Spatial heterogeneity of mesozooplankton along the tropical coastal waters


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Abstract
A survey along the coast of India (~1100 km stretch) between Benaulim (Goa) in the west coast and Thoothukudi (Tamil Nadu) in the east coast was conducted during summer 2014, to evaluate the mesozooplankton community structure. Zooplankton community was dominated by holoplanktonic forms representing 93.7% of the total zooplankton, while meroplanktonic forms constituted 6.3%. Zooplankton was generally dominated by copepods which contributed about 69%. In total, forty-eight species of copepods belonging to eighteen families dominated the zooplankton abundance, with a significant contribution of small-sized copepod genera, viz. Bestiolina, Parvocalanus, Acrocalanus, Corycaeus, Oncaea and Oithona. Total mesozooplankton and copepod density ranged from 80 ind. m⁻³ to 804 ind. m⁻³ and 28 ind. m⁻³ to 570 ind. m⁻³, respectively. Considerably higher abundance of cladocerans (Penilia avirostris and Evadne tergestina) with a significant contribution to zooplankton biomass (r² = 0.984, p < 0.01) compared to copepods was recorded along the east coast. The results of RDA analysis revealed that the sea surface temperature (SST), nutrients (SiO₂ and NO₃), dissolved oxygen (DO) and total suspended matter (TSM) were significant environmental variables (p < 0.05; 999 Monte Carlo permutations) associated with the community structure during pre-monsoon period. Both copepod diversity (H') and dominance (λ) index were higher along the west coast, suggesting the influence of high nutrient and organic input from riverine influx coupled with complex environmental features. The inverse relationship between chlorophyll-a and copepod diversity (H': r = -0.488, p < 0.01) substantiated the importance of grazing pressure in these coastal waters. In contrast, a positive relationship between chlorophyll-a and copepod dominance (λ: r = 0.434, p < 0.05) indicated that copepods abstained from grazing on phytoplankton. Further characterization of this variability in community structure along the coastal waters requires long-term monitoring at a lower taxonomic level.

1. Introduction
Coastal waters are highly productive and biodiversity-rich ecosystems with immense fishery potential on which the coastal fishers are dependent. However, extensive use of coastal waters along with the influence of other anthropogenic pressures (overexploitation, eutrophication, habitat destruction and fragmentation, coastal dumping, unregulated tourism and recreational activities) has led to severe threats to biodiversity (Eissa and Zaki, 2011; Warren et al., 2013), thereby impeding on the ecological integrity of the coast.

Mesozooplankton (0.2–20 mm) constitute a significant component of the heterotrophic plankton community in the coastal environment (Steinberg and Landry, 2017). They play a pivotal role in the trophodynamics of coastal ecosystems and transfer energy and carbon to the higher trophic levels (Jyothibabu et al., 2010; Steinberg and Landry, 2017; Leitao et al., 2019). Spatial heterogeneity of the plankton community structure is a fundamental feature defining patterns of population dynamics within ecosystem trophic webs, which in turn defined by the heterogeneity in the spatial attributes of tropical waters. The variability in the community structure is mainly due to the regional hydrography (Jagadeesan et al., 2013), geomorphology (Cornils et al., 2010), prey-predator dynamics (Sommer and Stibor, 2002), freshwater inputs and water exchanges through tides and currents (Jagadeesan et al., 2013, 2017a; McKinstry and Campbell, 2017; Karati et al., 2019).

Mesozooplankton are also considered as key indicators of prevailing environmental changes, however, identifying changes over some time in any particular area requires background knowledge of species abundance, distribution, and diversity (Jagadeesan et al., 2013).

Keywords:
Arabian sea
Community structure
Small-sized copepods
Diversity
Environmental variables
Alternative prey
Additionally, assessment of coastal health comprises numerous processes among which quantitative and qualitative estimation of zooplankton is identified as the most crucial (Richardson et al., 2015). Moreover, monitoring of zooplankton dynamics is considered as a precautionary mechanism of identifying any changes in the marine ecosystem (Bode et al., 2014; Sato et al., 2015; Steinberg and Landry, 2017). Among mesozooplankton, copepods typically predominate up to 70–90% of the mesozooplankton abundance and constitute a keystone trophic link in the food web, especially due to their species heterogeneity and diverse niche in the marine pelagic realm (Madhupratap et al., 2001a; Fernandes and Ramaiah, 2009; Rakhesh et al., 2015; Steinberg and Landry, 2017).

Recent studies explain that microzooplankton is major grazers of phytoplankton in most marine habitats (e.g. Calbet and Landry, 2004; Umani et al., 2005; Schmoker et al., 2013). On the other hand, in tropical waters, mesozooplankton played a significant role in the trophic food web, control large-sized phytoplankton standing stock and also able to feed on second-level producers of these waters (Calbet and Saiz, 2005; Isari et al., 2007; Jyothibabu et al., 2008; Schmoker et al., 2013; Steinberg and Landry, 2017). Consequently, their abundance, composition and environmental preference received considerable attention around the world (Relox et al., 2000; Criales-Herrández et al., 2008; Kurt and Polat, 2015; Al-Aidaroos et al., 2016; Torreblanca et al., 2016). Earlier studies of Indian waters exclusively focused on distribution, abundance and functional traits of mesozooplankton by emphasizing the copepod assemblage (Rakhesh et al., 2006, 2013) and highlighting their ecosystem service and water mass indication (Madhupratap et al., 2001b; Rakhesh et al., 2015; Jagadeesan et al., 2017a; Karati et al., 2019). However, the data provided is patchy and limited to regional interest (e.g. Padmavati and Goswami, 1996; Padmavati et al., 1998; Jyothibabu et al., 2006; Madhu et al., 2007; Fernandes and Ramaiah, 2009; Rakhesh et al., 2015; Jyothibabu et al., 2018). In this paper, we evaluate the hydrographical influence on the mesozooplankton abundance and community structure along the tropical coastal waters. We hypothesize that heterogeneity in the spatial attributes of tropical waters is important features defining community structure. Also, we
consider that single stretch observation of long coastline during the
stable environmental condition (pre-monsoon) will provide some
insight into the understanding of variability in the spatial distribution of
mesozooplankton.

2. Materials and methods

2.1. Study area

The present study was carried out along the stretch of ~1100 km
from Benaulim, Goa to Thoothukudi, Tamil Nadu, covering the lat-
titudinal distance of 15°N 73°E to 8°N 78°E (Fig. 1). The average monthly
total rainfall of Karnataka, Kerala and Tamil Nadu presents an annual
average of 3050.5 mm, 2350.8 mm and 784.4 mm respectively for the
period between 2010 and 2014 (Kothawale and Rajeevan, 2017), with a
higher rainfall during southwest monsoon (June to September), and
lower precipitation from pre-monsoon (Fig. 2). These neritic waters
experience varying hydrographical conditions and biological diversity.
Biogeochemistry of these waters is influenced by the high riverine
influx, the formation of mudbanks and frequent upwelling. Coastal up-
welling and river runoff have been identified as the two most important
factors regulating productivity of the Arabian Sea (Jyothibabu et al.,
2008, 2010; 2018). A considerable amount of freshwater influx from the
rivers of Kerala (Valapattanam, Chaliyar, Periyar, Kayamkulam, Kallada
and Perumathura River) and Karnataka (Sharavati, Gurupura and
Nethravati) have a profound impact on the nutrient enrichment and
overall productivity of the region (Smitha et al., 2008; Jyothibabu et al.,
2010). Cochin backwaters discharge about 2 × 10^10 m^3 y^-1 of fresh-
water into the coast (Srinivas et al., 2003), influencing the biogeo-
chemistry and coastal features of the region. The Kerala coast also
features mudbanks, a unique phenomenon that plays a vital role in the
regional economy (mudbank fishery) of the coastal belt by enhancing
nutrient concentration which in turn triggers a substantial tertiary
production of the region (Madhupratap et al., 2001a; Nair, 2015)
(Fig. 3). The fishery productivity of these regions contributes signifi-
cantly to the national economy while providing a livelihood for
approximately 40% of the country’s total fishermen population (Rao
et al., 2016). By contrast, the southeast coast is endowed with a group of
coral reef islands in the Gulf of Mannar. The region between
Kanyakumari to Thoothukudi encompasses ~40% of the Gulf of Mannar
(Dhanushkodi to Kanyakumari) biosphere reserve that extends up to
~300 km along Tamil Nadu coast (Joshi et al., 2016). The area is well
known for its rich biodiversity including coral reefs and lagoons that
attribute to a large number of finfish, crustaceans and molluscs
(Kumaraguru et al., 2006; Bavinck and Vivekanandan, 2011; Joshi et al.,
2016).

