

# Coastal sponge communities of the West Indian Ocean: taxonomic affinities, richness and diversity

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## Abstract

Sponges assemblages were sampled in four coastal study regions (Malindi, Kenya; Quirimba Archipelago, northern Mozambique; Inhaca Island, Southern Mozambique and Anakao, Madagascar) in the west Indian Ocean. Sponge species were counted in multiple 0.5 m<sup>2</sup> quadrats at depths of between 0 and 20 m at a number of sites within localities within each region. Despite the relatively small areas sampled, sponge samples comprised a total of 130 species and 70 genera of the classes Demospongiae and Calcarea. Sponges are clearly a major taxon in these regions in terms of numbers of species, percentage cover or biomass, although their ecology in the west Indian Ocean is virtually unknown. Nearly half of the genera, e.g. *Iotrochota*, found were species with a so-called Tethyan distribution. Most of the other genera were cosmopolitan, e.g. *Clathria*, but some were cold water (*Coelospheera*), Indo-Australian (*Ianthella*) or circum-African (*Crambe*). Many of the species encountered in the present study occurred in at least two study regions, many in more and could occupy large areas of substratum. Some of these, e.g. *Xestospongia exigua*, are commonly found throughout the Indo-west Pacific region where they also occupy much space. The endemism of the shallow water sponge faunas in East Africa (20–25%) seem to be high within the Indo-Pacific realm but are lower than northern Papua New Guinea. The tropical regions (Kenya and Northern Mozambique) were more speciose than subtropical regions (southern Mozambique and Madagascar) but not significantly more diverse (Shannon  $H'$ ). Although latitude was not a major influence on sponge community patterns, hard substratum assemblages did

form a cline from the tropics to Southern Mozambique, linked by Madagascar. Substratum nature (habitat) was most important in influencing the suite and number of species present. Sponge assemblages of soft substrata were much more dissimilar, both within and between habitats, than those on hard substrata. There was a predictable variability in species richness between hard substratum habitats: coral reefs being speciose and caves being less so. Our findings showed that both patterns and influences on species richness may be decoupled from those influencing diversity. In our data species richness, but not diversity, showed striking regional and bathymetric trends. In addition, sponge species richness mainly split at coral reef vs. non-reef habitats, whilst diversity divided principally into assemblages on hard and soft substrata. We consider this dichotomy of findings between species richness and diversity values to be important, as these are two principal measures used for the interpretation of biodiversity.

**Key words:** sponge, diversity richness, zonation, Madagascar, Mozambique

## Résumé

On a récolté des assemblages d'éponges dans quatre zones d'étude côtières (Malindi, Kenya; archipel de Quirimba, nord du Mozambique; île d'Inhaca, sud du Mozambique et; Anakao, Madagascar) de la partie occidentale de l'océan Indien. On a compté les espèces d'éponges sur de multiples quadrats de 0.5 m<sup>2</sup>, à des profondeurs allant de 0 à 20 m, en de nombreux endroits pour chaque région. Malgré la surface relativement restreinte des échantillons, les prélèvements comprenaient 130 espèces et 70 genres des classes Demospongiae et Calcarea. Les éponges sont à l'évidence un taxon majeur dans ces régions en termes de nombre d'espèces, de pourcentage de couverture ou de biomasse, même si leur écologie est

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à peu près inconnue dans l'ouest de l'océan indien. Près de la moitié des genres trouvés, ex. *Iotrochota*, étaient des espèces avec une distribution dite "Téthienne". La plupart des autres genres avaient une distribution cosmopolite, comme *Clathria*, mais certains étaient des genres d'eau froide (*Coelosphaera*), de la région indo-australienne (*Ianthella*) ou du pourtour africain (*Crambe*). De nombreuses espèces rencontrées lors de la présente étude se retrouvaient dans au moins deux régions différentes, de nombreuses dans plus de deux, et elles pouvaient occuper de grandes surfaces du substrat. Certaines d'entre elles, par exemple *Xestospongia exigua*, se trouvent communément dans toute la région indo-pacifique occidentale où elles occupent aussi de grands espaces. Le caractère endémique de la faune spongiaire de faible profondeur en Afrique de l'Est (20–25%) semble être élevé dans la zone indo-pacifique, mais il est plus bas que dans le nord de la Papouasie-Nouvelle Guinée. Les régions tropicales (Kenya et nord du Mozambique) abritaient plus d'espèces que les régions sub-tropicales (sud du Mozambique et Madagascar), mais n'étaient pas significativement plus diverses (*H'* de Shannon). Bien que la latitude n'exerce pas beaucoup d'influence sur les schémas des communautés d'éponges, les assemblages de substrats durs forment une courbe des tropiques vers le sud du Mozambique, liée par Madagascar. La nature du substrat (habitat) avait une influence plus importante sur la succession et le nombre des espèces présentes. Les assemblages d'éponges sur les substrats mous étaient beaucoup plus dissemblables, tant au sein qu'entre les habitats, que ceux des substrats durs. Il y avait une variabilité prévisible dans la richesse des espèces entre les habitats des substrats durs, les récifs coralliens étant plus riches et les grottes l'étant moins. Notre étude montre que l'on peut dissocier les patterns et les caractéristiques qui influencent la richesse des espèces de celles qui influencent leur diversité. Nos données sur la richesse des espèces, pas leur diversité, révèlent des tendances régionales et bathymétriques étonnantes. De plus, la richesse des espèces d'éponges se divisait principalement entre récifs coralliens *versus* habitats non coralliens, tandis que la diversité se divisait surtout entre assemblages de substrats mous ou durs. Nous estimons que cette dichotomie de nos découvertes entre richesse et diversité des espèces est importante, parce que ce sont deux mesures majeures utilisées pour l'interprétation de la biodiversité.

