

Biodiversity and biogeography pattern of benthic communities in the coastal basins of India

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Abstract

Our understanding of coastal biogeography patterns is presently limited to certain regions and marine groups. Comprehending the large-scale patterns and their underlying predictors are critical due to the changing environmental conditions. The Indian coast, bounded by two contrasting seas, the Bay of Bengal and Arabian Sea, offers an excellent opportunity to determine the most important factors influencing coastal biogeography patterns. Here we use distribution data of 2,581 species belonging to three benthic groups (polychaetes, gastropods and bivalves) to evaluate the role of environmental factors and coastal currents on the biogeography patterns. Data was obtained from the bioSearch database, developed under the Census of Marine Life programme. As measures of diversity, we used species richness as well as taxonomic distinctiveness indices. Multivariate analyses were used in identifying biodiversity patterns and correlated biogeography patterns with environmental factors. This paper points out a clear difference between the eastern and western basins of India, but also within the basins. Mainland and island fauna also showed a clear distinction. The biogeography of the Indian coast is best explained by temperature, habitat heterogeneity and coastline length. Spatiotemporal variability in the boundary currents also forms an effective barrier for the dispersal of planktonic larvae of benthic fauna. The study has identified a finer scale division of Indian coast that can help to effectively improve conservation plans. Our study is the first to attempt to understand benthic biogeography patterns of the Indian coast. The findings will be useful in guiding future biogeography studies of this unique and underexplored marine system.

Keywords: benthos, biogeography, coastal currents, diversity, environmental factors, habitat heterogeneity.

Introduction

Coastal ecosystems with their complex habitats host diverse taxa and account for 43% of the total global ecosystem services (Costanza et al. 1997). Despite the great economic and ecological importance of this ecosystem, a few studies have been carried out to understand the biogeography patterns of coastal fauna (Blanchette et al. 2008; Belanger et al. 2012). Over the last decade, an increase in the number of marine biogeography studies has improved our knowledge of biodiversity patterns and its underlying predictors (Pierrat et al. 2013). Among the environmental factors, temperature, salinity, primary productivity, habitat heterogeneity and dispersal have been identified as features that influence the coastal biogeography patterns (Kraan et al. 2010; Sellanes et al. 2010, 2013; Tittensor et al. 2010; Belanger et al. 2012; Compton et al. 2013; Pierrat et al. 2013 Waters et al. 2014; Barboza & Defeo 2015). It has been recognized that coastal boundary currents affect the dispersal of larvae and therefore are considered an important determinant of species distribution patterns (Coleman et al. 2013). Moreover, the species' ability to survive different environmental conditions during the planktonic larval stages will also be reflected in their distribution range (Lomolino et al. 2010).

The North Indian Ocean is recognised as one of the centre of endemism and at higher risk of anthropogenic activities (Roberts et al. 2002; Obura 2015). The Indian peninsula divides the North Indian Ocean into two smaller basins, the Bay of Bengal on the east and the Arabian Sea on the west. Based on the tectonic model, the coastal basin of India is further subdivided into nine coastal sedimentary basins (DGH 2007; Biswas 2012). Although the two seas of the North Indian Ocean are situated at the same latitude, they have contrasting environments. The Bay of Bengal is a region of positive water balance where the large amount of precipitation and river runoff, far exceeds evaporation. It receives a large amount of freshwater ($1.625 \times 10^{12} \text{ m}^3 \text{ yr}^{-1}$) from eight major rivers and some smaller rivers making it a region of low salinity with little annual variation (Ittekkot et al. 2003; Akhil et al. 2014). The rivers also carry a considerable amount of sediment causing high turbidity in the area. Sediment in the shelf region is predominantly clayey silt except towards the south, which is sandy (Rao & Wagle 1997). In the Arabian Sea, the inner shelf region is characterised by clay, whereas outer shelf by sand (Rao & Kessarkar 2001). Further, the Arabian Sea is one of the most productive regions of the world. As evaporation exceeds precipitation in the Arabian Sea, it results in a negative water balance. Salinity is higher in the northern Arabian Sea due to the spreading of the Persian Gulf water mass (Prasad et al. 2001), while the southeast Arabian Sea

is a region with the highest sea surface salinity variability and the one of the warmest regions of the world oceans (Joseph 1990). The Arabian Sea also has some of the most extreme coastal environments in the North Indian Ocean (Schils & Wilson 2006).

One of the most distinguishing features of the North Indian Ocean are the Asian monsoon winds that bring about seasonal reversal of surface circulation. The Somalia current along the Somali coast is the most energetic and best-documented amongst the seasonally reversing currents (Shankar et al. 2002). While the Western India Coastal Current (WICC) and Eastern India Coastal Current (EICC) along the India coast, although less energetic also show seasonal reversal (Shankar et al. 2002; Figure 1). The Western India Coastal current flows toward the equator during the Indian summer monsoon (May–September) and polewards during winter monsoon (November–February). Although the WICC flows equatorially, during the summer monsoon, the overall flow along the southwest coast is poleward (Amol et al. 2012). Further, the WICC, either flowing, equatorially or poleward it weakens north of 20°N (Amol et al. 2012). The East India coastal current flows poleward during February–August, and towards the equator from October–December. However, the poleward flow weakens during the summer monsoon (June–August) and it usually reverses at 19°N and often at 12°N (Durand et al. 2009; Mukherjee et al. 2014). Therefore, the coastal boundary currents show a spatiotemporal variation (Durand et al. 2009; Amol et al. 2012; Mukherjee et al. 2014). However, the seasonally reversing boundary currents along the Indian coast play a critical role in connecting the Arabian Sea and the Bay of Bengal basins (Shankar et al. 2002).

Moreover, the monsoon is the major recruitment period for most tropical benthic fauna (Alongi 1990; Gaonkar et al. 2013). Most benthic fauna have a complex life cycle including a planktonic larval stage and bottom-dwelling juvenile and adult benthic stages (Thiébaud et al. 1998). Thus, dispersal of most benthic organisms occurs primarily during the planktonic larval phase. The reversing monsoonal currents have the potential for dispersing the benthic larvae and connecting the two coastal basins of India. Levin & Dayton (2009) suggest that comparative studies from contrasting environments provide a unique opportunity to understand the influence of environmental and oceanography variables in driving the species diversity and distribution patterns.

The Indian subcontinent has a unique geological history, and is therefore of great interest to biogeographers and paleontologists (Ali & Aitchison 2008). India remained an isolated island for 30–40 million years during its journey from the Gondawana super-continent to its collision with Eurasia. Therefore, it is expected that flora and fauna of India have high levels of endemism and

hence often been left out of Asian biogeography studies (Kamei et al. 2012; Barley et al. 2015). Although there are extensive works on the terrestrial biogeography of India, marine systems have largely lagged behind (Köhler & Glaubrecht 2007; Barley et al. 2015). Therefore, the Indian subcontinent with its unique geological history and natural gradient in environmental features and complex oceanographic processes provides a useful model to understand the marine biogeography patterns and the underlying factors.

Discerning the large-scale marine biodiversity patterns is highly important due to changing environmental conditions, which affects the biotic and abiotic features of an ecosystem. However, there is a clear bias in the biogeography studies of the Indian Ocean, as most of the studies have been focused on few groups (fish and coral) and certain regions, such as the Indo-West Pacific, to understand connectivity between Indian and Pacific Ocean (e.g. Carpenter et al. 2011) or the large-scale pattern in the western Indian Ocean (Obura 2012; Tsang et al. 2012), Australia (Waters 2008; Coleman et al. 2013), South Africa (Anderson et al. 2009) and the Arabian Gulf region (Schils & Coppejans 2003; Schils & Wilson 2006; McMahon et al. 2012; DiBattista et al. 2016). In spite of the environmental heterogeneity along the Indian coast, the large-scale biodiversity patterns and the environmental factors that influence these patterns are largely unknown. Such studies are restricted to the role of currents in small-scale larval dispersal (George et al. 2011; Gaonkar et al. 2012) or genetic variation of some commercially important fishes (Menezes et al. 2002; Divya et al. 2012; Kumar et al. 2012; Kunal et al. 2013).

The current study aims to contribute to our understanding of coastal biogeography patterns of benthic species along the Indian coast. We predicted that the coastal basins of India would have low similarity due to the environmental heterogeneity and spatiotemporal variability of coastal currents. Accordingly, the objectives of the present study were to determine the biodiversity and biogeography patterns in the coastal basins of India using the distribution data of polychaetes, gastropods and bivalves. We used the species distribution data of three important macrobenthic groups (Polychaeta, Gastropoda and Bivalvia). These groups are the most dominant, diverse and widely distributed in most marine habitats and hence play an important role in ecosystem functioning (Glasby 2005; Rex et al. 2005). They are also among the best-documented benthic groups and exhibit great diversity in life-history traits, evolutionary history, and ecological characteristics, hence appropriate for biogeography studies. Moreover, comparative biogeography studies across taxonomic groups, even phylogenetically distant groups, which share a particular geographic region, provide realistic

evidence that the same factors account for the common speciation events and are therefore, useful to draw a logical conclusion in large-scale biodiversity patterns (Glasby 2005; Pierrat et al. 2013; Barley 2015). In general, few studies have focused on the relationship between regional environmental heterogeneity and the influence of surface circulation on the species assemblage at continental scale (Peguero-Icaza et al. 2011; Compton et al. 2013; Waters et al. 2014).

