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Surface mesozooplankton assemblages in a tropical coastal upwelling ecosystem: Southeastern Arabian Sea

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ABSTRACT

The spatio-temporal variation of mesozooplankton assemblages and the relative environmental variables were assessed in a coastal upwelling system. Remarkable seasonal variations were found in the mesozooplankton community structure and Chl-*a* concentration due to the seasonal shift in the environmental variables. Copepods were found to be the dominant group during the winter monsoon (WM) and spring inter monsoon (SIM) seasons whereas, cladocerans (*Evadne tergestina* and *Penilia avirostris*) were dominant during the summer monsoon (SM) which may be attributed to the availability of preferential food and favorable environmental conditions (viz., temperature and salinity etc.). Multivariate statistical analysis revealed that the distribution and their possible spatio-temporal pattern of dominant copepods (*Acrocalanus gibber, Acartia danae*, *Nanocalanus minor* and *Oncaea venusta*), siphonophores (*Chelophyes appendiculata* and *Diphyes chamissonis*) and pelagic tunicates (*Doliolida* sp.) synchronized with their specific food habits and adaptive mechanism. The present findings emphasize the significance of the trophic relationship between Chl-*a* concentration and mesozooplankton abundance in the coastal waters of Kochi, southeastern Arabian Sea.

1. Introduction

The continental shelf ecosystems are the transitional zones between the land and open ocean and receive a significant amount of anthropogenic runoff from the rivers (Rabalais et al., 1996). Further, the biogeochemistry in these shelves is mainly influenced by the physical process like coastal upwelling, oceanic currents (Chavez and Messié, 2009) ultimately affecting the plankton community structure and their function (Jyothibabu et al., 2010). The community structure of mesozooplankton in the coastal waters is influenced by the riverine influx and coastal upwelling processes. Thus, studies on mesozooplankton community structure and abundance in these environments has received considerable attention by several researchers from all over the world due to their importance in grazing pressure on phytoplankton, carbon and nutrient cycling and food web dynamics of higher trophic levels (Kuipers et al., 1993; Bode et al., 1998; Wiafe et al., 2008; Rakhesh et al., 2008; Kusum et al., 2014). The mesozooplankton distribution in the coastal waters is highly asymmetric (Rakhesh et al., 2008) due to the existence of complex biogeochemical processes in the upwelling zones. The knowledge of the abundance and composition of mesozooplankton and the relationship with the environmental parameters is essential for understanding of the ecological processes of a particular region (Sousa et al., 2008). Several studies have been reported from the temperate waters on the zooplankton dynamics with the influence of upwelling (Foster and Battaerd, 1985; Bradford-Grieve et al., 1993; Vargas and González, 2004), whereas such studies are fragmented in case of the tropical environments (Boyd and Smith, 1983; Hitchcock et al., 2002; Rakhesh et al., 2008). The dynamic process of coastal upwelling exhibit wide variation in the environmental and biological variables. In the present study, an attempt was made to study the role of upwelling on mesozooplankton biomass and abundance along the Kochi coast by calculating the upwelling index (Gonzalez-Nuevo et al., 2014) and the spatio-temporal variation of the environmental variables.

The coastal waters of Kochi, southeastern Arabian Sea are mainly influenced by the West Indian Coastal Current (WICC) during the monsoon and the East Indian Coastal Current (EICC) during the post-monsoon (Prasannakumar et al., 2004). Moreover, a significant runoff from the two major inlets of the Kochi backwaters during the summer monsoon (SM) influences the biogeochemistry of the coastal waters of Kochi, southeastern Arabian Sea. Both coastal upwelling and estuarine runoff, make the shelf waters of Kochi highly productive (Gupta et al.,

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2016) during the Nair et al. (1999) observed the signatures of nutrient enriched shelf waters and higher biological production during the winter monsoon (WM) to be persistent until the arrival of spring inter monsoon (SIM) for the shelf waters of the Arabian Sea. These oceanographic features play a vital role in the planktonic standing stock which influences the fishery production of this region (Manjusha et al., 2013).

Numerous studies have reported on the distribution and composition of zooplankton for the larger domain along the open and coastal waters of southeastern Arabian Sea (Nair et al., 1978; Madhupratap et al., 1996; Madhu et al., 2007; Jyothibabu et al., 2008, 2010; Habeebrehman et al., 2008; Devi et al., 2010; Kusum et al., 2014; Sooria et al., 2015; Vineetha et al., 2015; Jagadeesan et al., 2017). These studies focused mainly on the different aspects of zooplankton like grazing, secondary production during a particular season, microzooplankton ecology and most of the studies were mainly for the Kochi estuarine region pertaining to tidal aspects. Thus, the present study examined seasonal and upwelling induced changes on physical and chemical parameters and their influence on spatio-temporal changes in mesozooplankton distribution and community structure in the coastal waters of Kochi, southeastern Arabian Sea.

2. Materials and methods

The study was conducted along the coastal waters of Kochi, southeastern Arabian Sea using the research vessels *Sagar Manjusha* and *Sagar Purvi*. Seasonal sampling was carried out during the winter monsoon (WM – January), spring inter monsoon (SIM – April) and summer monsoon (SM – August) of 2015. Five transects orthogonal to the coast with 25 locations within the 10–50 m isobaths along 70 km stretch off Kochi, southeastern Arabian Sea were selected as sampling locations (Fig. 1).

Surface (~0.5 m) water samples were collected using Niskin sampler for the estimation of dissolved oxygen (DO), suspended particulate matter (SPM), nutrients and chlorophyll-a (Chl-*a*). Salinity and temperature was measured by deploying the Seabird CTD. DO was measured using the modified Winkler's method (Carrit and Carpenter, 1966). The water samples collected for dissolved nutrient analysis (except ammonia) were filtered through GF/F filter paper for removing the particulate matter and the filtrate was frozen at −20 °C until the analysis. Water samples were collected separately in 100 ml Nalgene bottles and frozen at −20 °C for the analysis of ammonia. For SPM, a known quantity of water sample was filtered through pre-weighted 0.22 µm Millipore polycarbonate membrane filter papers dried at 60 °C for 12hrs and reweighed. The difference in the two weights was considered as SPM (mg L^{-1}) (Kanuri et al., 2017). All the nutrients (i.e., ammonia, nitrite, nitrate, phosphate and silicate) were analyzed following standard spectrophotometric procedures (Grasshoff et al., 1999). For Chl-*a* analysis, 1 L of water sample was filtered through GF/F filter with a gentle vacuum (of ≤ 80 mm Hg) and then the filter was wrapped with an aluminum foil and frozen until analysis. Chl-*a* in the filter was extracted with 90% acetone at 4 °C in the dark for 24 h and analyzed spectrofluorometrically (Parson et al., 1984).

Mesozooplankton samples were collected by horizontally towing a zooplankton net (mesh size: 200 µm and mouth diameter: 75 cm) for approximately 10 min equipped with a flow meter to register the volume of water filtered. To avoid the large-scale variation in mesozooplankton diel vertical migration, all the samples were collected from morning 8.00 a.m. to early evening 4.00 p.m. Totally, 75 mesozooplankton samples were analyzed in this study. The collected samples were preserved with 5% buffered formalin. The preserved samples were used for the analysis of mesozooplankton biomass and identification. Mesozooplankton biomass was measured by volume displacement method described by Postel et al. (2000). The taxonomic composition of the samples was analyzed to the lowest possible taxa following identification manuals by Kasturirangan (1963) and Conway et al. (2003). The abundance was expressed as number of individuals per cubic meter (ind m^{-3}).