## Introduction

Global and regional patterns and trends in species diversity, both in time and space, have generated serious research and conservation discussion for a number of decades. The magnitude and rate of taxon increase with time seems to be robust (Jablonski, 1999). Strong evidence from certain taxa has suggested periodic bursts of speciation (see Jackson & Cheetham, 1990). Inter-oceanic differences in species numbers have rarely been compared directly, but for many taxa diversity is greatest in the Indo-West Pacific region (Stehli, McAlester & Helsley, 1967; Stehli & Wells, 1971; Briggs, 1987; van Soest, 1994). Interpretations of numbers of species per unit area have been confounded and complicated by various factors. These include taxonomic considerations and species ranges (e.g. Knowlton & Jackson, 1994), differential area with latitude (e.g. Rosenweig, 1995; Rhode, 1997), geological age (Clarke & Crame, 1996) and intensity of scientific sampling. As in the terrestrial environment, a marine latitudinal cline in species numbers in the northern hemisphere appears to be real (Pianka, 1966; Roy, Jablonski & Valentine, 1996; Clarke & Lidgard, 2000). In the southern hemisphere, patterns are less clear-cut and many taxa are well represented in the Southern Ocean (Clarke, 1992).

Sponges are one taxon that have been well represented globally in aquatic environs (above 2000 m) since the Cambrian period. They are, however, poorly represented in the literature, mainly because of their relative difficulty of identification. Like many other groups, sponges appear to be most speciose in the Indo-West Pacific (Hooper & Lévi, 1994; Van Soest, 1994) but may locally dominate assemblages in polar (Dayton, Robilliard & Paine, 1970), temperate (van Soest & Weinberg, 1980; Picton, 1991), sub-tropical (Sim, 1994) and tropical (Barnes, 1999) localities. The contribution of sponges to Caribbean coral reefs has been particularly well documented (Hartman & Goreau, 1970; Alcolado, 1990; Diaz, Alvarez & Laughlin, 1990; Schmahl, 1990; Wulff, 1995) whilst little beyond species lists and presence or absence, comparatively little is known from East African shores (Rützler, 1972; Thomas, 1979; van Soest, 1993, 1994). East African (or West Indian Ocean) sponges seem to have strongest affinities with Indonesia, rather than geographically closer areas of continental shelf such as India, the Red Sea, South Africa or West Africa (Van Soest, 1994). Despite the paucity of information, it is thought that East Africa sponges may have a particularly important contribution to coastal assemblages. In northern Mozam-

bique, sponges are one of the most speciose and diverse taxa (Barnes, 1999; Bell & Barnes, 2001) and may outnumber corals on the Barrier Reef of Madagascar (Vacelet & Vasseur, 1965, 1977; cf. Pichon, 1978; Gabri   *et al.*, 2000).

There is clearly a considerable heterogeneity in the current knowledge of extant (and fossil) sponges by region. Equally, a sharp divide is apparent between information known about deep water sponges and more poorly known, but richer, shallow water sponges. For example of the  $\approx 5000$  species estimated to be in the Australian region, only a third are known and the poorest represented area is shallow water cryptic species associated with corals (Hooper & L  vi, 1994). In addition there may be quite different patterns associated with shallow and deep water species, such as in level of endemism. Deep water sponges seem to share a greater level of commonality, possibly due to being relicts of a Palaeozoic Tethys Sea fauna (L  vi & L  vi, 1988). Like some other localities in the Indo-west Pacific Ocean, such as Papua New Guinea, an examination of the shallow water sponges of East Africa is needed, and may be useful for addressing global patterns and trends.

Apart from geographical region and bathymetry, many factors may influence the species richness or diversity of a taxon, such as the Porifera (sponges). These may include properties of the water mass, weather, or substratum type. As with ecological investigations on any taxon, the influence of various parameters on sponges must be accounted for simultaneously for powerful conclusions. In this study, we investigate the species composition of west Indian Ocean sponge assemblages using univariate and multivariate techniques. We ask: (i) are there significant differences in species richness between habitats, depths and regions and which are most speciose? (ii) How much overlap in habitat, depth and region is there of individual sponge taxa? (iii) Do suites of species form distinct clusters under multivariate analyses. If so, which of the environmental variables examined is most explanatory of such patterns? (iv) How distinct is the Madagascan sponge fauna considering its long period of separation (by deep channel) from East Africa or is faunal similarity more aligned with latitude? (v) How does species diversity (Shannon  $H'$  and  $J$ -values) change with environmental characteristics of sites?

### Study site and methods

Sponges were sampled in four coastal study regions (Malindi, Kenya [K]; Quirimba Archipelago, northern

Mozambique [Q]; Inhaca Island, Southern Mozambique [I], Anakao, Madagascar [A]) in the west Indian Ocean (Fig. 1). Additional minor observations were made at two other localities; Pemba [P], in northern Mozambique (50 km south of study locality 1) and Toliara [T], in south-west Madagascar (30 km north of study locality 3). Within each region, four localities were chosen, and within each locality three sites were chosen. Finally, within each site a minimum of 10 quadrats ( $0.5 \text{ m}^2$ ) were sampled at 5 m intervals at whatever depths were present within the confines of each site (0, 5, 10, 15 and 20 m). The scales investigated by the present study were region (100s km apart), locality (1 km apart), site (10s m apart) and quadrat (1 m apart). Both exposed and sheltered (coral reef) localities were selected within each region. Only two localities (one exposed and one sheltered) were studied at one region [I].

Species were photographed, and microcores taken (for spicule analysis). Sand, seagrass, mangrove and coral reef habitats were present and sampled at each study locality. The Mozambique mangroves were dominated by *Rhizophora mucronata*, while those in Madagascar were principally composed of *Avicennia marina*, but *Ceriops tagal* and *Sonneratia alba* amongst other trees were also present at both. Seagrasses were highly speciose at region Q (Mario Carvalho unpublished data) but fewer species are known at study regions I (Kalk, 1995) and T (Cooke, Ratamahenina & Ranaivoson *et al.*, 2000). *Thalassia hemprichii*, *Hathodula* sp. and *Cymodocea* sp. occur at all regions. Similarly, the coral reef habitat of Q was characterized by more than 55 coral genera (Barnes & Whittington, 1999), whilst fewer corals are known from I (Kalk, 1995). More than 200 coral species are known from the barrier reef between regions T and A (Pichon, 1978). At least three of the four main study regions have experienced large scale and regular environmental disturbance in the form of storms, floods and extensive bleaching and mortality of corals following the El ni  o events of the last decade (see e.g. Barnes & Whittington, 1999; Cooke *et al.*, 2000).