2.2. Coastal sampling

A total of 35 samples for water quality and mesozooplankton were
collected along the coast on-board CRV Sagar Purvi during the early
southwest monsoon (May and June 2014). Sampling was undertaken at
one station from Goa, five stations from Karnataka (KA), twelve stations
from north Kerala (N-KL), eleven stations from south Kerala (S-KL) and
six stations from south Tamil Nadu (S-TN). Considering the ecological
significance (riverine and backwaters inputs, the frequent occurrence of
mudbanks (Fig. 3), upwelling and coral reef ecosystems) and economic
importance (fishery production) of the region, samples were taken at 25
km intervals along N-KL and S-TN coast, whereas in KA coast, the
samples were collected at 50 km interval.

2.3. Hydrological parameters

Sea-surface temperature (SST), salinity, pH, dissolved oxygen (DO),
oxxygen saturation and turbidity were measured in situ using a pre-
calibrated water quality probe (HYDROLAB DSS, USA). Surface (0.5
m) seawater samples were collected using a 5 L Niskin sampler at each
station to examine the spatial variation in dissolved inorganic nutrients
(NO_3^- -N, NO_2^- -N, NO_3^- -N and SiO_2^- -Si), Chlorophyll a (chl-a), dissolved
organic carbon (DOC) and total suspended matter (TSM). Samples were
stored at −20 °C until analysis. In the laboratory, the concentrations of
seawater nutrients were estimated by following the analytical methods
of Grasshoff et al. (1999). For estimation of chl-a, 1l of seawater was
filtered onto 47 mm Whatman GF/F filter, extracted in 90% acetone for
12 h, and analysed spectrophotometrically (Gupta et al., 2008). DOC
concentrations in samples were measured using total organic carbon
analyzer (Vario TOC Cube) following high-temperature catalytic
oxidation method (Gupta et al., 2008; Robin et al., 2016). TSM was

Fig. 2. Monthly average rainfall for the period between 2010 and 2014 along the studied coastal states (Karnataka, Kerala and Tamil Nadu) of India showing higher rainfall during southwest monsoon (June to September).
measured by filtering a known volume of seawater through 0.45 μm cellulose acetate membrane filters (Millipore), rinsed with Milli-Q water and by taking the difference of initial and final weights of filter (Gupta et al., 2008).

2.4. Mesozooplankton sampling and processing

Mesozooplankton samples were collected at each location using a standard plankton net (200 μm mesh size and 60 cm diameter at the mouth) equipped with a digital flow meter (KC Denmark), hauled horizontally for 10 min. Sampling was undertaken during daylight hours (8.00 a.m.–4.00 p.m.) to offset extensive variation in mesozooplankton abundance caused by diel vertical migration. The collected samples were then immediately preserved in 4% buffered formaldehyde for identification and enumeration of mesozooplankton species. In the laboratory, subsamples were removed with 5 ml Henson-Stempel pipette for analysis (Bode et al., 2014). Three to four subsamples were analysed until at least 200 individuals were counted for each of the most abundant species (Machado et al., 2016) and the density was expressed as individuals per cubic meter (ind. m⁻³). Before the identification, the total zooplankton biomass was calculated using the settled volume method, where the collected sample was allowed to settle for 24 h until the measurement was recorded and the zooplankton biomass was expressed as ml m⁻³ (Geowamii, 2004; Boyer et al., 2009). To avoid the effect of large particles that are not part of the plankton, elements such as macroalgae, pieces of ships’ paint were removed (Campelo et al., 2019). The copepods in the samples were sorted, counted and identified up to the species level (Conway et al., 2003; Razous et al., 2005–2017) by using a stereomicroscope (NIKON SMZ25) and an inverted microscope (Leica DMIL LED). The preserved samples were labeled and stored at National Centre for Sustainable Coastal Management (NCSCM) repository.

2.5. Statistical analysis

Diversity index such as Margalef richness (d), Pielou’s evenness (J'), Shannon diversity (H') and Simpson dominance (i) was used to determine the spatial variation in copepod assemblage structure (Madhu et al., 2007). Spatial variation in the environmental variables was tested using one-way ANOVA and Kruskal-Wallis test based on the normality (Shapiro-Wilk test) and homogeneity of variances (Levene test) of the variables. Temperature, salinity, nitrite, nitrate, DOC, and chl-α data violate the assumptions of normality and homogeneity of variances, thus, these variables were tested with Kruskal-Wallis test. Multivariate analyses were employed on the copepod density data to ascertain the similarities among the sampling stations. Non-metric multidimensional scaling (nMDS) was performed using the Bray-Curtis similarity index after log (X+1) transformation of copepod density (Rakhesh et al., 2008). The analysis of similarity (ANOSIM) and similarity percentage (SIMPER) based on log (X+1) transformation of density was used to describe the variation in copepod species assemblage between the sampling regions (KA, N-KL, S-KL and S-TN) (Rakhesh et al., 2008; Clarke and Gorley, 2013). All these analyses, including diversity index, nMDS, ANOSIM and SIMPER, for copepod species were conducted in PRIMER v7 (Clarke and Gorley, 2015).

Principal Component Analysis (PCA) was performed on normalized environmental data to identify the general spatial structure across the regions (Liu et al., 2018; ter Braak and Smilauer, 2002). Redundancy Analyses (RDA) was applied to evaluate the effect of environmental variables on the patterns of copepod species and mesozooplankton community composition. PCA and RDA were preferred, since the values of gradient lengths expressed in standard deviation units of environmental variables and the taxonomic categories were <3, determined by detrended correspondence analyses (DCA) and detrended canonical correspondence analysis (DCCA), respectively, indicated a linear response (Leps; Smilauer, 2003). Significant environmental variables that explained the variability of the community structure were determined through forward-selected Monte Carlo analysis with 999 permutation tests at p < 0.05 (ter Braak and Smilauer, 2002). Mesozooplankton and copepod species that contributed >1% of the total abundance at least at one of the regions were log (X+1) transformed and conducted RDAs by centering and standardization procedure. Oxygen saturation (DO %) and turbidity (NTU) showed strong intercorrelation with dissolved oxygen (DO) and phosphate (PO₄-P), respectively, were excluded from the ordination analyses. PCA and RDA were performed using CANOCO for Windows 4.5 (ter Braak and Smilauer, 2002; Leps; Smilauer, 2003). Besides, Pearson correlation was carried out to understand the correlation between the biotic and abiotic components and linear regression analysis was performed to determine the association between the concentration of chl-α with species diversity and dominance index of copepods by using SPSS version 20 (Machado et al., 2016). Samples from Goa and Karnataka were pooled together for statistical analysis and data interpretation.
3. Results

3.1. Environmental variables

The southwest coast of India experienced a warm, humid climate during the sampling period, with average air temperature (30.43 ± 1.88 °C) higher than that of the sea-surface temperature (SST) (29.87 ± 1.25 °C). SST variation ranged from 27.41 °C to 31.64 °C, with lower values observed along the S-TN coast (Fig. 4a). The salinity ranged between 33.65 and 35.71 with minimum average observed at S-KL. The shelf waters were supersaturated concerning O$_2$ at S-KL (106.67 ± 5.25%) and S-TN (103.40 ± 2.97%) (Fig. 4b). A moderate negative relationship of DO with SST ($r = -0.477; p < 0.01$) and salinity ($r = -0.359; p < 0.05$), and weak positive correlation with pH ($r = 0.379; p < 0.05$) indicated possible influence of physical mixing and biological processes. Surface concentration of nitrate, phosphate and silicate varied from 1.01 μmol/l - 6.45 μmol/l (mean 2.7 ± 1.4 μmol/l), 0.18 μmol/l - 1.22 μmol/l (mean 0.7 ± 0.2 μmol/l), and, 0.57 μmol/l - 14.27 μmol/l (mean 7.0 ± 4 μmol/l), respectively, with peak values mostly at waters along S-KL coast. Lowest concentration in nitrate and phosphate were observed at KA coast, whereas, the highest silicate concentration was recorded at N-KL coast followed by KA (Table 1). Concentrations of chl-a ranged between 0.40 mg m$^{-3}$ and 4.07 mg m$^{-3}$ and were observed to be relatively higher at N-KL followed by S-KL (Fig. 4c). Spatial distribution of physicochemical and biological parameters is presented in Fig. 4a-i, whereas the pooled mean and standard deviation of the hydrographic parameters for the four different regions is given in Table 1.