In order to study the role of upwelling on the distribution of

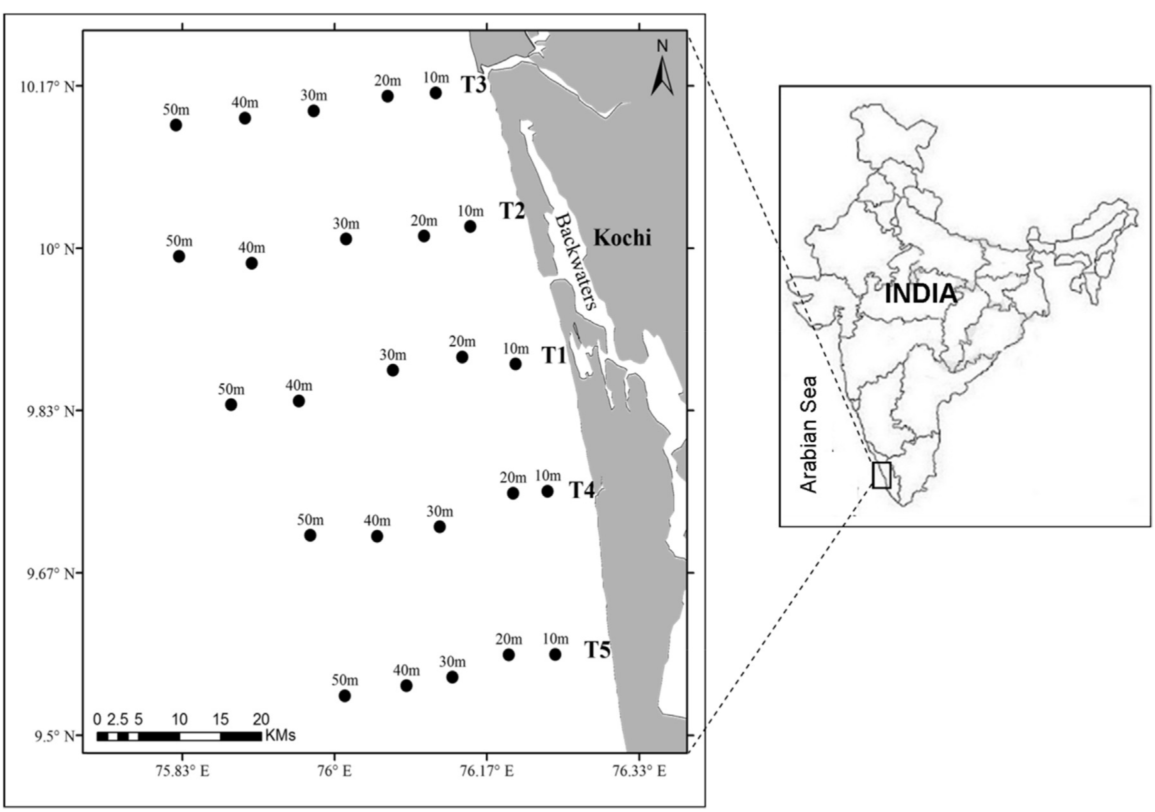

Fig. 1. Geographical map showing the sampling locations in the coastal waters of Kochi, southeastern Arabian Sea.

environmental variables and mesozooplankton biomass and abundance, upwelling index was calculated for the three seasons. The index was calculated by following the procedure of Gonzalez-Nuevo et al. (2014). The wind data required for the calculation of index was obtained from automatic weather station (AWS) installed on ships and on land at Kochi coast during 2014–2015. To understand the relationship between environmental and biological variables the Pearson correlation analysis was done. Diversity indices (viz., Shannon Weiner diversity index (H′ $\log_2$) and Simpson species richness (1-D)) were calculated for all the seasons and cluster analysis (CA), multi-dimensional scaling analysis (MDS) and similarity percentages analysis (SIMPER) was performed using the statistical software package PRIMER 6.0. To avoid extreme anomaly of mesozooplankton species data, the data was normalized using log (X + 1) transformation for cluster and MDS analysis. Canonical correspondence analysis (CCA) was performed to identify the influence of environmental variables on dominant mesozooplankton distribution by using the statistical program PAST v. 3.20.

3. Results and discussion

3.1. Spatio-temporal distribution of physical and chemical variables

All the physical and chemical variables showed distinct patterns during the different seasons of the study period. SST was found to be highest (31.25 ± 0.09 °C) during the SIM and lowest (26.02 ± 0.14 °C) during the SM (Table 1; Fig. 1). The SST of offshore waters was found to be lower than the near coastal waters except during the SM which might be due to the influence of freshwater discharge from the Kochi backwaters during the SM. The lower SST in the offshore waters during the SM when compared with the other seasons is due to the upwelled waters (Prasannakumar et al., 2004). During the SM season, the upwelling index was positive with a value of 2.2 which is a characteristic of upwelling signature, whereas for the WM and SIM the index was negative with values of −0.08 and −1.10 respectively indicating downwelling signature (Table 1).

The higher concentrations of nutrients and biological parameters and lower SST during the SM season may be attributed to both upwelling phenomena and also to land run off associated with river discharge. The surface salinity varied from 33.32 to 34.82 with an annual average of 33.88 ± 0.03. The mean surface salinity was found to be highest during the SM when compared with the other seasons (Table 1). The DO concentrations did not show any significant seasonal variations. The highest (256 μmol L^{-1}) and lowest (159 μmol L^{-1}) concentrations of DO were found during the SM. The mean SPM concentration was found to be higher (12.7 ± 0.5 mg L^{-1}) during the SM and lowest (9.8 ± 0.3 mg L^{-1}) during the WM. Generally, dissolved nutrients were found to be higher during the SM followed by the WM and SIM. The dissolved inorganic nitrogen (DIN) concentrations varied between 0.79 and 8.02 μmol L^{-1} with an average of 3.1 ± 0.22 μmol L^{-1}. Rao et al. (2017) reported nitrate as the dominant form among the DIN species for the coastal waters of southwest coast of India. Usually during the WM algal blooms crash leading to increased levels of ammonia. *Trichodesmium* blooms are common during the WM and can produce ammonium through the process of decomposition and nitrogen fixation (Chang et al., 2000). Similarly, high phosphate and silicate concentrations were observed during the SM followed by the SIM and WM (Table 1). The higher concentrations of nutrients during the SIM and SM might be due to the initiation of upwelling during the SIM at the shelf waters and its intensification during the SM (Gupta et al., 2016). A strong seasonal variability was exhibited in the distribution of Chl-*a* among the seasons. The highest (6.26 mg m^{-3}) and lowest (0.08 mg m^{-3}) Chl-*a* concentrations were found during the SM and WM respectively (Fig. 2). The seasonal variation of the environmental variables like salinity (r = 0.6; $p < 0.0001$), SiO_4 (r = 0.5; $p < 0.0001$), total nitrogen (r = 0.7; $p < 0.0001$) positively influenced the Chl-*a* concentration whereas temperature showed negative relation (r = −0.7; $p < 0.0001$) with Chl-*a* concentration. Nutrient enrichment during the upwelling season (SM season) was favorable for the phytoplankton production. The observed trends of Chl-*a* distribution were in accordance with the results reported by several researchers over the last five decades (Banse, 1968; Gupta et al., 2016; Kumar et al., 2018).

