



## Seasonal oceanographic phenomenon promotes hitchhiking among the plankton in a coastal marine ecosystem: A tropical perspective

Alfisa Siddique<sup>a</sup>, Aishee Bhowal<sup>a</sup>, Jasmine Purushothaman<sup>a,\*</sup>, Rakesh Madhusoodhanan<sup>b</sup>, Chelladurai Raghunathan<sup>a</sup>, Kailash Chandra<sup>a</sup>

<sup>a</sup> Protozoology Section, Zoological Survey of India, Kolkata 700053, India

<sup>b</sup> Ecosystem Based Management of Marine Resources, Environment & Life Sciences Research Centre, Kuwait Institute for Scientific Research, Salmiya 22017, Kuwait

### ARTICLE INFO

#### Keywords:

Epibiont  
Thermal inversion  
Winter monsoon  
Ocean stratification  
Bay of Bengal  
Tropical waters

### ABSTRACT

Epibiosis among plankton communities and the role of environmental forcing therein are discussed in this study. We hypothesized that a sub-surface thermal inversion phenomenon and associated hydrographical changes during winter monsoon promoted group/species-specific epibiosis among the plankton in the western Bay of Bengal. Plankton samples were collected from discrete depths along five transects placed perpendicular to the coast. Water column profiling revealed thermal inversion below the mixed layer depth along three southern transects (APB, APV and APK) and its absence along the two northern transects (ODP and ODG). Multivariate analysis revealed a significant difference in hydrographical properties between these areas. The warmer, highly saline waters of the thermal inversion layer, sandwiched at 10–20 m, between the colder, less saline waters of surface and bottom, supported higher density and diversity of epibionts on copepods and diatoms. The density of epibionts and intensity of epibiosis were significantly lower outside the thermal inversion layer and in the northern transects. Epibionts preferred copepods over diatoms and carnivorous/omnivorous copepods over herbivorous copepods of comparable size. These results suggest that hydrographical variability associated with thermal inversion during winter monsoon support epibiosis among the plankton in the coastal waters of the western Bay of Bengal (BoB). The present investigation is the first-ever study from a coastal marine ecosystem connecting hydrographical features with epibiosis among the plankton. Further studies are warranted to explore the higher frequency of epibiosis in the thermal inversion layer, the nutrient preference and indicator properties of epibionts, and their ecological role in the coastal and open ocean ecosystems.

### 1. Introduction

Epibiosis is an ecological commensal association between sessile phases of an organism (epibiont) attached to another living organism (basibiont), without trophic dependence on it (Wahl, 2009). This relationship is inter-specific and observed in marine and freshwater environments (Fernandez-Leborans, 2009). The most common epibionts are bacteria, algae, protozoans and small metazoans, whereas the basibionts include various plankton, benthos and meiobenthos (Gutt and Schickan, 1998; Fernandez-Leborans, 2004; Susetiono, 2006; Ghosh and Mandal, 2019; Purushothaman et al., 2020).

Several studies (Green and Shiel, 2000; Gilbert and Schröder, 2003; Purushothaman et al., 2020) have suggested host specificity of epibionts, with factors like water pollution boosting such relationships (Henebry and Ridgeway, 1979). Epibiosis is favourable for the epibiont in many

ways, like assisted transport to new territories and hosts, defence from predators, and an opportunity to obtain nutrients in a nutrient-rich environment (Wahl, 1989; Abelló et al., 1990; Gili et al., 1993). The detrimental effects reported on basibionts include decreased growth rate, restriction in movement and activity, increase in energy utilization, quicker sinking rate, and competition for food and resources (Henebry and Ridgeway, 1979; Wahl, 1989; Regali-Selegim and Godinho, 2004; Nanajkar et al., 2019). Epibionts may affect the physiological functions of the basibiont by occupying crucial organs like eyes and gills (Mikac et al., 2019). Even though some epibionts may prove to be disadvantageous to basibionts, they benefit basibionts by making them less vulnerable to their predators (Fernandez-Leborans and Gabilondo, 2007).

Epibiosis is ubiquitous in global oceans (Pane et al., 2014). Study on epibiosis in the Antarctic (Gutt and Schickan, 1998) suggest that epibionts are species-specific and prefer high mineral substratum since the

\* Corresponding author.

E-mail address: [jasbose@gmail.com](mailto:jasbose@gmail.com) (J. Purushothaman).

<https://doi.org/10.1016/j.ecolind.2021.107914>

Received 26 September 2020; Received in revised form 15 June 2021; Accepted 17 June 2021

Available online 19 June 2021

1470-160X/© 2021 The Authors.

Published by Elsevier Ltd.