In general, the mean temperature, phosphate, and silicate were...
significantly lower in the S-TN coast compared to the other stations. Higher turbidity (F3 ¼ 6.90; p < 0.001) and TSM (F3 ¼ 7.76; p < 0.05) were recorded on the west coast compared to S-TN coast. A significant positive relationship of turbidity with nitrate (r ¼ 0.350; p < 0.05) and phosphate (r = 0.650; p < 0.01) was observed. Besides, significant spatial variation was discernible in the hydrological parameters such as SST (H ¼ 15.2; p = 0.002) and DO (F3 ¼ 7.76; p < 0.001) and nutrients such as phosphate (F3 ¼ 4.22; p < 0.05) and silicate (F3 ¼ 11.24; p < 0.0001) commensurate with land-based inputs from major cities and towns along the coast. PCA analysis based on normalized environmental variables showed that PCA Axis 1 explained 26.1% of the variations (Fig. 5). The waters of S-TN coast and southernmost stations of Kerala (S-KL 8, 10 and 11) were characterized by relatively high DO and pH, whereas, TSM, SST and silicate exhibited a negative trend indicating lower values. On the other hand, PCA Axis 2 explained 20.5% of the variations, where N-KL coast (N-KL 8 to 11) and S-KL coast (S-KL 1 to 4) were characterized by high SST, TSM, DOC, nitrate and silicate.

3.2. Composition of mesozooplankton

A total of 28 taxa contributed to the total abundance of mesozooplankton. Zooplankton was dominated by holoplanktonic forms with 93.7%, predominant with copepods (68.5%), followed by Cladocera, Appendicularia (Oikopleura spp.), Lucifer sp. and Chaetognatha (17.1%, 2.5%, 1.9% and 1.2% respectively). On the other hand, meroplanktonic forms constituted with 6.3%, dominated by Decapod larvae (4.3%), other groups constituted about 1% each includes fish eggs, molluscan veliger and polychaete larvae. Percentage composition of mesozooplankton and copepod species is detailed in Fig. 6a-d. A total of 48 species of copepods were recorded in this study including 34 species of Calanoids, 11 Cyclopoids and 3 Harpacticoids. Out of eighteen families recorded, Pontellidae was the most diverse with eleven species followed by Paracalanidae with six species. Acartiidae and Centropagidae were represented by three species each (Supplementary Table 1). The species Acartia erythraea, Canthocalanus pauper, Centropages furcatus and Oncaea venusta were the most common among the copepod assemblage that occurred in all the samples. The predominant copepod genera that contributed to the total (89.9%) abundance were Bestiolina, Corycaeus, Acartia, Canthocalanus, Centropages, Oncaea, Acrocalanus, Temora and Oithona (Fig. 6d).

3.3. Spatial variation of mesozooplankton

Zooplankton density in the coastal waters from Goa (Benaulim) to S-TN (Thoothukudi) ranged between 80 ind. m−3 and 804 ind. m−3, while the respective zooplankton biomass ranged between 0.004 ml m−3 and 0.538 ml m−3 (Table 2). Mesozooplankton density was lowest along the S-TN coast (266 ± 199 ind. m−3) whereas, the highest was recorded at N-KL (424 ± 221 ind. m−3). In contrast, ichthyoplankton (fish eggs and larvae) density was higher along S-KL (4 ± 5 ind. m−3) and S-TN coast (3 ± 2 ind. m−3) compared to other locations (Fig. 7). On a spatial scale, the copepod family Temoridae dominated the S-TN waters, mainly represented by Temora turbinata. Along with copepods, Penilia avirostris, Oikopleura sp., chaetognaths and nauplii were important components of mesozooplankton that significantly determine the zooplankton biomass in KA and N-KL. However, in S-KL and S-TN, a moderate relationship was found between the abundant groups and zooplankton biomass (Table 3). Regression analysis of total mesozooplankton density

### Table 1

Spatial variation in environmental factors (mean ± SD) and minimum-maximum values (in parentheses) along the tropical coastal waters (KA: Karnataka; N-KL: North Kerala; S-KL: South Kerala; S-TN: South Tamil Nadu).

<table>
<thead>
<tr>
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<th>KA</th>
<th>N-KL</th>
<th>S-KL</th>
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<tr>
<td>SST (°C)</td>
<td>30.47 ± 0.38 (30.05-31.01)</td>
<td>30.58 ± 0.48 (30.07-31.64)</td>
<td>29.90 ± 1.18 (27.84-31.52)</td>
<td>27.77 ± 0.41 (27.41-28.58)</td>
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<tr>
<td>Salinity (PSU)</td>
<td>35.46 ± 0.16 (35.19-35.66)</td>
<td>35.49 ± 0.19 (35.13-35.71)</td>
<td>34.92 ± 0.7 (33.65-35.71)</td>
<td>35.21 ± 0.41 (34.67-35.65)</td>
</tr>
<tr>
<td>pH</td>
<td>7.91 ± 0.06 (7.81-7.99)</td>
<td>7.91 ± 0.05 (7.79-7.97)</td>
<td>7.92 ± 0.04 (7.84-8.8)</td>
<td>7.93 ± 0.04 (7.88-8)</td>
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<tr>
<td>DO (mg/l)</td>
<td>5.95 ± 0.37 (5.35-6.33)</td>
<td>5.99 ± 0.34 (5.62-6.96)</td>
<td>6.30 ± 0.32 (5.71-6.76)</td>
<td>6.67 ± 0.16 (6.42-6.83)</td>
</tr>
<tr>
<td>TSM (mg/l)</td>
<td>45.08 ± 5.67 (38.25-52)</td>
<td>49.83 ± 5.63 (40.25-63)</td>
<td>43.26 ± 12.43 (27.71-6)</td>
<td>36.56 ± 1.98 (33.4-39.4)</td>
</tr>
<tr>
<td>Turbidity (NTU)</td>
<td>11.47 ± 0.94 (10.3-12.8)</td>
<td>12.70 ± 1.49 (10.3-15)</td>
<td>13.87 ± 3 (11.17-15)</td>
<td>10.57 ± 1.03 (9.24-12.24)</td>
</tr>
<tr>
<td>NO2-N (μmol/l)</td>
<td>0.34 ± 0.06 (0.26-0.4)</td>
<td>0.42 ± 0.19 (0.18-0.74)</td>
<td>0.32 ± 0.12 (0.16-0.58)</td>
<td>0.32 ± 0.1 (0.19-0.47)</td>
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<tr>
<td>NO3-N (μmol/l)</td>
<td>1.96 ± 1.13 (1.01-3.42)</td>
<td>2.42 ± 0.74 (1.27-3.42)</td>
<td>3.63 ± 2.01 (1.25-6.45)</td>
<td>2.28 ± 0.17 (2.14-2.54)</td>
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<tr>
<td>PO4-P (μmol/l)</td>
<td>0.67 ± 0.26 (0.18-0.9)</td>
<td>0.75 ± 0.18 (0.41-0.99)</td>
<td>0.87 ± 0.27 (0.32-1.22)</td>
<td>0.48 ± 0.04 (0.43-0.54)</td>
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<tr>
<td>SiO2-C (μmol/l)</td>
<td>7.48 ± 3.6 (2.07-12.47)</td>
<td>10.07 ± 2.08 (6.07-13.2)</td>
<td>6.51 ± 4.03 (1.54-14.27)</td>
<td>1.44 ± 0.7 (0.57-2.4)</td>
</tr>
<tr>
<td>DOC (mg/l)</td>
<td>2.64 ± 0.48 (2.14-3.25)</td>
<td>3.09 ± 0.88 (2.15-5.26)</td>
<td>3.28 ± 1.59 (1.63-6.46)</td>
<td>2.29 ± 0.68 (1.86-3.66)</td>
</tr>
<tr>
<td>Chl-a (μg m−2)</td>
<td>0.89 ± 0.45 (0.4-1.5)</td>
<td>2.53 ± 1.26 (0.62-4.07)</td>
<td>2.30 ± 0.88 (1.13-3.88)</td>
<td>1.94 ± 0.92 (1.06-3.73)</td>
</tr>
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Fig. 5. Principal component analysis (PCA) biplot indicating relationships between environmental variables and different sampling points of the region (KA: Karnataka; N-KL: North Kerala; S-KL: South Kerala; S-TN: South Tamil Nadu). The environmental variables are represented in blue lines originating from the centroid of the PCA plot, and the sampling points are represented by various symbols as indicated in the plot. The direction of the lines indicates the increasing gradient of variables characterising the stations. The abbreviations of the variables are as follows: SST: sea surface water temperature (°ST); PSU: salinity; DO: dissolved oxygen; DO%: oxygen saturation; PO4: phosphate; SiO2-C: silicate; NO3-N: nitrite; NO2-N: nitrate; NTU: turbidity; TSM: total suspended matter; Chl-a: chlorophyll a; DOC: dissolved organic carbon. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

