Progress in Oceanography 156 (2017) 252–275

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

# Dominance of coastal upwelling over Mud Bank in shaping the mesozooplankton along the southwest coast of India during the Southwest Monsoon

L. Jagadeesan, R. Jyothibabu *, N. Arunpandi, C. Karnan, K.K. Balachandran

*CSIR- National Institute of Oceanography, Regional Centre, Kochi 682018, India*

A R T I C L E I N F O

*Article history:*
Received 8 February 2016
Received in revised form 29 June 2017
Accepted 11 July 2017
Available online 14 July 2017

*Keywords:*
Mud bank
Upwelling
Mesozooplankton
Copepods
Hydrography
Multivariate analysis

A B S T R A C T

Mud Banks are littoral zones along the Kerala (southwest) coast of India with increased suspended sediments during the Southwest Monsoon (SWM), which facilitate remarkable damping of incident waves creating a localized calm sea environment conducive for fishing activities. In this paper, we used the response of mesozooplankton community as a whole and copepod species in particular as a tool to characterize the relative importance of Coastal Upwelling and Mud Bank in shaping the biological manifestations along the southwest coast of India. The geographical area studied was off Alappuzha (Kerala coast) and altogether 18 field samplings (weekly/fortnightly) were carried out in three locations in the region (M1, M2 and M3) from the Pre-SWM to the Late-SWM of 2014. M1 was a reference location at the same depth contour (6 m) and 10 km north of location M2 that represented the region where the Mud Bank forms during the SWM. Location M3 was situated beyond the offshore boundary of the Mud Bank zone (12 m depth), perpendicular to location M2. The physical characteristics of the Mud Bank, such as relatively high suspended sediments and calm sea conditions, existed at M2 by mid-June and before that all the three locations had comparable physical characteristics in the water column. Coastal Upwelling was prevalent over all the three locations by early-June, characterized by cool and less oxygenated waters, more so in the subsurface waters. The mesozooplankton community in the study domain was composed of 15 heterogeneous groups; their biomass and abundance were high during the Peak- (av. $6.02 \pm 5.19$ ml m$^{-3}$ and av. $7285 \pm 3248$ No m$^{-3}$) and Late-SWM (av. $4.91 \pm 4.35$ ml m$^{-3}$ and av. $6802 \pm 2727$ No m$^{-3}$) compared to the Pre-SWM (av. $0.63 \pm 0.55$ ml m$^{-3}$ and av. $3045 \pm 1584$ No m$^{-3}$) and Early-SWM (av. $0.58 \pm 0.46$ ml m$^{-3}$ and av. $2047 \pm 1675$ No m$^{-3}$). Mesozooplankton abundance was dominated by copepods (>70%) and the number of larger zooplankton carnivores (medusae, siphonophores and chaetognaths) was found to be low (<5%). Altogether, 43 species of copepods were recorded from the present study. Based on the abundance and species distribution of copepods in all three locations, cluster and SIMPROF analyses delineated four environmental conditions (clusters) typical of Pre-SWM (cluster 1), Early-SWM (cluster 2), Peak-SWM (cluster 3) and Late-SWM (cluster 4). SIMPER analysis demarcated the discriminating species of copepods in the environmental clusters delineated by cluster/SIMPROF. The discriminating copepods were composed of *Acartia danae*, *A. erythraea*, *Centropages orsini* (cluster1); *Temora turbinata* (the upwelling indicator) (cluster 2); *Oithona similis* (cluster 3); *Temora turbinata*, *Pseudodiaptomus serricaudatus*, *Centropages tenuremis* (cluster 4). The dominance and distribution pattern of copepods observed in all three study locations were very similar and the detailed Multivariate Redundancy analysis confirmed the dominant influence of Coastal Upwelling and not the Mud Bank in structuring the mesozooplankton/copepod community in the study domain. The present study provides the first in-depth information on the mesozooplankton (especially copepods) from a Coastal Upwelling - Mud Bank system along the southwest coast of India, evidencing the dominant role of Coastal Upwelling in shaping the zooplankton community during the SWM.



## 1. Introduction

Mud Bank (Chakara) is a well-known but, enigmatic coastal feature that occurs annually during the Southwest Monsoon

* Corresponding author.
*E-mail address:* rjyothibabu@nio.org (R. Jyothibabu).

http://dx.doi.org/10.1016/j.pocean.2017.07.004
0079-6611/

(June - September) in fragmented stretches of the Kerala coast (Southwest coast of India). It is a unique feature attracting scientific and public interest from time immemorial principally due to the rich fishery associated with the event (Bristow, 1938; Du cane et al., 1938; Damodaran, 1973; Gopinathan and Qasim, 1974; Silas, 1984). Essentially, Mud Banks are semicircular patches of calm littoral waters carrying a relatively high load of suspended sediments. Their seaward extent typically occurs along the 10 m depth contour and their alongshore dimension is about 3–6 km (Kurup, 1977; Silas, 1984). The thick fluid muddy layer that exists close to the sea bottom during the Mud Bank facilitates damping of waves, making the environment conducive for fishing activities at a time that the rest of the region experiences strong monsoonal sea conditions unsuitable for fishing (Damodaran, 1973; Gopinathan and Qasim, 1974; Silas, 1984; Mallik et al., 1988). Even though Mud Banks occur in several places along the Kerala coast (Damodaran, 1973; Silas, 1984), the one that forms off Alappuzha receives special attention due to (a) its consistent occurrence every year and (b) large fisheries associated with it (Damodaran, 1973; Silas, 1984; NIO Report, 2008). Although a dozen hypotheses are in place to explain the formation of Mud Bank along the Kerala coast (Ramasastry and Myrland, 1959; Silas, 1984; Mathew et al., 1995; Manojkumar et al., 1998; Tatavarti et al., 1999; Narayana et al., 2001; Balachandran, 2004), all of them leave uncertainty in explaining one or the other characteristics of the Mud Bank that occurs along the Kerala coast. Nonetheless, it is a fact that large landings of fishes are associated with the Alappuzha Mud Bank event every year during the Southwest Monsoon period (Regunathan et al., 1984a,b). The Mud Bank region, due to its calm environment, serves predominantly as a launching and landing place for fishing vessels rather than an actual fishing ground itself (Regunathan et al., 1984a,b).

Upwelling in the nearshore waters along the Southwest coast of India begins by the onset of the Southwest Monsoon (June) and gets intensified during July - August (Madhupratap et al., 1996; Nair et al., 1992; Jyothibabu et al., 2008). Its presence during the Southwest Monsoon is indicated by the advection of cool, nutrient-rich, hypoxic subsurface waters towards the coast, leading to significantly high plankton biomass and production (Madhupratap et al., 1996, 2001; Smith and Madhupratap, 2005; Jyothibabu et al., 2006, 2008). Recent studies showed that both local wind stress and remote forcing contribute to the formation of coastal upwelling along the southwest coast of India (Gupta et al., 2016 and references therein). Certainly, the coastal upwelling areas possess immense socio-economic significance as they represent the regions of high fishery resources (Banse, 1959, 1968; Cury et al., 2000). World over, upwelling systems that occupy only 0.1% of the total oceanic area contribute around 20% of the world fish production (Cury et al., 2000). It is evident in the above description that coastal upwelling along the southwest (Kerala) coast of India during the Southwest Monsoon facilitate significant enhancement in plankton biomass.

Zooplankton are good indicators of hydrographical transformations in marine systems, as they respond to even subtle changes in the physical, chemical and biological properties in their surroundings (Queiroga and Blanton, 2004; Jagadeesan et al., 2013). Among around 15 zooplankton groups that normally occur in Indian seas, copepods generally contribute numerically 60–90% of the community and play a significant role in the planktonic food web (Jagadeesan et al., 2013). Their community/species response is considered to be a true indication of the prevailing hydrographical settings (Madhupratap et al., 1996; Jagadeesan et al., 2013). The current understanding is that the plankton biomass (both phyto - and zooplankton) in the inshore waters along the Southwest coast of India increases noticeably during the Southwest Monsoon period associated with intense coastal upwelling (NIO Report, 2008; Jyothibabu et al., 2008, 2010; Asha Devi et al., 2010). Similar is the case of the Alappuzha Mud Bank (present study area), wherein the water column becomes highly productive during the Southwest Monsoon (Mathew et al., 1977, 1984; Nair et al., 1984). As coastal upwelling and Mud Bank formation occurs during the same period (Southwest Monsoon), their specific role to enhance the plankton biomass is rather unclear. Therefore, in this study, we investigated the response of the mesozooplankton community as a whole and copepod species in particular to understand the specific biophysical roles of Mud Bank and coastal upwelling along the southwest coast of India during the Southwest Monsoon period.

The following aspects of the mesozooplankton community in the study region were considered with respect to the hydrographical settings; (a) temporal and spatial changes in biomass, abundance and composition of mesozooplankton (b) delineating the dominant and discriminating species of copepods during the different phases of hydrographical transformations associated with Mud Bank and coastal upwelling events, (c) the relative importance of coastal upwelling and the Mud Bank in shaping the copepod community (d) to verify whether there is a specialized zooplankton community adapted to the relatively turbid environment of the Mud Bank region.

## 2. Materials and methods

### 2.1. Environment and sampling

The Mud Bank area studied is located south of Alappuzha in Kerala, along the Southwest coast of India, between 9.25 to 9.43°N and 76.3–76.4°E. Baseline information on the biological characteristics of the Alappuzha Mud Bank is available in some of the historical studies on plankton (Mathew et al., 1977, 1984; Nair et al., 1984), benthos (Damodaran, 1973; Regunathan et al., 1984a) and fisheries (Regunathan et al., 1981, 1984b). In general, diatoms dominate throughout the Mud Bank phase, while dinoflagellates (especially *Noctiluca* sp.) occur abundantly and sporadically during the peak and late phases of the Mud Bank (Subrahmanyan et al., 1975; Nair et al., 1984). A review of the literature indicates that the phytoplankton successional pattern in the Mud Bank area is not very different from what exists all along the southwest coast of India during the Southwest Monsoon period governed by coastal upwelling (Subrahmanyan, 1959; Nair et al., 1992; Madhupratap and Parulekar, 1993; Naqvi et al., 1998; Sahayak et al., 2005). Compared to the phytoplankton community, studies on the mesozooplankton community from the Alappuzha Mud Bank is more generic in nature and basically deal with group level information (Mathew et al., 1977, 1984).

As a part of a focused study on the Mud Bank of Alappuzha in 2014 [Alappuzha Mud Bank Process Studies (AMPS)], 18 field samplings were carried out in three different locations (M1, M2 and M3) in the study domain off Alappuzha, southwest coast of India Fig. 1. Location M1 was a reference (non-Mud Bank) point at the same depth contour (6 m) but 10 km northward from M2 (Mud Bank location). Location M3 was situated beyond the offshore boundary of the Mud Bank (12 m depth) and perpendicular to the Mud Bank location M2. Field sampling at these three locations were carried out from April (Pre-Southwest Monsoon) to September 2014 (Late Southwest Monsoon) including 15 weekly samplings (April 22nd to 2nd August) and 3 biweekly samplings (16th August to 20th September). In total, four sampling phases were considered: Pre-Southwest Monsoon (Pre-SWM), Early-Southwest Monsoon (Early-SWM), Peak-Southwest Monsoon (Peak-SWM) and Late-Southwest Monsoon (Late-SWM).

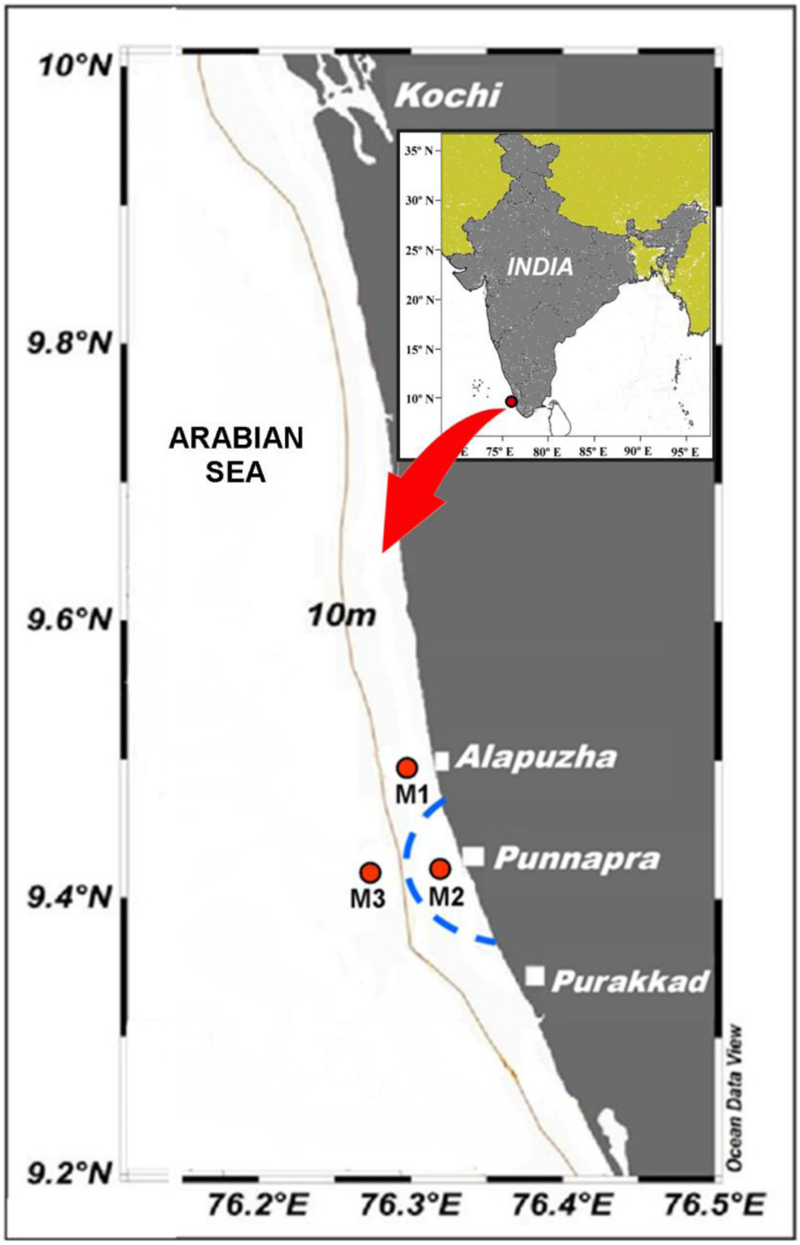


**Fig. 1.** Study domain and locations. Region where Mud Bank formed during the Southwest Monsoon (June – September) is indicated by thick, blue discontinuous semi-circle. Locations M2 represent the Mud Bank region and M1 a reference location at the same depth contour and 10 km far from the Mud Bank region. M3 was located beyond the offshore boundary of the Mud Bank, perpendicular to location M1. Weekly/biweekly time series sampling were carried out from all three locations (M1, M2 and M3) from the Pre-SWM (March) to the Late-SWM (September) in 2014.

### 2.2. Methods

In order to explain the general hydrographical setting, satellite data resources were utilized along with *in-situ* data. The rainfall (mm/day) in the study area was downloaded from Tropical Rainfall Measuring Mission (TRMM) using the Giovanni online portal of NASA (http://disc.sci.gsfc.nasa.gov/giovanni). The weekly mean data of precipitation was available in spatial color plots. Daily ocean surface wind data (ASCAT) was retrieved from the Ocean Watch LAS server (http://oceanwatch.pifsc.noaa.gov/las/servlets/index) and their weekly means and SD (standard deviations) were chosen to match the field sampling period. Vertical profiles of temperature and salinity in different sampling locations were measured using a calibrated Seabird Conductivity, Temperature and Depth (CTD) profiler (SEACAT SBE 19 plus). Water samples were collected from discrete depths using a 5L Niskin sampler (Hydrobios-Kiel) for chemical and biological parameters. Dissolved oxygen was measured following Winkler's method and nutrients using standard procedures of Grasshoff (1983). Chlorophyll *a* was measured using a calibrated Turner lab flourometer (Model: 7200–000, Trilogy, Turner designs, USA) following the JGOFS protocols (UNESCO, 1994). The CTD sensor chlorophyll *a* data was corrected using lab flourometer data (lab Chl. $a = 1.604^{*}$ CTD measured Chl. $a + 0.072$; $r = 0.88$; $P < 0.0001$) and used for generating the high resolution vertical profiles. Mesozooplankton samples were collected using a standard ring net with a mouth area of 0.3 $m^2$ and 200 μm mesh size. Samples were filtered through a 200 μm nylon sieve (Hydrobios) and the excess water in the samples was removed using blotting paper. The biomass of the mesozooplankton was measured as displacement volume (Postel et al., 2000).

Zooplankton samples were preserved in 4% formalin in filtered seawater for detailed taxonomic analysis. Zooplankton sub-samples (50%) were sorted and taxonomic group level abundance was estimated (Postel et al., 2000). Among various taxonomic groups, copepods were further analyzed and identified to the species level using standard literature (Kasturirangan, 1963; Conway et al., 2003; Sewell, 1999).

### 2.3. Data analysis

#### 2.3.1. Univariate analysis

Different univariate analyses were performed to compare the spatial and temporal differences in environmental and biological parameters in the study area. Initially, the data sets were tested for their homogeneity. Parametric ANOVA was used to compare the distribution of variables with homogenous distribution, whereas non-parametric ANOVA (Kruskal - Wallis ANOVA) was used to compare the distribution of variables with heterogeneous distribution. Tukeys HSD post hoc test (Zar, 1999) was used to compare the pair-wise significance in parametric ANOVA and Dunn's post hoc test for the pair-wise significance in the Kruskal-Wallis test (Zar, 1999). Tests of normality, parametric and nonparametric ANOVAs were carried out in XL stat pro.

#### 2.3.2. Segregation of locations

Cluster analysis was performed to segregate observations based on their similarity in distribution of copepod species. Observations within clusters represented similarity, whereas between represented clusters dissimilarity. For cluster analysis, data sets of copepod species abundance were initially log (X + 1) transformed to normalize differences in numerical abundance (Clarke and Warwick, 2001). The Bray - Curtis similarity matrix based on a group average method was used for the spatial grouping of observations. In addition to the cluster analysis, a Similarity Profile (SIMPROF) permutation test was also performed to identify significant species assemblages at stations ($p < 0.01$) (Clarke and Gorley, 2006). The Cluster/SIMPROF analysis in the present study was performed in PRIMER V6.

#### 2.3.3. Dominant species and simper analysis

Dominant species are the most common and numerically abundant species in each group of locations. The dominant species (common and numerically abundant species) of copepod in each group of locations were identified based on a standard procedure (Yang et al., 1999; Lin et al., 2011): $Y_i = (N_i/N) \times f_i$, where, $Y_i$ is the dominance of species $i$, $N_i$ is the number of individuals of species $i$ in all locations, N is the number of individuals of all species in all locations, and $f_i$ is the frequency of locations at which species $i$ occurs. Species of copepods with a $Y_i$ value greater than or equal to 0.02 were defined as dominant species (Yang et al., 1999; Lin et al., 2011). Discriminant species are the most characteristics/key species involved in dissimilarity between the groups of locations. A SIMPER (similarity Percentage) test was performed to identify the most characteristic/discriminating species involved in the dissimilarity pattern among the clusters. SIMPER analysis was performed on log (X + 1) transformed data sets of copepod abundance by Bray – Curtis similarity matrix. SIMPER analysis was performed in PRIMER V6.

