

Ecological Indications of Copepods to Oxygen-deficient Near-shore Waters

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Abstract

Dissolved oxygen deficiency and its impacts on marine organisms is an important research topic world over. In this study, we utilized the advantage of a shallow seasonal hypoxic zone occurring along the Southwest Coast of India. Also, we adopted the standard live staining technique to assess the ecological responses of copepods to oxygen-deficient waters. Based on 18 weekly/ biweekly sampling sessions in the nearshore-waters along the Southwest coast of India, spanning over the Pre-Southwest Monsoon (April) to Late-Southwest Monsoon (September) of 2014, this study showed a noticeable decrease in the total abundance of copepods in the hypoxic subsurface waters associated with coastal upwelling. This feature was noticed particularly during the Peak-Southwest Monsoon (July - August), which was contrary to the usual temporal abundance pattern of copepods in the aerated surface waters. During the Southwest Monsoon, the percentage of dead copepods was noticeably high in the study area, especially in the subsurface waters, due to the physiological stress from hypoxic waters. Indicator Value (IndVal) analysis of copepods demarcated 8 indicator species (IndVal >40) under different environmental conditions. During the Pre-Southwest Monsoon, the indicator species were *Acartia erythraea*, *A. danae*, *Centropages orsini* and *C. furcatus*, whereas *Oithona similis* was the indicator during the Peak- Southwest Monsoon. *Pseudodiaptomus serricaudatus* and *Centropages tenuiremis* were the indicators during the Late-Southwest Monsoon, whereas *Temora turbinata* was an indicator during both the Early- and Late- Southwest Monsoon periods. The overall pattern in the distribution of copepods evidenced the dominance of calanoids during the Pre-Southwest Monsoon and that of cyclopoids (*O. similis*, *Oithona* sp.) during the Peak-Southwest Monsoon. Multivariate analysis showed that the observed temporal shift in the composition and increase in the number of dead individuals of copepods in the study region were mainly governed by the coastal upwelling-associated hydrographical settings.

Key words: copepods, calanoid, cyclopoid, hypoxia, indicator species, coastal upwelling, Eastern Arabian Sea

1. Introduction

Oxygen-deficient (hypoxic to anoxic) waters exist in the Oxygen Minimum Zones (OMZs) of oceans as a consequence of intense and prolonged organic matter decomposition in poorly-mixed subsurface layers (Ekau et al., 2010; Levin et al., 2009). The major causative factor for these pollution events in the OMZs is believed to be the high organic production in the euphotic layer facilitated by natural or anthropogenic eutrophication events (Naqvi et al., 2000; 2006; Ekau et al., 2010; Levin et al., 2009). Studies in the past have raised an alarm about an imminent increase in the spread of oxygen-deficient zones across the globe (Diaz and Rosenberg, 2008; Stramma et al., 2008; 2010). In the northern Indian Ocean, the Arabian Sea has a well-defined thick perennial OMZ in the mid-depths (~150 - 1200 m), especially in its central and northern part, believed to have resulted from high plankton production in the euphotic layer during most of the year (9 out of 12 months), augmented by poor mixing in the subsurface waters (Naqvi et al., 2000; 2006; Ekau et al., 2010; Levin et al., 2009; Jyothibabu et al., 2010). The perennial mid-depth oxygen-deficient waters get elevated/expanded eastward during the Southwest Monsoon associated with coastal upwelling, causing the formation of seasonal oxygen-deficient zones in the nearshore waters along the west coast of India (Naqvi et al., 2000; Gupta et al., 2016; Jyothibabu et al., 2018). It has been documented that oxygen-deficient zones in the water column can significantly influence the distribution, predation and food web structure of organisms living in such environments (Longhurst, 1967; Pihl et al., 1992). However, the research community is still struggling to comprehend the adverse impacts of oxygen-deficient waters on organisms, mainly due to the inadequate discrete sampling of the OMZ pelagic community, which usually occurs along ocean mid-depths. It is a fact that world over, much more information in this regard is available for benthic organisms as compared to the pelagic ones (Banse, 1968; Ekau et al., 2010; Levin et al., 2009 and references therein).

Copepods are the most abundant crustaceans in the world oceans, usually contributing >60% of the total zooplankton abundance (Padmavati et al., 1998; Queiroga and Blanton, 2004; Jagadeesan et al., 2013). They act as a trophic link between phytoplankton and fishes in the food chain and thus, play a crucial role in ocean biogeochemical cycles (Campos et al., 2017). Usually, changes in the surroundings get reflected in the community composition, diversity, and geographical distribution of copepods (Queiroga and Blanton, 2004; Jagadeesan et al., 2013; Campos et al., 2017). Copepods are sensitive to even subtle changes in the environment and are, therefore, suitable indicator organisms of environmental change and ecosystem functioning (Campos et al., 2017). However, in the present study domain of the eastern Arabian Sea, information on copepods that inhabit the OMZ waters is

rather limited (Padmavati et al., 1998; Smith and Madhupratap, 2005) compared to those from the rest of the world (Smith, 1982; Smith et al., 1998; Ekau et al., 2010 and references therein). Most of the earlier studies on copepods from the eastern Arabian Sea focused mainly on their abundance and compositional aspects and, therefore, there is virtually no conclusive information available on how OMZs influence copepods in the region. One of the major reasons for the scarcity of such information, not only from Indian waters but from other parts of the world as well, seems to be the methodological inadequacy in assessing the physiological status of copepods living in the OMZ waters in the ocean mid-depths. In this context, studies on the physiological status (live and dead status) of plankton are advantageous in shallow OMZs in the near-shore waters as the sample collection from such shallow waters can be done rapidly, minimizing the sampling stress on the experimental organisms.

Studies elsewhere have presented the view that the response of copepods in OMZs could differ between taxa as many of them can avoid oxygen-deficient waters, whereas a few of them can adapt to the low oxygenated conditions (Castro et al., 1993; Auel and Verheye, 2007). Although some copepods (e.g., *Rhincalanus*, *Pleromamma*, *Heterorhabdus*, *Aetideopsis* etc.) can adapt to oxygen-deficient waters (Castro et al., 1993; Auel and Verheye, 2007), most others suffer from varying degrees of adverse impact due to the hypoxic waters (Roman et al., 1993; Invidia et al., 2004; Marcus et al., 2004). On individual level, hypoxia could cause physiological changes in copepods, thereby altering their life cycle performance, reproductive success, disease vulnerability and longevity (Ekau et al., 2010 and references therein). As mentioned before, copepods are susceptible to significant changes in the environment and such changes could even lead to their death (Cervetto et al., 1999; Elliot et al., 2013; Jagadeesan et al., 2013; Martinez et al., 2014). Although routine zooplankton studies assume all individuals in the natural samples to be live, the presence of dead individuals (carcasses) is undeniable (Tang et al., 2009; Elliot and Tang, 2011; Frangoulis et al., 2011; Jyothibabu et al., 2016). Some data are available on the composition and abundance of copepods in the OMZs of the Arabian Sea (Goswami and Padmavati, 1996; Smith and Madhupratap., 2005), but information on the physiological status of copepods in oxygen-deficient subsurface waters remains unknown. Some of the biological characteristics of the present study area investigated under the AMPS program have been published recently (Karnan et al., 2017; Arunpandi et al., 2017; Jagadeesan et al., 2017a; Jyothibabu et al., 2018); in this paper, emphasis has been given to the ecological response of copepods to the hypoxic subsurface waters during the Southwest Monsoon (June - September). Considering the above aspects, focused attempts have been made here to track the ecological response of copepods to the seasonal oxygen-deficient conditions in the

nearshore waters along the southwest coast of India during the Southwest Monsoon. The major objectives of the study are (a) to quantify the live and dead percentage of copepods (both adult and larvae) as an ecological response to the changing hydrographical setting and (b) to analyze the compositional changes of copepods, especially in the subsurface, so as to delineate the indicator species during different hydrographical settings.

2. Materials and Methods

2.1. Study area

The study area is located off Alappuzha in the south-central coast of Kerala, along the southwest coast of India between 9.25 to 9.43°N and 76.3 to 76.4°E. It is typical of the near-shore waters along the west coast of India, which is influenced by coastal upwelling during the Southwest Monsoon. Coastal upwelling causes high nutrient availability in the surface water column, promoting luxuriant growth of phytoplankton, especially during the Peak and Late Southwest Monsoon (Ramasastry and Myrland, 1959; Silas, 1984; Jagadeesan et al. 2017a; Karnan et al., 2017; Jyothibabu et al., 2018). This study forms a part of the investigation ‘Alappuzha Mud Bank Process Studies (AMPS)’, a multidisciplinary oceanography program of CSIR-National Institute of Oceanography, India, carried out in 2014.

In addition to coastal upwelling, another littoral oceanographic feature that exists along the Southwest (Kerala) coast of India, albeit in fragmented stretches, is that of the ‘Mud Bank.’ Mud Banks may be defined as patches of semicircular calm littoral waters close to the coast formed due to the presence of a bottom fluid muddy layer in the region (Gopinathan and Qasim, 1974; Silas, 1984; Mallik et al., 1988; Jyothibabu et al., 2018). This fluid muddy layer significantly attenuates wave energy, causing wave-less, smooth sea surface conditions (Mud Bank) conducive for fishing operations when the rest of the region is exposed to heavy monsoonal waves (Mallik et al., 1988). Field sampling exercises were carried out in three locations (M1, M2 and M3) in the study area (Figure 1); location M1 and M2 were in the onshore region (7m depth), but separated from each other by a distance of 8km. Location M3 was located relatively in the offshore (12 m depth) perpendicular to M2. 18 field sampling sessions in these three locations were carried out from April (Pre-Monsoon) to September 2014 (Late Southwest Monsoon), consisting of 15 weekly samplings (April 22nd to 2nd August) and 3 biweekly samplings (16th August to 20th September).

2.2. Sampling methods

Vertical profiles of temperature and salinity were obtained using a conductivity, temperature and depth (CTD) profiler to understand the temporal hydrographical transformations in the study domain.

Water samples collected from the surface (0.5m) and subsurface (6m in M1 and M2 and 10m in M3) waters using the Niskin samplers were used for measuring various chemical and biological parameters. Dissolved oxygen, nitrate and phosphate were measured based on standard procedures (Grasshoff, 1983). Chlorophyll *a* was measured using a Turner fluorometer following JGOFS protocol (UNESCO, 1994). Zooplankton samples were collected from two discrete layers, from the surface (0.5m) and the subsurface (6m in M1 and M2 and 10m in M3), adopting two different sampling methods. The surface sampling was done using horizontal tows of a standard meso-zooplankton net (200 μ m mesh size); on the other hand, the surface sampling consisted of two net tows: the first short duration tow (2 minutes) was for quantifying live and dead copepods while the second tow was for normal duration (10 minutes) for the quantitative estimations of copepods. As per the staining methods adopted (Elliot and Tang, 2009), only short duration tow has the desired efficiency to quantify the live and dead copepods, as the long duration net tows can cause further mortality of copepods. The samples obtained through short duration net tows were immediately processed with the neutral red staining procedure (Elliot and Tang, 2009) and then stored at -20°C until further microscopic analysis in the laboratory.

Mesozooplankton collected using long duration net tows were preserved in 4% formalin and processed further for biomass, composition and abundance estimations (Postel et al., 2000). Copepods were further analyzed and identified down to the species level using standard literature (Kasturirangan, 1963; Sewell, 1999). As the present study area was the nearshore waters along the Southwest coast of India, discrete zooplankton sampling from the subsurface waters using traditional plankton nets was impractical. For this reason, from each location, 100 liters of water samples were collected from the subsurface layers (6m in M1 and M2 and 10m in M3) using Niskin samplers, which were then screened through a 64 μ m bolting silk net. The zooplankton concentrated on the bolting silk net was directly stained with live stain (neutral red) as per standard procedure (Elliot and Tang, 2009; 2011). As the copepod sampling strategies were different in the surface and subsurface waters, a direct comparison of copepod quantitative data from the surface and subsurface was omitted in this study to avoid misinterpretations due to methodological differences. Alternatively, copepod data collected from the surface and the subsurface waters were treated separately to track the temporal variations in composition and ecological indications of copepods in the study domain.

