Journal of the Marine Biological Association of the United Kingdom, 2019, 99(1), 163–177. © Marine Biological Association of the United Kingdom, 2017
doi:10.1017/S0025315417001837

Influence of regional environment in guiding the spatial distribution of marine bivalves along the Indian coast

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Tropical coastal areas are amongst the most diverse ecosystems in the world. However, there are quite a few coasts that have rarely been studied for their macro-benthic diversity. The Indian coastline presents one such gap area. Two sub-parallel coastlines of India have a wide latitudinal span (8–23°N) and strikingly different physiographic environments. While the east coast receives a high siliciclastic input from large river systems flowing to the Bay of Bengal with fluctuating salinity, the west coast has a large shelf area and high productivity of the Arabian Sea. Such difference enables us to evaluate the effect of regional environmental parameters on marine molluscan diversity and distribution in an intra-tropical setting. Because of the wide latitudinal range, it is also possible to assess if spatial difference in species richness in such a regional scale follows the large-scale biodiversity pattern such as Latitudinal Biodiversity Gradient (LBG) despite inherent environmental variation. We used species distribution of marine bivalves, compiled using bioSearch and the Ocean Productivity database, to address this question. Our results show that intra-tropical species richness of marine bivalves is guided primarily by regional environmental parameters. Even with identical latitudinal extent, higher nutrient availability and larger shelf area, the west coast has significantly lower richness than the east coast; among environmental variables, productivity, salinity and coastline length emerged as significant predictors of species diversity. Moreover, a positive influence of a South Asian biodiversity hotspot on east coast fauna and a negative impact of the oxygen-depleted condition of Arabian Sea on west coast fauna, may have a significant contribution in developing such coastal variation in species richness. The latitudinal variation in species richness did not follow LBG. In contrast to the coast-specific diversity difference, species composition is not found to be dictated by coastal affiliation. The composition corresponds primarily to physiographic conditions. We identified three distinct eco-regions (north-western, southern, north-eastern) with characteristic species composition corresponding to unique physiography and productivity mechanism. The NW region has low siliciclastic input and high productivity associated with upwelling during winter cooling. The NE region has a distinctly high riverine input and salinity fluctuation. The southern region, in contrast, has well developed reefal system with moderate variation in salinity. Such correspondence underscores the importance of the regional environment in dictating the species diversity and distribution in the shallow marine realm.

Keywords: Biodiversity, latitudinal variation, species composition, Bay of Bengal, Arabian Sea

Submitted 5 June 2017; accepted 11 October 2017; first published online 21 November 2017

INTRODUCTION

Tropical and subtropical coastal areas are characterized by the highest species richness in the shallow marine realm (Crame, 2000a, b; Rex *et al.*, 2005). However, there are still gaps in our understanding of the regional controls of diversity after a long history of biodiversity studies, primarily because of the lack of research in some specific geographic areas of the tropics. The most severe knowledge gaps in biodiversity from shallow marine environments exist from the Indian Ocean (Crame, 2000a). For molluscan diversity, these major gaps include the African coast, the Indian coast and the oceanic islands (Stehli *et al.*, 1967; Crame, 2000a, b; Gray, 2001). Although efforts have been made to close the gap for other areas (Oliver, 2000; Oliver & Zuschin, 2001; Ashton *et al.*, 2003; Zuschin & Oliver, 2003, 2005; Zuschin Zauner & Zuschin, 2016; Steger *et al.*, 2017), limited efforts have been directed to study molluscan diversity of the Indian coast (Satyamurti, 1952, 1956; Venkataranman & Wafar, 2005; Ramakrishna & Dey, 2010). There is a plethora of studies on species that are important for aquaculture (Rao, 1969; Appukuttan, 1972; 1996; Alagarswami, 1974a; b; 1975, 1983; Mahadevan & Nayar, 1976; Dharmaraj & Nair, 1980; Mahadevan *et al.*, 1980; Nair & Dharmaraj, 1980; George *et al.*, 1986; Alagarswami *et al.*, 1987; Tanabe *et al.*, 2000; Kripa & Appukuttan, 2003; Kripa *et al.*, 2012) at a local scale from various sites along the Indian coast. Among marine benthos, bivalves have been taxonomically standardized, and their global diversity trends are representative of standing benthic invertebrate diversity trends reported for shelf faunas in general (Valentine & Jablonski, 2015). Moreover, they are often reported exhaustively due to their economic importance and are known to respond to oceanographic variables (Fernández *et al.*, 2009; Miller *et al.*, 2013). Despite these advantages that make bivalves an ideal group to study regional biodiversity, there has not been a single detailed study focusing on marine bivalves that evaluated the regional control on

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latitudinal and coastal variation in diversity along the Indian coast.

The Indian coastal region presents a unique scenario to evaluate the contribution of a regional environment on diversity profile of marine organisms, especially the marine benthos such as bivalves. Two of the coastlines of the Indian subcontinent have similar latitudinal spread of 15° (8–23°N). Such a wide latitudinal range is likely to demonstrate a biodiversity gradient conforming to global patterns such as the Latitudinal Biodiversity Gradient (LBG). However, the physiographic characters of the two coasts (east vs west) are strikingly different. Differences between the coasts primarily come from the distinct physical and chemical regimes of the Arabian Sea (west coast) and Bay of Bengal (east coast). These two enclosed basins differ primarily because of the differing amounts of freshwater and sediment influx. The Bay of Bengal receives large quantities of fresh water from hinterland rivers (an imposing 1.6 × 1012 m^3 year^{-1} compared with 0.3 × 1012 m^3 year^{-1} in the Arabian Sea (Subramanian, 1993)) as well as oceanic precipitation making its upper layers less saline (Shetye *et al.*, 1991; Shankar & Shetye, 2001). It also receives a substantial amount of siliciclastic input through the Ganga-Brahmaputra River system (Sangode *et al.*, 2001) and other major rivers such as the Mahanadi, Godavari, Krishna, Cauvery, Subarnarekha and Baitarani (Subramanian, 1996). The west coast, on the contrary, is dominated by the Indus river system with minor siliciclastic input from the Narmada and Tapi rivers (Chamyal *et al.*, 1997; Inam *et al.*, 2007; Marathe *et al.*, 2011). The associated suspended sediment discharge into the Bay of Bengal is estimated to be as high as 14 × 10^8 tonnes compared with ~2 × 10^8 tonnes in the Arabian Sea (Madhupratap *et al.*, 2003).

The physiographic characters that separate the east from west coast of India may have an important influence on marine biodiversity. Rivers are important factors in controlling productivity; the presence of larger rivers in a region leads to higher productivity, which in turn may affect marine species diversity and composition (Eadie *et al.*, 1994; Gallmetzer *et al.*, 2017). Suspension-feeding molluscs depend on primary productivity in the water column for food, which is also affected by nutrients carried in freshwater inflow of the rivers. Salinity, a functional parameter for biological diversity, is also controlled by river input. Although studies have suggested strong ties between salinity and biological diversity in marine ecosystems, they fail to come to a consensus about the exact nature (positive or negative) of the effect (Drouin *et al.*, 1985; Casamayor *et al.*, 2000). Apart from salinity and productivity, the suspended siliciclastic input from rivers often hinders bivalve growth and can dictate the population size of molluscan assemblages in a specific environment (Ellis *et al.*, 2002; Coco *et al.*, 2006).