Although the resolution of this study was at species level, the species of many genera were not identified. Identification was made using literature (de Laubenfels, 1954; L  vi, 1961; Vacelet & Vasseur, 1965; Vacelet, Vasseur & L  vi, 1976; Thomas, 1979; Pulitzer-Finali, 1993; Richmond, 1997) and specimens at the Frontier marine stations, collaborating local institutes and universities. The occurrence of sponge species was assessed using 10–20 quadrats ( $0.5 \text{ m}^2$ ) in each depth zone (0, 5, 10, 15 and

20 m where possible) of each site of each locality. At some sites, additional observations were recorded at 25 and 30 m depths. Most sites were only represented by a subset of the depth zones due to substratum profile. All habitats present at each site were sampled, but not all habitats (coral reef, sand, seagrass meadow, mangroves) were present in all zones of all study sites. The number (of individuals) and identification of all sponge species present and total space occupied (% cover) was recorded for each quadrat. Diversity of sponge species was analysed using the Shannon–Weiner information function outputting  $H'$  and  $J$ -values in base- $e$ . Clustering was analysed using dendrogram and ordination techniques on combined data of 10 quadrats for each depth of each site. Bray–Curtis similarity analysis, using hierarchical agglomerative group average clustering, was performed on the full species abundance data with the unweighted pair group method with arithmetic averages (UPGMA) and the PRIMER computer program (Plymouth Marine Laboratory). Data was  $\log(x + 1)$  transformed to reduce the importance of extreme values. Ordination of samples was performed using Correspondence Analysis upon transformed data (as above).

## Results

Sponges were a common, and in certain sites, dominant component of the sessile fauna and occasionally even a dominant component of the total fauna. A total of 130 species were recorded, belonging to 70 genera of the classes Demospongiae and Calcarea. A few genera were present at all depths of all regions, from intertidal shallows to 20 m, such as *Haliclona*, whilst others, e.g. *Plakinastrella*, were present at only one depth at one locality (Table 1). There was a significant small (quadrat) scale variability between sites and depths (within habitat and exposure types) in both the number of species and number of sponges (Kruskal–Wallis, all  $P < 0.01$ ). However, in only one study region, A, was there a significant difference between locality variation (locality 2 was characterized by a highly speciose assemblage occupying much of the primary space, see Table 2). At locality 2 [A] there were approximately fourfold as many species per unit area as in other localities (in region A) and more than twice the amount of space colonized by sponges. Overall, the two tropical regions were significantly more speciose (Kruskal–Wallis on reef quadrats,  $n = 32$ , d.f. = 1,  $H = 6.8$ ,  $P = 0.007$ ) and occupied more primary space (Kruskal–Wallis on reef quadrats,  $n = 32$ , d.f. = 1,  $H = 4.2$ ,  $P = 0.04$ ) than

the two subtropical regions. Only in region Q was there a significant difference between exposed and sheltered coral reefs in terms of the sponge species richness and space occupation. Values of both were proportionally higher at sheltered localities within this region (Kruskal–Wallis on Q reef quadrats,  $n = 10$ , d.f. = 1,  $H = 4$ ,  $P = 0.033$  (species) and  $n = 10$ , d.f. = 1,  $H = 5.07$  (space),  $P = 0.02$ ). Observations in the coastal environments at P and T suggested that the sponge communities of both localities were depauperate in terms of sponge abundance and richness.

Species richness also altered with depth and habitat (Fig. 2). Typically (for a given habitat) species richness was lowest in the intertidal zone and/or conversely the deepest end of the transect (20–30 m). Species richness generally peaked at 10–15 m depth in most habitats and regions. Coral reefs (Fig. 2a,b) were the most speciose habitat. Sand (Fig. 2c), mangroves and seagrass meadows (not illustrated), in contrast, were depauperate. The other hard substrata habitats, caves (Fig. 2d) and boulders (not illustrated), had intermediate species richness. These showed least change in species numbers with depth. There was little difference between regions in any of the study habitats, although generally they were ranked in latitudinal sequence (decreasing species richness with increasing latitude).

Diversity (Shannon  $H'$ ) values ranged from 3 (in exposed coral-reefs at A) to 0.8 (on sand at I). There was no significant difference between regions (within habitats) in species diversity and there was no obvious pattern with depth (Kruskal–Wallis, all  $P > 0.05$ ). Although Shannon  $H'$  values peaked at mid-study depth in some habitats, they were lowest in others. The range of values within each habitat was small (Fig. 3). Exposed and sheltered coral-reef habitats were the most diverse assemblages and were not significantly different (Kruskal–Wallis on reef quadrats,  $n = 34$ , d.f. = 1,  $H = 2.8$ ,  $P = 0.096$ ) from each other. The diversity of cave, boulder and seagrass habitats differed little, and with the exception of the intertidal zone, were all more diverse than those on sand. Mangrove values (not shown in Fig. 3, due to the lack of bathymetric range) were similar to those in seagrass meadows. The sponge assemblages of hard substratum habitats were therefore all more diverse than those on soft substratum. Evenness (Shannon  $J$ ) values ranged from 0.98 in intertidal caves to 0.67 on sand, but there were no significant differences between region, depth or habitat (Kruskal–Wallis, all  $P > 0.05$ ).