2.3. Data analysis

2.3.1. Temporal variation in copepod composition and abundance

Cluster and NMDS analyses were performed on separate observations based on the similarity of copepods species in surface layers. For cluster and NMDS analyses, copepod species abundance datasets were initially $\log(X+1)$ transformed to decrease their differences (Clarke and Warwick, 2001). The Bray - Curtis similarity matrix based on the group average method was used for the spatial grouping of observations. In addition to the cluster analysis, similarity profile (SIMPROF) permutation test was also performed to identify significant species assemblages in observations ($p < 0.01$) (Clarke and Gorley, 2006). Species of copepods that contributed more than 2% of the total community abundance were considered as the dominant ones.

2.3.2 Indicator species of copepods

Indicator (characteristic/representative) species of copepods in each group of observations were analyzed through Indicator value (IndVal) index (Dufrene and Legendre, 1997). IndVal essentially reflects whether the species assemblages are symmetric or asymmetric between different groups of observations. IndVal index reaches the maximum (100%) when all the individuals of a species occur in a single group of observations (center of distribution), which essentially represents the asymmetric distribution of that species between the groups. On the other hand, IndVal index reaches the lowest when the species are symmetrically distributed between the groups (Hunt and Hosie, 2006). According to Dufrene and Legendre, (1997), a minimum of 25% IndVal can be considered as the threshold level to determine IndVal species in a group of observations. In the present study, $\geq 40\%$ IndVal value was used as the threshold to demarcate the IndVal species.

2.3.4. Redundancy Analysis (RDA)

Inter-relationships between copepod abundance and physiological status with the environmental variables were analyzed using linear multivariate RDA based on the results of detrended correspondence analysis (< 2 axis gradient length) using CANOCO 4.5. The biological variables were log transformed and centered prior to the analysis. The ordination significance was tested with Monte Carlo permutation tests (499 unrestricted permutations) ($p < 0.05$). The results are presented as a Triplot attributed with overlay of dissolved oxygen (line contours). In RDA Triplot, samples are displayed by points, and species and quantitative environmental variables by arrows. The detailed Triplot interpretations were made following the RDA ordination explanation of Leps and Smilauer (2003).

3. Results

3.1. Hydrography induced by coastal upwelling

The hydrographical changes in the study area on a temporal scale is presented in Figure 2, wherein the entire sampling session has been separated into Pre-SWM (April-May), Early-SWM (June), Peak-SWM (July) and Late-SWM (August-September). During the Pre-SWM, water column was warmer ($>29.5\text{ }^{\circ}\text{C}$) compared to the rest of the period (Figure 2). The surface waters at all the three locations (M1, M2 and M3) showed a significant decline in its heat content by Early-SWM, which indicates that influence of coastal upwelling had commenced in the region. This significantly cool upwelled water mass persisted in the entire region till mid-August, with the surface waters showing increase in temperature ($>27^{\circ}\text{C}$) post that. In the subsurface layers (6m depth in M1 and M2 and 10m depth in M3), the temporal transformation in temperature associated with coastal upwelling was much more pronounced than that in the surface waters. The subsurface mean temperature in the study area was $\sim 29\text{ }^{\circ}\text{C}$ during the Pre-SWM, became $\sim 26^{\circ}\text{C}$ during the Early-SWM, and was $\sim 24^{\circ}\text{C}$ during the Peak-SWM and $\sim 25^{\circ}\text{C}$ during the Late-SWM (Table 1). Due to intense coastal upwelling, a significantly large drop in temperature ($\sim 6^{\circ}\text{C}$) was observed at all the three locations in a few weekly observations during the Peak-SWM. The salinity in the study area was always high (>32 psu), both in the surface and subsurface waters, and their distribution did not show any clear temporal trend except a marked decrease in the surface salinity level during the Late-SWM (Table 1).

Temporal variations in the vertical distribution of dissolved oxygen at all three locations (M1, M2 and M3) clearly indicated the manifestation of the coastal upwelling in the water column, especially in the subsurface waters (Figure 2). The surface waters in all the three locations were aerated throughout the sampling period with a dissolved oxygen concentration $> 140\text{ }\mu\text{M}$ ($> 4.40\text{ mg L}^{-1}$) due to effective air-sea exchange. The mean dissolved oxygen concentrations in the surface layers was the lowest during the Early-SWM compared to all other sampling periods. Dissolved oxygen in subsurface layers was $> 125\text{ }\mu\text{M}$ ($> 4.0\text{ mg L}^{-1}$) during the Pre-SWM, $< 70\text{ }\mu\text{M}$ ($< 2.24\text{ mg L}^{-1}$) during the Early-SWM, $< 35\text{ }\mu\text{M}$ ($< 1.12\text{ mg L}^{-1}$) during the Peak Southwest Monsoon and $< 120\text{ }\mu\text{M}$ ($< 3.84\text{ mg L}^{-1}$) during the Late - SWM. In a few weekly observations during the Peak-SWM period, the dissolved oxygen was found to be as low as $20\text{ }\mu\text{M}$ (0.64 mg L^{-1}) (Figure 2), an indication of the intense coastal upwelling that prevailed in the region. The temporal variations in the nutrient (nitrate and phosphate) concentration showed clear signatures of nutrient-enrichment, both in the surface and subsurface waters associated with coastal upwelling during the Southwest Monsoon (Table 1). Similar was the trend in the temporal variation of chlorophyll *a* in the surface and the subsurface

waters at all the three locations, with a prominent increase in their concentration during different phases of the Southwest Monsoon as a response to the enriched nutrient levels associated with the coastal upwelling (Table 2).

3.2. Biophysical response of copepods

This study observed that copepod composition in the subsurface waters was very similar to that in the surface samples throughout the study period. Altogether 43 species of copepods were recorded during the study, which consisted of 25 calanoids, 8 poecilostomatoids, 5 cyclopoids and 5 harpacticoids. Based on the composition and abundance of copepods, Bray Curtis similarity index-based cluster/SIMPROF overlaid NMDS analysis could delineate the sampling observations into four clusters at all the three locations (M1, M2 and M3), clearly demarcating different hydrographical phases involved in the sampling period (Figure 3). At all the three locations, Pre-SWM observations were grouped in cluster 1 (C1), Early-SWM observations in cluster 2 (C2), Peak-SWM in cluster 3 (C3) and Late-SWM observations in cluster 4 (C4). Individual contributions of copepods having more than 2% contribution to the total community abundance and their segregation in different clusters are presented in Table 3. *Acrocalanus* sp., *Paracalanus parvus*, and *Corycaeus danae* were found to be common in all the clusters. During the Pre-SWM (C1), *Acartia danae*, *A. erythraea*, *Centropages orsini* and *C. furcatus* were abundant, and they together contributed 55% of the total abundance. During Early - SWM (C2), *Temora turbinata*, *A. erythraea*, *A. danae* and *Oithona similis* were abundant. *O. similis* was the most abundant species during the Peak-SWM (C3) with a contribution varying from 60 to 80% of the total abundance. *Centropages tenuiremis*, *Pseudodiaptomus serricaudatus*, *Temora turbinata*, *Euterpina acutifrons* and *O. similis* were found to be abundant during the Late-SWM. Temporal variation in the abundance of copepods in the surface and subsurface waters at the locations M1, M2 and M3 is presented in Figure 4. The temporal variation in abundance of copepods in the surface waters showed a noticeable increase during the Peak and Late-SWM periods, whereas the trend was opposite in the subsurface waters, which showed a clear drop in copepod abundance during the Peak SWM (Figure 4). Copepod abundance in both surface and subsurface waters showed significant temporal variations at all the three locations, whereas spatial variation between the three locations during the sampling period was insignificant.

During the Pre-SWM, contribution of calanoids to the total abundance of copepods was rather significant (80-94%) as compared to the cyclopoids (<5%). By the onset of the SWM (Early-SWM), contribution of calanoids to the copepod total abundance decreased noticeably (63% - 80%) while the reverse was observed in the case of cyclopoids (13-20%). During the Peak-SWM, cyclopoid

contribution to the total community abundance increased significantly and became significantly high (63.8 - 82.1%) while the calanoid contribution during the period declined drastically (<22%). Interestingly, by the Late-SWM, calanoid contribution to the total community abundance increased tremendously and became the seasonal highest, while cyclopoid contribution decreased significantly and reached their Pre-SWM level (Figure 5). Similar to the surface waters, calanoid contribution to the total community abundance was noticeably high in the subsurface waters during the Pre-SWM and Early-SWM, whereas the cyclopoid contribution was the highest during the Peak-SWM (Figure 5). During the Late-SWM, calanoid contribution in the subsurface waters increased, but was lower than their level during the Pre-SWM. This temporal pattern in the contribution of calanoids and cyclopoids to the total copepod community abundance in the surface and subsurface waters was the same at all the three locations (M1, M2 and M3). *Oithona similis* was the most dominant cyclopoid found in the samples (70-80%) during the Peak-SWM in surface and subsurface layers (Supplementary material 1).

Results of IndVal analysis demarcated altogether 8 species of copepods, *Acartia danae*, *A. erythraea*, *Centropages orsini*, *C. furcatus*, *C. tenuiremis*, *Oithona similis*, *Temora turbinata* and *Pseudodiaptomus serricaudatus* as the major indicator species under different environmental conditions (Table 4). During the Pre-SWM, *A. erythraea*, *A. danae* and *C. orsini* were the indicator (IndVal) species at all the three locations. *Oithona similis* was the indicator (IndVal) species during the Peak-SWM. *P. serricaudatus* and *C. tenuiremis* were the indicator (IndVal) species during the Late-SWM. During both Early and Late-SWM periods, copepod *T. turbinata* was found to be the dominant species, but relatively high occurrences and IndVal values were encountered during the latter period. The seasonal shifts in species composition in the subsurface layers were comparable with the surface layers. At all the three locations during the Peak-SWM (C3), the contribution of cyclopoids was noticeably high as compared to the calanoids, harpacticoids and poecilostomatoids.

3.3. Ecological indications of copepods

Live and dead adults and larval copepods were quantified using the neutral red live stain, which has been presented in **Supplementary material 2 and 3**, respectively. This quantification was carried out for only adult copepods in the surface waters, whereas the analysis was carried out for both the adults and larval forms in the subsurface waters. After the incubation experiments, red-stained specimens were considered live while weakly- /un-stained ones were considered dead. The live and dead percentage of copepod adults in the surface and subsurface waters showed a noticeable increase in the percentage of the dead components during the SWM period, which was more pronounced in the case of the subsurface waters (Figure 6, Table 2). The highest percentage of the

dead copepods at all the three locations was in the subsurface waters during the Peak-SWM (Figure 6). The abundance of copepod larval stages in the subsurface waters was noticeably higher during the Pre-SWM and Peak-SWM periods compared to the Early and Peak-SWM periods (Figure 7). More importantly, it was very clear that the percentage of the dead copepods in M1, M2 and M3 significantly increased in the subsurface waters during the Peak-SWM, when hypoxic water was prevailing in the region (Figures 6 and 7).

3.4. Ecological interrelationships

Inter-relationships between the copepods (dominant and indicator species), their physiological status and the environmental conditions are presented in RDA Triplots (Figure 8), which are dissolved oxygen overlaid ordination plots. The results of the complete RDA have shown that salinity, temperature, dissolved oxygen and the nutrients could together explain 72.9 %, 76.4% and 75.8 % of the variations in copepod species distribution and their physiological status. The ordination significance of all the axes was tested by the Monte Carlo test, which showed that all the ordination axes of RDA in M1, M2 and M3 were significant [1.935 (M1), 2.015 (M2) and 2.064 (M3), respectively $P < 0.05$]. The axes of temperature, salinity and dissolved oxygen were oriented on the left-hand side of the plot with the Pre-SWM (C1). Early-SWM (C2) observations were oriented at the foremost position of the nutrient and turbidity axes and at the initial position along the decreasing gradients of dissolved oxygen and temperature, indicating the hydrographical transition from the Pre-SWM to SWM associated with the onset of the coastal upwelling. Decreasing gradients of temperature and dissolved oxygen and increasing gradients of turbidity and nutrients (nitrate and phosphate) were oriented on the right-hand side of the plot in case of the Early- SWM observations. The observations of the Peak-SWM (C3) period were oriented directly opposite to dissolved oxygen and temperature axes. The Late-SWM (C4) observations were oriented towards the lower right-hand side of the plot along with the nutrients, indicating the moderate level of dissolved oxygen and nutrients during the Late-SWM (C4).