### Table 2

Mesozooplankton density was lowest along the S-TN coast (266 ± 199 ind. m−3) whereas, the highest was recorded at N-KL (424 ± 221 ind. m−3). In contrast, ichthyoplankton (fish eggs and larvae) density was higher along S-KL (4 ± 5 ind. m−3) and S-TN coast (3 ± 2 ind. m−3) compared to other locations (Fig. 7). On a spatial scale, the copepod family Temoridae dominated the S-TN waters, mainly represented by Temora turbinata. Along with copepods, Penilia avirostris, Oikopleura sp., chaetognaths and nauplii were important components of mesozooplankton that significantly determine the zooplankton biomass in KA and N-KL. However, in S-KL and S-TN, a moderate relationship was found between the abundant groups and zooplankton biomass (Table 3). Regression analysis of total mesozooplankton density
Table 2
Mean (mean ± SD) and minimum-maximum values (in parentheses) for total mesozooplankton and other dominant taxa, and copepod species diversity index along the sampling regions (KA: Karnataka; N-KL: North Kerala; S-KL: South Kerala; S-TN: South Tamil Nadu). Density values are given as ind. m⁻³ and zooplankton biomass (settlement volume) as ml m⁻³.

<table>
<thead>
<tr>
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<th>S-KL</th>
<th>S-TN</th>
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<tbody>
<tr>
<td>Total mesozooplankton</td>
<td>284 ± 185 (80-519)</td>
<td>424 ± 221 (110-802)</td>
<td>334 ± 208 (85-804)</td>
<td>266 ± 199 (94-614)</td>
</tr>
<tr>
<td>Copepods</td>
<td>148 ± 116 (29-321)</td>
<td>255 ± 133 (58-480)</td>
<td>186 ± 151 (28-570)</td>
<td>91 ± 27 (60-124)</td>
</tr>
<tr>
<td>Chaetognatha</td>
<td>3 ± 4 (0.38-12)</td>
<td>4 ± 6 (0-19)</td>
<td>6 ± 5 (0-16)</td>
<td>2 ± 1 (0.84-5)</td>
</tr>
<tr>
<td>Decapod larvae</td>
<td>10 ± 15 (0.5-37)</td>
<td>18 ± 15 (2-54)</td>
<td>14 ± 18 (0.1-58)</td>
<td>18 ± 23 (1-62)</td>
</tr>
<tr>
<td>Oikopleura</td>
<td>5 ± 4 (0.25-10)</td>
<td>7 ± 5 (0-17)</td>
<td>11 ± 15 (0.5-47)</td>
<td>2 ± 1 (0-4)</td>
</tr>
<tr>
<td>Penilia avirostris</td>
<td>20 ± 22 (0.05-52)</td>
<td>36 ± 34 (0.35-89)</td>
<td>5 ± 12 (0.41)</td>
<td>25 ± 45 (0-114)</td>
</tr>
<tr>
<td>Evadne tergestina</td>
<td>28 ± 18 (9-52)</td>
<td>9 ± 6 (0-18)</td>
<td>33 ± 80 (0-267)</td>
<td>101 ± 138 (0-340)</td>
</tr>
<tr>
<td>Oikopleura sp.</td>
<td>5 ± 7 (0.25-18)</td>
<td>15 ± 20 (1-71)</td>
<td>6 ± 11 (0-39)</td>
<td>2 ± 1 (0.33-3)</td>
</tr>
<tr>
<td>Zooplankton biomass</td>
<td>0.09 ± 0.06 (0.02-0.18)</td>
<td>0.16 ± 0.09 (0.04-0.39)</td>
<td>0.14 ± 0.16 (0.004-0.54)</td>
<td>0.1 ± 0.04 (0.03-0.14)</td>
</tr>
<tr>
<td>Margalef richness (d)</td>
<td>4.16 ± 0.92 (3.23-5.37)</td>
<td>3.35 ± 0.7 (2.24-4.35)</td>
<td>3.16 ± 0.76 (2.37-4.89)</td>
<td>3.25 ± 0.65 (2.89-4.57)</td>
</tr>
<tr>
<td>Peilou’s evenness (J’)</td>
<td>0.72 ± 0.04 (0.65-0.77)</td>
<td>0.67 ± 0.1 (0.48-0.8)</td>
<td>0.69 ± 0.09 (0.51-0.79)</td>
<td>0.69 ± 0.09 (0.62-0.83)</td>
</tr>
<tr>
<td>Shannon diversity (H’)</td>
<td>3.11 ± 0.2 (2.81-3.45)</td>
<td>2.85 ± 0.55 (1.85-3.51)</td>
<td>2.77 ± 0.48 (1.94-3.53)</td>
<td>2.75 ± 0.46 (2.4-3.58)</td>
</tr>
<tr>
<td>Simpson dominance (J)</td>
<td>0.17 ± 0.02 (0.13-0.20)</td>
<td>0.23 ± 0.11 (0.12-0.45)</td>
<td>0.22 ± 0.08 (0.11-0.42)</td>
<td>0.22 ± 0.07 (0.11-0.30)</td>
</tr>
</tbody>
</table>

revealed its strong dependence on small-size copepods ($r^2 = 0.742, p < 0.05$ for KA; $r^2 = 0.844, p < 0.01$ for N-KL; and $r^2 = 0.580, p < 0.01$ for S-KL) along the western coast, whereas in S-TN, the relationship was meagre ($r^2 = 0.041; p > 0.05$).

Copepods were dominant in all the sampling stations except along S-TN coast, where cladocerans (47.23%) outnumbered the copepods with significant contribution from *Penilia avirostris* and *Evadne tergestina* to the total zooplankton density ($r^2 = 0.984; p < 0.01$). Copepod diversity showed a decreasing trend from Karnataka to Tamil Nadu coast; however, the abundance was the highest along N-KL coast. Shannon diversity ($H'$) ranged between 1.85 and 3.58 with the maximum recorded at KA, where richness ($d$) and evenness ($J'$) were found to be $4.16 ± 0.92$ and $0.72 ± 0.04$, respectively. The least diversity of copepod was recorded in S-TN coast. In contrast, the dominance ($J$) index was found to be highest at N-KL and lowest at KA (Table 2). Non-metric multidimensional scaling (nMDS) orientation (stress = 0.16) based on Bray-Curtis similarity index for copepod species at all the sampling sites indicated distinct variance in different coastal regions (Fig. 8). Clustering made with 50% resemblance level allowing the visualization of three groups of stations reflecting the structure of copepod assemblage. A large cluster was formed by clubbing KA and N-KL, including stations from the northern part of S-KL. Whereas, separation of S-TN coast along with the last station of S-KL and another one by the southernmost stations of S-KL (6, 7 and 9) is conspicuous from Fig. 8. Besides, the nMDS was confirmed by one-way ANOSIM which indicated that both mesozooplankton (Global $R = 0.18; p < 0.05$) and copepod (Global $R = 0.36; p < 0.01$) assemblage varied significantly between regions. Multiple pairwise comparisons revealed that the copepod assemblage significantly differs among pile KA and S-TN ($R = 0.844; p < 0.01$), N-KL and S-TN ($R = 0.942; p < 0.01$) and S-KL and S-TN ($R = 0.41; p < 0.01$). The
The highest dissimilarity was observed between N-KL and S-TN (58.18%). The most important discriminating species were Centropages furcatus, C. erythraea, and Temora turbinata. The densities contributed to more than 90% of the total average dissimilarities among three groups.