Table 1
Seasonal variation of environmental and biological variables in the coastal waters of Kochi, southeastern Arabian Sea.

	WM	SIM	SM	Annual
Temperature (°C)	28.5–29.73 (28.91 ± 0.06)	30.57–32.37 (31.25 ± 0.09)	24.21–26.98 (26.02 ± 0.14)	24.21–32.37 (28.73 ± 0.26)
Salinity	33.32–33.96 (33.64 ± 0.03)	33.46–34.31 (33.89 ± 0.05)	33.64–34.82 (34.11 ± 0.06)	33.32–34.82 (33.88 ± 0.03)
DO (μmol L^{-1})	184.43–206.6 (198.22 ± 1.03)	199.12–209.92 (204.12 ± 0.67)	159.56–256 (206.54 ± 5.19)	159.56–256 (202.91 ± 1.78)
SPM (mg L^{-1})	7–13 (9.8 ± 0.34)	6.5–15 (11.16 ± 0.35)	10–19 (12.74 ± 0.45)	6.5–19 (11.23 ± 0.26)
NH_4 (μmol L^{-1})	0.06–2.4 (1.32 ± 0.13)	0.04–1.45 (0.47 ± 0.06)	0.4–5.18 (2.38 ± 0.23)	0.04–5.18 (1.39 ± 0.13)
NO_2 (μmol L^{-1})	0.01–0.25 (0.07 ± 0.01)	0.01–0.56 (0.15 ± 0.03)	0.1–0.96 (0.35 ± 0.05)	0.01–0.96 (0.19 ± 0.02)
NO_3 (μmol L^{-1})	0.17–1.76 (0.76 ± 0.09)	0.65–3.48 (1.47 ± 0.14)	1.2–5.81 (2.89 ± 0.37)	0.17–5.81 (1.71 ± 0.17)
DIN (μmol L^{-1})	0.79–3.13 (2.09 ± 0.14)	0.88–4.16 (1.94 ± 0.16)	2.69–8.02 (5.27 ± 0.35)	0.79–8.02 (3.1 ± 0.22)
PO_4 (μmol L^{-1})	0.08–0.59 (0.28 ± 0.03)	0.08–1.84 (0.78 ± 0.11)	0.53–1.86 (0.92 ± 0.07)	0.08–1.86 (0.66 ± 0.06)
SiO_4 (μmol L^{-1})	0.84–6.89 (2.89 ± 0.33)	0.24–4.44 (2.09 ± 0.24)	1.89–12.74 (6.89 ± 0.77)	0.24–12.74 (3.95 ± 0.38)
Chl-*a* (mg m^{-3})	0.08–0.96 (0.22 ± 0.04)	0.09–0.6 (0.31 ± 0.03)	1.06–6.26 (4.16 ± 0.35)	0.08–6.26 (1.56 ± 0.24)
Mesozooplankton Abundance (ind m^{-3})	56–1195 (347 ± 54)	139–1319 (586 ± 76)	321–4480 (1610 ± 260)	56–4480 (848 ± 111)
Mesozooplankton biomass (ml m^{-3})	0.05–0.33 (0.16 ± 0.01)	0.01–0.16 (0.08 ± 0.01)	0.03–1.14 (0.27 ± 0.06)	0.01–1.14 (0.17 ± 0.02)
Upwelling index	−0.08	−1.10	2.2	−0.08 to 2.2

* WM: Winter Monsoon; SIM: Spring Inter Monsoon; SM: Summer Monsoon. Values in the open and parentheses represent the minimum - maximum and mean values ± standard error respectively.

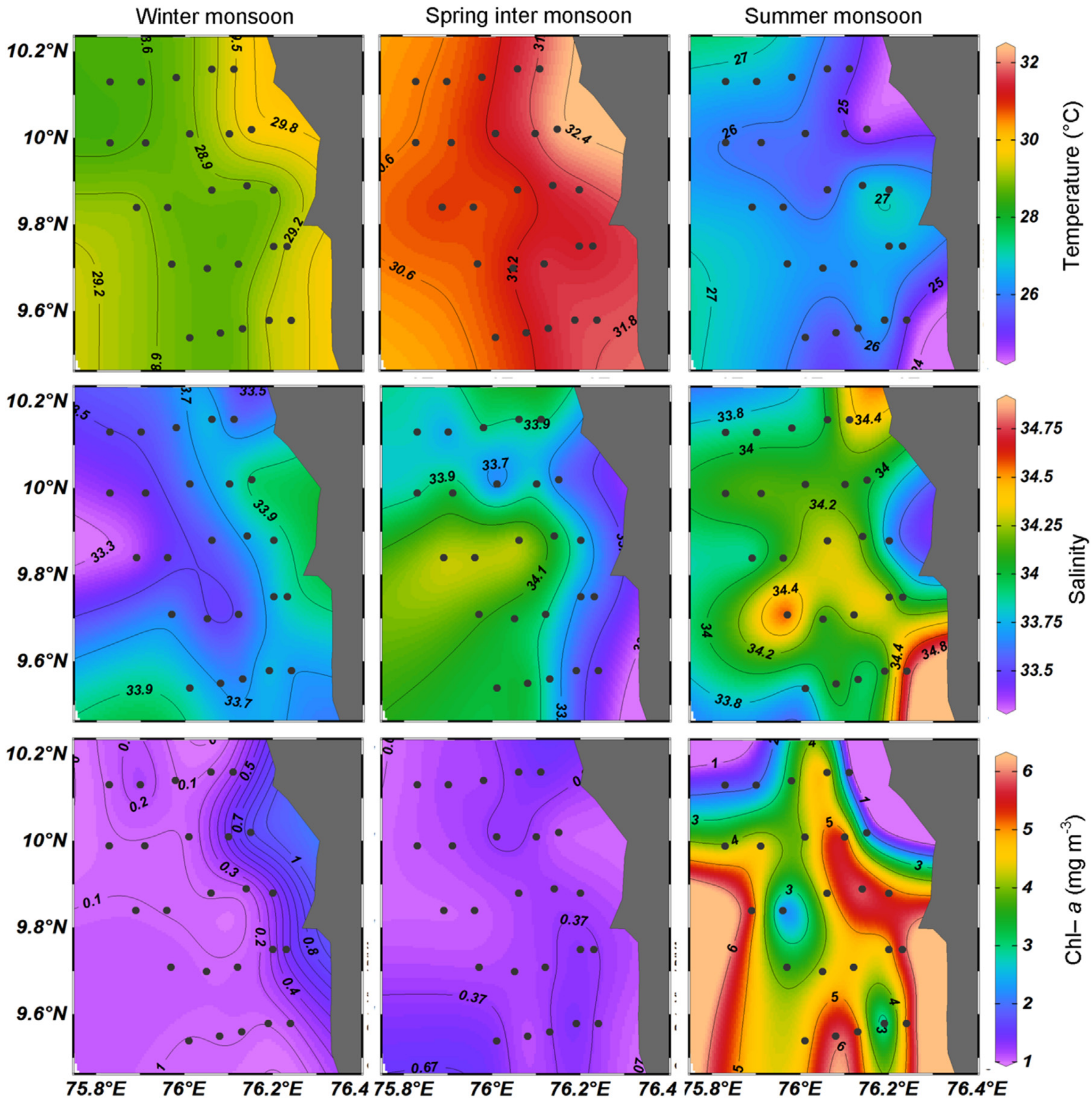

Fig. 2. Spatio-temporal variability of sea surface temperature, salinity and Chl-*a* in the coastal waters of Kochi, southeastern Arabian Sea.