Previous studies evaluating the effect of the physical environment on regional marine biodiversity have primarily been conducted in the temperate region and geographically concentrated in the coastal areas around the Mediterranean Sea (Astraldi *et al.*, 1995; Sabatés *et al.*, 2007) and Pacific (Bergen *et al.*, 2001) and Atlantic Oceans (Sanders, 1968; Boesch, 1979). Although many of these studies found a strong influence of various regional factors (such as sedimentation, coastal character, latitude) on marine diversity, the relationships were highly region specific, and thus cannot be used as generalized predictors for unexplored areas (Sanders, 1968). The Indian coastline, with its great variation in physical character and without exhaustive documentation of marine species, has rarely been explored for assessing the effect of regional environment on diversity. In a limited area of the north-western shelf of India, Jayaraj *et al.* (2007) evaluated environmental influences on macrobenthos and found a combination of factors (such as temperature, salinity, dissolved oxygen, sand and organic matter) explaining macrobenthos diversity. In their comprehensive study, Sivadas & Ingole (2016) have attempted to evaluate this effect around the entirety of India by documenting benthic communities of coastal basins of India. However, the coarse resolution of their study, fixed at basin scale, was insufficient to assess finer geographic controls on biodiversity that one expects along the Indian coastline due to its great geomorphological heterogeneity.

In this study, we attempted to evaluate the nature of diversity and species composition of marine bivalves along the coast of India in order to understand if intra-tropical marine diversity is guided by regional environmental parameters. It would also give us an opportunity to evaluate if this pattern is conformable with LBG. Using occurrence data of Recent bivalves from a database maintained by the National Institute of Oceanography, Goa, we addressed the following questions:

1. Can variation in species richness be explained by regional environmental parameters (such as productivity, salinity, temperature, coastal length and rivers)?
2. What dictates the variation in species composition along the coast?
3. Does the pattern of species richness follow the LBG?

MATERIALS AND METHODS

Diversity and ecology

We have collected pre-existing occurrence data from bioSearch (http://www.biosearch.in); it is a marine biodiversity database of India that is developed and maintained by the Bioinformatics Centre, National Institute of Oceanography, Goa, India. It has occurrence data of various marine groups reported from scientific cruises and other published literature. Occurrence, in our study, implies the number of times a species is reported from a latitudinal bin. It does not contain any information about the number of individuals or the sampling intensity. The database provided scientific name, along with taxonomic details, feeding habit, habitat, size and location. Location data are often supplemented by Google Earth for acquiring correct latitude and longitude. To standardize the quality of the data, we excluded the occurrences where the taxon was not identified to species level or the location name was not specific. Each coast is divided into 15 equally spaced latitude bins (Figure 1, Table 1) and occurrence of species in each bin is recorded. The bathymetric information is sparse; however, the majority of the occurrence is from shallow shelf setting. Occurrence from same location with bathymetric difference are treated as single occurrence. Taxonomic information was verified later using the World Register of Marine Species (WoRMS). The ecological information was collected from various sources including bioSearch, NMita and published literature; if details were unavailable at species level, genus level data were considered.

We recorded three ecological characteristics, namely, substrate relationship, type of attachment and feeding. All

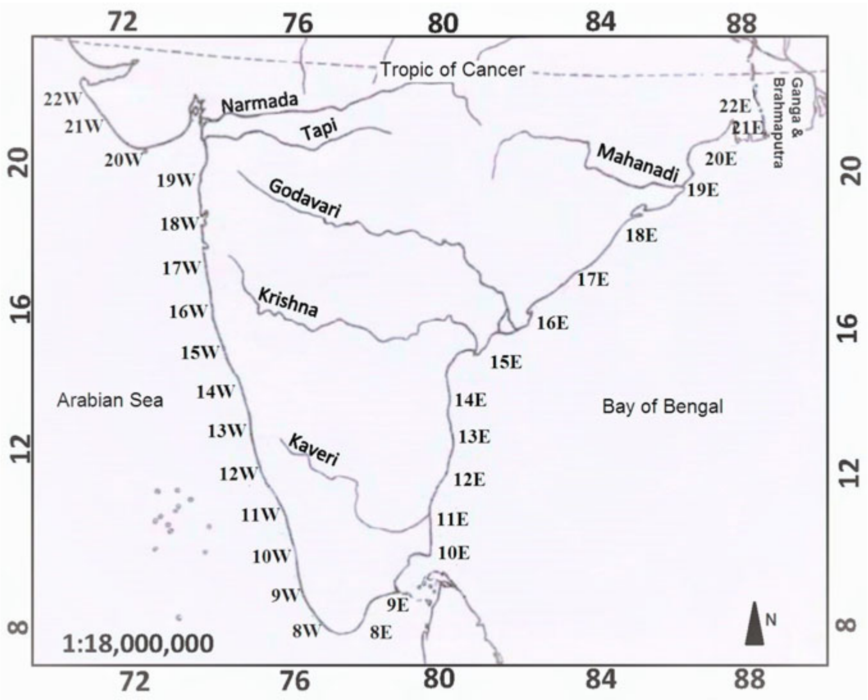

Fig. 1. Indian map showing the major rivers and latitudinal bins used for this study. The map is based on Survey of India Outline map (1996). Each bin is characterized by a specific name denoted by the latitude and the initials of the coast in which the bin is located.

bivalves are classified in the following substrate relationship: (1) Infaunal (Infaunal siphonate, Semi-infaunal, Infaunal asiphonate), (2) Epifaunal, (3) Others (Borer on or within hard substrates, Nestler on or within hard substrates). According to style of attachment, the species are divided into the following groups: (1) Byssally attached, (2) Cemented and

Table 1. Summary of bivalve diversity and environmental parameters in various latitudinal bins along the two coasts of India.

Latitude	Species richness	Occurrence	Rivers	Coastline length (km)	Temperature (°C)	Productivity (mg C m^{-2} day^{-1})	Salinity
22W	67	87	4	388	27.24	2403.6164	36.0125
21W	36	11	5	400	27.14	2053.7989	36.0025
20W	44	27	8	330	27.389	2333.9513	35.848
19W	70	71	3	174	27.641	2188.3939	35.8745
18W	60	21	5	235	27.955	1294.0732	35.5525
17W	51	1	3	124	28.187	1444.8986	35.533
16W	62	28	7	123	28.402	1013.7636	35.5253
15W	64	81	3	134	28.511	959.40704	35.2408
14W	49	39	5	138	28.525	1404.0882	34.6438
13W	35	6	5	122	28.51	1097.9712	34.5272
12W	36	20	5	120	28.629	535.4525	34.2261
11W	38	26	6	139	28.68	1264.941	34.2257
10W	37	14	3	120	28.483	1963.3682	33.8517
9W	44	42	1	116	28.454	1619.5527	34.2014
8W	27	35	1	166	28.216	1585.1812	34.4293
8E	50	41	2	165	27.97	1124.8526	34.3158
9E	206	446	3	295	28.102	1411.0814	33.8696
10E	108	37	2	181	28.305	1273.8081	33.3727
11E	124	89	6	118	28.262	834.7673	33.0352
12E	113	26	2	117	28.187	549.7318	33.3035
13E	138	143	2	123	28.236	667.3252	32.8184
14E	117	1	3	117	28.02	684.4264	31.2405
15E	118	7	5	223	28.069	760.8068	30.8612
16E	134	39	4	219	28.18	1175.0101	30.5957
17E	145	101	1	184	28.272	776.0350	30.9715
18E	108	2	4	172	28.360	657.0357	30.6322
19E	144	318	3	220	28.281	995.92901	29.6329
20E	127	133	5	163	27.866	1372.5198	28.9896
21E	118	425	5	281	27.664	2685.4977	28.0643
22E	56	119	4	115	27.654	2675.4977	28.0603

(3) Unattached. The bivalve species are classified into three groups based on their feeding behaviour: (1) Deposit feeders (subsurface and surface deposit feeder), (2) Suspension feeders, (3) Others (chemosymbiotic deposit feeder, predatory carnivores).

