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Nature of spatial heterogeneity of the coastal, marine ecoregions along the eastern coast of India

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The global marine environment is highly heterogeneous although the nature of heterogeneity can vary spatially. In this study, the nature and extent of spatial heterogeneity of the coastal, marine ecoregions along the Central-Eastern and South-Eastern coast of India (parts of Andhra Pradesh, Pondicherry and Tamil Nadu) was studied, which represent two different – Central-Eastern, and South-Eastern – coastal ecoregions. Several environmental (e.g., salinity, temperature, and nutrients of the ocean water, etc.) and physical (e.g., substrate type, energy condition of the coast) parameters were measured (quantitative as well as semi-quantitative approach) and analysed by using several bivariate and multivariate methods. Our results clearly point out that the Central-Eastern, and South-Eastern marine, coastal ecoregions of India are highly heterogeneous among themselves, and even smaller ecoregions (i.e., sub-ecoregions) within each of these larger ecoregions are also different from each other. Thus, each of these ecoregions is internally highly heterogeneous. In addition, there is no consistent spatio-latitudinal change in the environmental variables along the eastern coast of India.

Keywords. Indian molluscs; environmental variables; biogeographic provinces.

1. Introduction

Ecosystem is a natural functioning system where the abiotic and biotic factors interact with each other. This specific multidimensional space, where organisms inhabit, is defined by those biotic and abiotic variables. The major abiotic components of the marine environment include temperature, salinity, other chemical characters of water (Eh, pH), and different types of physical parameters (e.g., substrate, suspended sediment, energy condition, etc.), and primary productivity, among many others. Because each ecosystem differs in these abiotic and physical variables, each and every ecosystem differs significantly from others resulting in environmental heterogeneity (i.e., ecosystem heterogeneity). In the marine realm, because many of these aforementioned environmental factors (e.g., primary productivity, temperature, salinity) vary with latitudes as well as ocean basins, along with many other local variables, marine environmental heterogeneity is a global phenomenon and has been documented to vary spatially from local to global scale (Spalding *et al.* 2007). For example, the annual rainfall and sea surface temperature show spatio-latitudinal variation (NASA; https://www.nasa.gov/). Therefore, ocean salinity is also spatio-latitudinally variable (CATDS; https://www.catds.fr/). Due to variation in the environmental factors, different

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regions show different types of ecological conditions where organisms can thrive. May be for this reason, the famous latitudinal diversity gradient – high tropical diversity which declines towards the pole – appears to be less consistent (Clarke 1992; Roy *et al.* 2000).

The coastal region of India is about 7500 km that includes about 5500 km long mainland coastline, therefore offering a vast extent of the coastal region under the influence of highly variable latitudes and local environments (Kumar *et al.* 2006). The continental shelf along the west coast of India is wide, ranging from around 340 km in North to around 60 km in South; on the other hand, the shelf is narrower in the east coast of India (Kumar *et al.* 2006). The coastline includes rocky shores, open and barrier beaches, estuaries, bays, sandy splits, offshore islands, headlands and marshy lands (Ahmad 1972), resulting in sandy beaches, numerous tidal flats and marshy lands, and limited areas with rocky shores (Kumar *et al.* 2006), providing huge variation in substrate condition. Moreover, the coasts are bounded by Bay of Bengal in the east, Arabian Sea in the west, therefore providing wide range of oceanographic conditions (Wyrtki 1973). The major rivers which flow through the eastern part and have their sinks into Bay of Bengal are Ganga, Damodar, Mahanadi, Godavari, Kaveri, and the major rivers which flow through the west coast and which have their sinks into the Arabian Sea are Narmada and Tapi (NRSC 2017). The Bay of Bengal receives huge volume of fresh water from the eight major rivers and the smaller rivers make the region much less saline with minimal annual variation (Ittekot *et al.* 2003; Akhil *et al.* 2014). Similarly, sediment of the western continental shelf of India is mainly clayey silt and silt clay on the inner shelf and on the outer shelf, it is calcareous sand and the sedimentation rate at a particular site is mainly controlled by the proximity of it to the river mouths and it gradually decreases towards offshore (Pandarinath *et al.* 2001). The east coast of India is laden with high siliceous input due to the presence of the large river systems which flows to the Bay of Bengal and therefore results in salinity fluctuations whereas the west coast is enriched in high productivity because of the large shelf area of Arabian Sea (Sarkar *et al.* 2017). The reason that this dynamic geomorphological region is influenced by both the marine and terrestrial dynamics (Holland and Elmore 2008; Cisneros *et al.* 2011), the near-coastal, marine environment along the Indian coasts is highly heterogeneous (Jayaraman and Gogate 1957; Sivadas *et al.* 2012; Sivadas and Ingole 2016).

Spatio-latitudinal variation in different environmental factors along the Indian coasts has direct bearing on the coastal taxonomic and ecological diversities. For example, Perumal *et al.* (2009) found high correlation between salinity and species richness as well as population density of planktons in the Kaduviyar estuary, Nagapattinam, mainly because of salinity-controlled variation in different hydrographical parameters and chlorophyll – a content at that region. Similarly, Kannan and Kannan (1996) noticed that high fertility of Kottaipattinam and Kattumavadi of the Palk Bay is related to the presence of high proportion of dissolved oxygen, penetration of light, and the concentration of nutrients at these regions, as compared to the other parts of the Indian coastline. According to Sivadas *et al.* (2012), the two main factors which play a major role in the environmental heterogeneity of the macro faunal group of West coast of India are the annual tropical monsoon as well as the adjacent creeks' inputs which in turn influence the environmental gradient (also Sarkar *et al.* 2017). Levin and Dayton (2009), in a different note, suggested that comparative studies on diversity and distribution of species along the Arabian Sea and the Bay of Bengal should be performed because of their contrasting environmental conditions.