This is an open access article under the CC BY-NC-ND license

(<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

suspension-feeding behaviour of epibionts benefit from a raised substrate. Mikac et al. (2019) are the first to report an association between ciliates and polychaetes, where the ciliates benefit due to abundant food availability. The diversity and community structure of epibenthos and multi-level epibiosis from the White Sea was analyzed by Mikhaylova et al. (2019). From Indian waters, several studies are available on epibiosis, such as a symbiotic association of suctorian epibiont with marine nematodes (Matla estuary, Sundarbans, India; Ghosh and Mandal, 2019), the response of epibionts to habitat heterogeneity and anthropogenic disturbances (from a mangrove ecosystem; Ansari and Bhadury, 2017), and species-specific epibiont-basibiont association (from the west coast of India; Nanajkar et al., 2019). Despite their prevalence in eutrophic waters, the proliferation of epibionts concerning hydrographical variability is not yet fully understood (Manca et al., 1996). In the present study, epibiosis has been studied in plankton collected from the coastal waters of the northwestern Bay of Bengal (BoB) during the winter monsoon season, when the region reported a sub-surface thermal inversion phenomenon.

The BoB that constitutes the northeastern part of the Indian Ocean is a tropical semi-enclosed basin exposed to the seasonal reversal of monsoonal winds. South-westerly winds characterize the summer monsoon, and north-easterly winds the winter monsoon. Thermal inversion occurs during winter in the western BoB (Thadathil et al., 2002). When the sea surface temperature (SST) drops, a sub-surface warmer layer sandwiched between colder waters above and below is formed. Since the warmer layer is confined to the seasonal halocline, the salinity gain in the subsurface warmer layer maintains the stability of the water column. The sandwiched warmer layer limiting the vertical mixing and controlling the SST to alter the heat exchange with the atmosphere is referred to as the 'thermal inversion layer'. The major causes of thermal inversion are freshwater influx, surface heat flux and advection, seasonal winds, internal waves and currents (Shetye et al., 1996; Girishkumar et al., 2013). River runoff dilutes the upper oceanic layer and contributes to near-surface salinity stratification (Girishkumar et al., 2011). In turn, the salinity stratification improves the vertical stability of the upper water column and aids in maintaining a narrow-mixed layer (Thadathil et al., 2007; Girishkumar et al., 2013). The salinity stratification also facilitates the formation of a barrier layer below the mixed layer (Lukas and Lindstrom, 1991). The barrier layer is formed in the BoB during fall and attains a peak during winter (Rao and Sivakumar, 2003). Warming of the thermal inversion layer can be attributed to the narrow-mixed surface layer that allows shortwave radiations to penetrate the water column (Mignot et al., 2012). Furthermore, winter cooling leads to surface heat loss (Hastenrath and Lamb, 1979), resulting in convection currents in the thin surface layer.

The present study, keeping the ecological importance of sub-surface thermal inversion in view, investigates the influence of seasonal hydrographical variability supporting epibiosis in the coastal waters of the western BoB. Phytoplankton (diatoms) and zooplankton (ciliates and copepods) are the predominant taxa focussed here. Their roles as epibionts and basibionts and connecting their prevalence to hydrographical features are discussed for the first time from Indian waters.

## 2. Material and methods

### 2.1. Study area

As part of an investigation on the seasonal dynamics of microzooplankton, the present study was carried out during the winter monsoon along the coastal waters of the northwestern BoB. The lowest SST characterizes winter monsoon (or northeast monsoon) in the BoB due to net heat loss from the sea surface, stratified upper water column due to freshwater aided dilution of surface layers, and prevalence of cyclonic gyres (Babu and Rao, 2011; Chen et al., 2013). The impact of the northeast monsoon is more robust in the south than in the north of

the northwestern Bay (Ramage, 1971), making the surface water in the south less saline, which promotes the development of thermal inversion layer. Moreover, freshwater input along the coast generates estuarine features and attenuate exchange between the surface and deeper waters due to stratification. Although nutrients brought by the rivers enhance primary production in the coastal waters (Madhupratap et al., 2003), stratification due to low SST and sea surface salinity (SSS) prevents vertical mixing of nutrients in the water column. The stratification influences the coastal ecosystem function (Jyothibabu et al., 2004) when weak winds predominate the coastal waters during the winter monsoon. Chlorophyll *a* concentration (with Chl *a* maxima at 20 m depth) and average surface primary production during winter monsoon match the values in summer ( $0.17 \pm 0.14 \text{ mg/m}^3$ ;  $16.1 \pm 18.4 \text{ mgCm}^{-3} \text{ d}^{-1}$  respectively). The presence of a mature cyclonic eddy during winter monsoon has been reported between  $16^\circ$ – $20^\circ\text{E}$  latitude (Sabu et al., 2015). Two forces held responsible for the generation of eddy currents in this region are 1) wind forcing and unstable local baroclinicity and 2) Kelvin waves along the coast and westward-moving Rossby waves.

Several industries are located along the northeast coast releasing volumes of industrial effluents into the coastal Bay of Bengal. The coastal state of Andhra Pradesh alone accounts for one-third of the total pharmaceuticals production in India, and the city of Visakhapatnam is one of the central manufacturing hubs. A considerable amount of pharmaceutical effluents are discharged into the coastal waters of Visakhapatnam, which may affect the hydrography and biology of the coastal ecosystem (Shaik et al., 2017). Industrial activities in urban cities like Visakhapatnam and Kakinada have led to moderate to high trace metal enrichment in the coastal waters. Moreover, numerous fertilizer industries located close to and around the Kakinada Bay area can affect coastal water quality (Rao, 1999; Shaik et al., 2015). Agricultural runoff and water pollution due to other anthropogenic activities also affect the Mahanadi River-estuarine system of the coastal state of Odisha (Sundaray et al., 2006), the site of our northern transects. However, coastal eutrophication is prominent and widespread along Andhra Pradesh (AP) coast due to the dominance of industrial sectors in AP.