Environmental parameters

We collected environmental data from the Ocean Productivity database (http://www.science.oregonstate.edu/ocean.productivity/standard.product.php) for each latitudinal bin. The data source housed annual mean and range of net primary productivity (NPP), sea surface temperature (SST) and salinity. For counting numbers of rivers and measuring the length of the coastline, we used Google Earth images at the resolution of 1:20,500 (Table 1).

Analysis

We used species richness as a measure of species diversity in this study. Species richness is the total number of species in that particular latitudinal bin. Rarefied species richness curves are constructed from total number of occurrences and the confidence interval (calculated by bootstrap method) to evaluate the statistical distinctness of the rarefaction curves are calculated following the method proposed by Colwell *et al.* (2012). Along with observed species richness, we also used a range-through approach to calculate species richness for assessing latitudinal gradient; in this approach, if a species appears in two or more non-adjacent bins, they are assumed to be present in all the intermediate bins in that specific coast. We estimated the effect of environmental variables with multiple generalized linear models (GLMs) that analyses predictors simultaneously and evaluates their partial contributions to total variation in diversity (Quinn & Keough, 2002).

Similarities among latitudinal bins were calculated from a presence/absence matrix of the species in bins using the Sørensen similarity index. The Sørensen index implicitly incorporates differences in composition attributable to diversity gradients, ignoring relative magnitude of species gains and losses (Koleff *et al.*, 2003). The similarity matrices were clustered by unweighted pair group method using arithmetic averages (UPGMA), and visualized as a dendrogram. AU (Approximately Unbiased) *P*-value, which is computed by multiscale bootstrap resampling and hence is a better approximation to unbiased *P*-value, is used to compare groups in the dendrogram. Two-dimensional ordination assembles were created with non-metric multidimensional scaling (NMDS) using Sørensen similarity indices. To assess the relative importance of environmental parameters for distribution of all species, we used Redundancy Analysis (RDA). RDA can be thought of as the canonical extension of principal component analysis (PCA), where ordination vectors are constrained by multiple regression to be linear combinations of the original explanatory variables (Legendre & Legendre, 1998). The species distribution data were Hellinger distance-transformed (Legendre & Gallagher, 2001). This transformation enables us to analyse species distribution data by Euclidean-based ordination methods like RDA, hence it is a preferable alternative to chi-square based ordination methods, such as canonical correspondence analysis (CCA, Legendre & Gallagher, 2001). Significance of the canonical models, in terms of the first canonical axis and all canonical axes, was tested using 999 permutations. For cluster, NMDS and RDA analyses, we considered only those latitudinal bins where there is a minimum of 20 occurrences.

All univariate and multivariate analyses were performed in R (R Core Team, 2012). The ecological analyses were done using the packages Vegan and BiodiversityR in R platform.

RESULTS

Species diversity

We encountered a total of 2436 occurrences representing 417 species belonging to 183 genera. Out of these, 1927 occurrences are recorded from the east coast which represent 371 species (157 genera) and 509 occurrences are from the west coast representing 177 species (89 genera). Total number of families for the east and the west coast is 53 and 37 respectively. The most common five families are Veneridae, Teredinidae, Mytilidae, Tellinidae and Arcidae. There are 125 common species shared between the east and the west coast. The most common species is *Anadara antiquata* for the east coast and *Donax scortum* for the west coast.

The east coast has slightly higher median species richness per bin compared with the west coast (Figure 2; Wilcoxon rank sum test $W = 157.5$ and $P = 0.06$). To account for unequal occurrences between two coasts, we compared the rarefied species richness of the two coasts (Figure 3). The rarefied richness shows a significant difference between the east and the west coast. The difference is not significant in terms of relative abundance of various life modes (Figure 4).

There is no correlation between species richness and latitude for the east coast (Spearman's rho = 0.05 and $P = 0.84$); however, the west coast shows a significant positive correlation (Spearman's rho = 0.56 and $P = 0.03$) (Figure 5). When we run the analysis for the five most common families, Teredinidae (Spearman's rho = −0.670 and $P = 0.006$), Tellinidae (Spearman's rho = 0.748, $P = 0.0013$) and Arcidae (Spearman's rho = 0.7365, $P = 0.0017$) show a significant positive correlation for the west coast (Figure 6).

Life modes

The species represent a variety of life modes, attachment types and feeding styles (Table 2). Infaunal emerges to be the most common life mode. Comparison between the coasts shows that the east coast consists of a slightly higher proportion of

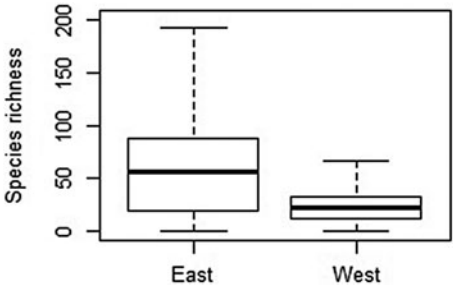

Fig. 2. Relationship between species richness (per latitudinal grid) and coast. The boxes are defined by 25th and 75th quantiles; thick line represents median value.

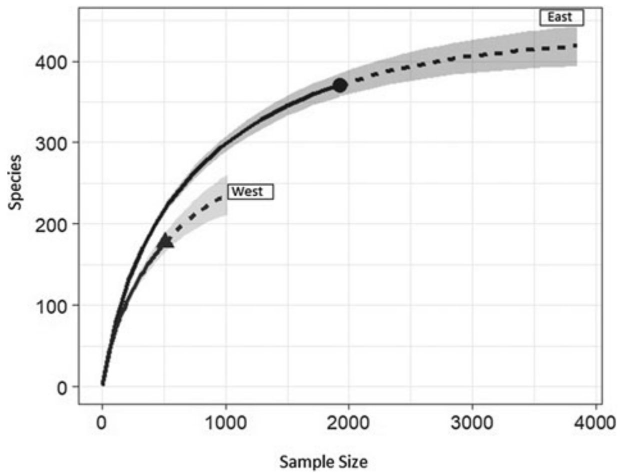

Fig. 3. Rarefied species richness for east and west coast with confidence intervals. The solid and dashed lines represent interpolated and extrapolated values respectively.

infaunal species than the west coast (Wilcoxon rank sum test, $W = 154$, $P = 0.08$). Among the epifaunal species, the east coast has a slightly higher proportion of cemented bivalves compared with the west coast. The two coasts do not show any significant difference in proportion of various feeding styles.

