa from neighbouring areas were also accumulated. An example of the former resulted from the drying of the Sunda Shelf in Indonesia during the Pleistocene period which effectively separated the Pacific from the Indian Ocean. This event promoted speciation in a number of mangrove-associated taxa which after the post-glacial sea-level rise contributed to enhance the diversity of these groups (Vermeij, 1978).

All other regions within the Indo-Pacific support less diversity. Examples of these less diverse areas include the central Pacific islands, the Red Sea and the western Indian Ocean, all of which demonstrate high levels of endemism. The development of marine biodiversity in these sub-provinces of the Indo-Pacific probably began with some of the widespread Tethyan biota. Subsequently, part of this taxa would have been lost during sea-level and other tectonic changes, while over time, additional species from the Malay-Indonesian region (which may have either existed since Tethyan times or developed subsequently) may have accumulated. Finally, these sub-provinces also developed their own unique biota through speciation.

The central Indo-Pacific region is characterised by thousands of islands of varying sizes and geology, a wide continental shelf and a rich diversity of coastal habitats. Geographical areas (provinces) defined in any study differ greatly in size, habitat diversity and extent, thus direct comparisons of diversity cannot be made. Abele (1982) demonstrated that the overall area of the four large tropical regions he examined (eastern Atlantic, western Atlantic, eastern Pacific and Indo-West Pacific) accounted for 98% of the variation in the number of crustacean species from these regions. He also found that shrimp species number in the West Indies was strongly related to the perimeter length of the islands.

While estimates of the coastal areas for the Indo-Pacific provinces considered for echinoderms in Table 2 may be difficult to obtain, coastline length data are given in Table 3, together with echinoderm species numbers for each of the provinces. Coastline length measurements for whole countries were mainly taken from Couper's (1989) *Times Atlas of the Oceans*, with portions of country coastlines forming part of provinces derived from estimates. Though these coastline length measurements may include an error of unknown dimension (but likely to be small, and equal to all data sets), they provide an opportunity to examine the presence of a relationship with echinoderm species

Table 3. Echinoderm species diversity and coastline length (km) for provinces within the Indo-Pacific

	WIO	E. Africa/ Madag.	WIO islands	Arabian Sea	Red Sea	Northern Australia	China Japan	Malay- Indonesia
Province codes	1	2	3	4	5	6	7	8
Species no.	419	373	215	191	224	460	457	606
Coastal length	11,612	10,754	858	6058	5730	12,800	18,844	89,654

Species number from Table 2; province coastline lengths based on Couper (1989) (see text); province codes relate to Figure 2.

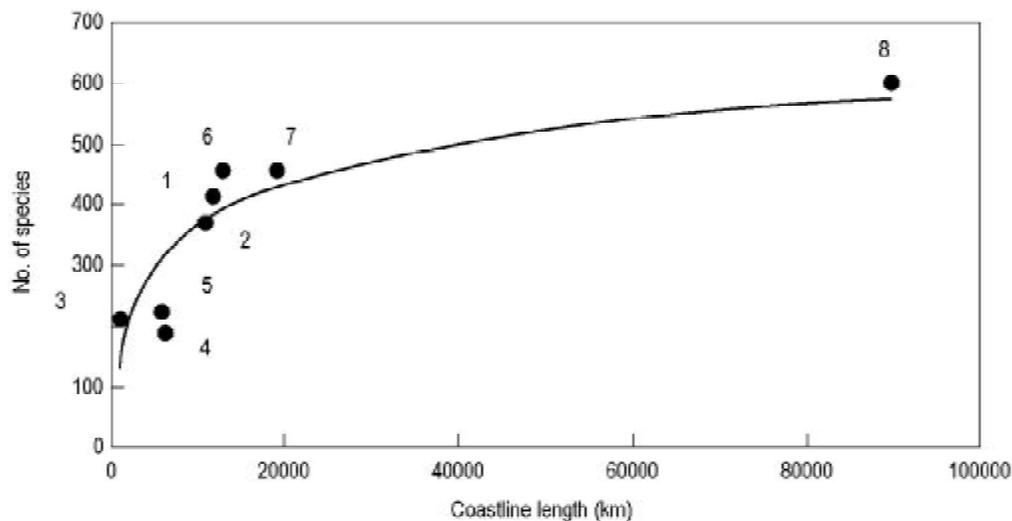


Figure 2. Echinoderm species number plotted against coastline length of Indo-Pacific provinces (see Table 3 for province codes)

number. A plot of these data against the number of species is shown in Figure 2. The relationship between coastline length and echinoderm species number is given by the formula $y = 97.062 \ln(x) - 523.21$, with $R^2 = 0.741$, indicating that species number is a strong function of coastline length.

