Marine Environmental Research 166 (2021) 105278

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: http://www.elsevier.com/locate/marenvrev

Response of macrozoobenthic communities to summer monsoon upwelling and related hypoxia in the south eastern Arabian Sea shelf

K.U. Abdul Jaleel [a,*], Usha V. Parameswaran [b], Aiswarya Gopal [b], Chippy Khader [b], V. N. Sanjeevan [b], Anil Kumar Vijayan [b], G.V.M. Gupta [b]

[a] CSIR-National Institute of Oceanography, Regional Centre – Kochi, Kerala, 682018, India
[b] Centre for Marine Living Resources & Ecology, Ministry of Earth Sciences, Puthuvype, Kochi, Kerala, 682508, India

ARTICLE INFO

Keywords:
Polychaetes
Summer monsoon
Seasonal oxygen deficiency
Continental shelf
Northern Indian ocean

ABSTRACT

Coastal upwelling in the south eastern Arabian Sea (SEAS) leads to oxygen depletion over the continental shelf during the summer monsoon season (June–September), with latitudinal gradients in intensity. Based on two surveys in the onset (June) and peak (August) phases of the summer monsoon, the present study evaluates the response of macrozoobenthic communities (size >500 μm) to upwelling and consequent hypoxia (dissolved oxygen <0.2 ml/l) in the central sector of the SEAS shelf (10–12°N, 30–200 m). From the onset to the peak monsoon, macrozoobenthic density increased five-fold in the mid-shelf (50 m water depth), and nearly doubled in the outer shelf (100 m water depth) and shelf edge (200 m water depth). This was found to be a direct consequence of recruitment and proliferation of opportunistic polychaetes, particularly the spionid *Paraprionospio pinnata*, which was the single dominant species (52–78%) at all depths during the peak monsoon. With the establishment of the monsoon, the shelf communities (particularly 50–100 m depth sites) are thus transformed from relatively diverse assemblages to dense, single-species dominated ones. The shelf-edge communities (150–200 m depths), which are impacted with the perennial Arabian Sea oxygen minimum zone, and therefore harbour opportunist-dominated communities year-round. It is postulated that larvae of hypoxia-tolerant taxa are transported from the shelf edge by the process of upwelling onto the shelf. The settlement and survival of these larvae are regulated by the nature of shelf sediments and by the prevailing hypoxia. Thus, substantial recruitment of opportunists occurred in the outer and mid-shelf (50–100 m), but not in the inner shelf (30 m), where sedimentation from river discharge hindered settlement and survival of juveniles.

1. Introduction

The south eastern Arabian Sea (SEAS) is an eastern boundary upwelling system, characterized by seasonal upwelling, which exhibits heterogeneity in its forcing mechanisms, initiation and propagation (Banse 1959; Smitha et al., 2008; Gupta et al., 2016). Around the southern tip of India (up to ~9°N), upwelling is a wind-driven process which initiates in March and reaches the surface around May (Smitha et al., 2008). With the onset of the summer monsoon (June), the process gradually extends towards the north (9–15°N), being regulated by longshore wind stress, coastally trapped Kelvin waves, and offshore propagating Rossby waves (McCreary et al., 1993; Banse 1959; Shankar and Shetye 1997; Gupta et al., 2016; Nampoothiri et al., 2020). Upwelling is moderate to intense between 9 and 13°N, and weak north of 13°N (Smitha et al., 2008). Across the SEAS, upwelling is intensified by the southwest (summer) monsoon winds in July/August and weakens towards the end of the monsoon (September) (Banse 1959; Nampoothiri et al., 2020). Upwelling induced nutrient enrichment in the euphotic zone (Sastry and D'Souza 1972) leads to high biological production over the SEAS shelf (Habeebrehman et al., 2008; Jyothibabu et al., 2010; Thomas et al., 2013). Studies along the SEAS reveal spatio-temporal variations in primary (Thomas et al., 2013) and secondary production (Habeebrehman et al., 2008; Jyothibabu et al., 2010) in the pelagic realm, with the progression of the monsoon and upwelling.

The process of upwelling in the SEAS brings cold, high saline, nutrient-rich, oxygen-depleted, sub-surface open-ocean waters onto the continental shelf. As a consequence of intense rainfall and terrestrial runoff, the upwelled waters are capped by a low saline warm water film, which results in strong stratification and prevents the replenishment of dissolved oxygen (DO) in the sub-surface (Naqvi et al., 2006; Rabalais

* Corresponding author.,
E-mail addresses: jaleel@nio.org, jaleelku06@gmail.com (K.U. Abdul Jaleel).

https://doi.org/10.1016/j.marenvres.2021.105278
Received 14 October 2020; Received in revised form 9 February 2021; Accepted 10 February 2021
Available online 15 February 2021
0141-1136/

et al., 2010). Furthermore, enhanced biological production causes high particulate flux to the sub-surface, which results in high biological oxygen demand. Thus, with the establishment of southwest monsoon and upwelling, the SEAS shelf is overlain with oxygen deficient waters (Naqvi et al., 2006; Gupta et al., 2016). A time series study confirmed the occurrence of hypoxic (<0.2 ml/l) waters in the sub-surface at 10°N (off Kochi) and anoxic conditions (~0 ml/l) at 13°N (off Mangalore) during the late summer monsoon (Gupta et al., 2016).

Oxygen depletion in the water column is known to have significant impacts on benthic fauna and their functioning (Diaz and Rosenberg 1995; Vaquer-Sunyer and Duarte 2008; Levin et al., 2009). With depleted oxygen levels, larger benthic taxa typically show avoidance or mortality, while the abundance of smaller, opportunistic taxa increases. Proliferation of opportunists sometimes ends with population crashes (Levin et al., 2009). The responses and tolerance of benthic invertebrates to hypoxia varies widely among taxa (Rosenberg et al., 1991; Diaz and Rosenberg 1995; Gray et al., 2002). Among macrozoobenthos (size >500 μm), the polychaetes are relatively more tolerant, while echinoderms and molluscs are generally most sensitive. The macrozoobenthos along the western Indian shelf are well described in terms of spatial variations in community structure (Joydas and Damodaran 2009, 2014; Musale and Desai 2011; Sivadas et al., 2020). However, information regarding their responses to the annually recurring upwelling events and hypoxia are very limited (Abdul Jaleel et al., 2015; Naidu et al., 2018; Parameswaran et al., 2018).

In general, sediment nature and oxygen availability are considered to be key factors determining distribution of benthic fauna on the SEAS shelf (Jayaraj et al., 2008; Joydas and Damodaran 2014; Parameswaran et al., 2018). Owing to the influence of hydrodynamic conditions and freshwater discharge, surficial sediments on the SEAS shelf show spatial heterogeneity, with little seasonal variation (Parameswaran et al., 2018). While sediments in the south (up to ~9°N) are predominantly sandy, the preponderance of finer sediments (silt and clay) increases towards the north, particularly in the inner shelf (Joydas and Damodaran 2014; Parameswaran et al., 2018). Dissolved oxygen concentration in bottom water shows significant spatial and seasonal variability in the SEAS, and upwelling related hypoxia is also more intense towards the north (Gupta et al., 2016; Parameswaran et al., 2018). In the sandy sediments of the southern SEAS (7–9°N), moderate oxygen depletion during the peak upwelling (August) coincided with recruitment of opportunistic polychaetes, along with a marked decrease in abundance of benthic crustaceans (Abdul Jaleel et al., 2015). Considering the latitudinal variations in sediment texture and intensity of upwelling-related hypoxia along the SEAS shelf, the present study evaluates the response of macrozoobenthic communities to upwelling in the central sector (10–12°N, 30–200 m water depth).