#### 2.3.4. Diversity indices

The diversity of the mesozooplankton community was represented using three common indices: (i) Pielou's evenness (Pielou, 1969), (ii) Simpson's dominance (Simpson, 1949) and (iii) Shannon Wiener diversity (Shannon and Weiner, 1963).

#### 2.3.5. Redundancy analysis (RDA)

The relationship between important species of copepod (dominant and discriminating species) and the environmental variables were analyzed using RDA (CANOCO 4.5). The data were initially analyzed using Detrended Correspondence Analysis (DCA) to select the appropriate ordination technique. The result of DCA showed an axis gradient length < 2 suggesting that the use of linear multivariate RDA (Leps and Smilauer, 2003) was suitable for the present data. The abundance of dominant and discriminate copepod species and chlorophyll *a* was log transformed prior to the analysis. Partial RDA was also carried out to determine the combinations of the variables that contribute most to the total variance of the biological components. The ordination significance was tested with Monte Carlo permutation tests (499 unrestricted permutations) ($p < 0.05$). Triplots with correlation scaling were prepared to represent the results of the RDA, in which samples are displayed by points, species and quantitative environmental variables by arrows. In Triplot, the relative directions of the copepod species arrows approximate their linear correlations; arrows pointing in the same direction correspond to variables having a high positive correlation; variables with a high negative correlation have arrows pointing in opposite directions. A similar approximation is used when comparing the arrows representing copepod species and environmental variables. If an arrow of an environmental variable orients in the similar direction of a copepod species, then that copepod species and the environmental variable are positively correlated. The sample points projected along with the parameter arrows indicate the approximate order of the samples in the increasing gradient of each environmental variable (when proceeding towards the arrow tip and beyond it). In Triplot, the ordinate system origin corresponds to the average value of a particular environmental/biological variable in each treatment. The angle between the environmental variables arrows approximate the correlations among those variables with the scaling focused on biological variables.

## 3. Results

### 3.1. Environmental Setting

#### 3.1.1. Physico-chemical environment

Surface winds in the study domain were low/moderate until the end of May (av. 3.5 m), increased in early June, and continued until the end of September (av. >5 m $s^{-1}$). Peak winds were observed during mid-June and late July (Fig. 2). In order to present the hydrographical characteristics of the study area with more clarity, all observations were categorized to represent Pre-SWM (April-May), Early-SWM (June), Peak-SWM (July) and Late-SWM (August-September). Table 1 shows a large change in SST (~6 °C) from Pre-SWM to Peak-SWM. Temporal variations in the vertical distribution of temperature in the water column at all locations (M1, M2 and M3) are presented in Fig. 2. The salient features are very similar in all locations throughout the observations: a warm water column prevailed during the Pre-SWM that was later replaced by cooler waters for the rest of the observation period.

Surface salinity showed noticeable temporal variations in all three locations, varying from 29.36 to 35.13 in M1; 27.17 to 35.16 in M2 and 31.28 to 35.38 in M3 (Table 1). The bottom salinity was always higher than the surface. Surface salinity was high during the Pre-SWM and Early-SWM, which subsequently fluctuated as a response to the rainfall and runoff (Table 2). During the Pre-SWM, fairly high concentration of dissolved oxygen was present in all sampling locations, with a clear decrease in bottom waters as compared to the surface (Table 2). The dissolved oxygen concen-

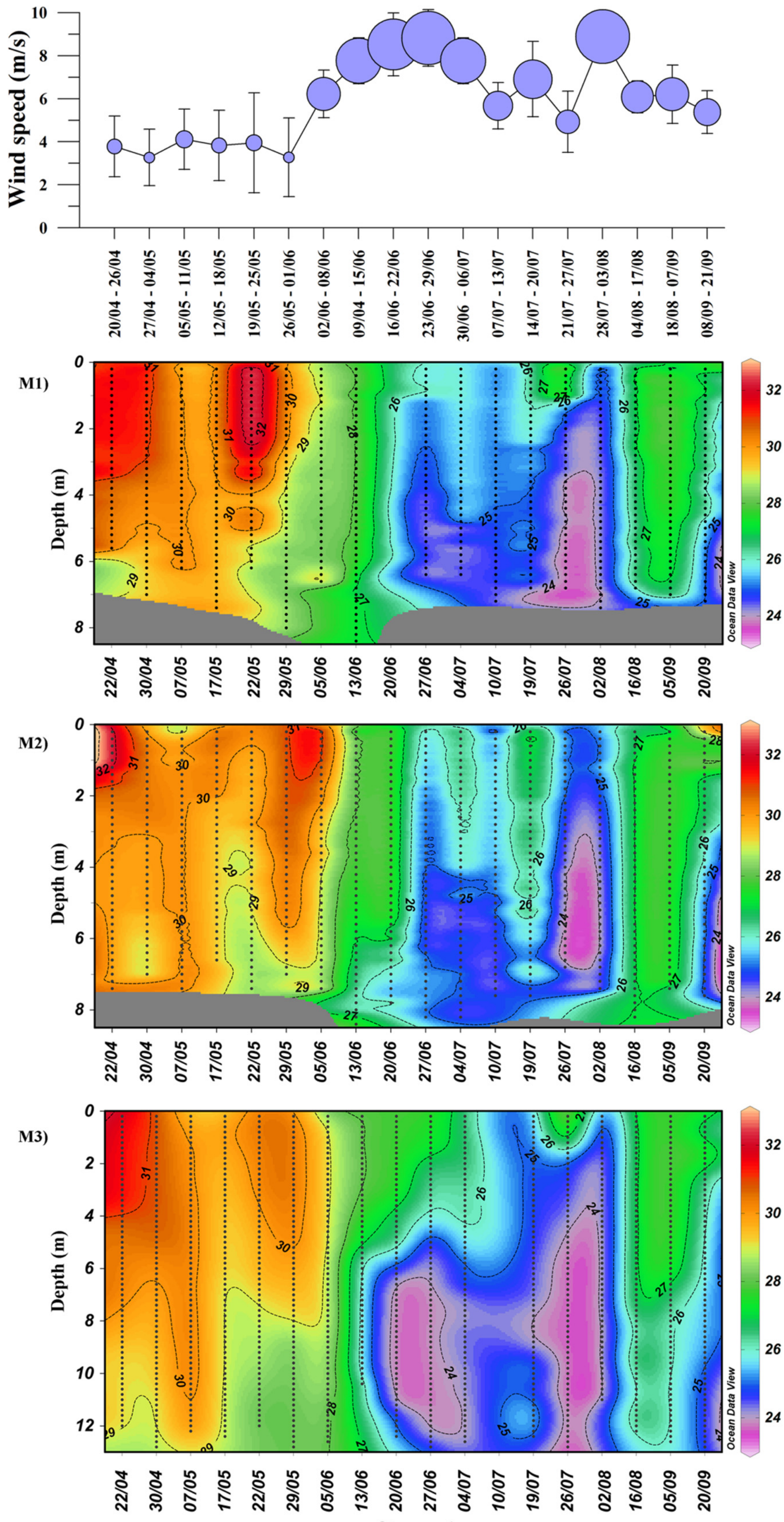


**Fig. 2.** Wind speed (line plots) and vertical distribution of temperature (°C) in locations M1, M2 and M3 during different observations. Water column temperature was high (>28.5) during the Pre- SWM, which decreased during Early-SWM (June) and become <25 °C during the Peak-SWM. Temperature increased by Late-SWM (August) but was still lower than the Pre-SWM condition. The mean and SD values of wind speed are presented.

**Table 1**
Minimum and maximum values of the measured parameters in M1, M2 and M3.

| SI. NO | Parameters | Depth | M1 | M2 | M3 |
|---|---|---|---|---|---|
| 1 | Temperature (°C) | S | 24.3–32.6 | 24.4–32.1 | 24.3–32.1 |
| | | B | 23.7–30.4 | 23.7–30.1 | 23.7–30.5 |
| 2 | Salinity | S | 29.36–35.13 | 27.17–35.16 | 31.28–35.38 |
| | | B | 33.67–35.47 | 31.29–35.55 | 34.29–35.39 |
| 3 | Turbidity (NTU) | S | 1.12–6.54 | 1.35–8.7 | 0.12–5.9 |
| | | B | 2.14–11.07 | 2.16–13.47 | 1.12–10.41 |
| 4 | DO (μM) | S | 129.3–251.9 | 104.4–234.0 | 138.4–355.7 |
| | | B | 3.0–178.1 | 6.3–104.4 | 6.7–185.85 |
| 5 | Nitrate (μM) | S | 0.02–6.2 | 0.01–14.6 | 0.07–13.4 |
| | | B | 0.07–8.8 | 0.14–14.6 | 0.03–20.6 |
| 6 | Phosphate (μM) | S | 0.16–1.8 | 0.17–1.5 | 0.21–3.05 |
| | | B | 0.40–2.0 | 0.3–2.02 | 0.5–2.05 |
| 7 | Chlorophyll *a* (μg/L) | S | 1.11–11.64 | 0.49–19.17 | 0.41–17.44 |
| | | B | 0.68–6.24 | 0.94–10.24 | 0.24–10.79 |

**Table 2**
Environmental parameters (Mean ± SD) in segregated clusters of locations M1, M2 and M3. S and B denote the surface and bottom waters, respectively.

| Location | Parameters | Depth | Pre-SWM (Cluster 1) | Early-SWM (Cluster 2) | Peak-SWM (Cluster 3) | Late-SWM (Cluster 4) |
|---|---|---|---|---|---|---|
| M1 | Temperature (°C) | S | 30.77 ± 1.21 | 27.45 ± 1.50 | 26.34 ± 1.30 | 26.46 ± 1.43 |
| | | B | 29.46 ± 0.75 | 26.82 ± 2.02 | 24.46 ± 0.65 | 25.75 ± 1.38 |
| | Salinity | S | 34.26 ± 0.64 | 34.71 ± 0.32 | 34.15 ± 0.43 | 32.80 ± 2.45 |
| | | B | 34.71 ± 0.42 | 35.01 ± 0.41 | 34.48 ± 0.28 | 34.40 ± 0.84 |
| | Dissolved oxygen (μM) | S | 190.48 ± 21.34 | 172.45 ± 68.90 | 178.65 ± 37.74 | 192.18 ± 20.90 |
| | | B | 153.64 ± 26.74 | 66.58 ± 51.53 | 32.12 ± 25.55 | 76.19 ± 58.83 |
| | Turbidity (NTU) | S | 1.66 ± 0.42 | 3.67 ± 0.62 | 5.76 ± 0.72 | 2.45 ± 1.06 |
| | | B | 2.42 ± 0.16 | 6.65 ± 2.24 | 11.59 ± 0.71 | 6.27 ± 0.86 |
| | Nitrate (μM) | S | 0.66 ± 0.94 | 1.18 ± 1.02 | 3.41 ± 2.13 | 1.39 ± 0.72 |
| | | B | 1.61 ± 1.76 | 3.65 ± 2.69 | 6.04 ± 3.27 | 3.49 ± 2.81 |
| | Phosphate (μM) | S | 0.57 ± 0.26 | 0.67 ± 0.44 | 1.17 ± 0.48 | 0.87 ± 0.42 |
| | | B | 0.66 ± 0.30 | 0.81 ± 0.41 | 1.63 ± 0.42 | 0.94 ± 0.40 |
| | Chlorophyll *a* (mg $m^{-3}$) | S | 1.77 ± 0.85 | 5.03 ± 2.62 | 9.3 ± 2.42 | 3.19 ± 1.84 |
| | | B | 1.76 ± 1.59 | 2.42 ± 1.04 | 5.20 ± 1.10 | 3.3 ± 0.49 |
| M2 | Temperature (°C) | S | 30.37 ± 1.11 | 27.58 ± 1.60 | 25.84 ± 1.43 | 27.06 ± 1.61 |
| | | B | 29.45 ± 0.58 | 26.88 ± 1.81 | 24.80 ± 0.95 | 25.89 ± 1.70 |
| | Salinity | S | 34.67 ± 0.23 | 33.85 ± 0.75 | 33.93 ± 0.89 | 32.93 ± 3.52 |
| | | B | 34.71 ± 0.53 | 34.63 ± 0.69 | 34.57 ± 0.30 | 34.10 ± 1.91 |
| | Dissolved oxygen (μM) | S | 175.06 ± 24.79 | 147.82 ± 30.52 | 199.75 ± 51.15 | 221.55 ± 34.39 |
| | | B | 128.34 ± 40.31 | 69.55 ± 17.54 | 34.41 ± 30.10 | 119.72 ± 76.25 |
| | Turbidity (NTU) | S | 1.72 ± 0.26 | 5.41 ± 0.76 | 6.74 ± 1.91 | 3.63 ± 1.96 |
| | | B | 3.15 ± 0.50 | 8.20 ± 2.60 | 12.85 ± 0.60 | 5.96 ± 1.72 |
| | Nitrate (μM) | S | 0.70 ± 0.69 | 4.21 ± 3.01 | 3.25 ± 3.19 | 1.15 ± 0.97 |
| | | B | 1.94 ± 1.02 | 5.60 ± 4.30 | 5.87 ± 4.40 | 3.91 ± 1.86 |
| | Phosphate (μM) | S | 0.52 ± 0.10 | 0.70 ± 0.24 | 1.19 ± 0.44 | 0.75 ± 0.47 |
| | | B | 0.66 ± 0.27 | 1.11 ± 0.42 | 1.64 ± 0.32 | 0.94 ± 0.48 |
| | Chlorophyll *a* (mg $m^{-3}$) | S | 2.66 ± 1.82 | 4.51 ± 2.92 | 10.72 ± 7.78 | 4.98 ± 4.51 |
| | | B | 2.09 ± 2.19 | 1.66 ± 0.68 | 5.70 ± 1.27 | 3.86 ± 1.83 |
| M3 | Temperature (°C) | S | 29.98 ± 1.36 | 27.52 ± 0.65 | 26.92 ± 2.08 | 26.72 ± 1.57 |
| | | B | 28.98 ± 0.76 | 24.33 ± 0.86 | 24.32 ± 0.79 | 25.26 ± 1.17 |
| | Salinity | S | 34.34 ± 0.65 | 34.29 ± 0.35 | 33.97 ± 0.49 | 32.91 ± 1.08 |
| | | B | 34.90 ± 0.40 | 35.02 ± 0.49 | 34.70 ± 0.11 | 35.30 ± 0.28 |
| | Dissolved oxygen (μM) | S | 181.22 ± 9.65 | 147.08 ± 12.30 | 225.53 ± 60.55 | 248.07 ± 73.72 |
| | | B | 146.80 ± 30.43 | 16.04 ± 11.13 | 29.94 ± 19.25 | 41.72 ± 25.23 |
| | Turbidity (NTU) | S | 0.61 ± 0.24 | 1.69 ± 0.72 | 3.72 ± 1.92 | 1.37 ± 1.31 |
| | | | 1.71 ± 0.78 | 10.18 ± 0.30 | 9.28 ± 0.71 | 6.24 ± 0.74 |
| | Nitrate (μM) | S | 0.37 ± 0.47 | 0.54 ± 0.42 | 1.72 ± 1.53 | 1.32 ± 1.13 |
| | | B | 2.28 ± 1.41 | 11.26 ± 5.44 | 11.11 ± 2.07 | 11.35 ± 8.51 |
| | Phosphate (μM) | S | 0.63 ± 0.58 | 1.05 ± 0.58 | 0.89 ± 0.24 | 1.01 ± 0.93 |
| | | B | 0.85 ± 0.24 | 1.68 ± 0.33 | 1.82 ± 0.23 | 1.27 ± 0.52 |
| | Chlorophyll *a* (mg $m^{-3}$) | S | 0.66 ± 0.20 | 7.38 ± 6.42 | 10.05 ± 7.63 | 3.97 ± 2.95 |
| | | B | 0.63 ± 0.36 | 2.13 ± 1.49 | 6.03 ± 3.01 | 2.82 ± 2.38 |

tration showed a significant drop in both the surface and bottom waters by the Early-SWM (Table 2). The largest drop (even in some cases <10 μM) in dissolved oxygen concentration occurred during the Peak-SWM in the bottom waters (Table 2), while surface oxygen concentrations increased in some cases (Table 2). By the Late-SWM bottom oxygen concentrations began to increase (Table 2).