3.2. Distribution of mesozooplankton biomass, abundance and faunal composition

The mesozooplankton biomass varied from 0.01 to 1.14 ml m^{-3} during the study period. The mean biomass was found to be highest during the SM (0.27 ± 0.06 ml m^{-3}) and lowest during the SIM (0.08 ± 0.01 ml m^{-3}) (Table 1; Fig. 3). The mesozooplankton abundance varied from 57 to 4480 ind m^{-3} (Table 1; Fig. 3) and the mean was found to be highest during the SM (1610 ± 260 ind m^{-3}) followed by the SIM (586 ± 76 ind m^{-3}) and WM (347 ± 54 ind m^{-3}). Generally, spatial distribution of mesozooplankton was higher in near coastal region (10–20 m) than the deeper coastal waters (30–50 m). However, such a variation was not seen during the SM (Fig. 3). The high abundance and low biomass during the SIM is due to the presence of a large number of small sized mesozooplankton. The observed trends in seasonal mesozooplankton abundance was in accordance with the earlier reported values for the Arabian Sea (Devi et al., 2010). The seasonal variation of mesozooplankton abundance showed significant relationship with Chl-*a* concentration (r = 0.51; $p < 0.0001$) and similar relationship was observed in a previous study in the Arabian Sea (Madhupratap et al., 2001).

The diversity indices showed distinct variation between the seasons. The Simpson index (0.86 ± 0.01) and Shannon Weiner index (2.48 ± 0.07) were relatively high during the WM as compared to the SIM (0.84 ± 0.02 and 2.38 ± 0.07) and SM (0.67 ± 0.05 and 1.87 ± 0.14). The diversity was higher in the near shore stations (10 and 20 m) except for the SM (Fig. 3). The diversity and richness during the WM showed an inverse relation to abundance and Chl-*a* concentration. The higher diversity during the WM could be due to the stable environmental conditions which are prevalent during the WM leading to succession of diversified plankton community. Further, the swarming of herbivorous cladocerans leads to the decline of some of the planktivorous organisms resulting in lower diversity and higher biomass during the SM (Abrantes et al., 2006; D'Costa and Pai, 2015). The influence of coastal upwelling on the ecology of mesozooplankton through higher production and lesser diversity was reflected during the SM. Similar findings of less diversified communities in upwelling regions have been characterized in other regions (Wiafe et al., 2008).

A total of 88 distinct taxa belonging to 16 groups were recorded during the study period (Table 2). The faunal composition of mesozooplankton varied markedly between the seasons. The maximum number of taxa were recorded during the WM (70) followed by SIM

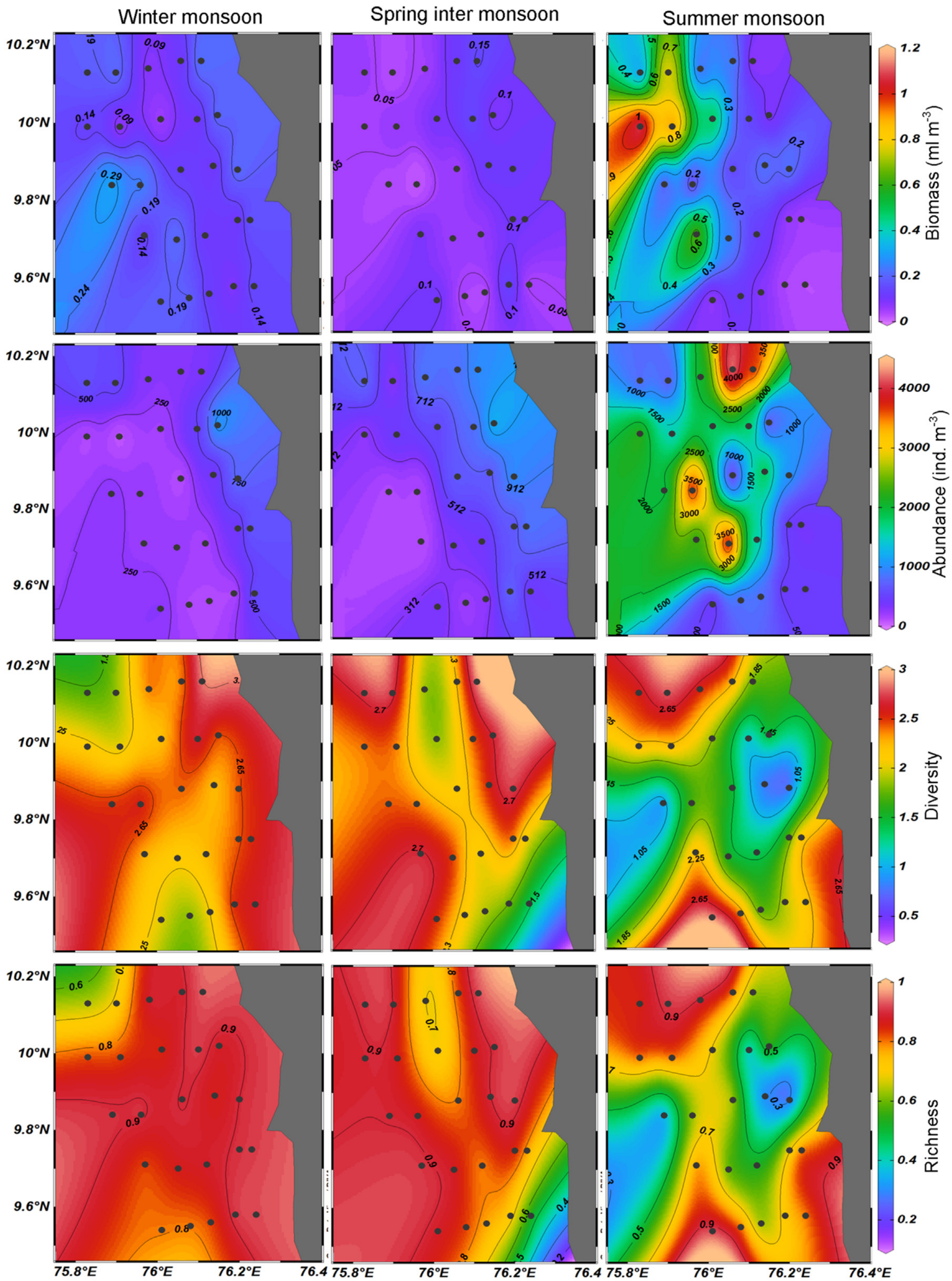

Fig. 3. Spatio-temporal variability of mesozooplankton biomass (ml m^{-3}), abundance (ind. m^{-3}), diversity and richness in the coastal waters of Kochi, southeastern Arabian Sea.