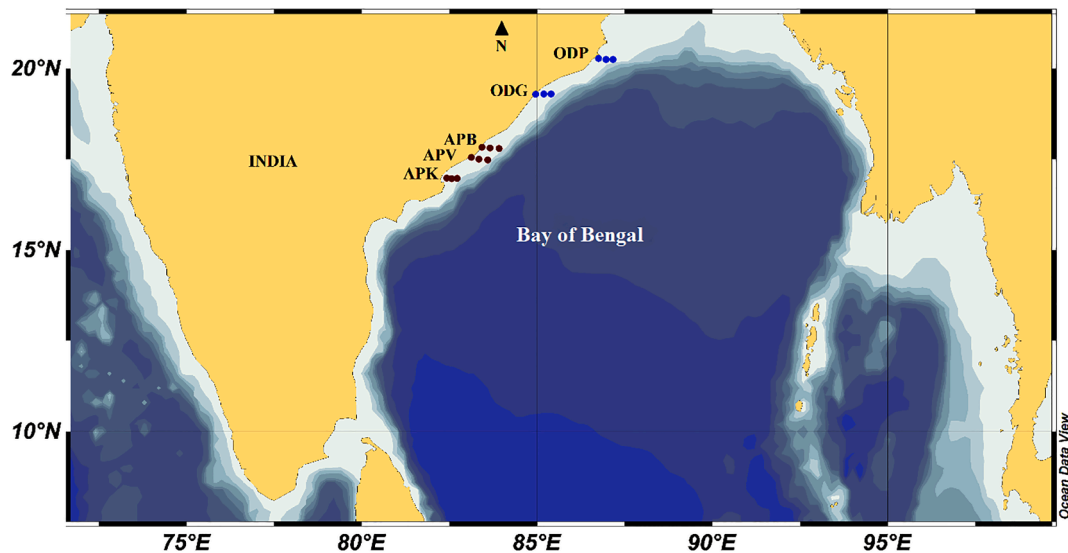
### 2.2. Sampling and sample processing

Water samples were collected from the surface (0 m), 10 m, 20 m and 30 m depths of five different transects (Tr), two northern, and three southern transects, designed perpendicularly to the coast [Tr A: Paradip (ODP); Tr B: Gopalpur (ODG); Tr C: Bheemunipatnam (APB); Tr D: Visakhapatnam (APV) and Tr E: Kakinada (APK)] (Fig. 1).

Temperature, salinity, light flux (PAR), and Chlorophyll fluorescence were measured by a Portable CTD (SBE Seabird). Mesozooplankton samples were collected using a WP (Working Party) plankton net with 200  $\mu\text{m}$  mesh size, equipped with a digital flow meter (GENERAL OCEANICS). Seawater samples were collected by Niskin sampler (5 L) from discrete depths for dissolved oxygen (DO), nutrients, Chl *a*, phytoplankton and microzooplankton taxonomic enumeration. Microzooplankton samples were collected from water samples filtered through a plankton net of 200  $\mu\text{m}$  and retained on 20  $\mu\text{m}$  mesh size.

Dissolved Oxygen (DO) was measured following the modified Winkler procedure (Grasshoff et al., 1999). Chl *a* was analyzed spectrophotometrically at wavelengths 750, 664, 647 and 630 nm (Strickland and Parsons, 1972). Nutrients (nitrate, nitrite, ammonium, silicate, and phosphate) were analyzed spectrophotometrically following Grasshoff et al. (1999). Phytoplankton and microzooplankton samples for taxonomic enumeration were preserved in 1–2% acidic Lugol's Iodine, whereas mesozooplankton samples were preserved in 5% buffered formaldehyde. In the laboratory, zooplankton biomass ( $\text{mg/m}^3$ ) and abundance ( $\text{ind./m}^3$ ) were calculated by taking account of the volume of water filtered through the net.

The phytoplankton and microzooplankton taxa were enumerated under an inverted microscope (Leica MC-120) using a Sedgewick-Rafter



**Fig. 1.** Map of the study area along the coastal waters of the Bay of Bengal. Blue dots indicate non-thermal inversion stations, and brown dots signify thermal inversion stations.

counting chamber at 100–200X magnification. Mesozooplankton taxa were identified using a stereo zoom microscope (Leica M125C). Epibionts were imaged using an inverted microscope (Leica MC-120) equipped with a digital camera and imaging software (LAS 4.12.0). An upright microscope (Nikon Eclipse Ni-U) was also used in the process. Plankton specimens, including epibionts and basibionts, were identified up to species level using standard taxonomic literature (Noble, 1929; Kahl, 1934; Krasske, 1941; Nagasawa and Warren, 1996; Fernandez-Leborans, 2011). All species names were verified for current taxonomic status using the online taxonomy verification platform, World Register of Marine Species (WoRMS, [www.marinespecies.org](http://www.marinespecies.org)).