Because all of these regions have their own types of physical and chemical variables, varying from local to regions scales, these regions have their own biodiversity (Subba Rao *et al.* 1991, 1992, Subba Rao and Dey 2000; Subba Rao 2003; Kannan and Kannan 1996; Kumar *et al.* 2006). According to Spalding *et al.* (2007), the vast coastal region of India can be subdivided into several sub-regions (or ecoregions), i.e., the coastal ecoregions of western India, southern India and Sri Lanka were designated in Marine Ecoregions of the World (MEOW). Sivadas and Ingole (2016) used this information of biogeographic distribution of three groups of benthic species (gastropods, bivalves and polychaetes) to divide these three large ecoregions into several smaller ecoregions. The newly proposed coastal mainland ecoregions were Northwest India, Central-Western India, Southwest India, Southeast India, Central-Eastern India, Northeastern India, and Northern Bay of Bengal (Sivadas and Ingole 2016). They predicted that the different coastal basins of India are not so much similar because of environmental heterogeneity and spatiotemporal variedness of coastal currents. On an account, Sivadas and Ingole (2016) considered only four environmental variables (sea surface temperature, salinity, dissolved oxygen and surface chlorophyll-a) in their study, while it is widely known that many other important variables like substrate characters, total dissolved solid, etc. should also be analysed to quantify environmental variability so that the result can be used to define the ecoregions, rather than using biogeographic distributions of cosmopolitan and eurytropic, euryhaline groups like molluscs.

We, being sceptic about the nature of these discrete and sharp boundaries between the two adjacent bioregions, we use multiple types of chemical variables to investigate the nature of environmental variability along the southeastern coast of India to better constrain the observations of ecoregions made by Sivadas and Ingole (2016). To do this, we subdivided each of these two bioregions into smaller ecoregions simply to verify whether these sub-regions can be classified into distinct groups or they show clear overlapping characters. If the boundaries are sharp, as demarcated by Sivadas and Ingole (2016), then all the smaller sub-regions should be environmentally homogeneous with minimum environmental heterogeneity, for which different types of environmental variables were considered in tandem.

2. Material and methods

2.1 *Study area*

The present study encompasses a part of the coastline of the eastern coast of India, along the coastal regions of Andhra Pradesh, Pondicherry and Tamil Nadu (figure 1). A total of twenty-five coastal locations – twelve places along Andhra

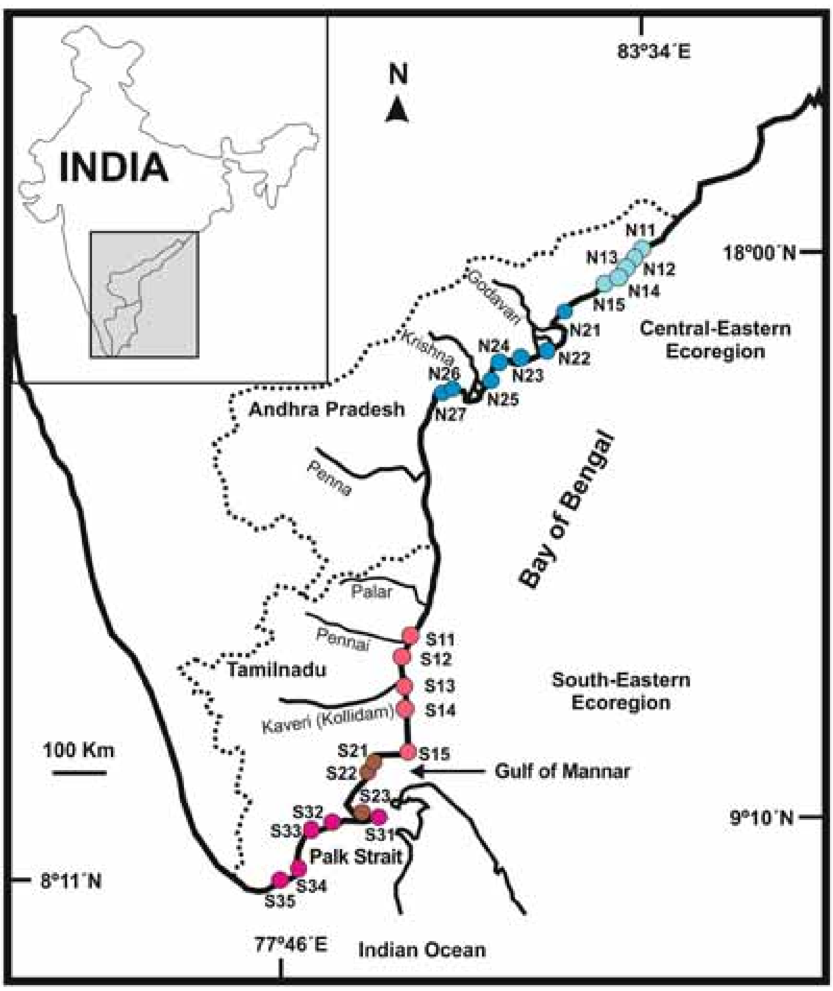

Figure 1. Map of the Indian coastline showing 25 study locations under the two marine ecoregions: Central-Eastern ecoregion (N11 to N27; blue circles) and South-Eastern ecoregion (S11 to S35; red circles) along with the important rivers and the ocean/water bodies. Note, the major rivers are shown.