Materials and Methods

Study Area

India (6°–23°N) has a coastline of ~7516.6 km in length and an Exclusive Economic Zone (EEZ) of 2.02 million km². This study encompassed the entire coastline of India, including the Andaman and Nicobar (AN) and Lakshadweep Islands (LK) in the east and west coast, respectively. Based on the tectonic model, the Indian coast is divided into coastal sedimentary basins (DGH 2007; Biswas 2012). We used the sedimentary basins as sampling units because tectonic events and subsequent geological events resulted in wide variations in the geological setup of different segments of the Indian margin (Bastia & Radhakrishnan 2012). It is known that the superposition of the palaeogeographic events influenced the biogeographic pattern (e.g. Cowman & Bellwood 2013). The sampling units consist of nine coastal basins, four along the west coast (Arabian Sea) and five in the east coast (Bay of Bengal) (Figure 2 and Table I). The basins were labelled as - the western basins WB 1-3 (from north to south), eastern basins EB 1-4 (from north to south), Lakshadweep (LK) and Andaman and Nicobar (AN).

Collection of Data

Species Distribution Data

Data was obtained from the marine biodiversity database (bioSearch.in) of India developed by the Bioinformatics Centre, CSIR-National Institute of Oceanography (CSIR-NIO). The Institute constructed the database as part of the Census of Marine life programme (Kakodkar et al. 2013). The main function of the Bioinformatics Centre, CSIR-NIO, is to collect marine biodiversity data of India from various sources and make it available through bioSearch database. Data is freely available to potential users (decision-makers, research community, educational institute and stakeholder) to encourage scientific research in marine biodiversity and biogeography and for its use in the effective management of the Indian marine ecosystem. The database encompasses data from bacteria to mammals in the Indian waters. The taxonomic and biogeography information for the

bioSearch was acquired from the Indian Ocean Node of the Ocean Biogeographic Information System (IndOBIS). Information on species distribution was compiled from published literatures (journals, monographs, books, species checklists, PhD theses and project reports) and also from the various ongoing research programmes of CSIR-NIO (Kakodkar et al. 2013). A total of 4,383 records were retrieved from the bioSearch database. To improve the quality of the data retrieved from the database, we checked the data for the following (1) records that were not identified to species level were excluded (2) records that were not geo-referenced to any of the basins were not considered (3) scientific names were standardised after excluding synonyms and checked for mis-spellings. The process left 2,581 records for the three benthic groups. The systematic of all the taxa was updated according to World Register of Marine Species (WoRMS). Basins that are divided into political sub region (KK basin) were combined (Table I). Species were classified into two different groups based on occurrence pattern. The common species were those that showed >50% occurrence; species recorded in a single basin were categorised as rare. We obtained temperature and salinity profile from the World Atlas 2013 (Schlitzer 2014). The ecoregion for India was re-drawn from Spalding's Marine Ecoregions of the World (Spalding 2007).

Environmental data

We focussed on three important environmental factors (temperature, salinity and chlorophyll-a) that have previously been shown to be strongly correlated with marine species richness (Tittensor et al. 2010; Belanger et al. 2012). We also investigated the influence of dissolved oxygen since upwelling and oxygen minimum zones are an important feature of the North Indian Ocean (Helly & Levin 2004; Naqvi et al. 2009). For each basin, we collected the long-term annual surface temperature, salinity, dissolved oxygen and surface chlorophyll-a data. Temperature, salinity and dissolved oxygen data were obtained from the World Ocean Atlas 2009 1° degree set and were averaged for each basin. The annual mean surface chlorophyll-a was obtained from SeaWifs, spanning the years from 1997 to 2009.

Habitat Availability and Heterogeneity

The coastline length was used as a proxy for the available near-shore habitat (Sanciango et al. 2013). The coastline length for each basin was obtained from Kumar (2006; Table I). We used the information on coral reefs, sea grass, mangroves, intertidal (rocky, sandy and muddy) and subtidal habitats from published literature to evaluate the habitat heterogeneity (Jagtap et al. 2003; Kathiresan & Qasim 2005; Venkataraman et al. 2003). For the purposes of simplicity in analysis and

interpretation, all the habitats were condensed into categories (Supplementary material, Table SI) and each category was given an arbitrary score. The coral reef, seagrass and mangrove habitats were assigned a score, depending on three criteria: the area, number of species and abundance (patchy or dense). The coral species were classified based on their morphology into four groups (Edinger & Risk 2000). A basin dominated by the massive and sub-massive morphological (stress-tolerant) group was given the lowest score (1) and when all the morphological groups were present, it was given the maximum score (4). Although the classification was used for conservation purpose, the morphological class was a reliable indicator of habitat complexity (Edinger & Risk 2000). The scores from each category were averaged for each habitat (coral reef, sea grass, mangroves). The reason for using different factors for scoring these habitats was because a single criterion does not capture the habitat heterogeneity. For example, although the KU basin has 20% of the total Indian mangrove area, the vegetation is sparse and patchy (Mandal et al 2008). Studies have shown that along with habitat area, structural complexity positively influences the species richness (Nagelkerken et al 2010).

For intertidal habitat, only two categories were created—presence and absence for each substrate type (rocky, sandy and mud). The shelf region was divided into inner shelf (up to 30 m) mid-shelf (40–50 m) and outer shelf (50–100 m). The dominant substrate type was collected from published literature (Rao & Wagle 1997; Rao & Kessarkar 2001) and was categorised into three groups (Fine, sandy and coralline debris, Table SI,). A final score, for each basin was obtained after summing the habitat scores that was used for further statistical analyses.

Data Analysis

In the present study, we used the average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+). Based on the data available, a separate master list was made for all the three benthic groups. The average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+) were calculated for each basin using the species presence/absence data (Clarke & Warwick 1998). The average taxonomic distinctness gives the degrees to which each species in a sample are taxonomically related to each other by measuring average path length between every pair of species through a taxonomic tree i.e. summing the path length connecting every pair of species in the list and dividing by the number of paths. The variation in taxonomic distinctness is the evenness to which the taxa are spread across the tree (Clarke & Warwick 2001). To test the departure from expected Δ^+ and Λ^+ , a 95% confidence funnel was generated. A theoretical mean (horizontal line in the Δ^+ and Λ^+

graphs) and variance of Δ^+ and Λ^+ is calculated by a 1000 simulation distribution, generated from the values obtained from subsampling species (m) from the master list. Although the theoretical mean remains the same, the variance increases as the m decreases. As a result, the 95% confidence interval takes the form of a 'funnel' (Rogers et al. 1999). The values of Δ^+ and Λ^+ from any set of samples are then related to this 95% confidence funnel. If each basin is a random selection from the master list, the Δ^+ and Λ^+ will fall within the confidence funnel indicating that the samples are diverse, i.e. high Δ^+ and Λ^+ . When the Δ^+ values fall below the theoretical mean, it indicates that the set of samples has a lower Δ^+ value than the entire area. The low value could be due to many species that are closely related, i.e. they belong to the same genera (high relatedness), although higher taxonomic category is well represented (different phyla/class/order). High Δ^+ value results when species are evenly distributed in the phylogenetic tree, i.e. even distribution of genera and species. Values of Λ^+ range from high, when several different orders are represented by a single species, but some genera are species rich whereas the ranges are low when all the species belong to different families but the same order (Clarke & Warwick 2001). The Λ^+ have values above 95% confidence funnel when a genus is well-diversified (many species in a single genus) compared to those represented by only a few or single species. A low diversity of Δ^+ values and high variation Λ^+ value (above the funnel) occurs when the samples are represented by species belonging to a single or a few genera and/or absence of a higher taxonomic category.

Finally, 95% probability contour (ellipse plot) of the joint Δ^+ and Λ^+ from a simulation distribution of random subsets of the master list from the region were plotted for each benthic group. The ellipse plot accounts for any correlation between Δ^+ and Λ^+ . The ellipses were based on m counts and are constructed to reflect the number of species seen at each coastal basin (values in parentheses in the plot). When the basins fall within the respective envelope, it indicates that there is no difference when compared to the master list from region. The basins are on the borderline of the envelope when there is decrease in Δ^+ and Λ^+ . Data points outside the respective envelope suggest a low Δ^+ and/or low Λ^+ and provide a statistical evidence of departure from the 'expected' value (Clarke & Warwick 2001). In the present study, the ellipse plots were divided into two component plots to improve the clarity. The taxonomic distinctness is applicable when comparing biodiversity at larger spatial scales where habitat heterogeneity and environmental disturbances influences the biodiversity patterns (Clarke & Warwick 2001). Hence, these diversity measures are finding wide application in

biogeographic studies (Baños-Picón et al. 2009; Tolimieri & Anderson 2010; Quiroz-Matinez & Salgado-Maldonado 2013).