Malindi -3, 2167 Inhaca Is. -26, 0278  
 40, 0167 32, 9044  
 Quirimba -12, 4089  
 40, 5992

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= Quirimba Archipelago = Inhaca Island

Table 1 Sponge taxa recorded with depth (m) and region. The symbols are ● (hard substratum) and ○ (soft substratum)

Species	Kenya (K) = Malindi					N. Mozambique (Q)					S. Mozambique (I)				SW Madagascar (A) = Anakao					
	0	5	10	15	20	0	5	10	15	20	0	5	10	15	0	5	10	15	20	
<del>Aaptos sp.</del>	○					○														
<del>Acanthella klethra</del>				●	●													●	●	
<del>Acanthella sp.</del>				●	●														●	
<del>Adocia atra</del>			○	●	●	○	●	●	●											
<del>Aplysilla sulfurea</del>								●					○			●	●	●	●	
<del>Aplysina sp.</del>						○	○													
<del>Astroclera willejana</del>								●				●	●		○	●	●			
<del>Axinella carteri</del>				●	●			●	●	●								●	●	
<del>Axinella sp.</del>								●	●											
<del>Axinyssa topsenti</del>	●	●	●	●		●														
<del>Biemna sp.</del>	○					○														
<del>Biemna fortis</del>	○	○				○	○													
<del>Callipelta sp.</del>															○	○	○			
<del>Callyspongia eonfoederata</del>		●	●	●	●	●	●	●	●			●	●							
<del>Callyspongia sp.</del>			●	●	●			●	●											
<del>Carteriospongia foliascens</del>	●					●						●								
<del>Chondrilla nucula</del>															○	●	○	●	●	
<del>Cribrachalina sp.1</del>								●	●											
<del>Cribrachalina sp.2</del>																				
<del>Clathrina darwinii</del>		○				○						○				●	●	●		
<del>Clathrina sp.</del>		○																		
<del>Clathria pulcherrima</del>													●					●	●	
<del>Clathria frondifera</del>	○					○														
<del>Clathria sp.</del>	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	
<del>Clathria sp.</del>				●				●	●											
<del>Ctiona sp.</del>	●	●				○					●	●	●	●	●	○	○		○	
<del>Cinachyrella voeltzkowii</del>	○					○														
<del>Ciocalypta sp.</del>	○					○	○					○	○							
<del>Ciocalypta crostrongilata</del>																			●	
<del>Coelosphaera sp.</del>								○							●	●		●		
<del>Crambe acuata</del>	●																			
<del>Crambe crambe</del>		●	●	●		●	●	●	●			●			●	●	●	●		
<del>Crambe sp.</del>			●					●	●											
<del>Cribrachalina sp.1</del>								●	●											
<del>Cribrachalina sp.2</del>								●												
<del>Discodermia sp.1</del>																		●		
<del>Discodermia sp.2</del>															○					
<del>Dysidea sp.1</del>	●	●	●	●		●	○	●	●	○		●	●	●	○	○	○	●		
<del>Dysidea sp.2</del>																			●	
<del>Echinodictyum sp.1</del>				●	●															
<del>Echinodictyum sp.2</del>								●	●	●									●	
<del>Ecionemia rotundum</del>												○			○					
<del>Erylus lendenfeldi</del>																	●	●		
<del>Gelliodes incrustans</del>	●	●	●	●	●	●	○	○	○	○	●	●	●	○	○	○	●	●	●	
<del>Gelliodes sp.1</del>								○	○	○										
<del>Gelliodes sp.2</del>																		●		
<del>Gellius cymiformis</del>															○	○				
<del>Geodia crustosa</del>	○					○	○	○	○	○										
<del>Halichondria sp.</del>											●	●	●	●	○	○	○	○	●	

Table 1 continued

Species	<i>Insindi</i> Kenya (K)					<i>Quissimba</i> N. Mozambique (Q)					<i>Inhaca</i> S. Mozambique (I)				<i>Anakao</i> SW Madagascar (A)					
	0	5	10	15	20	0	5	10	15	20	0	5	10	15	0	5	10	15	20	
<i>Haliclona</i> sp.1	○					○	○				○					○	○	○		
<i>Haliclona</i> sp.2	○	○	○			○	○	○	○		○									
<i>Haliclona</i> sp.3				●	●					●			●						●	●
<i>Haliclona</i> sp.4													●						●	●
<i>Haliclona</i> sp.5																			●	
<i>Hymedesmia</i> sp.1																		○		
<i>Hymedesmia</i> sp.2																		●		
<i>Hymeniacidon conulosa</i>	○	●	●	●		○	○				●	○	○		○	○	○			
<i>Ianthella basta</i>				●	●			●	●	●										
<i>Ianthella</i> sp.								●	●											●
<i>Iotrochota</i> sp.	●	●				●														
<i>Ircinia ramosa</i>		●	○					○	○				○	○						
<i>Ircinia</i> sp.				●	●					●									●	●
<i>Jaspis johnstoni</i>		●	●	●		●	○	●			●	●						●	●	●
<i>Jaspis</i> sp.				●			○	●										●	●	
<i>Kallypidion fascigera</i>		●	●	●	●			●	●	●										
<i>Laxosuberites arenosus</i>																		●	●	●
<i>Lendenfeldia dendyi</i>	●					●					●							●		○
<i>Lissodendoryx arenaria</i>						○	○	○	○	○								●	○	○
<i>Microciona</i> sp.1																		○	○	○
<i>Microciona</i> sp.2																			○	
<i>Mycale imperfecta</i>								●	●	●										●
<i>Mycale sulevoidea</i>																		●	●	●
<i>Mycale</i> sp.													○						○	
<i>Paratetilla</i> sp.																			○	
<i>Petrosia nigricans</i>		●									●	●	●		●	●	●	●	●	●
<i>Petrosia</i> sp.		●									●	●	●		●	●	●	●	●	●
<i>Phyllospongia dendyi</i>								○	○											●
<i>Phyllospongia foliascens</i>						○	○	○			○				○					
<i>Phyllospongia madagascariensis</i>													●		●	●				
<i>Placospongia melobesoides</i>	●					○		○			●	○			●					
<i>Plakinastrella</i> (1 species)																				●
<i>Plakortis nigra</i>	●	●	●	●	●	○	○	○	○	●										
<i>Plectroninia</i> sp.1									○	○										
<i>Plectroninia</i> sp.2								○	○	○									○	○
<i>Plectroninia</i> sp.3											●	●			○	○	○	○	○	○
<i>Plectroninia</i> sp.4																				○
<i>Prostylissa foetida</i>																			○	
<i>Pseudosuberites andrewsi</i>		○	○					○												
<i>Reniera</i> sp.											●	●	●		●	●	●	●	●	●
<i>Rhizochalina incrustans</i>											●	●	●		●	●	●	●	●	●
<i>Rhizochalina</i> sp.																		○		
<i>Sigmatocia amboinensis</i>						○	○	●	●	●										
<i>Speciospongia florida</i>	○					○														
<i>Spirastrella pachyspira</i>								○										●	●	●
<i>Spirastrella vagabunda</i>								○										●	●	●
<i>Spirastrella solida</i>																		●	●	●
<i>Spirastrella</i> sp.																		○		
<i>Strepsichordaia</i>				●	●					●	●									