RDA Triplot clearly displayed a large temporal change in the hydrographical setting in the study domain during the Early-SWM, displaying a noticeable change in the copepod community in the surface and subsurface layers. The similar and close orientation of chlorophyll *a* arrow with nutrients towards the decreasing gradients of dissolved oxygen and temperature represented the phytoplankton biomass accumulation during the upwelling period, especially during the Peak-SWM. The orientation of species arrows of the calanoids *Acatia danae*, *A. erythraea*, *Centropages orsini*, *C. furcatus*, and *Labidocera acuta* in the left-hand side of the Triplot with increasing gradients of temperature, dissolved oxygen and decreasing gradients of chlorophyll *a* indicated their dominance

during the Pre-SWM period. The orientation of species arrow of the cyclopoid *Oithona similis* towards the top right-hand side of the Triplot with decreasing gradients of temperature and dissolved oxygen represented the compositional shift of dominant copepods from calanoids to cyclopoids during the Peak-SWM associated with the coastal upwelling. Also, the orientation of the species arrow of *Oithona similis* closely followed the axis of the total copepods abundance, which indicated their significant contribution to the copepod community during the Peak-SWM.

The parameter arrows of *Pseudodiaptomus serricaudatus* and *Centropages tenuremis* were oriented at the right-hand side bottom of the Triplot, characterized by the decreasing gradients of temperature, salinity, and dissolved oxygen, and increasing gradients of nutrients and chlorophyll *a*, indicating that the abundance of these copepods was the highest during the Late-SWM. The upwelling indicator *Temora turbinata* first appeared in the study domain during the Early-SWM, reaching the peak abundance during the Late-SWM and hence, their parameter arrow in the Triplot was oriented towards the right-hand side down. The temporal change in the percentage of dead copepods as a response to the hydrographical transformation was very clear in RDA Triplot. The parameter arrows representing the percentages of dead copepod adults (both in the surface and subsurface) and larvae (subsurface) were oriented towards the decreasing gradients of dissolved oxygen and temperature. The axes of the copepods larval and adult abundance in the subsurface layers were oriented towards the Late-SWM observations, indicating their highest abundance during the period.

4. Discussion

An increase in turbidity all along the southwest coast of India during the SWM period is quite usual due to the inputs of numerous rivers that empty into the region. Even though these rivers are short (<100km length), they are numerous (around 50 numbers) and distributed widely, and therefore, their inputs have an impact on the inshore waters all along the southwest coast of India, especially north of the present study area (Muraleedharan et al., 2017). It is well-reflected in the present data that the entire water column was less turbid during the Pre-SWM and more turbid during the SWM period. Interestingly, in the present study area off Alappuzha (south-central part of Kerala coast), there is no significant river influx within 40km vicinity, and therefore, increased turbidity levels observed herein cannot be fully attributable to river influx. Another important aspect relevant in this context is the fluid muddy layer formation close to the bottom in the study domain during the Southwest Monsoon, which is associated with heavy monsoonal waves and the peculiarly viscous nature of the sediment in the region (Mallik et al., 1988; Shynu et al., 2017). In many fragmented stretches of the Kerala coast, this bottom fluid muddy layer attenuates the incident wave energy,

forming wave-less, calm localized zones very close to the shore line, traditionally known as Mud Banks (Mathew et al., 1995). The nature of the bottom fluid muddy layer leading to the formation of the Mud Bank in the present study area has been presented in detail in a few publications based on the data collected along with the present (AMPS) field sampling (Shynu et al., 2017; Jyothibabu et al., 2018). It is important to note that the fluid muddy layer and Mud Bank formation co-occur in the study domain with intense coastal upwelling processes during the Southwest Monsoon. Recent hydrobiological studies in AMPS have confirmed that most of the chemical and biological characteristics of the present study domain are governed by the intense coastal upwelling phenomenon and not the Mud Bank (Jyothibabu et al., 2018). The Mud Bank merely acts as a physical setting in the region wherein incident waves get attenuated, creating calm sea conditions during the Southwest Monsoon (Karnan et al., 2017; Jyothibabu et al., 2018).

Dissolved oxygen concentration in the surface and subsurface waters in the study domain was normoxic during the Pre-SWM. Subsurface dissolved oxygen concentrations decreased by the Early-SWM at all the three locations, given the cool waters and initiation of upwelling. The upwelling signatures along the southwest coast of India can be noticed beyond 100m depth in waters along the southwest coast of India between January and March, much before the setting of the SWM (Sharma, 1978; Gupta et al., 2016). The general belief to have emerged from OMZ research in the Arabian Sea is that the oxidation of the sinking, unutilized biological particles from the surface layers, availability of high subsurface production unutilized by higher trophic levels and the lack of advection of ocean mid-depths together lead to the formation of oxygen-deficient waters in the mid-ocean depths (Naqvi et al., 2006). However, the above reasoning for the formation of oxygen-deficient waters does not seem applicable here, given the report of depleted subsurface oxygen levels as early as June onwards, much before enhanced phytoplankton biomass even forms in the region. This also implies that the hypoxic waters prevalent in the three sampling locations throughout the SWM were caused by the coastal upwelling phenomenon, which advected the oxygen-deficient ocean mid-depth waters towards the Indian Southwestern Shelf (Gupta et al., 2016; Jagadeesan et al., 2017a). It is interesting to note that several historical studies in the past have clearly mentioned about the coastal upwelling-associated hypoxic waters in the region and their implications on the availability of rich fishery resource in the region during the Southwest Monsoon (Banse, 1959; Reghunathan et al., 1981).

One of the most significant observations to have emerged from the surface zooplankton studies under the AMPS program is the temporal change in the abundance and composition of copepods over the sampling period, which has been presented in detail by Jagadeesan et al (2017a) as a tool to

demarcate the dominant role of coastal upwelling and Mud Bank in the study domain. This surface zooplankton data was considered here to analyze whether there was any major compositional difference in copepods when compared to the subsurface waters, which were hypoxic during most part of the Southwest Monsoon period. Surprisingly, the subsurface zooplankton temporal data presented here showed a similar compositional pattern, but a different abundance pattern as compared to the surface waters. Abundance of copepods in the surface layer showed a noticeable increase during the Peak and late-SWM; however, in the subsurface layers, copepod abundance decreased significantly during the Peak-SWM. The temporal change in the abundance of copepods in the study area was significantly influenced by the coastal upwelling-associated hydrographical changes (Jagadeesan et al., 2017a). During the Pre-SWM, Early and Late-SWM period, calanoid copepods were clearly dominant in both surface and subsurface layers, whereas during the Peak-SWM period, cyclopoid copepods was more dominant in the community, showing a clear temporal shift in their composition. Temperature, salinity, dissolved oxygen and phytoplankton productivity are usually considered to be the most important parameters determining the survival, growth and reproduction of copepods. In the present study area, large temporal changes in the level of temperature, dissolved oxygen and phytoplankton productivity during the SWM were caused by coastal upwelling (Jagadeesan et al., 2017a).

During the Pre-SWM, *Acartia erythaea*, *A. danae*, *C. furcatus*, and *C. orisnii* were the dominant species, as evident from their highest IndVal indices during the period (C1). These copepods are typical inshore forms and hence, were present in the study domain throughout the study period. During the Pre-SWM, these copepods were efficient in utilizing the dominant microbial loop due to their carnivorous/omnivorous food habits (Jagadeesan et al., 2017b). However, by the Early-SWM, the abundance of *Acartia* and *Centropages* decreased in the study domain, when *Temora turbinata* (upwelling indicator) significantly increased in the region. It is interesting to note the appearance of *Pareucalanus attenuatus*, which is considered an offshore copepod, in the present study area during the SWM period. At the moment, it is difficult to attribute this to the upwelling-associated onshore advection of the subsurface waters as viewed by Peterson, (1998), as the available information indicates very weak upwelling intensity in the present study domain (Pillai et al., 1993). Hence, this aspect is quite intriguing and it is open to debate whether such slow onshore advection can possibly shift offshore copepods, which actually possess the ability to control their position in the water column through limited level of locomotion.

During the Early-SWM, the oxygen-deficient waters just appeared in the subsurface layers in the present study region; under such conditions, copepods exhibit two possible responses for their

survival. They may either migrate (escape) up from the subsurface hypoxic layer to normoxic surface layers, or they may attempt to adapt to the low oxygenated condition. Roman et al., (1993) reported only a few or no copepods in bottom layers during hypoxic conditions elsewhere. In the present case, the water column was shallow (8-12m) and, therefore, copepods mostly accumulated in the surface layers (habitat compression) to avoid subsurface oxygen-deficient waters; this was evident in the present data as there was a significant drop in copepod abundance in the subsurface during the SWM period (Figures 4; Supplementary material 4). The high accumulation of copepods in surface layers could possibly increase the predation-induced mortality, which could be the reason for the increased percentage of dead copepods in the present study domain during the Early-SWM. On the other hand, moderate levels of oxygen depletion in the sub-surface waters cause the sub-lethal effects of growth and reproduction, which likely reduces their total abundance. Although adult copepods of calanoids as well as cyclopoids can migrate effectively towards surface layers while oxygen-deficient waters persist in the subsurface waters, the latter have been reported to show higher survival success. Cyclopoids seem to enjoy better reproductive success than calanoids in nearshore hypoxic conditions with more egg hatchings and better nauplius survival (Elliot et al., 2013; Keister and Tuttle, 2013). A logical estimate on the poorer reproductive success of calanoids is presented below as they, unlike cyclopoids, release their eggs into the surroundings for hatching and larval development. Copepod eggs usually sink down at a rate of $\sim 20\text{m day}^{-1}$ (Uye, 1980) and their hatching time is around 0.5-1.0 day under 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 hypoxic layer before they hatch. Besides, it has been noticed earlier that hypoxia can suppress the copepod egg hatching (Uye et al., 1979; Lutz et al., 1992; Marcus and Lutz, 1994; Marcus et al., 1997; Choi et al., 2016).

In the present study, a sharp decline in copepod larvae was observed in the subsurface layers during the Early and Peak-SWM associated with low oxygenated waters, which corroborates the view that hypoxic conditions could retard the hatching of subitaneous/diapause eggs (Elliot et al., 2013; Choi et al., 2016; Roman et al., 1993). Although adult calanoids could have escaped from adverse subsurface hypoxic waters by avoidances mechanism such as upward movements, the reduced egg hatching and high mortality rate of larvae in the subsurface waters might have led to their overall decrease in abundance during the Peak-SWM. Cyclopoids also could migrate to surface layers during Early and Peak- Southwest Monsoon to avoid the subsurface hypoxia, but they have an edge over calanoids in such situations. Unlike common calanoids, most of the cyclopoids (e.g. *Oithona similis*) carry eggs in egg sacs until the nauplius gets hatched out. Therefore, cyclopoid

could move to the surface waters along with their progeny and had the opportunity to release their larvae into normoxic waters; therefore, they escaped the adverse effect of oxygen deficiency (Eiane and Ohman, 2004). This reproductive strategy of cyclopoid copepod *Oithona similis* was the main reason for their significantly high abundance in the present study domain during the Peak-SWM (Keister and Tuttle, 2013). It was observed in the present study that the abundance of larval and adult copepods in the subsurface layers increased by the Late-SWM period, which could be linked to the successful hatching of settled eggs when dissolved oxygen concentration improved. The experimental and field studies elsewhere have showed that successful hatching of the resting/settled eggs (>50 %) occur when oxygen conditions in the near-bottom waters increases after the hypoxia event (Choi et al., 2016). During the present study, the abundance of *Acartia* and other smaller calanoids have increased in the surface and subsurface waters during the Late-SWM, which can also be attributed to the resumption of normoxic conditions associated with the withdrawal of the upwelling process.