Table 1. *Details of sampling locations and their corresponding assigned sub-regions are presented.*

Sl. no.	Sampling sites	States/Union Territory	Sub-regions	Area codes	Latitudes	Longitudes
1	Konada Mohona	Andhra Pradesh	N1	N11	18°00′36″N	83°34′11.99″E
2	Bheemunipatnam			N12	17°53′49.5″N	83°27′14.4″E
3	Yarada			N13	17°39′36″N	83°16′48″E
4	Apikonda			N14	17°34′30″N	83°10′30″E
5	Rambilli			N15	17°27′39.6″N	82°57′36″E
6	Polavaram		N2	N21	17°1′15.6″N	82°17′34.8″E
7	Odalarevu			N22	16°25′12″N	81°58′48″E
8	Mollaripuram			N23	16°20′33.36″N	81°35′4.56″E
9	Manginipudi			N24	16°14′20.4″N	81°13′48″E
10	Koduru			N25	15°56′60″N	81.11°E
11	Suryalanka beach			N26	15°50′4″N	80°30′18″E
12	Ramapuram			N27	15°46′48″N	80°23′24″E
13	Pondicherry University beach	Pondicherry	S1	S11	12°0′57.64″N	79°51′43.42″E
14	Singharathope			S12	11°43′7.365″N	79°46′54.65″E
15	Thirumullaivasal			S13	11°16′4.922″N	79°50′29.89″E
16	Karaikal			S14	10°54′59.89″N	79°51′13.03″E
17	Kodiyakarai			S15	10°16′27″N	79°48′55.00″E
18	Manamelkudi	Tamil Nadu	S2	S21	10°2′16.75″N	79°15′59.12″E
19	Gopalpattinam			S22	9°55′29″N	79°09′08″E
20	Rameswaram			S23	9°19′13″N	79°19′52.41″E
21	Old Dhanushkodi		S3	S31	9°10′37.89″N	79°24′57.78″E
22	Allabhangulam			S32	9°9′13″N	78°37′35″E
23	Sippikulum			S33	8°59′37″N	78°15′05″E
24	Manapadu			S34	8°22′23″N	78°04′02″E
25	Avudaiyalpuram			S35	8°11′41.1″N	77°46′14.7″E

Pradesh, four places along Pondicherry, and nine places along Tamil Nadu were included in the present study (figure 1 and table 1). These 25 locations belong to the coastal ecoregions – Central-Eastern India and South-East India of Sivadas and Ingole (2016). These two geographically distant regions, separated by vast open ocean, are chosen to minimize the effects of any kind of gradual changes in environmental variables, and if the two ecoregions are actually different, the signal should be distinctly identified. Both of these ecoregions is geographically large (average length of about 770 km), covering a total of 3°–7° latitudinal variation. Because most of the environmental factors are directly related to latitudinal variation, it is, therefore, important to subdivide these ecoregions into smaller one-degree latitude bin. If the larger ecoregion is actually homogeneous, all of our smaller ecoregions should show similar environmental properties. For this reason, we further subdivided the two large ecoregion into five smaller-ecoregions (table 1).

The Central-Eastern India is subdivided into two sub-regions: (1) N1: from Konada Mohona to Rambilli (Andhra Pradesh) as all these locations are in close spatial proximity, i.e., within less than 1° latitudinal variation, and face the same open bay, the Bay of Bengal; (2) N2: from Polavaram to Ramapuram (Andhra Pradesh) as all the locations within this ecoregion belong to approximately the 15–16°N latitudinal bin, and face the same open bay, the Bay of Bengal (table 1 and figure 1). Similarly, the South-East India ecoregion was subdivided into three smaller regions – (1) S1: from the Pondicherry University beach to Kodiyakarai (Pondicherry/Tamil Nadu), as all these locations belong to approximately 10–12°N, and they face the Bay of Bengal; (2) S2: regions from Manamelkudi to Rameswaram (Tamil Nadu), as these locations belong to approximately 9°N latitudinal bin, and face a restricted bay, the Palk Strait; (3) S3: from Old Dhanuskodi to Avudaiyalpuram (Tamil Nadu), as the locations within S3 ecoregion belong to approximately 8–9°N bin and face a restricted gulf, the Gulf of Mannar and Indian Ocean in the south. It may be argued about the validity of separating S2 and S3. However, because physical barrier may actually control

Table 2. *Data of quantitative measures of abiotic environmental variables for the studied locations.*