Fig. 7. The density of mesozooplankton (dashed line with closed squares) and ichthyoplankton (continuous line with closed circles) along the sampling regions (KA: Karnataka; N-KL: North Kerala; S-KL: South Kerala; S-TN: South Tamil Nadu).

Table 3
Relationship between major mesozooplankton taxa and biomass-based on Pearson correlation coefficient (r) values at study regions (KA: Karnataka; N-KL: North Kerala; S-KL: South Kerala; S-TN: South Tamil Nadu).

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Zooplankton biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>KA</td>
</tr>
<tr>
<td>Copepods</td>
<td>0.886*</td>
</tr>
<tr>
<td>Chaetognaths</td>
<td>0.775</td>
</tr>
<tr>
<td>Decapods</td>
<td>0.416</td>
</tr>
<tr>
<td>Lucifer sp.</td>
<td>0.810</td>
</tr>
<tr>
<td>Penilia avirostris</td>
<td>0.841*</td>
</tr>
<tr>
<td>Evadne tergestina</td>
<td>–0.309</td>
</tr>
<tr>
<td>Nauplii</td>
<td>0.840*</td>
</tr>
<tr>
<td>Oikopleura sp.</td>
<td>0.859*</td>
</tr>
</tbody>
</table>

*p < 0.01; **p < 0.05.

Table 4
The discriminating species were composed of A. erythraea, C. pauper and F. gibbula in KA; B. similis in N-KL; C. furcatus and A. gibber in S-KL; T. turbinata and C. pauper in S-TN region.

3.4. Ecological relationship between physicochemical and biological variables

SIMPER analysis established the discriminating species of copepods in the regional sectors, described by dendrogram and confirmed by nMDS. Relationship between chl-α (phytoplankton) and dissolved nutrients (nitrate, phosphate and silicate) for the entire coastal stretch were statistically insignificant (r < 0.3, p > 0.05, n = 35) (Supplementary Fig. 1). The species-environment correlation for the RDA Axis 1 was 0.668 and 0.817 for mesozooplankton composition and copepod species, respectively. The cumulative explained variance for the first two axes accounted for about 63% of species-environmental relationship for both the taxonomic categories when treated separately (Supplementary Table 2). The first axis was strongly correlated with SiO4 and SST (p < 0.01; 999 Monte Carlo permutations), while moderately with NO3, the second axis with NO3 and PO4 (Table 5). The small-size copepod, total copepod and mesozooplankton density were mainly positively related to SiO4 and SST, the other groups related were bivalve veliger, Oikopleura sp., Penilia avirostris, chaetognaths and nauplii. The abundance of these taxa were mostly associated with the western coast, however, Evadne tergestina showed discrepancy and abundant towards the S-TN and S-KL (Fig. 9a). In the case of copepod assemblage structure, along with SiO4 and SST (p < 0.01; 999 Monte Carlo permutations), DO, TSM and NO2 were found to be significant variables (p < 0.05; 999 Monte Carlo permutations) correlated with the first axis (Table 5). The small-size copepod, Bestiolina similis coincide with TSM and SST but were negatively related to salinity indicating their abundance along the N-KL and S-KL region. Nonetheless, the small-sized copepod Parvocalanus cristatus and the demersal copepod species Pseudodiaptomus serricaudatus and Pseudodiaptomus compactus were positively correlated with DOC, despite the demersal species were restricted (contributed >1% of the relative abundance) to KA. Species such as Undinula vulgaris, Calanopia minor, Temora discudata, Camhocalanus pauper, Calanopia elliptica and Temora turbinata were showed positive relation to DO, Salinity and pH, however, exhibited relatively opposite trend with chl-α. Besides, the dominance index (J) was positively correlated to chl-α, whereas an opposite trend was exhibited to diversity (H′) and evenness index (J′) (Fig. 9b).

The present study on zooplankton revealed that the density was strongly governed by small-sized copepods, especially along the west coast. The relationship between chl-α and copepod diversity index showed a significant negative association (H′: r = –0.488, p < 0.01).
Table 5
SIMPER analysis (run with 30% cut off for low contributions) identifying per cent species contribution to the Bray Curtis dissimilarity metrics between the regions (KA: Karnataka; N-KL: North Kerala; S-KL: South Kerala; S-TN: South Tamil Nadu).

<table>
<thead>
<tr>
<th>Species</th>
<th>N-KL and S-KL (Ave. dissim = 42.68%)</th>
<th>Species</th>
<th>N-KL and S-TN (Ave. dissim = 53.86%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>KA and N-KL %</td>
<td>KA and S-TN %</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A.A A.A Contrib.</td>
<td>A.A A.A Contrib.</td>
<td></td>
</tr>
<tr>
<td>Bestiolina similis</td>
<td>3.64 2.25 8.43</td>
<td>Temora turbinata</td>
<td></td>
</tr>
<tr>
<td>Acrocalanus gibber</td>
<td>3.07 2.13 6.22</td>
<td>Bestiolina similis</td>
<td></td>
</tr>
<tr>
<td>Oncaea venusta</td>
<td>2.21 1.86 5.92</td>
<td>Farranula gibbula</td>
<td></td>
</tr>
<tr>
<td>Corycaeus crassiusculus</td>
<td>2.25 1.79 4.56</td>
<td>Ctenopelagicus minor</td>
<td></td>
</tr>
<tr>
<td>Centropages ornitii</td>
<td>1.72 1.36 4.28</td>
<td>Ctenopelagicus minor</td>
<td></td>
</tr>
<tr>
<td>Parvocalanus crassirostris</td>
<td>1.68 2.11 4.18</td>
<td>Subeucalanus subcrassus</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bestiolina similis</td>
<td>3.64 0.08 10.63</td>
<td>Temora turbinata</td>
<td></td>
</tr>
<tr>
<td>Farranula gibbula</td>
<td>3.07 0.54 7.26</td>
<td>Bestiolina similis</td>
<td></td>
</tr>
<tr>
<td>Temora turbinata</td>
<td>1.3 2.71 5.89</td>
<td>Farranula gibbula</td>
<td></td>
</tr>
<tr>
<td>Corycaeus crassiusculus</td>
<td>2.41 0.85 4.69</td>
<td>Oncaea venusta</td>
<td></td>
</tr>
<tr>
<td>Oncaea venusta</td>
<td>2.21 0.62 4.66</td>
<td>Cantocalanus pauper</td>
<td></td>
</tr>
</tbody>
</table>

A.A: Average Abundance.

Table 5
Results of redundancy analyses (RDA) for the taxonomic categories such as (a) mesozooplankton and (b) copepod species including their diversity index with the environmental variables. The p-values were obtained by forward-selected Monte Carlo analysis with 999 permutation tests at p < 0.05. Symbols for environmental variables are as in Fig. 5 and N.S. denotes not significant.