Turbidity in the water column showed large temporal variations (Fig. 3). It was the lowest during the Pre-SWM, increased during the Early-SWM, peaked during the Peak-SWM and decreased during the Late-SWM (Table 2). Even though the above spatial trend was similar in all locations, a noticeably higher concentration of turbidity was evident at M2 during the Peak-SWM period depicting the Mud Bank formation (Fig. 3; Table 2). During all

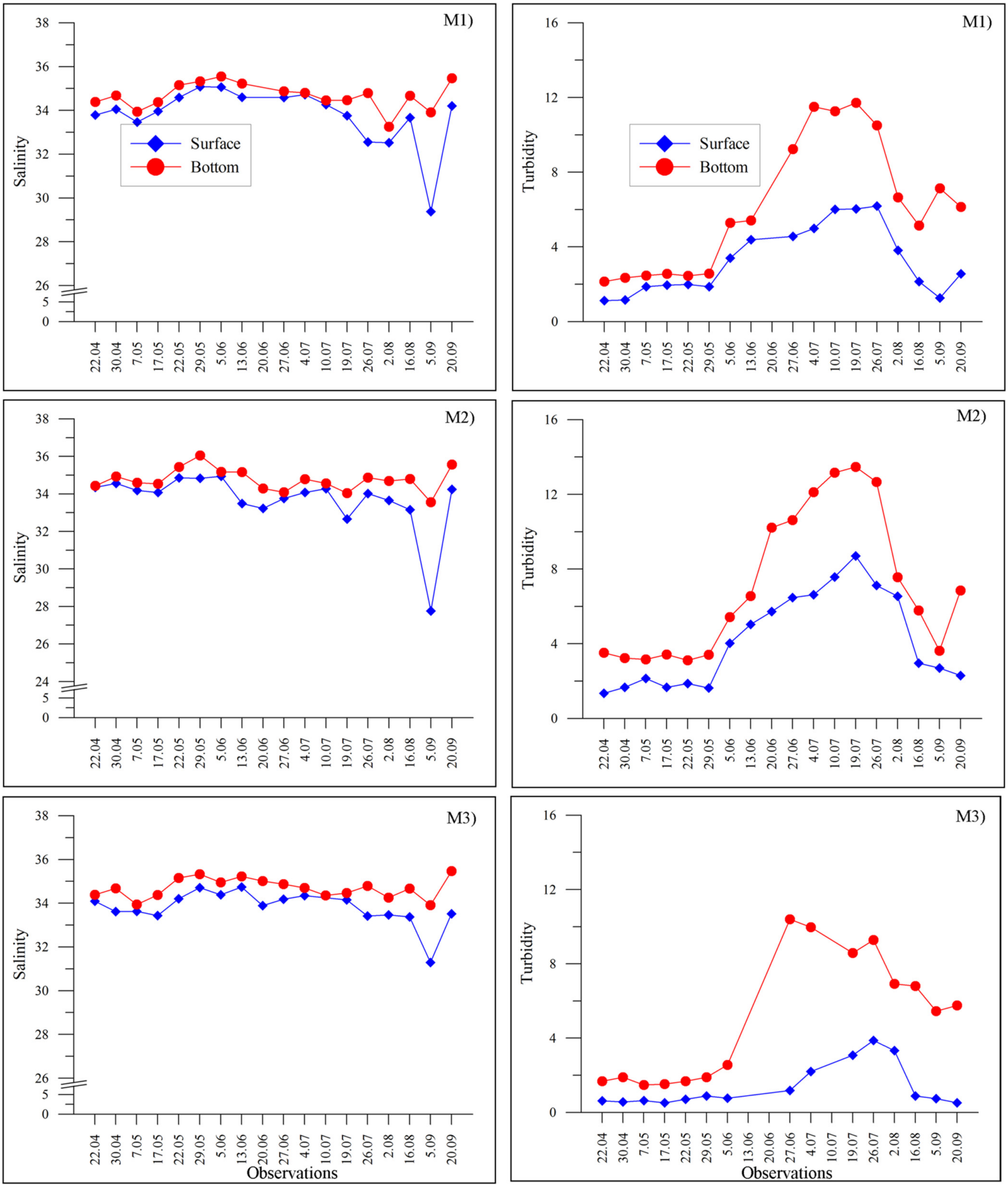


**Fig. 3.** Distribution of salinity and turbidity in M1, M2 and M3 locations during the study period.

the observations, turbidity was higher in bottom layers than in the surface at M1, M2 and M3. Nitrate and phosphate concentrations were low during the Pre-SWM at all locations sampled, increased during the Early-SWM and reached in highest levels by the Peak-SWM (Table 2). The distribution pattern of nutrients in all three locations was comparable in the subsurface waters with the values relatively higher than the surface layers. ANOVA showed minor spatial variations in temperature, dissolved oxygen and nutrients at M1, M2 and M3 ($P > 0.05$), but significant temporal variations during different seasons of the sampling (Pre-SWM, Early-SWM, Peak-SWM and Late-SWM) ($P < 0.01$).

### 3.2. Biological parameters

#### 3.2.1. Chlorophyll *a*

During the Pre-SWM, chlorophyll *a* concentration was moderate at M1 and M2, whereas it was relatively low at M3 (Fig. 4; Table 2) in surface and sub-surface layers. By Early-SWM, significant increase in chlorophyll *a* biomass was noticed at all three locations, and values at M3 had become comparable with M1 and M2 (Table 2). The chlorophyll *a* biomass continued to increase at all three locations, reaching exceptional levels during the Peak-SWM (Table 2). In the Late-SWM chlorophyll *a* decreased and reverted to the level of the Early-SWM. During the Early and Peak-SWM periods, accumulation of chlorophyll *a* biomass was significantly greater in the surface waters as compared to the sub-surface waters, but such a difference was not well marked during the Pre-SWM and the Late-SWM periods. Chlorophyll *a* spatial variation between locations (M1, M2 and M3) was insignificant ($P > 0.05$) throughout the study but, their temporal variation in all location between different seasons of the sampling was significant ($P < 0.05$).

#### 3.2.2. Mesozooplankton biomass and abundance

Mesozooplankton biomass in M1, M2 and M3 was <1.5 ml m$^{-3}$ during the Pre-SWM and Early-SWM periods, later increased into >10 ml m$^{-3}$ during the Peak-SWM and Late-SWM periods. Mesozooplankton abundance during the observation period ranged from 863 to 15,611 ind m$^{-3}$. Mesozooplankton abundance was low during the Pre-SWM compared to Peak- and Late-SWM periods. However, during the Early-SWM, the zooplankton biomass and abundance were low and comparable to the Pre-SWM period (Fig. 5). Similar to chlorophyll, the spatial variation of mesozooplankton biomass and abundance between M1, M2 and M3 was insignificant ($P > 0.05$), whereas their temporal variation in all locations between different phases of the sampling was significant ($P < 0.05$).

#### 3.2.3. Abundance of mesozooplankton groups

The mesozooplankton group abundances at M1, M2 and M3 during the Pre-SWM, Early-SWM, Peak-SWM and Late-SWM are presented in Table 3. Altogether, 15 groups contributed to the total

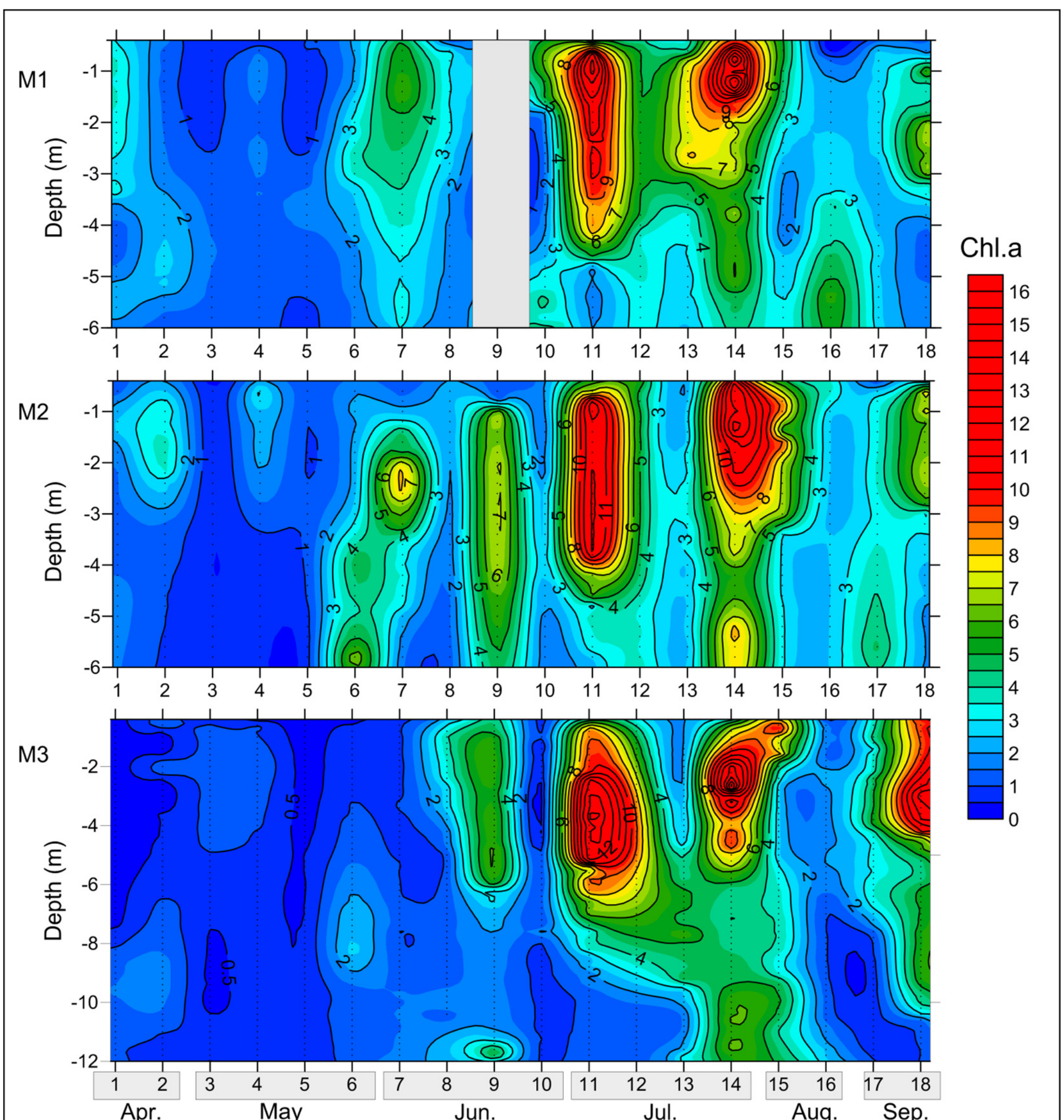


**Fig. 4.** The temporal pattern in the vertical distribution of chlorophyll *a* (mg m$^{-3}$) in M1, M2 and M3 locations.

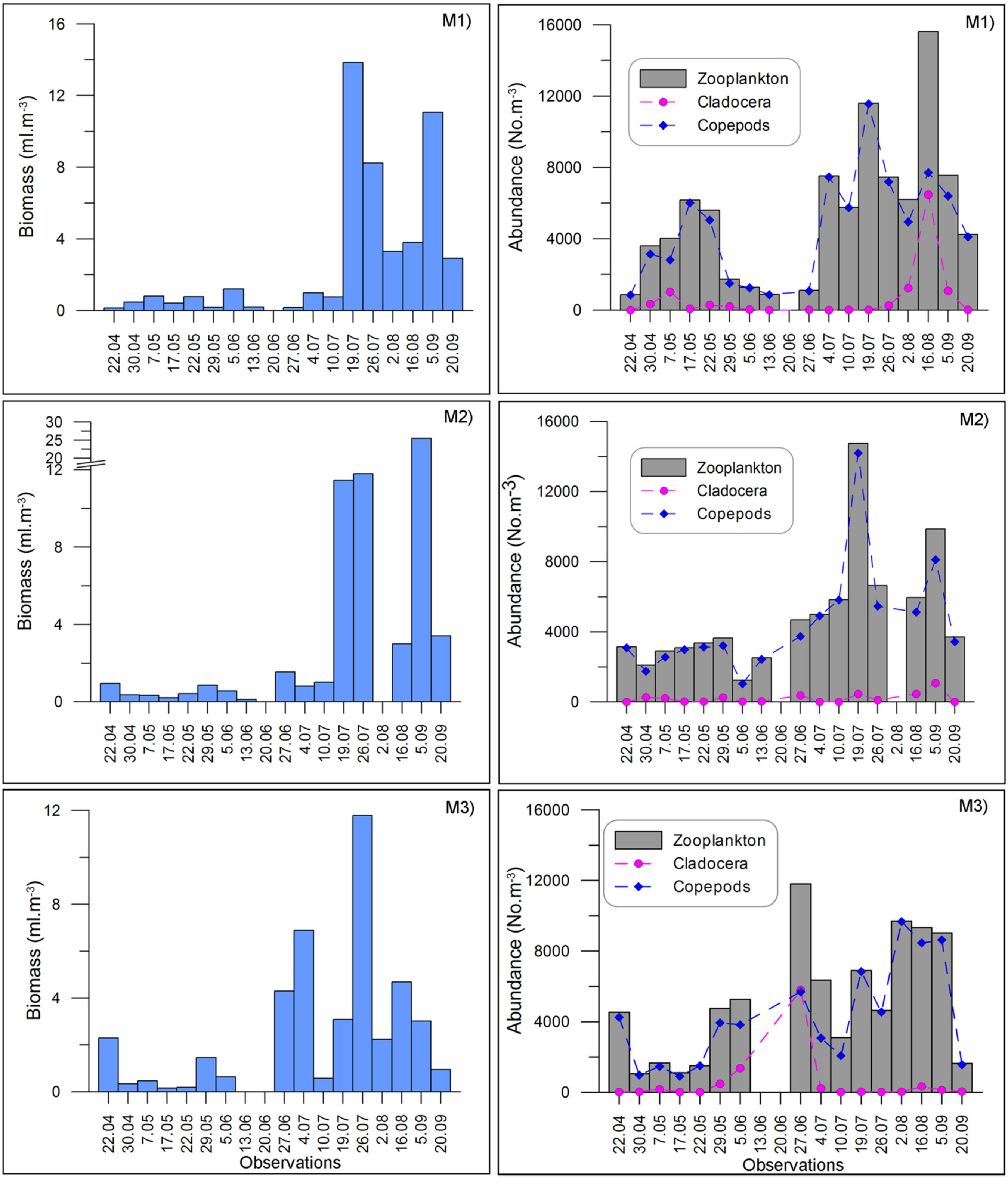


**Fig. 5.** Temporal distribution of zooplankton biomass (ml $m^{-3}$) and abundance (No $m^{-3}$) in M1, M2 and M3. The general trend is an increase in zooplankton biomass and abundance during the SWM period. Consider that there were 17 observations in location M1 and 16 observations each in locations M2 and M3.

abundance of mesozooplankton. Copepods contributed the majority (49–96%) to the total mesozooplankton abundance. Copepod abundance varied from 851 to 11,569 ind $m^{-3}$ at M1; 1402–14,187 ind $m^{-3}$ at M2 and 910–9672 ind $m^{-3}$ at M3. Copepod abundance was generally high during Peak- and Late-SWM compared to Pre-SWM and Early-SWM. During the Early-SWM, copepod abundance was lower at M1 and M2 compared to other seasons (Table 3). Siphonophores showed clear seasonality in distribution; they were absent during the Pre-SWM period, but they began to appear by the third week of June and

**Table 3**
Zooplankton group abundance (No $m^{-3}$) in M1, M2 and M3 during the Pre-SWM (cluster 1), Early–SWM (cluster 2), Peak-SWM (cluster 3), Late-SWM (cluster 4) Mean and SD (in parenthesis) are showed.

| Location | | Groups | Pre-SWM | Early-SWM | Peak-SWM | Late-SWM |
|---|---|---|---|---|---|---|
| M1 | 1. | Hydromedusae | – | 0.3 (0.2) | 0.4 (0.2) | 1.1 (0.8) |
| | 2. | Siphonophores | – | 0.2 (0.1) | 4.7 (3.5) | 148.6 (62.6) |
| | 3. | Chaetognaths | 18.8 (16.3) | 7.6 (5.8) | 8.6 (7.6) | 10.7 (9.3) |
| | 4 | Copepods | 3229 (1994) | 1065 (188) | 8341 (2490) | 5791 (1592) |
| | 5 | Cladocerans | 317 (269) | 9.8 (8.8) | 122.5 (54.5) | 2200 (2104) |
| | 6 | Lucifers | 45.1 (33.6) | 1.7 (1.5) | 5.4 (6.2) | 45.1 (90.2) |
| | 7 | Thaliaceans | 3.4 (2.2) | 0.3 (0.1) | 0.2 (0.1) | 33.7 (22.7) |
| | 8 | Appendicularians | 5.8 (3.9) | 0.5 (0.1) | 1.7 (2.3) | 48.3 (33.7) |
| | 9 | Ostracods | – | – | 0.8 (0.4) | 0.3 (0.1) |
| | 10 | Mysids | – | – | 0.6 (0.3) | 0.7 (0.2) |
| | 11 | Polychaete larvae | – | 0.5 (0.4) | 0.8 (0.5) | 0.3 (0.2) |
| | 12 | Decapod larvae | 39.3 (26.9) | 1.6 (1.3) | 3.9 (2.9) | 177.4 (122.7) |
| | 13 | Molluscans larvae | – | 3.52 (1.1) | 4.36 (1.65) | 1.31 (1.02) |
| | 14 | Fish Eggs | 11.4 (3.4) | 0.9 (0.4) | 0.6 (0.) | 22.5 (11.4) |
| | 15 | Fish larvae | – | 1.3 (0.5) | – | 1.1 (0.6) |
| M2 | 1 | Hydromedusae | – | 6.1 (4.5) | 1.9 (1.2) | 0.4 (0.7) |
| | 2 | Siphonophores | – | 6.3 (4.3) | 14.2 (12.4) | 86.5 (46.5) |
| | 3 | Chaetognaths | 34.5 (31.3) | 70.1 (55.8) | 9.9 (7.4) | 21.1 (14.4) |
| | 4 | Copepods | 3328 (1245) | 2403 (1347) | 7595 (4410) | 5554 (2366) |
| | 5 | Cladocerans | 124.4 (110.04) | 138 (104.2) | 215.9 (135.4) | 517.5 (434.4) |
| | 6 | Lucifers | 42.8 (41.9) | 20.3 (19.3) | 10.7 (5.3) | 98.7 (54.2) |
| | 7 | Thaliaceans | 1.8 (0.8) | 2.1 (1.1) | 0.2 (0.1) | 31.3 (14.6) |
| | 8 | Appendicularians | 3 (1.2) | 2.8 (1.6) | 12.1 (7.6) | 157.1 (67.54) |
| | 9 | Ostracods | – | 1.2 (0.4) | 0.8 (0.7) | 3.4 (1.2) |
| | 10 | Mysids | – | 0.8 (0.1) | 0.4 (0.2) | 4.1 (1.1) |
| | 11 | Polychaete larvae | – | 3.7 (2.2) | 7.9 (4.3) | 8.4 (7.9) |
| | 12 | Decapod larvae | 4.4 (2.4) | 65.6 (34.8) | 30.5 (22.3) | 26.2 (15.9) |
| | 13 | Molluscans larvae | – | 133.3 (110.3) | 65.4 (1.47) | 80.1 (76.56) |
| | 14 | Fish Eggs | 1.1 (0.6) | 16.5 (10.1) | 0.8 (0.7) | 0.4 (0.7) |
| | 15 | Fish larvae | 1.8 (1.) | – | – | 13.6 (11.4) |
| M3 | 1 | Hydromedusae | – | 0.2 (0.1) | 0.3 (0.1) | 0.5 (0.3) |
| | 2 | Siphonophore | – | 0.2 (0.1) | 0.5 (0.2) | 97.3 (43.1) |
| | 3 | Chaetognaths | 20.1 (18.5) | 145.9 (87.9) | 14.9 (11.1) | 10.3 (7.7) |
| | 4 | Copepods | 1817 (1382) | 4482 (1084) | 4881 (1553) | 7080 (3723) |
| | 5 | Cladocerans | 72.4 (43.5) | 2543 (2851) | 17.9 (7). | 126.1 (108.2) |
| | 6 | Lucifers | 30.6 (21.2) | 40.8 (36.1) | 10.6 (2.5) | 13.6 (0.8) |
| | 7 | Thaliaceans | 0.3 (0.1) | 0.2 (0.1) | 0.8 (0.6) | 10.7 (5.6) |
| | 8 | Appendicularians | 0.2 (0.1) | 4.2 (3.2) | 8.1 (6.4) | 47.9 (32.5) |
| | 9 | Ostracods | – | 0.4 (0.1) | 5.5 (2.8) | 3.4 (1.1) |
| | 10 | Mysids | – | 0.6 (0.2) | 0.4 (0.1) | 18.9 (4.6) |
| | 11 | Polychaete larvae | – | 0.8 (0.5) | 10.8 (4.1) | 3.2 (2.5) |
| | 12 | Decapod larvae | 68.3 (44.6) | 52.3 (42.2) | 8.4 (6.2) | 49.9 (33.5) |
| | 13 | Molluscans larvae | – | 13.1 (1.32) | 3.56 (2.12) | 1.12 (1.53) |
| | 14 | Fish Eggs | 47.7 (21.1) | 0.3 (0.1) | 407.8 (313.45) | 8.6 (7.1) |
| | 15 | Fish larvae | 0.8 (0.4) | – | 1.1 (0.2) | 0.41 (0.3) |

reached their maximum abundance in the first week of September. Cladocera contributions to the total mesozooplankton abundance were noticeable only during the Early-SWM at M3 and the Late-SWM at M1 and M2. Polychaetes larvae were absent during the Pre-SWM, but they appeared during the Early-SWM, Peak-SWM and Late-SWM in all three locations. Fish eggs were abundant in M3 during the Peak-SWM, but were of low key in M2 and M1. The other groups contributed to the total abundance were lucifers, chaetognaths, ostracods, thaliaceans, fish larvae, appendicularians and mysids, but together their contribution was <5% of the total abundance.

