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Diversity and distribution of echinoderms in the South Eastern Arabian Sea shelf under the influence of seasonal hypoxia

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ABSTRACT

The South Eastern Arabian Sea (SEAS) margin represents a tropical eastern boundary upwelling system, which is subjected to intense seasonal hypoxia in the continental shelf, and impingement of oxygen minimum zone (OMZ) along the continental slope. This paper provides the first comprehensive information on abundance, diversity and distribution patterns of echinoderms, which are highly sensitive to oxygen deficiency and anthropogenic disturbances, in the continental shelf (~20–250 m) of the SEAS. Results are based on depth stratified and seasonally resolved sampling at 241 sites, representing 8 latitudinal grids & 4 depth strata (from inner shelf to shelf edge) using naturalist dredge and Smith-McIntyre grab. Echinoderms were the numerically dominant group among epifauna (42%), with significant seasonal variations in relative abundance (71% during winter and 17% during summer monsoon). Fifty-five species of echinoderms were identified, among which ophiuroids showed highest diversity (24 species) followed by echinoids (11 species) and asteroids (8 species). Species richness of echinoderms was higher in the inner and mid shelf (20–80 m), while the group was nearly absent in the shelf edge (150–250 m). A significant negative correlation was noted between species richness and latitude, and three distinct sub-regions could be delineated based on species diversity and abundance. The observed distribution patterns were found to be determined chiefly by sediment texture and bottom water dissolved oxygen, along with anthropogenic disturbances (bottom trawling). Echinoderms showed maximum abundance and species richness in the well-oxygenated sandy sediments of the southern SEAS, and very low species richness and abundance in relatively silty sediments of the northern SEAS, which were characterised by high seasonal fluctuations in dissolved oxygen (seasonal hypoxia). The near absence of echinoderms in the shelf edge despite the availability of sandy substrates indicates that this group is more sensitive to the perennially low oxygen conditions prevailing here.

1. Introduction

Echinoderms are a distinct phylum of exclusively marine invertebrates, represented by ~7000 extant species which are widely distributed in the oceans, from intertidal to deep sea trenches (Pawson, 2007). Owing to their diverse feeding modes (detritivores, predators, filter feeders, etc.) and lifestyles (motile, grazing, burrowing, boring, etc.) echinoderms are important components of marine food webs, are instrumental in bioturbation of marine sediments (Belaústegui et al., 2017) and are of considerable ecological significance in marine ecosystems. The calcium carbonate exoskeletons of echinoderms make them particularly vulnerable to climate change induced ocean warming and acidification, which interfere with skeletal development in early life stages (Orr et al., 2005; Byrne and Prezslawski, 2013). The adaptive capacity of echinoderms to a changing ocean at various stages of development has received considerable attention in recent years (e.g. Karelitz et al., 2017). Their long evolutionary history (over 500 million years) and exceptional fossil record also makes echinoderms ideal model group for understanding the complex drivers of marine faunal evolution (Thuy et al., 2014; Belaústegui et al., 2017).

Studies on echinoderm distribution patterns vis-à-vis prevailing environmental regimes in tropical continental margins (which includes the continental shelf and slope) are scarce, at broad or narrow spatial scales (Entrambasaguas et al., 2008; Vázquez-Bader et al., 2008; Williams et al., 2010, etc.) when compared to other parts of the world ocean (Ellis et al., 2000; O'Hara and Poore, 2000; Howell et al., 2002; Freeman and Rogers, 2003; De Domenico et al., 2006, etc.). Latitudinal gradients in echinoderm abundance and species richness at larger

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spatial scales are found to be superseded by local hotspots, which are in turn sustained by local or regional processes like productivity regimes and evolutionary factors (Iken et al., 2010). This study underlines the importance of local environmental and ecological regimes, anthropogenic drivers (pollution, nutrient enrichment, etc.), as well as differing responses of echinoderm taxa in shaping distribution patterns, by influencing habitat and food availability.

The South Eastern Arabian Sea is an eastern boundary upwelling system (EBUS), with distinct oceanographic and biological features (Madhupratap et al., 2001; Luis and Kawamura, 2004; Jyothibabu et al., 2010) within the northern Indian Ocean. This monsoon driven ecosystem experiences two major seasons annually - the summer (June-September) and winter monsoon (November-February) monsoons (SM & WM), interspaced by fall (October) and spring (March-May) inter monsoons (FIM & SIM). The SM is characterized by strong south-westerly winds that drive southward flowing currents, the influence of moderate to intense coastal upwelling and consequent higher biological production (Banse, 1959; Gupta et al., 2016). The resultant high production (Habeebrehman et al., 2008; Thomas et al., 2013) and subsequent degradation of organic matter causes rapid utilization of dissolved oxygen from the upwelled waters, which are oxygen-poor to begin with. The formation of a low-saline film at the surface during the monsoon prevents oxygen penetration to the sub-surface waters, and results in formation of hypoxic (DO $<$ 0.2 ml/l) conditions over the continental shelf of the SEAS during this season (Naqvi et al., 2006; Abdul Jaleel et al., 2015; Gupta et al., 2016). The degree of oxygen depletion is largely influenced by the Arabian Sea oxygen minimum zone (OMZ), which forms a source of upwelled water in the EAS, and so, seasonal hypoxia is significantly more intense in the northern parts of the study area, where the OMZ is more intense (Naqvi et al., 2006; Gupta et al., 2016).

During WM, north-easterly winds drive the currents northwards, leading to the influx and spread of the low saline oligotrophic Bay of Bengal waters over the SEAS which results in reduced biological production (Prasannakumar et al., 2004). The FIM (October) and SIM (March-May) are short periods of transition, characterized by weak winds and sluggish circulation. During SIM, the weak winds and increased solar radiation intensify surface warming, stratification and oligotrophic conditions, which lead to proliferation of the filamentous algae of genus *Trichodesmium* (Padmakumar et al., 2010). The SEAS shelf is subjected to intense trawling (Naomi et al., 2011), except during the summer monsoon trawling ban (Vivekanandan et al., 2010), and echinoderms form significant portion of trawl by-catch in the region (Kurup et al., 2003).

Investigations on diversity, distribution and ecology of benthic macro- and meiofauna of the SEAS (Jayaraj et al., 2008; Joydas and Damodaran, 2009, 2014; Ingole et al., 2010; Sajan et al., 2010; Abdul Jaleel et al., 2014, 2015; Sivadas et al., 2016) clearly demonstrate bathymetric gradients in standing stock from shallower depths to the shelf edge and beyond, with a very low contribution from (infaunal) echinoderms. Abdul Jaleel et al. (2015) reported a recovery in standing stock of benthic macrofauna during the SM trawl ban period, as a result of recruitment of major polychaete taxa, which coincide their breeding window with the highly productive summer monsoon (SM) season. Zonation in epibenthic megafauna is also reported at bathyal depths (540–2000 m) in the North Eastern Arabian Sea (Hunter et al., 2011), under the influence of the Arabian Sea OMZ (~150–1200 m), with a high density of ophiuroids in the lower boundary of the OMZ (~800 m between 17 and 18°N). However, there is no comprehensive information on the species composition, diversity and distribution of the epifaunal echinoderms in the sizeable area of the SEAS shelf.

Under the present scenario of climate change induced ocean acidification, intensification of hypoxia (Diaz and Rosenberg, 2008) and habitat fragmentation to which echinoderms are less resilient (Desprez, 2000; Gray et al., 2002; Orr et al., 2005; Byrne and Prezslawski, 2013; Kaiser et al., 2006), documentation of their distribution and ecology is of critical importance. This is particularly relevant in the seasonally oscillating environmental and productivity regimes of the SEAS, which is characterised by seasonal (SM) hypoxia over the shelf and impingement of a perennial OMZ at bathyal depths (Diaz and Rosenberg, 2008; Helly and Levin, 2004; Hunter et al., 2011), and is also subjected to anthropogenic disturbances like intense bottom trawling (Vivekanandan et al., 2010).

The present study provides the first comprehensive information on abundance, diversity and distribution patterns of echinoderms in the SEAS continental shelf (~20–250 m), based on systematic and seasonally resolved sampling at 241 sites between 2005 and 2014. Along with data on hydrographic and sediment parameters, this dataset is used to test the following hypotheses: (i) significant spatial (bathymetric and latitudinal) and temporal heterogeneity exists in the echinoderm distribution in the South Eastern Arabian Sea (SEAS) shelf, and (ii) these patterns are affected by variations in observed environmental parameters as well as anthropogenic stressors (e.g. bottom trawling).

2. Materials & methods

The study area is located on the continental shelf (20 to ~200 m depth zone) in the South Eastern Arabian Sea (SEAS) off the southwest coast of India (7°–15°N, 73°–78°E). For the present study, the region was delimited into eight grids (G1-G8), representing c. 1° of latitude. Stratified seasonal sampling was carried out in each grid on board FORV *Sagar Sampada*, along the inner shelf (20–50 m), mid shelf (50–80 m), outer shelf (80–150 m) and shelf edge (150–250 m), covering summer monsoon (SM), fall inter monsoon (FIM), winter monsoon (WM) and spring inter monsoon (SIM) seasons. Benthic fauna were collected using a naturalist dredge (1 m × 0.3 m frame, 1 cm mesh bag) towed at 2 knots for 10 min and a Smith McIntyre Grab (0.1 and 0.2 m^2 bite area). Dredge samples (live) were sorted and enumerated on board, and echinoderms were preserved in 70% ethanol. Sediment samples from the grabs were sieved and preserved on board, followed by sorting and enumeration of major faunal groups in the shore lab. Data on salinity, temperature and dissolved oxygen concentration of bottom water were collected using the on-board CTD (SeaBird SBE-911). The CTD data on dissolved oxygen was validated using the Winkler method (Strickland and Parsons, 1972). Approximately 200 g of sediments were taken from grab samples at each station for analysis of sediment characteristics. During the study, 241 sites were covered in the SEAS shelf, through 112 dredge operations and 410 grab operations (Fig. 1, Suppl. table 1).

Faunal groups collected in the dredge hauls included echinoderms, molluscs (chiefly gastropods, cephalopods and bivalves), crustaceans (chiefly brachyuran crabs, prawns, hermit crabs and stomatopods), fishes, echiurans, nemertines, sponges and coelenterates. Samples in each taxonomic group was enumerated and expressed as individuals per haul (ind./haul). Owing to the nature of the sampling gear, the abundance data from dredge collections were considered as semi-quantitative. Sediment samples collected using the grab were sieved (0.5 mm test sieve), major taxonomic groups (polychaetes, crustaceans, molluscs, echinoderms and other groups) were sorted out, enumerated and abundance was expressed as ind./m^2.