Significantly high abundance of *Temora turbinata*, which is an indicator of coastal upwelling, was observed in the study domain during the Early- and Peak-SWM; this may be explained by analyzing the baseline reproduction cycle of their congeners. The congener, *Temora longicornis*, produces resting (diapause) eggs that remain viable in sediments over years or seasons (Marcus, 2005). These resting eggs hatch when the cool upwelled waters first appear in the near-bottom layers by Early-SWM, supplemented with high food availability in the water column. It was noted elsewhere that the successful recruitment of a specific copepod in all seasons depends on the hatching success of the resting eggs settled in the bottom during adverse conditions in the previous year (Hansen et al., 2010). Considering the above, it is quite likely that *Temora turbinata* in the present study domain could produce resting eggs during the late-SWM or end of SWM season associated with changes in temperature and food availability. These eggs might hatch during the late Pre-Monsoon/ Early Southwest Monsoon of the next year, depending on the first appearance of the upwelled waters in the near bottom, and dominate in the community during the period. However, we do accept the need for more focused studies in this direction to really comprehend the high abundance of *Temora turbinata* in the study area during the SWM period. It is pertinent to note here that the ecological indications of copepods presented in this paper do not represent a full year period as the study was restricted only to the Pre-SWM - Late-SWM period. It is evident in the present study that oxygen-deficient waters in the nearshore has a significant negative impact on the survival of copepod community as a whole. This observation needs to be comprehended with the imminent threat of the expanding oxygen-deficient zones in the global ocean due to the natural and anthropogenic causes (Diaz and Rosenberg,

2008; Stramma et al., 2008; 2010). Thus, the present observations point out that if the oxygen-deficient zones in the World Ocean increase over time, as highlighted in many studies (Diaz and Rosenberg, 2008; Stramma et al., 2008; 2010), it shall have the potential to disrupt the ocean biogeochemical cycles. It was clear in the present study that the oxygen-deficient waters could alter the composition and increase the mortality of copepods, which can have unforeseen negative implications on the lower level food web and thereby, the fish production, as most of the fishes consume copepods as their major food source (Gismervick, 2006; Campos et al., 2017).

5. Conclusion

Utilizing the advantage of a shallow seasonal hypoxic zone along the Southwest Coast of India and the standard live staining technique, this study investigated the responses of copepods to the oxygen-deficient subsurface waters. The results showed a noticeable decrease in the total abundance of copepods in the hypoxic subsurface waters during the Southwest Monsoon, which was contrary to their temporal abundance pattern in the aerated surface waters. When hypoxic waters existed in the subsurface waters during the SWM associated with coastal upwelling, the percentage of dead copepods (carcasses) increased noticeably, signifying the physiological stress of hypoxia on the organisms. The Indicator species (IndVal) analysis provided 8 species that were indicators of various environmental conditions. During the Pre-SWM, *A. erythraea*, *A. danae* and *C. orsini* were the indicator species at all the three locations. *O. similis* was the indicator species during the Peak-SWM. Copepods *P. serricaudatus* and *C. tenuiremis* were the indicator species during the Late-SWM. The copepod composition shifted from calanoids (*A. danae*, *A. erythraea*, *C. orsini*, *P. parvus*, and *A. gracilis*) during the Pre-SWM to cyclopoids (*O. similis* and *Oithona* sp.) during the Early and Peak-SWM. The overall result showed that hypoxic conditions had significantly impacted the copepod community structure in the study domain during the SWM. During the Late-SWM, calanoids regained their dominance over cyclopoids, which also indicated the withdrawal of coastal upwelling and increase in dissolved oxygen concentration in the subsurface waters. It has been showed here that the egg sac strategy of cyclopoids provides them an edge over calanoids in near-shore waters along the Southwest coast of India during the Early and Peak - SWM when oxygen deficiency prevails in the subsurface waters. This is the first in-depth study from the near-shore waters of the eastern Arabian Sea showing a clear seasonal compositional shift and increased percentage of dead copepods during the Southwest Monsoon, during coastal upwelling leads to low oxygenated waters in the subsurface.

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Data availability statement: *The datasets will be published in the public data repository of CSIR-National Institute of Oceanography (CSIR-NIO). It can be accessed by anybody after submission of individual request to Director CSIR-NIO or Scientist-in-charge of CSIR-NIO Regional Centre, Kochi, India as per the Institutional policy.*

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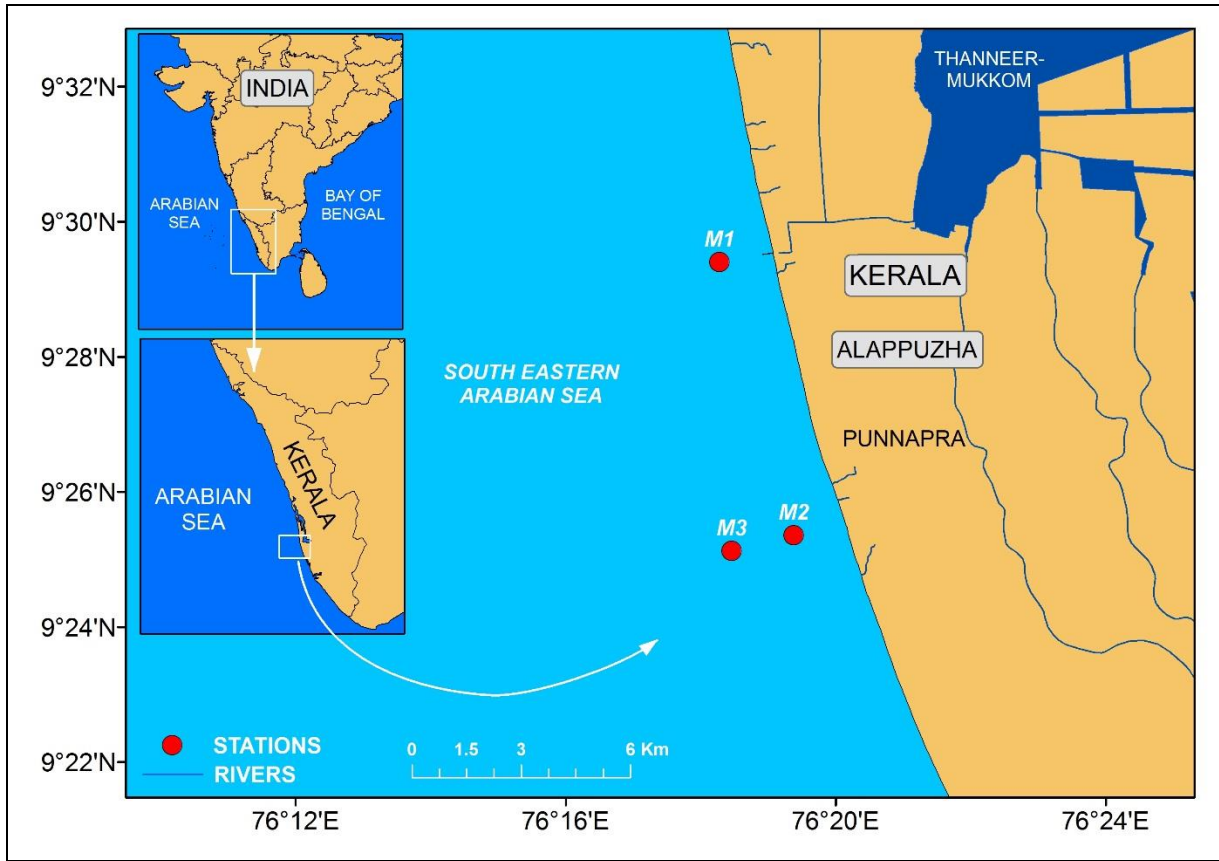


Figure 1 - Field sampling locations M1, M2 and M3 in the study area. Location M1 and M2 were in the onshore (7m depth) but, separated each other with a distance of 8km. Location M3 was situated relatively in the offshore (13 m depth) perpendicular to M2.

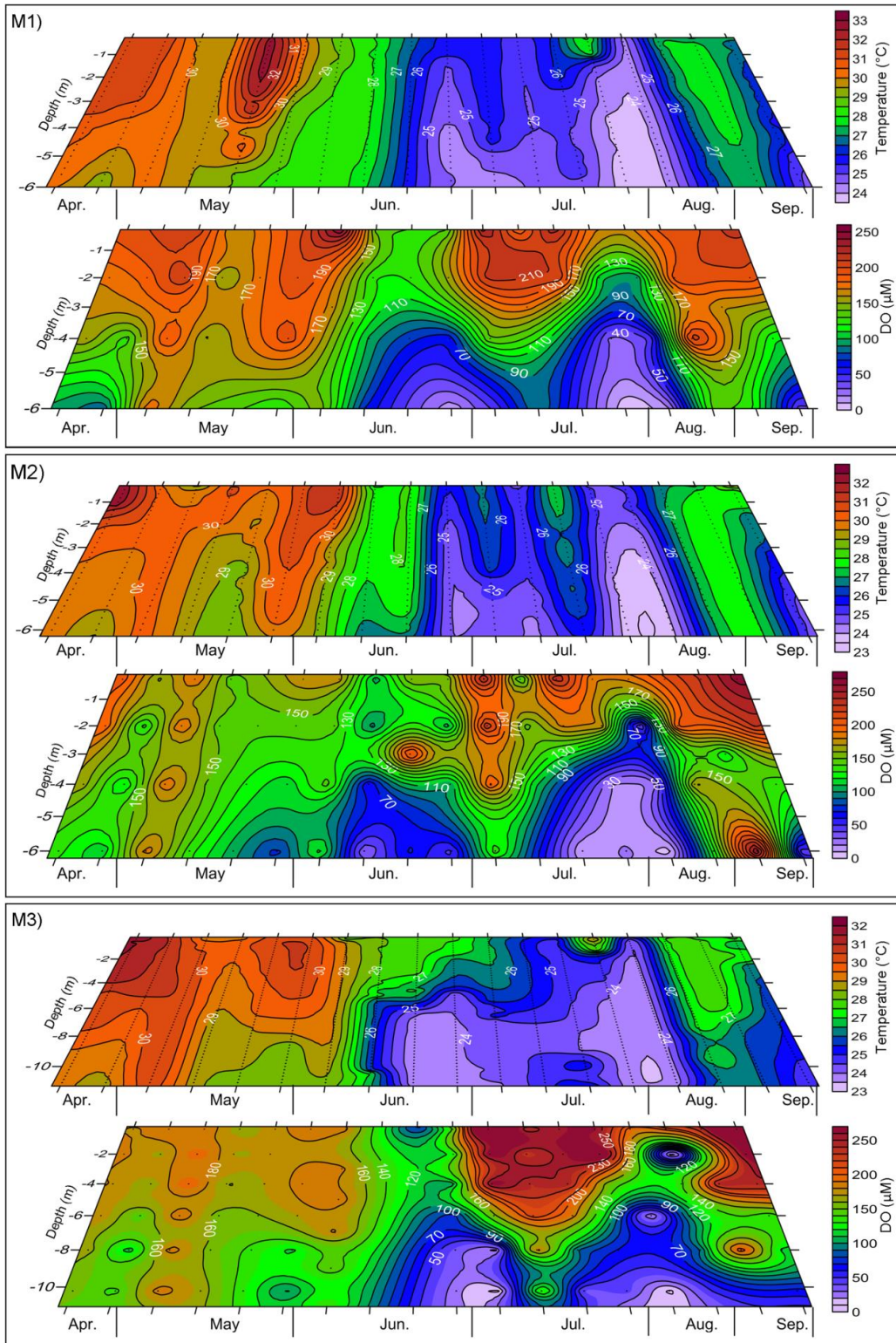


Figure 2 - Vertical distribution of temperature and dissolved oxygen in locations M1, M2 and M3 in the study domain. Temporal transformations in hydrography from a non-upwelling Pre-Monsoon (April - May) season to the upwelling Southwest Monsoon (June- September) season are evident at M1, M2 and M3. The color contours in the above panel representing each locations is the vertical distribution of temperature and the below panel dissolved oxygen.