### 2.3. Statistical analysis

The difference in environmental conditions between the areas showing the presence and absence of thermal inversion phenomenon was investigated using non-metric multivariate statistical procedures. For this purpose, data on environmental variables (water temperature, salinity, DO, PAR, and dissolved inorganic nutrients) and chlorophyll *a* were log-transformed and normalized before being used for the construction of a Euclidean distance-based similarity matrix for Agglomerative Hierarchical Cluster Analysis (AHCA), One-Way Analysis of Similarity (One-way ANOSIM), and Linkage Tree (LINKTREE) analyses. The One-way ANOSIM Global R-test checked for the significance of hydrographic assemblage patterns as revealed by the AHCA. LINKTREE analysis (powered with Similarity Profile test (SIMPROF;  $P_i$  statistics) and B statistics) is a non-metric, constrained divisive clustering procedure used to probe how abiotic variables explain particular sample clustering in a high-dimensional biotic/abiotic space. Here, the divisive binary clustering is performed to explain inequality (larger or smaller) on at least one of the abiotic variables used in the analysis. SIMPROF analysis helps search for new divisions until the probability level associated with the  $P_i$  value goes above the set significance level ( $P$ : 0.05). The best split is defined as that maximizes the ANOSIM R statistics between the groups. Here, the B% is the average of between-group rank dissimilarities, scaled to take 100% if the first division is a perfect split (i.e.,  $R = 1$ ) (Clarke et al., 2014). All the non-metric procedures were performed using the ecological statistical software PRIMER v.7.0.13 from PRIMER-E Ltd (Plymouth, UK). The Box-Whisker plots describing environmental variables, chlorophyll *a*, and plankton (with and without epibionts) were constructed using the statistical software GraphPad PRISM v. 5.01 (GraphPad Software Inc., UK).

## 3. Results

### 3.1. Hydrography

In the northern transects, sea surface temperature (SST) ranged between 23.58 and 24.60 °C (ca. 23.94 °C; CV: 0.02) off Paradip (ODP). Below 10 m depth (ca. 23.57 °C; CV: 0.0015), the temperature showed a gradual decrease up to 0.73 °C, reaching a minimum of 22.84 °C at 20 m. However, beneath 20 m, the temperature steadily increased and stabilized at 23 °C at 30 m depth. Similarly, the sea surface salinity (SSS) ranged from 27.16 to 27.66 (ca. 27.46; CV: 0.009), with a gradual increase, reaching a maximum of 28.61 at 30 m. The mean salinity gradient was 1.14 from the surface to 30 m depth (Fig. 2a).

Off Gopalpur (ODG), SST varied from 23.19 to 23.25 °C (ca. 23.21 °C; CV: 0.0012). The temperature increased with depth, reaching the highest at 30 m (23.89 °C). The SSS varied from 27.61 to 27.63 (ca. 27.62; CV: 0.001). Maximum salinity was noticed at 20 m (28.04). The salinity gradient made a difference of 0.42 between the surface and 20 m depth (Fig. 2b).

The SST varied between 25.92 and 26.10 °C (ca. 26.01 °C; CV: 0.003) off Bheemunipatnam (APB) in the southern transects. Beneath 10 m, the temperature increased from 26.03 °C to 26.53 °C up to 13 m. Below that, the temperature gradually decreased, reaching a minimum of 26.30 °C at 30 m. The change in temperature in the thermal inversion layer was 0.50 °C. SSS varied from 30.23 to 31.56 (ca. 30.89; CV: 0.022). Salinity slightly increased between 10 m (31.20) up to 13 m (32.77). Beyond 20 m, salinity (32.8) stabilized at 30 m depth. The salinity gradient recorded between 10 m and 13 m was 1.57. The initial increase in temperature and salinity below the surface mixed layer, followed by a gradual decrease below 20 m until a steady state is reached at 30 m, indicates the development of a thermal inversion layer off Bheemunipatnam (Fig. 2c).

Off Visakhapatnam (APV), SST varied from 25.69 to 25.94 °C (ca. 25.78 °C; CV: 0.005). Beyond 10 m, the temperature increased from 26.19 °C to 26.61 °C until 16 m. Below 16 m, the temperature decreased with depth, reaching 26.37 °C at 30 m. Salinity varied from 31.08 to 31.25 at the surface (ca. 31.16; CV: 0.003) and showed a steady increase from 8 m (31.61) up to 15 m (32.88). Salinity changes stabilized (at 32.6) at 30 m depth. The thermal inversion layer recorded a temperature gradient of 0.42 °C (between 10 m and 16 m) and a salinity gradient of 1.27 (Fig. 2d).