Sampling sites	Sub-regions	Area codes	Mean annual temperature (°C)	Salinity (ppt)	pH	Total dissolved solid (TDS) (ppt)	Sodium (Na) conc. (ppm)	Potassium (K) conc. (ppm)	Primary productivity (mg C/ m^2/ day)
Konada Mohona	N1	N11	28.4	30	7.54	37.1	886.65	28.81	657
Bheemunipatnam		N12	28.3	30	7.35	25.9	840.95	24.88	657
Yarada		N13	28.3	32	7.39	33.5	840.95	23.57	776
Apikonda		N14	28.3	31	7.53	37.9	822.66	24.88	776
Rambilli		N15	28.3	31	7.44	38.9	923.21	27.5	776
Polavaram	N2	N21	28.3	30	7.49	36.3	804.38	26.19	776
Odalarevu		N22	28.2	30	7.29	37.3	776.96	19.64	1175
Mollaripuram		N23	28.2	28	7.45	29.7	813.52	24.88	1175
Manginipudi		N24	28.2	33	6.9	36.8	795.24	22.26	1175
Koduru		N25	28.1	32	7.4	36.5	895.79	24.88	1175
Suryalanka beach		N26	28.1	32	7.48	37.4	932.35	23.57	761
Ramapuram		N27	28.1	32	7.44	37.4	786.11	20.95	761
Pondicherry University beach	S1	S11	28.2	30	7.58	35.7	804.38	22.26	550
Singharathope		S12	28.3	29	7.46	37.2	840.95	24.88	835
Thirumullaivasal		S13	28.3	30	7.42	37.6	813.52	24.88	835
Karaikal		S14	28.3	30	7.43	37.4	850.09	22.26	835
Kodiyakarai		S15	28.3	30	7.43	36.1	804.38	22.26	1273
Manamelkudi	S2	S21	28.3	30	7.6	32.7	831.81	24.88	1273
Gopalpattinam		S22	28.1	30	7.41	31.7	850.09	24.88	1273
Rameswaram		S23	28.1	31	7.47	39.2	840.95	26.19	1411
Old Dhanushkodi	S3	S31	28.1	31	7.53	35.1	868.37	26.19	1411
Allabhangulam		S32	28.1	31	7.46	32	804.38	24.88	1411
Sippikulum		S33	27.8	32	7.51	38.4	895.79	24.88	1411
Manapadu		S34	27.8	31	7.45	37.7	850.09	24.88	1125
Avudaiyalpuram		S35	27.8	34	7.47	32.9	886.65	24.88	1125

oceanographic currents and flow of nutrients, S2 and S3 are considered as two smaller regions, as these two are separated by a distinct barrier in the form of the small land bridge which is known as the Adam's Bridge (a chain of limestone shoals) between India and Sri Lanka.

2.2 *Quantification of environmental variables*

To quantify the nature of environmental heterogeneity along the studied region, 50 ml water samples were collected from those 25 locations, and corresponding geographical (i.e., latitudes and longitudes) and geopolitical (i.e., state names, and locations on Google Earth) information were noted (table 1). The various abiotic environmental factors concerning with the marine environment are temperature, salinity, sediment thickness, nutrient influx, nitrogen, phosphorus and potassium content, exchangeable sodium content of soil, acidity, alkalinity, total hardness, primary productivity, dissolved oxygen (DO) in water, biochemical oxygen demand (BOD) in water, chemical oxygen demand (COD) in water, the content of dissolved solids and suspended solids in water, the water holding capacity and organic carbon and organic matter of the sediments, among many others. However, how many of these influence coastal biodiversity in regional and global scale is poorly known. For the present study, the environmental variables that were quantified for each of the sampling sites were average annual temperature, salinity, pH, total dissolved solids (TDS), sodium (Na) and potassium (K) concentration, and primary productivity. For each of the 25 locations, handheld salinity refractometer was used for measuring salinity and a multi-parameter kit was used to calculate pH, and total dissolved solid (TDS) (table 2). In addition, Na and K concentration of each of the sample were estimated by flame photometer. The trace amounts of sodium and potassium were determined at a specific wavelength of 589 nm and 769 nm, respectively. Data for average annual temperature and primary productivity

Table 3. *Environmental characters and their variable states used for semi-quantitative analyses.*

Genre	Character names and details		Scores
Influence of river to the environment	Name of the water body	Indian ocean	0
		Bay of Bengal	1
		Gulf of Mannar	2
		Palk strait	3
	Character of water body	Open	0
		Intermediate	1
		Restricted	2
	Distance of the nearest river	<5 km S/N	0
		≥5–10 km S/N	1
		>10 km S/N	2
		No river present	3
	Number of nearest rivers	In between two rivers	0
		Beside one river	1
		Near one river	2
		No river	3
	Nature of tidal flat	Wide	0
		Moderate	1
		Narrow	2
Beach morphology	Nature of beach slope	High	0
		Medium	1
		Low	2
		Not well developed	3
	Nature of beach width	Very wide	0
		Wide	1
		Moderate	2
		Narrow	3
	Nature of substrate	Soft (sand)	0
		Soft (clay rich)	1
		Mixed (presence of any two types of substrates)	2
		Hard	3
Human influence	Distance from the nearest village	<5 km	0
		≤5–10 km	1
	Distance from the nearest industrial belt	<5 km	0
		≤5–10 km	1

were obtained from Ocean Productivity database (http://www.science.oregonstate.edu/ocean.productivity/) (table 2). Seasonal fluctuations of these variables are not considered and only the mean annual values are considered for the present analyses.