<table>
<thead>
<tr>
<th>Environmental variables</th>
<th>Variance explained</th>
<th>F-ratio</th>
<th>p-value</th>
<th>Correlation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Eigen value</td>
<td>Axis 1</td>
<td>Axis 2</td>
<td></td>
</tr>
<tr>
<td>(a) Mesozooplankton</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SST</td>
<td>0.31</td>
<td>4.49</td>
<td>&lt;0.01</td>
<td>0.711   -0.431</td>
</tr>
<tr>
<td>Salinity</td>
<td>0.42</td>
<td>0.96</td>
<td>NS</td>
<td>0.278   0.158</td>
</tr>
<tr>
<td>pH</td>
<td>0.25</td>
<td>1.00</td>
<td>NS</td>
<td>0.060   0.032</td>
</tr>
<tr>
<td>DO</td>
<td>0.39</td>
<td>1.14</td>
<td>NS</td>
<td>0.206   0.294</td>
</tr>
<tr>
<td>TSM</td>
<td>0.34</td>
<td>1.31</td>
<td>NS</td>
<td>0.276   0.267</td>
</tr>
<tr>
<td>NO3</td>
<td>0.38</td>
<td>2.07</td>
<td>NS</td>
<td>0.458   0.254</td>
</tr>
<tr>
<td>NO2</td>
<td>0.21</td>
<td>1.68</td>
<td>NS</td>
<td>0.036   0.710</td>
</tr>
<tr>
<td>CO3</td>
<td>0.28</td>
<td>1.55</td>
<td>NS</td>
<td>0.036   0.710</td>
</tr>
<tr>
<td>SiO3</td>
<td>0.16</td>
<td>6.24</td>
<td>NS</td>
<td>0.895   0.205</td>
</tr>
<tr>
<td>DOC</td>
<td>0.36</td>
<td>1.31</td>
<td>NS</td>
<td>0.240   0.441</td>
</tr>
<tr>
<td>nh-chl-a</td>
<td>0.41</td>
<td>0.68</td>
<td>NS</td>
<td>-0.066  0.025</td>
</tr>
<tr>
<td>Total</td>
<td>3.51</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

| (b) Copepod species     |                    |        |         |
| SST                     | 0.42               | 6.54   | NS      | -0.904  0.169 |
| Salinity                | 0.37               | 0.80   | NS      | 0.192   0.134 |
| pH                      | 0.45               | 1.03   | NS      | 0.186   0.340 |
| DO                      | 0.25               | 2.31   | <0.05   | -0.438  0.228 |
| TSM                     | 0.44               | 1.97   | <0.05   | -0.451  0.326 |
| NO3                     | 0.28               | 2.00   | <0.05   | -0.348  0.320 |
| NO2                     | 0.31               | 1.21   | NS      | 0.186   0.079 |
| PO4                     | 0.21               | 1.55   | NS      | -0.210  0.342 |
| SiO3                    | 0.17               | 6.78   | <0.01   | -0.922  0.033 |
| DOC                     | 0.40               | 1.37   | NS      | -0.378  0.139 |
| nh-chl-a                | 0.34               | 1.02   | NS      | -0.006  0.465 |
| Total                   | 3.64               |        |         |

indicating a low concentration of chl-a when the diversity of copepods were high (Fig. 10a). Whereas, a significant positive correlation between chl-a and copepod dominance ($\chi^2 = 0.434$, p < 0.05) suggested their preference over alternative energy sources (Fig. 10b). The density of copepods in the study area was significantly related to SST ($r = 0.344$, p < 0.05, n = 35). Density, on the other hand, did not show significant relation with chl-a and other parameters such as salinity, pH and DO ($r < 0.25$, p > 0.05, n = 35).

4. Discussion

4.1. Oceanographic conditions

Southeast Arabian Sea experiences low primary productivity during the early southwest monsoon resulting from weak winds, intense solar radiation and low water column nutrients (Jyothibabu et al., 2010, 2018; Jagadeesan et al., 2017a). The process of coastal upwelling results in cool and poorly oxygenated surface water that is rich in nutrients and affects the biological productivity of the region (Somoue et al., 2005; Bode et al., 2014; Jagadeesan et al., 2017a; Jyothibabu et al., 2018). However, the findings of the present study revealed that the existence of well-oxygenated water and high SST indicates weak or null upwelling (Fernandes and Ramahia, 2009), particularly during the sampling period. Preenu et al. (2017) established that the date of onset of monsoon over Kerala has a long term (1870–2014) mean of 1st June and standard deviation of 7–8 days which is mainly associated with SST anomalies. During the year 2014, the monsoon onset over 6th June in the southwest coast of India (Preenu et al., 2017) however, our sampling being undertaken during May, before the onset of monsoon. Accordingly, the higher salinity (mostly >35) obtained around the study area (Table 1) could be explained by the cumulative influence of warm SST and high rate of evaporation during pre-monsoon (Preenu et al., 2017; Behara et al., 2019). Salinity decrease in the southeastern Arabian Sea, in general, largely due to local rainfall and river runoff during southwest monsoon (Fig. 2) (Shankar et al., 2005; Madhu et al., 2007; Jyothibabu et al., 2008), the influence of prevailing coastal current and advection of low saline Bay of Bengal (BoB) water by winter monsoon current (Behara et al., 2019; Karati et al., 2019). Kerala coast receives an
important contribution from rivers; organic particles are imported into the waters of these rivers and drained from terrestrial environments. Although variation in the salinity showed lack of statistical significance, the regional comparison revealed relatively low level in the S-KL attributed to numerous river discharges (Jyothibabu et al., 2008, 2018; Rao et al., 2017) and the possible trace of intrusion from BoB high-salinity water (Behara et al., 2019; Karati et al., 2019). Higher TSM concentrations at both S-KL and N-KL, could be attributed to the inflow of riverine freshwater flux into the coast following the demise of the southwest monsoon (June to September) and post-monsoon (October to December) (Madhu et al., 2007; Rao et al., 2017). Such inputs can increase planktonic growth and support an economically important and biologically diverse fishery in the region. Further, a significant positive correlation between TSM and chl-α from N-KL (r = 0.599, p < 0.05) and S-KL (r = 0.625, p < 0.05) coast highlights the relative contribution of phytoplankton to TSM (Tang et al., 2013).

Factors such as the release of phosphorus from the mudbanks of Alleppey coast (Fig. 5), the influence of turbulent mixing, organic remineralisation and adsorption-desorption process in S-KL could explain the relatively higher concentration of inorganic phosphate and silicate along S-KL and N-KL coast respectively (Jyothibabu et al., 2018). Similarly, a high silicate concentration along the N-KL coast reinforces the important contribution of river discharge into coastal waters (Rao et al., 2017). These nutrients stimulate phytoplankton growth and enhance chl-α concentration during this period of the year along the Kerala coast. As depicted in the orientation analysis, the high DO concentration observed at S-KL and S-TN may be due to high photosynthetic production of oxygen supported by relatively low temperature (Figs. 5 and 9). Despite all the dynamic processes, the hydro-biological conditions of southwest coast were mostly governed by freshwater influx from the rivers (Rakhesh et al., 2015). Furthermore, the southern stretch of N-KL (stations 8 to 11) and the northern stretch of S-KL (stations 1 to 4, Fig. 1) were characterised by high DO and nitrate indicating the possible influence of land runoff from Cochin Backwater and other rivers (Ezhilarasan et al., 2018).

4.2. Mesozooplankton abundance and composition

This study presents a comprehensive record of the mesozooplankton community and copepod species composition, with relevance to the regional hydrological conditions. Mesozooplankton maxima differed significantly from earlier reported values of Padmavati et al. (1998)
from central and eastern Arabian Sea (Gujarat) (76,778 ind. m$^{-3}$). The present values, however, found to be consistent with the earlier studies from Goa to Gujarat (Padmavati and Goswami, 1996), Cochin backwaters (Madhu et al., 2007), Alappuzha, mudbanks and coastal upwelling region (Jyothibabu et al., 2018) and from discrete depths along coastal regions of the southern Arabian Sea during winter monsoon (Karati et al., 2019). The low density and biomass of zooplankton during the study period is consistent with the observation by Jyothibabu et al. (2018). The zooplankton density and biomass reported during the early-monsoon was 1087 ± 199 ind. m$^{-3}$ and <1.5 ml m$^{-3}$, respectively, due to the time lag involved in nutrient enrichment (Jyothibabu et al., 2018). The mean zooplankton density in the present study varied widely concerning those reported from other tropical regions viz. the Red Sea (Dorgham et al., 2012; Al-Aidaroos et al., 2016), South China Sea (Relox et al., 2000), Northern Chile Bay (Torreblanca et al., 2016), Central Peru (Criales-Hernandez et al., 2008) and elsewhere from the subtropical and temperate regions (Fig. 11). Variations in zooplankton density and dynamics of community structure across geographical boundaries could be attributed to (a) bioavailability of natural food (El-Sherbiny et al., 2007; McKinstry and Campbell, 2017), (b) fluctuation in environmental variables such as temperature, salinity, nutrients and rainfall (Jyothibabu et al., 2006, 2018; Madhu et al., 2007; Rombouts et al., 2009; Chang et al., 2014; McKinstry and Campbell, 2017), (c) upwelling events (Somoue et al., 2005; Karati et al., 2014) and (d) oxygen minimum layer (Criales-Hernandez et al., 2008; Madhupratap et al., 2001a; Karati et al., 2014). Furthermore, the differences in the zooplankton density might be due to the difference in the field sampling (vertical or horizontal tow), time and sampling gears used (type and mesh size) (Al-Aidaroos et al., 2016; Leitao et al., 2019).

