

Shallow-water holothuroid (Echinodermata: Holothuroidea) biodiversity and biogeography of the subtropical east coast of South Africa

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ABSTRACT: Due to increased market demands, some countries of the south-western Indian Ocean, including the subtropical east coast of South Africa (ECSA), have become vulnerable to blind exploitation of their sea cucumber resource. At least 55 species occur in the latter region. The present investigation uses cluster analyses of several β -diversity coefficients to determine the faunistic similarities between the holothuroids of ECSA with those of Mozambique, West Madagascar, the Mascarene Islands and East Madagascar. It is concluded that the holothuroid fauna of the South African east coast has a mixed composition, being most similar to that of Mozambique, West and North-East Madagascar. We here suggest that prevailing current patterns can to a large extent explain the compositional structure of the ECSA shallow-water holothuroid fauna.

1 INTRODUCTION

The southern African subcontinent, lying south of the Tropic of Capricorn, forms a small landmass narrowing gradually southwards. It is the meeting place of two of the world's greatest oceans and has thus received faunal invasions from both sides, producing a highly complex fauna. Although there are no large offshore islands to break the force of ocean swells, it nevertheless offers a variety of marine habitats. These, coupled with the narrow continental shelf, frequent up- and downwellings, warm and cold ocean currents and the mixing of these in the south-western corner, have resulted in unique conditions, especially in the temperate regions, where numerous endemics occur. As far as intertidal species are concerned there is a clear subtropical element on the east coast up to Port St Johns (ca. 31.5°S), a warm-temperate element on the south coast up to Cape Point, and a cold-temperate element on the west coast (Stephenson 1944, Day 1974 and others). However, if all shelf species (<200 m deep) are analysed, there is only a single temperate element in South Africa with little or no support for a cold-temperate province up the west coast into Namibia (Day 1967, Millard 1978, Thandar 1989, 1998, amongst others).

2 REVIEW OF PHYSICAL OCEANOGRAPHY

Although the current regime of South Africa is quite complex (amongst others Harris 1978, Brown &

Jarman 1978, Heydorn 1978, Thandar 1989, and for the east coast, amongst others, Schumann 1982, 1987, Lutjeharms et al. 2000a, b), some consensus exists as to its main pattern. Overall, two chief currents sweep the South African coastline: the southbound, West Boundary warm Agulhas Current (AC) that washes the east coast and the northbound, cold Benguela Current (BC) that flows along the western coastline (Fig. 1). However, in order to fully understand the role of current systems in the shaping of the fauna of the subtropical east coast of South Africa – the area stretching from $\pm 27^\circ\text{S}$ (Mozambique border) to $\pm 31.5^\circ\text{S}$ (Port St. John's) – a more detailed picture of the prevailing

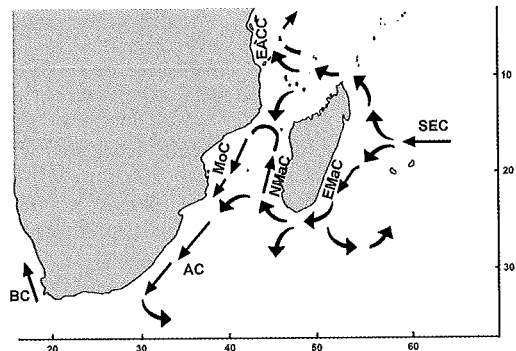


Figure 1. Map of southern Africa showing the main current systems (see text for current acronyms).

currents is needed. An excellent revision of the current patterns in the south-western Indian Ocean has recently been delivered by DiMarco et al. (2002). It here suffices to summarize their main conclusion (see also Fig. 1).

Flowing westward across the Indian Ocean, the South Equatorial Current (SEC), splits at the east coast of Madagascar at roughly 20°S. The northern branch follows the East Madagascar coast until a westward turn at the northern tip of Madagascar occurs. Here, the current bifurcates again (roughly at the Comores 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 bough 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 (especially during austral summer), forming the North Madagascar Current (NMaC). The latter flows into the Mozambique Channel where it retroflects counterclockwise to continue southwards, eventually ending in the AC. It thus seems that the AC on the east coast of southern Africa is formed mainly by the confluence of the MoC, the EMaC and the associated NMaC. The MoC-EMaC convergence is thought to take place near the KwaZulu-Natal-Mozambique border (±27°S).