Explanations for the relationship shown in Figure 2 between coastline length and species diversity are certain to include the influence that coastline length has on habitat heterogeneity which is known to strongly affect species diversity (Ricklefs, 1979; Williamson, 1988) and must itself be a function of length of coastline. However, certain coastlines in the Indian Ocean exist which are likely to fail to conform to the above. The western shores of India for example, though lengthy, are predominantly of fine sediments and prone to high freshwater influences, not suited to echinoderms.

To test the reliability of the relationship shown in Figure 2 more data are needed, especially within the coastline length ranges of 20,000–80,000km for which species diversity must also be ascertained. Although it cannot be concluded from the relationship derived from this brief analysis that echinoderm species diversity is simply a function of

the length of coastline sampled, the findings do indicate that further examination of this coastal perimeter effect may reveal interesting results.

REASONS FOR HIGH BIODIVERSITY

Differences between the biodiversity of the western Indian Ocean islands (Mascarenes and Seychelles) and that of the East Africa mainland and Madagascar are apparent. Particularly noticeable are the differences in the diversity of molluscs (and of echinoderms) and bivalves. From an analysis of the molluscan fauna of tropical continental and oceanic islands Kohn (1971) found a ratio of prosobranchs to bivalves of 2.2:1 for continental islands and 4.8:1 for oceanic islands, providing further evidence that in continental environments, a greater diversity and contribution of bivalves is manifest. Bivalves probably evolved in shallow, coastal, continental waters rich in suspended material (Salvat, 1967; Taylor, 1971) and their adaptive radiation into coral reef habitats has only been achieved by a few families involving relatively fewer genera (Morton, 1983). The echinoderm species diversity study by Richmond (1999) found that eastern Africa (including Madagascar) supported 373 species (with 81 endemics), while from the western Indian Ocean islands only 215 species (with 15 endemics) have to date been reported.

These differences are not surprising given the differences in the physical properties (size, geological history and location). Differences in habitat diversity and extent are also great. For example, the islands lack any significant development of mangrove forests and estuarine conditions common along parts of the mainland and Madagascar shores. The isolation of the islands (e.g. Mauritius and Réunion) however contributes to the overall diversity of the region by favouring speciation and endemism (see Barnes and Hughes, 1982). In addition, the presence of a mixed or boundary region off South Africa, contributes by providing an element of warm temperate taxa, thus increasing the biodiversity of the southwestern portion of the region. The remoteness of many of the smaller islands in the region from human habitation (and possible degradation as increasingly found on mainland shores) may also create reservoirs of intact communities and thus sources from which export of larvae to neighbouring degraded areas can take place.

FUTURE RESEARCH

The mangroves, seagrasses, macroalgae, scleractinian corals, the prosobranch molluscs and some of the bivalves, most of the decapod crustaceans, echinoderms and fish are taxonomic groups which can be considered to be reasonably well known. These account for about 75% of the total estimate of species of shallow-water taxa for the region (see Table 1). Even within these groups there remain areas under study, resolving taxonomic uncertainties and discovering new species. Among the remaining, lesser-known taxa, taxonomic and biogeographical studies will almost certainly reveal new species (or genera),

new records and progress towards resolving systematic ambiguities. During the work in preparing the guide book, previously undescribed species of macroalgae, Porifera, Octocoralia, Cirripedia, Amphipoda, Nudibranchia, Holothuria and Ascidiacea were found and have or are being described. At present, it is likely that any detailed study on marine invertebrate taxa in the western Indian Ocean will reveal new records for the region as well as new species.