*3.2.4. Copepods species distribution and community structure*

Altogether, 43 species of copepods were recorded in this study including 25 Calanoids, 8 Poecilostomatoids, 5 Cyclopoids and Harpacticoids each (Table 4). The species *Paracalanus parvus* and *Acrocalanus* sp. were present in all samples from M1, M2 and M3. Based on the distribution of the copepod species occurrence and abundance, cluster analysis by the Bray Curtis similarity index delineated the entire dataset into four clusters at M1, M2 and M3 (Fig. 6). SIMPROF permutation tests showed that the patterns of the delineation were significant ($P < 0.05$). Observations of Pre-SWM were assembled in cluster 1, Early-SWM in cluster 2, Peak-SWM in cluster 3 and Late-SWM in cluster 4.

Throughout the observations, the copepod abundance variation between the three locations was insignificant but, their temporal variation with in all three locations was significant ($P < 0.05$). At all three locations, copepod abundance was high in cluster 3 (Peak-SWM) as compared to other three clusters. The contribution of copepods species to the total abundance varied considerably among different clusters. Calanoid copepods contributed the majority of the total copepod abundance in cluster 1 (Pre-SWM), cluster 2 (Early-SWM) and cluster 4 (Late-SWM) at M1, M2 and M3. Cyclopoid copepod contribution to the total abundance was high compared to Calanoids in cluster 3 (Peak-SWM). During the Peak-SWM (cluster 3), *Oithona similis* alone contributed 60–80% to the total copepod abundance in M1, M2 and M3 (supplementary material 2). All the above indicate a clear dominance of Cyclopoids (*Oithona similis*) over Calanoids during the Peak-SWM. Copepod species distribution and their abundance in different clusters of M1, M2 and M3 is presented in Table 4. Copepod species diversity and richness were the highest during the Pre-SWM (cluster 1) and the lowest during the Peak-SWM (Fig. 7). The second highest diversity and

**Table 4**
Species of copepods and their mean abundance in various clusters (Cluster 1 – Pre-SWM; Cluster 2 - Early-SWM; Cluster 3 – Peak-SWM; Cluster 4 – Late-SWM) in M1, M2 and M3. Abundance symbols + denotes 0.1 to ≤50; ++ denotes 50.1 to ≤100; +++ denotes 100.1 to ≤200; * denotes 200.1 to ≤500; ** denotes 500.1 ≤ 1000; *** denotes 1000.1 to ≤5000; ### denotes >5000 and – denotes absence.

| SI. NO | *Species* | Location M1 (Clusters) | | | | Location M2 (Clusters) | | | | Location M3 (Clusters) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 |
| | **Order: Calanoida** | | | | | | | | | | | | |
| 1 | *Acartia danae* | *** | * | + | * | *** | +++ | + | ++ | ** | + | + | +++ |
| 2 | *Acartia erythraea* | ** | +++ | + | ++ | ** | ++ | + | + | ** | + | + | ++ |
| 3 | *Acartia spinicauda* | + | – | – | – | + | – | – | + | + | + | – | + |
| 4 | *Acrocalanus gibber* | + | + | + | + | + | + | + | + | + | + | + | + |
| 5 | *Acrocalanus gracilis* | + | + | +++ | +++ | + | + | +++ | ++ | ++ | ++ | ++ | ++ |
| 6 | *Acrocalanus longicornis* | + | + | ++ | + | + | + | + | ++ | + | + | + | + |
| 7 | *Acrocalanus monachus* | + | + | + | – | + | + | + | + | + | + | + | + |
| 8 | *Acrocalanus* sp. | +++ | +++ | ++ | * | ++ | ++ | * | ++ | ++ | +++ | +++ | +++ |
| 9 | *Candacia* sp. | + | – | – | – | + | – | – | – | + | – | – | – |
| 10 | *Centropages furcatus* | +++ | – | – | – | ++ | + | – | – | +++ | – | – | – |
| 11 | *Centropages orsini* | * | + | – | – | +++ | + | – | – | * | + | – | – |
| 12 | *Centropages tenuiremis* | – | – | – | * | – | – | ++ | ** | – | – | – | * |
| 13 | *Eucalanus* sp. | – | + | – | ++ | + | + | + | – | + | + | – | – |
| 14 | *Labidocera acuta* | ++ | – | – | – | ++ | – | – | – | ++ | + | – | + |
| 15 | *Labidocera minuta* | + | – | – | – | + | – | – | – | + | – | – | – |
| 16 | *Labidocera pectinata* | + | – | – | – | + | – | – | – | + | – | – | + |
| 17 | *Paracalanus parvus* | * | * | * | ** | ** | * | * | ** | * | ** | ** | ** |
| 18 | *Pareucalanus attenuatus* | – | + | – | – | + | ++ | + | + | + | +++ | – | ++ |
| 19 | *Pontella danae* | + | – | – | – | + | – | – | – | + | – | – | – |
| 20 | *Pontella securifer* | + | – | – | – | + | – | – | – | + | – | – | – |
| 21 | *Pseudodiaptomus serricaudatus* | – | – | – | *** | – | – | **++** | *** | – | + | ++ | *** |
| 22 | *Temora discaudata* | – | + | – | – | – | + | – | + | – | + | – | + |
| 23 | *Temora stylifera* | – | + | – | – | – | + | – | + | – | + | – | + |
| 24 | *Temora turbinata* | – | *** | + | ** | – | ** | **+** | *** | – | *** | + | *** |
| 25 | *Undinula vulgaris* | + | + | – | – | + | – | – | – | + | ++ | – | ++ |
| | **Order: Harpacticoida** | | | | | | | | | | | | |
| 26 | *Euterpina acutifrons* | – | + | – | * | + | + | + | ++ | + | + | + | * |
| 27 | *Macrosetella gracilis* | + | – | – | – | + | – | – | – | + | – | – | – |
| 28 | *Macrosetella oculata* | + | – | – | – | + | – | – | – | + | – | – | – |
| 29 | *Microsetella norvegica* | + | – | – | – | + | – | – | – | + | + | – | – |
| 30 | *Microsetella rosea* | + | – | – | – | + | – | – | – | + | – | – | – |
| | **Order: Cyclopoida** | | | | | | | | | | | | |
| 31 | *Oithona brevicornis* | – | – | + | + | + | – | – | – | – | – | + | – |
| 32 | *Oithona rigida* | – | – | + | + | + | – | – | – | – | ++ | + | + |
| 33 | *Oithona similis* | + | +++ | **###** | ** | + | ** | **###** | + | – | +++ | *** | ++ |
| 34 | *Oithona simplex* | – | – | + | + | – | – | + | – | + | – | + | – |
| 35 | *Oithona spinirostris* | – | – | + | – | – | + | – | + | + | – | – | – |
| | **Order: Poecilostomatoida** | | | | | | | | | | | | |
| 36 | *Corycaeus catus* | + | + | + | + | ++ | – | – | – | ++ | + | + | + |
| 37 | *Corycaeus danae* | + | ++ | + | + | +++ | +++ | + | – | +++ | ++ | + | + |
| 38 | *Corycaeus* sp. | + | + | ++ | +++ | + | + | * | ** | + | ++ | ++ | ++ |
| 39 | *Corycaeus speciosus* | + | + | + | + | ++ | – | – | – | + | + | + | + |
| 40 | *Farranula gibbula* | + | + | + | – | +++ | – | – | – | + | – | + | + |
| 41 | *Oncaea venusta* | – | + | + | – | + | ++ | + | ++ | + | + | + | +++ |
| 42 | *Sapphirina auronitens* | – | – | – | + | + | + | – | + | – | – | – | + |
| 43 | *Sapphirina ovatolanceolata* | – | – | – | + | – | – | + | + | – | – | – | + |

evenness was found during the Late-SWM period in M2 and M3 whereas, it was during the Early-SWM period in M1.

### 3.2.5. Dominant copepods and simper analysis

Dominant species in each cluster and their dominance values are presented in Table 5. *Acrocalanus* sp. *Paracalanus parvus* and *Corycaeus danae* were found dominant in all clusters of M1, M2 and M3. During the Pre-SWM (cluster 1), *Acartia danae*, *Acartia erythraea*, *Centropages orsini* were dominant in all three locations. In addition to these species *Labidocera acuta* was also found dominant during the Pre-SWM at location M1. During the Early-SWM (cluster 2), *Pareucalanus attenuatus*, *Temora turbinata, Acartia erythraea, A. danae* and *Oithona similis* were dominant in all three locations (Table 5). *Oithona similis* was the most dominant species during the Peak-SWM (cluster 3). *Centropages tenuiremis, Pseudodiaptomus serricaudatus, Temora turbinata, Euterpina acutifrons* and *Oithona similis* were found dominant during the Late-SWM in locations M1 and M2 (Table 5).

The results of the SIMPER analysis are presented in Fig. 8, which shows the dissimilarity percentage among the clusters and the key species responsible for the dissimilarity. The dissimilarity values (average dissimilarity/SD ≥ 2) demarcated 7 species as the leading discriminating species that defined the different clusters, consisted of *Acartia danae*, *A. erythraea*, *Centropages orsini, Oithona similis*, *Temora turbinata*, *Pseudodiaptomus serricaudatus*, *Centropages tenuremis*. The discriminating copepods were composed of *Acartia danae*, *A. erythraea*, *Centropages orsini* in cluster1; *Temora turbinata* (the upwelling indicator) in cluster 2; *Oithona similis* in cluster 3; *Temora turbinata*, *Pseudodiaptomus serricaudatus*, *Centropages tenuremis* in cluster 4.

### 3.3. Ecological inter-relationships

The present study discovered large temporal variations in hydrography associated with the SWM. This temporal difference in the environmental factors influenced the distribution of the

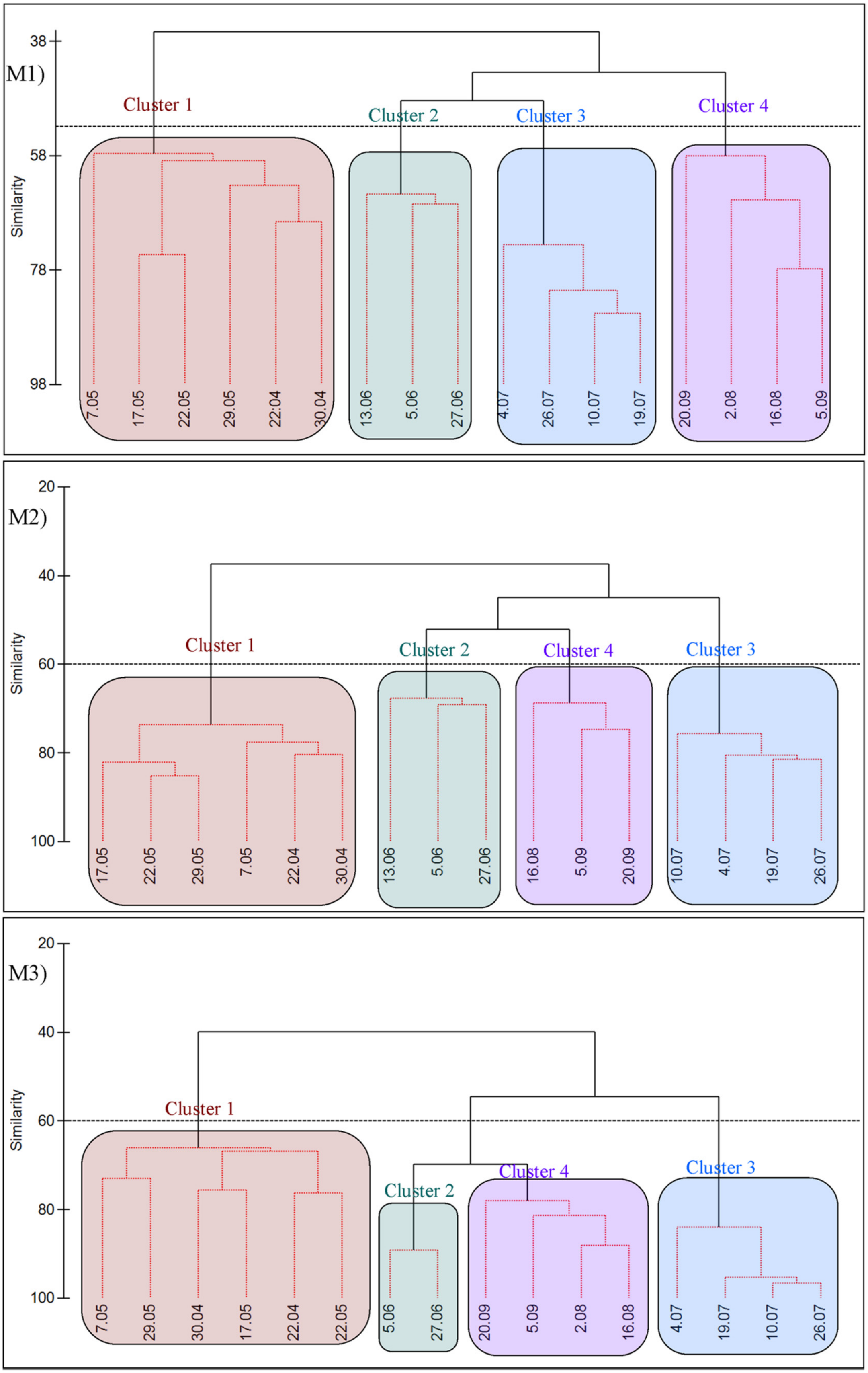


**Fig. 6.** Bray-curtis similarity based group average cluster/SIMPROF evidencing the assemblages of observations based on the distribution of copepod species abundance and distribution in M1, M2 and M3. The entire observations in M1, M2 and M3 were assembled into four clusters each representing the Pre-SWM (cluster 1), Early-SWM (cluster 2), Peak-SWM (cluster 3) and Late-SWM (cluster 4). In figure the black solid lines represents the significant grouping (SIMPROF, $P < 0.05$) of the observations and the red dotted lines showed insignificant grouping of locations (SIMPROF $P > 0.05$). The observations represents the date and month of collection. Consider that there were 17 observations in location M1 and 16 observations each in locations M2 and M3.

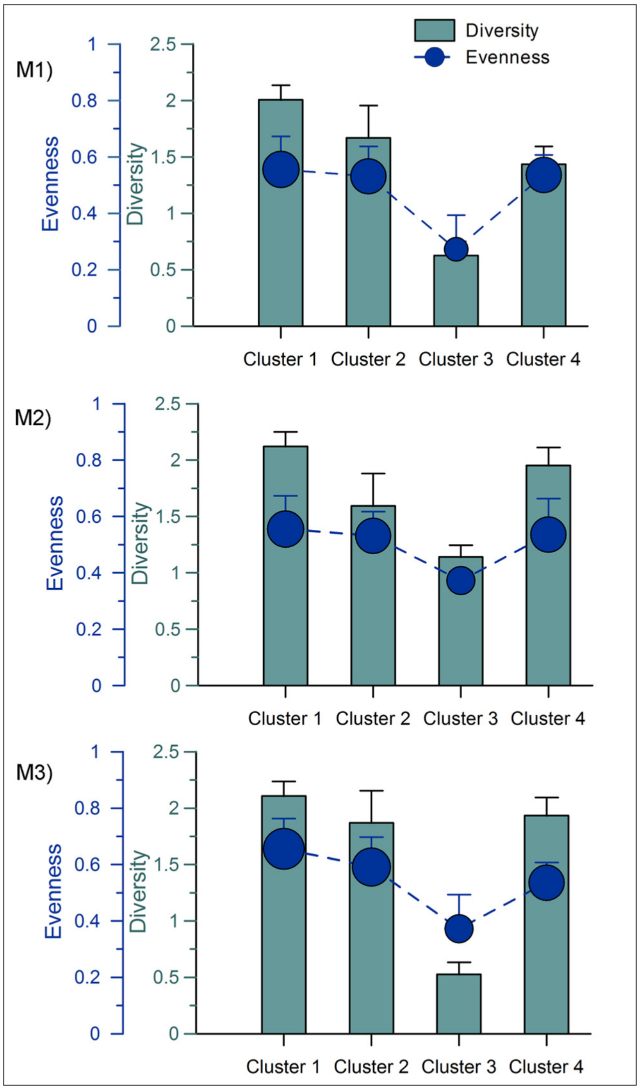


**Fig. 7.** Shannon diversity and Pielous evenness of copepods in temporally assembled clusters in M1, M2 and M3. The observations in clusters are same as in Fig. 6. Copepod species diversity and evenness was the highest in cluster 1, followed by clusters 2, 4 and 3.

dominant and discriminate species of copepods and chlorophyll *a* distribution in the study area. The ecological inter-relationships of the dominant and discriminating copepods at locations M1, M2 and M3 are presented in Fig. 9, in which the right-hand side panels show the temperature overlaid on the ordination plot. The results of the complete RDA has shown that environmental parameters collectively (salinity, turbidity temperature, dissolved oxygen and in nutrients) explained 85.8%, 86.8% and 89.1% of variations in copepod species distribution and chlorophyll *a* at M1, M2 and M3 locations. The ordination significance of all the axes were tested by a Monte Carlo procedure, which showed that all the ordination of RDA axes of M1, M2 and M3 ($F = 2.095$, 2.141 and 2.167 respectively) were significant ($P < 0.05$). The Monte Carlo permutation procedure in forward selection of environmental variables (499 permutations) showed that turbidity (surface and bottom), temperature (surface and bottom), DO (bottom) and nutrients (surface and bottom) are the most important variables ($P < 0.05$) at M1, M2 and M3. Partial RDA model was performed to find out the variance of biological parameters explained by environmental variables with single and combined approach. The analyses showed that temperature, dissolved oxygen and nutrients collectively (indicative of the coastal upwelling) could explain 67.5%, 70.6% and 68.9% variance of copepods species distribution and chlorophyll *a* in M1, M2 and M3, respectively. On the other hand, the analysis with turbidity as the environmental variable (indicative of Mud Bank) showed that it could explain only low variance of copepods species distribution and chlorophyll *a* in all three locations (36.4% in M1, 38.1% in M2 and 37.9% in M3).