Taxonomic identification of echinoderms was carried out using standard taxonomic references (detailed in Parameswaran et al., 2017). Data on presence and absence of echinoderm species from the 241 sites collected using both grab and dredge were pooled together in order to examine their distribution patterns in the SEAS shelf as a whole. Quantitative species abundance data from these two gears were not pooled, considering the fundamental differences in the gear types used in this study (i.e. towed sampling of epifauna and point sampling of infauna).

Sediment samples for texture and organic matter analysis were oven dried at 55 °C, and 10 g of dried samples were accurately weighed, treated with hydrogen peroxide to remove organic matter, dispersed

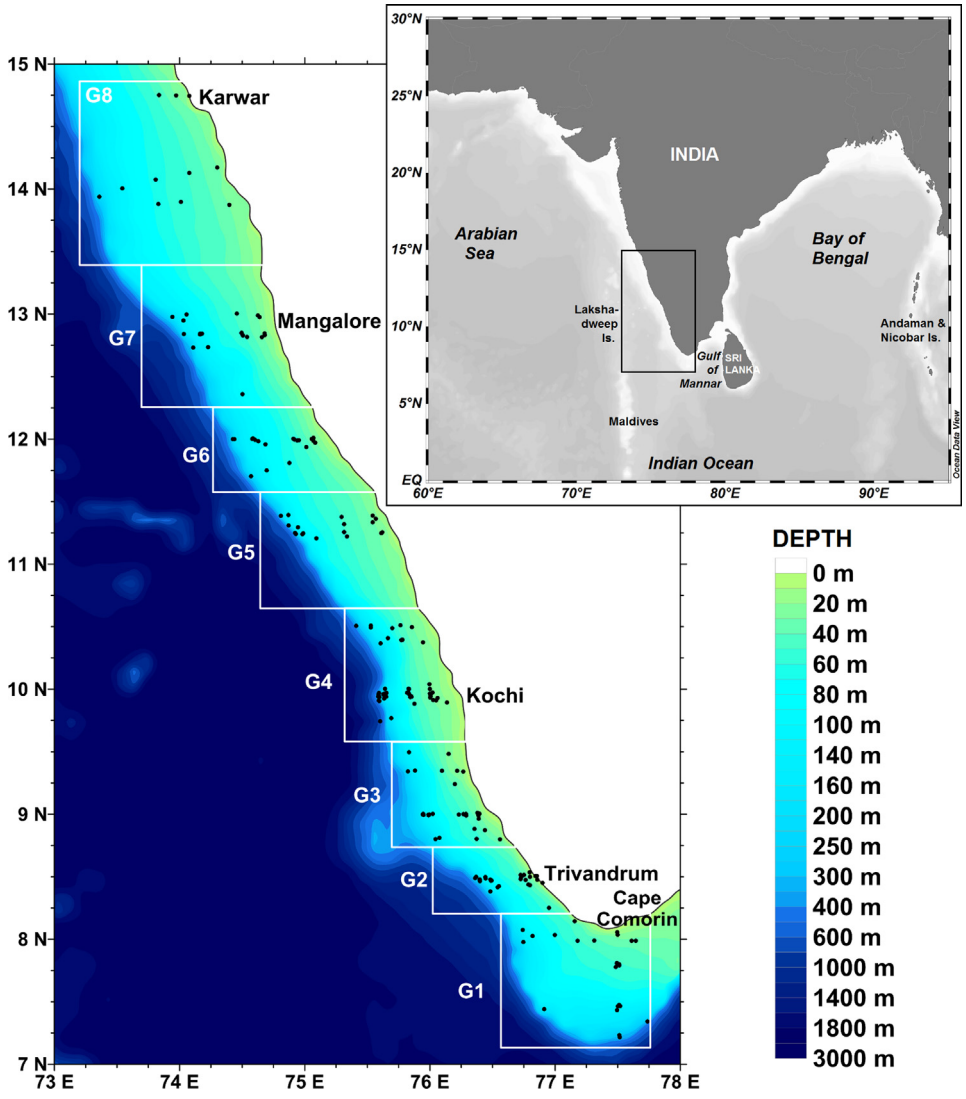

Fig. 1. Map of the south eastern Arabian Sea (SEAS) showing sampling sites and 8 assigned grids.

using sodium hexa-metaphosphate and kept overnight. Subsequently, sediment texture analysis was done using a CILAS 1180 Particle Size Analyser. The data on percentage composition of sand (grain size > 63 μm), silt (4–63 μm) and clay (< 4 μm) was taken along with median and mean grain size. Organic carbon of sediments was estimated by wet oxidation method (El-Wakeel and Riley, 1957), which measures the quantity of chromic acid required to oxidize the organic matter in a known quantity of sediment. A fixed quantity (0.2 g) of dried sediment was incubated at 100 °C for ~15 min with a fixed volume (10 ml) of chromic acid; and added to 200 ml of distilled water after cooling. The volume of chromic acid remaining was measured by titration against 0.2 mol l^{-1} ferrous ammonium sulphate solution with Phenolphthalein indicator. The procedure was simultaneously repeated without the sediment sample, in order to determine blank value. Deducting the titre value of the sample from the blank indicates the volume of chromic acid utilized. The organic carbon content is calculated from this, based on the equivalence of 1 ml of 0.2 mol l^{-1} ferrous ammonium sulphate to 1.15 × 0.6 mg of organic carbon (El-Wakeel and Riley, 1957). The values obtained were converted to organic matter (OM) by multiplication with the conversion factor (1.725) provided by Trask (1939) and expressed as percentage of sediment dry weight.

Bathymetric, latitudinal and seasonal variations in faunal abundance (using square-root transformation and Bray-Curtis similarity), echinoderm species composition (Kulczynski resemblance) and environmental parameters (log-transformation, normalisation and Euclidean distance) were tested using the PERMANOVA add-on in PRIMER-6 (Anderson et al., 2008). The quantitative data collected from dredge (ind./haul) and grab (ind./m^2) were analysed separately. The number of species collected in each sample was used as a direct measure of diversity in the present study. Sampling sufficiency was tested by employing species accumulation curve and species estimators (Chaos 2, which is based on numbers of rare species in presence-absence data, and Jacknife 1, which is based on number of species occurring in exactly one sample) using PRIMER-6 (Warwick and Clarke, 2006). The spatial and seasonal variations in environmental parameters (log transformed and normalised) was examined through a Principal Component Analysis (PCA) using PRIMER-6. The abundance of epifaunal echinoderms and species richness in each site were superimposed as bubbles on a bathymetric map of the study area (using SURFER 11) and the PCA (using PRIMER-6), respectively to elucidate environmental preference of echinoderms. Strength of correlation (Pearson's coefficient, r) between individual biological and environmental variables were tested using IBM SPSS 20. Echinoderm species were classified based on the feeding modes, such as detritivores, grazers, predators and suspension feeders (Meyer, 1982; Massin, 1982; De Ridder and Lawrence, 1982; Jangoux, 1982; Warner, 1982), in order to link observed distribution patterns with major food sources.

Table 1
Results of PERMANOVA test of environmental parameters for variations between depth, latitude & season (values in bold indicate statistical significance with $p < 0.05$).

Factor	Depth stratum		Latitude		Season	
	Pseudo-F	p	Pseudo-F	p	Pseudo-F	p
Dredge composition	0.990	0.467	**1.579**	**0.018**	**2.075**	**0.023**
Grab composition	**8.190**	**0.001**	1.417	0.108	**2.114**	**0.025**
Echinoderm abundance (dredge)	1.806	0.125	**1.717**	**0.038**	1.090	0.382
Echinoderm species (p/a)	**1.243**	**0.034**	**2.216**	**0.001**	1.159	0.322
Sediment texture	**11.606**	**0.001**	**11.728**	**0.001**	1.595	0.183
Organic matter	**14.037**	**0.001**	**20.298**	**0.001**	1.879	0.148
Median grain size	**19.943**	**0.001**	**17.657**	**0.001**	1.268	0.273
Salinity	**3.996**	**0.023**	**4.385**	**0.002**	**4.522**	**0.013**
Temperature	**350.180**	**0.001**	**4.607**	**0.006**	**97.718**	**0.001**
Dissolved oxygen	**76.117**	**0.001**	**4.530**	**0.001**	**166.990**	**0.001**

3. Results

3.1. Abundance of echinoderms

Echinoderms were represented in 69 of the 112 dredge hauls in the south eastern Arabian Sea (SEAS) shelf and were the numerically abundant epifaunal group (42%). Other fauna in the dredge were crustaceans (decapods such as brachyuran crabs, hermit crabs and prawns; 31%), molluscs (gastropods, bivalves and cephalopods; 19%) and teleost fishes (4%), along with coelenterates, nemertines, sponges, echiurans and polychaetes (cumulatively 4%). Considerable seasonal and latitudinal variations were noted in the composition of epifauna (PERMANOVA $p < 0.05$), while bathymetric variations were not statistically significant (Table 1). The mean abundance of epifauna was 132 ind./haul during summer monsoon (SM) and 120 ind./haul during winter monsoon (WM). The seasonal variations were due to significant differences in relative abundance of faunal groups. During SM, crustaceans (chiefly prawns and crabs) were the dominant group (58 ind./haul, 43%), followed by molluscs (40 ind./haul, 30%) and echinoderms (22 ind./haul, 17%). During WM, the relative abundance of echinoderms increased to 71% (85 ind./haul), while the contribution of crustaceans decreased to 15% (17 ind./haul) and molluscs to 6% (7 ind./haul).

Bathymetric variations in composition of epifauna were low and not significant (Table 1). In the inner shelf, molluscs (57 ind./haul, 61% of epifauna) and crustaceans (49 ind./haul, 36%) were the dominant groups, while echinoderms dominated in the mid shelf (49 ind./haul, 68%) and crustaceans dominated in the deeper strata (43 ind./haul, 46% at 80–150 m and 17 ind./haul, 70% at 150–250 m). Echinoderms were nearly absent in the shelf edge of the SEAS, being represented only at a single site in G3. With respect to latitude, highest abundance of epifauna was recorded in G3, owing to high abundance of echinoderms (54% of epifauna) in the mid-shelf (50–80 m). A progressive and statistically significant (Table 1) decline in the relative abundance of echinoderms from south to north was noted (from 65% in G1 to 2% in G8), with the notable exception of G7 (63%) accompanied by an overall increase in relative abundance of crustaceans and molluscs (Figs. 2b and 3).

