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ORIGINAL ARTICLE

Zoogeography of the shallow-water holothuroids of the western Indian Ocean

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ABSTRACT

Aim To analyse the zoogeography of the shallow-water holothuroids of the western Indian Ocean (WIO). Based on this analysis we ask to what extent differences in species' ability to disperse across potential barriers provide an explanation for holothuroid zoogeography.

Location Shallow-waters (50 m isobaths) of the WIO, extending from Suez to Cape Town and from the coastline of East Africa upward to 65° E.

Methods Data for the analysis were obtained from Samyn's (2003) monograph on the shallow-water sea cucumbers of the WIO. A species presence/absence matrix with a resolution of 1° latitude/longitude was constructed. These cells were assigned to eight coarser operational geographical units, which were delimited on the basis of published faunistic and geological borders. The analytical zoogeographical methods employed were cluster analysis on several β-diversity coefficients and parsimony analyses of endemicity. The influence of life-history strategies on the distribution pattern was analysed through examination of latitudinal and longitudinal gradients, and by plotting cumulative curves for species number against range size.

Results The shallow-water holothuroid fauna of the WIO can be split into several biogeographical units. To the north, we found evidence that the northern Red Sea holothuroid fauna differs from that of the southern Red Sea. The latter has closest affinity with south-east Arabia and the Persian Gulf, and thus the biogeographical barrier of Bab-el-Mandab nowadays seems to be of minor importance. The cold upwelling at the east coast of Somalia forms an effective barrier for holothuroids and especially those with lecitothrophic (short-lived) larvae. Even though the circumtropical biogeographical pattern is not well resolved, important taxonomic turnovers suggest that it is composed of several distinct subprovinces. Taxonomic turnover is at least partially dictated by the dispersion capacity of the different orders.

Main conclusions This study concludes that the WIO is best split into at least three biogeographical realms: (1) the Red Sea and associated Arab Basin, (2) the asymmetrical circumtropical region stretching from the horn of Africa to southern Mozambique, and (3) southern Africa. Conspicuous differences in dispersal abilities of the three dominant orders are identified. The biogeography of the WIO is best explained by: (1) species' dispersion ability, (2) the prevalent current patterns, and (3) to a lesser, geographically limited extent, recent geological history. As a serendipitous discovery, we found that Rapoport's rule does not hold in the WIO.

Keywords

Beta diversity, dispersion capacity, diversity gradients, Echinodermata, gamma diversity, Holothuroidea, parsimony analyses of endemicity, western Indian Ocean.

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INTRODUCTION

For several centuries, shallow-water holothuroids (mainly those belonging to the order Aspidochirotida Grube, 1840) have been fished to feed the sea cucumber or *beche-de-mer* trade in the Far East (Conand & Byrne, 1993; Conand, 1997, 1998a,b, 2001; Marshall *et al.*, 2001). The last decades, driven by the ever-increasing market demand, have witnessed relentless overharvesting, which to some extent has shifted to countries of the western Indian Ocean (WIO) (Samyn, 2000; Marshall *et al.*, 2001). Although biologists are only just beginning to grasp the functional roles of these invertebrates, they fear that the present rate of exploitation might cross critical thresholds, with knock-on effects for these ecosystems. Conservationists urge control and regulation of holothuroid fisheries, but their efforts are bound to fail due to a lack of qualitative and quantitative measurements of the biodiversity of this non-charismatic taxon. Until recently, this lack of information applied especially to the tropical east coast of Africa, for which only a handful of taxonomic and/or faunistic publications have appeared during the last two decades (Clark, 1984; Cherbonnier, 1988; Arakaki & Fagoonee, 1996; Rowe & Richmond, 1997). Our team has, in recent years, sampled intensively along the tropical coasts of Kenya and Pemba Island (Tanzania) and along the subtropical coast of KwaZulu-Natal (Republic of South Africa). As a result, we were able to re-evaluate local faunas (Samyn & Vanden Berghe, 2000; Samyn, 2000, 2003; Bolton *et al.*, 2001; Samyn & Thandar, 2003a,b; Thandar & Samyn, 2004a), describe several new taxa (Massin *et al.*, 1999, 2004; Samyn *et al.*, 2001; Samyn & Thandar, 2003a,b), revise some supraspecific taxa (Samyn & Massin, 2003; Massin *et al.*, 2004; Thandar & Samyn, 2004b) and detail some of the patterns of nested relationships among certain clades (Kerr *et al.*, 2005; Samyn *et al.*, in press). An analysis of the large-scale patterns of holothuroid species richness has, however, never been performed in the WIO. As convincingly argued elsewhere (e.g. O'Hara & Poore, 2000; Purvis & Hector, 2000), insight into this component of biodiversity can greatly enhance our understanding of the history of regional biota, can put ecological studies into their regional biogeographical context, and can provide a potential framework for future conservation initiatives. The present study is the first attempt to analyse the distribution of the shallow-water holothuroids of the WIO. The spadework for this analysis was laid down in the monograph of Samyn (2003), which is here transformed into a presence/absence data set for several *a priori* defined operational geographical units (OGUs).

The overall aim of our research is to determine the zoogeography of the shallow-water holothuroids of the WIO, and to evaluate the hypothesis that dispersion capacity is one of the main driving forces behind the retrieved zoogeographical pattern. As such analysis involves investigating the latitudinal ranges of species, we also were in the position to evaluate the validity of Rapoport's rule that dictates that the higher species richness of the tropics is linked with the smaller range size of the species inhabiting these latitudes.

GEOLOGY AND OCEANOGRAPHY OF THE WESTERN INDIAN OCEAN

It is well documented that the Indian Ocean was formed some 185–180 Ma by the Ferrar volcanism along the coast of present southern Mozambique (Courtillot *et al.*, 1999). This volcanism caused the drifting away of Australia and Antarctica to the east and south, respectively, while Africa (still linked with Madagascar, the Seychelles and India) moved north. By the late Cretaceous (*c.* 95 Ma), spreading in the Mascarene Basin pushed India (still linked with the Seychelles) rapidly (15 cm year^{-1}) to the north, leaving Madagascar behind. Later (60–65 Ma), India drifted apart from the Seychelles. The latter have since then retained their position. The pre-Cambrian granitic boulders of the northern islands evidence the historical association of the Seychelles with Africa. On the other hand, the southern Seychelles are made of fossilized coral of much younger Pleistocene origin (1.65 million to 10,000 years old); these are placed on top of the once active volcanoes of the Réunion plume. The more eastern islands of the WIO (La Réunion, Mauritius and Rodriguez Island; all placed on the Mascarene Ridge) also owe their existence to such relatively young (*c.* 15 Ma up to the present day for La Réunion) volcanic activity. Here again, the tops of the (by now) submerged volcanoes are covered with Pleistocene coralline sediments. Similar volcanic activity took place in the Mozambique Channel (*c.* 15 Ma) and formed the Comoros Islands (Mayotte being the oldest).

Yet another geological origin is suggested for the three main islands that fringe the Tanzanian coast (Pemba Island, Zanzibar and Mafia Island). Pemba Island, surrounded by relatively deep water (>200 m), is believed to have broken away from the continent through seafloor spreading in the Pemba rift some 10 Ma. Zanzibar and Mafia Island on the other hand are thought to be Pleistocene inshore reefs that are now separated from the mainland by shallow (<50 m) waters.

The geological origin of the Red Sea (and afterwards the Gulf of Aden) nowadays is interpreted in terms of two distinct phases of seafloor spreading (one between 30 and 15 Ma and one that continues to occur since *c.* 5 Ma) along the East African rift (Omar & Steckler, 1995; Courtillot *et al.*, 1999). The northern part of the Red Sea holds the Gulf of Suez and the Gulf of Aqaba; the former is recognized as an abandoned rift basin with <100-m water depths, while the latter is a young (spreading since 5 Ma), rapidly subsiding wrench basin with maximum water depth of 1850 m. The Persian Gulf is a sedimentary basin with shallow water (depth on average only some 30 m); it is thought to be a remnant of the Tethys Sea.