However, Bang & Pearce (in Heydorn 1978) have put forward the hypothesis that the EMaC forms the major component of the AC and that the MoC is of lesser importance than originally supposed and may even, at times, not be confluent with it. This is in some disagreement with the findings of others (see DiMarco et al. 2002) who, including DiMarco et al. regard the MoC as the main contributing agent to the AC, even if it is only in the form of southward flowing eddies.

The present investigation, through examination of species turnover (β-diversity) in pre-defined subregions of the south-west Indian Ocean, aims at determining if the South African Indo-Pacific fauna is derived by way of the EMaC (hypothesis of Bang & Pearce, in Heydorn 1978) or, alternatively by way of the MoC.

3 REVIEW OF BIODIVERSITY

Samyn & Thandar (2003a), in their recent analysis of the shallow-water echinoderm biodiversity of KwaZulu-Natal, commented that despite several efforts, the southern African echinoderm biodiversity and biogeography remain poorly investigated. The last most comprehensive work is that of Thandar (1989), who recorded 407 echinoderm species in southern Africa, including both shallow and deep-sea species, of which 108 were holothuroids. When only shelf forms (*i.e.* <200m deep) – single locality species excluded – were considered, the total number of

echinoderm species dropped to 263. Later, Thandar (1998) summarized the holothuroid biodiversity and biogeography of southern Africa, recording some 137 species with 79 species – single locality species excluded – restricted to the shelf. Of these 79 species about 40 were recorded from KwaZulu-Natal. Recent additions to the southern African east coast holothuroid fauna are mainly due to the works of Thandar (1996), Rajpal & Thandar (1998, 1999) and Thandar & Rajpal (1999) based on collections by the South African Museum, and *de novo* collections by SCUBA-gear by one of us (Y.S.), along the coast of KwaZulu-Natal (see Bolton et al. 2002, Samyn 2003, Samyn & Thandar 2003a, b, Samyn & Massin 2003, Massin et al. 2004). These and others still to be published records, have increased the number of shallow-water holothuroids from the east coast to 55 species (see Table 1).

While Samyn & Thandar's (2003a) effort aimed at understanding the shallow-water echinoderm biodiversity of KwaZulu-Natal, the current paper aims at recording the holothuroid biodiversity and faunistics of the South African subtropical east coast; revising its faunistic components; determining the similarity of its fauna to that of Mozambique, Madagascar and the Mascarene Islands; linking the observed patterns to prevailing currents; and calculating the degree of local endemicity in support of the subtropical province. Moreover, the oceanography of the Natal Bight, a region with apparent echinoderm paucity, is briefly discussed.

4 METHODS

4.1 Study area

For the purpose of this investigation, the east coast of South Africa (ECSA) is taken as that extent of the coastline south of the KwaZulu-Natal – Mozambique border (ca 27°S latitude) to Port St Johns (ca 31.5°S latitude).

In order to determine how the holothuroid fauna of ECSA relates to the rest of the south-west Indian Ocean, we compare its species composition to that of northern and southern Mozambique, West and East Madagascar and the Mascarene Islands, using various similarity coefficients. Six operational geographical units (OGU's) are here arbitrarily defined (Fig. 2): northern Mozambique (NMoz) (north of 20°S), southern Mozambique (SMoz), West Madagascar (WMad), East Madagascar (EMad), the Mascarene Islands (MIDs) and ECSA. A more detailed analysis of the hypothesis that current patterns can, at least partially, explain the faunistic relationships is investigated by subsequently dividing West and East Madagascar into respectively NWMad, SWMad, NEMad and SEMad (Fig. 2).

Table 1. Shallow-water holothuroids of the South African subtropical east coast and their faunistic components.