Off Kakinada (APK), SST varied from 25.46 to 26.43 °C (ca. 26 °C; CV: 0.019). Beyond 6 m, the temperature increased from 25.30 °C to

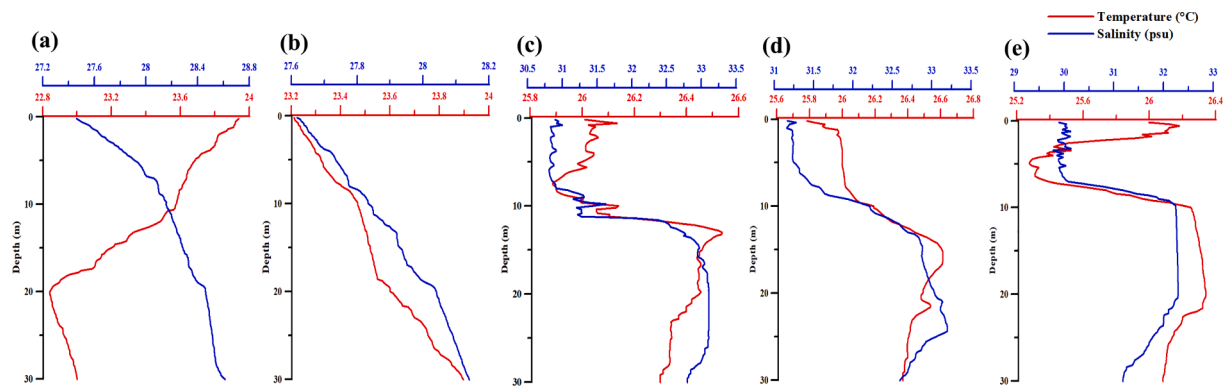


Fig. 2. Temperature and salinity profiles in the water column (a) ODP (b) ODG (c) APB (d) APV (e) APK.

26.26 °C until 11 m depth. Below this depth, the temperature decreased to 26.08 °C at 30 m depth. SSS varied from 29.85 to 29.95 (ca. 29.89; CV: 0.0012), and exhibited a steady increase from 7 m (30.09) up to 10 m (32.25). Beyond 11 m, salinity stabilized at 31.2. The temperature and salinity gradients observed in the thermal inversion layer were 0.95 °C and 2.16, respectively (Fig. 2e).

These observations suggested that at the time of sampling, southern waters off APB, APV and APK, experienced a sub-surface thermal inversion, which promoted the formation of a thermal barrier between the surface and deeper waters at 10–20 m depth (in APK, sub-surface thermal inversion was induced above 10 m). However, the thermal inversion phenomenon was absent in the northern transects off ODP and ODG.

High chlorophyll *a* (Chl *a*) was observed in the surface waters of southern (thermal inversion region) and northern (non-thermal inversion region) transects. In the northern waters, Chl *a* was homogeneously distributed in the upper 10 m (surface Chl *a* ca. 0.27 µg/l; CV: 0.13 off ODP, and ca. 0.23 µg/l; CV: 0.09 off ODG). The Chl *a* reduced to 0.22 µg/l (ODP) and 0.09 µg/l (ODG) at 30 m depth. In the surface waters of southern transects, Chl *a* concentration (surface Chl *a* ca. 0.11 µg/l, CV: 0.07 off APB; ca. 0.15 µg/l, CV: 0.13 off APV, and ca. 0.16 µg/l, CV: 0.09 off APK) were comparatively lower but exhibited consistent values. In the thermal inversion layer (10–20 m), Chl *a* ranged from 0.05 to 0.15 µg/l. At 30 m, the levels decreased substantially to 0.04–0.05 µg/l. Chl *a* concentration was higher in the northern transect than in the southern transect.

Dissolved oxygen (DO) was the highest in surface waters and decreased with an increase in depth in all stations. In the northern transects, the surface and deep (30 m) waters recorded mean DO concentration of 6.77 ml/l and 5.76 ml/l respectively (surface DO ca. 6.77 ml/l, CV: 0.003 off ODP; ca. 6.77 ml/l, CV: 0.03 off ODG). In the southern transects, the highest DO was reported in the surface waters off Visakhapatnam and the lowest off Bheemunipatnam (ca. 6.17 ml/l, CV: 0.02 off APB; ca. 7.30 ml/l, CV: 0.04 off APV, and ca. 6.32 ml/l, CV: 0.02 off APK). In the thermal inversion layer (10–20 m), mean DO levels decreased from 6.01 ml/l to 5.58 ml/l.

In the northern transects, despite a general decrease with depth, dissolved inorganic nitrogen and phosphorous concentrations were higher in the surface (off ODP: nitrate ca. 2.51 µM, CV: 0.08; nitrite ca. 0.73 µM, CV: 0.55; phosphate ca. 0.73 µM, CV: 0.27 and off ODG: nitrate ca. 2.44 µM, CV: 0.05; nitrite ca. 0.86 µM, CV: 0.09; phosphate ca. 0.63 µM, CV: 0.04) and in deeper layers (30 m) (off ODP nitrate: 2.74 µM, nitrite: 0.86 µM, phosphate: 0.91 µM, silicate: 17.29 µM and ammonium: 0.64 µM; off ODG nitrate: 2.69 µM, nitrite: 0.95 µM, phosphate: 0.90 µM, silicate: 17.22 µM and ammonium: 0.73 µM). Between 10 m and 20 m, nitrate levels did not vary much (2.29 µM to 2.43 µM). Silicate had the lowest concentration at the surface and the highest concentration in deeper waters. Conversely, in the southern transects, nitrate levels were comparatively lower in the surface waters (ca. 1.97 µM; CV: 0.317). In

the thermal inversion layer, mean nitrate concentration ranged from 2.56 µM and 3.24 µM, higher than that recorded from same depths at non-thermal inversion locations in the north. The highest concentration of nitrate was observed at 30 m depth (nitrate ca. 3.64 µM). Nitrite and phosphate showed a trend similar to nitrate. Silicate concentrations increased with increase in depth; the levels were higher in the northern transects (ca. 14.45 µM; CV: 0.27 at the surface to ca. 17.25 µM; CV: 0.003 at 30 m) when compared to southern transects (silicate ca. 3.64 µM; CV: 0.31 at the surface to ca. 7.34 µM; CV: 0.15 at 30 m). Ammonium levels recorded a similar trend, with the highest concentrations in deeper waters (30 m).