Echinoids were represented in 45 hauls, with high abundance in G2-G4 (Fig. 3a) which was due almost entirely to the exceptional abundance of the echinoids *Clypeaster rarispinus* and *Sculpsitechinus auritus* (max. 1316 ind./haul at G3, 49 m, WM). Ophiuroids were represented in 41 hauls (Fig. 3b), with high abundance throughout most of the study area and maximum of 240 ind./haul (*Amphioplus depressus*, G4, 106 m & G7, 53 m, SM). Asteroids were collected in 32 hauls (Fig. 3c), with relatively high abundance only in G1 (*Astropecten vappa* 130 ind./haul in G1, 48 m, WM). Holothurians were present in 18 hauls (Fig. 3d), with relatively low abundance (max. 21 ind./haul in G2 52 m, SM) and crinoids were represented only in 4 sites in the inner shelf (32–51 m) in G1 (max. 21 ind./haul, 49 m, WM). Apart from a single ophiuroid, collected at 155 m depth in G3, echinoderms were altogether absent at the 150–250 m depth stratum. Substantial populations of echinoderms were found only in the southern part of the study area, particularly in the mid-shelf (50–80 m) of G2 and G3, and within this region, seasonal and bathymetric variations were found to be statistically significant ($pF = 2.664$, $p = 0.021$).

Based on 410 grab samples from the SEAS shelf, polychaetes were found to be the dominant components among macro infauna (80% of total macrofaunal abundance), followed by crustaceans, molluscs and echinoderms. Mean abundance of echinoderms was 29 ind./m^2 (1% of total macrofaunal abundance). They were represented by adults of Ophiuroidea and Holothuroidea along with juveniles of certain species of Ophiuroidea (*Ophiura* sp.), Asteroidea (*Astropecten* spp.) and Echinoidea (*Clypeaster* spp., *Sculpsitechinus* sp.). The occurrence of these juveniles was noted between August and December. Seven species of ophiuroids (all of family Amphiuridae) and 2 species of holothurians (*Synaptula recta* and *Pseudocnus echinatus*) were represented only among the grab collections. The standing stock of macrofauna in the SEAS shelf showed significant bathymetric and seasonal variations (Table 1). Owing to the relative low contribution of echinoderms to macrofaunal abundance, comparable variations were not discernible in this group. However, echinoderms were notably absent among grab samples north of G3 during SM, except for *Amphioplus depressus* (Ophiuroidea, Amphiuridae) which occurred in high abundance (20–50 ind./m^2) at two sites in G4 & G7.

3.2. Species richness of echinoderms

In order to analyse the species diversity of echinoderms in the SEAS shelf, data from the dredge and grab collections were pooled to provide a presence-absence dataset of 55 echinoderm species in the 241 sites. Owing to the different methodology and sample size of dredge and grab

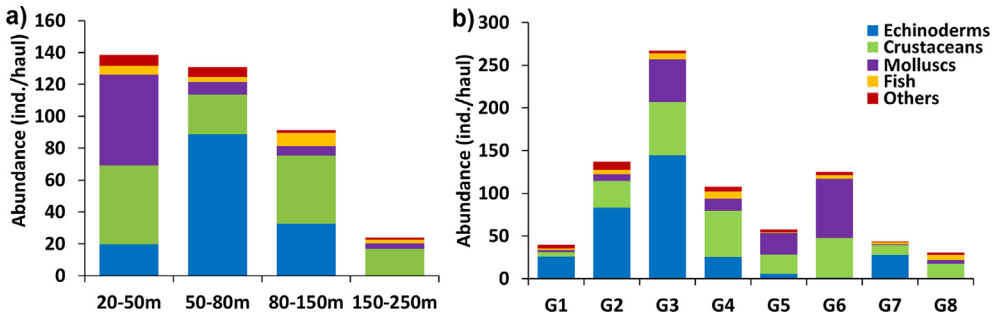

Fig. 2. Abundance of major groups among epifauna in (a) the four depth strata: 20–50 m, 50–80 m, 80–150 m and 150–250 m and (b) eight latitudinal grids: G1-G8 of the SEAS.

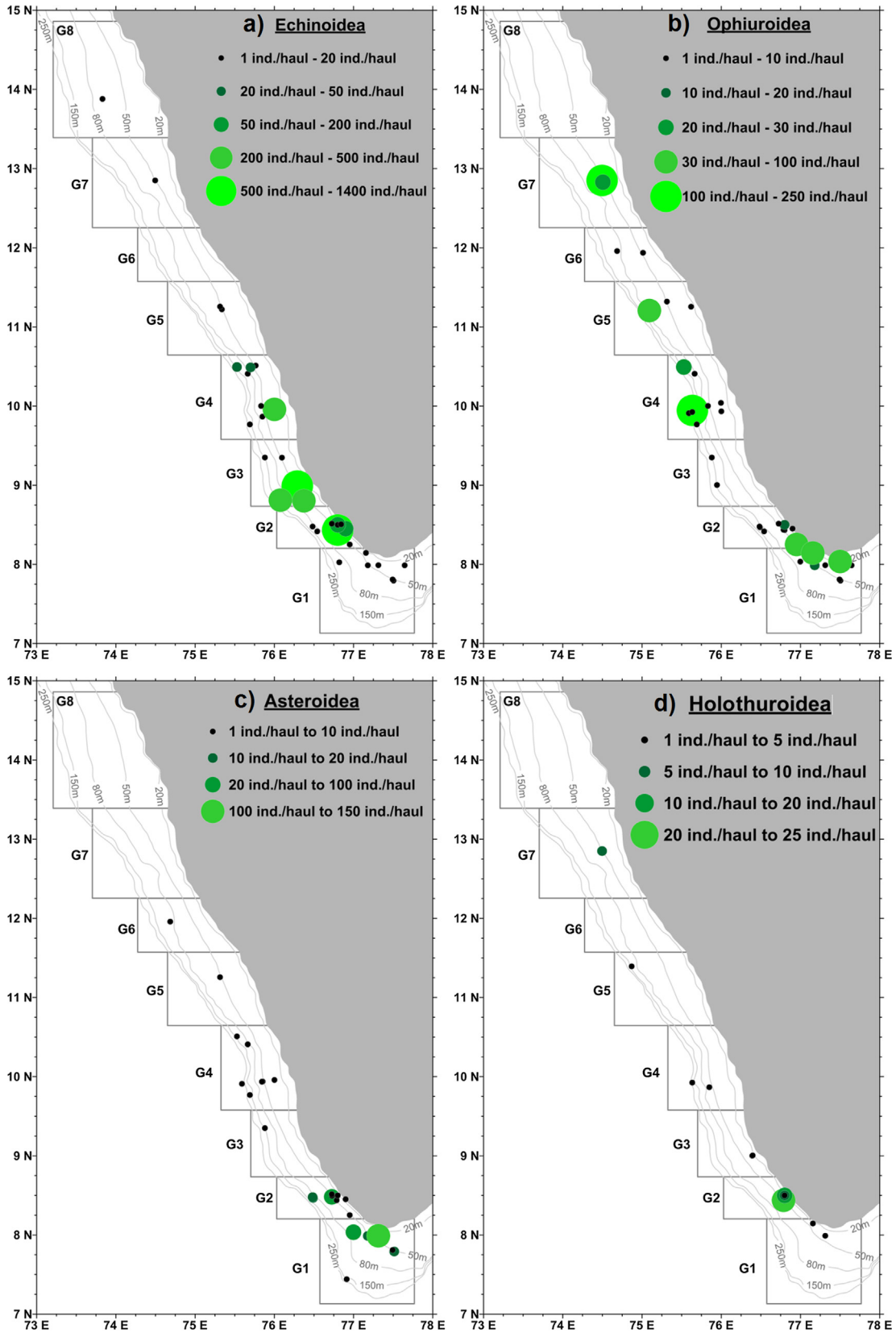

Fig. 3. Abundance of the five classes of echinoderms among epifauna in the SEAS shelf. (a) Echinoidea, (b) Ophiuroidea, (c) Asteroidea, and (d) Holothuroidea among epifauna in the SEAS shelf.

collections, attempts were not made to combine quantitative species distribution data from these two gears. Echinoderms were represented at 106 sites out of 241; and class Ophiuroidea exhibited highest richness (24 species), followed by Echinoidea (12 species) and Asteroidea (8 species). Holothurians and crinoids were represented by 5 and 6 species respectively. A species accumulation curve for the study area did not

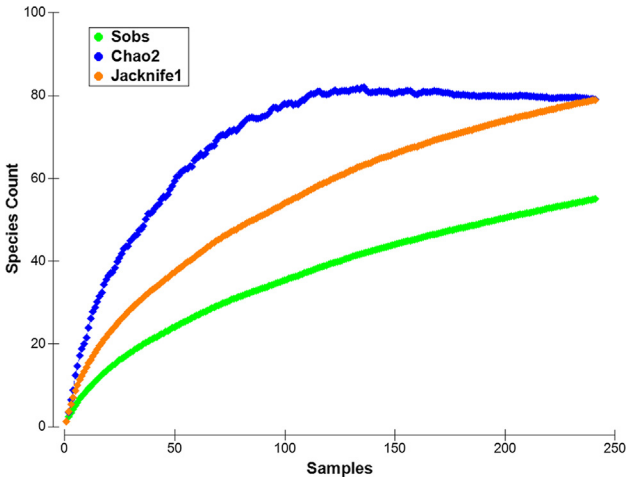

Fig. 4. Species accumulation curves of echinoderms, based on presence-absence of species in 241 sampling sites in the SEAS shelf, with Chao's second order and first order Jackknife species estimators.

attain the asymptote (Fig. 4), and estimators (Chaos 2 and Jacknife 1) predict the occurrence of up to 79 species (70% sampling sufficiency). The ophiuroids in the present study included epibionts *Ophiodaphne scripta* (on echinoids *Sculpsitechinus auritus* and *Clypeaster rarispinus*), *Ophiosphaera insignis* (on echinoid *Salmaciella dussumieri*), *Ophiacantha dallasii* and *Ophiopteron elegans* (on gorgonids).

Bathymetric and latitudinal variations in species distribution were found to be statistically significant ($p < 0.05$), while seasonal variations were not (Table 1). Species richness was high in the 20–80 m depth stratum (Fig. 5a). Only one species, *Ophiura kinbergi* (Ophiuroidea, Ophiuridae), was represented beyond 124 m depth (Table 2). Crinoids were collected only in the inner shelf (20–50 m), and holothurians showed highest richness at this depth range. Species richness of all classes decreased significantly at depths > 80 m. Highest species richness was recorded in G1 (50 species), and this included all the crinoids recorded in the study (Fig. 5b). Echinoderm species richness decreased progressively towards the north, particularly in the case of Asteroidea, Ophiuroidea and Echinoidea; and only 1 species, *Lovenia elongata* (Echinoidea, Loveniidae), was recorded in T8.

Out of the 55 species of echinoderms collected in the present study, 24 were known from a single sample, while the remaining 31 species were represented in two or more sites in the study area. The bathymetric and latitudinal ranges of these 31 species were examined in order to further explore distribution patterns in the SEAS shelf (Fig. 6a, b). The brittle star *Ophiura kinbergi*, showed widest bathymetric range in the SEAS shelf (31–155 m), and 13 other species also had a relatively wide distribution range, while the remaining sixteen showed relatively narrow ranges (Fig. 6a). The most significant depth-related pattern in echinoderm species distribution in the SEAS shelf was the absence of all but one species beyond 125 m and the complete absence of the group between 155 and 250 m, while between 20 and 125 m 14 species showed a wide distribution range.