The reality of the Pleistocene, with its glaciations, significant land rises and lowering of the sea level [according to some recent calculations, *c.* 20,000 yr bp the sea level was some 130 m lower than present day (Cutler *et al.*, 2003; see also Sidall *et al.*, 2003)], thus readily explains the occurrence of

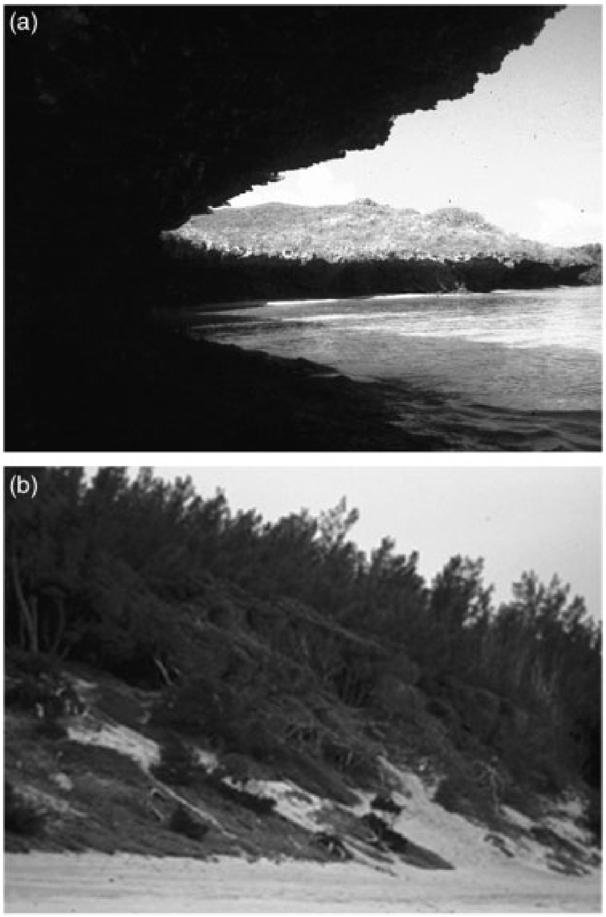

Figure 1 (a) Fossilized coral deposits of Pleistocene origin undercut by wave action can be found along large parts of the East African coastline (here at the Kiunga Reserve in northern Kenya); (b) south of the Zambezi Estuary the coastline forms vast stretches of sand beaches that are fringed by high dunes (here Sodwana Bay in South Africa).

fossilized coral reefs along most of the African continental shelf (Fig. 1a). In the Southern Hemisphere, at the mouth of the Zambezi river (Mozambique), that pattern is brusquely disrupted. While north of the Zambezi estuary the general settings are very similar to those of tropical East Africa, south of that point the coastline consists of low coastal plains that form vast sand beaches and dunes (Fig. 1b). South of the Zambezi estuary, coral growth is severely inhibited by the vast amounts of sediments discharged by the Zambezi River.

Coral outcrops (patch reefs) re-appear in southern Mozambique and more or less flourish around Inhaca and the northern parts of KwaZulu-Natal (South Africa). Still, it must be stressed that the coral growth around this region is limited and is not built on top of Pleistocene coralline deposits. As such, these deposits are best seen as sabellariid reefs rather than as true coral reefs. In the Northern Hemisphere, Pleistocene coralline deposits, and coral growth in general, are absent in the 1000 km of Somalian coastline south of Soccotra. Here, the seasonal cold upwelling during the south-east monsoon obstructs coral growth and reef formation (Glynn, 1993; Kemp, 1998).

The eustatic sea level changes in the Pleistocene are generally assumed to have had a major impact on the distribution of marine organisms (e.g. Adey & Steneck, 2001). For instance, it is believed that the Pleistocene drop in sea level emptied the very shallow Persian Gulf completely (Price, 1982 and references therein) and that today's Persian Gulf biota comprises obligate post-Pleistocene immigrants from the larger Indo-Pacific or recently evolved species. Similarly, the shallow (*c.* 137 m) and narrow (*c.* 18 km) passage to the Red Sea (Bab-el-Mandab) is thought to have dried up (Price, 1982; Kemp, 1998), or become very shallow (*c.* 15 m) during the last glacial maximum (Sirocko, 2003). Because this sea level drop at the very least severely restricted the amount of surface water flowing into the Red Sea, the possibility of active speciation within the Red Sea is strong.

Next to the geological processes, past and present oceanic current patterns (see Fig. 2) are undoubtedly worthy of attention when it comes to the distribution of marine organisms with free-living larvae, such as holothuroids. These current patterns are known to be under the influence of the prevailing, monsoon-dependent, wind patterns, the morphology of the continental shelf, and the Coriolis force (McClanahan, 1988). Flowing westward across the Indian Ocean, the South Equatorial Current (SEC), splits at the east coast of Madagascar at roughly 20° S (DiMarco *et al.*, 2002).

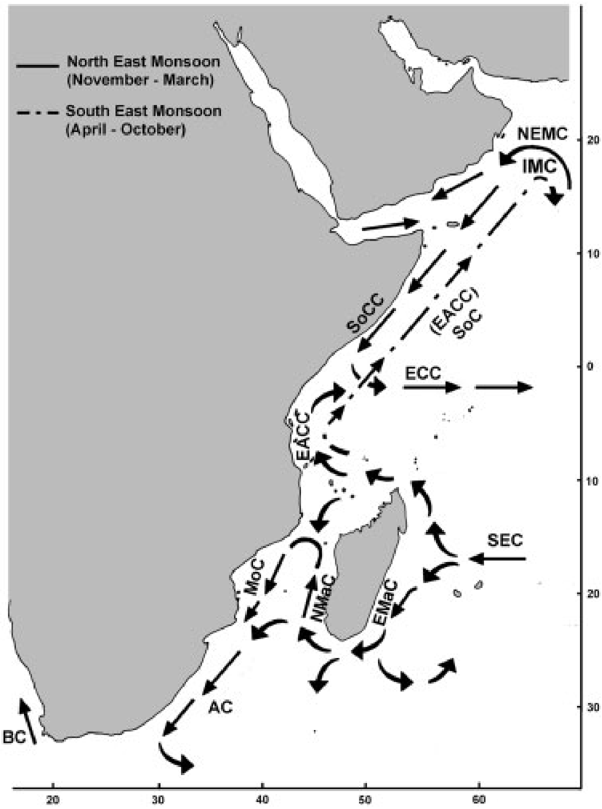

Figure 2 Prevailing currents in the western Indian Ocean (for abbreviations of the currents see Appendix 1). Position and temporal course of the currents were gathered from McClanahan (1988) and DiMarco *et al.* (2002).

The northern branch follows the east Madagascar coast until a westward turn at the northern tip of Madagascar occurs. The current then bifurcates again, roughly at the Comoros Islands, with one limb going north to form the East African Coastal Current (EACC) and the other south to form the Mozambique Current (MoC). The southern branch of the SEC, the East Madagascar Current (EMaC), flows along the east coast of Madagascar up to the most southern point of the island where it turns westward and possibly even northward into the Mozambique Channel, especially during the austral summer, forming the North Madagascar Current (NMaC). DiMarco *et al.* (2002) report that the acceleration of the narrow EMaC along the steep continental slope induces upwelling inshore, particularly at the southern end of Madagascar where the shelf widens. The NMaC retroflects anticlockwise in the Mozambique Channel and eventually fuses with the MoC. Near the border of KwaZulu-Natal (*c.* 27° S) the MoC converges with the remainder of the EMaC and forms the Agulhas Current (AC). This southbound current washes the east shores of southern Africa up to Cape Agulhas (*c.* 36° S) where it retroflects towards the Indian Ocean. The AC flows with a high-velocity and with a strong stability in its trajectory brought about by the very narrow and steep continental shelf along the east coast of southern Africa (Lutjeharms *et al.*, 2000). Between Cape Agulhas and the Cape Peninsula, the interaction of the AC and the cold Benguela Current (BC), sweeping the west coast of South Africa, and the prevailing trade winds cause important upwellings that result in important temperature fluctuations. In the northern part of the WIO the monsoonal regimes largely dictate the prevailing current patterns. During the south-east monsoon (April to October), the northwards flowing EACC flows along the Somali coast (forming the Somali Current; SoC) with a high velocity; it leaves the continent at the Gulf of Aden and passes South Arabia before joining the eastbound Indian Monsoon Current (IMC). During that time, increasing offshore winds north of the equator cause cold-water upwellings along the eastern of Somalia, with water temperatures as low as 13 °C (Currie *et al.*, 1973 in Kemp, 1998). During the north-east monsoon (from November to March), the north-east Monsoon Current (NEMC) flows westward across the Arabian Sea, from India to southern Arabia. The northern winds of the north-east monsoon slow the northerly water movement of the SoC and eventually reverse it, forming the Somali Counter Current (SoCC), which leaves the continent approximately at Malindi in Kenya (*c.* 4° S). It is roughly at the latter location that the SoCC joins the EACC and that the east flowing Equatorial Counter Current (ECC) is generated. This is accompanied by an upwelling at the northern Kenyan coast.