Though much of the taxa present in the waters of this region is well documented, very little about the biology of the organisms, their reproductive needs, feeding habits, interactions with other species and role in the ecology of their habitats is understood. We also know that we are losing taxa through habitat destruction, pollution and climatic events such as the most recent 1998 El Niño-induced coral bleaching. Larger animals such as the dugong and several marine turtles are locally threatened with extinction. Taxonomy should not therefore be the focus of marine research by regional scientists. The science of taxonomy requires many years of experience, access to extensive taxonomic collections, type material and specialised literature, most of which are not present in the region. Funding for taxonomic research has suffered considerably in many countries which previously contributed greatly to taxonomic knowledge (e.g. France and the United Kingdom) with the result that globally there has been a reduction in this field of biology. Funding for such research in the western Indian Ocean is not likely to develop significantly. The focus of regional marine scientists should instead reflect the region's needs. More specifically the priorities should be to develop effective methodologies and policies to conserve the marine biodiversity which we are already aware of. Effective policies to ensure benefits from bioprospecting activities should also be initiated.

The encouragement of specialist taxonomists to visit the region and add to the knowledge and collections should nevertheless continue, thus furthering our biodiversity knowledge and updating the taxonomy of the flora and fauna. There is a need to continually revise species checklists for the region by making them widely available to specialists. A significant contribution to this process was initiated in late 1996 by the Kenya-Belgium Project which has been compiling a database for a number of taxonomic groups. Under the MASDEA - Marine Species Database for Eastern Africa project approximately 22,890 distribution records, and 10,160 taxon records are currently entered. There are additional 500 family-level records, all derived from over 230 literature references. Such a database will greatly assist in the dissemination of information and is being expanded to cover other taxa. The production of freely distributed reports is currently being undertaken by Sida (Swedish International Development Agency) for mangroves, seagrasses and corals, using CD formats. World or regional species checklists and distribution records are also now available on the Internet for some groups e.g. Indian Ocean macroalgae (University of California Berkeley) and freshwater and marine isopods of the world (Smithsonian Institution). Together, these sources will, with time, greatly assist in developing a more precise estimate of the marine biodiversity for the region.

ACKNOWLEDGEMENTS

This paper is derived from a PhD thesis submitted to the University of Wales, Bangor. For their support and encouragement during the various stages of this work I thank most heartily Dr David Jones of the School of Ocean Sciences and Dr Olof Linden of the Sida/SAREC Regional Program. Assistance with identification of polychaetes was provided by Mr J. Coppock and Dr A.S.Y. Mackie (Zoology Department, National Museum of Wales - Cardiff). The identification of parts of the mollusc collection made in Zanzibar were verified by staff at the Natural History Museum (London) and Dr G. Oliver (National Museum of Wales - Cardiff) who also assisted greatly with literature and advice. Echinoderm identifications were verified by Dr F. Rowe. Dr E. Vanden Berghe provided a copy of the MASDEA database which contributed especially to the compilation of the mollusc species checklist. To all these and others who assisted, I am extremely grateful.

REFERENCES

- Abbott, I.A. 1995. The state of systematics of marine algae in tropical island Pacific, pp. 25–38. In: Maragos, J.E., Peterson, M.N.A., Eldredge, L.G., Bardach, J.E. & Takeuchi, H.F. (eds) *Marine and Coastal Biodiversity in the Tropical Island Pacific Region. Vol. 1. Species Systematics and Information Management Priorities*. Honolulu, Hawaii: Program on Environment East-West Centre.
- Abele, L.G. 1982. Biogeography, pp. 242–305. In: Abele, L.G. (ed.) *The Biology of Crustacea, Volume 1. Systematics, the Fossil Record and Biogeography*. Academic Press.
- Allen, G. 1991. *Damselfishes of the World*. New York: Merges Publishers.
- Barnes, R.S.K. & Hughes, R.N. 1982. *An Introduction to Marine Ecology*. Oxford: Blackwell. 339pp.
- Branch, G.M., Griffiths, C.L., Branch, M.L. & Beckely, L.E. 1994. *Two Oceans. Guide to the Marine Life of Southern Africa*. David Philip. 340pp.
- Briggs, J.C. 1974. *Marine Zoogeography*. New York: McGraw Hill.
- Bruce, A.J. 1984. Marine caridean shrimps of the Seychelles, pp. 141–168. In: Stoddart, D.R. (ed.) *Biogeography and Ecology of the Seychelles Islands*. The Hague: Dr W Junk Publishers.
- Bruce, A.J. 1998. New keys for the identification of Indo-West Pacific coral associated pontonine shrimps, with observations on their ecology. *Ophelia* 49 (1): 29–46.
- Carcasson, R.H. 1977. *A Field Guide to the Coral Reef Fishes of the Indian and West Pacific Oceans*. London: Collins.
- Claparède, E. 1867. On the structure of the Annelida, including a critical examination of the most recent works on this class of worms. *Ann. Mag. nat. Hist. Ser. 3*, 20 (119): 337–361.
- Clark, A.M. 1984. Echinodermata of the Seychelles, pp. 83–103. In: Stoddart, D.R. (ed.) *Biogeography and Ecology of the Seychelles Islands*. The Hague: Dr W. Junk Publ.
- Clark, A.M. & Rowe F.W.E. 1971. *Monograph of Shallow-water Indo-West Pacific Echinoderms*. London: The British Museum (Natural History). 234pp.
- Coppejans, E., De Clerck, O., Leliaert, F. & Dargent, O. (this volume). Progress of the taxonomic research on macroalgae (Chlorophyta, Phaeophyta and Rhodophyta) along the East African coast (including Zanzibar). Conference on Advances in Marine Sciences in Tanzania. June 28–July 1, 1999, Zanzibar.