The species having widest latitudinal distribution ranges were *Clypeaster rarispinus*, *Ophiura kinbergi*, *Amphioplus depressus* and *Leptopentacta imbricata* (~7°45′N to ~12°49′N, T1-T7). *Luidia hardwicki*, *Thyone dura*, *Amphipholis misera* and *Astropecten vappa* also showed relatively wide latitudinal range (Fig. 6b, Table 2). The aforementioned 8 widely distributed species, were the only echinoderms recorded between G4 and G7 in the present study, along with *Amphiura duncani*, which was only collected in G4 and G5. The echinoid *Lovenia elongata* was observed in G1 and G2 and was the only echinoderm species recorded in G8. Thirty-one species were found to occur only in G1 and 3 species (*Dougalopus echinatus*, *Ophiothrix proteus* and *Synaptula recta*) were represented only in G2 (Table 2).

The results indicate a clear latitudinal trend in distribution of species within the 20–150 m depth zone of the SEAS shelf. These variations were evident in an nMDS ordination (Kulcsynski resemblance) of species incidence data in the 8 grids (Fig. 7). In this plot, G8, with only one species (*Lovenia elongata*) being recorded, formed an outlier. The rest of the study area could be differentiated into three distinct sub-regions, at 65% similarity, based on species richness and composition. These are characterised below along with diversity estimators:

(i) The Cape Comorin sub-region (G1): characterised by highest species richness in the SEAS shelf (total 50 species), including all 6 crinoids identified in the present study, and 25 other species which were found only in this sub-region. Species estimators predict the occurrence of up to 87 species in this region, with intensified sampling (Fig. 8a).

(ii) The Trivandrum-Kollam sub-region (G2 & G3): characterised by intermediate richness (23 species), including widely distributed species of the SEAS shelf (*Ophiura kinbergi*, *Amphioplus depressus*, *Luidia hardwicki*, *Clypeaster rarispinus*, *Thyone dura* and *Leptopentacta imbricata*) and a few species exclusive to the southern SEAS (G1-G3). Species estimators predict up to 31 species in this region with further sampling (Fig. 8b).

(iii) The Kochi-Mangalore sub-region (G4-G7): characterised by low species richness (9 species). Apart from *Amphiura duncani*, which was unique to the region along with *Amphipholis misera* and *Astropecten vappa*, the 6 species that occurred here were the widely distributed taxa of the SEAS shelf (mentioned above). Species estimator values equalled the observed number of species in this sub-region, indicating that all possible species in the region have been collected in the study (Fig. 8c).

3.3. Linking echinoderm distribution to environmental conditions

The spatial and temporal variations in environmental parameters (sediment texture, grain size, organic matter content, bottom water

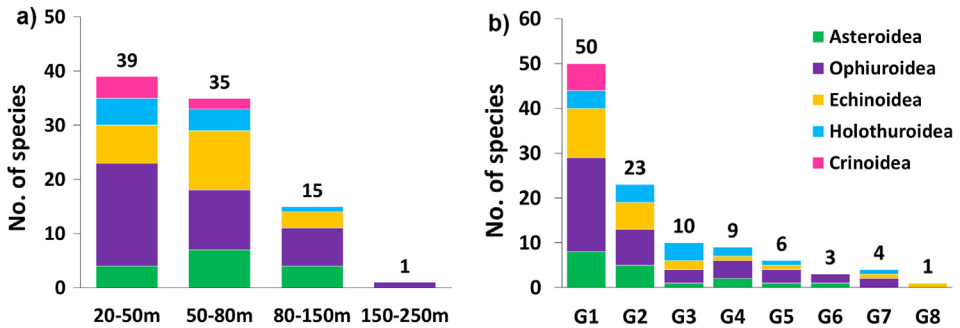

Fig. 5. Species richness of the five classes of echinoderms in the SEAS shelf. (a) Echinoidea, (b) Ophiuroidea, (c) Asteroidea, and (d) Holothuroidea epifauna in the four depth strata: 20–50 m, 50–80 m, 80–150 m and 150–250 m (a) and eight latitudinal grids: G1-G8 (b) of the SEAS.

Table 2
Region and depth of occurrence of echinoderm species in the SEAS shelf, along with feeding mode inferred from literature.[a]

Species	Region of occurrence								Depth range	Feeding mode[a]
	T1	T2	T3	T4	T5	T6	T7	T8		
Asteroidea										
Astropecten polyacanthus	+	+	−	−	−	−	−	−	50–52 m	Carnivore
Astropecten vappa	+	+	−	+	−	−	−	−	24–116 m	Carnivore
Astropecten hemprichi	+	−	−	−	−	−	−	−	52 m	Carnivore
Luidia denudata	+	−	−	−	−	−	−	−	53–113 m	Carnivore
Luidia hardwicki	+	+	+	+	+	+	−	−	33–111 m	Carnivore
Stellaster childreni	+	+	−	−	−	−	−	−	32–101 m	Mixed grazer
Heteronardoa carinata	+	−	−	−	−	−	−	−	50 m	Deposit feeder
Goniodiscaster forficulatus	+	+	−	−	−	−	−	−	52–124 m	Carnivore
Ophiuroidea										
Amphioplus depressus	+	+	+	+	+	+	+	−	24–100 m	Deposit feeder
Amphipholis misera	+	+	−	+	−	−	−	−	51–116 m	Deposit feeder
Amphiura ambigua	+	−	−	−	−	−	−	−	32–100 m	Deposit feeder
Amphiura constricta	+	+	−	−	−	−	−	−	52–106 m	Deposit feeder
Amphiura duncani	−	−	−	+	+	−	−	−	52–109 m	Deposit feeder
Amphiura micra	+	−	−	−	−	−	−	−	24 m	Deposit feeder
Amphiura heptacantha	+	−	−	−	−	−	−	−	31 m	Deposit feeder
Amphiura tenuis	+	−	−	−	−	−	−	−	24–53 m	Deposit feeder
Amphuira crispa	+	−	−	−	−	−	−	−	24 m	Deposit feeder
Dougalopus echinatus	−	+	−	−	−	−	−	−	49 m	Deposit feeder
Ophiodaphne scripta	+	+	+	−	−	−	−	−	38–111 m	Epibiont
Ophiosphaera insignis	+	−	−	−	−	−	−	−	49 m	Epibiont
Ophiacantha dallasi	+	−	−	−	−	−	−	−	49 m	Epibiont
Ophiocoma brevipes	+	−	−	−	−	−	−	−	49 m	Mixed grazer
Ophiopsila pantherina	+	−	−	−	−	−	−	−	49 m	Mixed grazer
Ophiarachnella infernalis	+	−	−	−	−	−	−	−	51 m	Carnivore
Ophioconis cupida	+	−	−	−	−	−	−	−	48–50 m	Carnivore
Ophiocnemis marmorata	+	+	−	−	−	−	−	−	49–52 m	Suspension feeder
Ophiopteron elegans	+	−	−	−	−	−	−	−	49 m	Epibiont
Ophiothrix proteus	−	+	−	−	−	−	−	−	52 m	Suspension feeder
Ophiothrix purpurea	+	−	−	−	−	−	−	−	51–52 m	Suspension feeder
Ophiothrix foveolata	+	−	−	−	−	−	−	−	49 m	Suspension feeder
Ophiothrix savignyi	+	−	−	−	−	−	−	−	31–52 m	Suspension feeder
Ophiura kinbergi	+	+	+	+	+	+	+	−	30–155 m	Carnivore
Echinoidea										
Stereocidaris alcocki	+	−	−	−	−	−	−	−	51 m	Mixed grazer
Paratrema doederleini	−	+	−	−	−	−	−	−	102 m	Mixed grazer
Salmaciella dussumieri	+	+	−	−	−	−	−	−	34–52 m	Mixed grazer
Salmacis virgulata	+	−	−	−	−	−	−	−	52 m	Mixed grazer
Echinoneus cyclostomus	+	−	−	−	−	−	−	−	30–51 m	Deposit feeder
Sculpsitechinus auritus	+	+	+	−	−	−	−	−	38–95 m	Deposit feeder
Clypeaster fervens	+	−	−	−	−	−	−	−	52 m	Deposit feeder
Clypeaster rarispinus	+	+	+	+	+	−	+	−	32–111 m	Deposit feeder
Clypeaster reticulatus	+	−	−	−	−	−	−	−	52 m	Deposit feeder
Echnolampas alexandri	+	+	−	−	−	−	−	−	30–50 m	Deposit feeder
Lovenia elongata	+	+	−	−	−	−	−	+	33–65 m	Deposit feeder
Nacospatangus alta	+	−	−	−	−	−	−	−	30–52 m	Deposit feeder
Holothuroidea										
Synaptula maculata	−	+	+	−	−	−	−	−	31–51 m	Deposit feeder
Leptopentacta imbricata	+	+	+	+	−	−	+	−	31–108 m	Deposit feeder
Pseudocnus echinatus	+	−	−	−	−	−	−	−	24 m	Deposit feeder
Stolus buccalis	+	+	+	−	−	−	−	−	30–52 m	Deposit feeder
Thyone dura	+	+	+	+	+	−	−	−	24–109 m	Deposit feeder
Crinoidea										
Antedon ?parviflora	+	−	−	−	−	−	−	−	49 m	Suspension feeder
Mastigometra micropoda	+	−	−	−	−	−	−	−	51 m	Suspension feeder
Cenometra bella	+	−	−	−	−	−	−	−	51 m	Suspension feeder
Petasometra helianthoides	+	−	−	−	−	−	−	−	49 m	Suspension feeder
Heterometra africana	+	−	−	−	−	−	−	−	49 m	Suspension feeder
Himerometra robustipinna	+	−	−	−	−	−	−	−	32 m	Suspension feeder

[a] *Sources:* Meyer (1982), Massin (1982), De Ridder and Lawrence (1982), Jangoux (1982), and Warner (1982).

salinity, temperature and dissolved oxygen) were examined using a Principal Component Analysis (PCA). Five principal components (PCs) explained 91.4% of variance among the sites (Table 3). Latitudinal variations in sediment texture, grain size (GS) and organic matter content (OM) were explained by PC1, while bathymetric and seasonal variations in bottom water dissolved oxygen (DO), salinity and temperature were resolved by PC2 (Fig. 9a, Tables 1 and 3).