Along with these quantifiable variables, we have also used several physical environmental variables which cannot be measured directly. Information of the following physical environmental variables was taken for each studied location: (1) because the character of the water body can have significant effect on local environment, names and character of the water body near the location (i.e., ocean/sea/bay) were noted; (2) as rivers acts as a major source of sediment and nutrients to the coasts, as well as acts as buffer for local temperature, salinity, and nutrient budgets, the total number of nearest rivers and their corresponding distance (south or north) were taken into account. Moreover, distance of the nearest village and nearest industrial belt (south or north) were also taken into account for similar reason; (3) to document the actual physical nature of the coast, the following variables were also noted – presence/absence of tidal flat, character of the beach (i.e., slope, width and substrate). Because these variables cannot have measurable values, all the physical environmental variables were condensed into characters and each of the characters were supplemented by character states, i.e., the observations were converted to a semi-quantitative grading scheme (tables 3 and 4). The

Table 4. *Semi-quantified, raw data of physical environmental variables used. Character states are mentioned in table 2.*

Sampling sites	Area codes	Name of water body	Nature of (ocean/ sea/bay)	Substrate type	Distance of nearest river (km)	Number of nearest river	Tidal flat character	Nature of beach slope	Nature of beach width	Nearest village distance (km)	Nearest industrial belt distance (km)
Konada Mohona	N11	1	0	0	2	1	0	2	1	1	0
Bheemunipatnam	N12	1	0	0	2	3	0	2	0	0	0
Yarada	N13	1	0	0	3	3	0	2	1	0	0
Apikonda	N14	1	0	0	3	3	0	1	1	0	0
Rambilli	N15	1	0	2	1	2	0	1	1	0	0
Polavaram	N21	1	0	0	2	2	0	1	0	0	0
Odalarevu	N22	1	0	1	1	0	1	2	2	0	0
Mollaripuram	N23	1	0	0	2	1	1	2	2	1	1
Manginipudi	N24	1	1	0	3	3	2	2	1	0	1
Koduru	N25	1	1	2	1	0	1	2	1	1	1
Suryalanka beach	N26	1	1	0	2	3	2	1	1	1	0
Ramapuram	N27	1	1	0	2	3	2	2	1	0	0
Pondicherry University beach	S11	1	0	0	2	0	1	1	3	0	0
Singharathope	S12	1	0	2	0	0	0	1	2	0	0
Thirumullaivasal	S13	1	0	2	1	0	0	1	2	0	1
Karaikal	S14	1	0	0	0	1	0	1	0	0	0
Kodiyakarai	S15	1	0	2	3	3	1	1	0	0	0
Manamelkudi	S21	3	2	2	3	3	2	2	3	0	1
Gopalpattinam	S22	3	2	1	2	2	2	2	3	0	0
Rameswaram	S23	3	2	2	2	2	2	3	3	0	0
Old Dhanushkodi	S31	2	2	2	3	3	2	0	1	1	1
Allabhangulam	S32	2	2	2	3	3	1	1	0	0	0
Sippikulum	S33	2	2	2	3	3	1	1	3	0	0
Manapadu	S34	2	2	0	3	3	1	0	2	0	1
Avudaiyalpuram	S35	0	2	0	3	3	1	0	3	0	1

data for the ocean/sea/bay, number of nearest rivers, tidal flat were obtained from Google Earth. The ocean/sea/bay was categorized into two groups – name (Indian Ocean, Bay of Bengal, Gulf of Mannar and Palk Strait) and character (open, intermediate and restricted). The influence of river was categorized into three groups – nearest river distance (<5 km S/N, ≥5–10 km S/N, >10 km S/N, and no river present), number of the nearest river (in between two rivers, beside one river, near one river and no river) and tidal flat (wide, moderate and narrow). Beach morphology was categorized into three groups – beach slope (high, medium, low and not well developed), beach width (very wide, wide, moderate and narrow) and substrate (soft-sandy, soft-clay rich, mixed, and hard-rocky). Human influence were grouped into two – nearest village (<5 km and ≤5–10 km) and nearest industrial belt (<5 km and ≤5–10 km). This semi-quantification of several environmental variables otherwise difficult to quantify, helped to use these variables in mathematical calculations and analyses.

2.3 *Data analysis and predictions*

Analyses were performed to find out the spatial and latitudinal variations of each of the environmental variable from north to south, and also to see within- and between-ecoregional variations. Box and whisker plots are used to visually identify the nature of variability of the quantifiable physical environmental factors. Kruskal–Wallis tests, with $\alpha = 0.05$, are performed to statistically compare the median values of these variables among themselves. For multivariate comparison, cluster analyses (Ward's Method) were used. The statistical analyses were performed using the open access software PAST3.0 (Hammer *et al.* 2001). Moreover, to visualize the clustering of locations in relation to those environmental variables, a Principal Component Analysis (PCA) of standardized covariance (correlation) matrices was used on R platform (R core team).

If the sub-regions are environmentally homogeneous and vary with respect to the nearby sub-region, all the northern (i.e., N1 and N2) sub-regions should show similar environmental characters. Similarly, all the southern (i.e., S1, S2, and S3) sub-regions also should be similar with each other, while they should be distinct from the northern sub-regions. Alternatively, if the environmental parameters defining these sub-regions show random clustering, it would indicate that these ecoregions are environmentally heterogeneous and random, and no distinct sub-regions or ecoregions can be identified, at least for these parts of India.