| Species | Comp* | Species | Comp* |
|---|-------|---|-------|
| Dendrochirotida Grube, 1840 | | Aspidochirotida Grube, 1840 | |
| Phylloporidae Oestergren, 1907 | | Stichopodidae Haeckel, 1896 | |
| Thyoninae Panning, 1949 | | <i>Neostichopus</i> Deichmann, 1948 | |
| <i>Stolus</i> Selenka, 1867 | | <i>N. grammatus</i> (H.L. Clark, 1923) | SAE |
| <i>S. buccalis</i> (Stimpson, 1856) | IWP | <i>Stichopus</i> Brandt, 1935 | |
| <i>S. conjungens</i> (Semper, 1868) | IWP | <i>S. herrmanni</i> Semper, 1868 | IWP |
| <i>S. kilberti</i> Rajpal & Thandar, 1999 | LE | <i>Thelenota</i> Brandt, 1935 | |
| <i>Thyone</i> Jaeger, 1833 | | <i>T. ananas</i> (Jaeger, 1833) | IWP |
| <i>T. comata</i> Cherbonnier, 1988 | SAE | Holothuriidae Ludwig, 1894 | |
| <i>T. venusta</i> Selenka, 1869 | WIO | <i>Actinopyga</i> Bronn, 1860 | |
| Phylloporinae Oestergren, 1907 | | <i>A. echinites</i> (Jaeger, 1833) | IWP |
| <i>Phylloporus</i> Grube, 1840 | | <i>A. mauritiana</i> (Quoy & Gaimard, 1833) | IWP |
| <i>P. (Phyllophorella) rosetta</i> Thandar 1994 | LE | <i>A. obesa</i> (Selenka, 1867) | IWP |
| <i>Selenkiella</i> Heding & Panning, 1954 | | <i>Bohadschia</i> Jaeger, 1833 | |
| <i>S. paradoxa</i> Cherbonnier, 1970 | SAE | <i>B. subrubra</i> (Quoy & Gaimard, 1833) | IWP |
| Semperiellinae Heding & Panning, 1954 | | <i>Holothuria</i> Linnaeus, 1767 | |
| <i>Massinium</i> Samyn & Thandar, 2003 | | <i>H. (Halodeima) atra</i> Jaeger, 1833 | IWP |
| <i>M. arthroprocessum</i> (Thandar, 1989) | SAE | <i>H. (H.) edulis</i> Lesson, 1830 | IWP |
| <i>M. maculosum</i> Samyn & Thandar, 2003 | LE | <i>H. (Lessonothuria) insignis</i> Ludwig, 1875 | IWP |
| Sclerodactylidae Panning, 1949 | | <i>H. (L.) pardalis</i> Selenka, 1867 | IWP |
| Cladolabinae Heding & Panning, 1954 | | <i>H. (Mertensiothuria) albofusca</i> Cherbonnier, 1988 | SAE |
| <i>Afrocucumis</i> Deichmann, 1944 | | <i>H. (M.) hilla</i> Lesson, 1830 | IWP |
| <i>A. africana</i> (Semper, 1868) | IWP | <i>H. (M.) leucospilota</i> (Brandt, 1835) | IWP |
| <i>Cladolabes</i> Brandt, 1835 | | <i>H. (Metriatyla) scabra</i> Jaeger, 1833 | IWP |
| <i>C. bifurcatus</i> (Deichmann, 1944) | SAE | <i>H. (Microthele) nobilis</i> (Selenka, 1867) | IWP |
| <i>Ohshimella</i> Heding & Panning, 1954 | | <i>H. (Platyperona) difficilis</i> Semper, 1868 | IWP |
| <i>O. ehrenbergi</i> (Selenka, 1867) | IWP | <i>H. (Selenkothuria) erinacea</i> Semper, 1868 | IWP |
| <i>O. turbinata</i> (Pearson, 1903) | WIO | <i>H. (S.) parva</i> Lampert, 1885 | WIO |
| Cucumariidae Ludwig, 1894 | | <i>H. (Semperothuria) cinerascens</i> (Brandt, 1835) | IP |
| Colochirinae Panning, 1949 | | <i>H. (Stauropora) pervicax</i> Selenka, 1867 | IWP |
| <i>Aslia</i> Rowe, 1970 | | <i>H. (Thymiosycia) arenicola</i> Semper, 1868 | IP |
| <i>A. spyrtdophora</i> (H.L. Clark, 1923) | SAE | <i>H. (T.) impatiens</i> (Forsk., 1775) | IP |
| <i>Pseudocnella</i> Thandar, 1987 | | <i>Labidodemas</i> Selenka, 1867 | |
| <i>P. sinorbis</i> (Cherbonnier, 1952) | SAE | <i>L. pertinax</i> (Ludwig, 1875) | IWP |
| <i>P. sykion</i> (Lampert, 1885) | SAE | <i>L. quadripartitum</i> Massin, Samyn & Thandar, 2003 | LE |
| <i>Trachycucumis</i> Thandar & Moodley, 2003 | | <i>L. rugosum</i> (Ludwig, 1875) | IP |
| <i>T. sp.</i> (Thandar, 1991) | | Apodida Brandt, 1835 | |
| <i>Trachasina</i> Thandar & Moodley, 2003 | | Synaptidae Oestergren, 1898 | |
| <i>T. crucifera</i> (Semper, 1867) | IP | <i>Euapta</i> Oestergren, 1898 | |
| Cucumariinae Ludwig, 1894 | | <i>E. godeffroyi</i> (Semper, 1868) | IWP |
| <i>Koehleria</i> Cherbonnier, 1988 | | <i>Leptosynapta</i> Verrill, 1867 | |
| <i>K. unica</i> Cherbonnier, 1988 | SAE | <i>L. naiga</i> Thandar & Rowe, 1989 | LE |
| <i>Pawsonellus</i> Thandar, 1986 | | <i>Patinapta</i> Heding, 1928 | |
| <i>P. africanus</i> Thandar, 1986 | LE | <i>P. crosslandi</i> Heding, 1929 | WIO |
| <i>Pseudocolochirus</i> Pearson, 1910 | | Chiridotidae Oestergren 1898 | |
| <i>P. violaceus</i> (Théel, 1886) | IWP | <i>Chiridota</i> Eschscholtz, 1829 | |
| <i>Roweia</i> Thandar, 1985 | | <i>C. rigida</i> Semper, 1868 | IWP |
| <i>R. frauenfeldi webbi</i> (Thandar, 1977) | SAE | <i>C. durbanensis</i> Thandar, 1996 | LE |
| <i>Staurothyone</i> H.L. Clark, 1938 | | <i>Polycheira</i> H.L. Clark, 1907 | |
| <i>S. rosacea</i> (Semper, 1869) | WIO | <i>P. fusca</i> (Quoy & Gaimard, 1833) | IWP |
| Thyonidiinae Heding & Panning, 1954 | | | |
| <i>Neocucumis</i> Deichmann, 1944 | | | |
| <i>N. kilburni</i> Rajpal & Thandar, 1998 | LE | | |