(57) and SM (56). A significant shift was observed between the major taxonomical groups with seasons, i.e., copepods (72%) followed by crustacean larvae (7.11%), chaetognaths (4.49%) and cladocerans (2.96%) were found to be the dominant groups among the total taxonomical composition during the WM. A gradual increase in the percentage of cladocerans with the maximum during the SM (50%) was observed, while there was a significant decline in copepods percentage from WM to SM (29%) (Fig. 4). However, such a phenomenon was not observed for the abundance of copepods, it was high during the SM (av. 466 ± 95 ind. m^{-3}) followed by SIM (369 ± 62 ind m^{-3}) and WM (266 ± 43 ind m^{-3}). The percentage composition and abundance of copepods and cladocerans showed a significant spatial variability

Table 2
Surface mesozooplankton taxa found in the coastal waters of Kochi, south-eastern Arabian Sea.

Taxa	WM	SIM	SM	Taxa	WM	SIM	SM
Copepods				*Copilia vitrea*	+	–	+
Acartia danae	+	+	+	*Corycaeus danae*	+	+	+
A. erythraea	+	+	+	*C. catus*	+	+	–
A. spinicauda	+	+	+	*C. speciosus*	+	–	–
Acrocalanus gibber	+	+	+	*Corycaeus* sp.	+	–	–
A. gracilis	–	–	+	*Farranula gibbula*	+	–	–
Calanopia elliptica	–	+	–	*Oncaea venusta*	+	+	+
Calanopia sp.	+	+	–	*Sapphirina ovatolanceolata*	+	+	+
Calocalanus pavo	+	+	–	**Crustacean larvae**			
Calanus tenuicornis	+	–	–	Copepodite	+	+	+
Calanus sp.	+	–	–	Zoea	+	+	+
Candacia discaudata	+	+	+	Nauplii	–	+	+
Candacia sp.	+	–	–	Shrimp larvae	+	+	+
Canthocalanus pauper	+	+	+	Barnacle larvae	–	+	+
Canthocalanus sp.	+	–	–	**Cumacean**	–	–	+
Centropages furcatus	+	+	+	**Cladocerans**			
C. calaninus	+	+	+	*Evadne tergestina*	+	+	+
C. orsini	+	+	–	*Penilia avirostris*	–	+	+
C. tenuiremis	–	–	+	**Ostracods**	+	–	+
Centropages sp.	+	–	–	**Polychaetes**	+	+	+
Eucalanus attenuatus	–	–	+	**Amphipods**	+	+	–
E. elongatus	+	–	+	**Chaetognaths**			
E. monachus	+	+	+	*Sagitta enflata*	+	+	+
Euchaeta wolfendeni	+	+	+	*Sagitta neglecta*	+	+	+
Labidocera pavo	+	–	–	*Sagitta robusta*	+	+	+
L. acuta	+	+	–	**Hydromedusae**			
L. minuta	–	+	–	*Aequorea* sp.	–	+	+
L. pectinata	+	+	–	*Eutima mira*	–	–	+
Labidocera sp.	+	–	–	*Liriope tetraphylla*	–	+	+
Metacalanus aurivilli	+	–	–	**Siphonophores**			
Nanocalanus minor	+	+	+	*Chelophyes appendiculata*	+	+	+
Paracalanus parvus	+	+	+	*Diphyes chamissonis*	+	+	+
Pontellina plumata	+	–	–	*Lensia* sp.	+	+	+
P. securifer	+	–	–	**Pelagic tunicates**			
Pontellopsis herdmani	+	+	–	*Oikopleura* sp.	+	+	+
Pseudodiaptomus aurivilli	–	–	+	*Salpa* sp.	–	+	–
P. serricaudatus	+	+	+	*Doliolida* sp.	+	–	+
Rhincalanus nasutus	+	–	+	**Ctenophors**	–	–	+
Scolecithrix danae	+	–	–	**Decapods**			
Temora discaudata	+	+	+	*Lucifer* sp.	+	+	–
T. stylifera	+	+	–	**Molluscan larvae**			
T. turbinata	+	–	+	Bivalve larvae	+	+	+
Undinula vulgaris	+	+	+	Gastropod larvae	+	+	–
Clytemnestra scutellata	+	–	+	*Creseis* sp.	+	+	–
Euterpina acutifrons	–	+	+	**Echinoderm larvae**			
Macrosetella gracilis	+	–	+	Bipinnaria larva	–	+	–
Microsetella sp.	+	+	–	**Ichthyoplankton**			
Miracia efferata	+	–	–	Fish eggs	+	+	+
Oithona brevicornis	+	–	+	Fish larvae	+	+	+
O. similis	+	+	+				

* WM: Winter Monsoon; SIM: Spring Inter Monsoon; SM: Summer Monsoon.

during the SM. The percentage of cladocerans were found to be high (78%) at nearshore waters when compared to the offshore waters, where the copepods (39%) were found to be the highest during the SM.

The taxonomic composition of mesozooplankton was dominated by copepods (57 species in 32 genera comprised of 42 calanoid, 8 Poecilostomatoid, 5 harpacticoid, and 2 cyclopoid species) followed by hydromedusae, siphonophores, chaetognaths and cladocerans. Copepods were dominant in term of species richness and numerical abundance demonstrating wide distribution in all the seasons. *Acartia danae, Acrocalanus gibber, Canthocalanus pauper, Centropages furcatus, C. calaninus, C. tenuiremis, C. orsini, Eucalanus monachus, Nanocalanus minor, Paracalanus parvus, Corycaeus catus, C. danae, Oncaea venusta* and *Undinula vulgaris* were numerically predominant copepods in all the seasons (Fig. 5). Species like *Scolecithrix danae* and *Pontellina securifer* were present only in the SM with low abundance (< 4 ind m^{-3}). The species *Acartia danae, Paracalanus parvus* and *Centropages calaninus* were dominant at near coastal waters (10 m) whereas *Acartia danae, Canthocalanus pauper, Corycaeus danae, Euchaeta wolfendeni, Nanocalanus minor, Temora discaudata* and *Undinula vulgaris* were common species at offshore locations (50 m).

The succession of herbivorous species like *Nanocalanus minor* and *Acrocalanus gibber* during the SM is linked to the high phytoplankton production (McKinnon, 1996; D'Costa et al., 2008). The higher abundance of *Acartia* spp. in the near coastal waters (at 10 and 20 m isobaths stations) demonstrates their adaptability in near coastal and estuarine habitats (Gajbhiye et al., 1991; Paffenhöfer and Stearns, 1988; Elliott et al., 2012). *Oncaea venusta* was found during all the seasons and was abundant at locations with low Chl-*a* (WM). The successful establishment of these copepods might be due to their adaptive feeding behavior on detritus matter, omnivores feeding habit (Yamaguchi et al., 2002). Further the higher abundance of herbivorous cladocerans, pelagic tunicates and other mesozooplankton during the SM could be linked to the higher phytoplankton production in the nutrient enriched waters (Mckinnon and Thorrold, 1993; Deibel and Paffenhöfer, 2009).