3. Results and discussion

Both Spalding *et al.* (2007) and Sivadas and Ingole (2016) considered the Krishna–Godavari basin of Andhra Pradesh and Cauvery basin of Tamil Nadu as two ecologically distinct bioregions, which they called as Central-Eastern India and Southeast India bioregions. However, our analyses does not support this conclusion. Considered separately, the five locations within the sub-region N1 show distinctness among themselves as they are poorly clustered – N11 and N12 are placed away from N13 and N14, and N15 is placed altogether at a different place (figure 2). Even in the PCA graphs, all of these locations are away from each other (figure 4). The cause of this heterogeneity is mostly because of high variation in K concentration and TDS values among them (table 2 and figure 3). Similarly, presence of nearby rivers and beach character also vary among these locations (table 4). Similar to N1, locations under the sub-region N2 are also heterogeneous – while three out of seven locations are clustered closely, the other four are clustered away from each other. More specifically, within N2, N22 and N24 are distinctly different from the rest; the strong heterogeneity is also evident in the PCA graphs (figures 2 and 4). Na concentration, productivity, and presence of nearby rivers causes the poor clustering of few locations (figure 3 and tables 2 and 4).

In case of inter-sub-regional comparison between N1 and N2, temperature is highly variable, and different (Mann-Whitney $U = 2$, $p = 0.01$), and other variables also show larger variation (figure 3). For example, salinity, pH, Na, and K moderately varies in both the sub-regions. The variation is relatively wide in terms of TDS in N1 and low in N2, and the variation in primary productivity in N1 is lower than in N2 (table 2 and figure 3). However, there are some degrees of overlapping between these two sub-regions identified in the clusters and PCA graphs. The small degree of overlapping, evident for quantitative and semi-quantitative measures are used, may simply represent the fact that they both represent the Central-East Indian ecoregion. As these sub-regions face the Bay of Bengal, presence of rivers

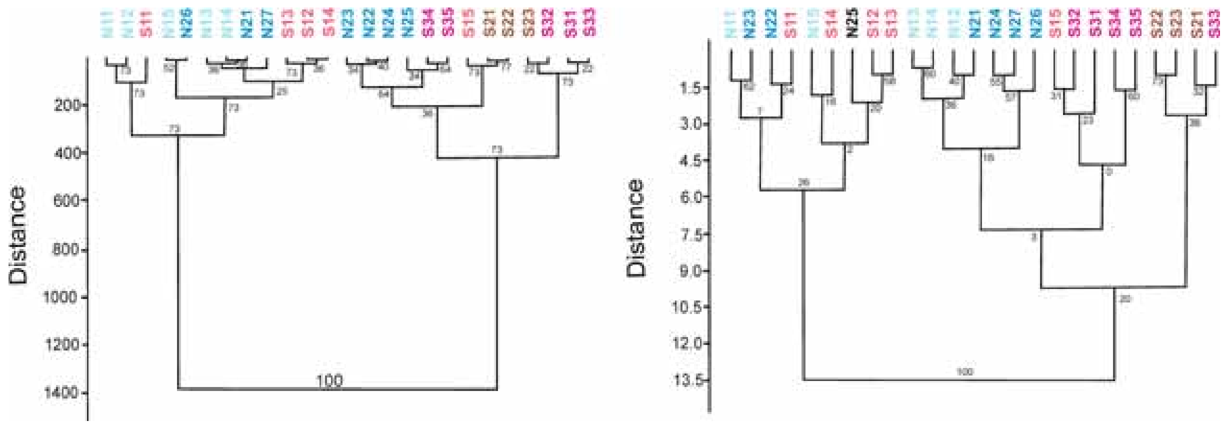

Figure 2. Cluster analysis of quantitative (left) and semi-quantitative (right) environmental variables based on Ward's method represent poor clustering of the studied locations. For colour coding, see figure 1.