Table 1 continued

Species	Kenya (K)					N. Mozambique (Q)					S. Mozambique (I)				SW Madagascar (A)					
	0	5	10	15	20	0	5	10	15	20	0	5	10	15	0	5	10	15	20	
<i>Spongia ceylonensis</i>						○	○	○												
<i>Strongylamma arenosa</i>																○	○			●
<i>Stylotella aurantium</i>								○	●											
<i>Tedania anhalens</i>	○	○				○	○	○	○											
<i>Tedania digitata</i>	○	○				○		○	○											
<i>Terpios granulosa</i>		●	●	●	●															
<i>Terpios sp.</i>	○										●	●			●	○	○	○	○	
<i>Tethya seychellensis</i>						●	●	●	●		●	●	●	●	●	●	●	●	●	
<i>Thalysias sp.</i>	○	○				○	○	○												
<i>Timea sp.1</i>															●	●	●	●	●	
<i>Timea sp.2</i>												●								
<i>Toxochalina sp.</i>														●					●	
<i>Ulosa rubra</i>															●					
<i>Xestospongia exigua</i>	●	●	●	●	●	●	●	●	●	●					●	●		●	●	
<i>Xestospongia testudinaria</i>		●	●	●				●	●	●									●	
<i>Xestospongia sp.</i>									●											

Table 2 Maximum no. sponge species and space occupation with site, exposure and depth in the four principal study regions. Values in parentheses in last two columns are the depths (m) at which maximum number of species and percentage cover occur

Locality	Site	Reef type	Site depths	Minimum sample size	Maximum no. species	Maximum % cover
<b>Kenya (K)</b>						
1	1	Exposed	0, 5	20	2 (0)	15 (0)
	2	Exposed	0, 5	20	4 (5)	10 (5)
	3	Exposed	0, 5	20	4 (5)	30 (0)
2	4	Exposed	10, 15	13	5 (15)	40 (15)
	5	Exposed	10, 15, 20	11	6 (15)	65 (15)
	6	Exposed	10, 15, 20	11	8 (15)	70 (20)
3	7	Sheltered	0, 5, 10, 15	14	2 (15)	25 (10)
	8	Sheltered	0, 5, 10	13	3 (0)	20 (10)
4	9	Sheltered	5, 10, 15	10	7 (15)	30 (15)
	10	Sheltered	10, 15, 20	10	5 (15)	40 (15)
<b>N. Mozambique (Q)</b>						
1	1	Exposed	10, 15	13	2 (15)	5 (10)
	2	Exposed	0, 5	14	8 (5)	85 (5)
	3	Exposed	0, 5, 10, 15, 20	11	5 (5)	20 (0)
2	4	Exposed	10, 15, 20	11	9 (15)	—
	5	Exposed	10, 15	9	5 (15)	40 (15)
	6	Exposed	10, 15	13	5 (15)	40 (15)
3	7	Sheltered	0, 5, 10, 15, 20	11	7 (10)	80 (15)
	8	Sheltered	5, 10, 15, 20	11	11 (15)	95 (15)
	9	Sheltered	5, 10, 15	10	9 (10)	55 (10)
4	10	Sheltered	0, 5, 10, 15	12	8 (10)	75 (15)
	11	Sheltered	0	15	4 (0)	15 (0)
	12	Sheltered	5, 10, 15	15	9 (10)	45 (10)
<b>S. Mozambique (I)</b>						
1	1	Exposed	0, 5	15	3 (5)	20 (5)
	2	Exposed	0, 5, 10, 15	10	3 (10)	35 (10)

Locality	Site	Reef type	Site depths	Minimum sample size	Maximum no. species	Maximum % cover
2	3	Sheltered	0, 5, 10, 15	12	4 (10)	30 (10)
	4	Sheltered	0, 5, 10, 15	15	2 (10)	25 (5)
<b>SW. Madagascar (A)</b>						
1	1	Exposed	10, 15, 20	10	2 (20)	10 (15)
	2	Exposed	0, 5, 10, 15	20	3 (5)	25 (5)
	3	Exposed	0, 5	20	2 (5)	20 (5)
2	4	Exposed	10, 15, 20	15	13 (15)	95 (15)
	5	Exposed	10, 15, 20	20	9 (15)	50 (15)
3	6	Sheltered	0, 5, 10	20	4 (10)	40 (10)
	7	Sheltered	0, 5, 10	20	3 (5)	15 (5)
4	8	Sheltered	0, 5, 10	15	3 (5)	25 (10)
	9	Sheltered	0, 5	15	3 (0)	20 (0)
	10	Sheltered	5, 10	10	4 (10)	20 (10)