The sediments of the inner shelf were predominantly sandy towards the south (Figs. 9a and 10, Suppl. table 2), with coarse biogenic sands (higher GS) in G1, siliceous sands in G2, and silty sands in G3 & G4, whereas towards the north (G5-G8) sediments were dominated by silt. In the mid-shelf, sandy sediments prevailed in the south (G1-G3), while

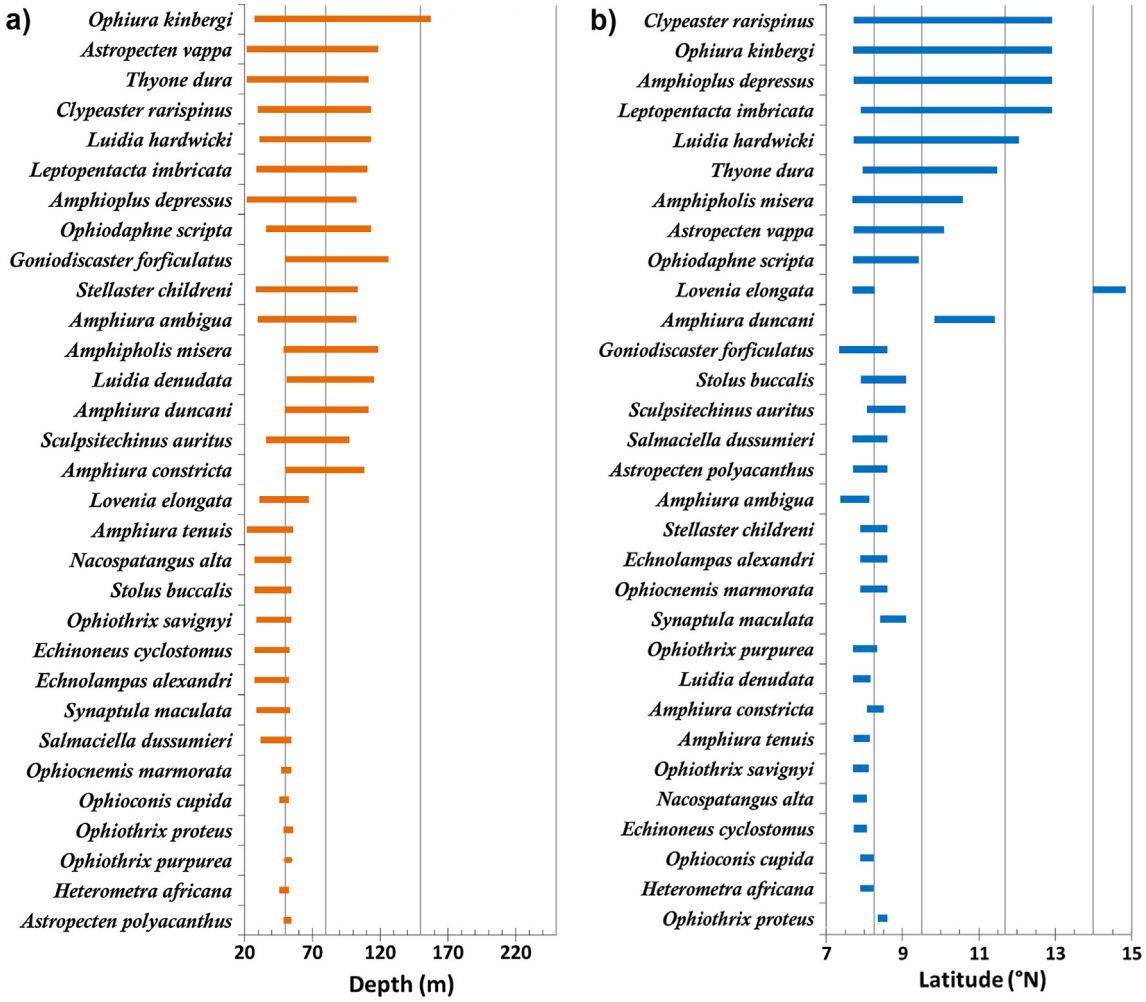

Fig. 6. Distribution ranges of echinoderms on the SEAS shelf. (a) Bathymetric, and (b) latitudinal distribution range.

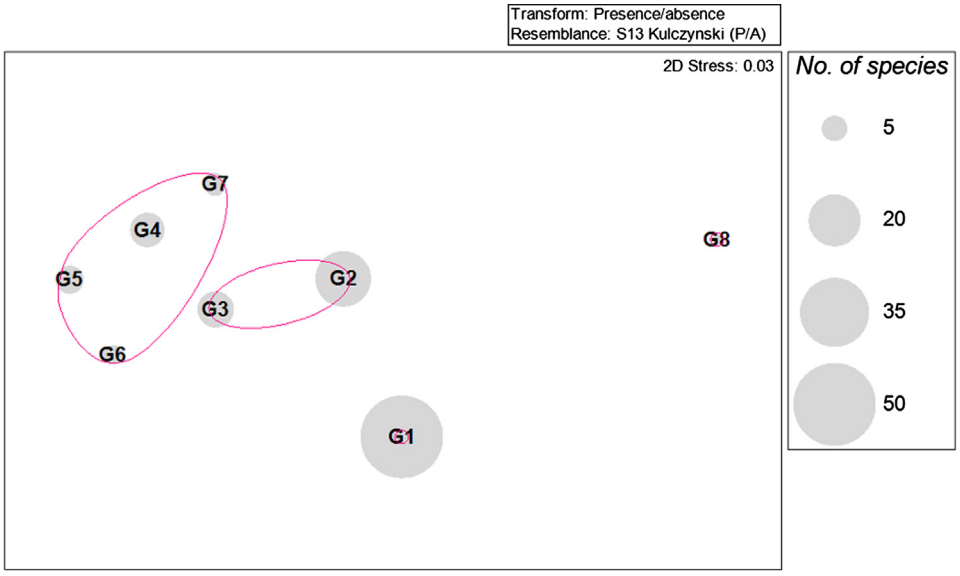

Fig. 7. Non-metric multi-dimensional scaling (nMDS) ordination based on Kulcsynski resemblance of species incidence data in the 8 grids of the SEAS, with similarity contours (65%), and species numbers superimposed as bubbles.

sediments were silty sand in the north (G4-G8). Along the outer shelf and shelf edge, sediments were heterogeneous, with higher sand content between G1 and G5 and a mixture of sand and silt between G6 and G8. In the study area, OM content of sediments ranged from 0.20 (G2, 33 m) to 8.57% (G7, 37 m), with an overall mean of 1.64 ± 1.36% and highest values in the inner shelf of the north (G5-G8). Spatial variations

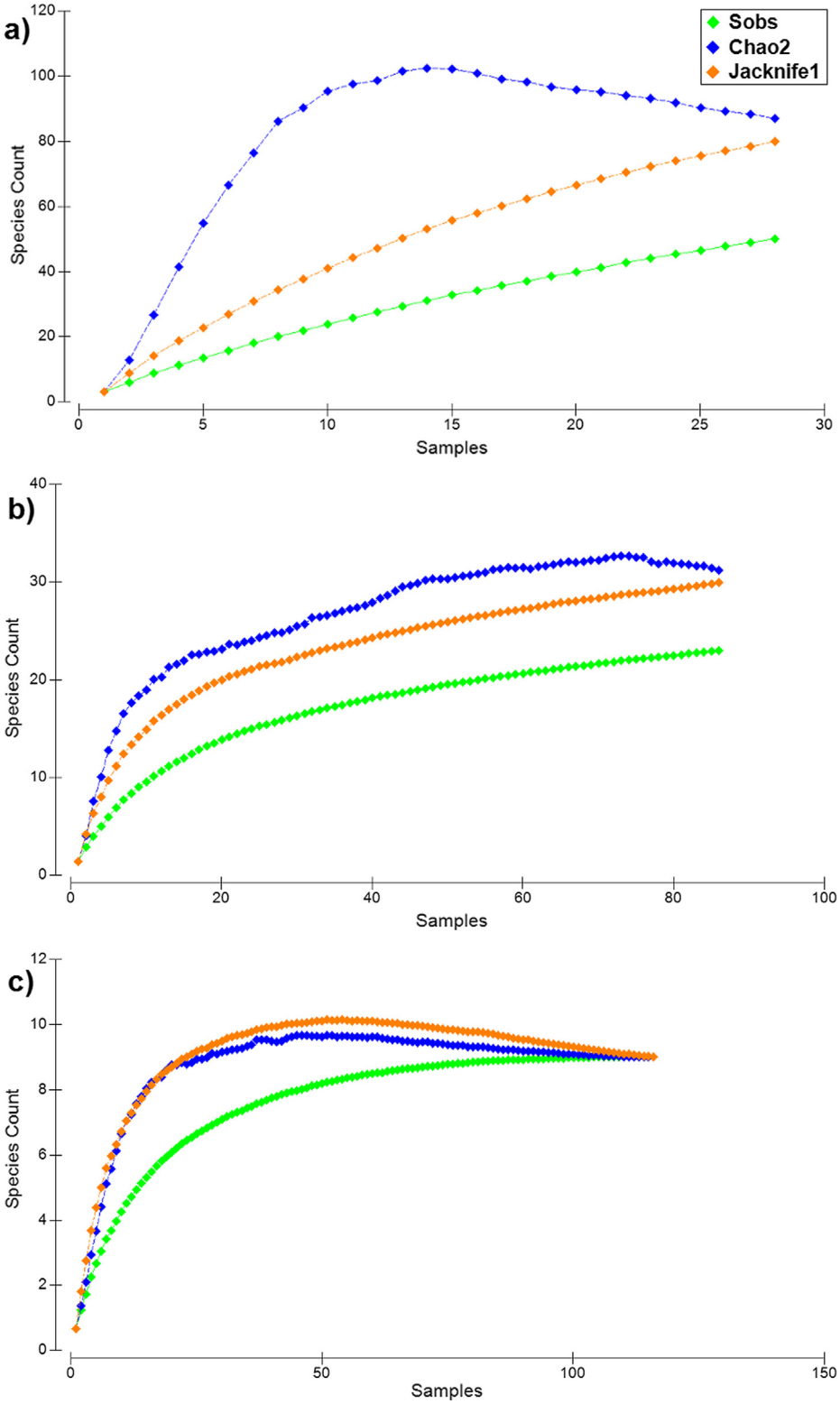

Fig. 8. Species accumulation curves based on the presence-absence of species in the three sub-regions delineated in the SEAS, (a) Cape sub-region, (b) Trivandrum-Kollam sub-region and (c) Kochi-Mangalore sub-region.

in OM reflected close correlation with proportion of finer sediments (OM & silt: $r = 0.784$, $p < 0.05$) and median grain size ($r = -0.549$, $p < 0.05$). Although seasonal variations were not statistically significant ($p > 0.05$), OM was relatively higher during FIM at most sites (Suppl. table 3).