- Cornelius, P. 1997. Class Scyphozoa, pp. 122–125. In: Richmond, M.D. (ed.) *A Guide to the Seashores of Eastern Africa and the Western Indian Ocean Islands*. Sida/Department for Research Cooperation, SAREC. 448pp.
- Couper, A. 1989. *The Times Atlas and Encyclopaedia of the Ocean*. Times Books Ltd. /Guild Publishing. 272pp.
- Day, J.H. 1967. A Monograph of the Polychaeta of Southern Africa. Part 1. Errantia; Part 2: Sedentaria. London: Trustees of the British Museum (Natural History). 878pp.
- Donaldson, T.J. 1985. Distribution and species richness patterns of Indo-West Pacific Cirrhitidae: Support for Woodland's hypothesis. In: Yyeno, T., Arai, R., Tanischi, T. & Matsuura, K. (eds) *Indo-Pacific Fish Biology. Proceedings of the 2nd International Conference on Indo-Pacific Fishes*. Tokyo National Museum, Ueno Park, Tokyo, July 29–August 3.
- Ekman, S. 1953. *Zoogeography of the Sea*. Sidgwich & Jackson Ltd. 416pp.
- Erdmann, M.V., Caldwell, R.L. & Moosa, M.K. 1998. Indonesian 'king of the sea' discovered. *Nature* 396pp.335.
- Fauchald, K. 1977. *The Polychaete Worms. Definitions and Keys to the Orders, Families and Genera*. Natural History Museum of Los Angeles County/Allan Hancock Foundation, University of Southern California. 186pp.
- Fiege, D. 1992. Polychaeta of the intertidal zone in the Ras Az-Zawr-Marduma Bay region, pp. 171–186. In: Establishment of a Marine Habitat and Wildlife Sanctuary for the Gulf Region. Final Report for Phase I. Jubail & Frankfurt a.M.
- Gardiner, J.S. 1907. The Percy Sladen Trust Expedition to the Indian Ocean in 1905, under the leadership of Mr J. Stanely Gardiner, No. 9. Description of the expedition. *Trans. Linn. Soc. Lond.* (2) *Zool.* 12: 11–175.
- Gaston, K.J. & Williams, P.H. 1993. Mapping the world's species – the higher taxon approach. *Biodiversity Letters* 1: 2–8.
- Gaston, K.J. & Spicer, 1998. *Biodiversity: An Introduction*. Oxford: Blackwell Science, 113pp.
- Gosliner, T.M., Behrens, D.W. & Williams, G.C. 1996. *Coral Reef Animals of the Indo-Pacific*. California: Sea Challengers, Monterey. 314pp.
- Gosliner, T.M. & Draheim, R. 1996. Indo-Pacific opisthobranch gastropod biogeography: How do we know what we don't know? *Am. Malac. Bull.* 12 (1–2): 37–43.
- Guerreiro, J., Freitas, S., Pereira, P. & Paula, J. 1996. Sediment macrobenthos of mangrove flats at Inhaca Island, Mozambique. *Cah. Biol. Mar.* 37 (4): 309–327.
- Guille, A., Laboute, P. & Menou, J.L. 1986. *Guide des étoiles de mer, oursins et autres échinodermes du lagon de Nouvelle-Calédonie*. Éditions de l'ORSTOM. Institut Français de Recherche Scientifique pour le Développement en Coopération. 238pp.
- Hartnoll, R.G. 1975. The Grapsidae and Ocypodidae (Decapoda: Brachyura) of Tanzania. *J. Zool. Lond.* 177: 305–328.
- den Hartog, J.C. 1997. Sea anemones, pp. 134–139. In: Richmond, M.D. (ed.) *A Guide to the Seashores of Eastern Africa and the western Indian Ocean Islands*. Sida/Department for Research Cooperation, SAREC. 448pp.
- Hayward, P. & Yonow, N. 1997. Miscellaneous phyla, pp. 322–325. In: Richmond, M.D. (ed.) *A Guide to the Seashores of Eastern Africa and the Western Indian Ocean Islands*. Sida/Department for Research Cooperation, SAREC. 448pp.
- Hove, H.A.T. 1994. Serpulidae (Annelida: Polychaeta) from the Seychelles and Amirantes Islands, pp. 107–116. In: Land, J. van der (ed.) *Oceanic Reefs of the Seychelles*. Report on a cruise of RV *Tyro* to the Seychelles in 1992 and 1993. Netherlands Indian Ocean Programme. Cruise Reports Vol. 2. National Museum of National History, Leiden.
- Hughes, R.N. & Gamble, J.C. 1977. A quantitative survey of the biota of intertidal soft substrata on Aldabra Atoll, Indian Ocean. *Phil. Trans. R. Soc. Ser. B.* 279: 327–355.
- Kalk, M. (ed.) 1995. *A Natural History of Inhaca Island, Mozambique*. Johannesburg: Witwatersrand University Press. 395pp.