The latitudinal distribution of life modes did not show any consistent pattern for either of the coasts (Figure 7). The same is true for attachment type and feeding style. Epifauna shows a significant correlation for both east (Spearman's rho $= -0.51$ and $P = 0.04$) and west coast (Spearman's rho $= 0.66$ and $P = 0.006$) (Figure 7). Among various epifaunal groups, only cemented bivalves show a significant positive correlation for west coast (Spearman's rho $= 0.76$ and $P = 0.0009$).

Species composition

Cluster analysis separated the bins into three detectable clusters: (a) north-eastern bins (b) southern bins, and (c) north-western bins. The southern bins are closer to north-western bins; north-eastern bins appear separated from the remaining areas. There is also a clear separation between north-western and southern bins (bootstrap = 96% and 99% respectively) (Figure 8). The southern coastal bins have slightly higher species richness (~25 per bin) with dominance of species

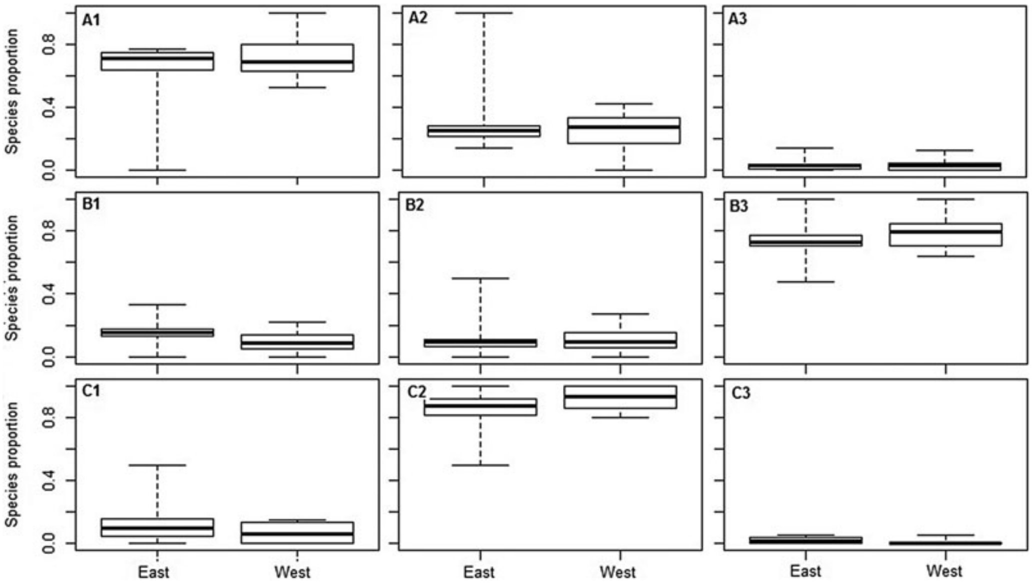

Fig. 4. Relative proportion of various ecological groups in two coasts. (A) Lifemode (1. Infauna, 2. Epifauna, 3. Others). (B) Attachment type (1. Byssally attached, 2. Cemented, 3. Unattached). (C) Feeding type (1. Deposit feeder, 2. Suspension feeder, 3. Others). The boxes are defined by 25th and 75th quantiles; thick line represents median value.

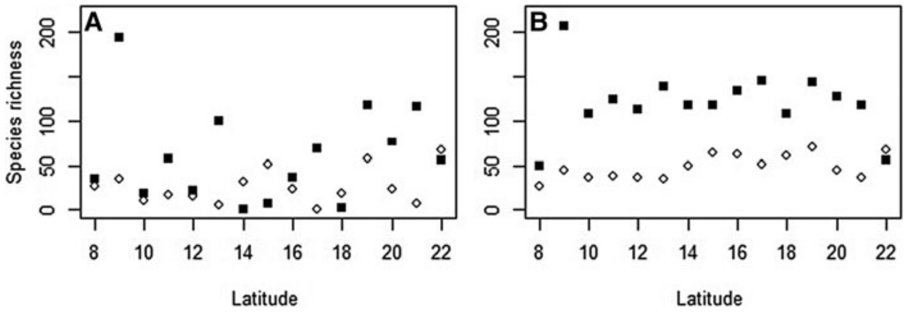

Fig. 5. Relationship between species richness and latitude from (A) actual occurrence, (B) range-through occurrence. West coast is represented by open diamonds and east coast is represented by solid squares.

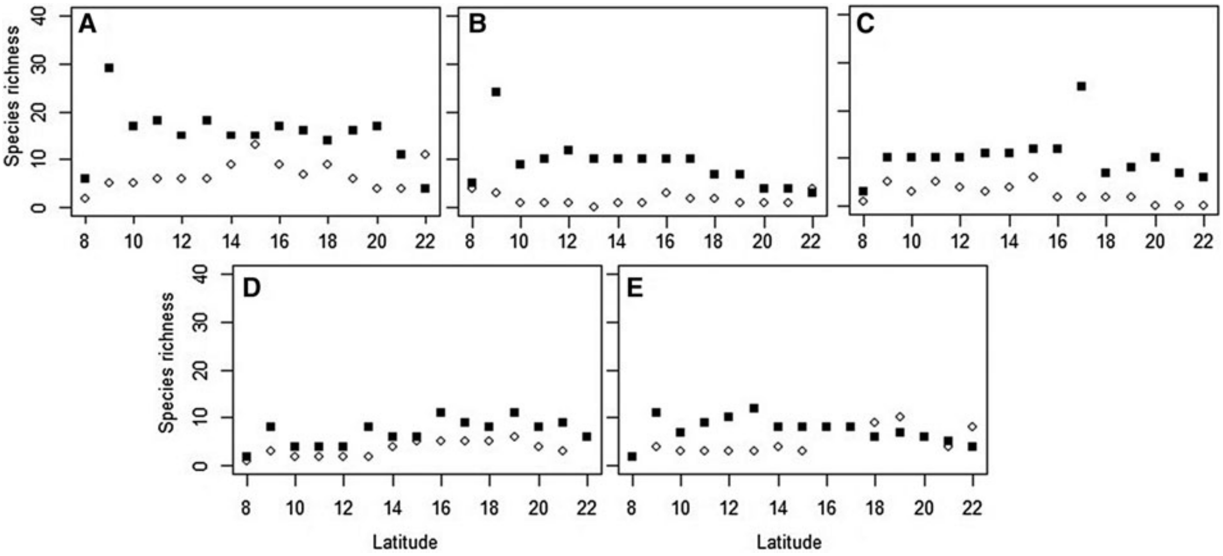

Fig. 6. Relationship between species richness (range through) and latitude for most common families. (A) Veneridae, (B) Teredinidae, (C) Tellinidae, (D) Mytilidae, (E) Arcidae. West coast is represented by open diamonds and east coast is represented by solid squares.

Table 2. Summary of distribution of bivalves of various ecological types in two coasts of India.

		East coast	West coast
Life mode	Infaunal	264	121
	Epifaunal	88	52
	Others	19	4
Attachment type	Byssally attached	74	30
	Cemented	26	17
	Unattached	271	130
Feeding style	Deposit feeder	47	22
	Suspension feeder	308	152
	Others	16	3

such as *Aspidopholas tubigera* and *Anadara antiquata*. The north-western bins show a high share of species such as *Meretrix meretrix* and *Luzonia philippinensis*. Some of the characteristic species in the cluster of the north-eastern bins are *Donax scortum* and *Donax incarnatus*. The clusters do not significantly differ in their share of any particular life mode, nature of attachment or feeding style.