In the present study cladocerans were represented by *Evadne tergestina* and *Penilia avirostris*. The mean abundance of *E. tergestina* was lowest (av. 10 ind;m^{-3}) during the WM and the abundance gradually increased during the SIM (av. 130 ind m^{-3}) and reached the peak during the SM (av.754 ind. m^{-3}). During the SM, seasonal swarming of cladocerans was abundant in near coastal waters, and the swarms reached peak densities (4166 ind;m^{-3}) at 20 m depth. However, *P. avirostris* appeared during the SIM with an average of 6 ind. m^{-3} and the abundance increased to an average of 44 ind m^{-3} during the SM. The increase of cladocerans during the SM might be due to the switch in reproductive behavior between parthenogenetic and gamogenetic reproduction under ambient environmental conditions such as temperature and salinity (Marazzo and Valentin, 2003; Kurt and Polat, 2013) which subsequently leads to increased food supply. *P. avirostris* feeds on smaller organisms and bacteria while *E. tergestina* preferentially feeds on large size phytoplankton (Marazzo and Valentin, 2001). In the present study, the Chl-*a* concentration was 82% higher during the SM and the seasonal variation of Chl-*a* was positively significant with seasonal variation of the mesozooplankton abundance ($r = 0.51$; $p < 0.0001$) and group cladocerans ($r = 0.6$; $p < 0.0001$) and ichthyoplankton ($r = 0.5$; $p < 0.0001$). These results suggest that the upwelling-induced high Chl-*a* in the coastal waters was favorable to the cladoceran community. Seasonal blooms of large size diatoms and dinoflagellates in the SM has been documented along the west coast of India (D'Silva et al., 2012). Thus, the availability of suitable food during the SM could lead to proliferation of the cladoceran populations. It is presumed that the *E. tergestina* swarm may affect the food web structure of the coastal ecosystems by their grazing pressure on phytoplankton community (Goes et al., 1999).

3.3. Influence of environmental variables on dominant mesozooplankton species distribution and assemblages

The relationship between environmental variables and dominant *meso*zooooplankton distribution was studied by canonical correspondence analysis (CCA). The CCA plots for the different seasons showing the relationship between the dominant mesozooplankton distribution

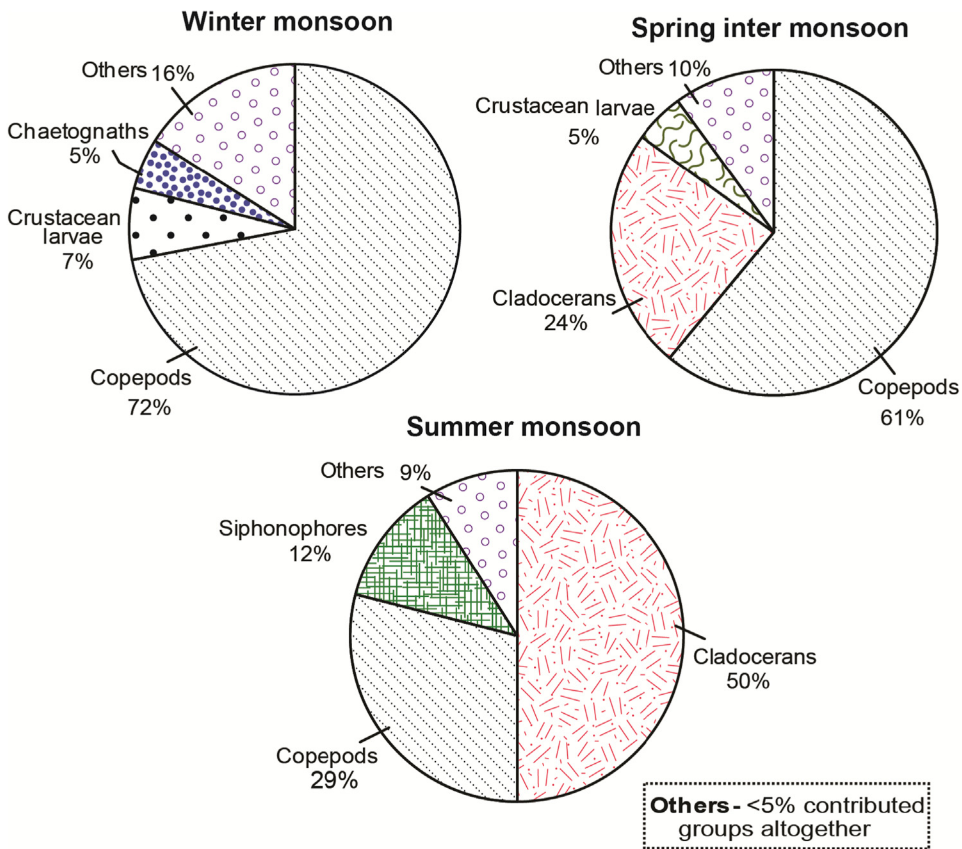

Fig. 4. Seasonal changes in the taxonomical composition of mesozooplankton abundance in the coastal waters of Kochi, southeastern Arabian Sea.

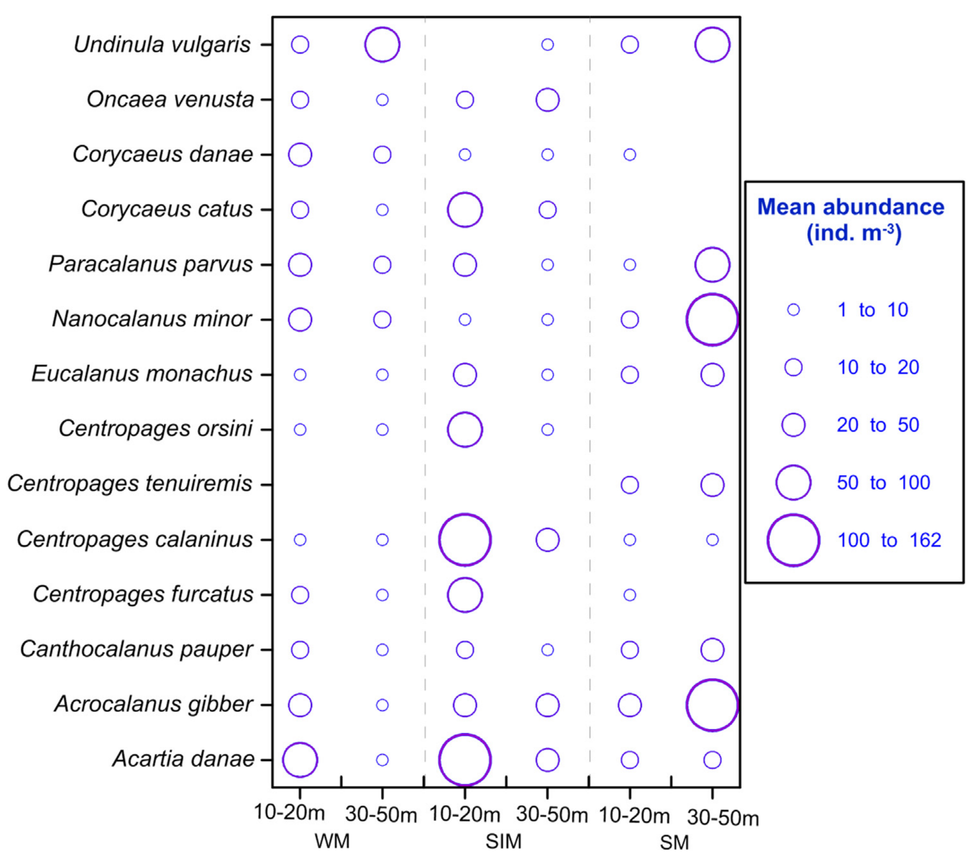

Fig. 5. Spatio-temporal variation in the distribution of dominant species of copepods in the coastal waters of Kochi, southeastern Arabian Sea.