* Components: IP = Indo Pacific, IWP = Indo-West Pacific, LE = local endemic, SAE = southern African endemic, WIO = West Indian Ocean.

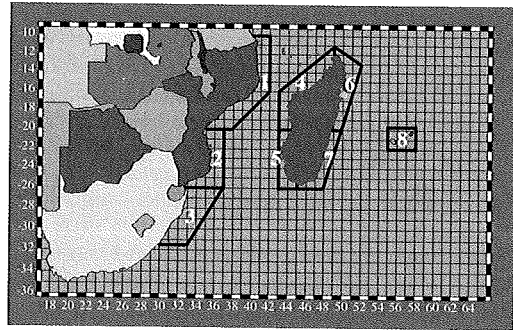


Figure 2. Map with the eight OGU's. 1 = NMOz; 2 = SMOz; 3 = ECSA; 4 = NWMad; 5 = SWMad; 6 = NEMad; 7 = SEMad and 8 = Mids (abbreviations in text).

4.2 Data acquisition

The bulk of the shallow-water distribution data is obtained from Samyn & Tallon (2003, see also Samyn 2003). Few other species, identified with certainty but not yet published, were also incorporated. All distribution data were transformed into a presence/absence dataset for each OGU. Uncertain species and/or records were omitted. The resulting dataset holds 171 species belonging to 52 genera, 7 families and 3 orders.

4.3 Analyses

The similarities amongst the OGU's were determined by calculating some of the more commonly used β -diversity coefficients: the Dice (or Sorenson), the Jaccard and the First and Second Kulczynski coefficients (see also Price 1982, Magurran 1988 and Samyn & Tallon 2003) of which the formulae are given below. Dendrograms were produced by hierarchical cluster analysis with average linkage (with SPSS v. 10 for Mac).

$$\text{Dice/Sorenson : } C_d = 2j/(a + b - j)$$

$$\text{Jaccard : } C_j = j/(a + b - j)$$

where a = no. of spp. in site A; b = no. of spp. in site B; j = no. of spp. in both sites

$$\text{1st Kulczynski : } C_{k1} = s/(u + v)$$

$$\text{2nd Kulczynski : } C_{k2} = 1/2 * [s/(s + u) + s/(s + v)]$$

where s = no. of spp. in sites A & B; u = A/B; v = B/A.