2. Sampling and analysis

Two surveys were carried out on the continental shelf of the central sector of the SEAS (10–12°N), during summer monsoon 2009 – once in June (onset of summer monsoon, OSM) and once in August (peak summer monsoon, PSM), onboard FORV *Sagar Sampada* (FORVSS Cruises 267 and 270). During both surveys, sediment samples and environmental data were collected along 3 transects perpendicular to the coast at 10°N (T1, off Kochi), 11°N (T2, off Calicut) and 12°N (T3, off Kannur). Four stations, at 30 m, 50 m, 100 m and 200 m water depths were covered in each transect (Fig. 1). At all stations, CTD (Sea Bird SBE 911) casts were made to collect temperature, salinity and dissolved oxygen (DO) profiles. Sampling was rendered impossible at the 200 m station off Kannur (T3) during the first collection, owing to bad weather. A modified Smith-McIntyre grab (with sample area 0.2 m^2) was deployed to collect sediment samples in duplicate at each site. A subsample for sediment texture and organic matter analyses was collected from the grab sample. The sediments were then washed through a 500 μm mesh sieve, and the retained material preserved in a buffered

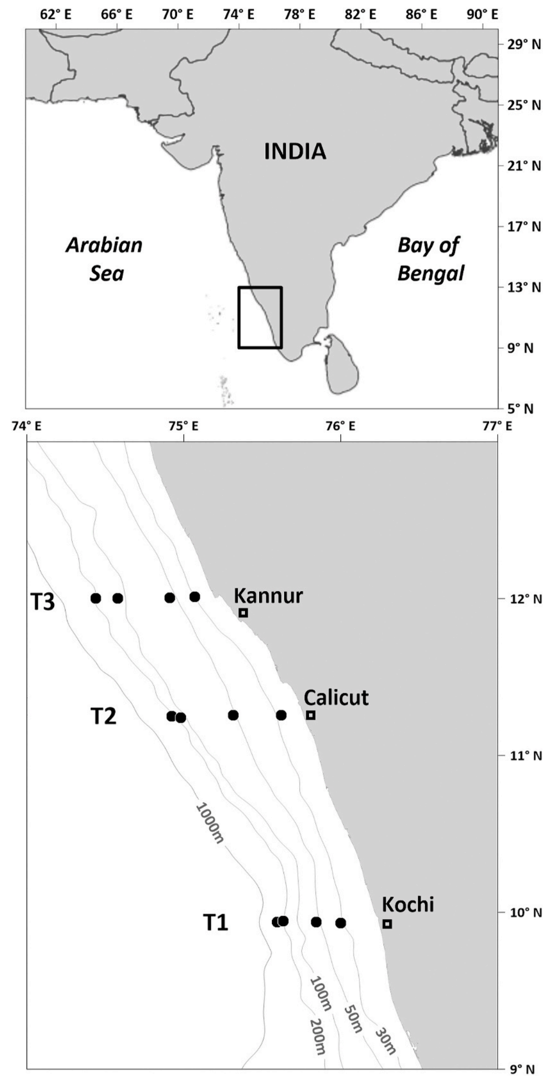

Fig. 1. Map of the study area in the South Eastern Arabian Sea showing the sampling sites in the three transects (T1-T3).

formaldehyde solution containing Rose Bengal stain, after treating with magnesium chloride solution. During the survey, which was carried out between 1st June and 20th August 2009, 23 stations were covered and a total of 40 grab samples were collected, between 10°N and 12°N.

In the shore lab, the sediment samples were again sieved (through a 500 μm mesh) and the macrozoobenthic organisms were isolated and sorted to group level (polychaetes, crustaceans, molluscs and others). They were then enumerated and density was expressed as individuals per square meters (ind.m^{-2}). The wet-weight biomass (gm^{-2}) of these groups in each grab was then measured on a Mettler Toledo (AB204-S) electronic balance. The polychaetes were first sorted to the family level and then further to the genus/species level using identification keys of Fauvel (1953), Day (1967) and Fauchald (1977). Sediment samples for texture and organic matter analysis were oven dried at 55 °C. For granulometry, 10 g of dried samples were accurately weighed, treated with hydrogen peroxide to remove organic matter and dispersed using sodium hexa-metaphosphate. The percentage composition of sand (grain size >63 μm), silt (4–63 μm) and clay (<4 μm) along with median grain size was then elucidated using a CILAS 1180 Particle Size Analyser. Organic carbon content of sediments was estimated by wet oxidation method (El Wakeel and Riley, 1957), converted to organic matter (OM) using the conversion factor (1.8) Trask (1955) and expressed as percentage of sediment dry weight.

Vertical profiles of temperature in the three transects during each survey were plotted using SURFER 15. A Principal Component Analysis (PCA) in PRIMER 6+ (Anderson et al., 2008) was employed to visualize spatio-temporal variations in the environmental parameters. Univariate diversity measures of polychaete species – species richness (S) and Shannon–Weiner diversity ($H' \log_2$) were calculated for each site using PRIMER 6+. Dominance (k-dominance) curves was plotted using PRIMER 6+ to visualize species dominance at each depth in each survey. The PERMANOVA test in PRIMER 6+ was used to test for bathymetric, latitudinal and seasonal variations in macrozoobenthic standing stock, polychaete species composition and diversity indices, as well as hydrographic (temperature, salinity and dissolved oxygen) and sediment (percentage of sand, silt and clay, median grain size and organic matter content) parameters. Square-root transformation and Bray-Curtis similarity were used for biological parameters while log-transformation, normalisation and Euclidean distance were employed for environmental parameters.

3. Results

3.1. Environmental parameters

Temperature of bottom water decreased significantly from the onset (OSM) to peak (PSM) phase of the summer monsoon at all sites, with the establishment of upwelling (Fig. 2, Tables 1 and 2). There was a significant decrease in salinity (Tables 1 and 2) towards the PSM, particularly in the near shore areas (30–50 m). The concentration of bottom water dissolved oxygen (DO) in the shelf region (30, 50 and 100 m depths) was much lower (<0.2 ml/l) during the PSM (Fig. 3, Table 1), when compared to the OSM (range: 0.32–1.2 ml/l). Meanwhile, DO was low (<0.2 ml/l) during both surveys along the shelf edge (200 m water depth). During OSM, the salinity, temperature and DO of bottom water showed a significant decreasing trend with increasing depth (Fig. 3, Tables 1 and 2), while such a trend was eliminated with the establishment of upwelling over the shelf during PSM. During both phases, bottom water DO decreased and salinity increased significantly (Table 2) from south to north.