- Kay, E.A. 1967. The composition and relationship of marine molluscan fauna of the Hawaiian Islands. *Venus* 25: 94–104.
- Kay, E.A. 1984. Patterns of speciation in the Indo-West Pacific, pp. 15–31. In: Raven, P.H., Radovsky, F.J. & Sohmer, S.H. (eds) *Biogeography of the Tropical Pacific*. Honolulu: Association of Systematics Collections and the Bernice P. Bishop Museum.
- Kelly-Borges, M. 1997. Sponges, pp. 106–117. In: Richmond, M.D. (ed.) *A Guide to the Seashores of Eastern Africa and the western Indian Ocean Islands*. Sida/Department for Research Cooperation, SAREC. 448pp.
- Kelly-Borges, M. & DeFelice, R. (in press). Sponges on the floating docks and piers of Pearl Harbour, Hawaii: Taxonomic and biogeographical status.
- Knox, G.A. 1977. The role of polychaetes in benthic soft-bottom communities, pp. 547–604. In: Reish, D. & Fauchald, K. (eds) *Essays on Polychaetous Annelids. In Memory of Dr Olga Hartman*. The Allan Hancock Foundation, University of Southern California.
- Kohn, A.J. 1971. Diversity, utilization of resources, and adaptive radiation in shallow-water marine invertebrates of tropical oceanic islands. *Limnol. Oceanogr.* 16 (2): 332–348.
- Ladd, H.S. 1960. Origin of the Pacific island molluscan fauna. *Amer. J. Sci.* 258 A: 137–150.
- Ledoyer, M. 1982. Crustacés amphipodes gammariens familles des Acanthanozomatidea à Gammaridae. *Faune de Madagascar* 59: 1–598.
- Ledoyer, M. 1986. Crustacés amphipodes gammariens familles des Haustoriidae à Vitjazianidae. *Faune de Madagascar* 59: 599–1112.
- Lewis, J.B. 1960. The fauna of rocky shores of Barbados, West Indies. *Canad. J. Zool.* 38: 391–435.
- Liao, Y. & Clark, A.M. (eds) 1995. *The Echinoderms of Southern China*. Beijing, New York: Science Press. 614 pp. + 23 pts.
- Lieske, E. & Myers, R. 1994. *Coral Reef Fishes. Indo-Pacific and Caribbean*. Harper Collins Publishers. 400pp.
- Mackie, A.S.Y. 1996. Taxonomy and phylogeny of spioniform polychaetes (Annelida). Göteborg University PhD thesis. 32pp.
- Macnae, W. 1968. A general account of the flora and fauna of the mangrove swamps and forests of the Indo-West Pacific region. *Adv. Mar. Biol.* 6: 73–270.
- Macnae, W. & Kalk, M. 1958. *A Natural History of Inhaca Island, Mozambique*. Johannesburg: Witwatersrand University Press, 163pp.
- Millard, N.A.H. & Bouillon, J. 1973. Hydroids from the Seychelles. *Mus. Roy. d'Afrique Centrale Ser. In-8. No. 206*: 6–106.
- Millard, N.A.H. & Bouillon, J. 1975. Additional hydroids from the Seychelles. *Ann. S. Afr. Mus.* 69: 1–15.
- Morton, B. 1983. Coral-associated bivalves of the Indo-Pacific, pp. 139–224. In: Russell-Hunter, W.D. (ed.) *The Mollusca Vol. 6. Ecology*. Academic Press Inc.
- Myers, A.A. 1996. Species and generic gamma-scale diversity in shallow-water marine Amphipoda with particular reference to the Mediterranean. *J. mar. biol. Ass. U.K.* 76: 195–202.
- Myers, A.A. 1997. Biogeographic barriers and the development of marine biodiversity. *Est. Coast. Shelf Sci.* 44: 241–248.
- Paulay, G. 1997. Diversity and distribution of reef organisms, pp. 298–353. In: Birkeland, C.E. (ed.) *Life and Death of Coral Reefs*. New York: Chapman & Hall.
- Pawson, D.L. 1995. Echinoderms of the tropical island Pacific: Status of their systematics and notes on their ecology and biogeography, pp. 171–192. In: Maragos, J.E., Peterson, M.N.A., Eldredge, L.G., Bardach, J.E. & Takeuchi, H.F. (eds) *Marine and Coastal Biodiversity in the Tropical Island Pacific Region. Vol. 1. Species Systematics and Information Management Priorities*. Honolulu, Hawaii: Program on Environment East-West Centre.
- Phillips, R.C. & Meñez, E.G. 1988. Seagrasses. *Smithson. Contr. Mar. Sci.* 34: 104pp.