In NMDS plot (stress value = 0.19), we found a separation between east and west coastal sites with few overlaps (Figure 9A); southern sites are in the area of overlap. The NMDS plot for the west coast, however, shows a clear separation between northern sites (above 15°N) and southern sites (Figure 9C) in contrast to the east coast (Figure 9B).

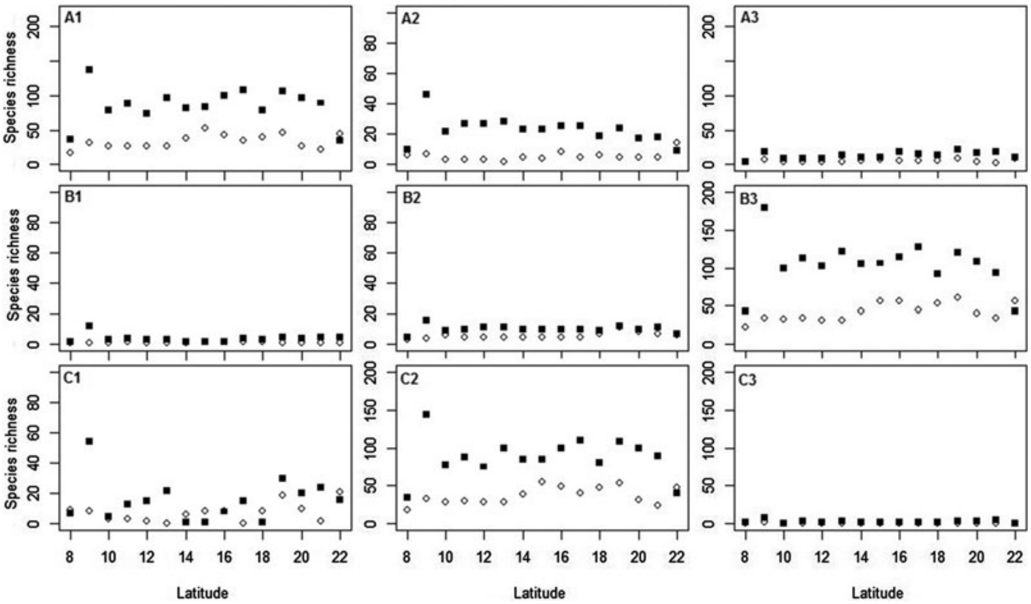

Fig. 7. Relationship between species richness (range-through) and latitude for various ecological guilds. The 1st column represents life mode (A1. Infauna, B1. Epifauna, C1. Other), the 2nd column represents attachment types (A2. Byssally attached, B2. Cemented, C2. Unattached) and the 3rd column represents feeding strategies (A3. Deposit feeders, B3. Suspension feeders, C3. Others). West coast is represented by open diamonds and east coast is represented by solid squares.

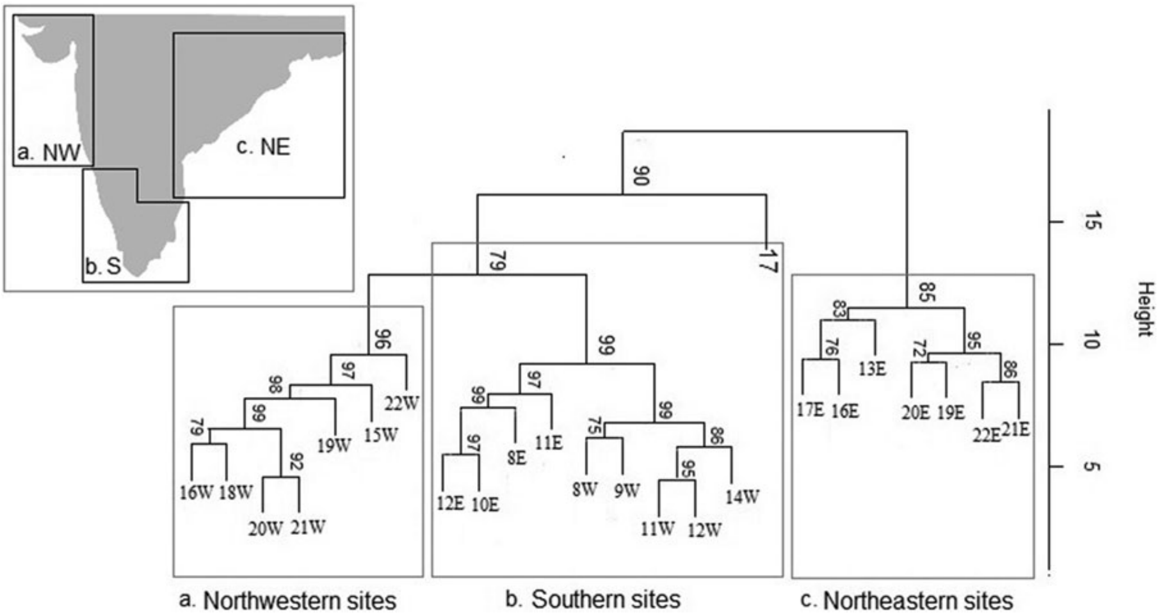

Fig. 8. Dendrogram constructed by UPGMA method using arithmetic averages, based on Sørensen matrices of presence/absence of 417 marine bivalve species from different coastal areas of India. The values at the base of the branches indicate the % bootstrap support (N = 10,000). The rectangles correspond to sub-regions along the Indian coast: a – north-western sites, b – southern sites, c – north-eastern sites.

Relationship between environment and species distribution

The relationship between species richness and environmental parameters as revealed by multiple GLM analysis shows salinity (mean and range), productivity (range) and coastline length to be significant predictors of species diversity (Table 3).

About 30% of the variation in distributions of presences and absences of bivalve species is explained by environmental variables using RDA on the Hellinger distance-transformed species data. A relatively high value of unconstrained variance (70%) is probably indicative of the limited explanatory power of the chosen environmental parameters for species composition. The first two axes are found to be significant in explaining the variation. Coastline length, salinity (mean), productivity (range), river and temperature (range) are found to be significant contributors (Adjusted $R^2 = 0.11$, Figure 10). With automatic forward selection, only salinity (mean) is selected as a significant predictor (Adjusted $R^2 = 0.07$, $P = 0.02$).

DISCUSSION

The diversity and composition of Indian marine bivalves have been studied previously at various local scales. Some studies reported bivalves from specific habitats such as coral reefs (Melvill, 1909; Hornell, 1922; Gravely, 1941; Ray, 1949; Satyamurti, 1956; Ganapati & Nagabhushanam, 1958; Kundu, 1965; Appukuttan, 1972), mangroves (Morton, 1984) and estuaries (Morton, 1977; Appukuttan, 1996). A few studies focused on the economically important bivalve species and associated conservation efforts (Rao, 1974; Kripa & Appukuttan, 2003). Various other studies reported overall diversity of organisms including bivalves from localities in the southern coast (Kurian, 1971; Khan *et al.*, 2010; Kundu *et al.*, 2010; Manokaran *et al.*, 2015), east coast (Ansari *et al.*, 1977; Mahapatro *et al.*, 2011), and west coast (Parulekar, 1973; Parulekar & Dwivedi, 1974; Parulekar & Wagh, 1975; Jayaraj *et al.*, 2007). Such studies conducted at a local scale, although common, may be limited in their utility in explaining larger patterns. Witman *et al.* (2004) emphasized that diversity of local scale (spatial scale of metres to hundreds of metres) must be affected by regional-scale processes (spatial scale of 200 to thousands of kilometres) because local communities are an integral part of larger biogeographic regions and hence affected by mechanisms operating at a regional scale. Our study attempts to understand the regional pattern of bivalve diversity of the Indian coast instead of trends observed only locally or globally (LBG) and to evaluate the role of the regional environment as a predictor in shaping this pattern.