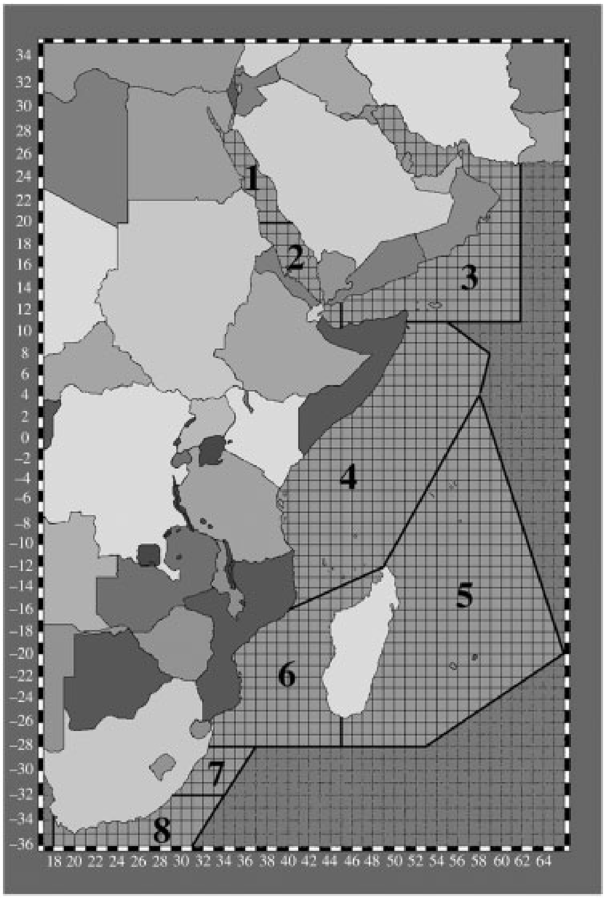

Figure 3 The western Indian Ocean (WIO), with the demarcation of the operational geographical units (OGUs). (1) Northern Red Sea (NRS) inclusive of the Gulfs of Suez and Aqaba, bounded at 20° N; (2) southern Red Sea (SRS), delimited to the east at 45° E; (3) Arab Basin (AB), inclusive of the Gulf of Aden, the Island of Soccotra and the Persian Gulf, bounded to the south at 11° N and to the east by the boundary between Iran and Pakistan; (4) Somali Basin (SB), inclusive of the Comoros Archipelago, bounded to the north-east by the Carlsberg ridge, to the south by the Comoros and to the south-west by Madagascar; (5) Mascarene Plateau (MP), bounded to the south at 28° S; (6) Mozambique Channel (MC), bounded to the south at 28° S; (7) Natal Province (NP), subtropical area delimited to the south at 32° S; (8) Cape Province (CP), delimited to the west at the Cape. The gridded cells are one longitudinal degree wide and one latitudinal degree long (*c.* 12,500 km^2 each); the shaded cells represent cells that fall outside our OGU definition; no records were scored in these cells. OGUs were defined by using published faunistic borders (Thandar, 1989; Kemp, 1998; Procheş & Marshall, 2002; Samyn & Thandar, 2003a,b) and tectonic ridges (Santini & Winterbottom, 2002).

MATERIALS AND METHODS

Study area

The WIO is here defined as the area ranging from Suez to Cape Town and from the coastline of East Africa eastwards to 65° E.

In order to describe the faunistics of this area in a standardized way, it was divided into cells of 1° latitude and longitude (Fig. 3). These cells were simultaneously assigned to eight coarser OGUs (terminology from De Grave, 2001), which were defined by published faunistic borders [Thandar, 1989 on the marine zoogeographical provinces of southern African (echinoderms); Kemp, 1998 on the zoogeography of the Red Sea/Gulf of Aden/North West Indian Ocean (chaetodontid fish); Procheş & Marshall, 2002 on the zoogeography of southern African intertidal Acari; Samyn & Thandar, 2003a,b on the delimatation of KwaZulu-Natal (North East South Africa) as the transition zone between temperate and tropical shallow-water echinoderms] and tectonic ridges (Santini & Winterbottom, 2002 defining these for the study of the zoogeography of Indo-western Pacific coral reef biota).

Data acquisition

Shallow-water (i.e. not deeper than the 50 m isobaths) holothuroid distribution data for the WIO were obtained from the monograph of Samyn (2003), and the distributions were transformed into a presence/absence data set for each OGU and for each 1° latitude/longitude cell. Uncertain species, as flagged by the above author were omitted from the analyses. As already noted by Samyn (2003), some records are so broadly defined in terms of location (e.g. location given as 'Red Sea') that they cannot be attributed to discrete 1° latitude/longitude cells. For such records we constructed one or several aggregation cells in each OGU; these conglomerate cells were only used in the 'coarse grain' (inter-OGU relationships) analyses, whereas in the 'fine-grain' (at the level of the 1° cells) analyses they were discarded. The resulting data set holds 235 species that belong to 63 genera, 12 families and four orders. Distribution records cover a total of 117 1° cells (eight of which being aggregation cells) (see Appendix S1 in Supplementary Material for complete data set).

Zoogeographical analyses

The shallow-water biotas of the WIO are generally believed to belong to the tropical Indo-West Pacific biogeographical province and to the South African Province (Briggs, 1974; Adey & Steneck, 2001). The zoogeographical value and the relation between the eight *a priori* selected OGUs were tested by performing hierarchical cluster analyses with several β-diversity coefficients as well as with parsimony analyses of endemicity (PAE) (Rosen, 1988). The utilized β-diversity coefficients are the Dice or Sorensen, the Jaccard and the first and second Kulczynski similarity coefficients (see Price, 1982; Magurran, 1988; Thandar & Samyn, 2004a for details). PAE was run under the heuristic search algorithm (10^6 replicates), using PAUP* (Swofford, 2002). By adding a hypothetical OGU outgroup – with all species coded as absent, implying that all cells were initially empty (Lundberg rooting) and that presences are new arrivals or new speciations – we were able to deduce historical OGU-relationships and make inferences on the direction of colonizations. As explained by Cracraft (1991; see also De Grave, 2001) this assumptive scenario is the only possibility when no fossil record is available. The robustness of the nodes in the PAE topology was investigated by bootstrapping with replicates encompassing 1000 data sets and with Bremer support indices (i.e. the number of additional records needed to collapse an internal branch). We applied Wagner and Dollo parsimony to the data set; the first allows the analysis to run unordered (taxa are allowed to colonize an OGU, disappear and re-colonize as many times as necessary), the second orders the colonization events (taxa can colonize an OGU only once, but can be lost independently in each OGU). As explained by De Grave (2001), Wagner parsimony thus allows inferences on long-distance dispersion, whilst Dollo-dispersion can only handle short-distance dispersion.

Understanding the zoogeographical provinces

As the dominant families in the present data set have different life-history strategies, we investigated if these reflect the observed zoogeographical pattern. Thorson (1950) recognized three major patterns of larval development in marine benthic invertebrates: planktotrophic, lecithotrophic and brooding. Many workers continue to use this simple division (e.g. Jeffery & Emlet, 2003), even though recently several refinements have been proposed to recognize and classify the bewildering diversity of larval and life-cycle patterns in echinoderms (e.g. McEdward & Janies, 1997; McEdward & Miner, 2001; Poulin *et al.*, 2001). Common to all these workers is the recognition that embryological as well as ecological components must be combined to arrive at a meaningful integrated picture. Thus, recently, matrices that sum up the above two components have become available, *albeit* for species that predominantly are absent in our data set. Table 1 represents an extrapolation of the data presented by McEdward & Miner (2001).

From this overview, it is clear that, until data become available for the species in our data set, the most meaningful criterion to be used is whether or not development is direct or indirect, that is with or without an auricularia larva. Species belonging to the aspidochirotid families Holothuriidae Ludwig, 1894 and Stichopodidae Haeckel, 1896 and to the apodid family Synaptidae Burmeister, 1837 typically have indirect development. Hereby the gastrula first develops into an auricularia, which undergoes metamorphosis to the doliolaria stage before settlement (Smiley *et al.*, 1991; Sewell & McEuen, 2002). On the other hand, species belonging to the dendrochirotid families and the apodid family Chiridotidae Oestergren, 1898 typically undergo direct development whereby the gastrula develops directly into the doliolaria larva (i.e. there is no auricularia stage) (Smiley *et al.*, 1991; Sewell & McEuen, 2002). Obviously, such raw division is a gross simplification of developmental diversity, but as long as no accurate additional data are available for all the species in our data set, we believe it is the most accurate approximation we can get.