- Price, A.R.G. 1982. Echinoderms of Saudi Arabia. Comparison between echinoderm faunas of Arabian Sea, SE Arabia, Red Sea and Gulfs of Aqaba and Suez. *Fauna Saudi Arabia* 4: 3–21.
- Randall, J.E. 1995. Zoogeographic analysis of the inshore Hawaiian fish fauna, pp. 193–203. In: Maragos, J.E., Peterson, M.N.A., Eldredge, L.G., Bardach, J.E. & Takeuchi, H.F. (eds) *Marine and Coastal Biodiversity in the Tropical Island Pacific region. Vol. 1. Species Systematics and Information Management Priorities*. Honolulu, Hawaii: Program on Environment East-West Centre.
- Richmond, M.D. (ed.) 1997. *A Guide to the Seashores of Eastern Africa and the Western Indian Ocean Islands*. Sida/Department for Research Cooperation, SAREC. 448pp.
- Richmond, M.D. 1999. The Biodiversity and Biogeography of shallow-water flora and fauna of the western Indian Ocean with special reference to the Polychaeta, Mollusca and Echinodermata. PhD thesis. University of Wales - Bangor, School of Ocean Sciences. 235pp.
- Ricklefs, R.E. 1979. *Ecology*. New York: Chiron Press.
- Riegl, B. 1995. Description of four new species of hard coral genus *Acropora* Oken, 1815 (Scleractinia: Astrocoeniina: Acroporidae) from south-east Africa. *Zool. J. Linn. Soc.* 113: 229–247.
- Rosen, B.R. 1971. The distribution of reef coral genera in the Red Sea and Indian Ocean, pp. 263–300. In: Stoddart, D.R. & Young, M. (eds) *Regional Variation in Indian Ocean Coral Reefs. Symp. Zool. Soc. Lond.* 28: 584pp.
- Rowe, F.W.E. 1985. Preliminary analysis of distribution patterns of Australia's non endemic, tropical echinoderms. In: Keegan, B.F. & O'Connor, B.D.S. (eds) *Echinodermata*. Rotterdam: A.A. Balkema.
- Roy, K., Jablonski, D. & Valentine, J.W. 1996. Higher taxa in biodiversity studies: Patterns from eastern Pacific marine molluscs. *Phil. Trans. Roy. Soc. Lond. Ser. B* 351: 1605–1613.
- Salm, R. 1995. Marine biodiversity of the western Indian Ocean: Status and conservation framework, pp. 101–130. In: Linden, O. (ed.) *Workshop and Policy Conference on Integrated Coastal Zone Management in Eastern Africa including the Island States. C.M.C. Conference Proceedings*. 371pp. Metro Manila, Philippines.
- Salvat, B. 1967. Importance de la faune malacologique dans les atolls Polynésiens. *Cah. Pac.* 11: 7–49.
- Schleyer, M. 1997a. Subclass Octocorallia, pp. 128–133. In: Richmond, M.D. (ed.) *A Guide to the Seashores of Eastern Africa and the Western Indian Ocean Islands*. Sida/Department for Research Cooperation, SAREC. 448pp.
- Schleyer, M. 1997b. Order Scleractinia, pp. 140–153. In: Richmond, M.D. (ed.) *A Guide to the Seashores of Eastern Africa and the western Indian Ocean Islands*. Sida/Department for Research Cooperation, SAREC. 448pp.
- Sheppard, C.R.C. 1987. Coral species of the Indian Ocean and adjacent seas: A synonymised compilation and some regional distribution patterns. *Atoll Res. Bull.* 307: 1–32.
- Sheppard, C.R.C. 1998. Biodiversity patterns in Indian Ocean corals, and effects of taxonomic error in data. *Biodiv. Conserv.* 7: 22pp.
- Silva, P.C., Basson, P.W. & Moe, R.L. 1996. Catalogue of benthic marine algae of the Indian Ocean. University of California, Publications in Botany, 79. Univ. California. 1259pp. (also, Internet website: <http://ucjeps.herb.berkeley.edu/rlmoe/tioc/ioctoc.html>).
- Sloan, N.A., Clark, A.M. & Taylor, J.D. 1979. The echinoderms of Aldabra and their habitats. *Bull. Br. Mus. (Nat. Hist.) Zool.* 37 (2): 81–128.
- Smith, M.M. & Heemstra, P.C. (eds) 1995. *Smith's Sea Fishes*. Johannesburg: Southern Book Publishers. 1047 pp.
- Taylor, J.D. 1971. Intertidal zonation at Aldabra Atoll. *Phil. Trans. Roy. Soc. Lond. B.* 260: 173–213.