The texture and organic matter (OM) content of surficial sediments showed significant bathymetric variations, while temporal and latitudinal variations were not significant (Fig. 4, Tables 1 and 2). Sediments in the 30 m contour were silty (75–80%), with moderate clay content (19–23%) and median grain size (mdGS) of 9.95–11.68 μm (mean ± SD: 10.74 ± 0.67 μm). The exception was at T1 (PSM), where texture was sandy (85% sand, 11% silt, mdGS 142.2 μm). In the rest of the study area, sediments were silty sand (49–76% sand, 16–39% silt, 5–10% clay, mdGS 60.62–157.61 μm). The OM content of sediments ranged between 0.54 and 5.38% (Fig. 4, Table 1), with higher values in the silty sediments of the 30 m contour, reflecting the strong correlation of OM with sediment texture (OM and mdGS: $R^2 = 0.734$).

The spatio-temporal variations in environmental parameters were

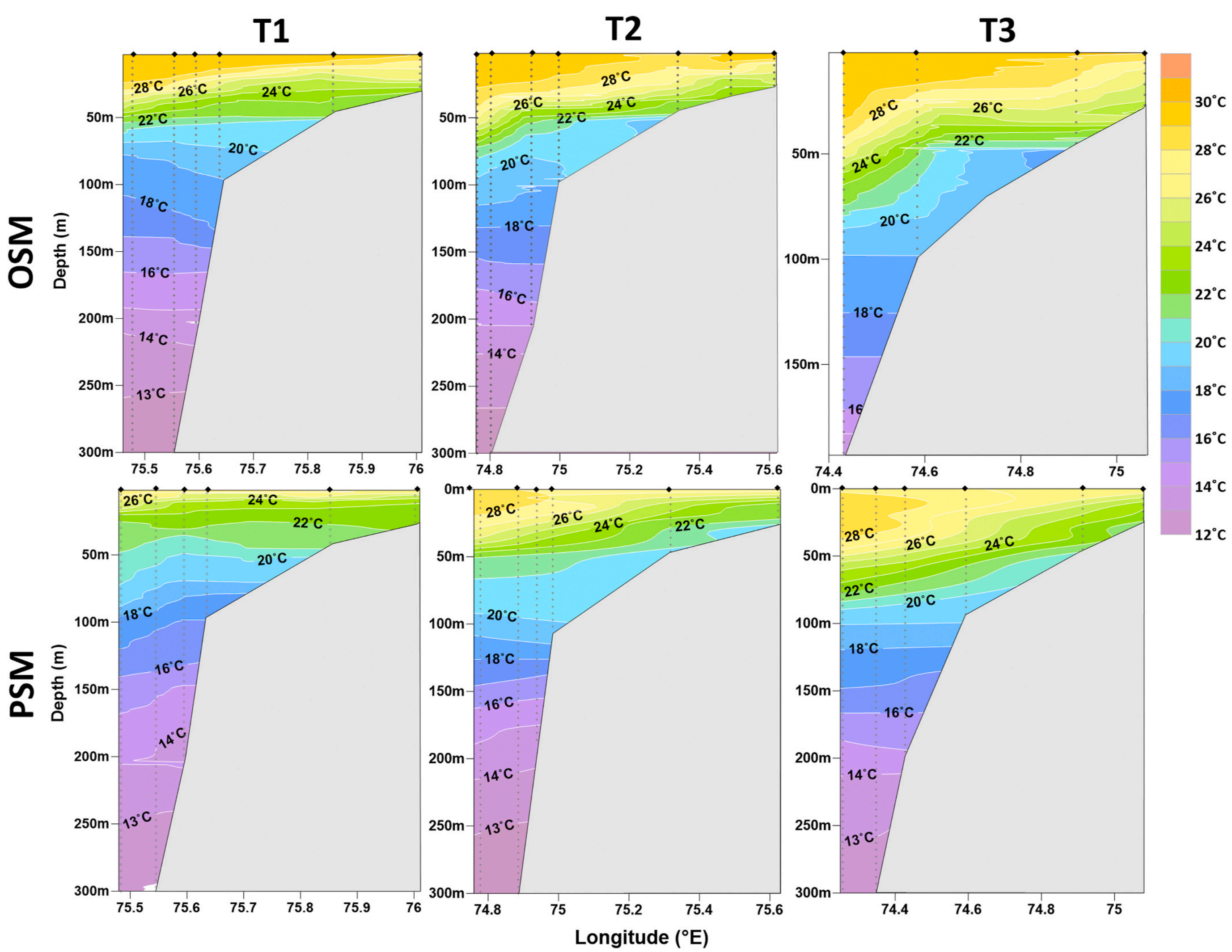

Fig. 2. Vertical profiles of temperature (°C) along the three transects during the onset (OSM) and peak (PSM) phases of the summer monsoon.

Table 1
Environmental parameters (mean ± SD) at each depth stratum during the onset (OSM) and peak (PSM) phases of the summer monsoon.

	30 m		50 m		100 m		200 m	
	OSM	PSM	OSM	PSM	OSM	PSM	OSM	PSM
Temperature (°C)	24.17 ± 0.62	22.31 ± 0.02	22.47 ± 0.62	21.48 ± 0.04	19.11 ± 0.25	18.92 ± 1.44	15.07	14.18 ± 0.74
Salinity	35.49 ± 0.22	34.94 ± 0.06	35.36 ± 0.13	34.93 ± 0.05	35.08 ± 0.09	34.91 ± 0.01	35.07	35.08 ± 0.03
Dissolved Oxygen (ml/l)	1.11 ± 0.16	0.11 ± 0.02	0.83 ± 0.19	0.11 ± 0.03	0.41 ± 0.08	0.26 ± 0.06	0.2	0.15 ± 0.02
Organic Matter (%)	4.41 ± 0.91	3.07 ± 2.28	1.32 ± 0.26	1.07 ± 0.47	1.73 ± 1.04	1.7 ± 0.15	2.02	2.04 ± 0.45
Sand (%)	1.1 ± 0.9	28.7 ± 49.2	62.7 ± 5.3	63.3 ± 13.3	62.7 ± 22.9	56.7 ± 15.1	61.2	57.5 ± 5.1
Silt (%)	77.1 ± 2.9	56.3 ± 38.8	27.9 ± 4.9	28.3 ± 10.4	30.3 ± 22.4	35.9 ± 13.1	32.9	35.4 ± 4.1
Clay (%)	21.8 ± 2.1	15.1 ± 10.4	9.4 ± 0.6	8.4 ± 3.2	6.9 ± 0.9	7.4 ± 2.3	5.9	7.1 ± 1.5
Median grain size (μm)	10.8 ± 0.9	54.5 ± 75.9	111.8 ± 17.5	99.9 ± 46.6	113.1 ± 57.5	75.1 ± 25.8	89.9	78.3 ± 9.9

Table 2
Results of PERMANOVA tests for significant variations in environmental and biological parameters (values in bold indicate statistical significance).