We analysed the role of these two opposing life histories by determining the dispersion capacity of the three dominant orders and of the two opposing life-history strategies. This was done by constructing cumulative curves for species number against range size, the latter expressed as the number of cells within a species' extent of occurrence (Roberts *et al.*, 2002). If life history (and therefore dispersion capacity) is indeed ruling the zoogeography, then it should, at least partially, reflect the

Table 1 Overview of developmental patterns and larval type(s) as presented by the families in the data set (after McEdward & Miner, 2001)

	Developmental pattern			
Order and family	Morphogenesis	Nutrition	Habitat	Larval type(s)
Apodida				
Synaptidae	Indirect	Planktotrophic	Planctonic	Auricularia, doliolaria
Chiridotidae	Direct	Lecithotrophic	Benthic	Doliolaria, if auricularia present then reduced
Aspidochirotida				
Holothuriidae	Indirect	Planktotrophic	Planctonic	Auricularia, doliolaria
Stichopodidae	Indirect	Planktotrophic	Planctonic	Auricularia, doliolaria
Dendrochirotida				
Cucumariidae	? Direct	? Lecithotrophic	? Benthic	? Doliolaria and/or vitellaria
Phyllophoridae	? Direct	? Lecithotrophic	? Benthic	? Vitellaria
Psolidae	? Direct	? Lecithotrophic	? Benthic	? Doliolaria only
Rhopalodinidae	?	?	?	?
Sclerodactylidae	? Direct	? Lecithotrophic	?	?

species turnover as observed across latitudinal and longitudinal gradients. We also investigated how the taxonomic composition (at the level of the order) behaves across latitudes and longitudes. Moreover, we examined how the different orders contribute to each OGU by relating the total species richness to the number of species within each order. By calculating the bootstrapped 95% confidence limits (as computed by random allocation of each order to local sites from the total WIO species pool) we determined if the contributions of each order to each OGU falls within the bounds of what is predictable were the WIO a homogeneous region (see also Bellwood & Hughes, 2001).

RESULTS

Describing biodiversity

Of Samyn's (2003) data set, 235 species – belonging to 63 genera, 12 families and four orders – were analysed. In total, 117 1° cells (thus nearly 1.5×10^6 km^2) in the study region contained holothuroid species. We assessed the completeness of this data set by constructing a species accumulation curve for the WIO (Fig. 4). The absence of an asymptote shows that with each additional sampling expedition new records continue to be found, although the velocity of discovery is diminishing. The punctuated leap of species numbers in the late 1980s is best seen as a more gradual accumulation of species, because this punctuated leap corresponds with Cherbonnier's (1988) monograph on Malagasy holothuroids, a major work that spans more than a century of sampling. The last additions can largely be credited to *de novo* sampling in Kenya and KwaZulu-Natal. The success of the last additions undoubtedly is related to our use of SCUBA gear (see also Thandar & Samyn, 2004a).

Species richness across cells is so patchy that a pattern can hardly be discerned. The Red Sea (with the majority of available cells not investigated), tropical East Africa (Kenya, northern Tanzania, the Seychelles and northern Mozambique), relatively isolated parts of Madagascar (Nosy Be, Tuléar and to a lesser extent Fort Dauphin), Mauritius and subtropical south-east Africa (KwaZulu-Natal and the Cape) can be called rich in species; south-east Arabia (including the Persian Gulf), the Gulf of Aden, the Somali coast, the central coast of Mozambique and large parts of eastern south Africa appear to be species poor.

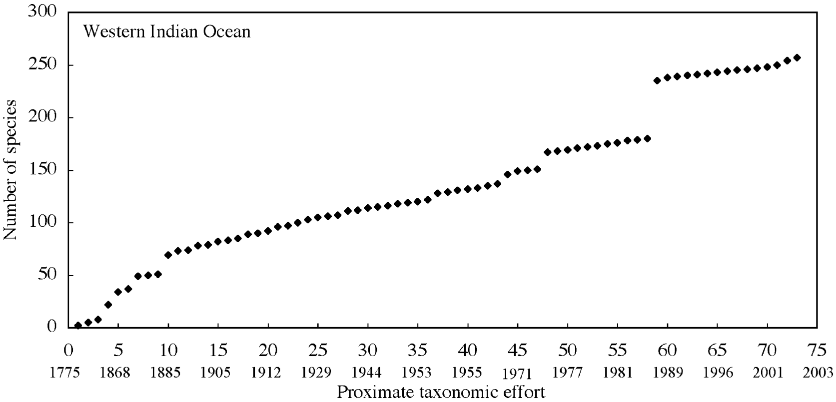

Figure 4 Species accumulation curves for the complete WIO based on holothuroid publications. Proximate taxonomic effort is ordered chronologically whereby the publication date of each fifth paper is also indicated (note that the series is approximately linear in regard to effort and not in regard to publication date).

Zoogeography

Clustering with the Dice (or Sorensen), the Jaccard and the first Kulczynski coefficients all returned the same topology (Fig. 5a), while the dendrogram calculated on the second Kulczynski coefficient gave a topology that differed only in the position of the MC (abbreviations of OGUs are given in Appendix 1) (Fig. 5b). The NRS and SRS, together with the AB have the highest faunistic similarity, irrespective of the choice of β-diversity index. To a lesser extent this also applies to the MP and the SB. Furthermore, the CP always came out as being clearly different from the rest of the WIO (similarity coefficients of 0.1 irrespective of the β-diversity coefficient utilized). The NP is further shown to act as the transition zone between the Cape Province and the rest of the WIO.

Parsimony analysis – performed with paup* (Swofford, 2002) under the heuristic search mode with random addition sequence with 10^6 replicates and with all species equally weighted – on the 235 taxa in the data set revealed that only 113 of them are distributed in a parsimony informative way (i.e. shared by two or more OGUs but not all OGUs together; or in other words OGU autapomorphies and OGU symplesiomorphies excluded). Parsimony analysis of endemicity under Wagner parsimony produced a single most parsimonious area cladogram with a tree length of 201 steps, a consistency index (CI) of 0.562 and a retention index (RI) of 0.567 (Fig. 6a). PAE under Dollo parsimony generated two most parsimonious trees with tree length 240, CI = 0.471 and RI = 0.74 (Fig. 6b for the strict consensus view).

Both the PAE under Dollo (dispersion obstructed) and the PAE under Wagner parsimony (dispersion permitted) present the CP and the NP as basal clades. Also, the (NRS,SRS,AB) branch returns as a sister clade to the tropical (MP,MC,SB) branch. Dollo and Wagner parsimony differed from each other in the position of the SRS and in the relation between MP, MC and SB. Under the Wagner parsimony the SRS is placed as sister area to the (AB,NRS) clade whereas under the Dollo parsimony the NRS is sister to the (AB,SRS) clade. Another

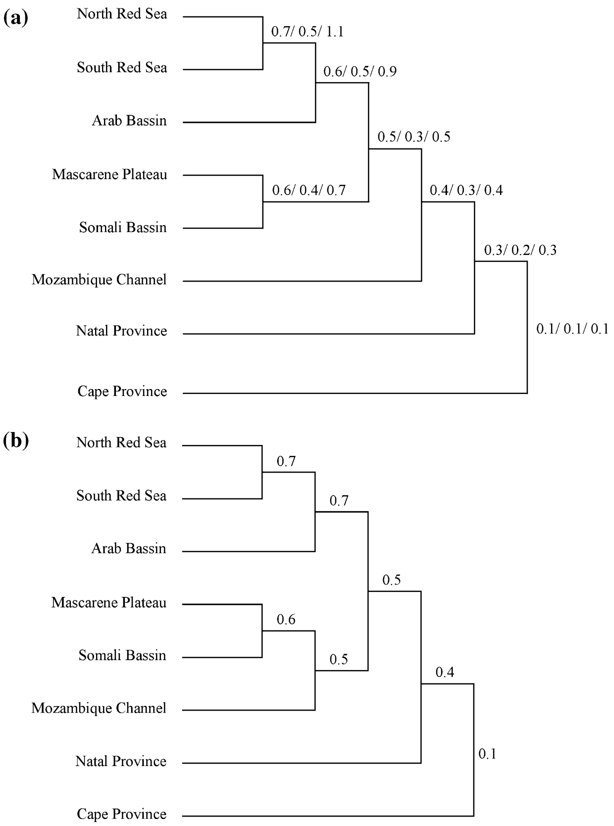

Figure 5 Dendrogram using average linkage (between OGUs) produced by clustering with commonly used β-diversity indices such as (a) the Dice, the Jaccard and the first Kulczynski coefficient, and (b) the second Kulczynski coefficient. Numbers are the respective similarity coefficients.