Compared to northern transects, thermal inversion induced stratification of the water column in southern transects prevented vertical mixing of nutrients, thus attenuating the infusion of nutrients into the euphotic zone resulting in low nutrient concentration in the surface waters.

### 3.2. Phytoplankton and zooplankton distribution

Phytoplankton abundance in the southern transects was higher than that recorded from the northern locations. Their mean cell density at surface (0 m), 10 m, 20 m and 30 m depths of northern (and southern) transects were 25.83 × 10<sup>3</sup> cells/L (30.56 × 10<sup>3</sup> × 10<sup>3</sup> cells/L), 25.5 × 10<sup>3</sup> cells/L (32.44 × 10<sup>3</sup> cells/L), 25.75 × 10<sup>3</sup> cells/L (22.17 × 10<sup>3</sup> cells/L), and 19 × 10<sup>3</sup> cells/L (20 × 10<sup>3</sup> cells/L) respectively. The highest phytoplankton abundance was recorded from 10 m depth off APV in the south. Conversely, zooplankton distribution (biomass and abundance) exhibited an inverse trend with the maximum stock at 30 m depth (mean: 2681.82 mg m<sup>-3</sup>; 4161.41 ind. m<sup>-3</sup>) and minimum at the surface (mean: 338.42 mg m<sup>-3</sup>; 1151.56 ind. m<sup>-3</sup>) along the southern transects. In the thermal inversion layer, zooplankton biomass (and abundance) increased from 1051.44 mg m<sup>-3</sup> (1856.72 ind. m<sup>-3</sup>) at 10 m depth to 2590.83 mg m<sup>-3</sup> (3540.47 ind. m<sup>-3</sup>) at 20 m. On the contrary, in the northern transects, where thermal inversion was absent, zooplankton stock was higher in the surface (mean: 1374.88 mg m<sup>-3</sup>; 18936.64 ind. m<sup>-3</sup>) and 10 m depth (mean: 1408.56 mg m<sup>-3</sup>; 10693.19 ind. m<sup>-3</sup>) and decreased substantially at 20 m (mean: 961.27 mg m<sup>-3</sup>; 6080.54 ind. m<sup>-3</sup>) and 30 m depths (mean: 652.97 mg m<sup>-3</sup>; 5440.73 ind. m<sup>-3</sup>). Thus, zooplankton distribution in the water column exhibited contrasting trends in thermal inversion regions and non-thermal inversion regions.

### 3.3. Spatial trends in epibiont distribution

Epibiosis and epibiont abundance and diversity were higher throughout the water column in southern waters, while in the north, a single species represented the epibionts. The number of epibionts associated with individual copepod varied from 2 to 12 cells off APK and from 1 to 16 cells off APV in the southern transects. Likewise, epibiont density per phytoplankton cell ranged from 1 to 4 cells in the

north and 1–10 cells in the south. Off APB and APV, epibionts mainly were found attached to plankton collected from above (surface–10 m) the thermal inversion layer (at 10–20 m). Off APK, their maximal association with phytoplankton was noticed at surface–10 m, and on copepods at the surface layers (0.2 m) and again at 20 m.

In the northern transects, the epibiont-basibiont association was species-specific between the chained centric diatom *Chaetoceros coarctatus* (basibiont) and the peritrichous ciliate, *Vorticella oceanica* (epibiont). The highest abundance of *V. oceanica* was recorded off ODP at the surface and 10 m depths. Whenever epibiosis was recorded, a single diatom cell of *C. coarctatus* supported at least three cells of *V. oceanica*. Off ODG, epibiosis was observed only at 20 m depth. Unlike northern transects, the diversity of epibionts and basibionts were significantly higher in the south. Peritrichous ciliates (*V. oceanica*), suctorian ciliates (*Ephelota plana*, *Ephelota gigantea* and *Ephelota gemmipara*), and a species of epizoic pennate diatom (*Pseudohimantidium pacificum*) were the major epibionts, while calanoid and cyclopoid copepods were the major basibionts. Like northern waters, *V. oceanica* was associated with the chained centric diatom *C. coarctatus* only (mean density: 3 epibionts. cell<sup>-1</sup>).