The findings corroborated that copepods were most abundant in the west coast as reported by earlier studies from estuarine (Jyothibabu et al., 2006, 2018; Madhu et al., 2007), coastal (Karati et al., 2019) and offshore areas with sporadic dominance of other zooplankton groups (Padmavati et al., 1998; Madhupratap et al., 2001a; Fernandes and Ramaiah, 2014) as in the present study. In the tropical regions, small-sized copepods contribute to the bulk of zooplankton abundance (Rakhesh et al., 2013; Piontkovski et al., 2013; Li et al., 2016). Similarly, in the present study, high zooplankton abundance was mainly attributed to the small-sized copepods (51.2%), Bestiolina, Parvocalanulus, Acrocalanus, Corycaeus, Oncaea and Oithona along with other co-occurring species (Canthocalanus pauper, Centropages furcatus, Centropages ornithi and Temora turbinata). Besides, Acartia erythraea, C. pauper, C. furcatus and Corycaeus sp. were neritic copepods widely distributed in the coastal waters of India (Madhu et al., 2007; Rakhesh et al., 2008; Cornills et al., 2010; Fernandes and Ramaiah, 2014; Jyothibabu et al., 2006, 2018) playing a crucial role in the neritic food web (Turner, 2004; Rakhesh et al., 2013; Li et al., 2016).

4.3. Spatial heterogeneity and copepod distribution

The study of copepod species from the tropical coastal waters of Goa to Thoothukudi showed significant heterogeneity in spatial diversity, possibly caused by a large array of environmental influences. Variation in environmental forces such as physicochemical factors, the bioavailability of natural food and geographical location are expressed in distinct spatial heterogeneity of copepod assemblage at coastal waters. The conditions of each station may have a significant impact on the community structure, which in turn alter the general pattern of the studied region (Machado et al., 2016; Leitao et al., 2019; Karati et al., 2019). In case of the present study region, the conditions such as riverine freshwater influx, advection of neighbouring water mass, the influence of coastal currents, coastal local upwelling and a rich source of unequivocal food concentration were identified as the potential spatial features may contribute to the observed heterogeneity in the community assemblage and distribution.

Spatial heterogeneity in copepod assemblage was apparent among the regions investigated with diversity decrease geographically from north to south and also from west to east and the highest be recorded at KA and least diversity registered at S-TN coast. The observed dissimilarity in copepods assemblage structure was mainly attributed to neritic species such as A. erythraea, C. pauper, Farranula gibbula, Bestiolina similis, C. furcatus, Acrocalanus gibber and T. turbinata, reasonably most of these species are strongly associated with RDA Axis 1 (Fig. 9b). The neritic waters are influenced by high river influx, the formation of mudbanks and frequent upwelling has been identified as the most important factors regulating productivity of the Arabian Sea (Jyothibabu et al., 2008, 2010; 2018). In general, low density and high diversity for copepod species occurred in the coastal waters of KA. This result is based on the taxonomic composition of copepod population, with a mixed size-gradient contributed by small-sized copepods, Paracalanidae (27%) and other families such as Centropagidae (12.6%), Calanidae (12.5%), Acartiidae (7.8%) and Subeucalanidae (4.5%), considered coastal larger-body calanoid copepods (Jyothibabu et al., 2010; Bode et al., 2014; McKinstry and Campbell, 2017) (Supplementary Table 1) resulting in sustainable utilization of the available resources (McKinstry and Campbell, 2017). Furthermore, Penilia avirostris (Cladocera), although typical inhabitant of neritic waters, their ability to adapt for a flexible range of feeding diet including small and elongated diatoms and microzooplankton (Umanai et al., 2005; Piontkovski et al., 2013) and being a warm water species sequester higher abundance (Sommer and Sommer, 2006; Ozdemir and Orhan, 2012), consequently evidencing the trophic niche available for other communities. The results of RDA analysis also showed a strong relation between P. avirostris and temperature (Fig. 9a).

The areas with higher copepod diversity are characterized by warm water, lower oxygen concentrations and primary production (Rombouts et al., 2009; Fernandes and Ramaiah, 2009), that was concomitant with the conditions at KA coast. The coastal system dominated with river influx, these estuarine-coastal systems, in general, tends to decrease the...
overall diversity of the region due to the colonization and dominance by few opportunistic species adapted to endure the natural variability (Montoya-Maya and Strydom, 2009; Araujo et al., 2016; Salvador and Bersano, 2017). In contradiction, the relatively low influence of river input (~14 rivers drain into the coast compared to >50 numbers in Kerala) and associated low phytoplankton production presented stable hydrological structures that also ensure the availability of higher vertical niche (Rombouts et al., 2009; Jyothibabu et al., 2010; Rao et al., 2017). The verified occurrence of demersal copepod family the Pseudodiaptomidae during daytime in the subsurface waters related to other regions suggested the prevalence of such vertical niche (Cornils et al., 2010) and, hence could support high diversity (Rombouts et al., 2009). For instance, it is important to note that abundance of other estuarine-coastal families, the Acartiidae was prominent (Montoya-Maya and Strydom, 2009; Salvador and Bersano, 2017); however, except for F. gibbula (10.6%), none of the other species occurred greater than 10% of relative abundance.

Leitao et al., 2019), along the southwest coast which is enriched with river discharges (Rao et al., 2017; Jyothibabu et al., 2018; Sato et al., 2015), as opposed to other regions, in particular to S-TN. Further, the high concentration of silicate and TSM along this coast highlights the important contribution of river discharge into coastal waters (Rao et al., 2017), and the later could be a source of nutrients for the detritivorous zooplankton (Fernandes and Ramaiah, 2009). RDA also indicated that these environmental variables are significant contributors influencing on the copepod species assemblage (\( p < 0.05; 999 \) Monte Carlo permutations) (Table 5) and also reinforce the importance of river influx on the zooplankton community structure. Moreover, predation of planktivorous fish in the coastal areas might have sustained the abundance of small-sized copepods, which in turn serves as important prey for fish larvae, and other planktivores (Turner, 2004; Nair, 2015; Sato et al., 2015; McKinstry and Campbell, 2017). Higher biomass of copepod communities could explain high fishery potential from the south of 15°N. This signifies the importance of food web interactions in sustaining commercially important planktivorous fishes such as sardines (Sardinella longiceps), mackerels (Rastrelliger kanagura) and anchovies (Engraulis ringens, Engraulis mordax). Stolephorus watieri, Stolephorus commersonii and Stolephorus indicus) along the southwest coast of India (Madhupratap et al., 2001b; Nair, 2015).

The coastal region of S-KL is extremely complex, undergoes regular oscillation, affected by combined effects from mudbanks explained by the higher concentration of inorganic phosphate (Madhupratap et al., 2001b; Nair, 2015; Jyothibabu et al., 2018), local rainfall and river runoff (Shankar et al., 2005) and advection of low-salinity BoB water during winter monsoon period (Behara et al., 2019). Karati et al. (2019) demonstrate that intrusion of BoB water and coastal circulation during winter monsoon is an important factor for shaping the spatial structure of zooplankton distribution and abundance in the coastal Arabian Sea. Concomitantly, the low salinity observed in the S-KL indicates the residence of low-salinity BoB water during the study period. The exchange of water masses between these ocean basins add complexity to its hydrography and critical to the pattern of zooplankton community structure (Karati et al., 2019). Furthermore, Jyothibabu et al. (2018) suggested that mudbanks in the S-KL has been characterised by high turbidity and serene sea surface conditions during southwest monsoon have significant influence on planktonic productivity.