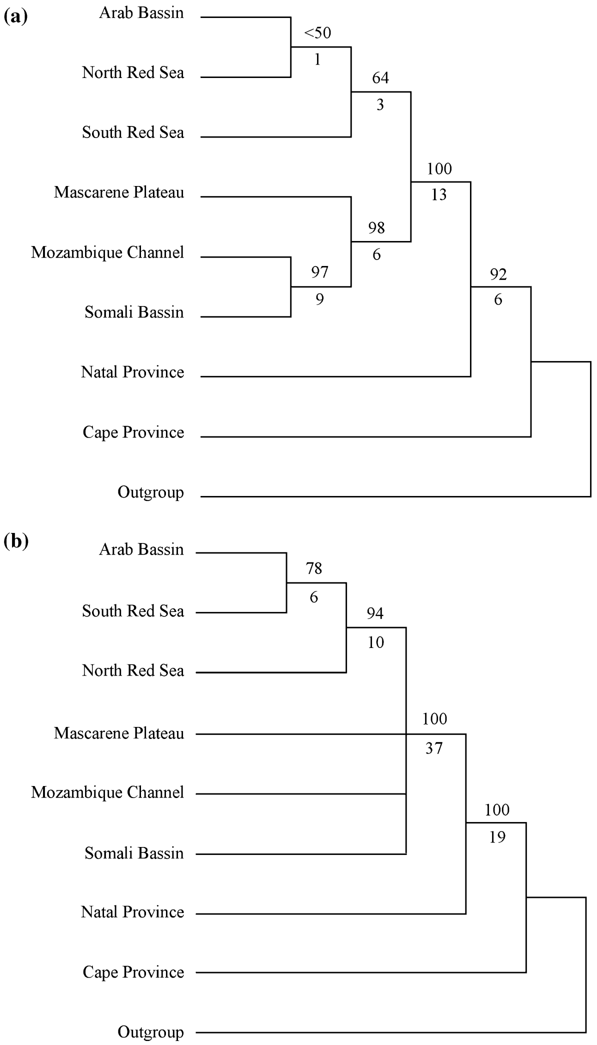

Figure 6 OGU cladograms: (a) single most parsimonious cladogram as obtained under Wagner parsimony, and (b) strict consensus tree of the two most parsimonious cladograms as obtained under the Dollo parsimony. Numbers above branches represent bootstrap percentage; numbers below branches represent Bremer support. The outgroup is coded as all species absent from each cell.

difference between both parsimony approaches entails the relationships between the tropical OGUs, which returned as unresolved under the Dollo criterion whereas under the Wagner criterion the clade (MP,(MC,SB)) was uncovered. Using Wagner parsimony, bootstrap percentages and Bremer supports for and within the (SRS(NRS,AB)) clade proved low (bootstrap support = 64%; Bremer support = 3). On the other hand, the ((AB,SRS)NRS) clade as obtained with Dollo parsimony received high support for both indices (bootstrap support = 94%; Bremer support = 10). Using Wagner parsimony, bootstrap and Bremer support for the (MP(MC,SB)) clade is also high (bootstrap support = 98%; Bremer support = 6). The latter topology, together with the (MC(SB(MP))) topology was one of the most parsimonuous topologies uncovered under the Dollo parsimony. The support for the (tropical OGU, Red Sea, AB) clade was very high, both under Wagner (bootstrap support = 100%; Bremer support = 13) and Dollo parsimony (bootstrap support = 100%; Bremer support = 37).

Given the differences between Dollo and Wagner parsimony further exploration of the link between life-history strategy and zoogeography is justified. Thus, we plotted the geographical spreading of the three orders across the latitudinal and the longitudinal gradient of the WIO (Figs 7 & 8). These plots reveal that species turnover between OGUs is largely governed by a taxic turnover at the level of the order. This applies especially to the ratio of aspidochirotids to dendrochirotids over the latitudinal gradient and is especially visible around 32° S, where the transition between the CP and the NP is located. Similar inverse trends , although smaller in amplitude, occur around 29° S (transition between NP and MC), around 15° S (transition between MC and SB), around 6–7° S (within the SB and the MP), around the equator (within the SB and the MP), around 10° N (transition between SB and AB) and around 20° N (more or less at the transition between SRS and NRS). The trend line of the apodid/aspidochirotid proportion is less obvious to interpret, but it seems to change around 18° S (transition between MC and SB), around 8° S (within the SB and MP) and around 10° S (transition between SB and AB). No firm extrapolations can be made for the east coast of Somalia (1–11° N), for this regions is too poorly investigated; the only study being that of Tortonese (1980). At higher northern latitudes, the simultaneous rise of apodids and (although less pronounced) dendrochirotids also needs mentioning as it corresponds roughly (*c.* 20° N) to the pre-defined border between the north and south Red Sea. Similar trends can be observed along the longitudinal gradient (Fig. 8). Again the most obvious taxonomic turnover occurs in the CP–NP transition (*c.* 30–32° E). Also noteworthy is the minor shift around 45° E [both the transition between AB and SRS and between MP and MC/SB(partim)].

Understanding the zoogeographical patterns

The correspondence between life-history strategy and range size of the dominant orders is clearly visible from the plot of range size vs. the cumulative species richness (Fig. 9). Dendrochirotids (with their lecithotrophic doliolaria and direct development) reach the asymptotic range size after 23 cells, while the aspidochirotids (with their planctotrophic auricularia and indirect development) reach this saturation point only after 45 cells. Apodids (with both types of development) are generally positioned somewhat in between but reach their asymptotic range size at 18 cells (at 10 cells for the lecithotrophic Chiridotidae) (Fig. 9). By splitting the data on the basis of the life history rather than at the level of the orders,

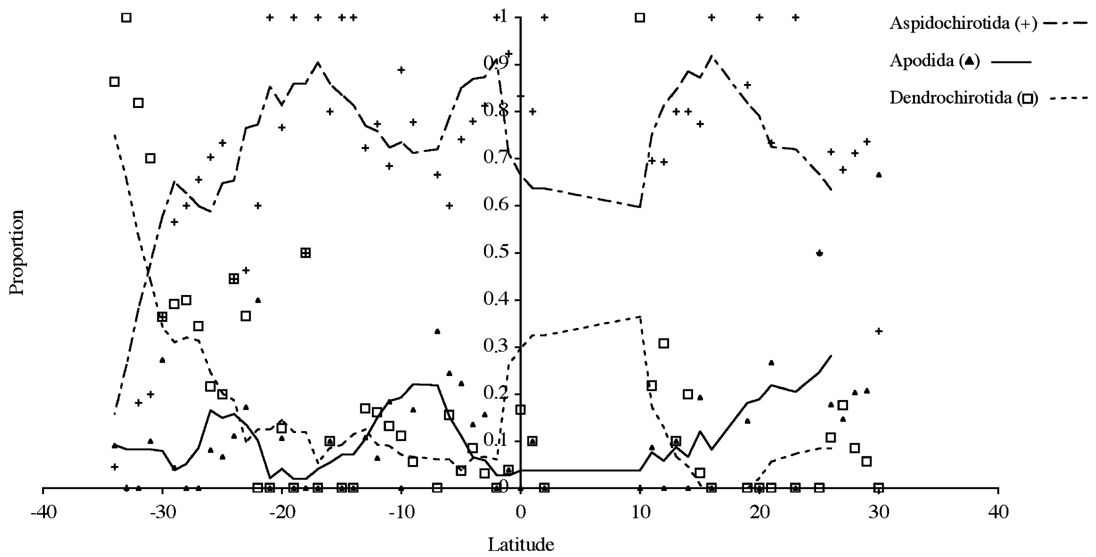

Figure 7 Proportional contributions of the dominant orders across the investigated latitudinal gradient. Negative latitudes represent southern latitudes; positive values are northern latitudes. The curves represent the moving average (with period five).

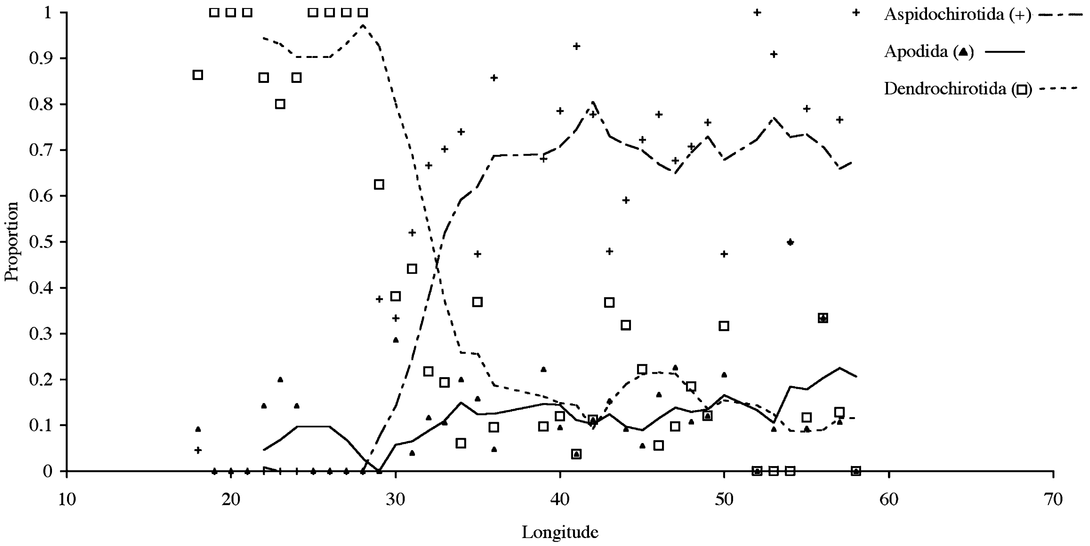

Figure 8 Proportional contributions of the dominant orders across the investigated longitudinal gradient. Longitudes represent degrees east. The curves represent the moving average (with period five).