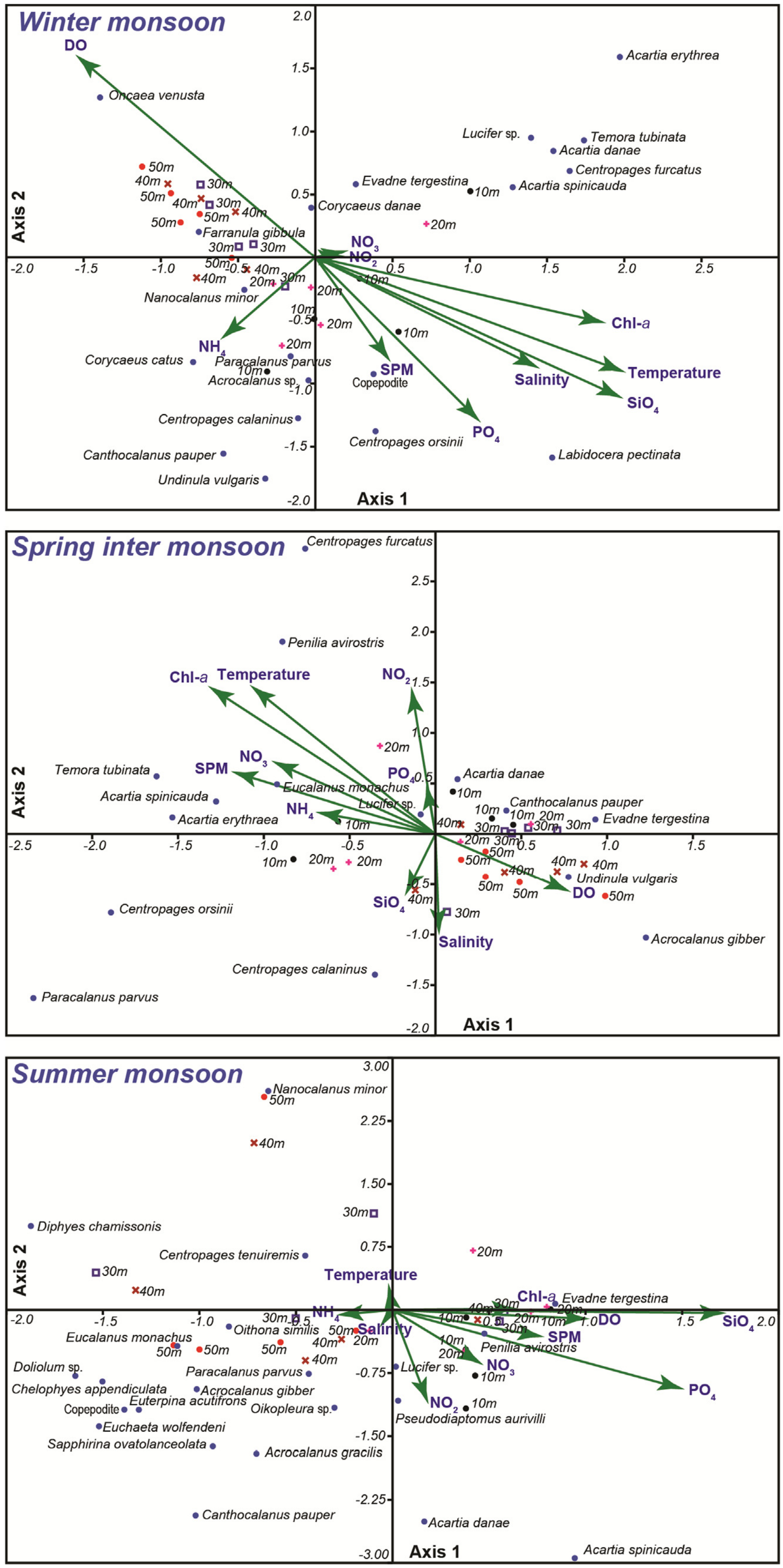

Fig. 6. Canonical correspondence analysis (CCA) triplots for dominant mesozooplankton abundance and environmental variables (Environmental variables are represented by arrows. The number indicates depth contour of the sampling stations. Mesozooplankton species are depicted by points).