Table 2 continued

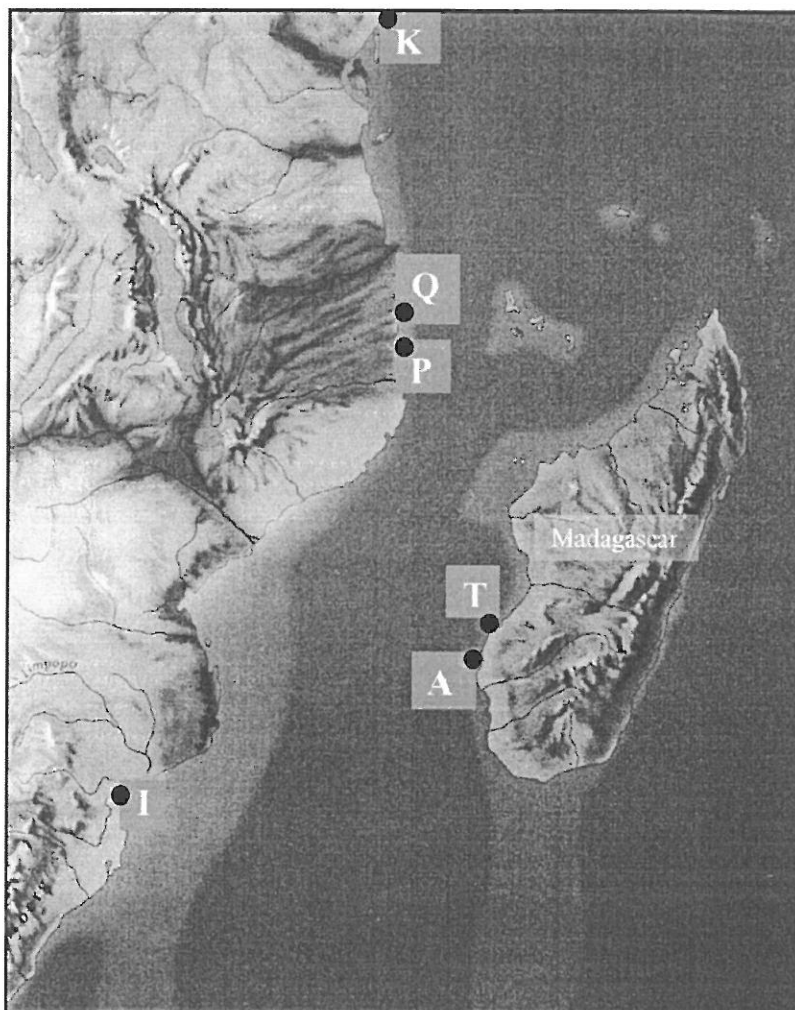


Fig 1 The position of the study regions in the West Indian Ocean. The identity of these are K (Malindi, Kenya), Q (Quirimba Archipelago, Mozambique), A (Anakao, Madagascar), I (Inhaca Island, Mozambique). The positions of two other localities (Pemba and Toliara), mentioned in the text, are shown as P and T, respectively



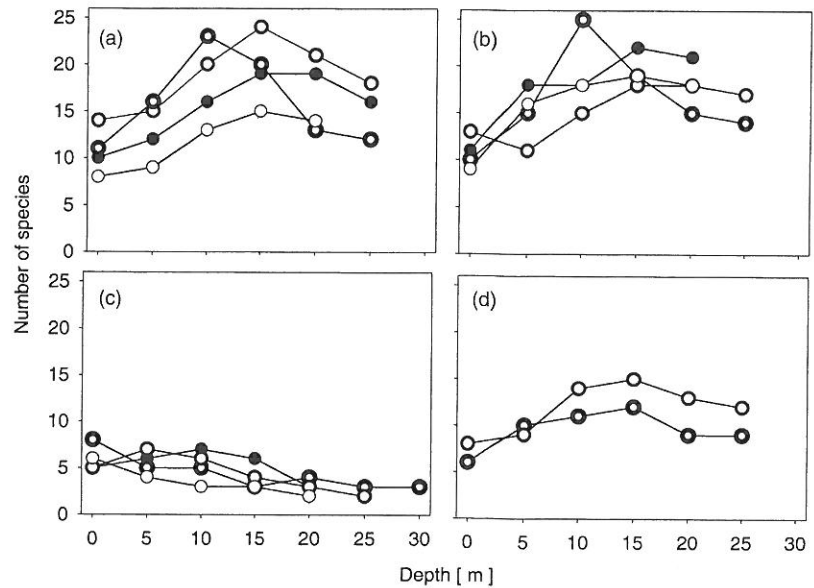


Fig 2 Species richness with depth, habitat and study region. Data are total numbers of species. The symbols are ● (Kenya), ● (N. Mozambique), ○ (S. Mozambique) and ○ (Madagascar). The habitats are exposed coral reef (a), sheltered coral reef (b), soft substrata (c) and caves (d)

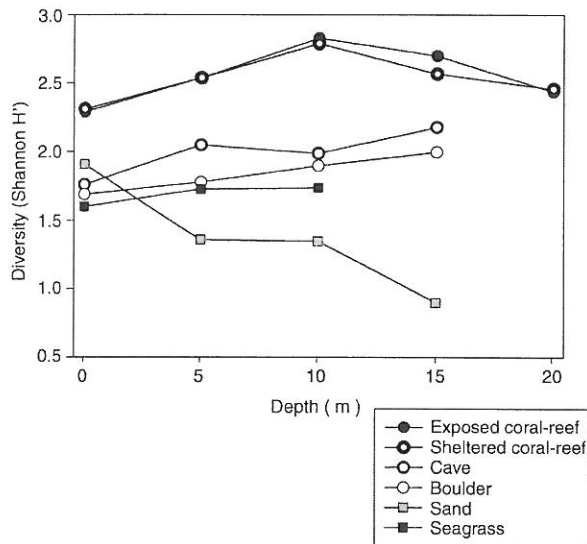


Fig 3 Species diversity with depth, habitat and study region. Data are for region Q only (patterns for other regions are similar). Symbols are shown on the plot