To compare the large-scale geographic pattern using presence/absence (incidence) species data, we used two different cluster analyses i.e. Jaccard (Jaccard 1908) similarity and Theta (Θ^+) dissimilarity analysis. Of the different similarity/dissimilarity matrices based on presence/absence species data for biogeographic classification, Jaccard gives similar and lowest number of poorly informative structure (Murguía & Villaseñor 2003). The poor informative structures are “those with three pairs of operative geographical units equal in values or those in which the similarity coefficient cannot be applied because the denominator is zero” (Murguía & Villaseñor 2003). The Jaccard Similarity Index (JSI) is defined as the ratio of number of species shared by two regions to the number of species present in either one of them.

$$JSI = 100 \times \frac{a}{a + b + c}$$

Where, a is the number of species present in both the samples; b implies the number of species present in region 1 but absent in region 2; c represents the number absent in region 1 but present in region 2; (Clarke & Gorley 2006). The Theta (Θ^+) dissimilarity cluster analysis takes into consideration the taxonomic relationship of species found in each region (Clarke & Warwick 1998). The Theta dissimilarity or ‘optimal mapping coefficient’ is a natural extension of Kulczynski presence/absence dissimilarity and separately calculates the mean path length between all species in sample 1 and their nearest relations in sample 2, and vice versa, and then averages the two means (Clarke & Warwick 1998). It is useful in ordinating samples from widely distributed biogeographic regions with a few, if any, shared species, but will have common taxa at higher taxonomic order (Clarke & Warwick 1998).

$$\Theta^+ = \frac{1}{2} \left[\frac{\sum_{i=1}^{s_1} \min\{\omega_{ij}\}}{s_1} + \frac{\sum_{j=1}^{s_2} \min\{\omega_{ij}\}}{s_2} \right]$$

Where, there are s_1 species present in region 1 and s_2 species in region 2, ω_{ij} is the distance through the tree from species i of region 1 to species j of region 2. Therefore, two regions with no species in common, can have a dissimilarity value <100 . If two samples tend to have species in similar genera or families to each other then taxonomic dissimilarity is low, whilst if they do not share many evolutionary branches the dissimilarity will remain large (Clarke et al. 2006). The biogeography pattern was then determined through cluster analysis and non-metric multidimensional scaling

(nMDS) based on Jaccard and Θ^+ similarity/dissimilarity matrices, where similar regions are clustered (Manly 1991; Clarke & Ainsworth, 1993).

The Principal Component Analysis (PCA) was performed to identify the environmental factors that characterised the study area. We also performed the PCA to visualise the patterns of distribution of abiotic characteristics and the species number which was used as a supplementary variable. To predict the role of environmental variables on the biogeography patterns, we used the non-parametric Mantle-type test, the RELATE analyses. The RELATE analyses tests the agreement in the multivariate patterns between two similarity matrices i.e. benthic group similarity matrices (based on Jaccard similarity) and the environmental similarity matrices based on Euclidean distance. The analyses use the Spearman's rank correlation (ρ) to determine the significant relation between the two similarity matrices. The BIOta ENVironmnet matching (BIO-ENV) procedure was used to find which combination of environmental variables best explains the observed benthic biodiversity patterns. All the environmental data was normalised prior to the RELATE and BEST analyses. The statistical analyses were performed using PRIMER v6 (Plymouth Routines in Multivariate Ecological Research) (Clarke & Gorley 2006) and STATISTICA 10 software packages.

Results

Polychaete biodiversity and biogeography pattern

The Polychaeta was represented by 564 species belonging to 54 families and 262 genera. The eastern basin, EB4, recorded the highest species richness with 255 species followed by WB 3 (160 species) and AN (157 species; Figure 3). Three hundred and twenty-one species had single area occurrence, of which 35% were from EB 4 and 17% in AN (Table II). In general, the Nerididae was the most diverse family (71 species). Nerididae were dominant in all the basins except for WB 1 and LK where, Eunicidae dominated. Simulation test on Δ^+ using funnels showed that the values for individual basin generally fell within the 95% funnel, except for AN basin which was significantly below the expected value ($P = 0.4\%$; Figure 4a). The values for WB 1-2 and EB 1-2 were lying below the mean value indicating that the diversity in terms of taxonomic distinctness was generally lower than expected. However, the values did not show a statistically significant departure from the null hypothesis ($p > 5\%$). The Λ^+ values for EB1 ($P = 2.6\%$) and AN basin ($P = 3.6\%$) was higher than the expected and was located above the funnel (Figure 4b). The simulation test for Δ^+ and Λ^+ values using the ellipse plot showed that the species richness fell within the 95% confidence contour (figure not shown). The skewness of ellipses suggested a negative correlation between Δ^+ and Λ^+

which was confirmed by the high correlation coefficient ($r = -0.74$). Combining both the measures of taxonomic distinctness suggests that in the AN basin, high values of Λ^+ and low Δ^+ resulted from the evenness at higher taxa. However, the distribution at lower taxa is less even with dominance of certain genera, e.g. *Perinereis*, *Eunice*, *Chloeia*, *Phyllodoce*, *Polydora*, *Lepidonotus* had more than three species.

The cluster based on the dissimilarity coefficient of taxonomic distinctness (Theta) shows a large cluster of the Island and mainland basins (Figure S1a). The mainland clusters in turn are subdivided, into smaller subgroups of (1) the western basins of WB 2 and 3 (20% dissimilarity) which in turn clustered with the eastern EB 4 at 22% dissimilarity and (2) eastern basins of EB 1 and 2 clustered at 24% dissimilarity. The Islands (AN and LK) clustered with low dissimilarity of 20%. The nMDS plot also distinguishes the same group of the basins as observed in the cluster (Figure S1b). The application of species similarity matrix data (Jaccard's similarity) on polychaete distribution data shows three groups, but not closely related as shown by the low similarity value (Figure 5 a and b). The western basins of WB 2 and 3 clustered at 30% similarity, the eastern basins of EB 1 and 2 at 22% and the islands, AN and LK, clustered at 26% similarity. The basins of EB 3 and 4 and WB 1 stand alone in the cluster.

Gastropod biodiversity and biogeography pattern

A total of 1435 gastropod species belonging to 142 families and 473 genera were reported from the Indian region. Of the total species reported, 62% had a single basin distribution. The Andaman and Nicobar basins recorded the highest number of rare species 439 (49%) followed by the EB 4 with 24% (216 species; Table II). The Muricidae (116 species) was the most diverse gastropod family. The Cypraedidae (76 species), Nassariidae (75 species) and Mitridae (51 species) were the other dominant families. Of the 142 families, only 14 had a representative in all the basins. The average taxonomic distinctness of gastropods showed that WB 2 ($P = 0.2\%$), LK ($P = 0.2\%$) and AN ($P = 0.2\%$) basins departed from the 95% confidence funnel (Figure 4c). Moreover, the Λ^+ of these basins ($P = 0.2\%$) were above the above 95% confidence funnel (Figure 4d). A closer look at the data from these basins indicates a widespread representation at higher taxa. However, the unevenness in the distribution of genera and species resulted in the Δ^+ falling significantly below the 95% funnel. For, example in the AN basin, all the 48 species of the family Conidae belong to the single genus *Conus*. In the LK basin, 33 out of the 51 gastropod families were represented by a single genus. In the elliptical plot, the deviation of the LK basin was due to the low Δ^+ and high Λ^+ values.

Based on the Θ^+ cluster analysis, three regions were observed (Figure S1c): the western basins and the eastern EB 4 basin formed a large group (22%), the Island basins (21%) and the northeastern basins of EB 1 and 2 (20%). The clustering of the basins based on the Θ^+ cluster analysis are further illustrated in the nMDS plot (Figure S1d). The Jaccard similarity cluster based on the gastropod species show three groups—(a) The western basins of WB 2 and 3 clustered at 26.5% similarity and was joined by WB 1 basin at 21.59% similarity (b) The Eastern group composed of the gastropod fauna from EB 1 and 2 basins (28%) which in turn was linked to the EB 3 basin at 21% similarity and (c) the AN and EB 4 basins with 21% similarity (Figure 5 c and d).