	Monsoon phase		Depth		Latitude	
	Pseudo-F	p	Pseudo-F	p	Pseudo-F	p
Temperature	**15.168**	**0.01**	**192.35**	**0.001**	2.552	0.165
Salinity	**232.14**	**0.001**	**25.607**	**0.002**	**23.526**	**0.003**
Dissolved oxygen	**1716.5**	**0.001**	**238.6**	**0.001**	**41.143**	**0.002**
Sediment texture	0.2887	0.701	**4.887**	**0.035**	1.096	0.398
Sediment grain size	0.038	0.844	**8.184**	**0.026**	0.810	0.481
Organic matter	0.769	0.442	**4.607**	**0.07**	0.649	0.549
Macrozoobenthic density	**4.341**	**0.043**	**38.695**	**0.001**	1.067	0.424
Macrozoobenthic **biomass**	1.176	0.341	**22.968**	**0.001**	1.712	0.25
Polychaete species composition	**2.641**	**0.01**	**4.851**	**0.001**	**1.895**	**0.03**
Polychaete species richness (S)	**4.676**	**0.033**	**47.056**	**0.001**	**3.951**	**0.027**
Polychaete species diversity (H′)	2.206	0.154	**3.172**	**0.028**	2.043	0.133

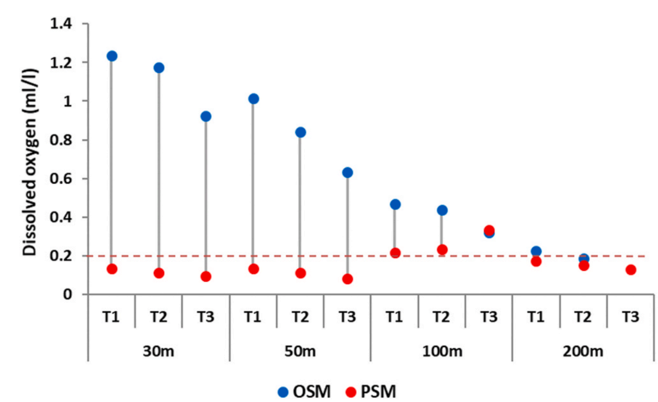

Fig. 3. Bottom water dissolved oxygen (ml/l) at the sampling sites during the onset (OSM) and peak (PSM) phases of the summer monsoon.

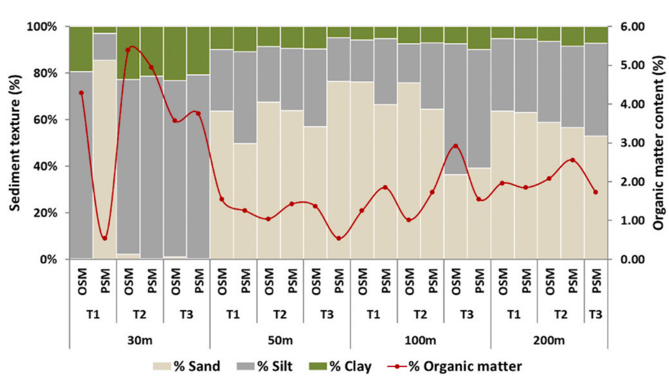

Fig. 4. Sediment texture (% of sand, silt and clay) and organic matter content (%) at the sampling sites during the onset (OSM) and peak (PSM) phases of the summer monsoon.

visualised using a principal component analysis (PCA). The principal components (PCs) 1 and 2 together explained 83.9% of variance among sampling sites. The factors loading strongly in PC1 (Fig. 5, Table 3) were sediment texture, grain size and OM content, which showed bathymetric variations in the study area but did not show any significant temporal variations. The PC1 axis, thus separated the silty sites (30 m depth) with appreciable clay and OM from the relatively sandy sites of the 50–200 m contours. The hydrographic parameters of bottom water, which showed significant temporal variations within the inner shelf (30–50 m contours), loaded strongly on PC2 (Fig. 5, Table 3). This axis, thus, separated the inner shelf sites during the OSM and PSM. During OSM, these sites were characterized by relatively higher temperature, salinity and DO, while during PSM, hydrographic conditions were comparable with

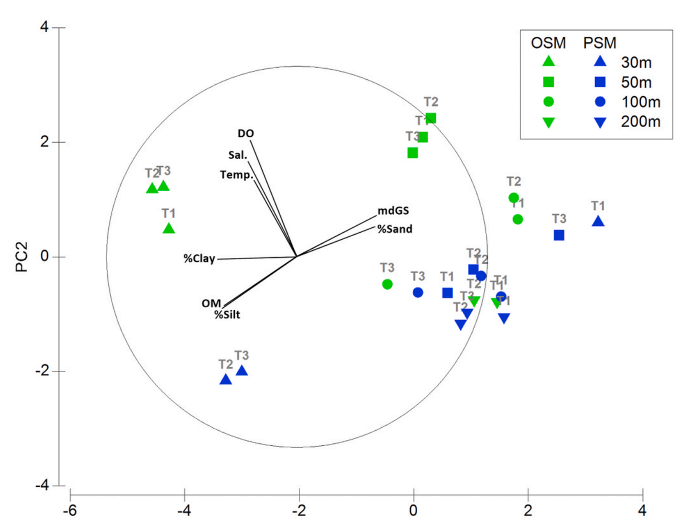

Fig. 5. Principal component analysis (PCA) of environmental parameters in the sampling sites during the onset (OSM) and peak (PSM) phases of the summer monsoon.

Table 3
Results of Principal Component Analysis of environmental factors: eigenvector values.

Vector name	Variable	PC 1	PC 2
Sal.	**Salinity**	−0.259	**0.501**
DO	**Dissolved Oxygen**	−0.245	**0.608**
Temp.	**Temperature**	−0.227	**0.402**
OM	**Organic Matter**	**−0.387**	−0.264
%Sand	**%Sand**	**0.411**	0.159
%Silt	**%Silt**	**−0.394**	−0.272
%Clay	**%Clay**	**−0.418**	−0.013
MdGS	**Median grain size**	**0.416**	0.217

the outer shelf (100 m) and shelf edge (200 m) sites. Such a temporal separation was weak in the outer shelf (100 m) and altogether absent at the shelf edge (200 m).

3.2. Standing stock of macrozoobenthos

During the study, significant temporal variation was noted in the macrozoobenthic density, but not in biomass (Fig. 6, Tables 2 and 4). The density of macrozoobenthos during the OSM ranged between 18 and 1175 ind. m^{-2} (mean ± SD: 716 ± 517 ind. m^{-2}) and biomass ranged between 0.13 and 12.73 g m^{-2} (5.44 ± 5.17 g m^{-2}). During PSM, density ranged between 20 and 10140 ind. m^{-2} (2135 ± 2848 ind. m^{-2}) and biomass between 0.39 and 32.84 g m^{-2} (8.17 ± 9.58 g m^{-2}). Significant bathymetric variations in density and biomass were noted during both phases of the monsoon (Fig. 6). Macrozoobenthic density and biomass