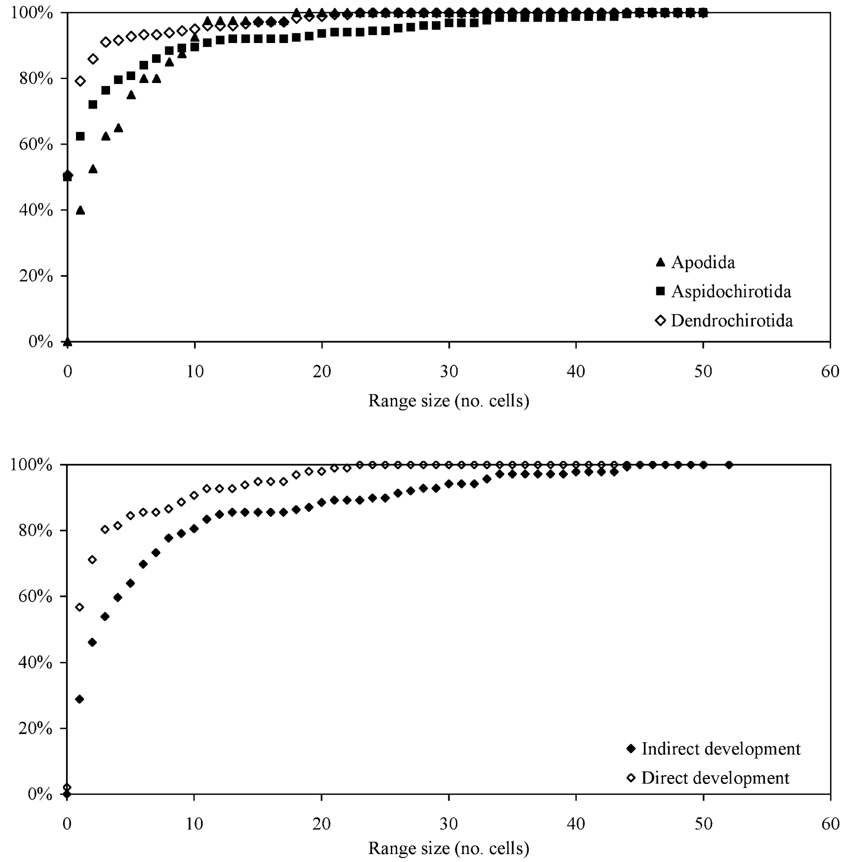

Figure 9 Dispersion capacity (number of cells occupied) vs. cumulative species richness: (left) for the three dominant orders; (right) for holothuroids with lecithotrophic (Dendrochirotida and the apodid family Chiridotidae) and planctotrophic larvae (Aspidochirotida and the apodid family Synaptidae).

the above pattern was made even more visible; species with lecithotrophic larvae are range restricted after 23 cells, while those with planktotrophic larvae reach this saturation only after 45 cells (Fig. 9).

The significance of life-history traits is further analysed by calculating the proportional contribution of the three dominant orders across the species richness of all sampled locations in the WIO. Our results show that the contribution of the orders varies considerably for each OGU and that moreover these values do not fall within the bounds predicted by random allocation of species to local sites from the global species pool (bootstrapped 95% confidence limits based on random selection of species from the total species pool for each total species richness, 235 iterations were employed; see also Bellwood & Hughes, 2001) (Fig. 10).

More specifically, in the Red Sea, Somali Basin, Mascarene Plateau and to a lesser extent also the Mozambique Channel, the proportion of aspidochirotids is markedly higher than predicted by random allocation were the WIO homogenous. Conversely, more dendrochirotids than expected are found in the Cape Province and to a lesser extent also the Natal Province. For the apodids, the pattern largely matches the expected one.

DISCUSSION

Quality of the data set

A major problem for a study like the present one is that one needs a data set that is rigid both in quantity (number of taxa, representative sampling efforts) and in quality (correct taxonomy and location of records). Unfortunately these parameters are hard to control and (more often than not) will require a formidable sampling, taxonomic and systematic effort (see also Vecchione *et al.*, 2000). This is conclusively shown by Fig. 4: each additional sampling in a WIO area continues to bring additional records, even today. For instance, Samyn (2003) roughly doubled the number of Kenyan holothuroids, and Samyn & Thandar (2003a,b) were able to add nearly 25% to

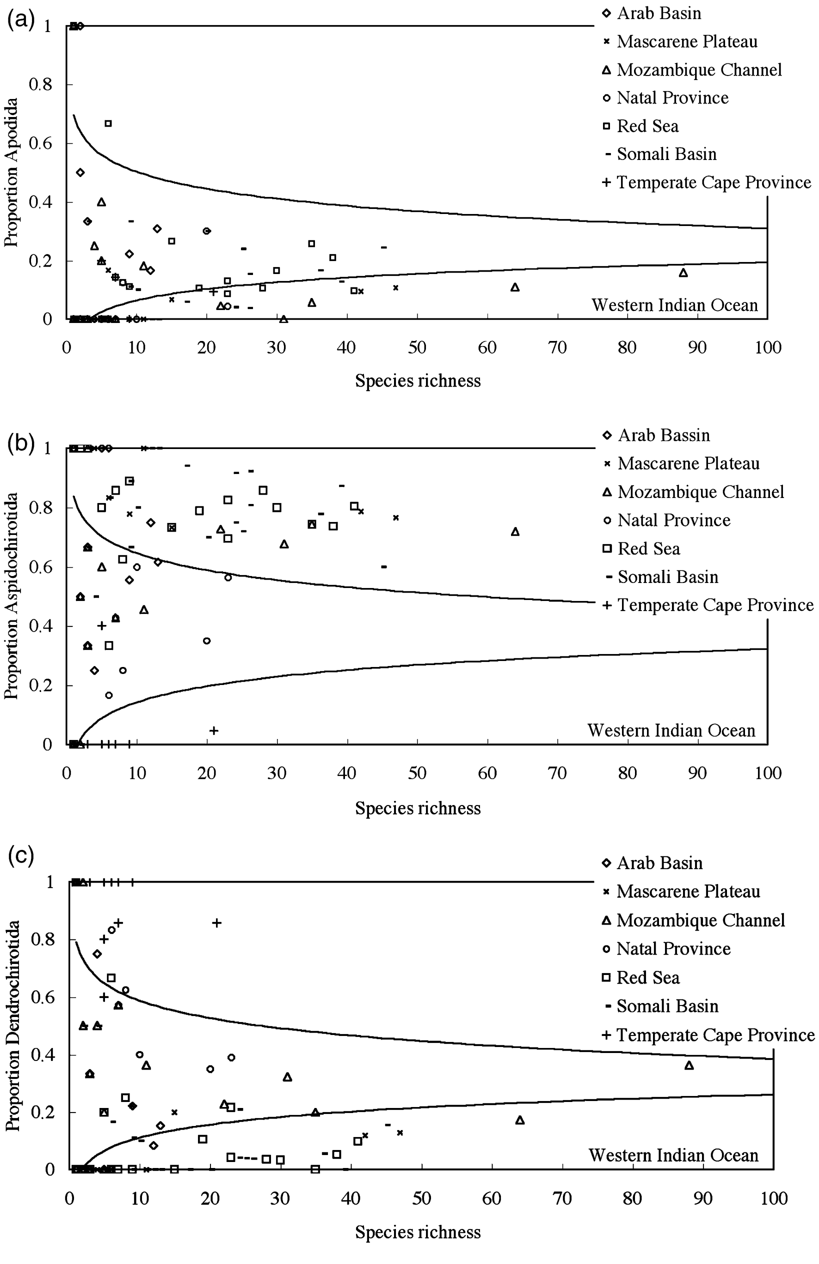

Figure 10 Contribution to the total species pool of the three dominant orders across the range of total species richnesses. Each data point represents 1° latitude/longitude cell; different marking symbols indicate separate OGUs (northern and southern Red Sea are here lumped for clarity). Upper and lower lines are bootstrapped 95% confidence limits based on random selection of species from the total species pool. Bootstrapping was based on 235 iterations for each total species richness value, using estimated total species pools for the three dominant orders in the data set.

the holothuroid fauna of KwaZulu-Natal (even though this is one of the best-studied stretches of coast along the African continent). Moreover, analyses of endemicity patterns (Y. Samyn, unpubl. data) have revealed that the faunal lists as employed here underestimate rare species. On the other hand, even though the present data set is based on an extensively researched taxonomic and systematic foundation (Samyn, 2003), we cannot, with absolute certainty, exclude the possibility that some of the records will subsequently have to be omitted. Such can be exemplified with Cherbonnier's (1988) monograph on the holothuroids of Madagascar, an *opus* that is generally accepted as the standard for East Africa. Despite its grandeur in temporal and geographical scope (it spans more than a century of sampling and covers a considerable part of larger Madagascar), more than a third (45 of 122) of the species treated in this work were new to science. However, in 40% of the cases (18 of 45) these descriptions were based on only a single specimen and in *c.* 16% of the cases (7 of 45) on only two specimens. Therefore, it can be expected that several of these newly erected species will turn out to be but synonyms of existing species. This observation is further strengthened by the fact that: (1) many of these specimens are remarkably small, thus not precluding the possibility that they are but juveniles of already established species of which the intraspecific variation is inadequately known; (2) some of them are obviously erroneously classified and thus have not been compared with their natural sister-species (e.g. *Opheodesoma sinevirga* Cherbonnier, 1988 obviously belongs to the genus *Euapta* Oestergren, 1898). Moreover, as most of Cherbonnier's (1988) new species have not been found again (C. Massin, pers. comm.), the possibility of synonymity remains. Nevertheless, until we, or colleagues, have accumulated convincing proof for such lumping, we *must* retain them as valid. Simultaneously, the contrasting situation also has to be borne in mind. Indeed, some supposedly well-known species increasingly reveal themselves as sibling species. This was recently discovered to be the case in *Labidodemas semperianum* Selenka, 1867 (Massin *et al.*, 2004), in *Holothuria arenicola* Semper, 1868 (unpubl. data) and in *Massinium magnum* (Ludwig, 1882) (unpubl. data). Undoubtedly, comprehension and prediction of such species will to a large extend depend on our understanding of the factors that explain the zoogeographical distributions.