Along the SEAS shelf, hydrographic parameters of bottom water showed significant bathymetric and seasonal variations (Table 1), which were reflected in the PCA plot (Fig. 8a). In general, bottom water salinity increased from the inner shelf to the shelf edge, while DO and temperature decreased (Fig. 9a, Suppl. table 3). During SM, temperature of bottom water decreased and salinity increased in the inner, mid and outer shelf, as a result of coastal upwelling across the SEAS. At

Table 3
Results of Principal Component Analysis (PCA).

Principle components		PC1	PC2	PC3	PC4	PC5
Eigenvalue		4.53	2.30	1.08	0.74	0.50
Cumulative % of variation explained		45.3	68.3	79.1	86.5	91.4
Variables	Depth	0.119	**0.519**	−0.050	**−0.605**	0.137
	Latitude (Lat.)	**−0.314**	0.103	**0.401**	−0.160	**−0.811**
	Salinity	−0.065	**0.223**	**0.830**	0.148	**0.402**
	Temperature (Temp.)	−0.060	**−0.619**	0.217	−0.007	−0.032
	Dissolved oxygen (DO)	0.001	**−0.517**	0.110	**−0.673**	0.194
	Sand (%)	**0.413**	0.056	0.034	−0.196	−0.254
	Silt (%)	**−0.409**	0.074	−0.200	−0.147	−0.057
	Clay (%)	**−0.422**	0.006	−0.177	0.086	0.107
	Organic matter (OM)	**−0.395**	0.109	0.062	−0.255	0.186
	Median grain size (GS)	**0.456**	0.003	0.114	−0.042	−0.099

these depths, oxygen depleted conditions were observed during SM, with DO concentration falling below 0.5 ml/l (22.32 µM) in the northern and central regions, and even below 0.2 ml/l (8.93 µM) in G7 and G8 (Fig. 11, Suppl. table 3). No seasonal variations were observed in the shelf edge (~0.2 ml/l), where low-oxygen conditions prevail throughout the year.

Abundance of epifaunal echinoderms correlated positively with bottom water DO ($r = 0.311$, $p < 0.05$), while that of crustaceans and molluscs showed positive correlation with silt and clay content ($p < 0.05$). In order to link the distribution of echinoderm species in the SEAS to the prevailing environmental conditions, the number of species collected from each site were superimposed as bubbles on the PCA plot (Fig. 9b). Species abundance and richness were highest in the inner and mid shelf (20–80 m) of the southern SEAS (G1-G3), which was characterised by sandy sediments, and relatively high DO throughout the year (Figs. 3 and 9b). Echinoderm species were poorly represented in the silty inner and mid shelf (20–80 m) sediments of the north (G4-G8), where seasonal (SM) hypoxia was pronounced. Intermediate abundance and richness were noted in the relatively sandy

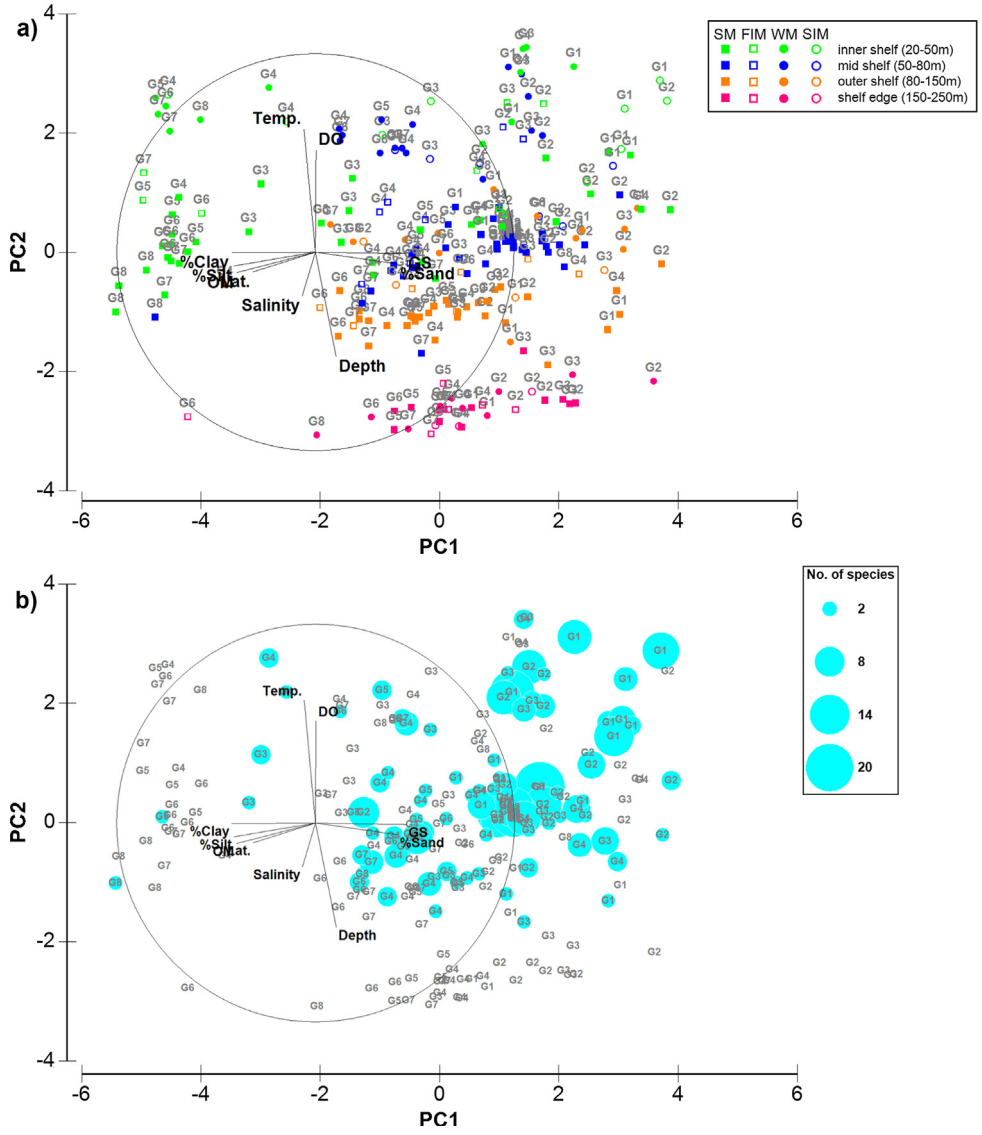

Fig. 9. (a) Results of Principal Component Analysis (PCA) showing spatial and temporal variations in environmental factors in the sampling sites and (b) same plot with superimposed bubbles indicating species richness at each site.

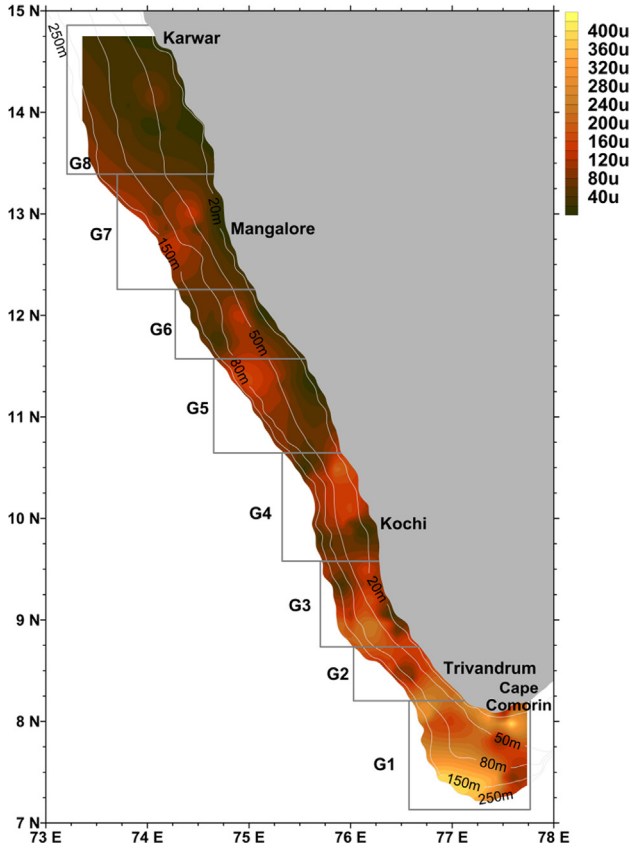

Fig. 10. Map of the SEAS shelf showing the mean grain size of sediments.

sediments of the outer shelf (80–150 m), particularly between G1 and G4. Echinoderms were almost absent under the perennially low oxygen conditions of the shelf edge, despite the predominantly sandy sediments.

3.4. Feeding ecology of echinoderms

The echinoderm species represented in the study area were classified as carnivores, mixed grazers, deposit feeders and suspension feeders (Table 2), based on the main food sources of these taxa, as inferred from literature (Meyer, 1982; Massin, 1982; De Ridder and Lawrence, 1982; Jangoux, 1982; Warner, 1982). The epibiotic ophiuroids (*Ophiodaphne scripta*, *Ophiosphaera insignis*, *Ophiacantha dallasii* and *Ophiopteron elegans*) were treated separately, since their distribution is linked with that of their hosts and assuming that they depended partially or wholly on their hosts for feeding. The asteroid *Heteronardoa carinata*, which is described as a 'substrate film feeder' (Jangoux, 1982), and holothurians, which were all small (1–3 cm length) and wholly or partially burrowing forms, are referred to the broad group of deposit feeder.

Though the deposit feeding forms were widely represented in the study area, most species showed affinity to the sandy inner shelf sediments of the southern region (G1-G3) as well as the mid and outer shelf (50–150 m) of the north, despite the relatively low sedimentary OM. The majority of these deposit feeders (clypeasterid echinoids and amphiurid ophiuroids) are surface feeders, which rely on freshly deposited OM at the sediment surface; and these included most widely distributed species of the study area (*Clypeaster rarispinus* and *Amphioplus depressus*). The holothurians were interphase feeders, filtering or collecting food from the sediment-water interphase, and they showed affinity mostly to sandy sediments between G1 and G4 (20–80 m). The spatangoid echinoids (*Lovenia elongata* and *Nacospatangus alta*), are deep-burrowing forms, which ingest subsurface sediments and extract OM from them; and were found to prefer finer sands (GS ~100–200 μm) with some silt content (4–20% silt). In the silty sediments of the northern grids (G4-G8, 20–50 m), a few deposit feeding echinoids were represented (*Lovenia elongata* at 33 m of G8, *Clypeaster rarispinus* at 34 m in G4); and holothurians (*Synaptula recta*, *Stolus buccalis* and *Leptopentacta imbricata*) were also found to occur in relatively silty sediments of G3 (30–32 m, SM).