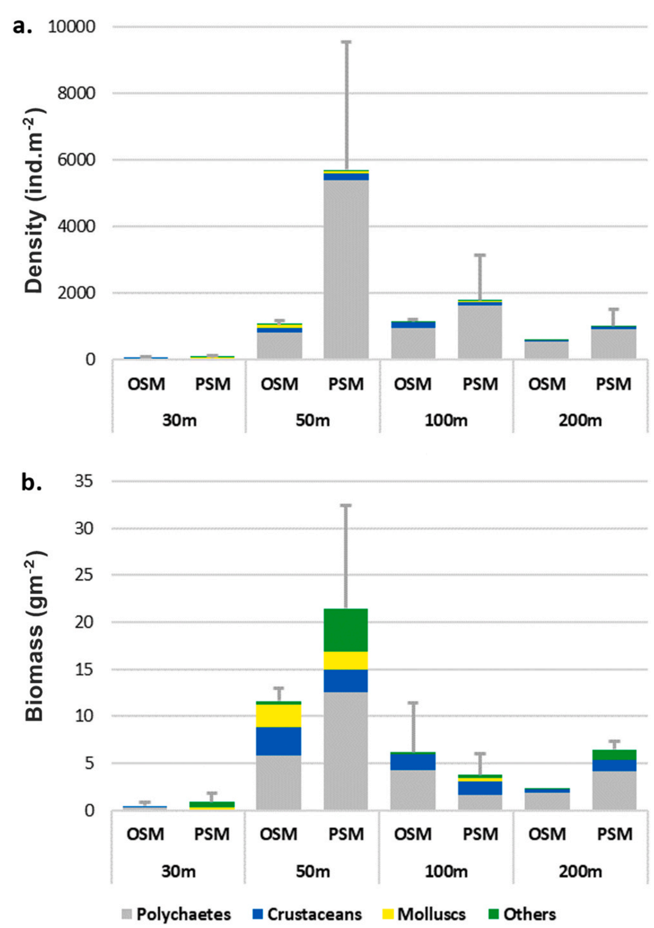

Fig. 6. Mean macrozoobenthic density (a) and biomass (b) at each depth stratum during the onset (OSM) and peak (PSM) phases of the summer monsoon. Error bars represent standard deviation.

was very low in the inner shelf (30 m) sites in both phases (Fig. 6, Table 4). During the OSM, highest density was recorded in the middle and outer shelf (50 m and 100 m), while biomass was significantly higher in the mid-shelf (Fig. 6, Table 4). During the PSM, density and biomass was markedly higher in the mid-shelf (50 m).

Towards the PSM, density of macrozoobenthos increased five folds in the mid-shelf (50 m) and nearly doubled in the outer shelf and shelf edge (100–200 m). Polychaetes constituted the bulk of macrozoobenthos during the study, with their relative abundance increasing from 84% (OSM) to 94% (PSM) (Fig. 7). Concurrently, the relative abundance of crustaceans decreased from 12% (OSM) to 4% (PSM). The marked increase in standing stock during PSM reflected the increase in polychaete standing stock, while a comparable increase was not noted in crustaceans (Table 4). The molluscs, which were altogether absent at 30, 100 and 200 m depth sites during OSM, were represented at all 30 m sites and most 100 m sites during PSM (Fig. 7).

3.3. Species composition of polychaetes

A total of 173 polychaete species belonging to 36 families were recorded during the present study. Significant temporal, bathymetric and latitudinal variations were noted in species richness (S) of polychaetes (Table 2). The temporal variations (between monsoon phases) were more prominent within each depth class (pseudo-F = 4.507, p = 0.007). During both surveys, polychaete species richness was lowest at the 30 m sites, while it was highest in the 50 and 100 m sites (Fig. 8a). Species numbers decreased towards the PSM in the inshore sites (30 m), as well as the outer shelf sites (100 m) of T1 and T2, while it increased at all other sites (Fig. 8a). Along the middle and outer shelf (50 and 100 m), a consistent decrease in species richness was noted from south to north during both surveys (Fig. 8a).

The Shannon-Weiner diversity index (H′) showed significant bathymetric variations (Table 2) and within each depth stratum, temporal variations in H′ were also found to be significant (pseudo-F = 2.410, p = 0.025). During the OSM, highest values were observed at the 50 m and 100 m depths (Fig. 8b). During the PSM, H' decreased significantly in the inner, middle and outer shelf (30–100 m sites) (Fig. 8b). The significant decrease in species diversity during the PSM was a result of high species dominance (Fig. 9).

The aforementioned variations in diversity indices reflected the significant temporal, bathymetric and latitudinal variations in species composition of polychaetes (Table 2). Of the 173 species observed in the present study, 122 species were represented in the OSM and 129 in the PSM. The most species rich families in the study area were the Spionidae, Paraonidae, Cirratulidae, Ampharetidae, Terebellidae, Lumbrineridae and Onuphidae. In general, the inner shelf (30 m) sites were characterized by low species richness and diversity; with only 12 species being represented in the OSM and 5 species in the PSM. At this depth, the community was chiefly represented by *Aglaophamus dibranchis* (21%), *Lumbrineris* spp. (21%), *Prionospio* spp. (18%) and *Paraprionospio pinnata* (11%) during the OSM. During the PSM, the spionids dominated (70%), with *P. pinnata* constituting the bulk (56%).

Moderate to high species richness and diversity of polychaetes was observed in the mid-shelf (50 m) during both phases (Fig. 8). During the OSM, the 50 m sites were characterized by a diverse assemblage of polychaetes, including magelonids (18%), spionids (17%), paraonids (15%), lumbrinerids (8%), pilargids (8%), capitellids (6%) and cirratulids (6%). At the same depth, spionids (87%), particularly *P. pinnata* (78%, mean density 4230 ind./m^2), exhibited very high dominance during the PSM.

Along the outer shelf (100 m), polychaete assemblages were species-rich during the OSM and showed relatively lower diversity during the PSM (Fig. 8). Though spionids dominated in both surveys (OSM: 58%, PSM: 72%), 6 species of *Prionospio* contributed to the family's abundance (52%) and *Paraprionospio pinnata* represented <1% of polychaetes during the OSM. The latter was the single dominant species (52%)

Table 4
Density (ind.m^{-2}) and biomass (gm^{-2}) of macrozoobenthic groups (mean ± SD) at each depth stratum during the onset (OSM) and peak (PSM) phases of the summer monsoon.

	Depths	Survey	Polychaetes	Crustaceans	Molluscs	Others	Total
Density **(ind./m^{-2})**	**30m**	**OSM**	41 ± 24	15 ± 13	0	0	56 ± 36
		PSM	43 ± 63	8 ± 9	6 ± 4	1 ± 1	57 ± 55
	50m	**OSM**	824 ± 170	140 ± 43	80 ± 96	5 ± 9	1049 ± 109
		PSM	5404 ± 3760	189 ± 87	84 ± 96	35 ± 26	5713 ± 3835
	100m	**OSM**	951 ± 92	158 ± 119	0	22 ± 33	1131 ± 74
		PSM	1629 ± 1350	113 ± 24	24 ± 38	3 ± 3	1769 ± 1357
	200m	**OSM**	528	53	0	4	584
		PSM	930 ± 507	68 ± 14	0	3 ± 3	1001 ± 499
Biomass (g/m^{-2})	**30m**	**OSM**	0.36 ± 0.25	0.14 ± 0.15	0	0	0.50 ± 0.40
		PSM	0.18 ± 0.08	0.01 ± 0.01	0.20 ± 0.16	0.58 ± 1.01	0.91 ± 0.88
	50m	**OSM**	5.83 ± 1.88	3.08 ± 3.09	2.34 ± 1.63	0.42 ± 0.72	11.66 ± 1.29
		PSM	12.54 ± 7.57	2.45 ± 3.02	1.93 ± 1.49	4.56 ± 0.49	21.49 ± 10.97
	100m	**OSM**	4.29 ± 4.51	1.69 ± 1.07	0	0.20 ± 0.18	6.18 ± 5.19
		PSM	1.67 ± 0.81	1.44 ± 1.05	0.39 ± 0.57	0.29 ± 0.31	3.789 ± 2.27
	200m	**OSM**	1.94	0.34	0	0.14	2.42
		PSM	4.24 ± 1.45	1.10 ± 0.77	0	1.17 ± 1.92	6.51 ± 0.89