Investigating inter-OGU relationships

Patterns of biodiversity have been actively researched ever since the pioneering work of Darwin (1859) and Wallace (1860). In a recent review, Gaston (2000) concluded that lately there has been a shift of focus from local to geographical scale and a move from descriptive to causal biogeography. The present study follows that trend and investigates the inter-OGU relationships by hierarchical clustering of β-diversity indices and by performing PAE. Both analytical zoogeographical methods basically measure the same thing, namely that if two OGUs share the same species, they are more closely related than those OGUs that do not share the same species. However, whereas similarity coefficients quantify the faunistic similarity between the faunas of any two existing OGUs and thus provide a measure of current species turnover (β-diversity), PAE allows recovery of historical relationships between the biota of any two OGUs (Rosen, 1988; De Grave, 2001). PAE has the additional advantage that it can operate with two parsimony options (Wagner and Dollo) which allows differential gauging of the dispersion capacity (long- and short-range, respectively). PAE, which does not require an *a priori* phylogeny, thus basically acts as an analogue of true cladistic biogeography (the discipline that searches for the correspondence between phylogenies and area relationships). It must, however, be stressed that PAE can only act as a surrogate of cladistic biogeography. Despite this, until robust phylogenetic hypotheses for the majority of holothuroids become available, PAE provides an invaluable tool for deciphering historical interactions. As our two analytical zoogeographical methods measure the relationship between any two bioassociational units, it can hardly surprise us that the main differences between the two approaches are found in the crown topologies rather than in the overall topology.

A first important observation comes from the area-dendrograms obtained through clustering with similarity coefficients (Fig. 5). By and large, we prefer the topology as obtained with the second Kulczynski coefficient (Fig. 5b) because this coefficient is known to behave more robustly when disproportionate species numbers are considered (Price, 1982 and references therein; Samyn & Thandar, 2003a,b; Thandar & Samyn, 2004a). This clustering shows that species turnover is lowest (largest similarity coefficients) within and between the (NRS, SRS, AB) and the (SB, MP and MC) branches. On the other hand, species turnover is at its largest at the southern extreme, i.e. at the boundary between CP and NP. The intermediate position of the NP, between the (NRS, SRS, AB, MC, SB, MP) and the CP branches, once again demonstrates that it acts as a bleeding zone between the Indo-Pacific and the South African Province (see also Thandar, 1989; Samyn & Thandar, 2003a,b). The parsimony-based analyses provide complementary insights into the biogeographical evolution of the subject taxa. Dollo and Wagner parsimony exposed some important differences. It must be stressed that disparity does not necessarily favour one scenario over another. For instance Dollo parsimony returned ((AB,SRS),NRS) whilst Wagner gave back ((AB,NRS),SRS) as the topology for the Red Sea, Arab Basin region. Dollo parsimony (dispersion restricted) thus indicates that the SRS has more affinity with the AB, while Wagner parsimony (dispersion allowed) reveals that taxa from the AB can reach the NRS. These observations in combination with the similarity coefficients indicate that the narrow and shallow passage between the Red Sea and the Gulf of Aden, the zoogeographical barrier of the Bab-el-Mandab (Briggs, 1974; Price, 1982), is, at least nowadays, of minor significance in the dispersion of shallow-water holothuroids. This observation is in agreement with Kemp's (1998) postulate on the biogeography of the chaetodontid fish from the Soccotra Archipelago.

The hypothesis that the north and south Red Sea faunas are separated by a zoogeographical barrier around 20° N (Kemp, 1998 and references therein) is harder to prove given the paucity of distribution data from the central part of the Red Sea. Nevertheless, figure seven indicates that at roughly that latitude, quite a few aspidochirotids are replaced by apodids and to a lesser extent dendrochirotids. Closer examination indicates that the majority of these apodids belong to the family Synaptidae, which have the ability to disperse over longer distances, thanks to their planktotrophic larvae. This explains why our PAE under Wagner parsimony (dispersion not constricted) put the Arab Basin and the north Red Sea in one clade. In fact, the reality of long-range dispersion of Indo-Pacific species through the Red Sea is evidenced by the Lessepsian migrations of *Holothuria impatiens* (Forskål, 1775), *Holothuria poli* Delle Chiaje, 1823 and *Leptosynapta inhaerens* (O.F. Müller, 1776) (Tortonese, 1953) and by the fact that the majority of holothuroids at the most northern extreme of the Red Sea (the Gulfs of Aqaba and Suez) belong to the aspidochirotids and the apodids (again mainly the Synaptidae) (Samyn, 2003). Further, as indicated by Fig. 6b, the Arab Basin and the southern Red Sea are intimately connected. However, whether this region has to be seen as a distinct biogeographical region [an extension from the centre of endemism in Oman (Randall & Hoover, 1995)], as postulated by Kemp (1998), cannot be decided here, for the simple reason that we lack detailed holothuroid species lists from most of south-east Arabia.

The relationships between the circumtropical OGUs (Mascarene plateau, Somali Basin and the Mozambique Channel) differed between each analysis. The similarity coefficients teach us that the Mascarene Plateau (roughly composed of the Seychelles, Mauritius, Réunion and the eastern side of Madagascar) and the Somali Basin are always positioned in the same cluster; the Mozambique Channel is according to the second Kulczynski coefficient most similar to that cluster (Fig. 5b). Here the PAE returned a fully resolved picture only under Wagner parsimony; under Dollo parsimony two most parsimonious trees were recovered [i.e. (CP,(NP,(MC,(SB,(MP,(NRS,(SRS,AB))))))) and (CP,(NP,(MP,(SB,MC),(NRS,(SRS,AB))))))]. Potential reasons for such ambiguity are plentiful, but the most straightforward one can readily be read from Fig. 7, which shows that at several latitudes important order turnovers occur within the Somali Basin and the Mascarene Plateau (one from 18 to 8° S; one from 8 to 1° S and one from 1° S to 10° N), which thus possibly hold several as yet unrecognized biogeographical units. Undoubtedly, *de novo* sampling in these regions (e.g. the poorly known Comoros, Mafia Island and Somali Coast) can reveal if these observations are truth or artefact. Be that as it may, it is clear that the circumtropical OGUs are to a large extent connected to each other.

Now we come to the question of the causality of the observed patterns. It is generally assumed (Bakus, 1973) that dendrochirotids inhabit temperate rather than tropical waters, while for aspidochirotids the reverse situation exists. The reason for this has been attributed to the feeding habit of the orders (Bakus, 1973 and many subsequent authors): dendrochirotids being suspension-feeders and thus by and large preferring colder, richer water, whereas aspidochirotids and apodids (family Synaptidae, not Chiridotidae which are burrowing) are epibenthic deposit feeders preferring warmer waters, where they act as 'vacuum cleaners'. Levin (1999), however, disregarded the above explanation and claimed that the low density of dendrochirotids in the tropics has to be attributed to: (1) an absence of attachment sites; (2) weak wave action and high sedimentation; and (3) competitive exclusion by aspidochirotids. We do not want to go into too much detail, but it has been long known (Darwin, 1845) that coral reefs flourish in a large circumtropical belt (Stoddart & Yonge, 1971). These biogenic constructs provide the required attachment sites, are subject to strong wave action (e.g. atolls), and are found exactly at locations where there is little sedimentation.

Given the patterns sketched above, it is now clear that important taxonomic turnovers occur within the latitudinal and longitudinal gradient of the WIO, which is not all that homogeneous an area as has long been thought (Briggs, 1974). As shown by Fig. 9, there exists a considerable discrepancy in dispersion capacity between the species with planktotrophic and the species with lecithotrophic larvae. By combining this dispersion capacity with the prevalent currents (Fig. 2) and the geological history we can now arrive at an integrated picture.