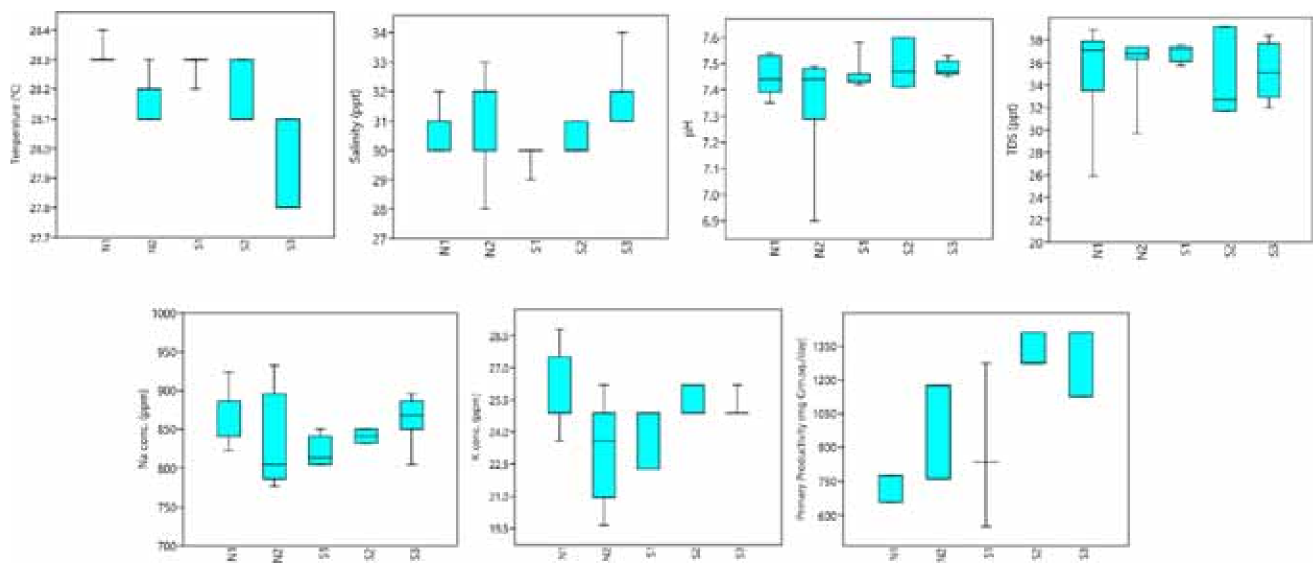

Figure 3. Box and whisker plots representing the spatio-environmental variation in different abiotic factors. x-axes represent the five smaller sub-regions – N1, N2 under the Central-Eastern ecoregion, and S1, S2, S3 under the South-Eastern ecoregion. Boxes in the upper and middle panels of the figures were defined by the 25th and 75th percent quantiles, and whiskers represented 95% confidence intervals.

has a strong influence – salinity fluctuations in relation to river discharge, modifying substrate characters, sediment supply, and beach characters – on the overall physico-chemical environment of these sub-regions. These suggest that – (1) the locations within the smaller sub-region N1 and N2 are environmentally heterogeneous, rejecting the hypothesis that N1 or N2 could be considered as one sub-region; (2) when considered together, N1 and N2 show some degree of overall similarities, but they show very large heterogeneity.

The southern sub-regions are relatively more homogeneous than N1 and N2. The sub-region S1 has five locations, among which S12, S13, and S14 are very similar among each other, while S15 is totally distinct (figure 2). This is also evident in the PCA plot, where all the locations of the sub-region S1 are distinctly away from each other (figure 4). This happened because of distinct nature of Na concentration and primary productivity of S15 (table 2 and figure 3). In S1, except for temperature which remains same throughout, all the other abiotic environmental factors show more or less moderate variation which results in the weak clustering. This variability may be explained by the influence of the Bay of Bengal from the north and the Indian Ocean from the south and it is also seen that the places of S1 experiences a large influence of the rivers at many locations (figure 1). Similar to S1, all the locations of the sub-region S2

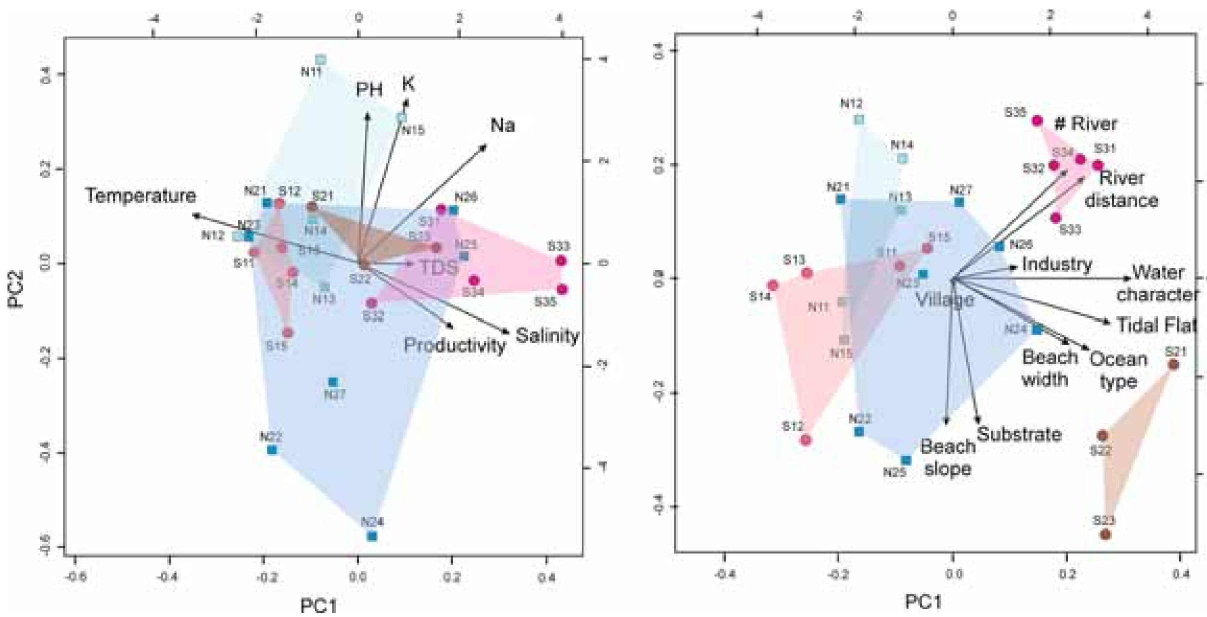

Figure 4. Principal Component Analyses (PCA) biplot using quantitative (left) and semi-quantitative (right) variables suggest that the studied locations along the eastern coast of India are environmentally heterogeneous. Quantitative variables abbreviations: K = Potassium concentration, Na = Sodium concentration, TDS = total dissolved solid, Productivity = primary productivity, Temperature = mean annual temperature. Semi-quantitative variables abbreviations: # River = number of the nearest rivers, River distance = distance of nearest river(s), Industry = distance from the nearest industrial belt, Water character = character of the water body, Tidal flat = nature of the tidal flat, Ocean type = name of the water type, Beach width = nature of beach width, Substrate = nature of substrate, Village = distance of the nearest village. For detailed description of these semi-quantitative variables, see table 3. For colour coding, see figure 1.