In RDA Triplot, samples are displayed by points, environmental and biological variables by solid and dotted arrows, respectively (Fig. 9). The RDA triplot clearly shows the distribution and inter-relationships of the physico-chemical and biological parameters during various observations. In triplots, dissolved oxygen and temperature were closely located in the left-hand side with Pre-SWM (cluster 1) observations. For SWM observations (Clusters 2, 3 and 4) nutrients (nitrate, phosphate) and turbidity were oriented on the right hand side of the Triplot showing their marked differences from the Pre-SWM sampling (cluster 1). The Peak-SWM observations (cluster 3) were located on the top of the right-hand side of the triplot, and these observations were characterized by extremely low DO, low temperature, high nutrients (nitrate and phosphate) and high turbidity. The Early-SWM (cluster 2) and Late-SWM (cluster 4) were characterized by moderate levels of DO, temperature, nitrate and phosphate. The Triplot orientation pattern mentioned above was similar in all three locations.

The Triplots showed the orientation of the species arrows of *Acatia danae*, *Acartia erythraea*, *Centropages orsini*, *Labidocera acuta* and *Centropages furcatus* to the left-hand side along with increasing gradients of temperature, DO and salinity, which indicated the dominance of these copepods during the Pre-SWM. The arrows representing *Oithona similis and* Chlorophyll *a* are oriented in the top right-hand side associated with decreasing gradients of temperature and dissolved oxygen. Along with them was the increasing gradient of nutrients (nitrate and phosphate) and turbidity, all these represented the Peak-SWM, the period with significantly high abundance/concentration of *Oithona similis* and chlorophyll *a* in all three locations. The orientation of the arrows representing *Pseudodiaptomus serricaudatus* and *Centropages tenuremis* on the bottom right-hand side of the Triplot, along with decreasing concentrations of temperature, salinity, dissolved oxygen and positive gradients of nutrients indicated that these copepod species dominated during the Late-SWM. The abundance of 6 discriminating species (*Acartia danae*, *Acartia erythraea*, *Centropages orsini*, *Temora turbinata*, *Pseudodiaptomus serricaudatus* and *Oithona similis*) were overlaid as bubbles to visualize their distributional differences among the cluster observations in locations M1 (Fig. 10), M2 (Fig. 11) and M3 (Fig. 12). It is clear in these figures that the pattern of abundance of all discriminating species of copepods was similar in all three locations. *Acartia danae*, *A. erythraea* and *Centropages orsini* were abundant during the Pre-SWM period. *Temora turbinata* was high during Early- (cluster 2) and Late-SWM period. *Oithona similis* was high during the Peak-SWM and *Pseudodiaptomus serricaudatus* during the Late-SWM period.

## 4. Discussion

During the Pre-SWM period, the Southeastern Arabian Sea experiences strong heating because of weak winds and intense solar radiation. The ocean surface layer is thermally stratified, resulting in a scarcity of nutrients in the upper euphotic zone, which eventually leads to relatively low phytoplankton biomass and production (Bhattathiri et al., 1996; Jyothibabu et al., 2010). Coastal upwelling begins during the onset of the SWM and is intensified by July (Madhupratap et al., 1990; Nair et al., 1992; Smith et al., 1998; Stelfox et al., 1999; Jyothibabu et al., 2008). In addition

**Table 5**
List of dominant species of copepods and their dominance values (in parenthesis) in Locations M1, M and M3. Abbreviations: *P. attenuatus - Pareucalanus attenuatus; C. tenuiremis – Centropages tenuiremis; P. serricaudatus - Pseudodiaptomus serricaudatus.*

| Location | Pre-SWM | Early-SWM | Peak-SWM | Late-SWM |
|---|---|---|---|---|
| M1 | *Acartia danae* (0.38)<br>*Acartia erythraea* (0.21)<br>*Acrocalanus* sp. (0.06)<br>*Centropages furcatus* (0.03)<br>*Centropages orsini* (0.03)<br>*Corycaeus danae* (0.02)<br>*Labidocera acuta* (0.02)<br>*Paracalanus parvus* (0.15) | *Acartia danae* (0.05)<br>*Acartia erythraea* (0.04)<br>*Acrocalanus* sp. (0.03)<br>*Corycaeus danae* (0.03)<br>*Oithona similis* (0.04)<br>*P. attenuatus* (0.02)<br>*Paracalanus parvus* (0.24)<br>*Temora turbinata* (0.34)<br>*Undinula vulgaris* (0.02) | *Acrocalanus* sp. (0.02)<br>*Oithona similis* (0.93)<br>*Paracalanus parvus* (0.03) | *Acrocalanus* sp. (0.05)<br>*C. tenuiremis* (0.03)<br>*Corycaeus danae* (0.02)<br>*Euterpina acutifrons* (0.02)<br>*Oithona similis* (0.04)<br>*P. serricaudatus* (0.34)<br>*Paracalanus parvus* (0.14)<br>*Temora turbinata* (0.16) |
| M2 | *Acartia danae* (0.32)<br>*Acartia erythraea* (0.19)<br>*Acrocalanus* sp. (0.10)<br>*Centropages orsini* (0.04)<br>*Corycaeus danae* (0.03)<br>*Paracalanus parvus* (0.18) | *Acartia danae* (0.05)<br>*Acartia erythraea* (0.02)<br>*Acrocalanus* s. (0.02)<br>*Corycaeus danae* (0.05)<br>*Oithona similis* (0.04)<br>*P. attenuatus* (0.04)<br>*Paracalanus parvus (0.14)*<br>*Temora turbinata (0.16)* | *Acrocalanus* sp. (0.06)<br>*Oithona similis* (0.76)<br>*Paracalanus parvus* (0.07) | *Acrocalanus* sp. (0.05)<br>*C. tenuiremis* (0.11)<br>*Corycaeus danae* (0.02)<br>*Euterpina acutifrons* (0.02)<br>*Oithona similis* (0.04)<br>*P. serricaudatus* (0.26)<br>*Paracalanus parvus* (0.10)<br>*Temora turbinata* (0.28) |
| M3 | *Acartia danae* (0.35)<br>*Acartia erythraea* (0.17)<br>*Acrocalanus* sp. (0.07)<br>*Centropages orsini* (0.03)<br>*Corycaeus danae* (0.05)<br>*Paracalanus parvus* (0.12) | *Acartia danae* (0.12)<br>*Acartia erythraea* (0.17)<br>*Acrocalanus* sp. (0.03)<br>*Corycaeus danae* (0.02)<br>*Oithona similis* (0.02)<br>*P. attenuatus* (0.02)<br>*Paracalanus parvus* (0.24)<br>*Temora turbinata* (0.36) | *Acrocalanus* sp. (0.06)<br>*Oithona similis* (0.56)<br>*Paracalanus parvus* (0.17) | *Acrocalanus* sp. (0.03)<br>*C. tenuiremis* (0.13)<br>*Corycaeus* sp. (0.02)<br>*Euterpina acutifrons* (0.02)<br>*P. serricaudatus* (0.34)<br>*Paracalanus parvus* (0.14)<br>*Temora turbinata* (0.16) |

to the upwelling, riverine inputs increase the concentrations of nutrients and enhance the phytoplankton production in the near shore waters along the southwest coast of India (Nair et al., 1992; Sawant and Madhupratap, 1996; Jyothibabu et al., 2008). The pattern of large elevation of nutrients and higher phytoplankton production was reported all along the southwest coast of India including the Mud Bank locations during the SWM (Subrahmanyan et al., 1975; Subrahmanyan, 1959; Nair et al., 1984; Madhupratap et al., 1990, 1996; Nair et al., 1992; Jyothibabu et al., 2010).

The well-known coastal upwelling along the Southwest coast of India begins in June, intensifies in July-August, and weakens by September (Banse, 1959; Madhupratap et al., 1990; Shetye et al., 1990; Madhupratap and Parulekar, 1993; Madhupratap et al., 1996, 2001; Jyothibabu et al., 2008). In the present study, coastal upwelling signatures such as cold and poorly oxygenated waters were very clear at all three locations by early June (Early-SWM). Upwelling intensified in July (Peak-SWM), shown by a significant drop in temperature and dissolved oxygen concentrations especially in sub-surface waters. By August (Late-SWM), the subsurface temperature and dissolved oxygen increased compared to the peak upwelling period and became comparable to the values during June. During the SWM, flooding of several rivers along the southwest coast of India cause a drop in salinity of the near shore waters (Banse, 1968; Madhupratap et al., 1990; Nair et al., 1992; Madhupratap and Parulekar, 1993), this evidence was well seen in the present study as lower sea surface salinity during the SWM as compared to the Pre-SWM. Sea surface salinity showed fluctuations during the SWM period with the lowest value occurring during early-September (Late-SWM). Turbidity in the entire study domain was the lowest during the Pre-SWM compared to the SWM periods. An increase in turbidity in the near shore waters along the Southwest coast of India is expected due to high river runoff during the SWM. However, the typical Mud Bank signatures of increased suspended sediments with dampened waves were found only at location M2 during the SWM associated with a thick fluid muddy layer formation in the bottom. The formation and the nature of the fluid muddy layer leading to the formation of the Mud Bank in the present study area has recently been studied and presented in detail (Shynu et al., 2017; Jyothibabu et al., 2017). Nonetheless, there was a clear and similar temporal hydrographical transformation in all three locations throughout the study period, which caused defined variations in the plankton components in the water column.

As described in the introduction section, there are more than a dozen hypotheses in place to explain the physical mechanism involved in the formation, sustenance and dissipation of the Alappuzha mud bank (Murty et al., 1984). However, it is curious to understand how comparable hydrography existed in all three locations during the present study especially during the Southwest Monsoon period when a Mud Bank was persistent only in M2 location. This feature seems to result from the coastal upwelling prevalent in all three locations. As coastal upwelling was prevalent in all three locations, the onshore advection of the subsurface waters and their overturn in the surface waters happen in more or less same magnitude in larger spatial extent. Ramasastry and Myrland (1959) proposed this onshore advection of the subsurface upwelled waters as the physical mechanism that lifts the bottom mud triggering the formation of the mudbank. Considering the very feeble velocity of the upwelled waters and also the widespread occurrence of the coastal upwelling in the study domain, Verma and Kurup (1969) overruled the above proposition arguing that the onshore movement of the upwelled water is very feeble and therefore upwelled water cannot lift the bottom mud and sustain it in the water column to form the mud banks. However, the upwelling associated onshore advection of the subsurface waters and its overturn in the surface eventually cause similar hydrographical characteristics in a larger spatial extent in the study domain, and hence in all three sampling locations considered in the present study.

In the present study, chlorophyll *a* was low during the Pre-SWM period, increased by the Early-SWM, and reached the highest concentrations during the Peak-SWM period in both Mudbank and Non-Mud Bank locations. The Pre-SWM period is generally considered biologically less productive compared to all the phases of SWM due to nutrient enrichment that occurs during the latter period (Smith et al., 1998; Banse et al., 1996; Smith and Madhupratap,

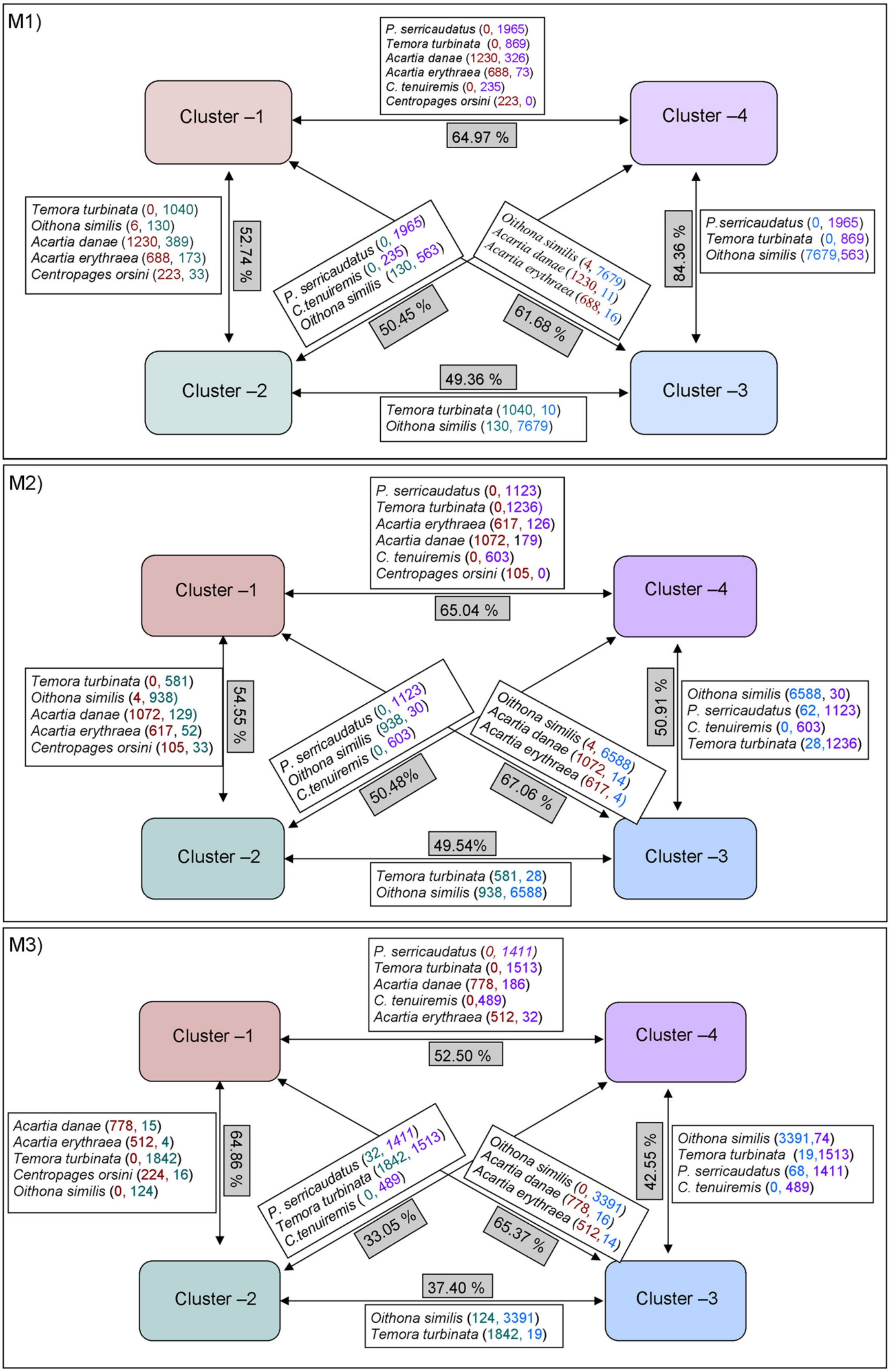


**Fig. 8.** SIMPER analysis showing the dissimilarity percentage between different clusters and the dominant species responsible for such dissimilarities (Cumulative cut of level 75%) are shown in text boxes. The dissimilarity percentage between the clusters (blue large boxes) are shown in small grey boxes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

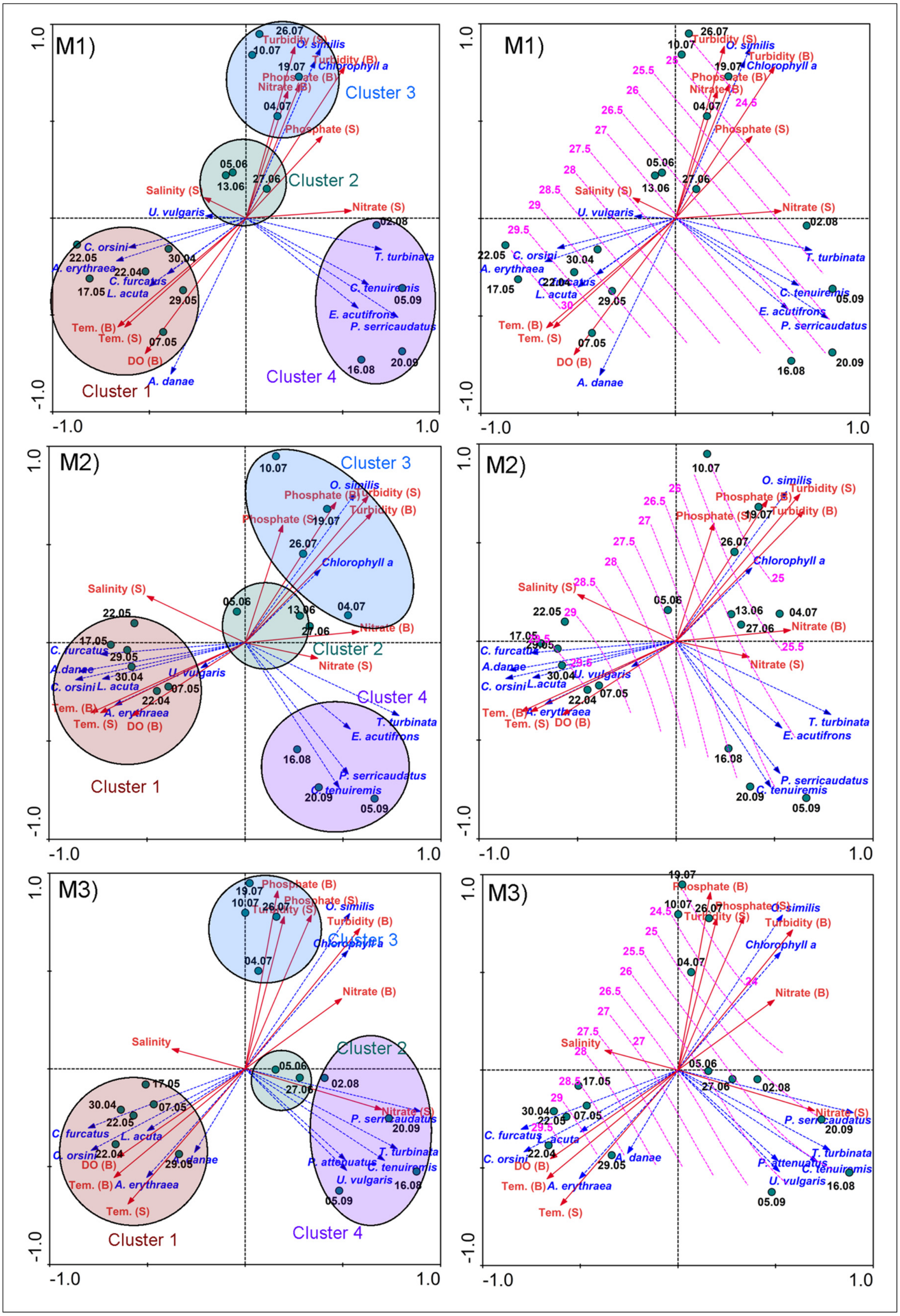

**Fig. 9.** RDA Triplot showing the inter-relationships of environmental and biological parameters in M1, M2 and M3. The environmental variables are represented in red solid arrows, biological variables in blue dotted lines and field sampling as small blue filled circles. Panels in the right hand side represent temperature (subsurface) overlaid RDA plot visualizes more precisely how chemical and biological variables responded to large spatial changes that occurred during the study period extending from the Pre-SWM (March) to the Late-SWM (September). The direction of arrows indicates the increasing gradient of that variable. (S) and (B) indicate surface and bottom (6 m in M1 and M2 and 12 m in M3) waters. The dates of the sampling are represented in the Triplot.