5 RESULTS

When only six OGU's (East and West Madagascar not split into their respective northern and southern parts) are considered, clustering with the Dice, the Jaccard and the 1st Kulczynski coefficients all give the same

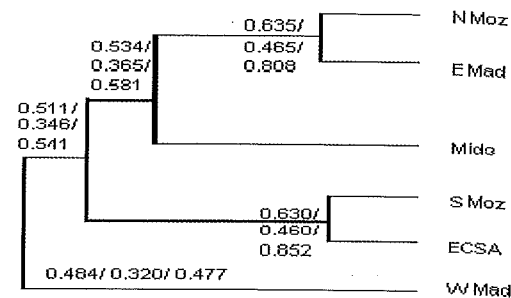


Figure 3. Dendrogram of holothuroid assemblage relationships in the south-west Indian Ocean using average linkage (between six OGU's) produced by clustering with the Dice, the Jaccard and the first Kulczynski coefficients. Numbers indicate the respective similarity coefficients.

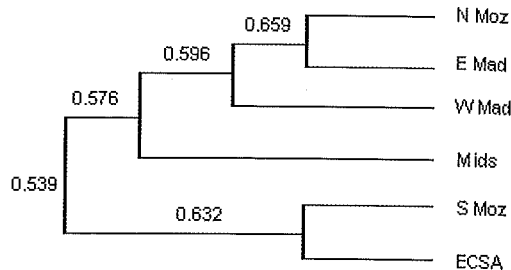


Figure 4. Dendrogram of holothuroid assemblage relationships in the south-west Indian Ocean using average linkage (between six OGU's) produced by clustering with the second Kulczynski coefficient.

topology (Fig. 3). WMad returns as most dissimilar from the other OGU's; NMOz & EMad on the one hand and SMOz & ECSA on the other, share the most species. Mids is more similar to the NMOz-EMad grouping than to the SMOz-ECSA cluster.

Application of the 2nd Kulczynski coefficient (Fig. 4), which behaves more robustly when disproportionate species numbers are considered, shows that WMad clusters with the NMOz-EMad group as well as with the Mids. Once again SMOz and ECSA share more species with each other than with the northern OGU's.

Cluster analyses, using the Dice, the Jaccard and the 1st Kulczynski coefficients, with East and West Madagascar further split into northern and southern parts, again exposes just one topology (Fig. 5). Here, the hierarchical clustering returns the following topology: SMOz and NMOz are more similar to each other than to ECSA; NWMad and SWMad cluster together and are most similar to the NMOz-SMOz-ECSA grouping; Mids groups with the continental and WMad cluster rather than with the more nearby NEMad-SEMad cluster; NEMad and SEMad are more similar to each other than to any of the other OGU's.

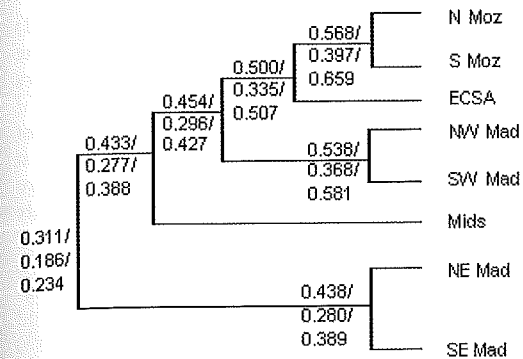


Figure 5. Dendrogram of holothuroid assemblage relationships in the south-west Indian Ocean using average linkage (between eight OGU's) produced by clustering with the Dice, the Jaccard and the first Kulczynski coefficients. Numbers indicate the respective similarity coefficients.

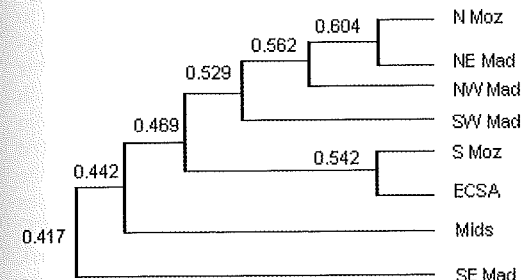


Figure 6. Dendrogram of holothuroid assemblage relationships in the south-west Indian Ocean using average linkage (between eight OGU's) produced by clustering with the second Kulczynski coefficient.