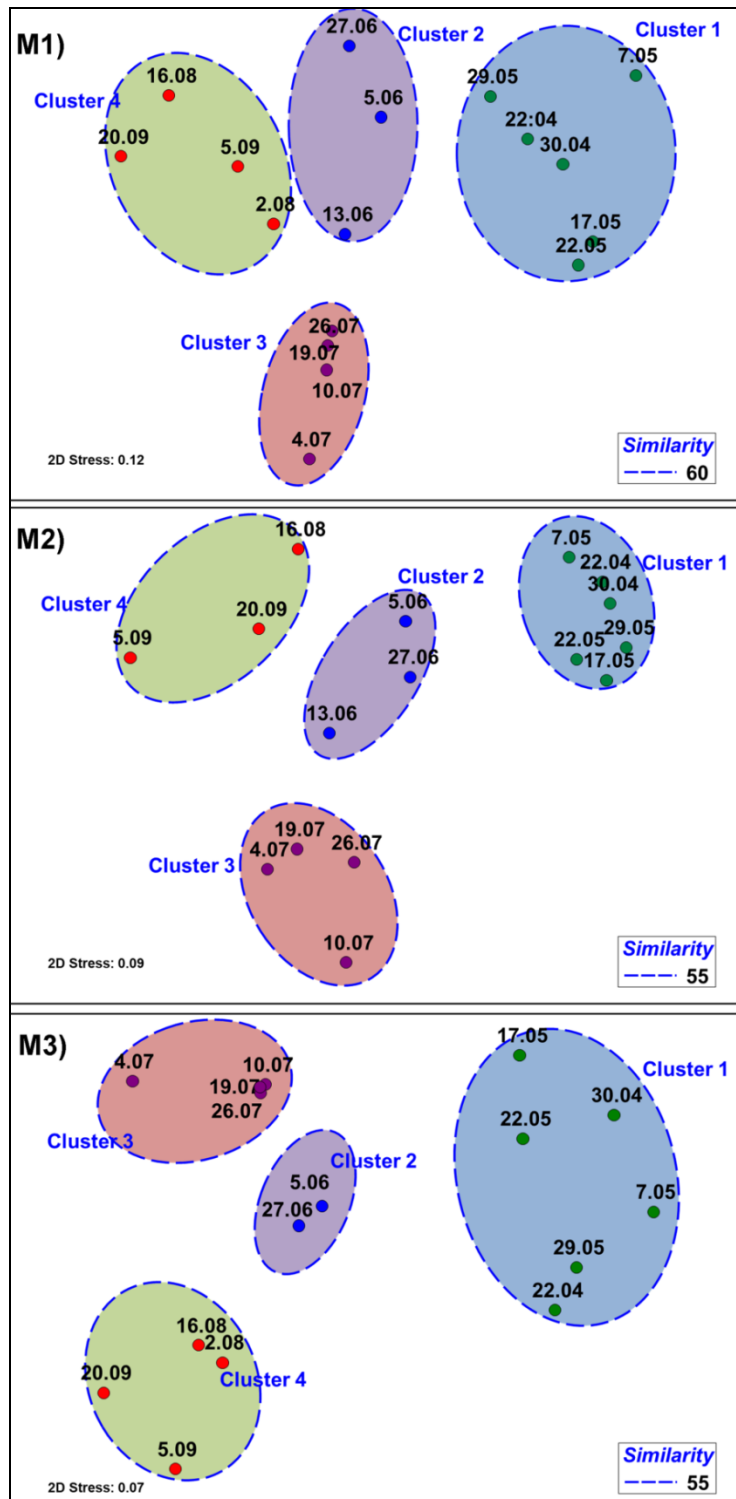


Figure 3 - The grouping of samples/observations based on the composition of copepods in the surface waters in location M1, M2, and M3. Four clusters were evident in all three locations sampled indicating four species assemblages indicating different environmental settings.

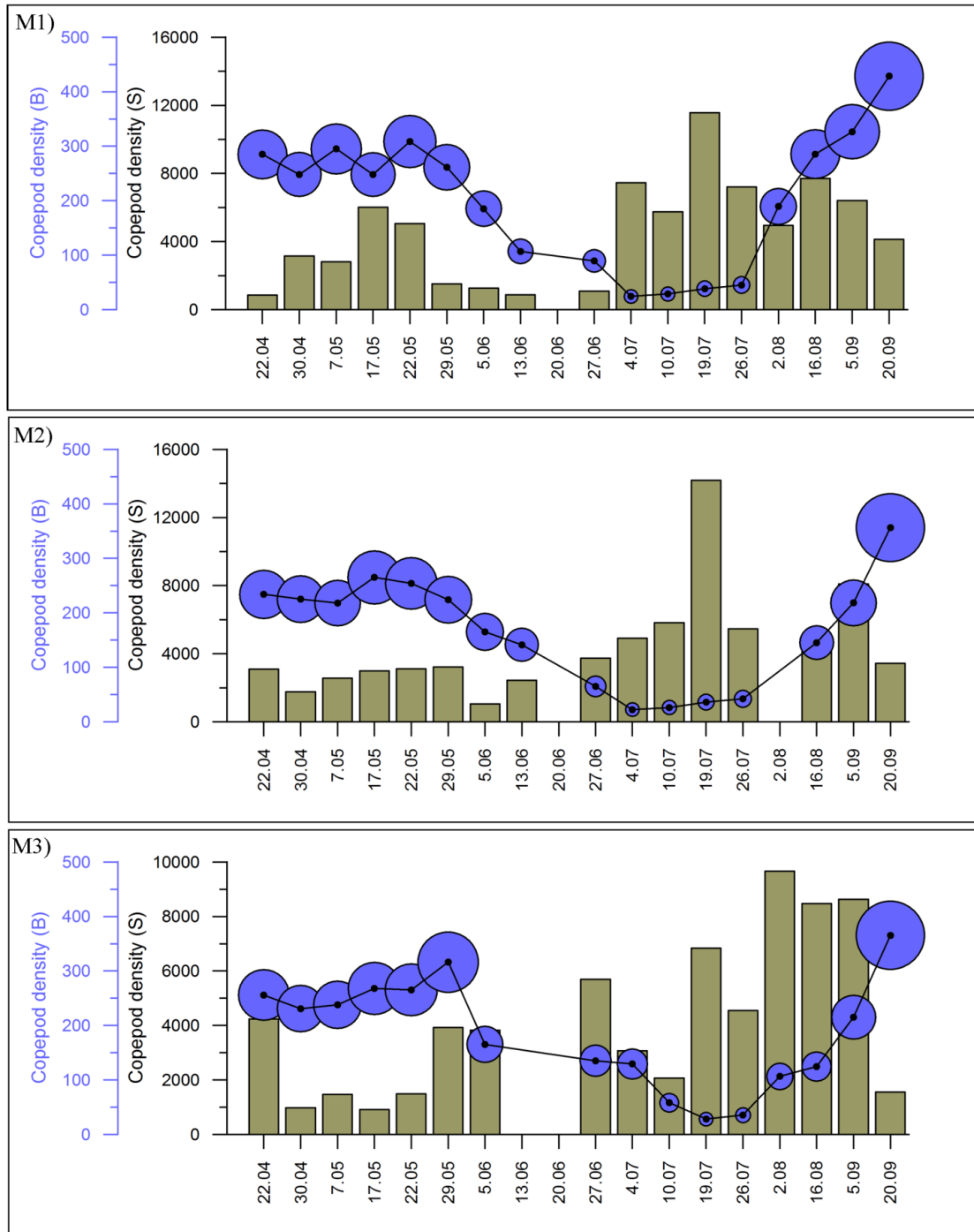


Figure 4 - Temporal variations of copepod density in the surface (No.m^{-3}) and sub-surface (No.100 L^{-1}) waters. Bars indicate the surface abundance values and blue bubbles the subsurface in locations M1, M2 and M3. S - Surface and B - Bottom/Subsurface.

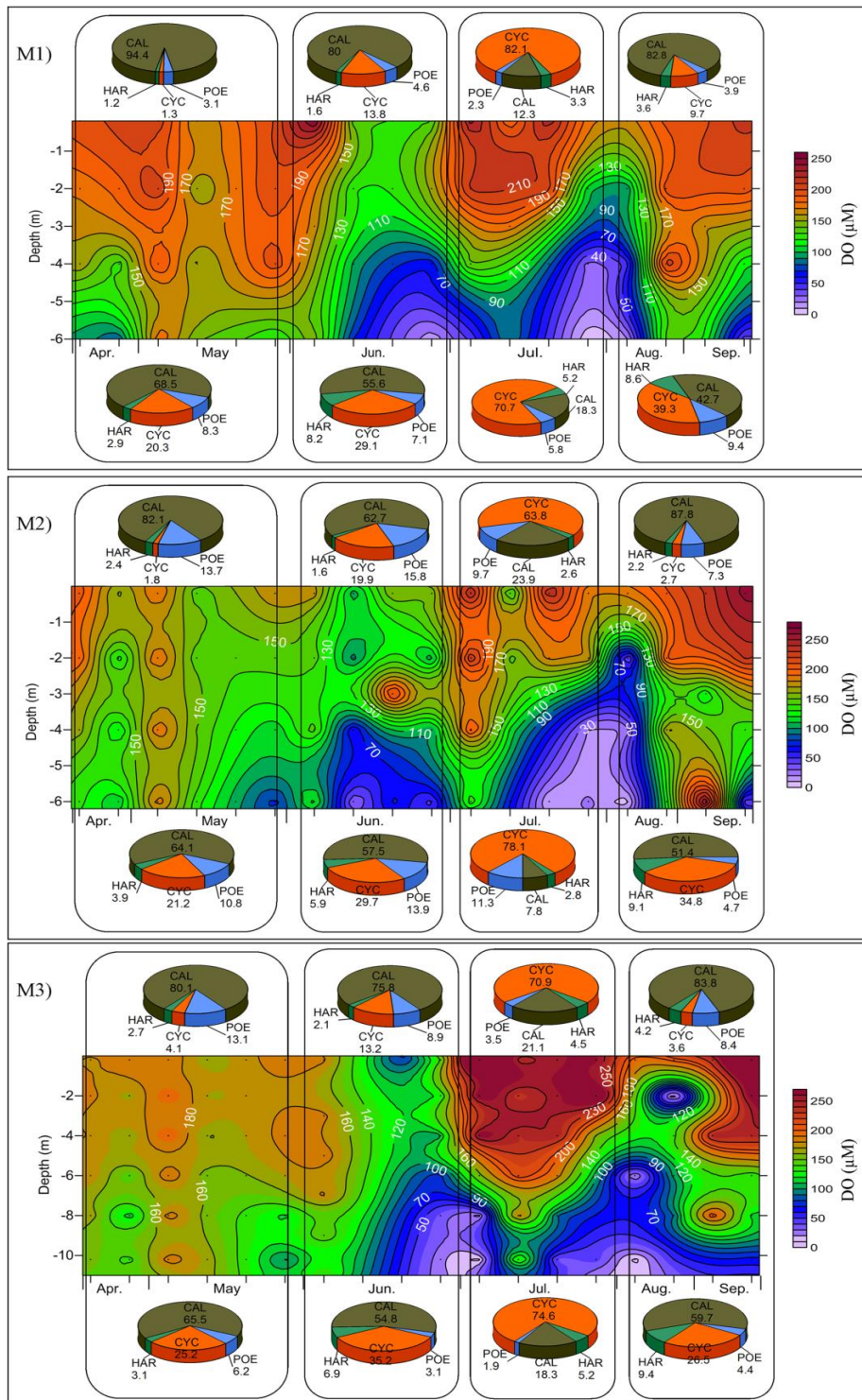


Figure 5 - Temporal variations in the percentage contribution of different copepod orders to the total copepod density in the surface and sub-surface waters. The contour plot at the central panels in all three locations represent the temporal variation in the vertical distribution of dissolved oxygen in the water column. The percentage pie diagrams in the upper and lower panels in each locations detail the percentages of different copepod orders in the surface and subsurface waters respectively. Abbreviations: CAL - Calanoids, POE - Poecilostomatoids, HAR - Harpacticoids, CYC - Cyclopooids.