On the other hand, a mixed assemblage contributed by Paracalanidae (B. similis) and Cladocera (Eucyclops teregestina) in S-KL, evidencing the synergetic effect of estuarine influence and intrusions of neighbouring water mass on the assemblage structure (Anjusha et al., 2013). Although a significant difference in copepod assemblage was evident when compared to S-TN coast (Table 4 & Supplementary Table 1), however, the variation remained to be moderate (R = 0.41; \( p < 0.01 \)). Besides, the occurrence of neritic copepods, such as C. pauper, Undinula vulgaris, Candacia discoidata, Calanopia minor, Temora discoidata and T. turbinata, which were relatively abundant found in S-TN coast (Fig. 9b) suggested that probable impact of water mass exchange on copepod assemblage in S-KL during the study period. Thus, patterns obtained in this study reflect the distributions and abundances of copepod species resulted in the conspicuous separation of southernmost stations of S-KL (Fig. 8). Moreover, the prevalence of similar environmental conditions between the N-KL and the S-KL may contribute to the lack of a statistically significant variation (ANOSIM, \( p > 0.05 \)) indicating the river influx was the main determinant for community structure, although water mass exchange was of some importance.

The studied region of S-TN has been endowed with high biomass benthic habitats (coral reef and seagrass ecosystem) known for its rich biodiversity and support a large number of finfish, crustaceans and molluscs (Kumaraguru et al., 2006; Bavinck and Vivekanandan, 2011; Joshi et al., 2016). Despite the significant difference in the copepod assemblage and low density at S-TN coast related to favourable conditions, such as low temperature and phytoplankton production (evidenced by the high concentration of DO and chl-\(a \)) (Fig. 9b), favouring cladoceran swarm (P. avirostris and E. teregestina). High zooplankton biomass at a similar condition of low temperature and high DO have been previously described (Fernandes and Ramaiah, 2014). Similarly, high abundance of T. turbinata and U. vulgaris at surface waters has been described as an indicator of upwelling (Rakhesh et al., 2008; Jagadeesan et al., 2013; Anjusha et al., 2013), and such opportunistic copepods are suspension feeders on phytoplankton and other particles efficient in exploiting favourable nutritional conditions (Wu et al., 2010). Although they belong to a different taxonomic group, their dominance in the ambient environmental condition reflects the importance of the functional trait, the efficient herbivore (Kurt and Polat, 2012; Anjusha et al., 2013), in determining the successful co-occurrence in the region (Machado et al., 2016).

The distribution of E. teregestina was closely related to a lower temperature, which is characteristically herbivores and additive competitor for resources of copepods (Sommer and Stibor, 2002; Kurt and Polat, 2012), in contrast, El-Sherbiny et al. (2007) and Cornils et al. (2010) reported their abundance in the warm eutrophic environment. Ezhilarasan et al. (2018) found a similar result to the western coast suggesting their abundance could consistently be related to the ambient temperature, salinity and chl-\(a \). Also, these species are wide-spread marine cladocerans that inhabit neritic waters circumglobally (Isari et al., 2007; Cornils et al., 2010; Piontkovski et al., 2013). Consequently, the substantial growth in the population of E. teregestina (41.8%) and P. avirostris (10.2%) along the S-TN coast could be attributed to parthenogenetic regeneration, causing swarming of monospecific female populations which outnumbered copepods (Tang et al., 1995; Isari et al., 2007; Ezhilarasan et al., 2018). Comparable to earlier studies, Madhupratap et al. (2001a) observed great swarms of ostracods along the northern Arabian Sea, however in the oceanic waters of BoB swarms of echinoderm larvae (60%) replaced the copepod dominance, related to their slower swimming behaviour and dispersal by surface (Fernandes and Ramaiah, 2014). However, further time-series monitoring is necessary to ascertain whether the abundance of cladocerans over copepods observed here is cyclical or sporadic.

4.4. Copepod assemblage and trophic structure

In general, biological uptake is responsible for the depletion of nutrient concentrations in the surface waters; however, such a relationship was not evident in the present study. Insignificant relationship (\( p > 0.05, r < 0.3, n = 35 \)) of chl-\(a \) with seawater nutrients (nitrate, phosphate and silicate) suggest surplus nutrient leaching from soft sediments of mudbanks, riverine influx, and other land-based sources (Supplementary Fig. 1). However, all nutrients showed negative correlations in S-KL with DO indicating biological uptake of nutrients with the photosynthetic release of oxygen. Moreover, in N-KL, chl-\(a \) showed linear relation with DOC, indicating its origin from primary production, but in S-KL, no such relationship is evident probably due to allochthonous inputs (Krishna et al., 2015). Regression analysis revealed that dissolved silicate (\( p < 0.05 \)) had a significant relation with chl-\(a \), whereas the influences of the remaining factors were limited.

The coupling of high mesozooplankton abundance and high ichthyoplankton density recorded at S-KL waters in the present study was consistent with those reported by Madhu et al. (2007). These results further signify the role of tropical estuaries in sustaining the aquatic food web and the associated fishery potential of the region. The results of RDA and Pearson correlation analysis indicated that an inverse relationship among the diversity and dominance index and diversity index with chl-\(a \) (Fig. 9b). These relationships could be assumed as higher grazing pressure over phytoplankton standing crop under highly diverse conditions. In contrast, a positive relationship between chl-\(a \) and dominance index suggested that the phytoplankton stock remained un-grazed due to the dominance of small size copepods (Bestiolina, Parvocalanus, Oithona, Oncaea, and Corycaeus). Small-sized copepods may rely on microplanktonic organisms by adopting omnivorous conditions.
feeding habits, to meet their nutritional requirements (Turner, 2004; Jagadeesan et al., 2017b). The size of the prey has a significant role in the feeding habit of copepods as they can preferentially select larger food particles to improve their feeding efficiency (Jagadeesan et al., 2017b; Liu et al., 2010). Despite the clear reductions in copepod diversity, ecologically important predators (small-sized copepods) efficiently sustain the material fluxes by playing a crucial trophic role in the region (Fig. 10a and b). Chl-a have been considered as a proxy for phytoplankton biomass available to copepods, therefore, the relationship between copepod diversity index and chl-a indicates that the region is more stable in terms of planktonic productivity as suggested by Rombouts et al. (2009). Furthermore, an extensive study on feeding strategy of copepods and their response to microbial food components (Wu et al., 2010; Steinberg and Landry, 2017), could minimize the knowledge gap and provide a better understanding of the trophodynamics of this unique food web.

5. Conclusions

The present study evaluated the spatial heterogeneity of mesozooplankton abundance and community structure on a long coastline with a single stretch observation during pre-monsoon. The limited sampling effort concluded that the studied region presents a significant spatial heterogeneity in the community assemble, with high diversity restricted to KA coast, high abundance occurred along N-KL and S-KL coast and low diversity in S-TN coast, governed by hydrographic dynamics, which could be to differences in the spatial attributes. The river influx was the main determinant for zooplankton community structure, despite the influence of different water mass and mainly affected by local oceanographic conditions. However, the observed spatial heterogeneity due to the swelling effect of certain groups, separating S-TN coast perhaps not confirmed by our inadequate sampling effort from single cruise to address these kinds of processes. The environmental variables such as sea surface temperature, nutrients (SiO\(_2\) and NO\(_2\)), dissolved oxygen and total suspended matter were significant influencing factors for the mesozooplankton community structure during pre-monsoon. Mesozooplankton abundance revealed its strong dependence on small size copepods. Despite, the contrasting relationship of copepod diversity and dominance index with chlorophyll a concentration presented a clear insight into the prevalent trophodynamic structure of the region. Characterizing these patterns of variability and the effect of change in community structure, especially of small copepods, require long-term monitoring at a lower taxonomic level. The region of southwest coast is a potential zone for planktivorous fishes, therefore, the information on mesozooplankton distribution could reinforce to understand their spawning habitat and recruitment success. Furthermore, the study signifies the need for an increased understanding of the unique geospatial features on mesozooplankton distribution and abundance.

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.

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Appendix A. Supplementary data

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