Regional controls of species richness

The two coasts of India, despite being located in the same latitudinal range, show a significant difference in species richness as demonstrated by our study. We recorded a high average regional diversity of bivalves in this region that is comparable to other tropical hotspots such as the Red Sea (Zuschin & Oliver, 2005); the richness in the east coast is higher than Red Sea richness whereas the west coast has a lower diversity. A similar pattern of coastal difference in diversity around India has been observed in a global compilation (Valentine & Jablonski, 2015) although slightly different values of species richness were reported. The average inter-coastal variation in species richness is twice the magnitude of intra-coastal variation (Figure 5). Such coastal differences in richness appear to relate well with the physiographic difference between these two Indian coasts. However, it is important to assess the underlying mechanism for generating coastal differences in species richness.

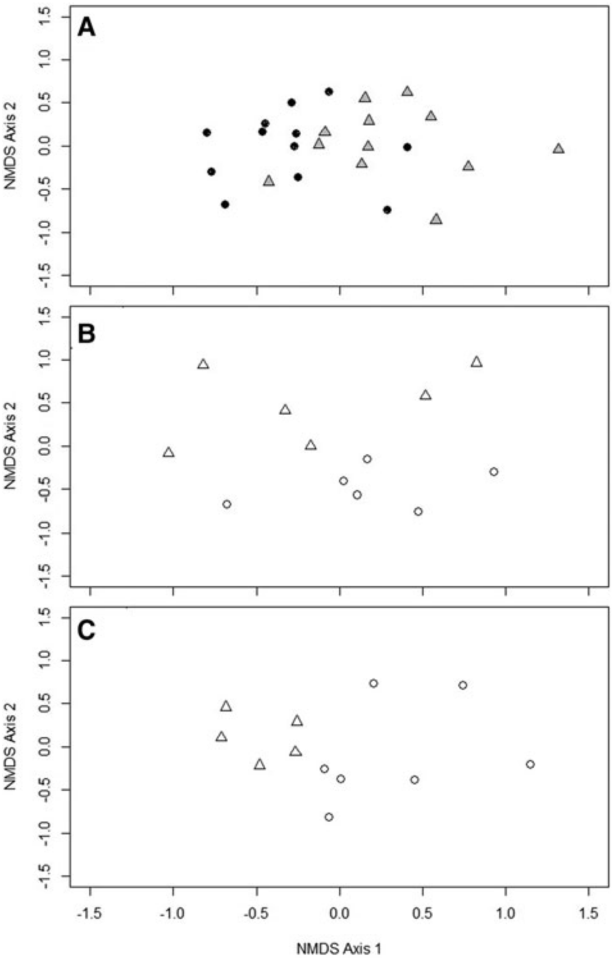

Fig. 9. Ordination in two dimensions performed using non-metric multidimensional scaling, using Sørensen similarity indices calculated from a presence/absence matrix of marine bivalve species at different latitudinal bins along the two coasts of India. (A) For all sites where the solid circles represent east coast and the solid triangles represent the west coast. (B) For east coast. (C) For west coast. The open circles represent the northern sites and the open triangles represent the southern sites.

Productivity has often been used to explain the diversity of shallow marine fauna. Many suspension-feeding organisms are known to thrive under high productivity, and there is a strong positive correlation between eutrophication and bivalve diversity throughout the Indo-West Pacific tropical province (Vermeij, 1990; Taylor, 1997). It is also observed that a highly diverse benthic community is more likely to be supported by a stable primary production than a fluctuating production summing up to a higher value of annual productivity (Valentine & Jablonski, 2015). Hence seasonal fluctuation in productivity plays an important role in shaping the diversity profile. The inverse relationship between productivity and richness as shown by our GLM points to the fact that the highly productive Arabian sea borders the species-poor west coast; this inverse relationship probably indicates a strong seasonal influence along the Indian coast. Although the west coast has relatively low productivity during 5 months of the year (March to May, September to October), the productivity changes drastically with the onset of the summer monsoon (June–September). Influenced by the south-westerly winds, the surface waters move away from the coast and are replaced by colder, nutrient-rich and often oxygen-poor waters from the subsurface. This leads to a rapid increase in productivity (Madhupratap *et al.*, 2001). During winter (November–February), the cold continental air blowing towards the northern Arabian Sea causes cooling and hence the dense surface water sinks. This leads to a convective mixing resulting in a rise in productivity in the surface layer (Kumar & Prasad, 1996; Madhupratap *et al.*, 1996). The species-rich east coast bordered by the Bay of Bengal, on the contrary, is characterized by low but stable productivity. Although the riverine flux contributes nutrients to the Bay of Bengal, they are thought to be lost to the deep because of its narrow shelf (Qasim, 1977; Sengupta *et al.*, 1977; Radhakrishna *et al.*, 1978). Moreover, dominant cold core eddies and thermocline oscillations are observed during the summer monsoon in the Bay of Bengal and coastal region (Madhupratap *et al.*, 2003). These oscillations are capped by a prevalent low saline upper regime which prevented nutrients from surfacing in spite of the river plumes. Consequently, the primary productivity range (3.0–8.7 g C m^{-2} day^{-1}) from the inshore waters of the east coast during monsoon (Nair *et al.*, 1973) is significantly lower than the productivity range (44–280 g C m^{-2} day^{-1}) reported from the west coast (Bhattathiri *et al.*, 1996); this also points to a more stable productivity profile of the east coast that can support high benthic diversity in comparison to highly fluctuating values of west coast productivity.

The influence of a river, although intuitive, is difficult to evaluate in our study since we could not distinguish between rivers with different sediment output. This could explain the apparent insignificant contribution of rivers in explaining species richness. River input, however, could be

Table 3. The results of multiple GLM on the relationship between species richness (range-through) and various environmental variables for latitudinal bins.

	Estimate	**SE**	***t* value**	**Pr(>|*t*|)**
Intercept	1046.616325	940.3793812	1.112972431	0.278298537
Productivity (mean)	0.006970872	0.014657408	0.47558696	0.639278461
Productivity (range)	**−0.024309958**	**0.01061119**	**−2.290973777**	**0.032408689**
Salinity (mean)	**−28.81102194**	**7.796514822**	**−3.695371919**	**0.001342783**
Salinity (range)	**−19.09011668**	**8.214030338**	**−2.324086459**	**0.03023476**
Temperature (mean)	3.478686973	28.71482976	0.121146007	0.904727092
Temperature (range)	−29.45146346	15.30219257	−1.924656439	0.067927106
Coastline length	**0.202086683**	**0.092157576**	**2.192838525**	**0.039720691**
Rivers	−2.856701772	3.263467669	−0.875357767	0.391281693

The significant results are in bold.