Carnivorous forms were similarly well represented in sandy sediments, particularly in the southern SEAS, and in areas with higher macrofaunal abundance. Two widely distributed echinoderms of the SEAS shelf, *Ophiura kinbergi* and *Luidia hardwicki* are carnivore or scavenger of small-sized benthic fauna (including other echinoderms). Grazers (regular echinoids) and suspension feeders (crinoids and ophiotrichid ophiuroids) were sparsely represented in the SEAS shelf; the former showing affinity to the finer sands of the inner and mid shelf (20–80 m) of G2 & G3, and the latter being found only in the coarse coralline sands of G1 (20–80 m).

4. Discussion

The Arabian Sea is among the most productive ecosystems in the world. Its eastern boundary, off the west coast of India, is strongly influenced by the seasonally reversing monsoon winds and currents, and experiences moderate coastal upwelling and high biological production during the summer monsoon (Banse, 1959; Luis and Kawamura, 2004; Habeebrehman et al., 2008; Thomas et al., 2013). The benthic fauna of

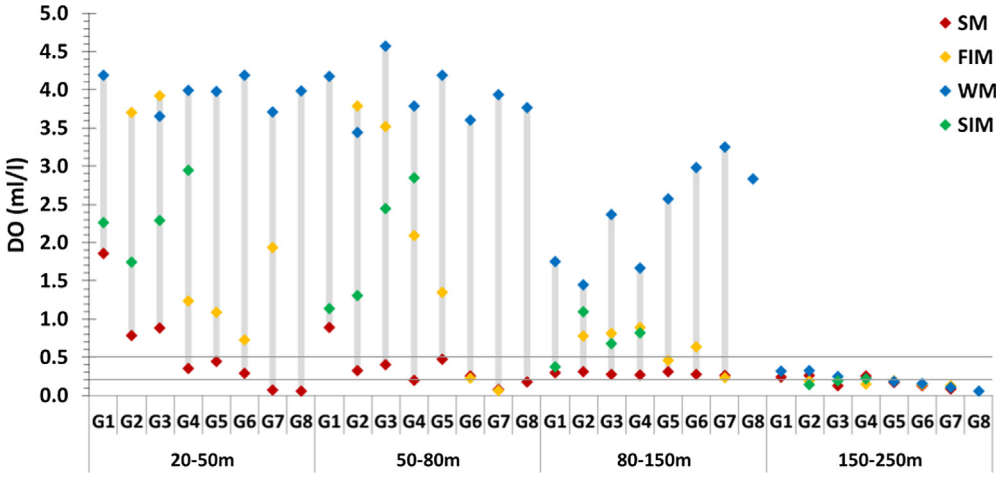

Fig. 11. Scatter plot showing spatial and temporal ranges in bottom water dissolved oxygen (ml/l) in the SEAS shelf.

this region are well studied, particularly macrofaunal polychaetes and meiofaunal nematodes (Jayaraj et al., 2008; Joydas and Damodaran, 2009, 2014; Sajan et al., 2010; Abdul Jaleel et al., 2014, 2015), while little information is available on the epifaunal communities of the region. This paper presents results of the first systematic attempt to understand the distribution of epifauna in the south eastern Arabian Sea (SEAS) continental shelf (~20–250 m). Emphasis is placed on the echinoderms, which were the dominant group (42%), as observed in many parts of the world (Feder et al., 2005; Ruhl, 2007; Bluhm et al., 2009).

Based on extensive and seasonally resolved surveys, covering a sizeable area of the eastern Arabian Sea shelf using multiple gears, the present study revealed spatio-temporal variations in abundance and composition of benthic fauna. Similar patterns are reported for macro infauna of the region (Jayaraj et al., 2008; Joydas and Damodaran, 2009, 2014). Crustaceans and molluscs also formed important components among benthos, and they dominated among epifauna in some areas. Epifaunal abundance decreased with depth and were dominated by molluscs in the inner shelf (20–50 m) and by echinoderms in the mid shelf (50–80 m), while crustaceans dominated in the outer shelf and shelf edge (80–250 m). The abundance of epifauna was highest at ~9°N (G3), owing to the exceptionally high abundance of echinoderms. In general, relative abundance of echinoderms decreased from south to north. Abundance of epifaunal echinoderms was much higher in the winter monsoon (WM) than the summer monsoon (SM), which resulted in the significant variations observed in overall faunal composition. Among infauna, density of echinoderms was lower during SM, and the group was nearly absent in the northern part of the study area (~10°–15°N). A concurrent increase in standing stock of polychaetes (Thomas et al., 2006; Sivadas et al., 2016), and a decline in that of crustaceans is reported in the study area (Abdul Jaleel et al., 2015).

Ambient oceanographic conditions are known to play important roles in structuring marine benthic communities (Rosenberg, 1995; Nordberg et al., 2001; Khan et al., 2010). In the SEAS shelf, salinity and temperature of bottom water exhibited seasonal and spatial variations. Coastal upwelling during the SM, brings cold, high-saline, nutrient rich waters on to the shelf (Banse, 1959; Gupta et al., 2016) which resulted in lower bottom water temperature up to ~150 m. A consistent decrease in bottom water temperature with increasing depth is well reported in the EAS shelf (Jayaraj et al., 2008; Joydas and Damodaran, 2014; Abdul Jaleel et al., 2015). Apart from the coastal upwelling, bottom water salinity was also influenced by intrusion of water masses from the Persian Gulf, Bay of Bengal and equatorial Indian Ocean (Luis and Kawamura, 2004; Prasannakumar et al., 2004). While seasonal variations were noted in both temperature and salinity, the amplitude of variations were relatively low (~5 °C and 0.6, respectively). High salinity is reported along the shelf break of the SEAS margin (Shenoi et al., 2004), without significant seasonal variations (Abdul Jaleel et al., 2014), and similar observations were made in the present study also.

Dissolved oxygen of bottom water is known to be an important structuring factor for benthos in tropical continental margins (Levin, 2003; Levin et al., 2009) and below upwelling areas (Cowie, 2005), including the EAS (Ingole et al., 2010; Hunter et al., 2011; Abdul Jaleel et al., 2014, 2015; Joydas and Damodaran, 2014). Wide variation in bottom water DO was noted between SM & WM. During WM, a bathymetric gradient of decreasing DO with increasing depth was evident, while during SM, much of the study area was under moderate to intense hypoxia (DO < 0.5 ml/l), more noticeable in the north of 10°N (G4-G8). Seasonal hypoxia in the bottom water of the SEAS shelf is previously reported (Abdul Jaleel et al., 2015) and is attributed to the oxygen-poor nature of upwelled water and formation of a low-saline film at the surface which limits ventilation, coupled with high production and subsequent degradation of OM during SM (Banse, 1959; Naqvi et al., 2006; Gupta et al., 2016). The hypoxic conditions disappear along the shelf during FIM with the withdrawal of upwelling. Perennial oxygen-deficiency (< 0.2 ml/l north of 10°N) is noted in bottom water along the shelf edge and is attributed to the southward extension of the Arabian Sea OMZ (Abdul Jaleel et al., 2014).

Availability of suitable substrates and ample food resources also play key role in determining the distribution of benthic fauna (Sanders, 1958; Gray, 1974); and the composition and texture of sediments are of great importance in soft-bottom benthos of the SEAS (Jayaraj et al., 2008; Abdul Jaleel et al., 2014). Benthic taxa are also known to show selectivity with respect to sediment grain size (Ellis et al., 2000; Freeman and Rogers, 2003). Sediment texture in the SEAS shelf showed significant spatial variations, under the influence of hydrodynamic processes. Terrestrial sediment input was found to influence the sediment texture along the inner SEAS shelf (Rao and Wagle, 1997; Jayaraj et al., 2008; Ingole et al., 2010). The northern part of the study area (~11–15°N) receives inputs from several rivers, and in these regions, inner shelf sediments were dominantly silty (median grain size 12.07 ± 2.27 μm). Two major estuaries of the west coast of India, the Cochin Estuary and Ashtamudi Lake, open to the sea at ~9 and 10°N, respectively, and around the estuary mouths, mixture of silt and sand was noted, with minor seasonal variations. A combination of factors are known to act in estuarine systems, including the trapping of coarser sediments within the estuaries and flocculation around the estuary mouths (Rao and Wagle, 1997). Seasonal variations around the estuary mouth may be attributed to the increase in terrestrial discharge during the SM. Further south, terrigeneous sands (median grain size 253.36 ± 90.85 μm in G2) and calcareous sand with hard substrates (median grain size 346.00 ± 206.73 μm in G1) could be observed. The coastal topography south of 9°N caused offshore transport of sediments away from the coast and the low sedimentation rates result in a 'no-clay zone', which favour growth of corals around the Cape (Rao and Wagle, 1997), which contributed biogenic materials such as shells and coral fragments to sediments. Beyond 50 m depth, the texture became progressively sandy throughout the study area, and sediments beyond 150 m were uniformly sandy (median grain size 110–220 μm). Occurrence of sandy sediments at around 50 m depth, as well as presence of relict sands between 100 m and 200 m depths of the SEAS are widely reported (Rao and Wagle, 1997; Jayaraj et al., 2008; Ingole et al., 2010; Abdul Jaleel et al., 2014, 2015).

The SEAS is an eastern boundary upwelling system (EBUS), with seasonally high production during SM (Banse, 1959; Habeebrehman et al., 2008; Thomas et al., 2013; Gupta et al., 2016). The supply of OM to the seafloor is governed by the seasonally fluctuating surface production, while OM settlement is strongly influenced by the dynamics of the water column (Calvert, 1987). During the present study, OM values did not differ significantly between SM & WM, unlike other seasonally varying factors. Rather, highest OM values were noted during FIM (October), immediately following the highly productive SM. The strong SM circulation may hinder OM flux to the bottom during this high productive season (Abdul Jaleel et al., 2015), while the quiescent conditions of the subsequent season (FIM) could favour OM settlement. Following settlement, the retention of OM is strongly influenced by the sediment texture, with finer sediment particles (clay & silt) retaining more OM by sorption, lamination and packing (Keil and Hedges, 1993; Cowie, 2005; Abdul Jaleel et al., 2014).