Bivalve biodiversity and biogeography pattern

The Bivalvia was represented by 582 species belonging to 57 families and 229 genera. The distribution of species followed the pattern of Gastropoda and Polychaeta with highest species richness in AN (110) and EB 4 (63; Figure 3). Similarly, the highest number of rare species were recorded in AN (37%) and EB 4 (21%; Table II). In general, the Veneridae (85 species) was the most dominant family except in LK and KG basins where Teredinidae dominated. The simulation test on Λ^+ using the 95% funnel for bivalves is shown in Figure 4e. In most of the basins, the Δ^+ values were close to the lower limit while AN and EB4 was above the simulated mean value, but within the 95% funnel. However, Δ^+ of EB 3 basin was the lowest and departed significantly ($P = 3.6\%$) from the mean value under the null hypothesis. The variation in taxonomic distinctness for the study area is displayed in Figure 4f. The Λ^+ showed a similar trend to gastropods and polychaetes in which the values for many basins were significantly above the expected mean and was above the 95% funnel. All the western basins (WB 1-3) and EB 3 and 4 from the eastern basin had the Λ^+ value significantly above the upper limit of the funnel. The highest Λ^+ values were for LK (462.80) and EB 3 (461.53) at a significance level of 0.2%. The Λ^+ for WB 1–3 and EB 4 basins were 388.53 ($P = 4.6\%$), 405.4 ($P = 2.4\%$), 418.59 ($P = 0.8\%$) and 372.92 ($P = 4.4\%$), respectively. The high Λ^+ values in LK and EB 3 were also reflected in the elliptical plot, as they were outside the probability ellipse.

The cluster based on the Θ^+ dissimilarity matrix of bivalve species divided the region into two groups (Figure S1e-f). The western subgroup consisted of the bivalve species from WB 2 and 3 basins (14%) that in turn clustered to the WB 1 and EB 4 (13%) group at a low dissimilarity of 17%. The eastern subgroup consisted of the EB 1 and 2 (15%). Interestingly, the bivalve regionalisation based on Jaccard's clustering, showed some differences from that of polychaetes and gastropods (Figure 5e and f). Three regions were recognised: the eastern basins of EB 1 and 2 clustered at 34%

similarity; the second group consisting of the western basins of WB 2 and 3 (36%) and the third group composed of the eastern EB 4 basin and western WB1 basin (32%). The islands and KG basin did not link to any of the cluster.

Environmental Data

The PCA of benthic species richness data and environmental factors showed that the first two components accounted for 78% of the variance. The first component accounted for 53 % of the total variance and segregates the BE basin from the other basins (Figure 6 a–b). The first component was mainly correlated with surface dissolved oxygen, chlorophyll-a, habitat heterogeneity and temperature. The second axis showed differences within the western basin and separated the WB 1 from WB 2–3 which was associated with salinity and coastline length.

The RELATE analysis confirmed that the benthic group similarity matrices and environmental parameters had a similar multivariate pattern. The degree of correlation between matrices was significant for gastropods ($\rho = 0.58$; $P = 0.8\%$) and polychaetes ($\rho = 0.36$; $P = 4.9\%$) while the bivalve matrices showed a low correlation (Table III). In general, the BIO–ENV routine showed that temperature, salinity, habitat heterogeneity and coastline length showed the highest rank correlation (Table III) with the benthic species similarity matrices. The BIO–ENV analysis indicates that a combined effect of temperature and habitat heterogeneity accounted for the highest correlation with gastropod distribution (Table III). The combination of environmental factors that explained the polychaete distribution patterns were temperature, habitat heterogeneity and coastline length. Although, the rank correlation with the bivalve similarity matrix was not significant ($\rho = 0.34$; $P = 12.7\%$), temperature and habitat heterogeneity showed the best correlation (Table III).

Discussion

Benthic Biodiversity Patterns

The Indian coast, bounded by two contrasting seas, the Bay of Bengal and Arabian Sea, offers an excellent opportunity to determine the most important factors influencing coastal biogeography patterns. The role of this environmental complexity in influencing the coastal biogeography was studied using three major benthic groups. The highest species richness and number of rare species was recorded in the EB 4 and AN basins. The high diversity in these basins was also confirmed from the results of taxonomic distinctness indices. The EB 4 basin not only supported more species (high Δ^+) but also showed an even distribution at the higher taxonomic level (high Λ^+). The AN basin also

had high species number and showed higher Λ^+ value but had low Δ^+ for gastropods and polychaetes. The high values of Λ^+ in the AN basin were probably due to the wide-spread representation of higher taxa, however some genera were extremely species-rich resulting in the low Δ^+ (Clarke & Warwick 2001). For, example all the 48 species in the Conidae (Gastropoda) belong to a single genus *Conus*, while many of the genera (*Nerita*, *Terebra*, *Mitra*) were represented by more than five species. Similarly, polychaetes were represented by several genera (e.g. *Perinereis*, *Eunice*, *Chloeia*, *Phyllodoce*, *Polydora*, *Lepidonotus*) with more than three species.

Benthic Biogeography Patterns

The present study identified that temperature, habitat heterogeneity and coastline length best explained the biogeography patterns of benthic groups along the Indian coast. Of the three benthic groups, polychaetes and gastropods showed a significant correlation with the environmental factors. Despite a lack of significant correlation between the bivalves and environmental factors, temperature, habitat heterogeneity and coastline length showed highest correlation (Table III). Several studies have explored the environmental factors that determine the marine biodiversity patterns. Belanger et al. (2012) and Tittensor et al. (2010) used the global-scale data to identify the environmental predictors of biodiversity patterns. In the study of Tittensor et al. (2010), temperature was the only environmental predictor that was highly related to the species richness of all the 13 taxa studied. However, habitat availability and historical factors were also important for coastal species (Tittensor et al., 2010). Belanger et al. (2012) observed that the temperature, salinity and productivity explained 80–89% of variability in the shallow water benthic organism. Similarly, Compton et al. (2013) observed that the temperature gradient and productivity played an important role in the diverse assemblage along the contrasting continental margin of New Zealand. The global biodiversity patterns based on the sandy beach macrofauna also confirms the role of temperature and habitat availability in structuring the benthic communities (Barboza & Defeo 2015). Likewise, Sanciangco et al. (2013) observed that habitat availability and heterogeneity, and sea surface temperature were highly correlated with species richness in the tropical Indo-Pacific. Other areas also provide evidence that habitat heterogeneity appears to influence regional benthic diversity and distribution patterns (Kraan et al. 2010; Sellanes et al. 2010; Sanciangco et al. 2013). Therefore, on a regional scale, habitat heterogeneity and habitat availability may become important environmental factors that influence the distribution of species.

The groupings of the coastal basins observed in the study are consistent with the natural environmental gradient of the Indian coast, was evident from the RELATE, BIO-ENV and PCA analyses. For example, the grouping of EB4 and AN which are characterised by the most diverse habitats along the Indian coast. Moreover, in all the three benthic groups, richness peaked in those two basins. The importance of habitat heterogeneity in increasing the species richness has been described for other regions (Sanciango et al. 2013). The EB4 basin is located at the southern tip of the Indian subcontinent, hence influenced by the Arabian Sea and the Bay Bengal and the open ocean circulation making it a transition zone (Rao et al. 2011). Moreover, the complex topography favours the development of diverse habitats where different species can co-occur. Although the AN basin is located in the Indian Ocean, it is influenced by the western Pacific Ocean via North-westerly through flow in the Strait of Malacca (Kimura & Satapoomin 2009). The AN basin is about ~189 km northwest of Sumatra while it is ~2500 km from the Indian coast. As a result, the region is represented by fauna of the Indian and Pacific Oceans (Kilburn 2002; Kimura & Satapoomin 2009). This is an island ecosystem, where the area, island shape, habitat diversity, distance from mainland, inter-island distance, island history, dispersal and human activities play an important role in the species diversity (Whittaker et al. 2008; Fattorini 2009).

Moreover, regions with diverse habitats are generally associated with both generalist and specialist species (e.g. EB4 and AN). As habitat heterogeneity reduces, as seen in WB 2-3 and EB 1-3, the generalist species characterised by wider dispersal range, efficient colonizing abilities and wide range of environmental tolerance represent the region (Keith et al. 2013). The western (WB 2-3) and other eastern basins (EB 1-3) are characterised by less diverse habitats. Environmental factors also showed a variation which accounted for the differences within and also between the western and eastern basins. The northern Bay of Bengal (EB 1) separated from rest of the eastern basins, was characterised by high dissolved oxygen and chlorophyll-a, and low salinity with little annual variation due to the major rivers in the region (Table I and Figure 1). River discharge, in addition to decreasing the salinity and increasing the turbidity in the coastal environment, may act as a dispersal barrier for many benthic species (Teske et al. 2011). Moreover, the EICC shows a spatiotemporal variation (Durand et al. 2009; Mukherjee et al. 2014) and this discontinuity of the coastal boundary current along the east coast may reduce the long-distance dispersal by retaining the larvae within the system and influence the distribution of the benthic fauna.

A similar gradient in the environmental factors and coastal currents could explain the low similarity among the western basins (Figure 6). Although WB1 showed similarity with the WB 2 and 3, it had its own characteristic species and environmental features. Salinity and temperature showed a north-south gradient from WB1 to WB3 (Figure 1). Similarly, biological productivity also showed a spatiotemporal variation (Lévy et al. 2007). Moreover, the WB1 has a more diverse habitat compared to the WB 2 and 3. As the WB1 has the longest coastline and broadest continental shelf, it is dominated by small-scale processes (Shetye & Gouveia, 1998). Further, the weak WICC north of 20°N and eddies in the Gulf mouth effectively restricts larval dispersal (Babu et al. 2005; George et al. 2011).