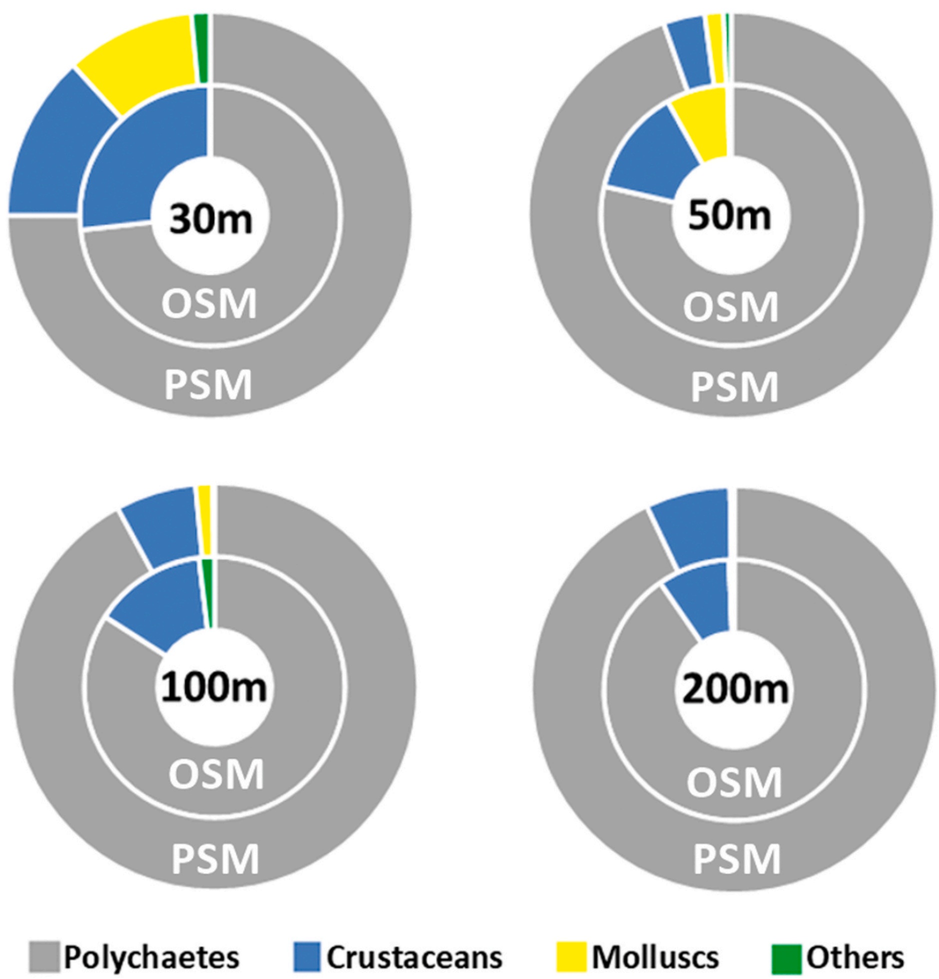

Fig. 7. Relative composition of macrozoobenthic groups at each depth stratum during the onset (OSM) and peak (PSM) phases of the summer monsoon.

during the PSM, followed by *Prionospio* sp.1 (9%). The shelf edge sites (200 m) exhibited relatively lower species richness and diversity than the middle and outer shelf during both phases, and temporal variations in species composition were not observed (Fig. 8). In both phases, the shelf edge communities were characterized by the relatively high abundance of *Prionospio* sp.1 (35%), *Paraonis* sp.1 (22%) and *Cossura* sp.1 (13%).

4. Discussion

Oceanographic processes in the South Eastern Arabian Sea (SEAS) are determined by the seasonally oscillating (summer-winter) monsoon system, which strongly influence its biological characteristics from the basin to meso-scale (Smitha et al., 2008; Habeebrehman et al., 2008; Jyothibabu et al. 2010, 2018; Thomas et al., 2013; Gupta et al., 2016). The summer monsoon (June–September) causes drastic changes in the

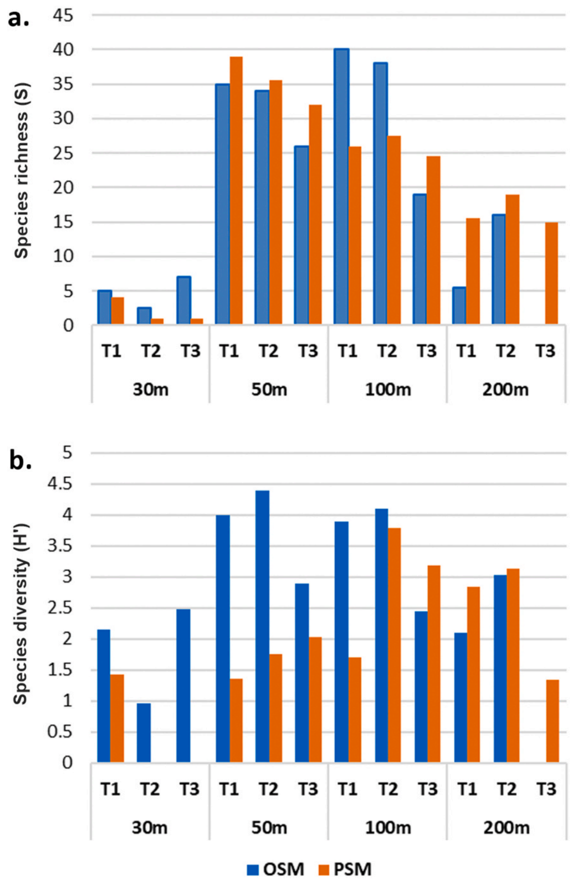

Fig. 8. Polychaete species richness (a) and diversity (b) at the sampling sites during the onset (OSM) and peak (PSM) phases of the summer monsoon.