However, when employing the 2nd Kulczynski coefficient (Fig. 6), NMOz and NEMad show the highest faunistic similarity ($C_{k2} = 0.604$), closely followed by NMOz-NEMad-NWMad ($C_{k2} = 0.562$) and the SMOz-ECSA association ($C_{k2} = 0.542$). The fauna of SWMad is most similar to that of the NMOz-NEMad-NWMad cluster ($C_{k2} = 0.529$), while the SMOz-ECSA grouping appears quite dissimilar from the above faunal assemblage ($C_{k2} = 0.469$). The same applies for Mids and especially SEMad, which return as most dissimilar from all other OGU's ($C_{k2} = 0.442$ and 0.417 respectively).

6 DISCUSSION

6.1 Quality and reliability of the dataset

For a study of this nature one requires rigid data on the number of taxa, their correct identifications, the number of sampling localities and efforts, and the

distribution ranges. For example, our additions of several new species and records collected off the KwaZulu-Natal coast, significantly improved the dataset. Nevertheless, species described on only a single specimen or from a single locality in the study area unmistakably give a negative bias to the faunistic relationships we here uncovered. As such, further *in situ* inventories undoubtedly will allow the recovery of additional records of poorly known species and thus will permit a more precise and robust evaluation of the faunistic similarities. However, given the fact that (over) exploitation currently threatens the holothuroid fauna of the western Indian Ocean, we must urgently understand the faunistics in order to protect the fauna in a scientifically correct way (see also Samyn 2000).

6.2 Regional similarities

Prior to discussing the regional similarities between the arbitrarily defined OGU's, it must be noted that the inter-OGU variability is relatively small (cfr. Figs 3-6, where all β -diversity coefficients are relatively large and have a narrow spreading), suggesting that the study area is rather homogeneous in terms of species composition.

Results obtained in the analyses of the six OGU's, irrespective of the similarity coefficient used (Figs 3, 4), invariably show that NMOz & EMad on the one hand, and SMOz & ECSA on the other, have the highest similarity in species composition. The grouping of NMOz with EMad can readily be explained by the SEC which, when bifurcating at the east coast of Madagascar (around 20°S), has its northern branch turning westward at the most northern point of Madagascar, reaching NMOz (Fig. 1). The cluster of SMOz with ECSA is explainable due to the southward flowing Mozambique-Agulhas Current system. The positions of WMad and Mids, on the other hand, are more difficult to interpret. Here we have to remember the disproportionate large number of species that have been reported from the latter two OGU's. Indeed, the descriptions of many new endemics from Mauritius by Haacke (1880), many never found again, and the many single specimen new species described by Cherbonnier (1988) from WMad, undoubtedly have pushed the faunistic similarity to a lower level.

Clustering of the six original OGU's using the second Kulczynski coefficient (Fig. 4), places Mids and WMad in the same cluster as NMOz and EMad. Such clustering again roughly reflects current patterns. Indeed, the SEC brings species across the Indian Ocean into Mids and then into EMad where the SEC bifurcates into north- and southbound branches. The northern limb of the SEC turns westward at the tip of Madagascar and flows up to the continent where it again splits into a northern (forming the EACC) and a southern branch (forming the MoC). This southern

limb (the MoC) can be considered the responsible vector for bringing EMad species into NMOz and WMad. This connectivity is further strengthened by the action of the southbound branch of the SEC, the EMaC (and associated NMaC). This current, which at the southern tip of Madagascar turns west and then northwards (especially during austral summer) into the Mozambique Channel, perhaps reaches as far as NMOz and thus could also bring species in from MIDs and EMad.