Although the reversing of monsoonal currents of the North Indian Ocean has the potential to connect the different biogeographic regions (Obura 2012), the low species similarity in our study may be due to the strong spatiotemporal variability in the coastal current patterns (Durand et al 2009; Amol et al. 2012; Mukherjee et al. 2014). However, even if there is mixing of the two water masses during a particular season, the difference in the environmental factors will allow only species with wider environmental tolerance to recruit successfully. This is evident from only ~32% (34% Polychaeta; 30% Gastropoda; 33% Bivalvia) of the species being common between the western and eastern basins, which is further confirmed from the genetic studies (Menezes et al. 2002; Divya et al. 2012; Kumar et al. 2012; Kunal et al. 2013) and larval dispersal (George et al. 2011). Therefore, in dynamic systems, the species are evolutionarily adapted to maximize recruitment success by avoiding various limiting factors such as food availability and variation in circulation pattern (Peguero-Icaza et al. 2011; Garavelli et al. 2012). The importance of seasonal reversing currents and tolerance of the larvae have been observed (Anderson et al. 2009; Obura 2012; Peguero-Icaza et al. 2011). To evaluate the influence of the boundary currents on the coastal biogeography patterns, oceanographic models are required, which was currently beyond our technical capabilities. However, the spatiotemporal variability observed in the boundary current patterns appears to influence the observed biodiversity patterns.

The other possible reasons for the low similarity in the regions could be the strong coastal upwelling and Oxygen Minimum Zones, which are important biogeography barriers (Wilson 2000). The Arabian Sea is one of the major upwelling regions and also has the largest and most intense Oxygen Minimum Zones of the world (Helly & Levin 2004; Naqvi et al. 2009). We also found a greater difference between the EB4 and adjacent eastern basins but more similarity between the WB 2–3 and

EB4. This difference could be due to the only ‘hard barrier’, the Pamban Pass and Ramsethu located between the Gulf of Mannar and Palk Bay region of the EB 4. This subsurface barrier separates the Gulf of Mannar and Palk Bay region of EB 4 (Rao et al. 2011), which may further limit the movement of benthic larvae within the eastern basin and from the eastern to western basins and vice versa. This is evident from the restricted southern flow of low saline and cooler Bay of Bengal water into the Gulf of Mannar (Rao et al. 2011) and differences in the zooplankton community (Jagadeesan et al. 2013). Therefore, the present study confirms that environmental factors, habitat heterogeneity and availability, and oceanographic features interact to influence the coastal benthic diversity pattern (Sellanes et al. 2010; Sanciangco et al. 2013; Waters et al. 2014).

Although the species number showed differences between the Islands, they clustered, based on Theta dissimilarity for gastropods and polychaetes (Figure S1a-b), which suggests a possibility of gene flow between the islands. De Grave (2001) reported similarity in the Pontoniid of Maldives (including Lakshadweep) and AN. Amongst the two Islands, high diversity and a number of rare species were observed in the AN. Although both the islands are considered to be of recent origin they have different geomorphological features (Malik et al. 2006; Wagle & Kunte 1999). Therefore, larger area, more diverse habitat, geographical proximity to high diversity regions of AN than the low-lying smaller island of LK may explain why they formed distinct regions.

Comparative biogeography pattern

A comparison of the biogeography pattern among the benthic groups was done using the Jaccard analysis. Although it showed some similarity in the clustering pattern, differences were also observed. The adjacent basins of WB 2–3 and EB 1–2 clustered for all the three groups and confirm the well-recognized concept in biogeography studies that the similarity between regions decreases or decays with geographic distance (Nekola & Brown 2007). Further, the polychaete and gastropod clusters are more similar (Figure 5b and d). Polychaetes and gastropods may be sharing a common evolutionary history or ecological traits. The gastropods in the present study were dominated by the carnivorous families and were similar to the other assemblages reported worldwide (Braco et al. 2010). The most dominant Muricidae family feed on epifaunal bivalves and sedentary/slow moving gastropods (Braco et al. 2010). While the other dominant gastropod family such as Conidae, Terebridae and Turridae prefer to feed on polychaetes such as Terebellidae, Sabellidae, Nerididae and Eunicidae (Braco et al. 2010). The highest diversity of these gastropod families was observed in the AN and EB 4 basins that also recorded the highest diversity of those polychaete families.

Previous studies have reported differences in the biogeography patterns between gastropods and bivalves (e.g. Pierrat et al. 2013). Our study confirms the importance of using several groups for testing a biogeography hypothesis. Similar biogeography pattern with widespread taxonomic groups provide evidence that different groups have been shaped by a similar environmental gradient or the same historical factors and hence reflect common speciation events (Glasby 2005; Pierrat et al. 2013; Barley 2015)

Bioregions for the Indian coastal basins

Most of the biogeography studies concluded that there is an east-west difference in the marine community of India. The bioregion for the Indian coast is that proposed by Kilburn (2002) and Spalding et al. (2007). According to Spalding et al. (2007), the western and south-Indian shelf was considered as a single province and subdivided into the western and south Indian ecoregions (Figure 7a). The Bay of Bengal Province consisted of the East India and North Bay of Bengal ecoregion. The Andaman and Nicobar ecoregion was part of the Andaman Province and Lakshadweep Island was part of the central Indian Ocean Island province. While Kilburn (2002), tentatively proposed four subregions based on the limited molluscan fauna and environmental factors. The subregions were (1) the Delta coast comprising of most of Orissa coast (EB 2), West Bengal (EB 1) and Bangladesh characterised by an estuarine coast rich in mangrove, low saline and high turbid conditions (2) the South-east coast (EB4 basin) (3) the Southwest coast of India (south of WB 3 basin) and (4) the North-west coast of India (WB 1 and 2). Our results complement the subregions recognised by Kilburn (2002), although a number of finer scale regions were identified (Figure 5). The results of cluster analysis suggested that the Spalding's western Indian ecoregion (North-west coast of Kilburn) can be split into two regions, namely the WB 1 and a central WB 2 and part (north) of the WB 3 (Figure 7b). The south India ecoregion may be sub-divided into SW (south WB 3 basin) and SE ecoregion (EB 4 basin) as suggested by Kilburn (2002). Since the diverse ecosystems in the EB 4 basin supports a more diverse benthic community (Figure 3). Similarly, we identified a smaller scale division within the Eastern Indian ecoregion i.e. EB 2 and 3. This finer scale division of the ecoregions are supported by the environmental gradient and current patterns. Further work based on an integrated approach (biodiversity, biophysical models, molecular approach) will be needed to confirm the finer scale division of the ecoregions along the Indian coast.

Conclusion

The present study is the first on the biogeography patterns of three benthic groups from the Indian coastal basins. Although the Indian coastal basins are small and situated at the same latitude, the various barriers accounted for the weak similarity. Our results suggest that the benthic biogeography patterns appear to be shaped by the interaction of environmental and oceanographic process. The ‘soft’ barriers included differences in temperature, habitat heterogeneity, habitat availability and spatiotemporal variation in the boundary currents. Upwelling, Oxygen Minimum Zone and freshwater discharge could also influence the species distribution pattern. The only ‘hard’ barrier, the Pamban pass, may restrict the dispersal of marine fauna and may influence the biodiversity distribution pattern. The study confirmed the proposed ecoregion for India, although we also identified finer scale divisions. Defining such smaller provinces help to efficiently improve conservation plans at local and regional scales. There are limitations to the study, as the present research is just at a starting point to understand the marine biogeography of India. The greatest limitation was due to the unequal sampling efforts along the Indian coast. The differences in the species richness and similarity/dissimilarity between the basins may reflect differences in the unequal sampling intensity and methods. The MU, KK, CA and AN have been well sampled, but studies are few from the other regions. Some of the observed patterns will undoubtedly change as a result of the continuous sampling, particularly from areas that are poorly studied. Since sampling techniques along with dispersal, evolution and environmental complexity play an important role in the observed biogeography patterns, the results of the present study need to be looked at with prudence. Nevertheless, similar patterns of benthic groups, coastal environmental conditions and current patterns provide evidence for the existence and generality of observed patterns. Our finding will be useful in guiding future biogeography studies of this unique and underexplored marine system using functional traits, biophysical models, field studies and molecular approach.