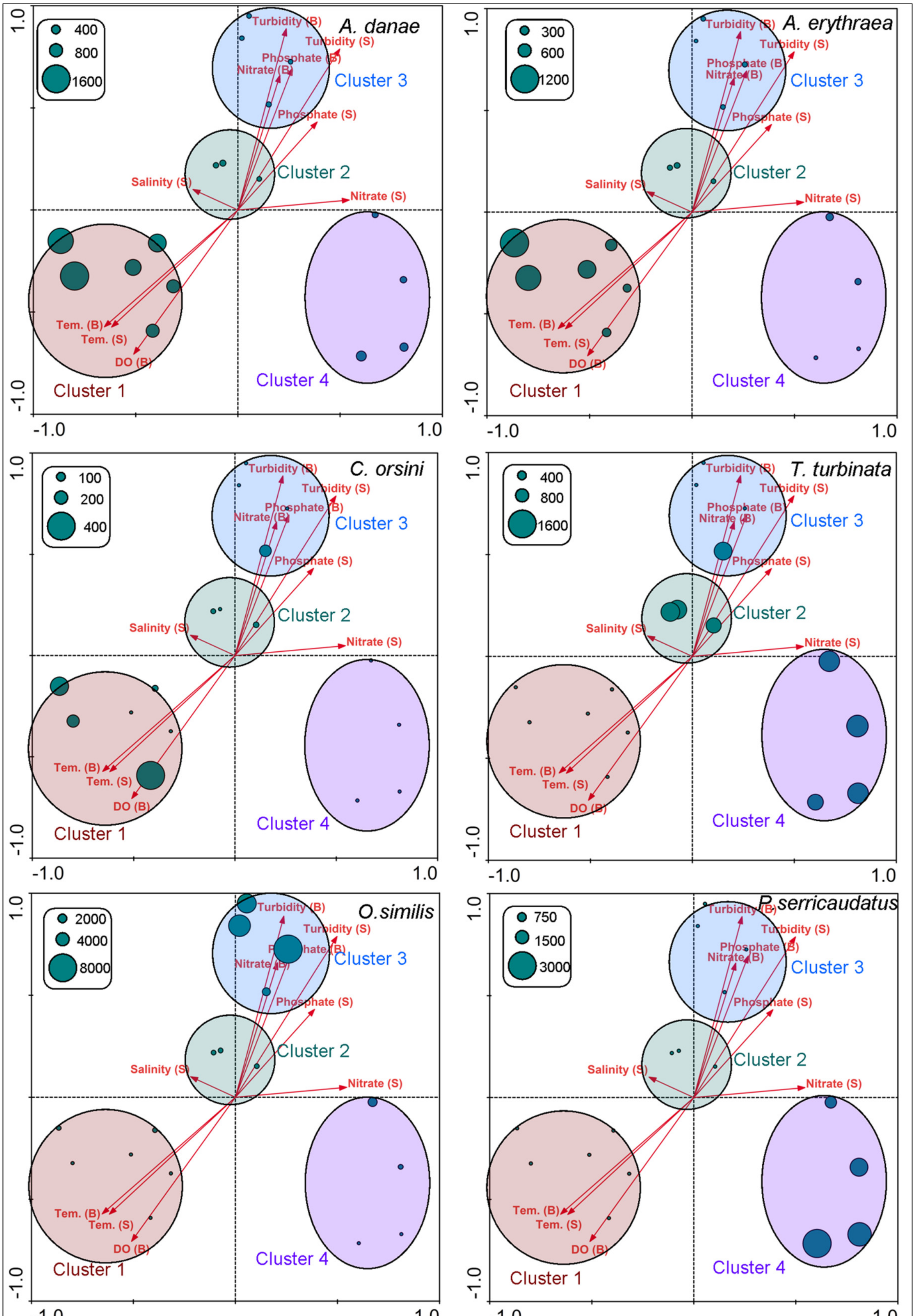


**Fig. 10.** Species abundance (bubbles) overlaid attribution RDA plot visualizing the influence of sequential transformation of the dominant copepods M1 along with varying environmental conditions during different phases of the sampling period. The sampling observations (bubble positions) are accordance's with the Fig. 9 (M1). The values of the bubble sizes are proportional to the reference bubbles in the inset in each panel.

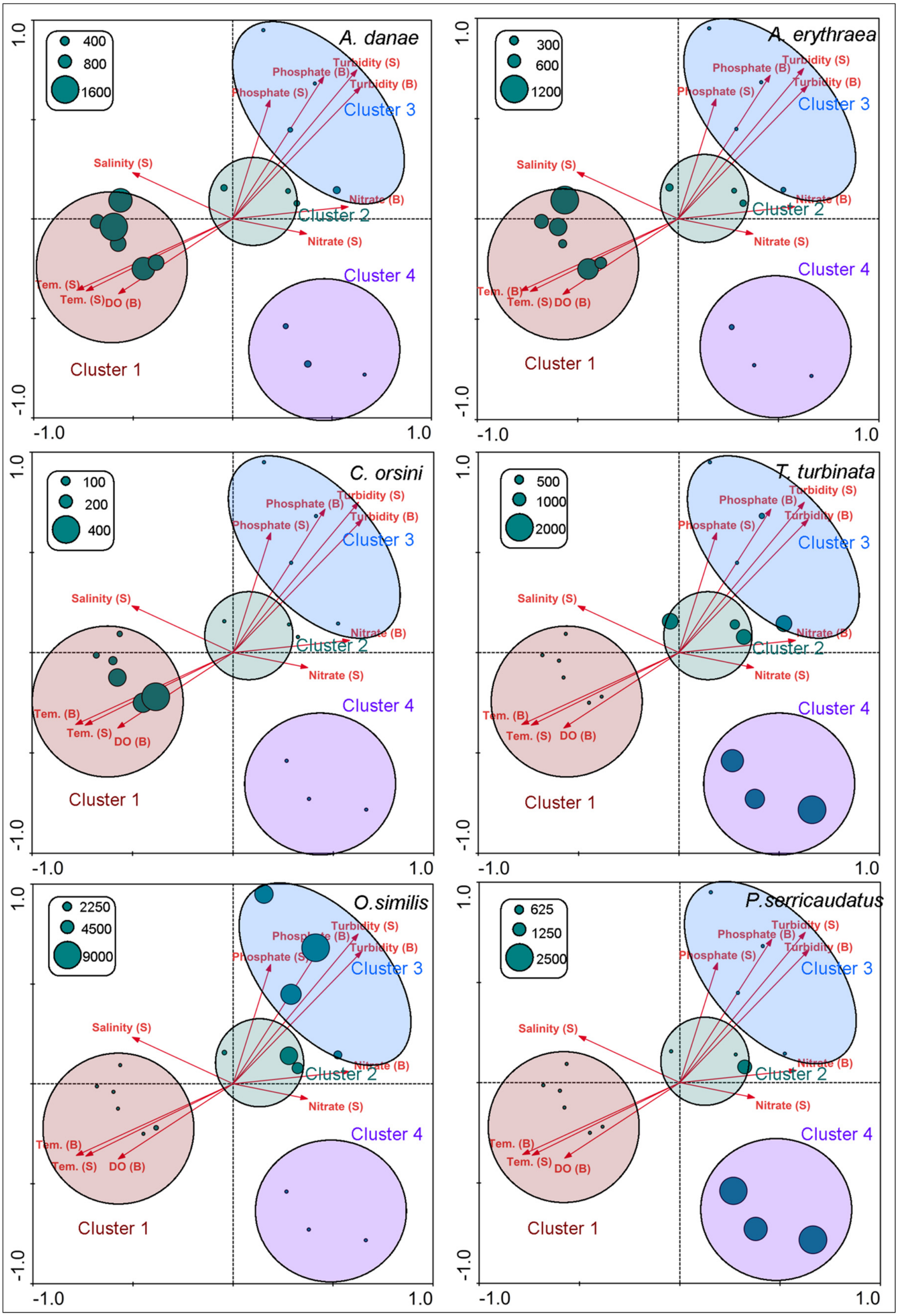


**Fig. 11.** Species abundance (bubbles) overlaid attribution RDA plot visualizing the sequential transformation of the dominant copepods M2 along with varying environmental conditions during different phases of the sampling period. The sampling observations (bubble positions) are accordance's with the Fig. 9 (M2). The value of the bubble sizes are proportional to the reference bubbles in the inset in each panels.

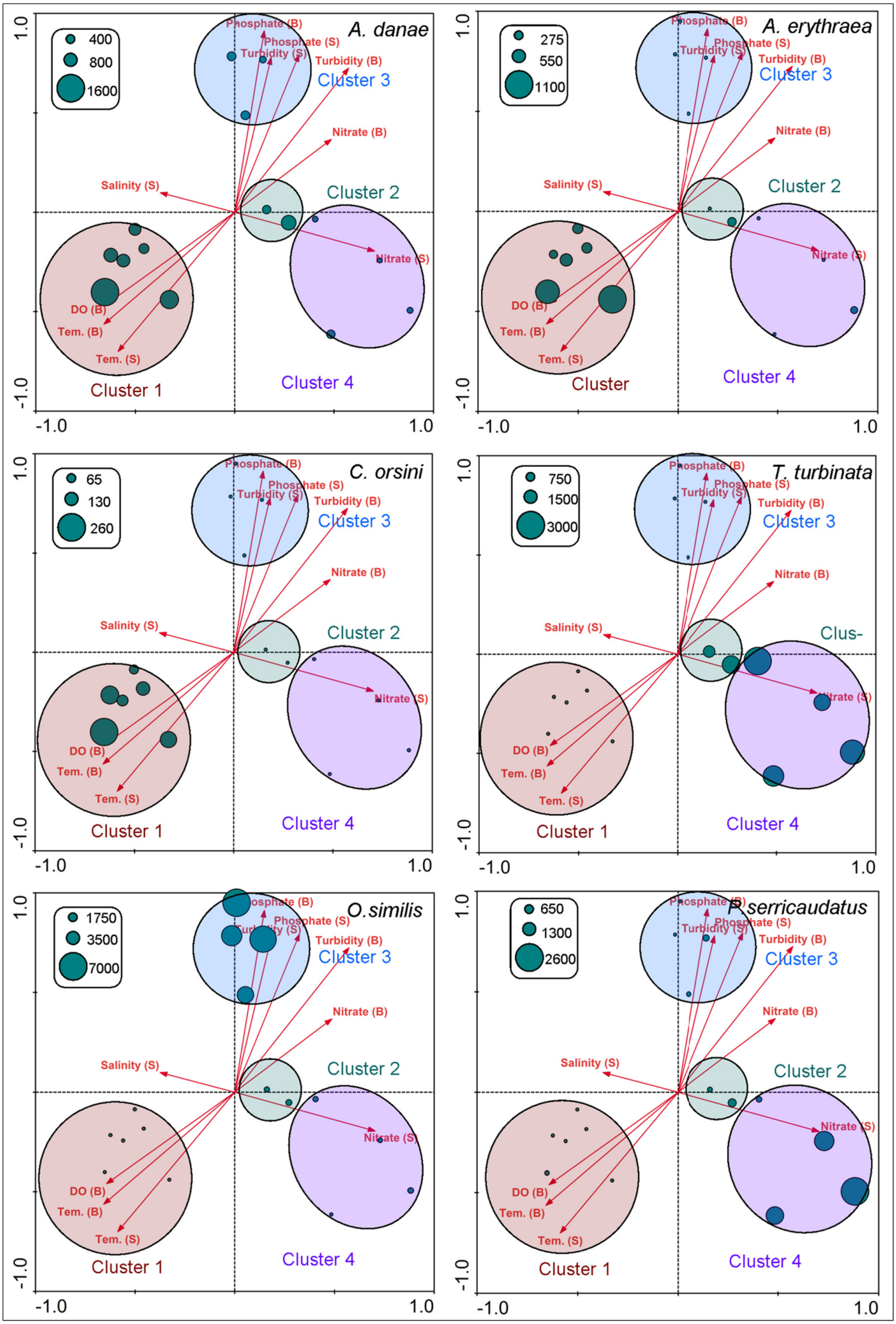


**Fig. 12.** Species abundance (bubbles) overlaid attribution RDA plot visualizing the sequential transformation of the dominant copepods M3 along with varying environmental conditions during different phases of the sampling period. The sampling observations (bubble positions) are accordance's with the Fig. 9 (M3). The value of the bubble sizes are proportional to the reference bubbles in the inset in each panels.

2005; Jyothibabu et al., 2006, 2008). Significantly high abundance and even blooms of diatoms such as *Fragillaria* and *Coscinodiscus* are common along the west coast of India during the SWM period (Madhupratap and Parulekar, 1993) and these large phytoplankton forms are considered as the main reason behind the large fishery stock along the southwest coast of India (Nair and Subrahmanyan, 1955; Subrahmanyan, 1973; Regunathan et al., 1984a,b; Madhupratap et al., 1996; Pillai et al., 2003). The spatial distributional differences of the chlorophyll *a* in the Mud Bank and the Non-Mud Bank locations were comparable, whereas, their temporal changes with in all locations was significant and this is similar to the already known pattern along the southwest coast of India including the Mud Bank (Nair and Subrahmanyan, 1955; Subrahmanyan, 1973; Nair et al., 1984; Madhupratap et al., 1996). Productivity associated with coastal upwelling and runoff alters the vertical distribution of dissolved oxygen in the subsurface and bottom waters (Madhupratap et al., 1990; Naqvi et al., 2006; Jyothibabu et al., 2006). The overall belief is that the oxidation of the sinking, unutilized particles (especially the larger diatoms) *Fragilaria* and *Coscinodiscus* from the surface, availability of high subsurface production without utilization by higher trophic levels and the lack of advection of deeper waters together contribute to the hypoxia in the eastern Arabian Sea (Naqvi et al., 2006). However, the above contention does not seem very relevant in the present case, as there were low oxygenated waters at the subsurface in the present study area from June onwards, much prior to the formation of the high phytoplankton stock in the region. This also implies that hypoxic waters prevalent in the three sampling locations throughout the Southwest Monsoon were caused by coastal upwelling. Similar conclusions are available from a recent time series study elsewhere in the study domain (Gupta et al., 2016).

Hydrographical transformations and associated changes in phytoplankton biomass and production influence the mesozooplankton diversity and production (Smith and Madhupratap, 2005; Jyothibabu et al., 2006; Jagadeesan et al., 2013). The significance of the present study is that this is the first detailed study about the mesozooplankton community in a region affected by both coastal upwelling and Mud Bank processes, whereas earlier studies deal with the mesozooplankton community response to seasonal changes in hydrography of the larger domain (Madhupratap et al., 1990; Nair et al., 1992). Earlier studies of the coastal region found that mesozooplankton biomass and abundance are generally higher during the Late-SWM period as compared to Pre-SWM conditions (Madhupratap et al., 1990). The seasonal pattern of mesozooplankton observed in the present study in the Mud Bank and the Non-Mud Bank locations were in good agreement with earlier studies (Mathew et al., 1984; Jyothibabu et al., 2006; Madhupratap et al., 1990) and the values were comparable to earlier observations in the inshore waters of the southwest coast of India (Madhupratap, 1987; Padmavati and Goswami, 1996; Madhu et al., 2007). The present study showed that the mesozooplankton biomass, which was low during the Pre-SWM and Early-SWM periods (<2 ml $m^{-3}$) at M1, M2 and M3, then increased significantly during the Peak-SWM period (>10 ml $m^{-3}$). We also found that the spatial differences of the mesozooplankton biomass were insignificant among M1, M2 and M3. Mesozooplankton abundance followed a similar pattern of biomass: it was high during the Peak- and Late- SWM periods as compared to the Pre-SWM at M1 and M2 locations. A general lag in increase in mesozooplankton biomass is evident as compared to the phytoplankton during the Early-SWM period, which is quite usual in marine systems due to the different generation times of both components (Madhupratap et al., 2001; Smith and Madhupratap, 2005; Jyothibabu et al., 2008). The contribution of different zooplankton groups to the total abundance varied between Pre-SWM and SWM periods in the Mud Bank and Non-Mud Bank locations and similar observations were recorded earlier for the general abundance in deeper Arabian Sea (Madhupratap et al., 1996; Smith and Madhupratap, 2005; Jyothibabu et al., 2008).

Copepods contributed the majority to the total mesozooplankton abundance in the study domain as noticed in earlier studies (Smith et al., 1998; Stelfox et al., 1999; Madhupratap et al., 1996; Padmavati and Goswami; 1996; Smith and Madhupratap, 2005). The appearance of hydromedusae and siphonophores in all three locations during the Peak-SWM was related to Coastal Upwelling (Madhupratap et al., 1990; Jagadeesan et al., 2013). During the Late-SWM period, the abundance of siphonophores increased in all three locations. High abundance of gelatinous zooplankton was reported before in Alappuzha Mud Bank (Mathew et al., 1984) as well as from the entire southwest coast of India (Madhupratap et al., 1996). Increased cladocera abundance was noticed during the SWM period, especially during the Late-SWM when sea surface salinity was low due to increased river influx. Swarms of cladocerans in the inshore waters along the west coast of the India during the Late-Monsoon period associated with low salinity and high phytoplankton abundances were reported earlier (Padmavati and Goswami, 1996; Naomi et al., 1990; Haridevan et al., 2015). The appearance of polychaete larva showed clear seasonality, occurring only during the SWM period in the Mud Bank and Non-Mud Bank locations. High production of the larvae is an indication of the availability of suitable food in the water column (Yoshinaga et al., 2010). Alternatively, subsurface hypoxia during coastal upwelling events might be responsible for the high abundance of the polychaete larvae in the surface waters as in the case of Puget Sound estuary (Keister and Tuttle, 2013). High abundance of fish eggs were found during Peak-SWM in M3, which corresponded to the peak reproductive period of fishes along the west coast of India during upwelling (Madhupratap et al., 1994; Preetha, 2015).

Upwelling begins in the inshore waters along the southwest coast of India in June (Madhupratap et al., 1990; Jyothibabu et al., 2008). Available studies on mesozooplankton from the southwest coast of India (Madhupratap et al., 1990, 2001; Jyothibabu et al., 2008) mostly represent the effects of the later phase of seasonal upwelling on the copepod community, while information for the onset and intense phase of upwelling is not available so far. The fine resolution samplings in the present study were useful to track changes in the copepod species composition especially during the transition period from the Pre-SWM to SWM conditions. The copepod distribution showed significant differences among the observations. The high resolution spatial sampling of the present study provided details about copepod abundance: their abundance decreased during the transition phase of Pre-SWM to Early-SWM period at M1 and M2 locations. This decrease corresponded with a shift in their community composition (Madhupratap et al., 2001; Rakhesh et al., 2006; Rakesh et al., 2008; Jagadeesan et al., 2013). Copepod total abundance was high during the Peak-SWM (Cluster 3) and Late-SWM (Cluster 4) as compared to the Pre-SWM period (Cluster 1) in M1, M2 and M3. More importantly, the abundance and composition of copepods remained similar in the Mud Bank and Non-Mudbank locations. *Paracalanus parvus* and *Acrocalanus* sp., were the common inshore coastal forms in Indian waters (Padmavati and Goswami, 1996; Jagadeesan et al., 2013) and their presence was found throughout the sampling period in the present study.