- Thandar, A.S. 1989. Zoogeography of the southern African echinoderm fauna. *S. Afr. Tydskr. Dierk.* 24 (4): 311–313.
- Thresher, R.E., Colin, P.L. & Bell, L.J. 1989. Planktonic duration, distribution and population structure of western and central Pacific damselfishes (Pomacentridae). *Copeia* 2: 420–434.
- van Soest, R.W.M. 1994. Demosponge distribution patterns, pp. 213–223. In: van Soest, R.W.M., van Kempen, Th. M.G. & Braekman, J.C. (eds) *Sponges in Time and Space*. Rotterdam: Balkema.
- Vermeij, G. 1972. Endemism and environment: Some shore molluscs of the tropical Atlantic. *Amer. Nat.* 106: 89–101.
- Vermeij, G. 1973a. West Indian molluscan communities in rocky intertidal zone: A morphological approach. *Bull. Mar. Sci.* 23: 351–386.
- Vermeij, G. 1973b. Molluscs in mangrove swamps: Physiognomy, diversity and regional differences. *Syst. Zool.* 22: 609–624.
- Vermeij, G. 1978. *Biogeography and Adaptation. Patterns of Marine Life*. Harvard Univ. Press. 332pp.
- Veron, J.E.N. 1995. *Corals in Time and Space*. Cambridge University Press.
- Wellington, G.M. & Victor, B.C. 1989. Planktonic larval duration of one hundred species of Pacific and Atlantic damselfish (Pomacentridae). *Mar. Biol.* 101: 557–567.
- Williams, P.H. & Humphries, C.J. 1996. Comparing character diversity among biotas, pp. 54–76. In: Gaston, K.J. (ed.) *Biodiversity: A Biology of Numbers and Differences*. Oxford: Blackwell Science.
- Williamson, M. 1988. Relationship of species number to area, disturbance and other variables, pp. 91–115. In: Myers, A.A. & Giller, P.S. (eds) *Analytical Biogeography*. Chapman & Hall.