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Table I Geomorphological details of the study area

Basins	Coastal States	¹ Basin Area Km ²	² Coastline (Km)	³ Substratum (%)				Major Rivers	⁴ Rainfall (cm)	⁵ Run off (m ³ sec ⁻¹)
				Sandy	Rocky	Muddy	Marshy			
Western (Arabian Sea)										
Kachchh (WB1)	Gujarat (GJ)	28000	1214.7	28	21	29	22	Narmada Tapti	1533	162272
Mumbai (WB2)	Maharashtra (MH)	116000	652.6	17	37	46	-	Bhima	2708	2363
Konkan-Kerala (WB3)	Goa (GA)		151	44	21	35	-	Mandovi-Zuari	300	
	Karnataka (KA)		280	75	11	14	-	Kalinadi	531	12834
	Kerala (KL)		569.7	80	5	15	-	Periyar	2955	16186
Lakshadweep (LK)	Lakshadweep (LK)	--	132						1653	
Total		580000	3000				-		10265	
Eastern (Bay of Bengal)										
Bengal (EB1)	West Bengal (WB)	32000	157.5	-	-	51	49	Ganga	153285	120372
Mahanadi (EB2)	Orissa (OR)	14000	476.4	57	-	33	10	Mahanadi	1491	188335
Krishna- Godavari(EB3)	Andhra Pradesh (AP)	24000	973.7	38	3	52	7	Krishna		164174
								Godavari		306118
Cauvery (EB4)	Tamil Nadu (TN)	30000	937.5	57	5	38	-	Cauvery	1022	23506
Andaman (AN)	Andaman & Nicobar (AN)	41000	1962						2806	
Total		141000	4507.1						233705	
Mainland			5413.1							
Island			2094							
Total			7507.1							

¹ Director General of Hydrocarbon Govt. Of India (www.dghindia.org); ² Naval Hydrographic Office; ³Kumar 2006; ⁴Indian Meteorological Department (IMD); ⁵ www.nelson.wisc.edu/sage/data-and-models/riverdata/index.php.

Basins	Polychaeta	Gastropoda	Bivalvia
Kachchh (WB1)	1.25	8.17	7.33
Mumbai (WB2)	7.79	4.14	4.00
Konkan-Kerala (WB3)	14.33	1.68	3.67
Lakshadweep (LK)	6.85	6.61	6.33
Bengal (EB1)	7.17	1.68	4.00
Mahanadi (EB 2)	5.61	3.36	10.33
Krishna-Godavari (EB3)	4.67	1.01	6.67
Cauvery (EB 4)	35	24	21
Andaman (AN)	17	49	37

Table III Results of RELATE and BIOENV based on Spearman's correlation.

Benthic Group	RELATE		BEST		Environmental Parameters
	ρ	P (%)	ρ	P (%)	
Bivalvia	0.34	12.7	0.58	12.9	Temperature, Habitat heterogeneity, coastline length
			0.55		Temperature, Habitat heterogeneity
Gastropoda	0.58	0.8	0.67	2.4	Temperature, Habitat heterogeneity, coastline length
			0.66		Habitat heterogeneity, coastline length
Polychaeta	0.36	4.9	0.57	5	Temperature, Habitat heterogeneity
			0.52		Temperature, Habitat heterogeneity, coastline length

FIGURE CAPTIONS

Figure 1 Surface temperature and salinity gradient derived from ODV data (Schlitzer 2014) with schematic representation of circulation pattern in the North Indian Ocean (Shankar et al. 2002) during northeast monsoon (a) and southwest monsoon (b) EICC-East India Coastal Current; WICC-West India Coastal Current; SMC Summer Monsoon Current; WMC Winter Monsoon Current; LL Lakshadweep Low; LH Lakshadweep High.

Figure 2 (a) Map of India showing the coastal states (abbreviation as in Table I) and (b) coastal sedimentary basins WB1-Kacheh; WB2-Mumbai; WB3-Konkan Kerala; LK-Lakshadweep; EB1-Bengal; EB2-Mahanadi; EB3-Krishna Godavari; EB4-Cauvery; and AN-Andaman and Nicobar (Source: DGH 2006-07) WB Western Basin and EB Eastern Basin.

Figure 3 Species richness of benthic groups in the Indian coastal basins. Abbreviations as given in Figure 2.

Figure 4 The 95% confidence funnel showing the observed Δ^+ and Λ^+ from the master list of Polychaete (a-b); Gastropoda (c-d) and Bivalvia (e-f) Expected mean indicated by the line in the middle of the funnel. Basin abbreviations as given in Figure 2.

Figure 5 Cluster and nMDS based on Jaccard similarity on the species incidence data for Polychaeta (a-b); Gastropoda (c-d) and Bivalvia (e-f) Basin abbreviations as given in Figure 2.

Figure 6 PCA biplot plot illustrating the association of benthic species richness and environmental factors (a) and basin distribution in the biplot (b). T-temperature; S-salinity; DO-dissolved oxygen, HH-habitat heterogeneity; CL-coastline length; B_sp. Bivalvia species richness; G_sp. Gastropoda species richness; P_sp. Polychaeta species richness. Basin abbreviations as given in Figure 2.

Figure 7 (a) Ecoregion for India based on Marine Ecoregions of the World (MEOW) (Spalding et al. 2007)—Western India; southern India and Sri Lanka; Maldives including Lakshadweep Islands; Eastern India; Northern Bay of Bengal (108); and Andaman and Nicobar Island. Numbers are ecoregion codes (Spalding 2007). (b) Finer scale division of MEOW based on the present study—Northwest India (1); Central western India (2); Southwest India (3); Lakshadweep (4) Southeast India (5); Central Eastern India (6); North Eastern India (7); North Bay of Bengal (8); Andaman and Nicobar (9).

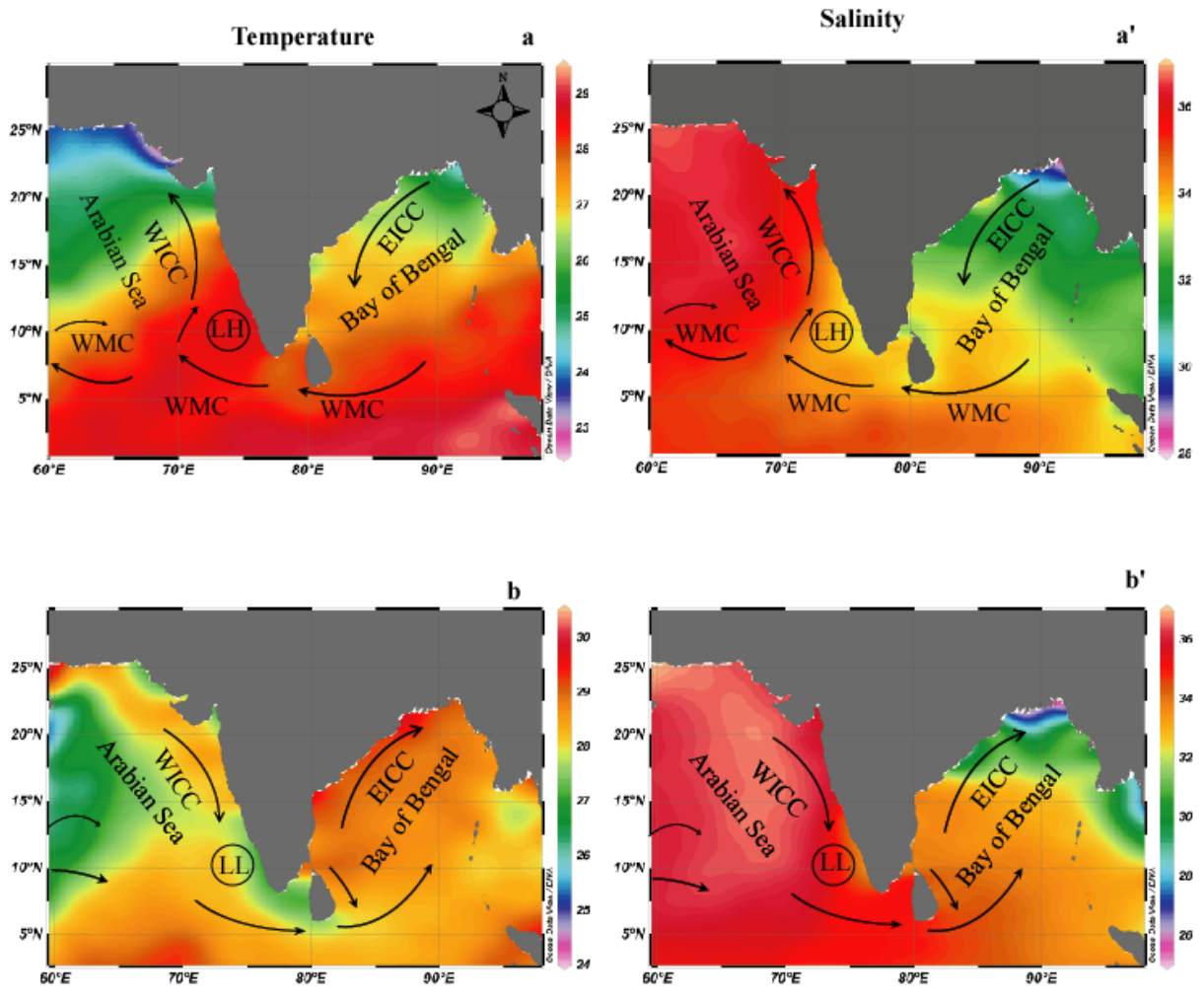


Fig.1.