are different from each other, which is also seen in the PCA plots (figure 4). In comparison, the three locations of the sub-region S3 (i.e., S31, S32, and S33) are quite similar, while the other two are clustered differently (figure 2). In terms of the PCA graphs, S3 locations are similar when the semi-quantitative variables are considered, but are somewhat different when only the quantitative variables are considered. Even S2 and S3 are similar in their physical environments such as beach environment, influence of rivers and human settlements, rainfall, wind speed and ocean currents, they are poorly clustered (table 4). Between S2 and S3, temperature remains same throughout S2 and is almost same differing by one degree in S3; there is a similar range of variation throughout these two sub-regions for salinity ($H = 7.65$, $p = 0.08$) and pH ($H = 3.37$, $p = 0.50$), TDS ($H = 0.47$, $p = 0.98$), Na ($H = 4.74$, $p = 0.31$), and K ($H = 6.79$, $p = 0.10$) concentration (figure 3). Based on these observations, the following can be concluded: (1) S1 is completely different from S2 and S3, and S2 and S3 show some degree of similarity. However, little variation among S2 and S3 locations occur because of the restricted natures of Gulf of Mannar and Palk Straits, as well as these regions have least influence of rivers. As a result, nutrient supply and sedimentation rate are low, promoting relatively better homogeneity; (2) even they represent the same bioregion (i.e., South-Eastern India bioregion), they cluster differently, questioning the homogeneous nature of this bioregion (figure 4). It therefore appears that these southern locations are although influenced greatly by the presence of restricted bays and sedimentation patterns, the local factors play greater influence to retain location-specific heterogeneity (Sarkar *et al.* 2017). Probably for this reason, many unrelated locations of different sub-regions are clustered together.

Use of multivariate analysis like PCA does not reveal any spatio-latitudinal gradient (figure 4). When all five sub-regions are considered for the plot of the quantitative variables only, as many as five PC axes are required to explain ∼85% variations. The two PCA axes account for only about 55% variations (PC1 = 28.64%, PC2 = 26.09%). Even more, all of the PC axes indicate better correlation with more than one environmental variable (figure 4). Similarly, when the semi-quantitative variables are used, the first two axes explain only about 53% variability (PC1 = 33.21%, PC2 = 20.18%), and at least five axes are required to explain about 85% of the total variation. Considering all results, the main conclusions are: (1) the two larger ecoregions are not environmentally distinct. Even more, smaller ecoregions within each of these larger ecoregions are also different from each other; (2) biogeographic vicinity does not guarantee ecological and environmental similarity, and distantly located places may show similar environmental condition, diluting any environmental gradient. Even, N1 and N2 together also cannot be regarded as a single cluster and thus Central-Eastern ecoregion is heterogeneous in nature; (3) the northern part of the South-Eastern ecoregion show relatively good homogeneity. However, it is totally distinct from the southern part of the South-Eastern ecoregion. So, as a whole, South-Eastern ecoregion is also heterogeneous in nature. However, S23 and S31 are almost similar in nature and S2 and S3 may represent homogeneity but different from S1. Thus, the South-Eastern ecoregion may have two parts – the northern part, i.e., S1 and the southern part, i.e., S2 and S3.

This type of environmental heterogeneity happens because of the fact that several local environmental factors influencing or disrupting the spatio-latitudinal trend (Sivadas and Ingole 2016; Sarkar *et al.* 2017). The most important local environmental factor is the influence of the rivers in the regions, including the wind speed and the ocean currents and also the influence of villages and industries situated near by the coastal regions. River discharge is responsible for the decrease in salinity and the increase in turbidity in coastal ecosystem (Teske *et al.* 2011). Also, due to the high human influence (villages as well as industries), the nutrient load is high which makes the regions highly heterogeneous. There are many other reasons for the heterogeneity of the coastal environment which can be strong coastal upwelling as well as Oxygen Minimum Zones (Wilson 2000). The other environmental factors which influences the spatio-latitudinal trend are soil pH, organic carbon content, nitrogen, phosphorus and potassium content. The wave heights as well as the current speed are some of the main factors which drive the rate of the sediment transport which influence the local environment (Kumar *et al.* 2006). In a few earlier studies, it is also seen that the surface oceanic circulation influences the heterogeneity of the regional environment (Levin and Dayton 2009; Compton *et al.* 2013; Waters *et al.* 2014). Therefore, when the various physical and abiotic environmental factors are studied, it is clearly discernible that the regional and local controls support variation in environmental parameters. Hence, it is unlikely to identify two regions as distinct and separate by sharp boundaries, as suggested by Sivadas and Ingole (2016). However, because the present study used a different set of environmental indices, as compared to Sivadas and Ingole (2016), the fine-scale separation, based on sharp boundary, of different sub-regions by these two works may not match, although they both show some degree of similarities when considered as a part of the global ecosystem.

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