Sponge assemblage composition altered with many factors. Certain genera (and species) were associated with either tropical (e.g. *Pseudosuberites*) or subtropical (e.g. *Ecionemia*) conditions (Table 1). Furthermore, some genera (and therefore associated species) were only recorded in particular regions (e.g. *Strongylamma* in Madagascar), depths (e.g. *Axinella* at 15–20 m), habitats (e.g. *Cinachyrella* on sand-rock) or a combination of these (e.g. *Lendenfeldia*

only found in intertidal coral reefs). Analysis using a Bray Curtis dendrogram showed distinct clusters centred around habitats and regions (Fig. 4a). The two major groupings (> 95% dissimilarity) represented the assemblages of soft ( $\alpha$  in Fig. 4a) and hard substrata ( $\beta$ ,  $\gamma$ ,  $\delta$  in Fig. 4a). Within the soft substratum cluster, the mangrove, seagrass and sand habitats all formed subgroupings with typically only  $\approx 20\%$  similarity. In all of these habitat groupings, the Madagascar (region A) assemblages were the most dissimilar from those of other regions. The hard substratum cluster split into subtropical ( $\beta$ ) and tropical ( $\gamma$ ,  $\delta$ ) groupings with just 12% similarity. Within the subtropical grouping further splitting was primarily on the basis of region ( $\beta$ ,  $\beta_2$ ), whereas in the tropical grouping further splits were along habitat and bathymetric gradients ( $\gamma$ – $\gamma_3$ ,  $\delta$ ). The most dissimilar grouping to all others and within the cluster were the sponge assemblages on sand. The assemblages with the highest degree of similarity (70–80%) were those of the caves and boulders (at region Q). The sharp dichotomy between the soft and hard substratum assemblages was reiterated by correspondence analysis (Fig. 4b). The relative similarity of hard substratum assemblages was more apparent in the correspondence analysis although groups were still distinct in this cluster. Essentially the cluster forms a cline from tropical assemblages to those in the subtropics with those in Madagascar (region A) linking the groups. As in the Bray Curtis dendrogram the tropical and subtropical caves were quite distinct from each other.

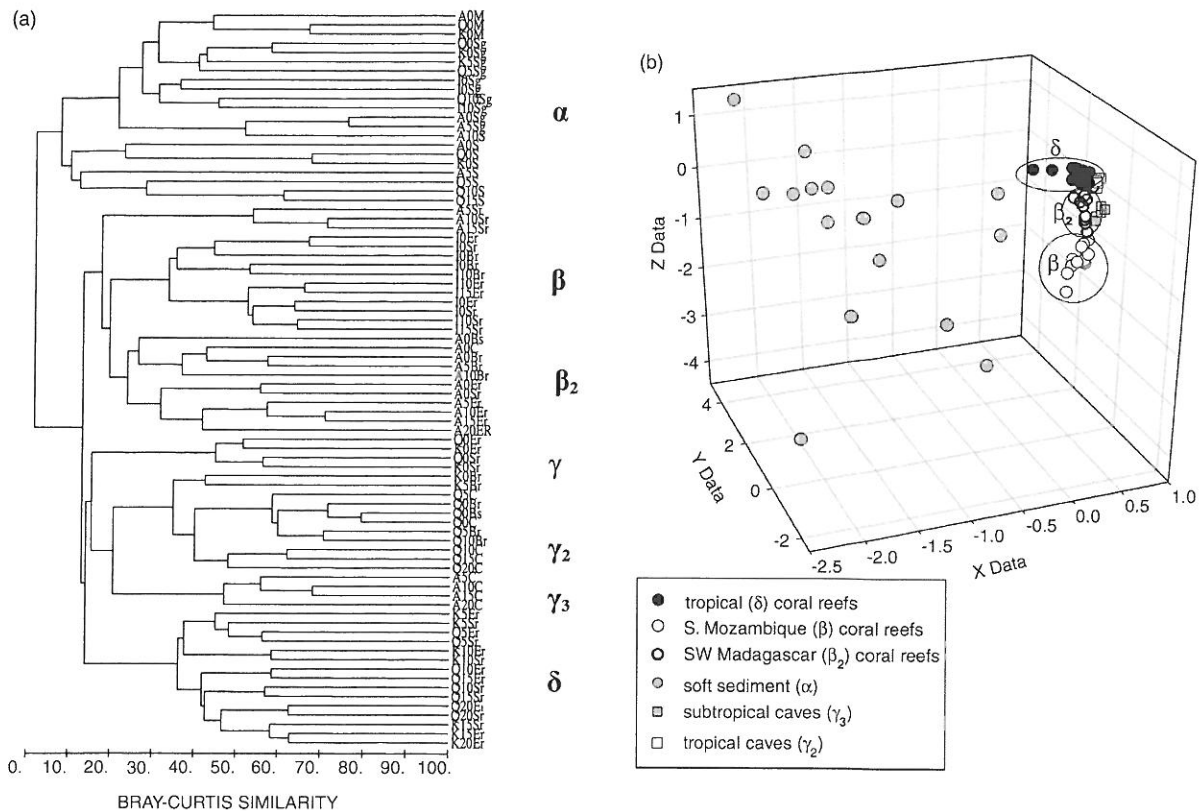


Fig 4 (a) Dendrogram of sponge assemblage similarity with depth and habitat in the four study regions. Correspondence analysis (b) showed the same clustering as the Bray–Curtis analysis. The main groupings are indicated by Greek letters (see text). The first three Eigenvalues explain 74, 6 and 5% of the total variance, respectively. Therefore the plot explains 85% of the total variance

**Discussion**

More sponges, as with many other taxa (Briggs, 1987), are known from the tropical Indo–West Pacific region than elsewhere (see Rützler, 1972; Van Soest, 1993, 1994; Hooper & Lévi, 1994). Sponge species richness of regions is typically high in the tropics and lower in temperate regions for various reasons (see Bakus & Ormsby, 1994). Species richness does, however, seem to be quite patchy, with some temperate areas richer than adjacent tropical areas along the same continental coast (see Van Soest, 1994). Both polar regions are also comparatively rich in species (Van Soest, 1994), though not in shallow water (Bakus & Ormsby, 1994). Despite this, there is no clear dichotomy in diversity even between tropical and nontropical studies (Bell & Barnes, 2001). In the present study too, both tropical regions (Kenya and Northern Mozambique) were more speciose than subtropical regions (southern