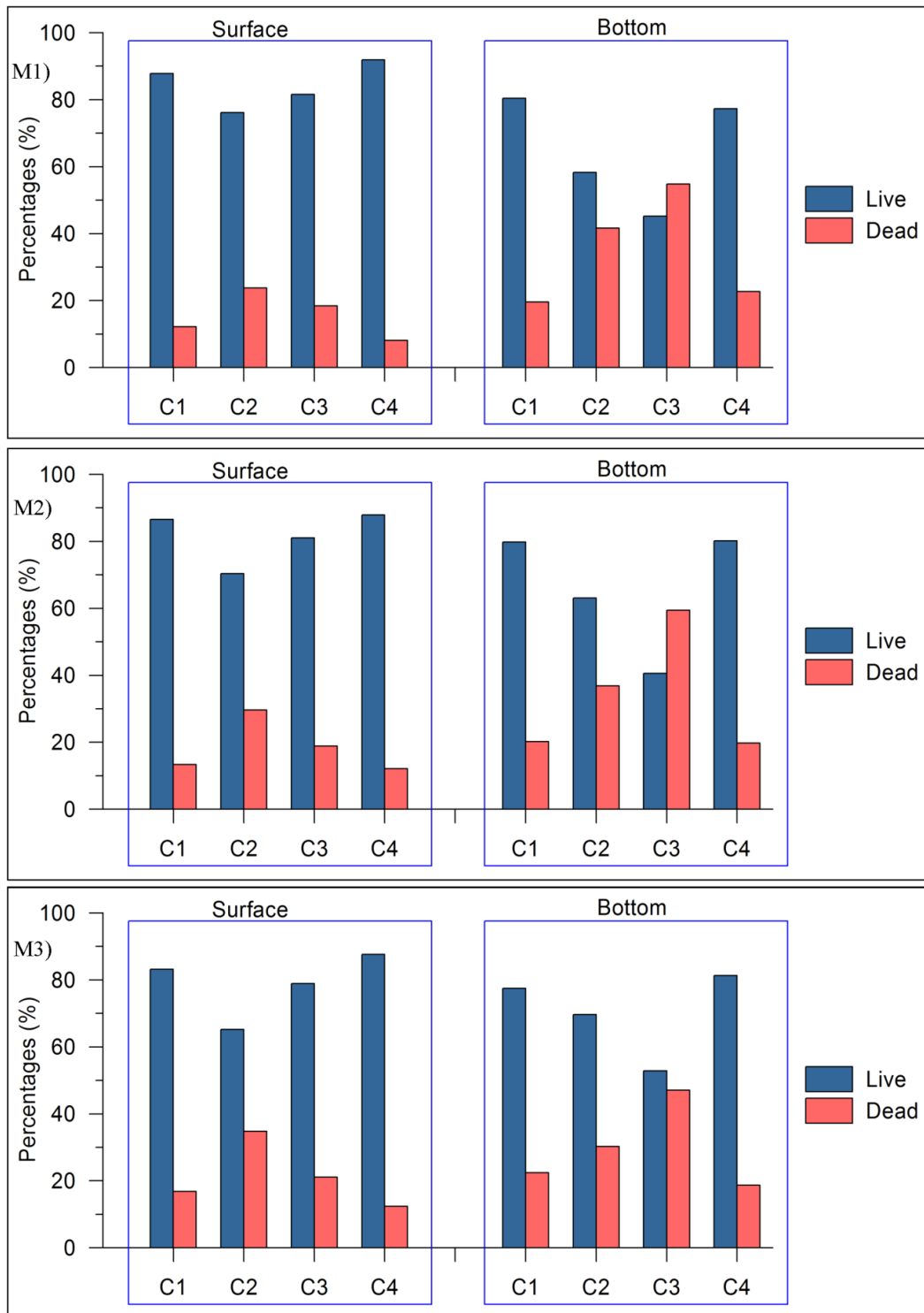


Figure 6 - Temporal variations in the percentage contribution of live and dead copepods in the surface and bottom/sub-surface waters. Environmental clusters from 1 to 4 is abbreviated as C1, C2, C3 and C4. The percentage of dead copepods showed a noticeable increase during C2 and C3 especially in the subsurface / bottom waters.

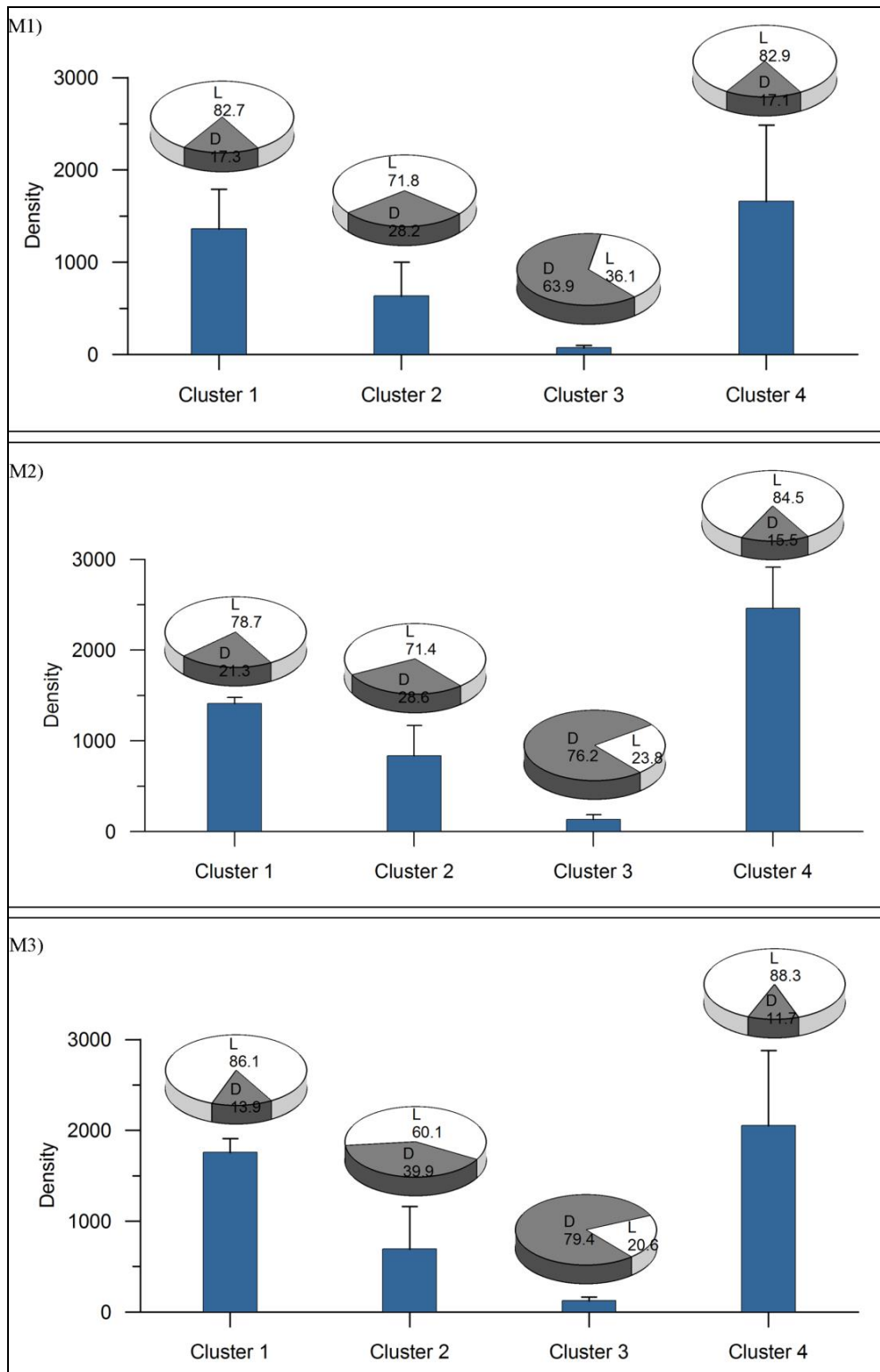


Figure 7 - Temporal variations in the copepod larval abundance (No. 100L⁻¹) and percentage contribution of live and dead copepod larval stages in the sub-surface waters. This analysis was not carried out in the surface waters as the plankton sample collection using 200µm mesh size net made it impossible to quantify the larval stages of copepods that are predominantly less than 200 µm in size.

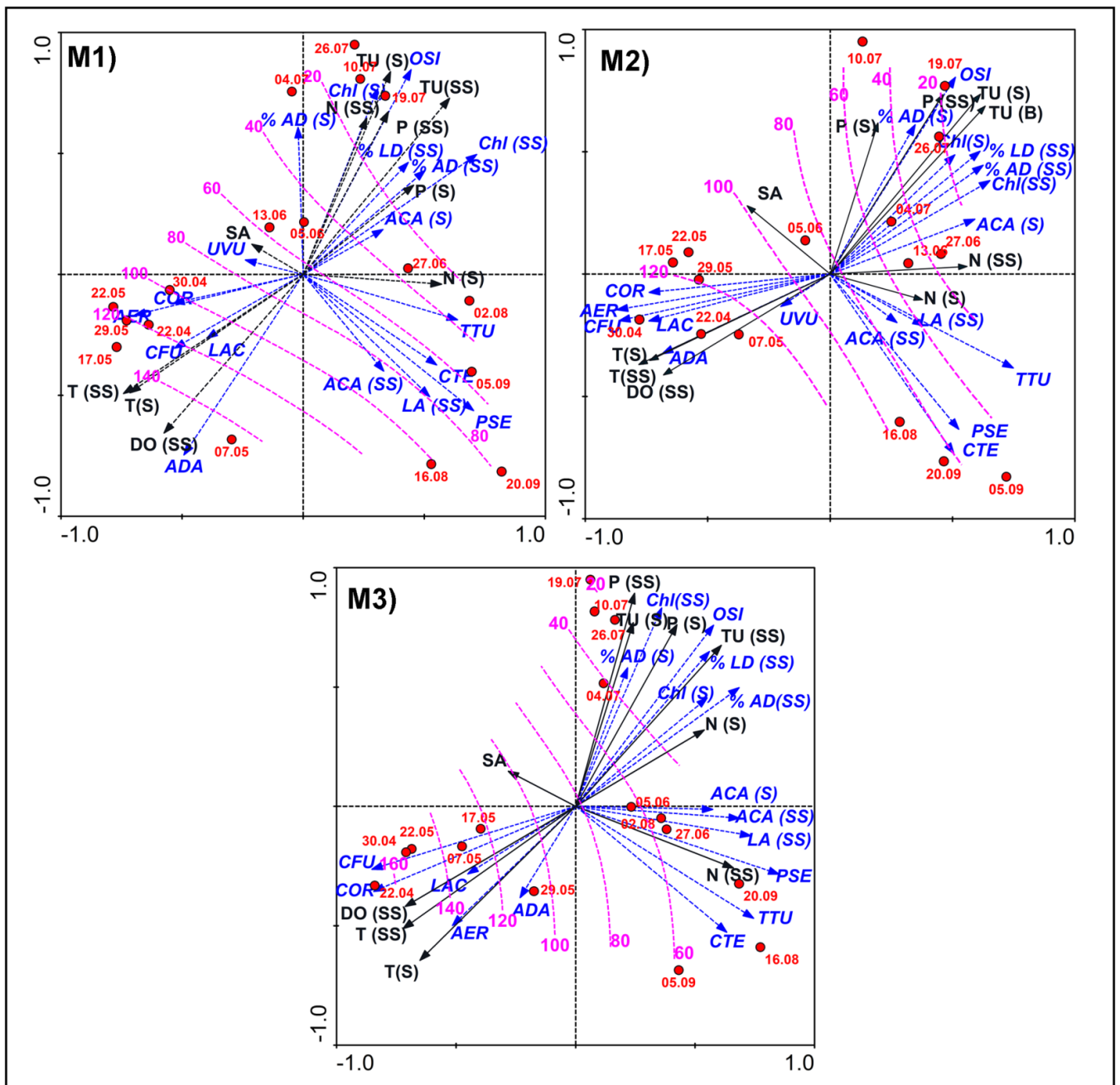


Figure 8 - RDA Triplot explains the interrelationship of environmental parameters (solid black arrows) and biophysical and physiological responses of copepods (dotted blue arrows) in M1, M2 and M3 locations in the study area. Dissolved oxygen (purple dotted lines) overlaid attribution Triplot have been presented. The red dots represent the date of sampling. Abbreviations: (S) - Surface; (SS) - Sub-surface; T - Temperature; SA - Salinity; DO - Dissolved Oxygen; NO₃ - Nitrate; PO₄ - Phosphate; TU- Turbidity; Chl. *a* - Chlorophyll *a*; UVU - *Undinula vulgaris*; COR - *Centropages orsini*; CFU - *C. furcatus*; CTE - *C. tenuiremis*; PSR- *Pseudodiaptomus serricaudatus*; TTU - *Temora turbinata*; LAC - *Labidocera acuta*; AER - *Acartia erythraea*; ADA - *A. danae*; EAU - *Euterpina acutifrons*; OSI - *Oithona similis*; SA - Surface abundance of copepods; LA (SS) - Larval abundances in subsurface; ACA (SS) - Adult copepods abundances in sub surface; % AD - Percentage of the carcasses in Adult; %LD - Percentages of the carcasses in Larval stages.