In order to test the hypothesis that the different current systems operating in the south-west Indian Ocean influence the faunistic relationships, EMad and WMad were subsequently split into northern and southern parts. The clustering obtained with the Dice, the Jaccard and the first Kulczynski coefficients (Fig. 5) in this situation becomes even more skewed because of disproportionate numbers of species and thus only the dendrogram based on the second Kulczynski coefficient (Fig. 6) is here discussed. Classification with the latter coefficient groups NMOz with NEMad, NWMad and SWMad on the one hand and SMOz and ECSA on the other; MIDs and especially SEMad return as most dissimilar in species composition. Since SEMad does not cluster with NEMad, an important species turnover must occur at the East-Madagascar bifurcation point of the SEC. The clustering of the ECSA-SMOz assemblage with the NMOz-NEMad-NWMad-SWMad grouping rather than with SEMad, seems to indicate that fewer ECSA species have come in with the EMaC (and associated NMaC) than with the MoC. Thus, the majority of ECSA species have come in from the north, through the Mozambique Channel, *i.e.*, mainly from SMOz, NMOz, NEMad and WMad. The relatively low second Kulczynski coefficient ($C_{k2} = 0.469$) between the SMOz-ECSA and the NMOz-NEMad-NWMad-SWMad clusters might be an indication that SMOz and ECSA have received species from yet another location: the warm temperate province, south of ECSA. A vector for such transport is the Agulhas Counter Current (ACC), flowing northward from the Cape up to roughly Durban, in combination with the recurrent eddies in the Natal Bight (see below). The present dataset does not hold data on the stretch of coast south of 31.5°S and thus verification of this scenario is here not possible. However, since Samyn & Tallon (2003) have conclusively demonstrated that the faunistic similarity between the temperate South African region and ECSA is very small, the action of the ACC (or the recurrent eddies) appear to be negligible in transporting warm temperate species into the ECSA region.

Given the flow of the NMaC (as a northern retroflexion of the EMaC), which connects SEMad with WMad, it is enigmatic why the holothuroid faunas of the latter two OGU's are not more interconnected. Somehow, a yet to be identified barrier between these two OGU's must be in place. DiMarco et al. (2000 and

Lutjeharms & Machu 2000, in DiMarco et al. 2002) have already provided us with some clues as to the nature of this barrier. According to these authors the acceleration of the narrow southbound part of the EMaC along the steep continental slope of East Madagascar induces upwelling inshore, especially at the southern most part of Madagascar where the shore widens. This phenomenon, which may significantly lower the sea temperature, possibly reflects the filter we are looking for. Whether this possible barrier affects warm water-loving, benthic-feeding species (belonging to the aspidochirotid families Holothuriidae and Stichopodidae and to the apodid family Synaptidae) differently than cold water-loving, suspension-feeding species (belonging to the dendrochirotid families and to the apodid family Chiridotidae), needs further investigations. Herefore taxonomic composition (at the level of the families) across latitudes and longitudes should be examined.

In conclusion, we can state that the fauna of ECSA is most similar to that of SMOz and to a lesser extent to that of WMad and NEMad (which is, due to the current system, intimately connected with NMOz). This similarity results from tropical stragglers moving south and south-west (with the flow of the MoC), either from northern Mozambique and West Madagascar (linked with NEMad) respectively. However, since the Mozambique-Agulhas Current cools as it progresses (surface water temperatures of between 28°–22°C between southern Mozambique and Port St. Johns), the limits attained by each species is defined by the increasing coldness of the water (Thandar 1989). From our dataset it can be seen that about 30 holothuroid species occurring in southern Mozambique have this far not been recorded from the subtropical east coast of South Africa and about 20 species occurring in north-east coast of South Africa fail to move south, beyond the St. Lucia estuary. This corresponds largely to the results obtained by Samyn & Thandar (2003a) on the echinoderm fauna of KwaZulu-Natal.

6.3 Faunal components

Of the 55 species of shallow-water holothuroids currently known from the east coast of South Africa, 31 species are Indo-Pacific, 5 West Indian Ocean, 11 southern African (including S. Madagascar) endemics and 8 local (ECSA) endemics (Table 1). When West Indian Ocean species are lumped with the Indo-Pacific species we obtain a 65.5% Indo-Pacific component as opposed to a 34.5% endemic component, different from the figures given by Samyn & Thandar (2003a) for KwaZulu-Natal echinoderms (73% and 21% respectively). The local endemic component (8 species) makes up about 15% of the fauna of ECSA, but when we add to these the five local SMOz endemics, this figure rises to 18%, close to 20% required by

Clark (1946), Ekman (1967) and others to justify Australian provinces. Briggs (1974, 1999), on the other hand, suggested a figure as low as 10%. Thus the area between SMOz and Port St Johns in South Africa is correctly treated as a subtropical province.