The distribution of epifauna in the SEAS shelf was found to be influenced by a combination of sedimentary and hydrographic parameters. The sandy sediments between 7° and 9°30′N (G1-G3) harboured good density of echinoderms, most of which are known to prefer sandy sediments (Pomory et al., 1995; Ellis et al., 2000; Ambrose et al., 2001; Freeman and Rogers, 2003) and this resulted in the high epifaunal abundance in the region. Echinoderms are also among the group most sensitive to low-oxygen conditions, and show mortality or avoidance behaviour (Alongi, 1990; Rosenberg et al., 1991; Diaz and Rosenberg, 1995; Ganesh and Raman, 2007; Levin et al., 2009). Under oxygen depleted conditions, epifauna are vulnerable than infauna, and mobile forms more vulnerable than sessile forms (Riedel et al., 2013). In the SEAS, echinoderm abundance (among epifauna and infauna) was

correlated with bottom water DO. The group was nearly absent under intense hypoxic conditions (~9°30′–15°N), but were relatively well represented in this region during the WM. Echinoderms were absent even in the sandy sediments of the shelf edge (~150–250 m), owing to the perennial oxygen depleted conditions. Complete absence of echinoderms among infauna around 200 m depth in the EAS has also been reported by Joydas and Damodaran (2014). These observations suggest that DO levels have a greater role in determining echinoderm distribution in the SEAS, than the availability of suitable substrates. Crustaceans and molluscs are less vulnerable to low-oxygen related stress (Diaz and Rosenberg, 1995), and these groups were capable of withstanding the seasonal shelf hypoxia in the northern grids and established as the dominant taxa among epifauna. Moreover, small decapods (prawns and ghost shrimps) dominated among crustaceans in the north; being detritivores, they are ideally placed to utilize the higher OM within the silty sediments in the northern SEAS. The most hypoxia-tolerant taxon among the benthos are the polychaetes (Diaz and Rosenberg, 1995; Levin, 2003; Abdul Jaleel et al., 2014), and this group dominated among the infauna in the SEAS shelf (Jayaraj et al., 2008; Joydas and Damodaran, 2009, 2014). The taxonomic and functional diversity of this group among SEAS benthos is well studied.

The SEAS shelf is subjected to anthropogenic disturbance in the form of intense bottom trawling, except the trawl-ban period (45–52 days) during the SM (Vivekanandan et al., 2010). Around 4000 bottom trawlers are reported to operate from the Kerala state (7°–12°30′N) alone (Naomi et al., 2011). Several scientific studies have raised serious concerns on the damages to benthic habitats by bottom trawling gears (Kaiser et al., 2006; Queirós et al., 2006; Tillin et al., 2006; Abdul Jaleel et al., 2015). Echinoderms are known to be sensitive to trawling disturbances (Bergman and Hup, 1992), and represent a significant portion of trawl by-catch in the SEAS (Kurup et al., 2003; Bijukumar and Deepthi, 2006). In general, impacts of trawling disturbances are known to depend on the type of trawling gear, intensity of trawling, nature of substrate or habitat and the taxa (Kaiser et al., 2006). In sandy sediments, habitat restoration and faunal recovery is known to take place more rapidly than in 'muddy' sediments after trawl cessation (Dernie et al., 2003; Kaiser et al., 2006). This may be a factor contributing to the dominance of echinoderms (particularly echinoids) in the sandy sediments of the south and their paucity in the relatively silty sediments of the north.

Fast growing and rapidly reproducing faunal groups, most notably polychaetes, are known to quickly recoup after trawling disturbance (Kaiser et al., 2006; Shephard et al., 2010). In the SEAS shelf, recovery in polychaete standing stock is reported within the 45-day trawling ban period (Abdul Jaleel et al., 2015). Being gonochoric and relatively slow-growing organisms, which often attain sexual maturity after 1–3 years (Kasyanov, 2001), echinoderms typically take longer time to recover from trawling disturbances (Sardà et al., 2000; Desprez, 2000). Unlike the polychaetes, recovery of echinoderms were not noted in the SEAS across the trawl-ban period. This could be due to the longer generation time of this group, and the inhibition of larval settlement under the prevailing hypoxic conditions of the SM. This is supported by the occurrence of juvenile (post-settlement stage) echinoderms during late-SM, FIM & early-WM, following withdrawal of hypoxic conditions. Molluscs, which are equally vulnerable to trawling disturbance owing to their shells (Dimitriadis et al., 2014) but are more resilient to low-DO stress also showed signs of recoupment during the trawl-ban (Abdul Jaleel et al., 2015). More realistic assessment of the impact of bottom trawling on echinoderms in the SEAS shelf can be achieved only through comparison with areas free from trawling disturbance (Protected Areas). However, such protected areas have not been designated thus far in the SEAS.

The SEAS shelf is characterised by the availability of a wide variety of habitats for benthic fauna, which may be expected to harbour distinct faunal assemblages. The taxonomic and functional diversity of echinoderm species in the region were analysed to elucidate distribution patterns. A total of 5477 individuals were collected in the present study, representing 55 species. Highest species richness was observed around Cape Comorin, which encompassed a large number of rare species, while only one species was found to occur around Karwar (G8). Between Trivandrum and Mangalore (G2-G7), intermediate richness was encountered, with occurrence of some common species and a few rare ones.

Distribution of echinoderm species were linked with the availability of suitable habitats as well as food resources. Among the irregular echinoids, the burrowing deposit feeding cake urchin, *Sculpsitechinus auritus*, and spatangoid heart urchins *Lovenia elongata* and *Nacospatangus alta*, were restricted to the southern part of the study area, preferring to burrow in sandy sediments (Jones et al., 1987). *Lovenia elongata* was the only echinoderm occurring in the relatively silty inner and mid shelf sediments around G8. Being a deposit feeder that lies completely buried in sediments, this species may be supported by the high OM content in this region. The deposit feeding species *Clypeaster rarispinus* (Echinoidea), *Amphioplus depressus* (Ophiuroidea) and *Leptopentacta imbricata* (Holothuroidea) were among the most widely distributed echinoderms in the study area. They occurred in sandy as well as silty sand sediments across most of the SEAS shelf. These interphase (holothurians), and deposit feeding (clypeasterids and amphiurids) forms possibly take advantage of freshly deposited OM at the sediment surface and the suspended OM at the benthic boundary layer. The consistent occurrence of these species between ~10° and 14°N latitudes, where SM hypoxia is known to be intense (Naqvi et al., 2006), indicates that they were relatively less vulnerable to stress related to oxygen-deficiency.

The Asteroidea found in the study area were chiefly carnivores (*Astropecten* spp. and *Luidia* spp.), as were the brittle stars of family Ophiodermatidae and Ophiuridae. Amongst these taxa, the ophiodermatids were restricted to the Cape region and *Astropecten* spp. were found between 8° and 9°30′N. Dense macrofaunal assemblages are reported in this region (Joydas and Damodaran, 2014), which would form ideal prey for the aforementioned carnivores. Being actively motile, these species are likely to have higher oxygen demand (Ambrose et al., 2001), and therefore occurred in the relatively well-oxygenated southern region. By contrast, the starfish *Luidia hardwicki* and brittle star *Ophiura kinbergi* were widely distributed in the SEAS, occurring in both sandy and silty sediments. Individual of *L. hardwicki* were often collected with one or more arms broken off and in various stages of regeneration. Being among the larger echinoderms occurring in the study area, *L. hardwicki* are most likely to have sustained sub-lethal damage from trawling gear. Large numbers of regenerating individuals are reported among *Luidia* in other intensely trawled areas (Pomory and Lares, 2000), and they are known to have high regeneration capacity (Lawrence, 1991; Lawrence and Vasquez, 1996; Pomory and Lares, 2000). Members of genus *Ophiura* have planktotrophic larvae that can survive up to 10 months in plankton, before settling in suitable habitats (Dahm, 1993). The wide distribution of *O. kinbergi* in the study area may be due to such a reproductive strategy, which enables propagules to avoid hypoxic conditions of the seafloor during SM, and facilitates settlement and development after withdrawal of hypoxia. The Echinoidea of the SEAS also included a few regular sea urchins like *Salmaciella dussumieri* and *Salmacis virgulata*, which were restricted to the sandy inner and mid shelf sediments of the south, having higher DO and less intense hypoxia during SM. Being epifaunal opportunistic grazers, these species may be feeding on the macrofauna, surficial OM or perhaps on organisms encrusting upon hard substrates off the Cape.

Crinoids, which are sessile passive filter feeders, was represented only in the calcareous sandy sediments of the Cape region. The topography of the shoreline around the western side of the Cape ensures little or no sedimentation near the coast (Rao and Wagle, 1997; Luis and Kawamura, 2004), which would hinder the filter feeding activities of the crinoids. The availability of rocks and boulders for attachment around the Cape (Rao and Wagle, 1997) are also ideally suited for the

crinoids. Similarly, filter-feeding brittle stars of family Ophiotrichidae and Ophiocomidae were also restricted to this region. Ophiotrichids position themselves with their arms raised upwards and using tube feet for filtering and often form dense aggregations in areas with strong currents (Warner and Woodley, 1975; Warner, 1979).

Only four species among the brittle stars are known to exhibit conspicuous dimorphism with respect to size and morphology. In all four, the male is smaller and is an epibiont on the female. Of these, two species – *Ophiodaphne scripta* and *Ophiosphaera insignis* were recorded in the present study (G1-G3), the latter being represented by a single female individual. Both these species are reported widely to be epibionts on sea urchins (Kroh and Thuy, 2013; Parameswaran et al., 2013). The brittle stars possibly derive protection among the spines of the echinoids (Kroh and Thuy, 2013) and are presumed to depend on the ciliary currents of the host for nutrition (Parameswaran et al., 2013). The sexual dimorphism in these species may be linked to their epibiotic habit, having evolved to overcome reproductive barrier that arises when the proximity of conspecific individuals is directly dependant on the proximity of host organisms.

Based on the echinoderms species distribution pattern observed in the present study, three major sub-regions (Cape, Trivandrum-Kollam and Kochi-Mangalore) are delineated within the SEAS shelf, with distinct species composition. The coarse sands with biogenic materials, and well oxygenated conditions off the Cape (7°–8°N) harboured highest richness of echinoderms, a majority of which are unique to this sub-region. This sub-region is characterised by heterogeneous habitats, which could support multiple functional niches (Gooday Andrew et al., 2010; Levin et al., 2010; Williams et al., 2010), and all feeding types are well represented here. Intermediate richness is found between Trivandrum and Kollam (8°–9°30′N), with a few characteristic species and a dominance of sand dollars *Clypeaster rarispinus* and *Sculpsitechinus auritus* in the finer sands with relatively high DO. The Kochi and Mangalore sub-region (9°30′-13°30′N) is characterised by the occurrence of only 9 species, most of which are the widely distributed species in the study area (e.g. *Ophiura kinbergi*, *Amphioplus depressus* and *Clypeaster rarispinus*). These were the only species which could withstand the intense hypoxia and trawling in this sub-region and establish relatively stable populations.

The present study provides baseline information on echinoderm abundance, diversity and distribution in a poorly studied tropical continental margin and also gives insights into the major factors influencing them. Echinoderm abundance and richness were determined chiefly by the nature of the substrate and bottom water dissolved oxygen. Only a few species were able to overcome wide seasonal oscillations in bottom DO, as well as the continuous and intense bottom trawling across major parts of the SEAS, owing to their long generation time and a general dearth of opportunistic taxa among echinoderms. Around the Cape, where the stress from seasonal hypoxia and intense bottom trawling eased, exceptionally high echinoderm diversity could be observed. These results indicate that echinoderms, which play key roles in functioning of marine ecosystems, are among the groups facing most significant threats from natural and anthropogenic disturbances.

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