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

Table 1 - Physico-chemical and biological parameters at the surface and subsurface in M1, M2 and M3. S - Surface, SS - Sub-surface

Parameters	Layer	Pre-Monsoon	Early-SWM	Peak- SWM	Late-SWM	
M1	Chlorophyll a	S	1.77 ± 0.85	5.03 ± 2.62	9.3 ± 2.42	3.19 ± 1.84
		SS	1.76 ± 1.59	2.42 ± 1.04	5.20 ± 1.10	3.3 ± 0.49
	Copepod abundance (A)	S	3229 ± 1994	1065 ± 188	8341 ± 2490	5791 ± 1592
		SS	285 ± 33	127 ± 51	44 ± 28	297 ± 115
	Larval abundances	SS	1361 ± 430	635 ± 365	74 ± 25	1660 ± 826
	Dead % in adult copepods	S	12.2 ± 7.1	25.5 ± 3.0	21.4 ± 6.2	8.2 ± 2.6
SS		17 ± 5.4	38.4 ± 11.9	60 ± 8.3	22.8 ± 4.4	
Dead % in Larval stages	SS	17.0 ± 0.2	28.2 ± 3.6	63.9 ± 7.9	17.1 ± 2.3	
M2	Chlorophyll a	S	2.66 ± 1.82	4.51 ± 2.92	10.72 ± 7.78	4.98 ± 4.51
		SS	2.09 ± 2.19	1.66 ± 0.68	5.70 ± 1.27	3.86 ± 1.83
	Copepod abundance (A)	S	3328 ± 1245	2403 ± 1347	7595 ± 4410	5554 ± 2366
		SS	239 ± 21	124 ± 52	32 ± 9	240 ± 107
	Larval abundances	SS	1411 ± 66	836 ± 331	135 ± 52	2463 ± 452
	Dead % in adult copepods	S	13.4 ± 5.9	29.60 ± 1.8	26.6 ± 5.1	12.00 ± 4.2
SS		19.7 ± 10.2	31.9 ± 13.1	55.4 ± 3.6	19.8 ± 6.1	
Dead % in Larval stages	SS	21.3 ± 9.9	28.6 ± 3.3	76.2 ± 8.1	15.5 ± 0.9	
M3	Chlorophyll a	S	0.66 ± 0.20	7.38 ± 6.42	10.05 ± 7.63	3.97 ± 2.95
		SS	0.63 ± 0.36	2.13 ± 1.49	6.03 ± 3.01	2.82 ± 2.38
	Copepod Abundance (A)	S	1817 ± 1382	4482 ± 1084	4881 ± 1553	7080 ± 3723
		SS	290 ± 36	143 ± 19	41 ± 15	203 ± 118
	Larval abundances	SS	1757 ± 152	696 ± 464	128 ± 36	2050 ± 823
	Adult Dead	S	16.8 ± 4.45	28.8 ± 2.5	31.1 ± 3.7	12.4 ± 4.4
SS		22.5 ± 8.6	25.3 ± 7.3	60.3 ± 3.1	18.7 ± 8.3	
Larval Dead	SS	13.9 ± 1.5	39.9 ± 2.8	79.4 ± 5.2	11.7 ± 4.7	

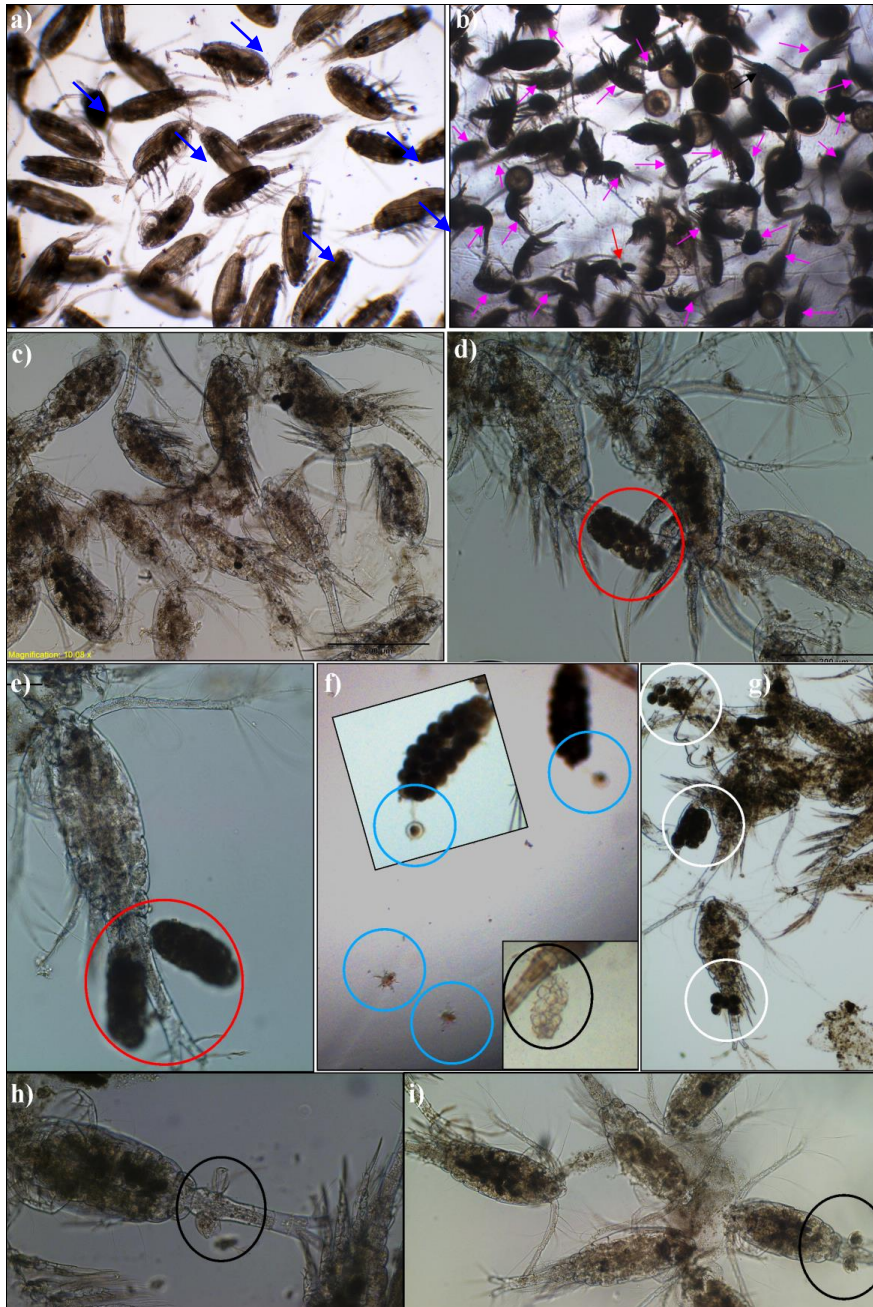
Table 2 - Temporal variations in biological parameters in M1, M2 and M3. S - Surface, SS - Sub-surface.

SI. NO	Species	Location M1 (Clusters)				Location M2 (Clusters)				Location M3 (Clusters)			
		1	2	3	4	1	2	3	4	1	2	3	4
1	<i>Acartia danae</i>	**	+++	+	++	**	+++	+	++	**	+++	++	++
2	<i>A. erythraea</i>	**	++	+	+	*	++	+	+	*	-	+	+
3	<i>Acrocalanus sp.</i>	+++	*	+++	+++	*	++	+++	++	+++	+++	*	++
4	<i>Centropages furcatus</i>	+++	-	-	-	++	+	-	-	++	-	-	-
5	<i>C. orsini</i>	+++	+	-	-	++	+	-	-	++	-	-	-
6	<i>C. tenuiremis</i>	-	-	-	++	-	-	-	*	-	-	-	++
7	<i>Labidocera acuta</i>	++	-	-	-	+	-	-	-	++	+	-	-
8	<i>Paracalanus parvus</i>	*	*	++	*	*	*	*	++	*	*	*	*
9	<i>P. attenuatus</i>	-	+	-	-	+	++	-	-	+	++	-	+
10	<i>Pseudodiaptomus serricaudatus</i>	-	-	-	**	-	-	++	**	-	-	++	*
11	<i>Temora turbinata</i>	-	**	+	*	-	**	+	**	-	+	*	*
12	<i>Undinula vulgaris</i>	+	++	-	-	+	-	-	-	+	++	-	+
13	<i>Euterpina acutifrons</i>	-	+	-	++	+	+	+	++	+	+	+	++
14	<i>Oithona similis</i>	+	++	***	++	+	+++	***	++	-	+	**	*
15	<i>Corycaeus danae</i>	++	++	+	++	++	+++	+	+	++	+++	++	+++

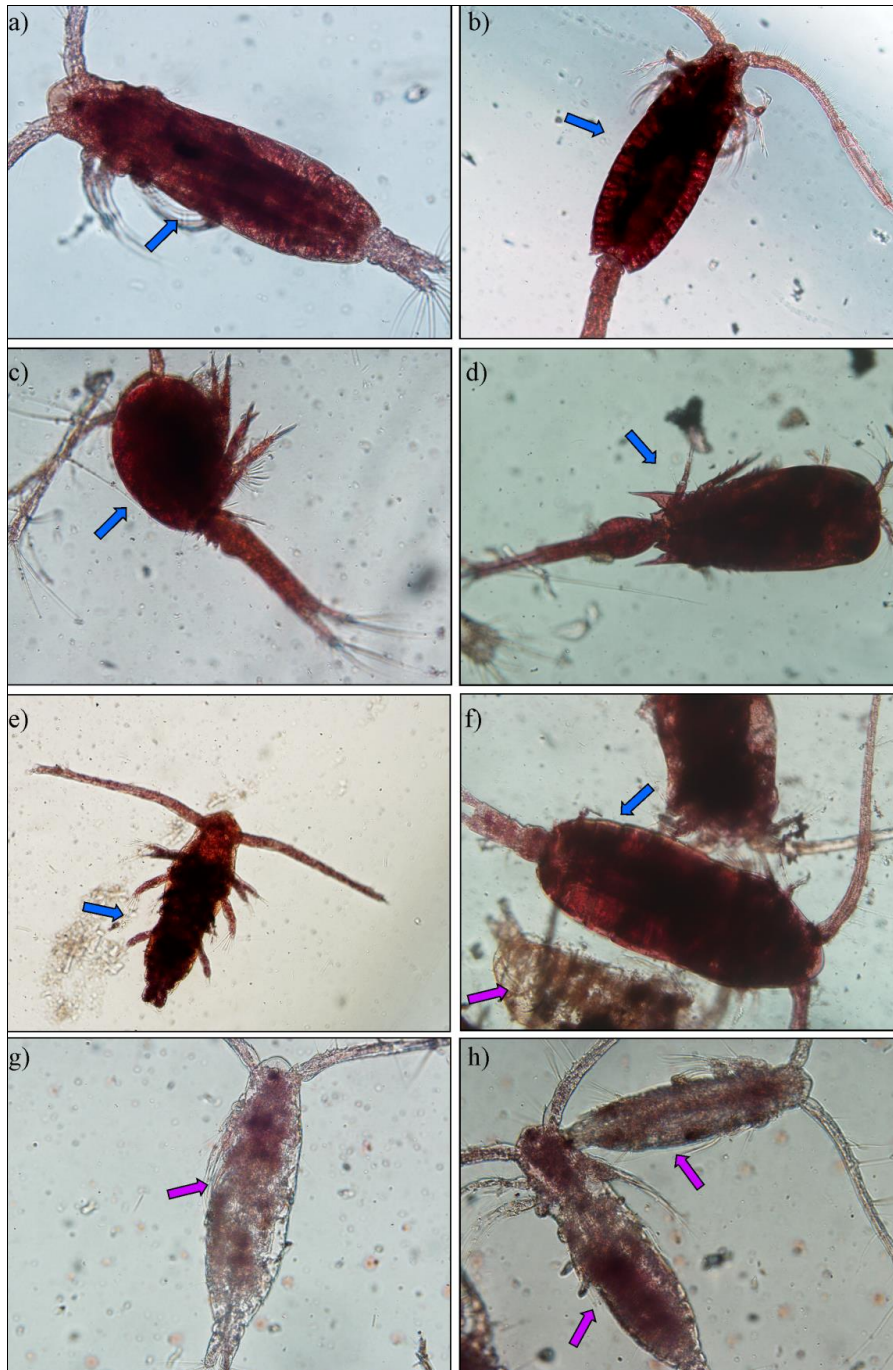
Table 3 - Dominant copepods (contributes >2% in the total community abundance in any one of the cluster) and their percentages of contribution to the total abundances in M1, M2 and M3. Symbols: + contribution ≤1%; ++ denotes 1.1 to ≤ 5% ; +++ denotes 5.1 to ≤ 10%; Cluster 1 - Pre-SWM; Cluster 2 - Early-SWM; Cluster 3 - Peak-SWM; Cluster 4 - Late-SWM.