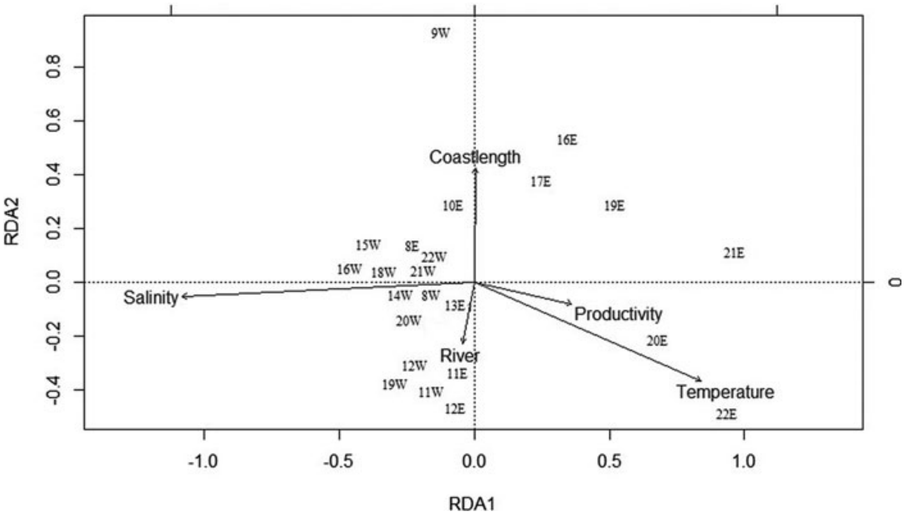

Fig. 10. RDA biplot showing the relationship between environmental variables and the sites.

estimated from salinity which is heavily influenced by the large rivers. The east coast is characterized by an extremely high river input, hence low salinity; this influenced our GLM result, which demonstrated a negative correlation between salinity and species richness. Several studies have shown that an increase in salinity causes a decrease in trend of biological diversity for microbial organisms (Casamayor *et al.*, 2000; Jungblut *et al.*, 2005; Rothrock & Garcia-Pichel, 2005; Abed *et al.*, 2007). This is also true for molluscs who have well-defined relationships between species distributions and physicochemical variables such as salinity (Montagna & Kalke, 1995). A similar pattern of inverse relationship between species richness and salinity (and productivity) range has been observed for global distribution and has been linked to low seasonality and species richness (Valentine & Jablonski, 2015).

The positive correlation between species richness and coastline length, as supported by our GLM result, is a trend that has also been universally observed in space and time. Such a positive relationship is used to explain global marine biodiversity increases during geological times of continental breakup (Peters, 2005). Coastline length has also been found to be an important predictor for Recent biodiversity of diverse marine groups globally (Tittensor *et al.*, 2010). Such dependence is attributed to the higher availability of important habitat features in a longer coastline that is expected to influence positively both abundance and richness of coastal species (Rosenzweig, 1995). Recent studies on marine diversity, including the present one, demonstrate that the same is operational even at a regional scale (Sivadas & Ingole, 2016).

Another important regional parameter, imparting a probable control over the species richness, might be the location of the nearest biodiversity hotspot. Crame (2000a, b) has documented the presence of a bivalve biodiversity hotspot near the Indonesian archipelago and claimed that species are radiating from there. He put this as a mechanism to explain the clines of species richness decreasing radially from this area in a north-south latitudinal pattern and east-west longitudinal pattern. The east coast is more likely to be influenced by this hotspot due to geographic proximity. The west coast, on the other hand, is relatively near to high diversity areas such as the Red Sea but is not expected to show as high an influence as the east coast due to two factors. The first one is the fact that the Bay of Bengal is partially connected to the Pacific Ocean through Australasian seaways and hence contributes to physical, chemical and biological exchanges (Madhupratap *et al.*, 2003). The Arabian Sea has a relatively closed circulation with limited exchange. The second reason is the difference between the size of species pool that each hotspot is hosting. The West Pacific is a much larger species pool compared with the western Indian Ocean (Jablonski *et al.*, 2017). A greater biological exchange of the Bay of Bengal with one of the largest species pools of the West Pacific is expected to result in a non-uniform increase in species richness of the east coast compared with the west coast. Another factor that may have contributed to the low species-richness of the west coast is the influence of an oxygen minimum zone (OMZ) in the Arabian Sea (Naqvi, 1987; Cook *et al.*, 2000; Levin *et al.*, 2000; Stramma *et al.*, 2008). In explaining a relatively low marine benthic diversity (primarily polychaete-bivalve assemblage) of coastal locations from the Arabian Sea in comparison to those from Bay of Bengal, Sanders (1968) identified the low-oxygen minimum layer that exists throughout the northern Arabian Sea at 100 to 200-m depth as the causal factor. This oxygen-depleted water is pushed towards the continental shelf in the west of India and may create a severely stressed condition for the bottom fauna (Nigam *et al.*, 2007). It is important to note that an OMZ is less likely to affect benthos of very shallow depth (<100 m) such as the one of the present study and hence probably is not appropriate to explain intra-coast variation in species richness. This might probably explain why do we see higher species richness in the northern west coast where the intensity of the OMZ is high (Slater & Kroopnick, 1984). However, the overall influence of a shallow OMZ is quite strong on west coast fauna (Levin, 2003). Both of these factors, a positive influence of South Asian biodiversity hotspot on east coast species richness and a negative impact of oxygen-depleted conditions of the Arabian Sea on west coast fauna, may have significant contribution in developing the coastal variation in species richness.

Controls of compositional variation

Regional environmental parameters cannot explain the species association satisfactorily. The major canonical axes of species variation from the RDA correlated with salinity primarily in our data set. However, because of the high contribution of unconstrained variance, the model has limited exploratory power.

The species composition within each coast tends to vary and they do not follow any gradient. We identified three distinct eco-regions along the Indian coast with characteristic species composition corresponding to unique physiography and productivity mechanism of the regions, namely the north-western, southern and north-eastern eco-regions. These eco-regions based on bivalve composition have not been established before and differ from globally established ecoregions (Spalding *et al.*, 2007).

Compositionally the north-eastern and north-western regions are different from the southern region as revealed by the cluster analysis. The southern eco-region shows a characteristic fauna dominated by borers such as *Aspidopholas tubigera* while north-western and north-eastern regions are dominated by species such as *Meretrix meretrix* and various species of *Donax* respectively. Such compositional difference is most likely to be developed because of the distinct physiographic characters of these three regions. The north-eastern region is characterized by high siliciclastic input from large rivers and variable salinity while the north-western region is characterized by low siliciclastic input, high salinity and large shelf area. The average sediment input in the north-eastern region is in the order of 1.4×10^9 *t* and has a significant proportion of suspended sediment load (Subramanian, 1996; Ganesh & Raman, 2007). The north-western region receives an order of magnitude less than that of the east coast and has a latitudinal variation in sediment grain size (Jayaraj *et al.*, 2007). The separation between northern and southern bins could also be an indirect result of distinct oceanographic features. It has already been established that the southern area is distinctly different from the northern Arabian Sea and Bay of Bengal in terms of chlorophyll concentration, productivity and shelf area (Calvert *et al.*, 1995; Dey & Singh, 2003; Ganesh & Raman, 2007). Moreover, the global distribution of coral reefs clearly shows a continuous presence of reef build up in the southern region from Kollam (8°N) extending up to Rameshwaram (9°N) (UNEP-WCMC, 2010). Reefs are known to facilitate diversity of a region and hence this explains the higher average species richness in the southern eco-region. The reefs also explain the dominance of borers in this region that thrive on hard substrate provided by the reef structure.