Bellwood & Hughes (2001), Roberts *et al.* (2002) and many others have conclusively shown that within the Indo-Pacific, species richnesses peak in the East Indies triangle (EIT). Away from this local zenith, species numbers rapidly tail off towards the eastern Pacific and the WIO. An almost uncountable number of hypotheses have been put forward to explain this pattern, but (as any scholarly textbook will tell) they come in three main forms: (1) centre of origin and dispersion; (2) centre of accumulation and (3) centre of survival. Whatever the correct explanation is for the origin of the EIT, it seems clear that nowadays the WIO fauna is – through the SEC and NEMC – to a lesser or larger extent connected with the EIT. Such connectivity is supported by the fact that most of the shallow-water WIO holothuroids are clearly related to some Indo-Pacific species and that most of the WIO genera are shared with other areas in the Indo-Pacific (Thandar, 1989). By analysing the current patterns within the WIO (see Fig. 2) in conjunction with the dispersion capacity, the crown clades in the PAE-obtained biogeographical units can largely be explained. These PAE analyses reveal that the Red Sea/Arab Basin holothuroids are derived from the WIO *sensu stricto* (thus without CP). In the Red Sea/Arab Basin region species can come in from the east (carried by the NEMC) and from the south (with the SoC). The paucity of stepping stones along the northern Arabian Sea and the cold upwelling along the east coast of Somalia act as a filter for species with limited dispersion capacity and as such explain why the proportion of dendrochirotids is lower than expected in this region (see Fig. 10). A similar situation exists in the circumtropical OGUs MP, MC and SB where disproportionately high ratios of aspidochirotids/dendrochirotids are found. Here again, it can be assumed that species with long-lived larvae have been more successful at surviving the journey across the Indian Ocean. Towards the more southern OGUs the proportion of species with lecithotrophic larvae increases steadily. This cannot (at least not to the same extent) be explained through the same dispersion mechanism (i.e. coming from the EIT) for these communities are dispersion limited, i.e. they contain many local endemics (Thandar, 1989, 1998; Thandar & Samyn, 2004a). Rather, as can be deduced from the PAE, these faunas are the oldest (although we cannot substantiate this with hard evidence such as fossils), and thus are best seen as relicts of historical distributions. However, the fact that the faunas of southern Australia, New Zealand, Antarctica and South America show no clear relationships with the WIO fauna indicates that it was not Mesozoic and early Cenozoic plate tectonics that shaped the distribution pattern (Thandar, 1989; see also De Grave, 2001). Nevertheless, assigning a relict status to the CP/NP fauna is in (partial) agreement with Santini & Winterbottom's (2002) vicariant scenario. These authors give evidence that part of the Indo-Pacific fauna (inclusive of the EIT) has originated from ancient lineages within the WIO. We cannot substantiate Santini & Winterbottom's (2002) decision to place the Red Sea/Arab Basin as the cradle of the WIO fauna, for we found that this area was sister to the tropical OGU clade in our PAE analyses. Rather, we believe that the (geologically recent) Pleistocene glacial swings have not only led to the closure of the Red Sea at the Bab-el-Mandab and to the complete evaporation of the Persian Gulf, but also to some rather extensive species range shifts that have trapped species in refugia such as the Red Sea and the southern WIO. Roy *et al.* (1998) have demonstrated, for Atlantic and eastern Pacific prosobranch gastropods, that post-Pleistocene latitudinal diversity gradients are significantly correlated with average sea surface temperature. If the latter is true for the WIO as well, then it becomes clear why the low temperature-loving, suspension-feeding dendrochirotids are doing so well at high southern latitudes and why they are doing so poorly in the Red Sea/Arab Basin biogeographical unit. It thus seems that in the former area they have become so well established (and to a large degree isolated) that they now constitute an active evolutionary centre with a high level of local endemism (Thandar & Samyn, 2004a), while in the latter they have been competitively excluded by the better adapted high temperature-loving, epibenthic aspidochirotids.

Rapoport's rule

The present study also had one serendipitous finding, namely that Rapoport's rule (see Gaston *et al.*, 1998) cannot be upheld across the latitudinal gradient studied here. The distribution we unveiled indeed clearly showed that, in a narrow circumtropical band, the majority of the holothuroid fauna belongs to the order Aspidochirotida (see also Samyn, 2003). Previously, Levin (1999) has recovered the same pattern in global holothuroid distributions. This pattern is contradictory to the rule that dictates that species' range sizes decrease towards lower latitudes, i.e. Rapoport's rule (Gaston *et al.*, 1998). We found conclusive evidence that aspidochirotids have the largest dispersion capacity (and thus range size) amongst shallow-water WIO holothuroids (Fig. 9). Our observations are again in agreement with those of Roy *et al.* (1998) who – based on an analysis of the geographical ranges of nearly 4000 species of marine prosobranch gastropods living on the shelves of the western Atlantic and eastern Pacific Ocean – found that the median latitudinal ranges of species are greater not in high but in low latitudes. Gaston *et al.* (1998), in their recent review, concluded that evidence for Rapoport's rule is equivocal at best. If valid at all, it is so only on local scales and only at higher latitudes. As we have only analysed a latitudinal range of 64° (30° N to 34° S), we cannot falsify the latter statement. Nevertheless, the present study adds to the evidence that in the circumtropical belt, Rapoport's rule cannot be upheld and thus most probably deserves its epitaph (Gaston *et al.*, 1998).

CONCLUSIONS

Describing and understanding the patterns of biodiversity always involves gross abstractions because these patterns are subject to an interrelated web of causal parameters (physical variables such as area, depth, temperature and geological history, as well as biological variables such as productivity, dispersion capacity, extinction and speciation) that operate at different scales. The present study provides the first description and a tentative understanding of the biodiversity patterns as revealed by shallow-water holothuroids of the WIO. The WIO can roughly be divided in three larger biogeographical realms: the Red Sea and associated Arab Basin, an asymmetrical circumtropical region stretching from the horn of Africa to southern Mozambique and the temperate Cape province. The subtropical Natal Basin acts as the bleeding zone between the tropical and temperate provinces. This study has revealed that the dispersion capacity of the taxa involved is one of the main causal factors required to explain the zoogeographical pattern described herein.

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BIOSKETCHES

Yves Samyn obtained his PhD (2003) at the Free University of Brussels (VUB), Belgium. His principal areas of research are sea cucumber taxonomy, systematics (with some excursions into phylogeny) and zoogeography. He attempts to frame his findings into conservation initiatives. Since 1999 he has (co)authored numerous peer-reviewed scientific papers on these topics. He is currently a tutor at the Belgian National Focal Point to the Global Taxonomy Initiative (Royal Belgian Institute of Natural Sciences, Brussels) where he is helping to install taxonomic capacity in developing countries.

Irena Tallon obtained her MSc (1993) at the Free University of Brussels (VUB), Belgium. Since 1999, she has voluntarily participated in several expeditions to collect echinoderms in South Africa. Her broad knowledge of data management and data bases was utilized here to construct and analyse the data set. She is currently a research fellow of the Learning and Guidance Centre of the Faculty of Sciences at the VUB.

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Appendix 1 Alphabetical list of abbreviations used

AB	Arab Basin (see Fig. 3)
AC	Agulhas Current (see Fig. 2)
BC	Benguela Current (see Fig. 2)
CI	consistency index
CP	Cape Province (see Fig. 3)
EACC	East African Coastal Current (see Fig. 2)
ECC	Equatorial Counter Current (see Fig. 2)
EMaC	East Madagascar Current (see Fig. 2)
IMC	Indian Monsoon Current (see Fig. 2)
MC	Mozambique Channel (see Fig. 3)
MoC	Mozambique Current (see Fig. 2)
MP	Mascarene Plateau (see Fig. 3)
NEMC	north-east Monsoon Current (see Fig. 2)
NMaC	North Madagascar Current (see Fig. 2)
NP	Natal Province (see Fig. 3)
NRS	northern Red Sea (see Fig. 3)
OGU	operational geographical unit
PAE	parsimony analyses of endemicity
RI	retention index
SB	Somali Basin (see Fig. 3)
SEC	South Equatorial Current (see Fig. 2)
SoC	Somali Current (see Fig. 2)
SoCC	Somali Counter Current (see Fig. 2)
SRS	southern Red Sea (see Fig. 3)
WIO	western Indian Ocean; here arbitrary defined as the area ranging from Suez to Cape Town and from the East African coast to 65° E (see Fig. 3)

SUPPLEMENTARY MATERIAL

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/JBI/JBI1295/JBI1295sm.htm

Appendix S1 Shallow-water holothuroid species of the western Indian Ocean arranged into a presence/absence matrix with 1° latitude/longitude cells grouped into recognized OGUs.