Location	Pre-SWM	Early-SWM	Peak-SWM	Late-SWM
M1	<i>Acartia danae</i> (78.9) <i>A. erythraea</i> (70.5) <i>Centropages furcatus</i> (56.5) <i>C. orsini</i> (51.4)	<i>Temora turbinata</i> (48.4)	<i>Oithona similis</i> (84.1)	<i>C. tenuiremis</i> (76.4) <i>P. serricaudatus</i> (96.5) <i>T. turbinata</i> (51.4)
M2	<i>A. danae</i> (83.4) <i>A. erythraea</i> (79.9) <i>C. furcatus</i> (87.4) <i>C. orsini</i> (91.3)	<i>T. turbinata</i> (44.1)	<i>O. similis</i> (85.9)	<i>C. tenuiremis</i> (74.1) <i>P. serricaudatus</i> (96.4) <i>T. turbinata</i> (55.1)
M3	<i>A. danae</i> (78.8) <i>A. erythraea</i> (59.8) <i>C. furcatus</i> (73.3) <i>C. orsini</i> (86.5)	<i>T. turbinata</i> (46.5)	<i>O. similis</i> (79.5)	<i>C. tenuiremis</i> (81.1) <i>P. serricaudatus</i> (98.5) <i>T. turbinata</i> (53.2)

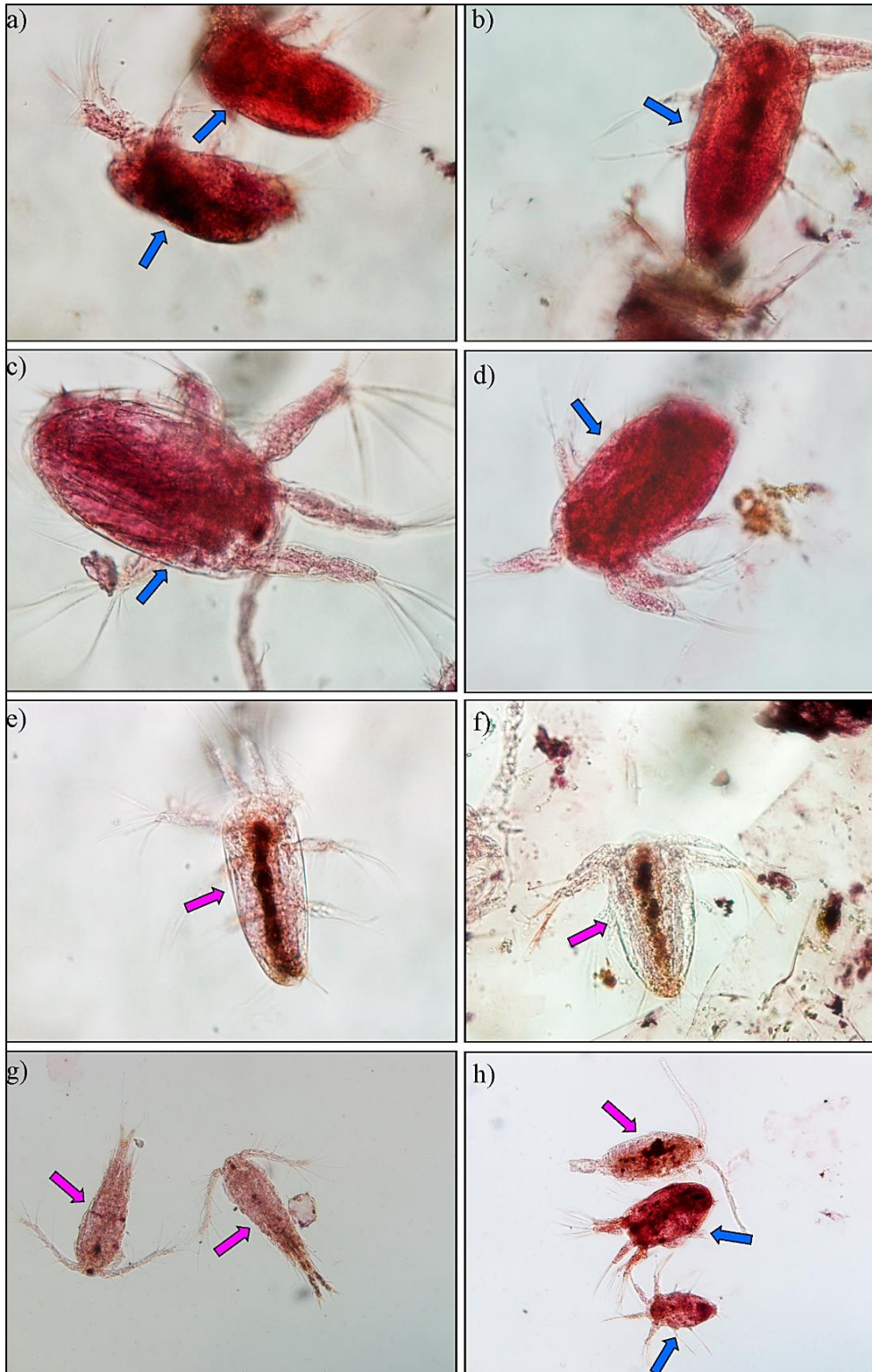
Table 4 - Indicator species of copepods (IndVal >40) and their IndVal indices (in parenthesis) in various cluster assemblages. Abbreviations: *P. attenuatus* - *Pareucalanus attenuatus*, *C. tenuiremis* - *Centropages tenuiremis*, *P. serricaudatus* - *Pseudodiaptomus serricaudatus*.



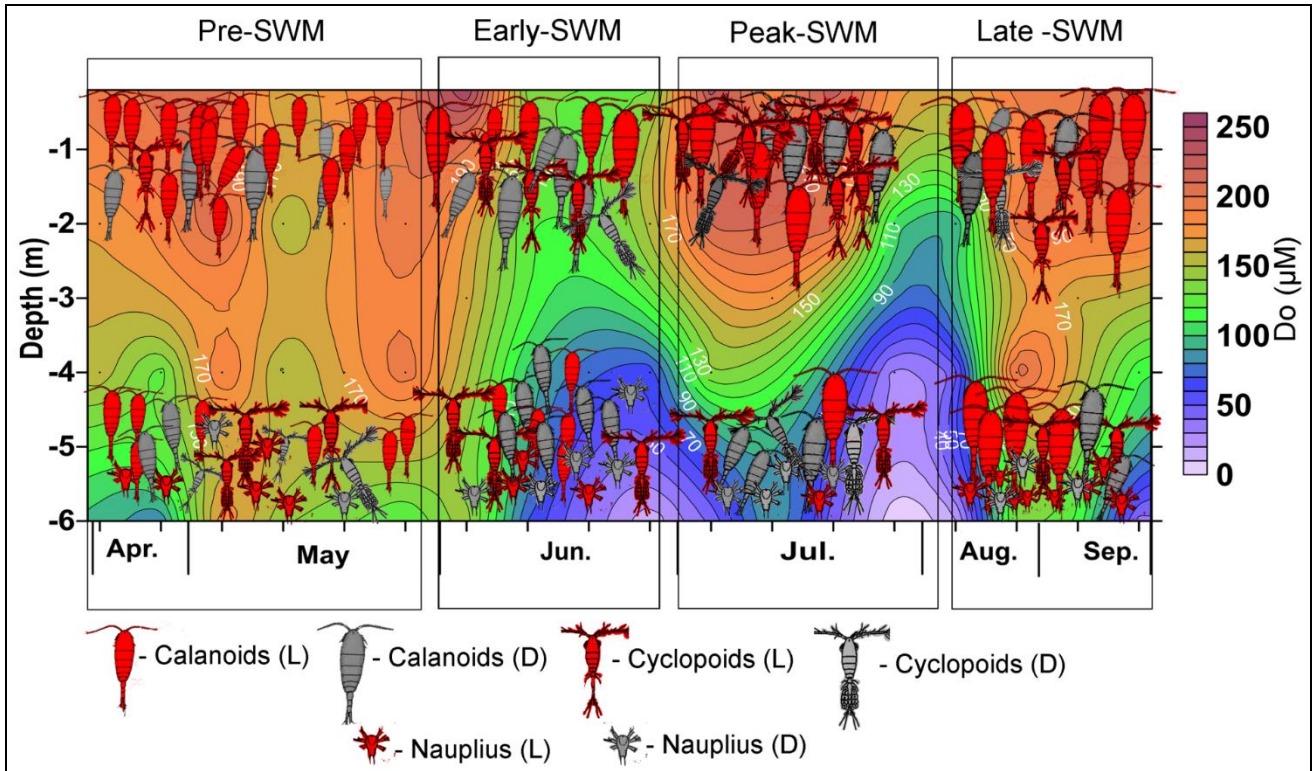
Supplementary Material 1 – Microscopic view of sorted zooplankton. Panel (a) and (b) show major compositional shift of copepods during different phases of the sampling. Calanoids (blue arrows) dominated the community except during the peak and Late Southwest Monsoon when cyclopoids (pink arrows in panel b) dominated the community. Panel (c) high magnification natural samples representing the Peak-SWM period. Panels (d-I) details the reproductive adaptation of Cyclopoid copepods over Calanoids copepods. In cyclopoids, eggs are matured inside of the egg sacs. Generally cyclopoids have two egg sacs and they are attached in the first urosomal segment (red circles). Panel (f) shows the laboratory incubated cyclopoid copepods releasing their nauplius from the matured eggs (blue circles). Panel (h and i) show empty egg sac (black circles) after the successful hatching of nauplii. This clearly shows that the shows that better reproductive adaptation favouring the cyclopoids in surviving hypoxic waters are depicted in subsequent figures.



Supplementary Material 2 - Differential staining of live and dead of copepods using the live stain neutral red. Stained individuals represent the live fraction (blue arrows) and unstained/weakly stained individuals (pink arrows) represent the dead fraction of the copepod community in the study domain.



Supplementary Material 3 - Differential staining of live and dead naupli and copepodite stages of copepods using the live stain neutral red. Stained individuals represent the live fraction (blue arrows) and unstained/weakly stained individuals (pink arrows) represent the dead fraction of the larval copepods in the study domain.



Supplementary Material 4 - Major compositional shift of copepods during the sampling period. Cyclopoid dominated during the Southwest Monsoon and calanoids during the peak and Late Southwest Monsoon. The better reproductive adaptation favouring the cyclopoids in surviving hypoxic waters are depicted in subsequent figures.