Mozambique and Madagascar) but not significantly different in terms of diversity (Shannon  $H'$  values). Other major taxa which have been extensively studied in East Africa, principally the corals, molluscs and decapod crustaceans, have, like the sponges, typically been found to be rich, diverse and abundant. Corals, particularly those of hermatypic nature, are probably the best studied marine group with respect to patterns in 'biodiversity' (see Sheppard, 1998 for a modern review). Corals in northern Mozambique have proved to be extremely taxa rich (Barnes & Whittington, 1999), more so than predicted by Stehli & Wells (1971), but are comparatively depauperate in southern Mozambique and South Africa (Kalk, 1995). About 200 (coral) species and 54 genera are known from Madagascar (Pichon, 1972, 1978) but surprisingly, considering the latitude span, there is negligible difference in northern and southern coral reef taxa richness. Gastropod molluscs are collected for food by coastal peo-

ple. Local diversity is reflected in the variety of species gleaned in north (Barnes *et al.*, 1998) and south Mozambique (De Boer, 2000) and Madagascar (Rabesandratana, 1985). Measuring mollusc diversity patterns is complicated by the heavy fishing pressure and associated faunal rarity along parts of the coast, such as much of Tanzania (Horrill, Darwall & Ngoile, 1996). Certainly in the northern hemisphere, gastropod molluscs show a clear latitudinal cline with highest diversity about 10°N and lowest in the Arctic (Roy *et al.*, 1996). Decapod crustaceans have also been the subject of many taxonomic and ecological studies, particularly from south Kenya to South Africa (Crosnier, 1962; Hartnoll, 1975; Vannini & Valmori, 1981; Branch *et al.*, 1994; Barnes, 1997). In contrast coral patterns, Crosnier (1962) found northern Madagascar (tropical) decapods to be more speciose and diverse than those in southern Madagascar (subtropical). Equivalent comparisons in Mozambique, which spans the same latitudes, are difficult because of a paucity of literature.

Almost half (31/70) of the genera found in this East African study comprised species with a so-called Tethyan distribution (see van Soest, 1994), of which 58% were widespread and the remainder restricted to subtropical-tropical areas, apart from *Iotrochota* (which is restricted to the tropics). Most of the other genera were cosmopolitan, e.g. *Clathria* and *Haliclona*, but three were cold water (*Coelosphaera*, *Hymedesmia*, *Pseudosuberites*), four were Indo-Australian (the Ianthellidae) and one circum-African (*Crambe*). Although there were discernable differences between tropical and subtropical localities examined in the present study, interpreting these was complicated, as latitude was not the major influence. It was, however, notable that hard substratum assemblages essentially formed a cline (Fig. 4b) from the tropics to Southern Mozambique, linked by Madagascar. As found elsewhere, both inside and outside the study area (Barnes, 1999 and Diaz *et al.*, 1990, respectively), the type of substratum (habitat) was the most important factor governing the suite and number of species present. In the present study, the sponge assemblages of soft substrata were much more dissimilar, both within and between habitats than those on hard substrata (see Figs 4a, b). Even within substratum types there may be substantial differences in species richness due to variability in water flow (Bell & Barnes, 2000) or ambient light regime (Jaubert & Vasseur, 1974; Uriz, Rosell & Martin, 1992). There was a predictable variability in species richness between hard substratum habitats: coral reefs being speciose and caves being less so (see Fig. 2). Marine

caves have been described from various parts of the world as being species rich (see Vacelet & Vasseur, 1965, 1977; Vasseur, 1974; Babiloni, Uriz & Gili, 1989; Corriero *et al.*, 2000). Usually, however, this is relative to adjacent species-poor areas, in contrast to the present study. The negative correlation observed between light intensity and sponge species richness (Uriz *et al.*, 1992) may explain the decreased sponge diversity in the intertidal zones (in the study areas). Why there was a decrease deeper than 10–15 m was not clear.

Many of the species/genera encountered in the present study occurred in at least two study regions, many in more, and occupying large areas of substratum. Some of these, e.g. *Xestospongia exigua*, are commonly found throughout the Indo-west Pacific region similarly occupying much space. The success of such species is largely thought to be due to the production of toxic allelochemicals (see Bakus & Ormsby, 1994, and references therein). Of the genera encountered in this East African study even 40% were in common with those found at 33°N around a Korean Island (although < 5% of the identified species were in common; data from Sim, 1994). Endemicity of shallow water sponge faunas in East Africa (see Vacelet & Vasseur, 1977) may be lower than some other Indo-Pacific areas, e.g. northern Papua New Guinea (Bakus & Ormsby, 1994), but are typically higher than other central and west Pacific localities which have been measured to date (van Soest, 1990). Much explanation of such patterns is considered to have historical explanations, such as isolation through tectonic or sea level movement. It is of note that despite splitting from India later than East Africa, the sponge fauna of Madagascar seems to be more similar to that of East Africa (not surprising, considering its geographical proximity) and Indonesia than India (see Van Soest, 1994). As in previous studies (e.g. Vacelet & Vasseur, 1965, 1977) the Madagascan sponges (species composition) were found to overlap substantially with those known in East Africa. Unlike most studies comparing animal taxa from region to region, the present study gains some comparative power in having relatively constant sampling regimes or effort between localities. The present study has shown that factors influencing species richness may be decoupled from those influencing diversity. For example, region and bathymetry have striking effects on species richness, but not on diversity and the main dichotomy with substratum was between coral reef and non-reef habitats in species richness but between hard and soft in species diversity. Why patterns in these two measures should be decoupled is at present unclear but

should merit serious further research considering their use in quantification of biodiversity. This taxon clearly comprises a major portion of the shallow water fauna of East Africa and as such should be considered when planning coastal management plans. Only by modelling these factors with more levels and including factors such as light irradiation, substratum profile and biological determinants, e.g. predation, will a better understanding of the East African wide sponge ecology be approached.

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