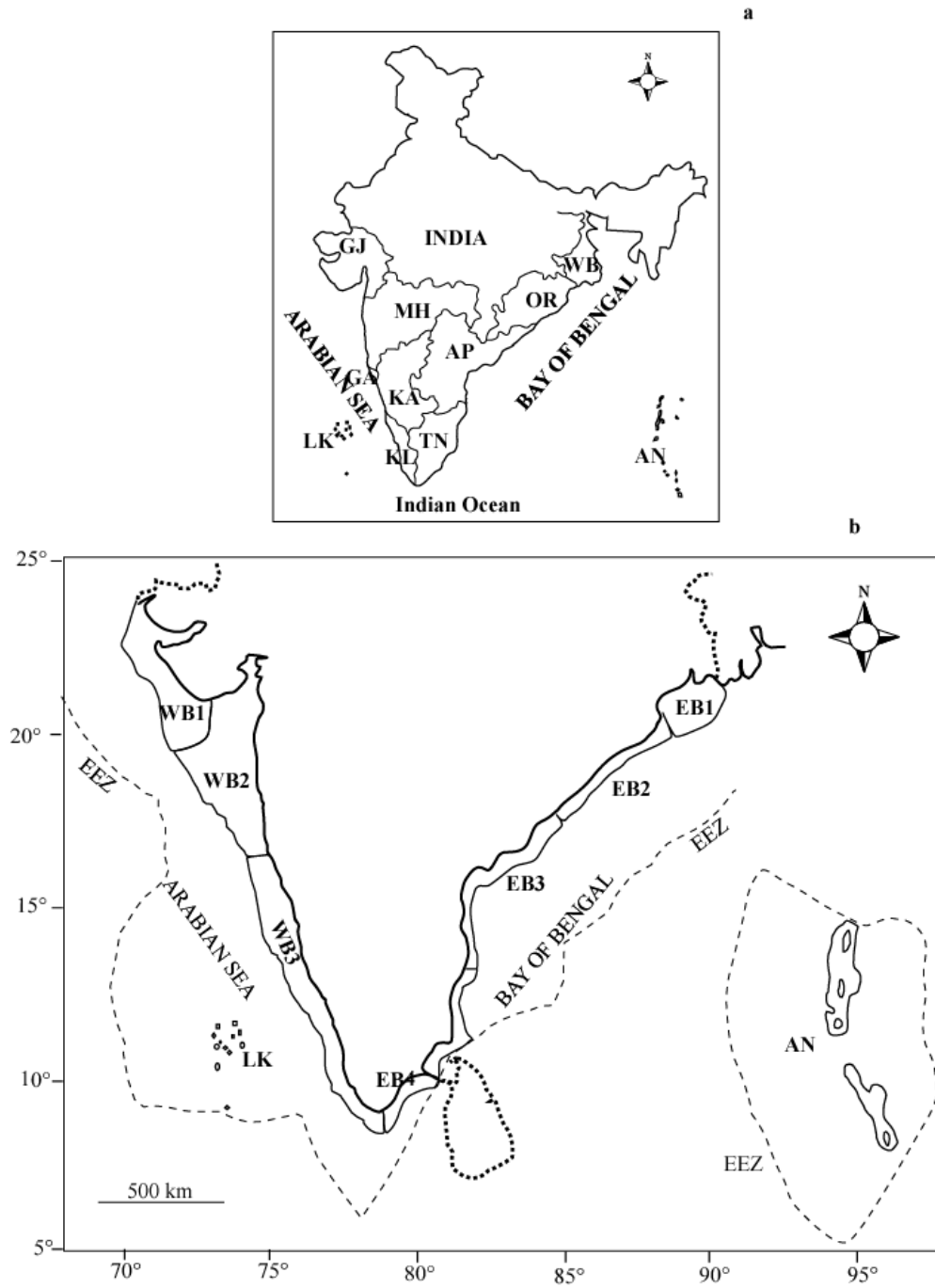


Fig. 2.

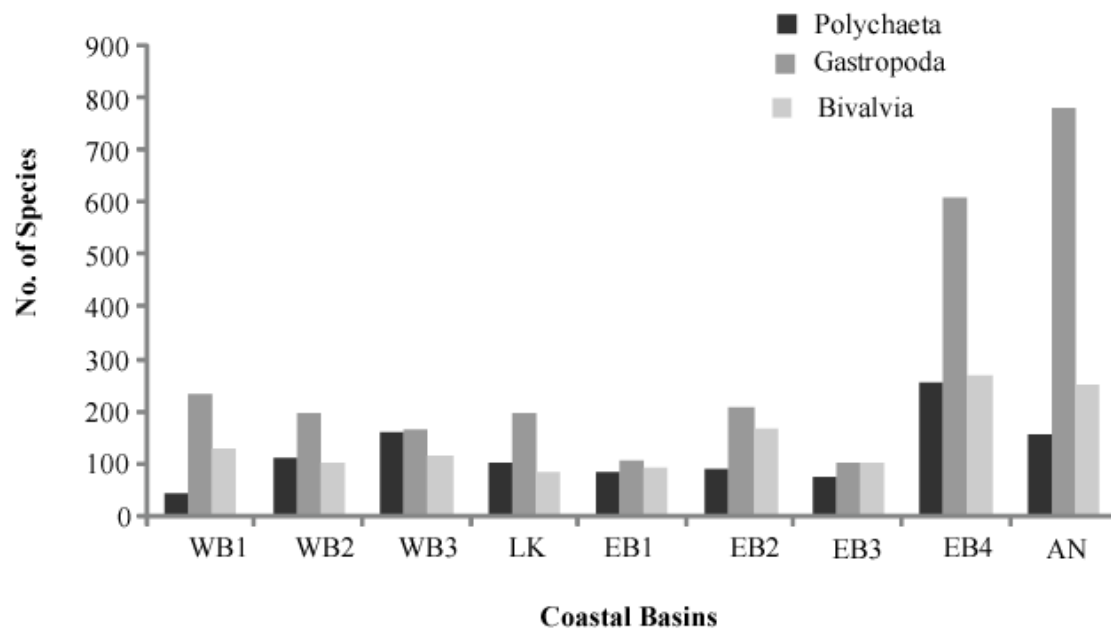


Fig.3.

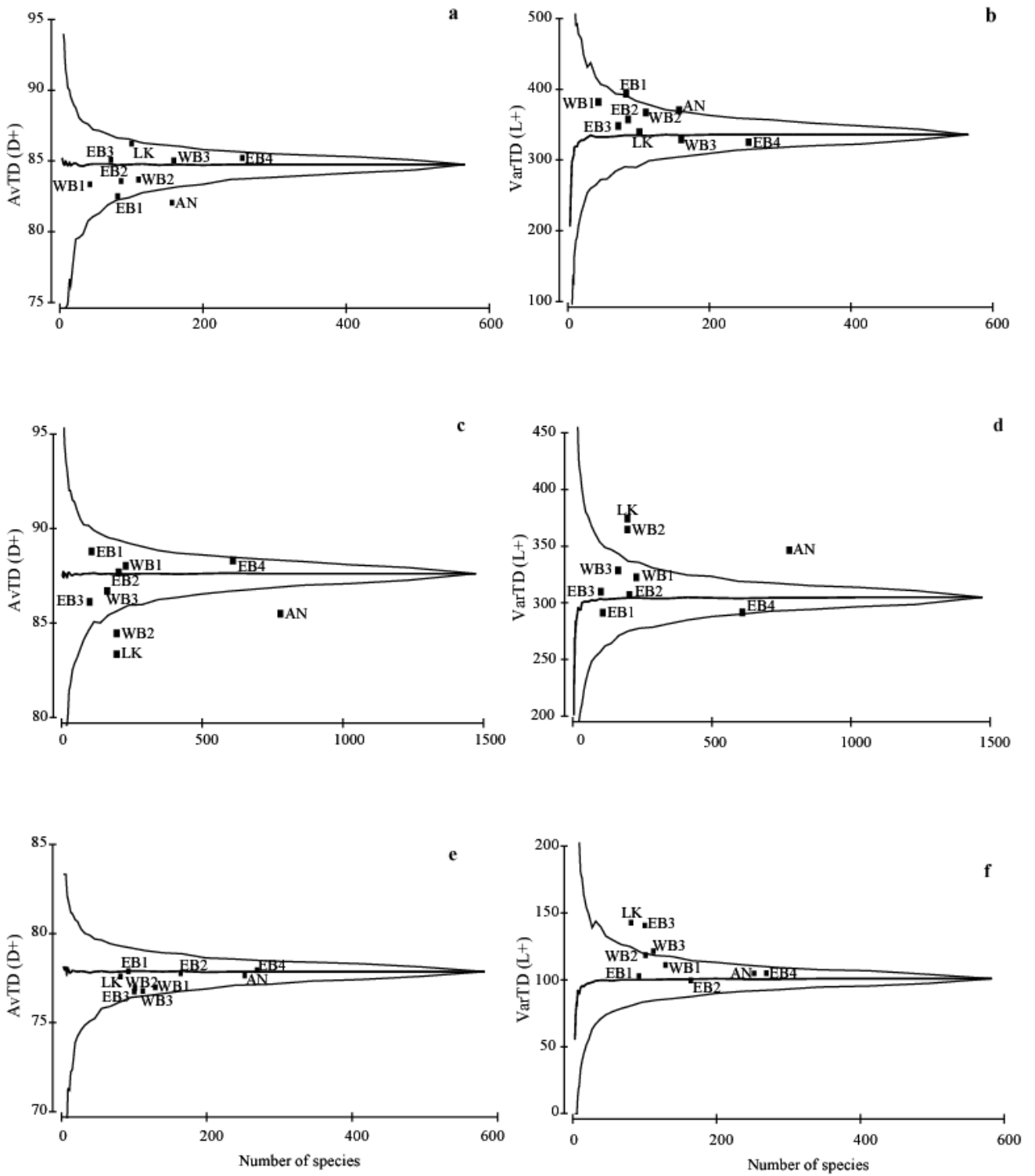


Fig. 4.