6.4 The Natal Bight

Despite much work on the east coast of South Africa by both oceanographers and marine biologists alike, the interpretation of its faunistics is not easy. This has recently been pointed out for the KwaZulu-Natal echinoderms by Samyn & Thandar (2003a), who also alluded to the paucity of the fauna in the Natal Bight. This area (Fig. 7) is a stretch of about 160 km of coastline between Cape St Lucia in the north to just south of Durban in the south (Meyer et al. 2002), with a high species turnover north and south of these points respectively (Samyn & Thandar 2003a). Off-shore of the northern part of this region lies the meeting place of the MoC and EMaC to form the AC (Fig. 1), drastically affecting the oceanography here. The latter current flows close inshore, due to the narrow continental shelf, but as it reaches Cape St. Lucia it moves off-shore. Here, the change in the trajectory of the current induces frequent upwellings, lowering the surface-water temperature to some extent. In addition, the shallower shelf and the increased river discharges induce high levels of turbidity, especially at

the mouth of the Tugela, KwaZulu-Natal's largest river. Here the shelf reaches its widest point, extending some 40 km off-shore (Schumann 1987.) Just off this point to Cape St. Lucia and just south of Durban, recurrent eddies are generated, making the Bight a variable current region with sporadic, patchy and small-scale upwelling (Malan & Schumann 1979) with correspondingly patchy nutrient distribution. These factors, in combination, may drastically influence the distribution patterns of the various species. In fact, only a few intertidal species of holothuroids, mostly southern African and local endemics, have been recorded from this region. While this may be a reflection of the low degree of sampling, possibly due to turbid, shark-infested waters, it is clear that there is grave paucity of holothuroids and other echinoderms in this region. According to Schumann (1982) there can be frequent temperature changes of 5°C or more over a period of a day. This may prevent tropical species from becoming established here. The cooler water temperatures, in addition to recurrent eddies and frequent current reversals, are perhaps responsible for the extension of the ranges of the southern warm-temperate suspension-feeding dendrochirotid up the east coast, with some species reaching southern Mozambique and even southern Madagascar.

7 CONCLUSIONS

Describing and understanding patterns of biodiversity always involve gross abstractions because these patterns are subject to several environmental and historical factors that contribute to faunal distribution patterns (most notably physical variables as habitat availability, depth, water temperature and geological history and also biological variables such as productivity, dispersion capacity, extinction and speciation) that operate at different scales. The present paper nevertheless demonstrates a correlation between the present day current patterns and the regional biogeography.

ACKNOWLEDGEMENTS

Financial and other support from the Flemish Community [Bilateral (International) Scientific and technological Cooperation; project numbers BIL98/84 and BIL01/46], the National Research Foundation (South Africa) and the university of KwaZulu-Natal (South Africa) and the Vrije Universiteit Brussel (Belgium) is greatly acknowledged. We are also greatly indebted to Peter Timm of Triton Divers, Sodwana Bay, who took one of us (Y.S.) to the non-tourist trap dive spots in his back garden. We also wish to thank Irena Tallon, Tim O'Hara and an anonymous referee for providing excellent feedback on the draft version of this paper.

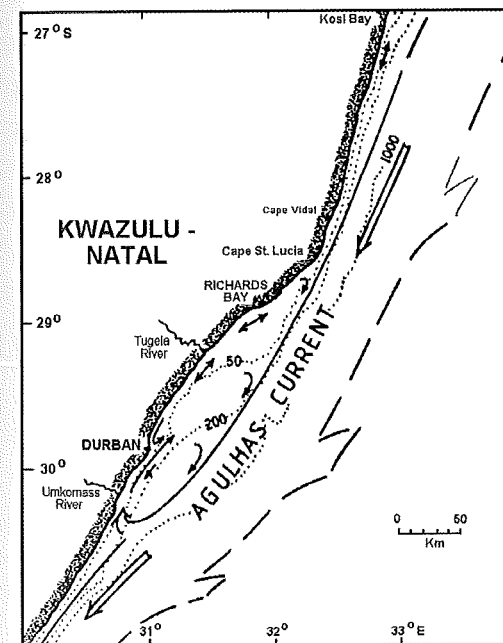


Figure 7. Mean current structures off the Natal Bight (after Schumann 1987).

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