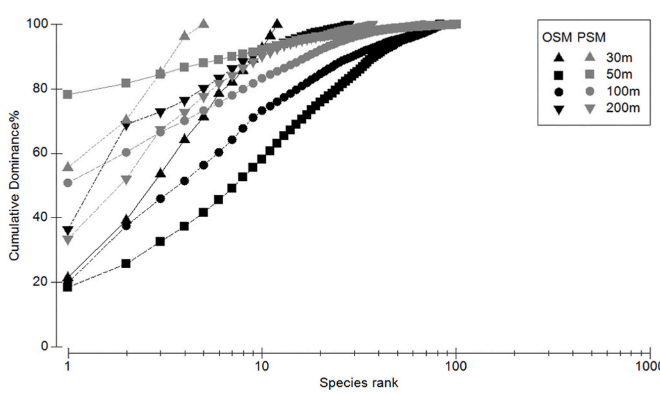

Fig. 9. Cumulative dominance curves of polychaete species at each depth stratum during the onset (OSM) and peak (PSM) phases of the summer monsoon.

physical and chemical characteristics of the water column, which includes reversal of circulation patterns, moderate to intense coastal upwelling as well as oxygen depletion (Gupta et al., 2016). During this season, the west coast of the Indian peninsula receives substantial rainfall, which ultimately drains into the Arabian Sea. The SEAS, thus, receives freshwater, sediments as well as organic load from the Western Ghats and adjacent coastal plains. The influence of coastal upwelling and terrestrial inputs are evident in the hydrographic and sediment characteristics in the present study. Temperature of bottom water recorded a significant drop in the entire study area, from the onset (OSM) to the peak of the summer monsoon (PSM) as a result of coastal upwelling (Habeebrehman et al., 2008, Thomas et al., 2013; Abdul Jaleel et al., 2015; Jacob et al., 2016; Gupta et al., 2016). Despite the coastal upwelling process delivering high-saline waters onto the shelf (Gupta et al., 2016), relatively lower salinity was recorded in the inshore areas of the present study (30–50 m water depth), possibly owing to the heavy terrestrial run-off. These sites were located close to the mouths of major estuaries and rivers (viz. the Cochin Estuary, Chaliyar River, Kadalundi River and Valapattanam River). Concurrent observations in the southern SEAS (7–9° N), where river discharge is significantly lower, recorded little change in bottom water salinity with the progression of the monsoon (Abdul Jaleel et al., 2015).

During the OSM, bottom water DO in the inner and mid shelf (30–50 m water depth) was ~1 ml/l, and with the establishment of shelf hypoxia, the values were <0.2 ml/l at all sites during PSM (mean: 0.11 ± 0.02 ml/l). The oxygen depletion was found to intensify towards the north (<0.1 ml/l at 12°N), in agreement with previous works (Jacob et al., 2016; Gupta et al., 2016; Parameswaran et al., 2018). The SEAS shelf edge is impinged with the perennial Arabian Sea oxygen minimum zone (OMZ) (Joydas and Damodaran 2014; Abdul Jaleel et al., 2014), and during the present study, bottom DO remained ≤0.2 ml/l, with no significant temporal variations.

Near shore sediments in the SEAS are, in general, influenced by terrestrial inputs, without prominent seasonal variations (Rao and Wagle 1997; Jayaraj et al., 2008; Joydas and Damodaran 2009; Abdul Jaleel et al., 2015). The dominance of finer sediments at the 30 m sites (except T1), with high organic matter (OM), showed the influence of river plumes (Chaliyar, Kadalundi and Valapattanam Rivers), which deliver finer sediments (10.75 ± 0.67 μm) to the near shore areas. Seasonal variations in sediment composition are reported around the mouth of the Cochin estuary (T1), which is a large and complex estuarine system with intense anthropogenic activities (e.g., dredging) (Rehitha et al., 2017; Parameswaran et al., 2018). In the present study, the nearshore sediments (30 m) of T1 were silty (80%) in the OSM, while sand dominated in the PSM (85%). Away from riverine and estuarine influences (50–200 m water depth), the surface sediments of the study area were uniformly silty sand with relatively lower OM content.

During the present study, a significant increase in macrofaunal density was observed towards the PSM in the 50, 100 and 200 m depth sites, while such temporal trends were absent in the inner shelf (30 m depth). Other studies in the western Indian shelf have also reported an increase in macrofaunal abundance during the summer monsoon season (Abdul Jaleel et al., 2015; Naidu et al., 2018; Rehitha et al., 2019). The lack of corresponding increase in standing stock in the inner shelf (30 m) is attributed to the high sedimentation associated with terrestrial discharge. The prominent increase in macrofaunal density, particularly in the middle and outer shelf (50–100 m) as well as shelf edge (200 m), was caused by the substantial increase in polychaete abundance which is attributed to the recruitment of certain polychaetes during the highly productive south west monsoon season (Abdul Jaleel et al., 2015). A similar recoupment was not observed in the case of crustaceans; their standing stock was relatively low throughout the study. The hypoxic conditions existing during the PSM, to which crustaceans are more sensitive, may be deterring their reproduction and settlement (Diaz and Rosenberg 1995; Vaquer-Sunyer and Duarte 2008; Levin et al., 2009). In the southern sector of the SEAS (7–9°N), where seasonal hypoxia is less intense, the density of crustaceans was found to increase towards the peak of the monsoon (Abdul Jaleel et al., 2015). Echinoderms, which are more sensitive to hypoxia are reported to be altogether absent in the central SEAS during the peak summer monsoon (Parameswaran et al., 2018). In the present study also, this group was absent towards the PSM. The molluscs, which were nearly absent in the study area during the OSM, showed a marginal recoupment and were collected in low abundance at many sites in the PSM. Being vulnerable to the intense trawling activities in the central SEAS, the recovery of this group can be attributed to the temporary cessation of trawling (annual trawl-ban period) between June and August (Dimitriadis et al., 2014; Abdul Jaleel et al., 2015). The relative resilience of molluscs to oxygen depletion (Diaz and Rosenberg 1995) may also be a factor influencing the increase in their abundance towards the PSM.

In the SEAS, the winter monsoon (November–February) and spring inter-monsoon seasons (March–May) are periods of relatively stable hydrodynamics (Luis and Kawamura, 2004). This supports the establishment of stable macrozoobenthic communities, well suited to thrive in the shelf sediments (Joydas and Damodaran 2009; Naidu et al., 2018). Thus, during the onset of the summer monsoon (OSM), polychaete communities were represented by a diverse assemblage of deposit feeders (spionids, capitellids, ampharetids, paraonids, magelonids, cirratulids and cossurids), along with omnivorous and predatory taxa (lumbrinerids, pilargids and nephtyids), with varying densities (Joydas and Damodaran 2009, 2014; Naidu et al., 2018). While density and diversity were low in the silty inner shelf (30 m) sediments, values were higher in the silty sands of the middle and outer shelf (50–100 m), with a relative dominance of spionids (58%) at 100 m depth sites. With the onset of the summer monsoon upwelling and establishment of hypoxia, communities along the entire shelf (30–100 m) became dominated by spionids (70–87%), especially *Paraprionospio pinnata* (52–78%). Surface deposit feeders, such as spionids, are known to attain dominance in sediments subjected to recurring hypoxia (Rabalais and Baustian, 2020). Among the spionids, *P. pinnata* is well known to proliferate and attain dominance under low-oxygen conditions (Abdul Jaleel et al., 2014; Ingole et al., 2010; Jayaraj et al., 2008; Joydas and Damodaran, 2009; Levin, 2003; Levin et al., 2009; Naidu et al., 2018; Quiroga et al., 2007). The increase in the abundance of spionids was a direct result of recruitment (Abdul Jaleel et al., 2015), as indicated by the prevalence of juveniles in sediments.