The separation in species associations along the west coast as revealed by NMDS, coincides with the 15°N latitude. Such compositional difference is also observed for fishes where planktivores dominate below 15°N and carnivores are more abundant above it (Madhupratap *et al.*, 2001). The 15°N barrier separates the productivity mechanism of the Arabian Sea. Seasonally higher productivity in the eastern Arabian Sea is mainly through upwelling during summer and cooling during winter. The summer upwelling has impact up to about 15°N along the southern coast, whereas the winter cooling is restricted to north of 15°N (Madhupratap *et al.*, 2001).

Latitudinal variation

One of the most important biodiversity patterns recognized globally is the latitudinal biodiversity gradient (LBG) (Roy *et al.*, 1998; 2000; Jablonski *et al.*, 2006; Roy & Goldberg 2007). The LBG is the observed monotonic decrease in species richness from equator to pole for terrestrial (Lawton *et al.*, 1998; Gaston, 2000; Weir & Schluter, 2007) as well as marine organisms (Roy *et al.*, 1994, 1998). However, the extent of such a gradient within a limited regional scale, especially in the species-rich tropics, remains unknown (Jablonski, 1993; Roy *et al.*, 1994, 1998; Coates, 1998; Kendall & Aschan, 1993; Roy & Goldberg 2007). In a detailed review on issues of Recent marine diversity, Gray (2001) cautioned against accepting the established trend based on data from North America as other continents with different geological history may result in a different trend. Therefore, it is pertinent to assess the nature of an established biogeographic pattern in an intra-tropical setting outside North America.

Our study of the variation in bivalve biodiversity did not find any consistent pattern of latitudinal variation within the 15° latitudinal span; while the east coast did not show any gradient, the gradient observed in the west coast is opposite to that of the predicted pattern by LBG. Such a non-conformity with LBG is not unusual (Kendall & Aschan, 1993; Poore & Wilson, 1993; Valdovinos *et al.*, 2003). Often specific taxa show a deviation from the standard LBG (Hillebrand, 2004; Stevens, 2006). Krug *et al.* (2007) emphasized the importance of specific families in providing insights into the general pattern of diversity dynamics. However, none of the dominant families in our data set showed any clear pattern for either of the coasts that supports or refutes the LBG. In order to rule out any bias introduced by a specific ecological group, we evaluated the gradient for individual ecological groups; this does not show any significant gradient either. It is clear, therefore, that the variation in species richness along Indian coast does not follow a global pattern such as the LBG. The consistent latitudinal decline in species richness along the west coast, however, is a unique feature of this area. The distinction from west to east is difficult to explain but could be attributed to couple of factors such as homogeneity of the coastal environment along the west coast in contrast to the east coast that is fragmented by multiple rivers creating habitat heterogeneity along the coast.

Issues with scale and sampling

It is important to note that global diversity patterns such as the LBG could be scale-dependent and larger-scale studies are expected to yield clearer patterns than studies on a smaller spatial scale. Hillebrand (2004), for example, predicted that gradients on regional scales are expected to be significantly stronger and steeper than on local scales. The observed lack of clear pattern in gradient could, therefore, be due to the limited spatial scale of our study.

Our data might also have inherent issues regarding sampling. A strong positive correlation between occurrence vs species richness at different latitudinal bins and difference in overall occurrence between the two coasts (Figure 11) points to the existence of such issue. A significantly high species occurrence from the east coast in comparison to the west coast also makes it difficult to understand the true difference in species diversity between the two. However, corrective

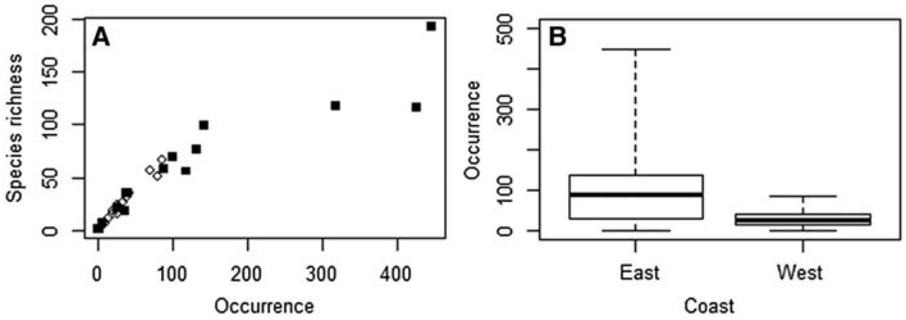

Fig. 11. (A) Relationship between species richness and occurrence from various latitudinal bins. West coast is represented by open diamonds and east coast is represented by solid squares. (B) Relationship between occurrence and coast. The boxes are defined by 25th and 75th quantiles; thick line represents median value.

measures, such as rarefaction and range-through conversion, do not change the results significantly. Moreover, the difference between the diversity from observed occurrences vs range-through occurrences (Figure 5) suggests that the east coast is more unevenly sampled than the west coast. These observations lead us to believe that the data are most likely showing a true biological signal. The only way to resolve this debate calls for a controlled exhaustive physical sampling and subsequent analysis which we are planning to do in future.

CONCLUSION

Gray (2001) mentioned the urgent need to study biodiversity in coastal systems on local and regional scales to evaluate the validity of general ecological patterns. Such studies are particularly rare in tropical areas. The present study attempts to fill the gap.

The present study demonstrates that the species richness of Recent marine bivalves within the tropics is largely governed by regional conditions. The east coast has a significantly higher species richness compared with the west coast. A combination of factors, such as higher coastal length, stable productivity and greater degree of biological exchange with the South Asian biodiversity hotspot may have created the higher species richness in the east coast. The lower richness of the west coast may have been caused by factors such as fluctuation in productivity, a lower degree of biological exchange with the neighbouring biological hotspot and a negative impact of oxygen-depleted conditions of the Arabian Sea. Species composition, instead of showing strict coastal affinity, reveals three distinct (north-eastern, north-western and southern) eco-regions. These regions largely correspond to regional character (such as river activity, salinity, presence of reef, circulation patterns). The details of the pattern may still be difficult to capture from these data with dissimilar occurrence; a detailed abundance data from controlled sampling and of higher resolution is needed to understand the finer pattern.

ACKNOWLEDGEMENTS

D.C. would like to thank Dr S. Prasanna Kumar, NIO for discussion on oceanographic aspects. Comments from Martin Zuschin and Adam Tomašových on an earlier version of the draft greatly improved the manuscript. We are grateful to two anonymous reviewers for their in-depth review and suggestions.

FINANCIAL SUPPORT

This project was funded by Academic Research Fund of IISER Kolkata (ARF 2013-14). D.S. and M.B. are supported by the doctoral fellowship and PBIP fellowship of IISER Kolkata, respectively.

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