Off APB, each cell of *C. coarctatus* hosted an average of five cells of *V. oceanica* (Fig. 3a). The maximal epibiont-basibiont association was observed at the surface and 10 m depth. Off APV, the occurrence of epibionts on phytoplankton was lower than that reported off APB and northern transects. Only one out of eight cells of *C. coarctatus* possessed epibionts at a density of 3 cells.cell<sup>-1</sup>. The marine stalked epizoic diatom, *P. pacificum*, was attached to the cyclopoid copepod *Ditrichocorycaeus asiaticus* (mean: 16 cells.ind<sup>-1</sup>) with the help of a mucilaginous stalk arising from the end of its frustules (Fig. 3b). Their association was observed only in the surface waters. Conversely, the suctorian ciliates were epibiotic on calanoid copepods only. *Ephelota plana* cells were associated with *Centropages orsinii* (6 cells.ind<sup>-1</sup>), *Euchaeta concinna* (2 cells.ind<sup>-1</sup>) and *Labidocera bengalensis* (2 cells.ind<sup>-1</sup>) at 10 m and 30 m depths (Fig. 3c). *Ephelota gemmipara* was epibiotic on *Canthocalanus pauper* (1 cell.ind<sup>-1</sup>) and *Centropages orsinii* (1 cell.ind<sup>-1</sup>) at 0 m and 30 m depths (Fig. 3d). In comparison, *Ephelota gigantea* was exclusively associated with *Euchaeta concinna* (1 cell.ind<sup>-1</sup>) at 30 m depth (Fig. 3e, Table 1).

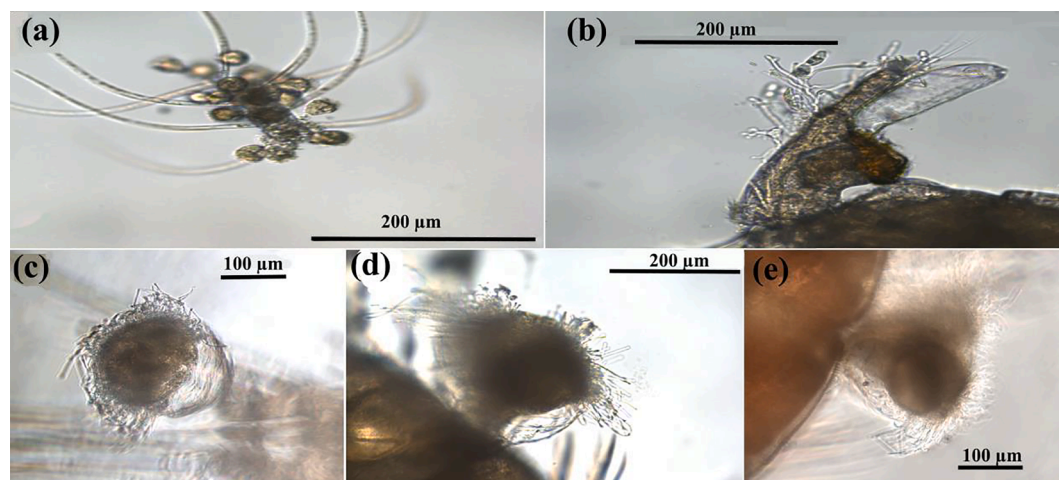
In the southernmost transect off APK, each *C. coarctatus* cell possessed an average of six cells of *V. oceanica* throughout the water column. *P. pacificum* was found attached to the urosome of the copepod *D. asiaticus* (9 cells. ind<sup>-1</sup>) in the surface waters. Cells of the suctorian ciliate *E. plana* were reported from the surface and 20 m depths, adhering to the calanoid copepods *Labidocera kroyeri* (1 cell. ind<sup>-1</sup>) and

*E. concinna* (2 cells. ind<sup>-1</sup>), while *E. gigantea* associated exclusively with *Euchaeta concinna* at 20 m depth with a frequency of one cell per copepod (Table 1).

As observed in our study, the ciliate species *V. oceanica* was the most abundant epibiont on phytoplankton, especially on chained centric diatoms like *C. coarctatus*. Such diatoms have better morphological modifications (in the form of adaptations suited for a symbiotic lifestyle) and higher substrate area (for epibiont attachment) compared to non-chain forming phytoplankton without much morphological complexity (like *Ceratocorys horrida* and *Pleurosigma diversistriatum*). Coastal waters off APK reported the highest occurrence of *V. oceanica* on phytoplankton. Conversely, carnivorous copepods were the most preferred hosts for the epizoic pennate diatom *P. pacificum*. Off APV and APK, *P. pacificum* was associated with copepods. The basibiont copepods made up 5–13% of total copepod density off APV and 9–15% off APK. In comparison, 10–18% of microphytoplankton stock (cell density-based) off APB and 6–22% of microphytoplankton off APK sustained the peritrichous ciliate *V. oceanica*. These results suggest a species-specific association of epibionts with microphytoplankton and copepods.