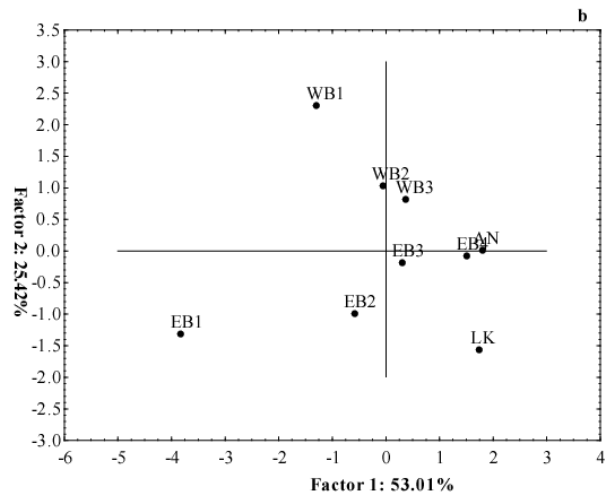
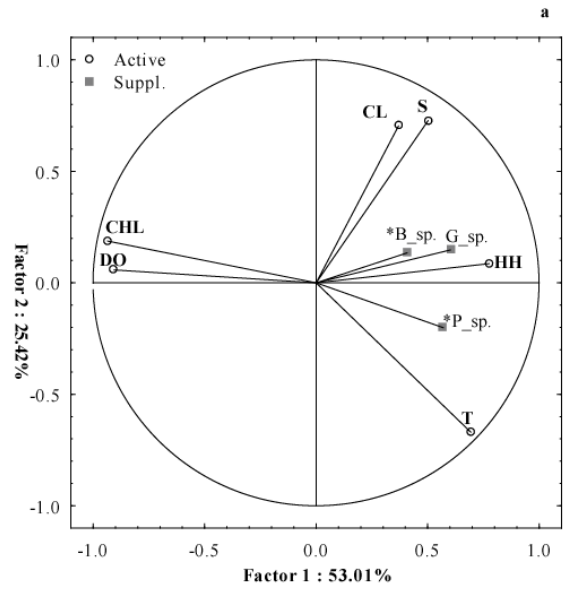


Fig. 6

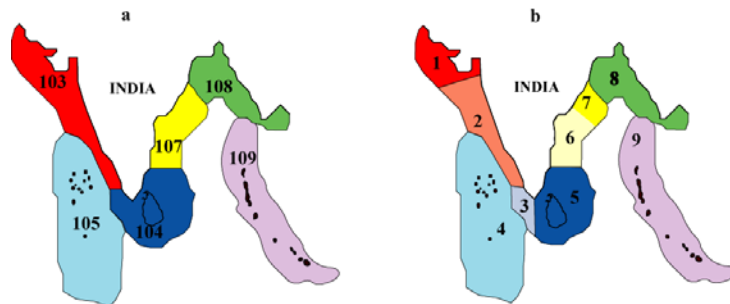
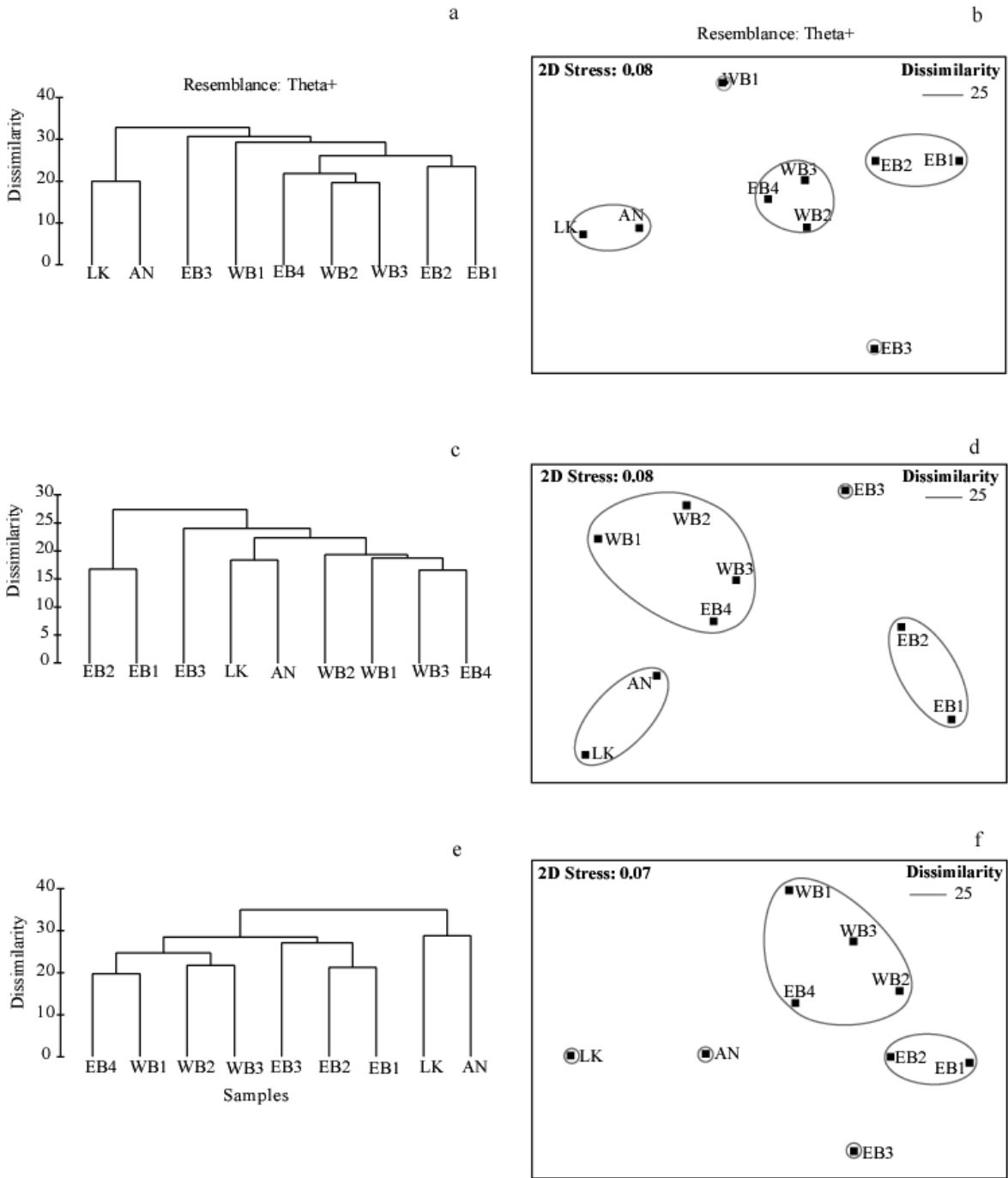


Fig. 7

Table SI Categories and scores for habitat			
Habitat	HH measures	Category	Scores
Coral Reef	Area cover %	< 60	1
		> 60	2
	Dominant Coral morphotype	Massive and submassive corals	1
		Monospecific stands of foliose and branching non- <i>Acropora</i> corals	2
		Branching and tabular <i>Acropora</i> corals	3
		Mixed coral morphology reefs	4
	Distribution	Patchy	1
Fringing		2	
Mangroves	Area cover %	< 20	1
		> 20	2
	Distribution	Patchy	1
		Dense	2
	Species richness	< 40	1
		41-50	2
> 50		3	
Sea grass	Area cover %	< 60	1
		> 60	2
	Species richness	< 40	1
		40-50	2
		> 50	3
	Distribution	Patchy	1
		Dense	2
Intertidal	Sandy, rocky or muddy	Absent	0
		Present	1
Shelf	Dominant substrate	Fine (silt and clay)	1
		Coral debris	2
		Sand	3



Suppl. Fig. 1 Cluster and nMDS based on Theta dissimilarity on the species incidence data for Polychaeta (a-b), Gastropoda (c-d) and Bivalvia (e-f). Basin abbreviations as given in Figure 2.