Copepod species *Acartia danae*, *A. erythraea* and *Centropages orsini*, *C. furcatus* and *Labidocera acuta* were abundant during the Pre-SWM period in the Mud Bank and the Non-Mud Bank locations. These species are typical coastal forms and they abundantly occur in the lower reaches of estuaries and inshore waters along the east and west coasts of India (Madhupratap et al., 1992;

Achuthankutty et al., 1997; Rakhesh et al., 2006). The Pre-SWM is a relatively low productive period (Madhupratap et al., 1996; Jyothibabu et al., 2006) during which the microbial loop food web plays an important role in providing nutrition to the higher trophic levels (Tiselius 1989; Burkill et al., 1993; Madhupratap et al., 1996; Landry et al., 1998; Ramaiah et al., 2005; Jyothibabu et al., 2006, 2010). *Acartia danae*, *Acartia erythraea*, *Labidocera acuta* and *Centropages orsini* are herbivorous/omnivorous and their high abundance during the Pre-SWM points towards their linkage with the microbial loop for nutrition (Tiselius, 1989; Stoecker and Egloff, 1987; Madhupratap et al., 1990; Rakhesh et al., 2006). The shift in species of copepod during the transition from the Pre-SWM to the Peak-SWM was evident in the present study (both the Mud Bank and Non-Mud Bank) and such a seasonal shifts were proposed earlier also from various coastal waters of India (Madhupratap, 1987; Madhupratap et al., 1996; Padmavati and Goswami, 1996; Jagadeesan et al., 2013). The discriminate species analysis emphasized the appearance of *Temora turbinata* during the Early-SWM (cluster 2) and the high abundance during the Late-SWM (Cluster 4) in Mud Bank and Non-Mud Bank locations. This species is an upwelling indicator and they are opportunistic, capable of exploiting upwelling - induced high phytoplankton stocks prevailing along the west coast of India during the SWM (Madhupratap et al., 1990, 1992). Their presence in the Gulf of Mannar and Palk Bay during the SWM associated with the upwelled waters advected by Monsoon Current has been reported recently (Jagadeesan et al., 2013; Anjusha et al., 2013). The predominance of opportunistic species of copepods, exploiting their favorable nutritional conditions has been reported earlier from many other regions such as the east coast of India (Rakesh et al., 2008), off Rio de Janerio (Lopez et al., 1999), northern Taiwan (Lo et al., 2004) and north eastern China Sea (Tseng et al., 2008). During such proliferation, the community diversity and evenness decrease as observed in the present study (Madhupratap et al., 1996; Jagadeesan et al., 2013).

One of the most important observations during the present study on seasonal copepod composition was the high abundance of cyclopoid copepods (especially *Oithona similis*) in the entire study area during the Peak-SWM. It is noticed earlier that the ability to tolerate low oxygen conditions differs among various species of copepods and their life stages (Roman et al., 1993). In general, copepods can respond in two ways to hypoxia, they can either adapt to the situation or move away from the adverse condition. It is fundamental to consider that the recruitment of copepod stock mainly depends upon the reproductive success and survival of the nauplius. Calanoid copepods (*Acartia, Paracalanus, Acrocalanus* and *Centropages*) release their eggs into the surroundings for hatching out and larval development. It is estimated earlier that copepod eggs sink down at a rate of $\sim$20 m day$^{-1}$ (Uye, 1980) and their hatching time is around 0.5–1.0 day in normal conditions (Uye, 1980; Yoshida et al., 2012). Considering the shallow depth of the present study area (6m in M1, M2 and 12m in M3), it is quite likely that the calanoid eggs reach the near bottom layer before they hatch out. It was noticed earlier that hypoxia could suppress the copepod egg hatching (Uye, 1980; Lutz et al., 1992; Marcus and Lutz, 1994; Marcus et al., 1997; Choi et al., 2016) and found that hatching success of copepods in hypoxic conditions could be as low as <10% of the aerated normal condition (Marcus and Lutz, 1994; Marcus et al., 1997; Choi et al., 2016). Hypoxia also causes high mortality of copepod nauplius due to the low efficiency of the larvae to survive in low oxygenated conditions (Elliott et al., 2013; Choi et al., 2016). Even though adult calanoids could escape the hypoxic sub-surface waters by some avoidances mechanism such as movements towards the surface waters, their reduced egg hatching success and high mortality rate of nauplius in hypoxic sub-surface waters might reduce the overall community abundance during the Peak-SWM. Like Calanoids, Cyclopoids also could migrate to surface layers to avoid the sub-surface hypoxia. Interesting to note here is the fact that most of the cyclopoid copepods (*Oithona similis*) carry their eggs in egg sacs until the nauplius gets hatched out. Therefore, cyclopoid nauplius released into the surface waters are unlikely to face the adverse effect of the subsurface hypoxia and this could be the reason why high abundance of cyclopoid copepod *Oithona similis* was found during the Peak-SWM of the present study (Eiane and Ohman, 2004). Similar observations of high abundance of *Oithona similis* in the surface waters associated with bottom hypoxia was reported from the coastal waters of Puget Sound estuary (Keister and Tuttle, 2013). The high abundance of *Oithona similis* in the inshore surface waters was coincident with upwelling associated- hypoxia, as elaborated above, is the first report from Indian waters. In earlier studies, the concentration of *Oithona similis* in the surface waters was considered just as a seasonal feature of the SWM without unraveling the underlying cause. This pattern of distribution was shown in the RDA Triplot of all three locations: the increasing gradients of the species axis of *Oithona similis* was oriented to the opposite side of the bottom dissolved oxygen and temperature.

A few earlier studies along the southwest coast of India reported high carnivorous plankton contributions during the SWM period (Madhupratap et al., 1990; Jagadeesan et al., 2013). This seasonal picture is true with *Oithona similis*, which is a carnivore (Madhupratap et al., 1996; Rakhesh et al., 2006) and found abundantly during the Peak-SWM in the present study. The Late-SWM was characterized by *Temora turbinata, Centropages tenuremis* and *Pseudodiaptomus serricaudatus*, which are opportunistic coastal species capable of forming swarms during favorable environmental conditions (Madhupratap et al., 1996; Jagadeesan et al., 2013). The physical signatures of upwelling and nutrient enrichment in the surface waters weakened during the Late-SWM, but increased mesozooplankton biomass was found up to October. This is primarily due to the time lag between nutrient enrichment, phytoplankton proliferation and zooplankton biomass accumulation and almost a month time lag was noticed in earlier studies as well (Madhupratap et al., 1992; Jyothibabu et al., 2008; MLR Plankton Atlas, 2011).

Distribution of dominant and discriminant species of copepods in M1, M2 and M3 was similar and their spatial differences were statistically insignificant, however the temporal differences of zooplankton biomass, zooplankton/copepods abundances were significant within M1, M2 and M3. These indicate the following (a) the environmental processes operating in all the three locations during the various phases of the sampling period were the same and (b) there were significant temporal variations in the hydrography during different phases of the sampling period. These features were clearly represented in the RDA analyses that the environmental variables explains that the $\sim$85% variance of dominant and discriminant copepod species distribution and chlorophyll *a* in the study domain. Partial RDA model shows that temperature, dissolved oxygen and nutrients together could explain 67.5%, 70.6% and 68.9% variance of copepods species distribution and chlorophyll *a* in M1, M2 and M3 respectively. It is very clear in the hydrography data presented and also in the results of the RDA analyses that the temporal differences in temperature, dissolved oxygen and nutrients were significantly influenced by upwelling processes in both Mud Bank and Non-Mudbank locations. Turbidity influenced variance of copepods species distribution and chlorophyll *a* was low and more importantly, comparable in both the Mud Bank and the Non-Mud Bank locations. Relatively high turbidity was found only in the Mud Bank. All the above strongly suggest the dominant influence of coastal upwelling associated hydrography in structuring the mesozooplankton/copepod community in the entire study domain including the Mud Bank location.

Many historical as well as recent studies have presented a comprehensive view about how upwelled hypoxic waters influence the fishery resources along the Southwest coast of India during the Southwest Monsoon (Banse, 1959; UNDP/FAO, 1976; Reghunathan et al., 1981, 1984b; Gupta et al., 2016; Karnan et al., 2017). It is realistic to consider here that diverse fishes have differences in their adaptive capabilities to deal with hypoxic, upwelled waters (Pihl et al., 1991; Rabalais and Turner, 2001). It is believed in the case of coastal upwelling along the west coast of India that the initial rising of upwelled hypoxic waters in the outer continental shelf tends to concentrate shrimp and other demersal resources towards the inner continental shelf and later onshore spreading of the hypoxic waters force the fishes present there to perform vertical movements towards surface layers to avoid hypoxic waters (Banse, 1959; Reghunathan et al., 1981, 1984b; Gupta et al., 2016; Karnan et al., 2017). Another possibility relevant in the present context is that many small pelagics on their usual schooling movement in the near-shore waters, usually against the currents, carry out upward movement to avoid subsurface hypoxic waters, eventually making their increased availability in the surface layers (Reghunathan et al., 1981, 1984b; Karnan et al., 2017). A detailed discussion on the above aspect in relation to coastal upwelling, plankton food web structure and fishery resources along the southwest coast of India has been presented in Karnan et al. (2017).

## 5. Conclusion

The response of mesozooplankton community, especially copepods, to the hydrographical transformations along the southwest coast of India caused by coastal upwelling and the Mud Bank is presented. The weekly/biweekly study focused on three locations (M1, M2 and M3). Mud Bank characteristics of relatively high suspended sediments and calm sea conditions existed at M2 by mid-June and before that all three locations had comparable water column characteristics. Coastal upwelling characterized by a cool and less oxygenated water column was prevalent over all the three locations by early-June. The mesozooplankton community in the study domain was composed of 15 heterogeneous groups; their biomass and abundance were high during the Peak- (av. $6.02 \pm 5.19$ ml m$^{-3}$ and av. $7285 \pm 3248$ No m$^{-3}$) and Late-SWM (av. $4.91 \pm 4.35$ ml m$^{-3}$ and av. $6802 \pm 2727$ No m$^{-3}$) as compared to the Pre-SWM (av. $0.63 \pm 0.55$ ml m$^{-3}$ and av. $3045 \pm 1584$ No m$^{-3}$) and Early-SWM (av. $0.58 \pm 0.46$ ml m$^{-3}$ and av. $2047 \pm 1675$ No m$^{-3}$). Mesozooplankton abundance was chiefly by copepods (>70%) and the number of larger zooplanktonic carnivores (medusae, siphonophores and chaetognaths) was found to be low (<5%). Following multivariate analyses, it was possible to segregate copepods into 4 clusters representative of Pre-SWM (cluster 1), Early-SWM (cluster 2), Pre-SWM (cluster 3) and Late-SWM (cluster 4). In all three sampling locations, discriminant copepods consisted of *Acartia danae*, *A. erythraea* and *Centropages orsini* (Pre-SWM); *Temora turbinata* (Early-SWM); *Oithona similis* (Peak-SWM); *Temora turbinata*, *Pseudodiaptomus serricaudatus*, and *Centropages tenuremis* (Late-SWM). The copepod dominance and distribution patterns observed in all three locations (M1, M2 and M3) were similar and the detailed Multivariate Redundancy analysis indicated the dominant influence of coastal upwelling associated hydrography in structuring the mesozooplankton/copepod community in the study domain including the Mud Bank location. This would mean that Mud Bank does not really matter at all to the mesozooplankton community in the study domain and it is just coincidently happening during the SWM, when coastal upwelling is predominant in the region. The present study provided the first in-depth information of the zooplankton, especially copepods, from a coastal upwelling – Mud Bank system along the southwest coast of India evidencing the dominant role of coastal upwelling in shaping the zooplankton community. On the other hand, the development of the Mud Bank is beneficial for fishing as it allows for a reliable launching and landing area for boats to access productive fishing grounds nearby that are enhanced by coastal upwelling.

## Acknowledgements

The authors thank the Directors, CSIR-National Institute of Oceanography (NIO) and ICAR- Central Marine Fisheries Research Institute (CMFRI) India for facilities. The authors thank the Scientist - in - Charge, CSIR NIO RC Kochi for encouragement. We are thankful to all our colleagues in CSIR-NIO and ICAR- CMFRI, India who helped to carry out the field sampling successfully. We sincerely thank Prof. Sharon L Smith and the other two anonymous reviewers for their useful comments and directions to improve the first version of the manuscript. The first author thanks CSIR for providing Senior Research Fellow funding. This is NIO contribution 6074.

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pocean.2017.07.004.

## References

Achuthankutty, C.T., Ramaiah, N., Padmavati, G., 1997. Zooplankton variability and copepod assemblage in the coastal and estuarine waters of Goa along the central west coast of India. Intergovernmental Oceanographic Commission 1, workshop report no. 142 (eds) Pierrot-Bults A. C. and Vander Spoel S., UNESCO, Paris, pp. 1–11.

Anjusha, A., Jyothibabu, R., Jagadeesan, L., Mohan, A.P., Sudheesh, K., Krishna, K., Ullas, N., Deepak, M.P., 2013. Trophic efficiency of plankton food webs, Observations from the Gulf of Mannar and the Palk Bay, Southeast Coast of India. J. Mar. Syst. 115–116, 40–61.

Asha Devi, C.R., Jyothibabu, R., Sabu, P., Jacob, J., Habeebrehman, H., Prabhakaran, M. P., Jayalakshmi, K.J., Achuthankutty, C.T., 2010. Seasonal variations and trophic ecology of microzooplankton in the South-eastern Arabian Sea. Cont. Shelf Res. 30, 1070–1084.

Balachandran, K.K., 2004. Does subterraneous flow initiate Mud Banks along the southwest coast of India. Estuar. Coast. Shelf Sci. 59, 589–598.

Banse, K., 1959. On the upwelling and bottom trawling off the southwest coast of India. J. Marine Biol. Assoc. India 1, 33–49.

Banse, K., 1968. Hydrography of the Arabian Sea shelf of India and Pakistan and effects on demersal fishes. Deep-Sea Res. I 15, 45–79.

Banse, K., Vijayaraghavan, Sumitra., Madhupratap, M., 1996. On the possible causes of the seasonal phytoplankton blooms along the southwest coast of India. Indian J. Mar. Sci. 25, 283–289.

Bhattathiri, P.M.A., Pant, A., Sawant, S., Gauns, M., Matondkar, S.G.P., Mohanraju, R., 1996. Phytoplankton production and chlorophyll distribution in the eastern and central Arabian Sea in 1994–1995. Curr. Sci. 71, 869–877.

Burkill, P.H., Leakey, R.J.G., Owens, N.P., Mantoura, R.F.C., 1993. *Synechococcus* and its importance to the microbial food web of the Northwestern Indian Ocean. Deep-Sea Res. II 40, 773–782.

Bristow, R.C., 1938. History of Malabar Mud Banks, Ernakulum, Cochin Government Press, vol. 174, pp. 55.

Choi, K.H., Jang, M.C., Shin, H.H., Lee, W.J., Shin, K., 2016. In situ hatching success of calanoid copepod eggs in hypoxic sediments of a coastal bay. J. Coastal Res. 32, 333–338.

Clarke, K.R., Warwick, R.M., 2001. Changes in Marine Communities – An Approach to Statistical Analysis and Interpretation. PRIMER-E LTD, Plymouth Marine Laboratory, UK., p. 171.

Clarke, K.R., Gorley, R.N., 2006. PRIMER (Plymouth Routine In Multivariate Ecological Research). User Manual/Tutorial V6, 1–90.

Conway, D., White, R., Hugues-Dit-Ciles, J., Gallienne, C., Robins, D., 2003. Guide to the Coastal and Surface Zooplankton of the South Western Indian Ocean. Occasional Publication No. 15, Marine biological Association of the United Kingdom, p. 354.

Cury, P., Bakun, A., Crawford, R.J.M., Jarre, A., Quinones, R.A., Shannon, L.J., Verheye, H.M., 2000. Small pelagic in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. ICES J. Mar. Sci. 57, 603–618.

Damodaran, R., 1973. Studies on the benthos of the mudbank regions of Kerala coast. Bulletin Department of Marine Science, University of Cochin, vol. 6, pp. 61–126.

Du Cane, C.G., Bristow, R.C., Brown, C.J., Keen, B.A., Russel, E.W., 1938. Report of Special Committee on the Movement of Mud Banks. Cochin Government Press, Cochin, India, p. 126.

Eiane, K., Ohman, M.D., 2004. Stage-specific mortality of *Calanus finmarchicus*, *Pseudocalanus elongatus* and *Oithona similis* on Fladen Ground, North Sea, during a spring bloom. Mar. Ecol. Prog. Ser. 268, 183–193.

Elliott, D.T., Pierson, J.J., Roman, M.R., 2013. Copepods and hypoxia in Chesapeake Bay: abundance, vertical position and non-predatory mortality. J. Plankton Res. 35, 1027–1034.

Gopinathan, C.K., Qasim, S.Z., 1974. Mud banks of Kerala – their formation and characteristics. Indian J. Mar. Sci. 3, 105–114.

Grasshoff, K., 1983. Methods of Seawater Analysis. In: Grasshoff, K., Ehrhardt, M., Kremling, K., (Eds.) Weinheim, Verlag Chemie, pp. 419.

Gupta, G.V.M., Sudheesh, V., Sudharma, K.V., Saravanane, N., Dhanya, V., Dhanya, K. R., Lakshmi, G., Sudhakar, M., Naqvi, S.W.A., 2016. Evolution to decay of upwelling and associated biogeochemistry over the southeastern Arabian Sea shelf. J. Geophys. Res., Biogeosci. 121, 159–175.

Haridevan, G., Jyothibabu, R., Arunpandi, N., Jagadeesan, L., Biju, A., 2015. Influence of salinity on the life table demography of a rare Cladocera *Latonopsis australis*. Environ. Monit. Assess. 643 (187), 1–15.

Jagadeesan, L., Jyothibabu, R., Anjusha, A., Mohan, A.P., Madhu, N.V., Muraleedharan, K.R., Sudheesh, K., 2013. Ocean currents structuring the mesozooplankton in the Gulf of Mannar and the Palk Bay, southeast coast of India. Prog. Oceanogr. 110, 27–48.