The shelf-edge communities, which are under the influence of the perennial Arabian Sea OMZ were typified by a few species of spionids, paraonids and cossurids, with little seasonal variations in species composition (Abdul Jaleel et al., 2014; Joydas and Damodaran 2014). These taxa, most notably *Paraprionospio pinnata*, are r-selected opportunists with specific adaptations like extended branchiae and smaller-sized bodies which make them well suited to thrive under OMZ conditions (Levin, 2003; Abdul Jaleel et al., 2014). Their planktotrophic larvae are capable of surviving in the water column for extended periods, even in oxygen depleted waters (Yokoyama 1990, 1995; Powers et al., 2001). Like early life stages of most benthic invertebrates, these larvae rely on cilia for propulsion, which renders them at the mercy of horizontal currents (Shanks et al., 2003). They may be transported from the outer shelf and shelf edge (100–200 m) along with the upwelled waters, on to the shelf (Shanks et al., 2003). The high planktonic biomass in the water column (Jyothibabu et al., 2010) may support their survival. Aggregation of spionid larvae is reported along upwelling fronts in the SEAS (Abdul Jaleel et al., 2015) and other parts of the world as well (Shanks et al., 2003). At the end of their planktonic phase, these propagules settle in suitable substrates on the continental shelf (Shanks et al., 2003), even in the prevailing hypoxic conditions. Their settlement and survival in the shelf sediments would be facilitated by the concurrence of the annual ban on bottom trawling between June and August (Abdul Jaleel et al., 2015). Thus, towards the peak summer monsoon, significant enrichment of *P. pinnata* populations occurred in the silty sand sediments with freshly settled organic matter in the middle and outer shelf (50–100 m) (Baustian and Rabalais, 2009). Even though organic matter availability was higher in the inner-shelf (30 m), the unconsolidated clayey-silt sediments and high rate of sedimentation due to river discharge, would hinder the settlement and survival of post-larvae in substantial numbers. Notwithstanding, some enhancement in the population of *P. pinnata* still occurred here, as they were the single dominant species even at these sites (>75%). Thus, shelf-edge populations of opportunistic polychaetes play a key role in regulating shelf communities during the summer monsoon by supplying larvae of hypoxia-tolerant taxa.

In the southern part of the SE Arabian Sea (7–9°N), a three to four-fold increase in macrozoobenthic density was observed in the inner and mid-shelf (30–50 m), owing to an increase in density of opportunistic polychaetes (spionids, capitellids, cirratulids, pilargids, amphinomids etc.) during the peak summer monsoon (Abdul Jaleel et al., 2015). In that region, examination of planktonic larvae as well as benthic fauna have shown that the summer monsoon is a peak breeding window for hypoxia-tolerant opportunists, including spionids. However, a single-species dominance by *P. pinnata* did not occur there (7–9°N), as observed in the present study (10–12°N). A major factor causing this distinction is the northward increase in intensity of seasonal hypoxia in the SEAS (Parameswaran et al., 2018). Observations during the same period (August 2009, PSM) recorded an average DO of 0.62 ± 0.65 ml/l in the inner and mid-shelf (30–50 m) of the southern sector (Abdul Jaleel et al., 2015), while the value was much lower (0.11 ± 0.02 ml/l) in the central sector (present study). While the process of upwelling may be delivering larvae of opportunistic taxa onto the SEAS shelf as a whole, their settlement and survival are strongly regulated by latitudinal variation in the intensity of upwelling-induced hypoxia as well as in sediment nature. In the south (7–9°N), where the hypoxia was less intense, successful recruitment of a relatively diverse assemblage of polychaetes occurred in the sandy shelf sediments (<100 m) (Abdul Jaleel et al., 2015). This was true even in the nearshore areas (30 m), which were relatively free from the influence of river discharge and sedimentation, unlike isobathic sites further north (10–12°N) (Rao and Wagle 1997). The intense hypoxia in the central sector led to recruitment of only a few taxa (primarily spionids), among which a single species (*Paraprionospio pinnata*) was overwhelmingly dominant. Here, recruitment success was strongly regulated by the sediment nature. While inter-specific interactions (competition, predation etc.) play a major role in regulating community composition under stable conditions (i.e., OSM), they are overridden by species-specific factors like tolerance and adaptations under adverse conditions like hypoxia. A five-fold increase in macrozoobenthic density occurred in the sandy silt sediments of the mid-shelf (50 m) but no significant variations were seen in the inner shelf, where sedimentation due to riverine and estuarine discharge is high during the monsoon. The present study thus reveals that community level changes during the summer monsoon, as a result of terrestrial discharge, upwelling and related hypoxia are very different in two contiguous geographic regions (southern and central sectors) within the SE Arabian Sea.

5. Conclusions

The present study provides one of the first insights into the changes in macrozoobenthic standing stock and community composition in the south eastern Arabian Sea shelf (off the southwest coast of India, 30–200 m water depth) due to summer monsoon upwelling. Between 10 and 12°N latitudes, significant bathymetric variations were noted in standing stock and community composition, with relatively high polychaete diversity, during the onset of the summer monsoon. With the establishment of upwelling and consequent hypoxia, the standing stock increased significantly in the shelf, except at the 30 m depth. This was a direct result of increase in density of the hypoxia-tolerant spionid polychaetes, particularly *Paraprionospio pinnata*. In the near-shore areas, influence of freshwater discharge during the monsoon and consequent sedimentation prevented the establishment of such adapted taxa, and density remained very low throughout the monsoon season. It is postulated that the outer shelf and shelf edge communities, which are impacted with the perennial Arabian Sea OMZ, play a major role in regulating the aforementioned community changes in the shelf, by supplying larvae of adapted taxa. Within the SE Arabian Sea shelf, the summer monsoon processes including freshwater discharge and upwelling-related hypoxia show significant latitudinal variations, and therefore elicit distinct responses in the macrozoobenthic communities in the southern (7–9°N) and central (10–12°N) sectors. From a small area in the SE Arabian Sea, the present study demonstrates how benthic communities are impacted by gradients in oxygen depletion. It provides an indirect insight into the changes that can be expected with the predicted intensification of oxygen depletion in the world ocean. In this regard, further studies are warranted on the recruitment of opportunistic polychaetes and the supply of larvae to the continental shelf sediments using an integrated approach.

Funding

The work was carried out under the Marine Living Resources Programme (MLRP) funded by the Ministry of Earth Sciences, Government of India.

Author statement

Abdul Jaleel K. U.: Conceptualization, Validation, Formal analysis, Investigation, Data curation, Writing - Original Draft, Writing - Review & Editing, Supervision; **Usha V. Parameswaran:** Formal analysis, Investigation, Writing - Original Draft, Writing - Review & Editing, Visualization; **Aiswarya Gopal:** Formal analysis, Investigation, Writing - Original Draft, Writing - Review & Editing; **Chippy Khader:** Formal analysis, Investigation; **Sanjeevan V. N.:** Conceptualization, Project administration; **Anil Kumar Vijayan:** Project administration, Writing - Review & Editing; **G. V. M. Gupta:** Project administration, Writing - Review & Editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors thank the current and former Directors of the Centre for Marine Living Resources and Ecology, Kochi for their support and encouragement. AJKU acknowledges the support of the Director, CSIR, National Institute of Oceanography and Scientist-in-Charge of CSIR-NIO Regional Centre, Kochi. The support of scientists, as well as research and support staff at CMLRE and on-board FORV *Sagar Sampada* is acknowledged with gratitude. Sediment texture analysis was carried out at the National Centre for Earth Science Studies (NCESS), Ministry of Earth Sciences. This is NIO contribution no. 6683 and CMLRE contribution no. 133.

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