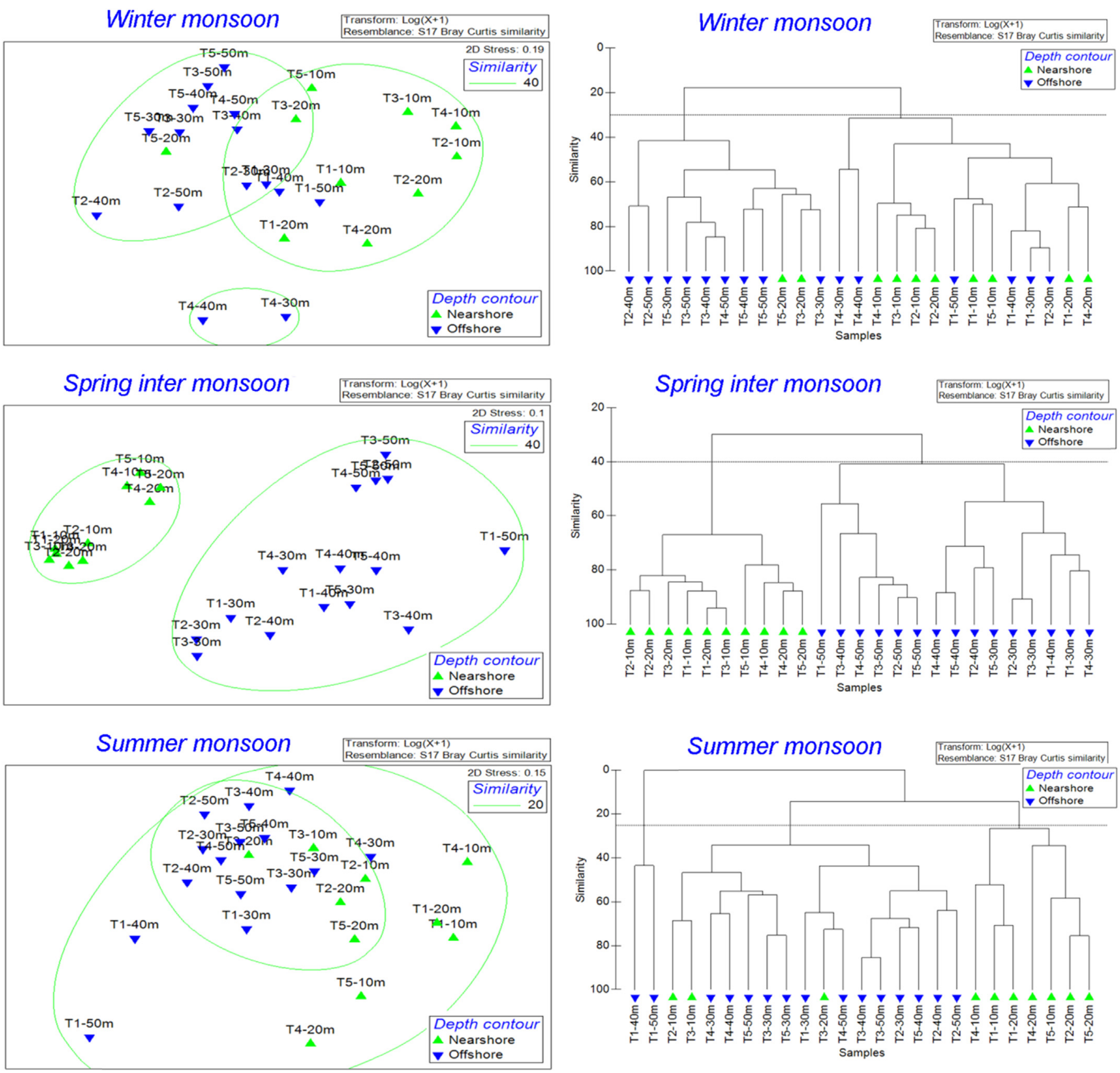

Fig. 7. Spatial patterns of dominant mesozooplankton assemblages based on metric multidimensional scaling and cluster analysis.

and environmental variables are shown in Fig. 6. The correlation between the dominant species distribution and environmental variables was explained in the first and second canonical ordination. The eigenvalues for axis 1 (λ_{WM} = 0.38, λ_{SIM} = 0.16 and λ_{SM} = 0.38) and axis 2 (λ_{WM} = 0.21, λ_{SIM} = 0.09 and λ_{SM} = 0.16) describe total cumulative variance of 63.06%, 58.4% and 68.69% for the WM, SIM and SM, respectively. During the WM season, CCA ordination axis, indicated that *Acartia danae*, *Acartia erythraea* and *Acartia spinicauda* were abundant in the near coastal waters, where temperature, salinity, SPM and nutrients were favorable environmental variables for these species (Fig. 6). *Oncaea venusta* and *Farranula gibbula* were associated with high DO in offshore waters (40–50 m depth). During the SIM season, species like *Acartia danae*, *Acartia erythraea, Acartia spinicauda, Canthocalanus pauper, Centropages orsinii, Paracalanus parvus, Eucalanus monachous, Lucifer* sp. *and Evadne tergestina* were abundant in near coastal waters, where temperature, Chl-*a*, nitrate, nitrite and SPM were conducive environmental variables. *Undinula vulgaris* and *Acrocalanus gibber* were abundant in offshore waters and were positively correlated with DO (Fig. 6). However, during the SM most of the species were abundant in offshore waters than the near coastal waters. Copepods species (O*ithona similis, Eucalanus monachus, Paracalanus parvus, Acrocalanus gibber, Canthocalanus pauper, Eucalanus monachus, Euterpina acutifrons, Euchaeta wolfendeni, Nanocalanus minor, Sapphirina ovatolanceolata* and Centropages tenuiremis), siphonophores (*Diphyes chamissonis* and *Chelophyes appendiculata*) and pelagic tunicate (*Doliolum* sp.) were dominant in offshore waters whereas copepods (*Acartia danae*, *Acartia spinicauda* and *Pseudodiaptomus aurivilli*), Cladocerans (*Evadne tergestina* and *Penilia avirostris*) and *Lucifer* sp. were abundant in near coastal waters, wherein the concentrations of Chl-*a* and nutrients (like silicate, phosphate, nitrate and nitrite) were high (Fig. 6).

In order to understand the spatial characteristics of dominant mesozooplankton distribution, multidimensional scaling (MDS) and cluster analysis (CA) were performed for the three seasons. The Bray Curtis similarities of MDS results showed grouping of stations based on the abundance of dominant species. During the WM and SIM, the dominant species showed two different spatial assemblages at 40% similarity (Fig. 7). These two different groups are mainly near coastal (10–20 m) and offshore stations (30–50 m). A few sampling stations did not show clear spatial differences between the near coastal and offshore waters during the WM. However, in the SIM clear spatial separation between the near coastal and offshore waters was seen. Similarity percentage analysis (SIMPER) was done to reveal the common and dominant species assemblages between the cluster groups. For both the WM and SIM, SIMPER showed higher diversity in near coastal stations cluster grouping than the offshore stations cluster. *Acrocalanus* sp., *Oncaea venusta*, *Paracalanus parvus*, *Evadne tergestina*, *Centropages calaninus*, *Acartia danae*, *Undinula vulgaris* and *Centropages furcatus* contributed 60% of the cumulative percentage in near coastal stations whereas *Oncaea venusta, Paracalanus parvus, Corycaeus danae, Acartia danae, Acrocalanus gibber* and *E. tergestina* were the dominant species in offshore stations.

During the SM, MDS and CA plots did not show any clear spatial pattern between the near coastal and offshore stations groupings at 20% similarity. Further, it was clearly seen that some of the dominant species were distributed homogenously and many of the species were dominant in offshore waters than the near coastal waters (Fig. 7). The high abundance of mesozooplankton throughout the entire study region was due to the high Chl-*a* concentration during the SM. SIMPER test showed that *E. tergestina* was a common and dominant species with 43% and 18% of cumulative percentage in near coastal and offshore stations respectively whereas in offshore stations, herbivorous copepods (*Acrocalanus gibber* and *Eucalanus monachus),* carnivorous siphonophores (*Chelophyes appendiculata* and *Diphyes chamissonis*) and pelagic tunicate (*Doliolida* sp.) were abundant. The abundance of carnivorous siphonophores in offshore waters is in accordance with the abundance of prey (copepods) concentration (Lo et al., 2012). Further, the abundance of pelagic tunicates in offshore waters might be due to their higher grazing efficiency in accordance with less suspended particulate matter (SPM) in offshore waters (Zeldis et al., 1995).

4. Conclusion

The present study elucidates that the distribution and abundance of mesozooplankton community is influenced by the seasonal changes in the coastal waters of Kochi, southeastern Arabian Sea. Specific food habits and physiological adaptation may be responsible for modulating the variations in mesozooplankton biomass and community structure. Thus, an understanding of the mesozooplankton community in coastal pelagic ecosystems is useful to predict the mesozooplankton carbon cycling. These major changes in the pelagic food web can ultimately impact the biogeochemical cycling. Hence, future research should address the role of mesozooplankton community in the pelagic food web, which can bring out better understanding on the food web ecology of the coastal waters of Kochi, southeastern Arabian Sea.

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