Jyothibabu, R., Asha Devi, C.R., Madhu, N.V., Sabu, P., Jayalakshmy, K.V., Jacob, Josia., Habeebrehman, H., Prabhakaran, M.P., Balasubramanian, T., Nair, K.K.C., 2008. The response of microzooplankton (20–200 μm) to coastal upwelling and summer stratification in the southeastern Arabian Sea. Cont. Shelf Res. 28, 653–671.

Jyothibabu, R., Madhu, N.V., Habeebrehman, H., Jayalakshmy, K.V., Nair, K.K.C., Achuthankutty, C.T., 2010. Re-evaluation of 'paradox of mesozooplankton' in the eastern Arabian Sea based on ship and satellite observations. J. Mar. Syst. 81, 235–251.

Jyothibabu, R., Madhu, N.V., Jayalakshmi, K.V., Balachandran, K.K., Shiyas, C.A., Martin, G.D., Nair, K.K.C., 2006. Impact of large river influx on microzooplankton and its implications on the food web of tropical estuary (Cochin backwaters – India). Estuar. Coast. Shelf Sci. 69, 505–518.

Jyothibabu, R., Balachandran, K.K., Jagadeesan, L., Karnan, C., Arunpandi, N., Naqvi, S. W.A., 2017. Mud Banks along the Southwest coast of India are not muddy for plankton (under review).

Karnan, C., Jyothibabu, R., Arunpandi, N., Jagadeesan, L., Muraleedharan, K.R., Pratihari, A.K., Balachandran, K.K., Naqvi, S.W.A., 2017. Discriminating the Biophysical impacts of Coastal Upwelling and Mud Banks along the Southwest Coast of India. J. Mar. Syst. 172, 24–42.

Kasturirangan, L.R., 1963. A key for the identification of the more common planktonic Copepoda of the Indian coastal waters, Publication No.2. Indian National Committee on Oceanic Research, pp. 1–87.

Keister, J.E., Tuttle, L.B., 2013. Effects of bottom-layer hypoxia on spatial distributions and community structure of mesozooplankton in a sub-estuary of Puget Sound, Washington, USA. Limnol. Oceanogr. 58, 667–680.

Kurup, P.G., 1977. Studies on the physical aspects of Mud Banks along the Kerala coast with reference to the Purakkad Mud Bank. Bulletin of the Department of Marine Science, vol. 8, pp. 1–72.

Landry, M.R., Brown, S.L., Campbell, L., Constantinou, J., Liu, H., 1998. Spatial patterns in phytoplankton growth and microzooplankton grazing in the Arabian Sea during monsoon forcing. Deep-Sea Res. II 45, 2353–2368.

Leps, J., Smilauer, P.S., 2003. Multivariate analysis of ecological data using CANOCA. Cambridge University Press, Cambridge, UK. pp. 283.

Lin, D., Xiu, Q.L., Hong, D.F., Yan, H.D., Zhuo, X.H., Chen, J., 2011. Calanoid copepods assemblages in Pearl River Estuary of China in summer, Relationships between species distribution and environmental variables. Estuar. Coast. Shelf Sci. 93, 259–267.

Lo, W.T., Hwang, J.S., Chen, Q.C., 2004. Spatial variations of copepods in the surface waters of southeastern Taiwan Strait. Zool. Stud. 43, 218–228.

Lopez, R.M., Brandini, F.P., Gaeta, S.A., 1999. Distribution pattern of epipelagic copepods off Rio de Janeiro (SE Brasil) in summer 1991/1992 and winter 1992. Hydrobiologia 411, 161–174.

Lutz, R.V., Marcus, N.H., Chanton, J.P., 1992. Effects of low oxygen concentrations on the hatching and viability of eggs of marine calanoid copepods. Mar. Biol. 114, 241–247.

Madhu, N.V., Jyothibabu, R., Balachandran, K.K., Honey, U.K., Martin, G.D., Vijay, J.G., Shiyas, C.A., Gupta, G.V.M., Achuthankutty, C.T., 2007. Monsoonal impact on planktonic standing stock and abundance in a tropical estuary (Cochin backwaters – India). Estuar. Coast. Shelf Sci. 73, 54–64.

Madhupratap, M., 1987. Status and strategy of zooplankton of tropical Indian estuaries. A review. Bull. Plankton Soc. Jpn. 34, 65–81.

Madhupratap, M., Gopalakrishnan, T.C., Haridas, P., Nair, K.K.C., Aravindakshan, P.N., Padmavati, G., Paul, S., 1996. Lack of seasonal and geographic variation in mesozooplankton biomass in the Arabian Sea and its structure in the mixed layer. Curr. Sci. 71, 863–868.

Madhupratap, M., Nair, S.R., Haridas, P., Padmavati, G., 1990. Response of zooplankton to physical changes in the environment, coastal upwelling along the central west coast of India. J. Coastal Res. 6, 413–426.

Madhupratap, M., Gopalakrishnan, T.C., Haridas, P., Nair, K.K.C., 2001. Mesozooplankton biomass, composition and distribution in the Arabian Sea during the Fall Intermonsoon, implications of oxygen gradients. Deep-Sea Res. II 48, 1345–1368.

Madhupratap, M., Haridas, P., Ramaiah, N., Achuthankutty, C.T., 1992. Zooplankton of the southwest coast of India, abundance, composition, temporal and spatial variability in 1987. In: Desai, B.N. (Ed.), Oceanography of the Indian Ocean. Oxford & IBH, New Delhi, pp. 99–112.

Madhupratap, M., Parulekar, A.H., 1993. Biological processes of Northern Indian Ocean. In: Ittekkot, V., Nair, R.R. (Eds.), Monsoon Biogeochemistry, Sonderband, SCOPE/UNEP, vol. 76, pp. 51–83.

Madhupratap, M., Shetye, S.R., Nair, K.N.V., Nair, S.R.S., 1994. Oil Sardine and Indian Mackerel, their fishery, problems and coastal oceanography. Curr. Sci. 66, 340–348.

Mallik, T.K., Mukherji, K.K., Ramachandran, K.K., 1988. Sedimentology of the Kerala mud banks (fluid muds?). Mar. Geol. 80, 99–118.

Manojkumar, P., Narayana, A.C., Tatavarti, R., 1998. Mud Bank dynamics, physical properties of sediments. J. Geol. Soc. Indian 51, 793–798.

Marcus, N.H., Lutz, R.V., 1994. Effects of anoxia on the viability of subitaneous eggs of planktonic copepods. Mar. Biol. 12, 83–87.

Marcus, N.H., Lutz, R.V., Chanton, J.P., 1997. Impact of anoxia and sulphide on the viability of eggs of three planktonic copepods. Mar. Ecol. Prog. Ser. 146, 291–295.

Mathew, J., Baba, M., Kurian, N.P., 1995. Mud Banks of southwest coast of India I, Wave characteristics. J. Coastal Res. 11, 168–178.

Mathew, K.J., Gopinathan, C.P., Raghunathan, A., Rao, D.S., Murty, A.V.S., 1984. Ecology of Mud Banks – Zooplankton. Bull. Central Mar. Fisheries Res. Inst., India 31, 35–39.

Mathew, K.J., Gopinathan, C.P., Rao, D.S., Regunathan, A., Murty, A.V.S., 1977. Diurnal variations in the distribution of zooplankton in relation to currents and other ecological parameters of the Mud bank of Alleppey, Kerala. Proceedings of the Symposium of Warm Water Zooplankton Special Publications, National Institute of Oceanography, Goa, pp. 250–263.

MLR Plankton Atlas, 2011. Atlas on environmental parameters and productivity of the Indian EEZ and adjoining seas. Nair, K.K.C. (Ed.), Centre for Marine Living Resources and Ecology, Ministry of Earth Sciences, New Delhi, pp. 294.

Murty, A.V.S., Rao, D.S., Reghunathan, A., Gopinathan, C.P., Mathew, K.J., 1984. Ecology of Mudbanks-Hypothesis on mudbanks. Bull. Central Mar. Fisheries Res. Inst. 31, 8–20.

Nair, P.V.R., Gopinathan, C.P., Balachandran, V.K., Mathew, K.J., Regunathan, A., Rao, D.S., Murty, A.V.S., 1984. Ecology of Mudbanks – Phytoplankton productivity in Alleppey mudbank. Bull. Central Mar. Fisheries Res. Inst. 31, 28–34.

Nair, S.R.S., Devassy, V.P., Madhupratap, M., 1992. Blooms of phytoplankton along the west coast of India associated with nutrient enrichment and the response of zooplankton. Sci. Total Environ., 819–828

Nair, V.R., Subrahmanyan, R., 1955. The diatom *Fragilaria oceanica* Cleve, an indicator of abundance of the Indian oil Sardine, *Sardinella longiceps*. Curr. Sci. 2, 41–42.

Naomi, T.S., Antony, G., Mathew, K.J., 1990. Studies on the distribution of cladocera in the eastern Arabian Sea and Bay of Bengal. Proceedings of first workshop scientific results FORV Sagar Sampada, India 5–7, pp. 85–93.

Naqvi, S.W.A., George, M.D., Narvekar, P.V., Jayakumar, D.A., Shailaja, M.S., Sardessai, S., Sarma, V.V.S., Shenoy, D.M., Naik, H., Maheswaran, P.A., Krishnakumari, K., Rajesh, G., Sudhir, A.K., Binu, M.S., 1998. Severe fish mortality associated with 'red tide' observed in the sea off Cochin. Curr. Sci. 75, 543–544.

Naqvi, S.W.A., Naik, H., Jayakumar, D.A., Shailaja, M.S., Narvekar, P.V., 2006. Seasonal Oxygen Deficiency Over the Western Continental Shelf of India Past and Present Water Column Anoxia, vol. 64. Springer, Netherlands, pp. 195–224.

Narayana, A.C., Manojkumar, P., Tatavarti, R., 2001. Beach dynamics related to the Ambalapuzha Mud Bank along the southwest coast of India. In: McAnally, W.H., Mehta, A.J. (Eds.), Coastal and Estuarine Fine Sediment Processes, Elsevier Science BV. pp. 495–507.

NIO Report, 2008. Near – Shore Dynamics of the Southwest Coast of India With Special References to Upwelling and Mud Bank. Centre for Marine Living Resources and Ecology (MoES), Kochi, p. 257.

Padmavati, G., Goswami, S.C., 1996. Zooplankton production, composition and diversity in the coastal waters of Goa. Indian J. Mar. Sci. 25, 91–97.

Pielou, E., 1969. The measurement of diversity in different types of biological collections. J. Theor. Biol. 13, 131–144.

Pillai, N.G.K., Ganga, U., Jayaprakash, A.A., 2003. Indian Oil Sardine. In M. Mohan Joseph, A.A. Jayaprakash (Eds.), Status of exploited marine fishery resources of India. Central Marine Fisheries Research Institute, Cochin, pp. 18–24.

Pihl, L., Baden, S.P., Diaz, R.J., 1991. Effects of periodic hypoxia on distribution of demersal fish and crustaceans. Mar. Biol. 108, 349–360.

Postel, L., Fock, H., Hagen, W., 2000. Biomass and abundance, ICES Zooplankton Methodology manual. In: Harris, R.P., Wiebe, P.H., Leiz, J., Skjoldal, et al., (Eds.). Academic Press, pp. 193–213.

Preetha, G.N., 2015. Studies on small pelagic fishes along the Kerala coast with respect to the Potential Fishery Zone (PFZ) advisories, Ph.D., thesis, Mangalore University, pp. 1–172.

Queiroga, H., Blanton, J., 2004. Interactions between behavior and physical forcing in the control of horizontal transport of decapod crustaceans larvae. Adv. Mar. Biol. 47, 107–204.

Rabalais, N.N., Turner, R.E., 2001. Coastal hypoxia: consequences for living resources and ecosystems. American Geophysical Union. http://dx.doi.org/10.1029/CE058.

Rakesh, M., Raman, A.V., Kalavati, C., Subramanian, B.R., Sharma, V.S., Sunitha Babu, E., Sateesh, N., 2008. Zooplankton community structure across an eddy-generated upwelling band close to a tropical bay-mangrove ecosystem. Mar. Biol. 154, 953–972.

Rakhesh, M., Raman, A.V., Sudarsan, D., 2006. Discriminating zooplankton assemblages in neritic and oceanic waters, a case for the northeast coast of India, Bay of Bengal. Marine Environ. Res. 63, 93–109.
Ramaiah, N., Raghukumar, S., Mangesh, G., Madhupratap, M., 2005. Seasonal variations in carbon biomass of bacteria, thraustochytrids and microzooplankton in the Northern Arabian Sea. Deep Sea Res. II 52, 1910–1921.
Ramasastry, A.A., Myrland, P., 1959. Distribution of temperature, salinity and density in the Arabian Sea along the South Malabar Coast (South India) during the post-monsoon season. Indian J. Fisheries 6, 223–255.
Regunathan, A., Mathew, K.J., Kurup, N.S., Murty, A.V.S., 1981. Monsoon fishery and Mud Banks of Kerala coast. Bull. Central Mar. Fisheries Res. Inst. 30, 37–41.
Regunathan, A., Gopinathan, C.P., Mathew, K.J., Rao, D.S., Murty, A.V.S., 1984a. Ecology of Mud Banks - Benthos. Bull. Central Mar. Fisheries Res. Inst., India 31, 40–45.
Regunathan, A., Mathew, K.J., Rao, D.S., Gopinathan, C.P., Kurian, N.P., Murty, A.V.S., 1984b. Fish and Fisheries of the Mudbanks. Bull. Central Mar. Fisheries Res. Inst., India 31, 60–71.
Roman, M.R., Gauzens, A.L., Rhinehart, W.K., White, J.R., 1993. Effects of low-oxygen waters on Chesapeake Bay zooplankton. Limnol. Oceanogr. 38, 1603–1614.
Sahayak, S., Jyothibabu, R., Jayalakshmi, K.J., Habeebrehman, H., Sabu, P., Prabhakaran, M.P., Jasmine, P., Shaiju, P., Rejomon, G., Thresiamma, J., Nair, K. K.C., 2005. Red tide of *Noctiluca miliaris* off south of Thiruvananthapuram subsequent to the 'stench event' at the southern Kerala coast. Curr. Sci. 89, 1472–1473.
Sawant, S., Madhupratap, M., 1996. Seasonality and composition of phytoplankton in the Arabian Sea. Curr. Sci. 71, 869–873.
Sewell, R., 1999. The Copepoda of Indian Seas. Biotech Books, Delhi, India, pp. 1–407.
Shannon, C.E., Weiner, W., 1963. The mathematical theory of communication. University of Illinos. pp. 239.
Shetye, S.R., Gouveia, A.D., Shenoi, S.S.C., Sundar, D., Michael, G.S., Almeida, A.M., Santhanam, K., 1990. Hydrography and circulation off the west coast of India during the southwest monsoon 1987. J. Mar. Res. 48, 359–378.
Shynu, R., Rao, V.P., Kessserkar, P.N., Naqvi, S.W.A., Dineshkumar, P.K., 2017. Suspended matter and fluid muds off Alappuzha, Southwest coast of India. Estuar. Coast. Shelf. Sci. 185, 31–43.
Silas, E.G., 1984. Mud Banks of Kerala – Karnataka – Need for integrated study. Bull. Central Mar. Fisheries Res. Inst. 31, 1–2.
Simpson, E.H., 1949. Measurement of diversity. Nature, London 163, 688.
Smith, S.L., Madhupratap, M., 2005. Mesozooplankton of the Arabian Sea, Patterns influenced by seasons, upwelling, and oxygen concentrations. Prog. Oceanogr. 65, 214–239.
Smith, S., Roman, M., Prusova, I., Wishner, K., Gowing, M., Codispoti, L.A., Barber, R., Marra, J., Flagg, C., 1998. Seasonal response of zooplankton to monsoonal reversal in the Arabian Sea. Deep-Sea Res. II 45, 2369–2403.
Stelfox, C.E., Burkill, P.H., Edwards, E.S., Harris, R.P., Sleigh, M.A., 1999. The structure of zooplankton communities, in 2 to 2000 μm size range, in the Arabian Sea during and after the SW monsoon, 1994. Deep-Sea Res. II 46, 815–842.
Stoecker, D.K., Egloff, D.A., 1987. Predation by *Acartia tonsa* Dana on planktonic ciliates and rotifers. J. Exp. Mar. Biol. Ecol. 110, 53–68.
Subrahmanyan, R., 1959. Studies on the phytoplankton of the west coast of India. Proceed. Indian Acad. Sci. 1, 187.
Subrahmanyan, R., 1973. Hydrography and plankton as indicators of marine resources. Proceedings of the symposium on living resources of the seas around India. Mandapam, Central Marine Fisheries Research Institute - Special publications 199–228.
Subrahmanyan, R., Gopinathan, C.P., Pillai, C.T., 1975. Phytoplankton of the Indian Ocean, some Ecological problems. J. Mar. Biol. Assoc. India 17, 608–612.
Tatavarti, R., Narayana, A.C., Manojkumar, P., Chand, S., 1999. Mud Bank regime off the Kerala coast during monsoon and non-monsoon seasons. J. Earth Syst. Sci. 108, 57–68.
Tiselius, P., 1989. Contribution of aloricate ciliates to the diet of *Acartia clausi* and *Centropages hamatus* in coastal waters. Mar. Ecol. Prog. Ser. 56, 49–56.
Tseng, L., Dahms, H., Chen, Q., Hwang, J., 2008. Copepod assemblages of the northern South China Sea. Crustaceana 81, 1–22.
UNDP/FAO, 1976. Oil sardine larvae. UNDP/FAO Pelagic Fisheries Project (IND 69/593). Progress Report No. 15.
UNESCO, 1994. Protocols for the Joint Global Ocean Flux Study (JGOFS). Core Measurements. UNESCO, Paris 29, pp. 170.
Uye, S., 1980. Development of neritic copepods *Acartia clausi* and *A. steuri*. 1. Some environmental factors affecting egg development and the nature of resting eggs. Bull. Plankton Soc. Jpn. 27, 1–9.
Verma, U.P., Kurup, P.G., 1969. Formation of Chakara (Mud Bank) in the Kerala coast. Curr. Sci. 38, 559–560.
Yang, G.M., He, D.H., Wang, C.S., Miao, Y.T., Yu, H.H., 1999. Study on the biological oceanography characteristics of planktonic copepods in the waters north of Taiwan, II. Community characteristics. Acta Oceanol. Sinca 21, 72–80.
Yoshida, T., Liong, C.F., Majid, A.M., Toda, T., Othman, B.H.R., 2012. Temperature effects on the egg development time and hatching success of three *Acartia* species (Copepoda: Calanoida) from the strait of Malacca. Zool. Stud. 51, 644–654.
Yoshinaga, M.Y., Sumida, P.Y.G., Silveira, I.C.A., Ciotti, Á.M., Gaeta, S.A., Pacheco, L.F. C.M., Koettker, A.G., 2010. Vertical distribution of benthic invertebrate larvae during an upwelling event along a transect off the tropical Brazilian continental margin. J. Mar. Syst. 79, 124–133.
Zar, J.H., 1999. Biostatistical Analysis. Prentice-Hall, Upper Saddle River, p. 660.