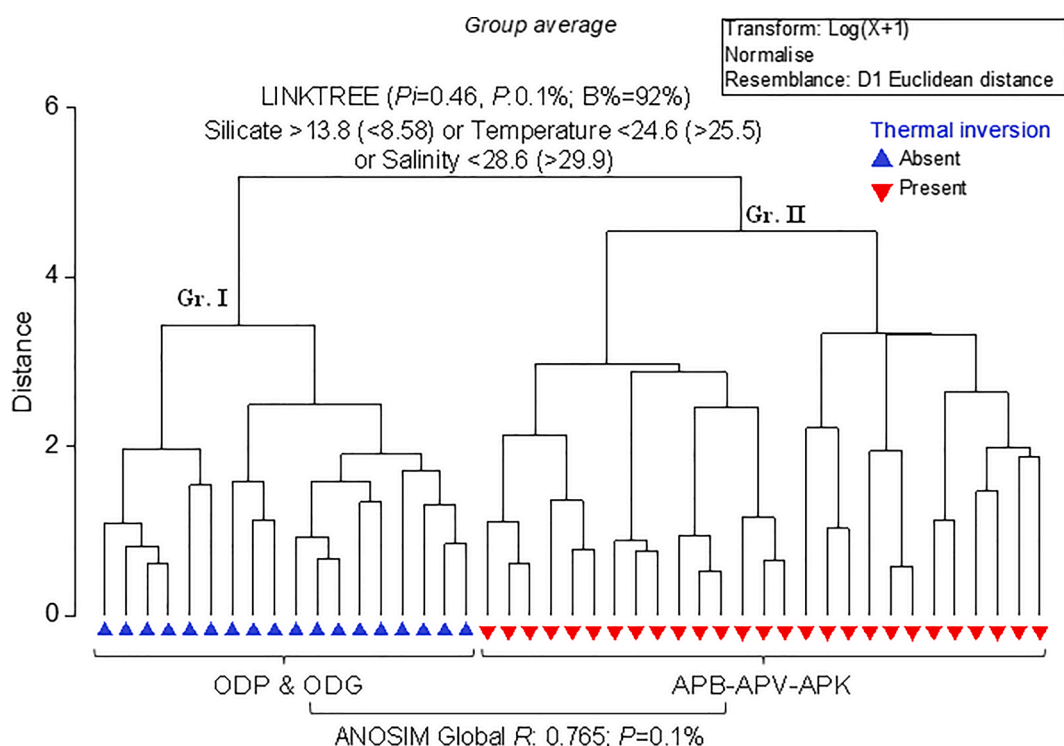
More epibionts were attached to phytoplankton and copepods in the southern transects' warmer, highly saline waters, characterized by lower copepod density but higher phytoplankton, nitrate + nitrite and phosphate levels. Conversely, silicate and ammonium were higher in the colder, low-saline waters of the northern transects, where signatures of sub-surface thermal inversion were absent at the time of sampling. Multivariate analysis revealed significant differences in water quality between southern and northern transects and the environmental variables responsible for that disparity (Fig. 4).

In this study, the highest copepod density was reported from the northern transects. Despite the dominance of carnivores (49–64%; ca. 57%), the small herbivorous copepod *Bestiolina similis* was the single most abundant species. Likewise, the dinoflagellate *Tripes furca* was the predominant phytoplankton taxon. Although present in low abundance on phytoplankton, epibionts were absent on copepods in the north and off APB. Despite the lower copepod density, more epibionts were associated with copepods off APV and APK, especially on carnivorous taxa like *Ditrichocorycaeus asiaticus* (off APV) and *Euchaeta concinna* (off APK). Off APV and APK, the carnivorous taxa constituted 63–73% (ca. 68%) of total copepod density, whereas off APB, their relative abundance has reduced to 19–34% (ca. 26%). Off APK, all the basibiont copepods were predominantly carnivorous (*Centropages orsinii*, *Ditrichocorycaeus asiaticus*, *Euchaeta concinna*, *Labidocera bengalensis* and *Labidocera kroyeri*) with mean epibiont density ranging from 0.1 to 8.3 cells per copepod. Together, these species contributed 85–90% (ca. 96%) of the total



**Fig. 3.** Light micrograph (LM) of epibiontic species (a) *V. oceanica* on *C. coarctatus*. Scale bar: 200  $\mu$ m, 200 X magnification (b) *P. pacificum* on *D. asiaticus*. Scale bar: 200  $\mu$ m, 200 X magnification (c) *E. plana* on *C. orsinii*. Scale bar: 100  $\mu$ m, 200 X magnification (d) *E. gemmipara* on *C. pauper*. Scale bar: 200  $\mu$ m, 400 X magnification (e) *E. gigantea* on *E. concinna*. Scale bar: 100  $\mu$ m, 200 X magnification.





**Fig. 4.** AHCA showing grouping of sampling locations based on their physicochemical and Chlorophyll-a characteristics. One-Way ANOSIM test revealed a significant difference in water quality in the presence and absence of sub-surface thermal inversion phenomenon. LINKTREE analysis confirmed the ANOSIM results with a SIMPROF test and B-statistics and accounted for variables mainly responsible for the grouping pattern. For each variable, values outside the parenthesis qualify Gr. I, while that inside qualify Gr. II.

carnivorous copepod population. Off APV, they made up 52–61% (ca. 57%) of carnivorous copepods (with 0.03–10.2 epibionts per copepod). The only calanoid copepod with epibionts was *Canthocalanus pauper* (0.03–3.1 epibionts per copepod). These findings suggest that the same epibiont species prefers carnivorous copepods over herbivorous ones of comparable size (Fig. 5, Fig. 6, Table 1).

#### 4. Discussion

The frequency of epibiosis and diversity and spatial structuring of epibionts in winter plankton samples stirred our interest in background factors and oceanographic features supporting such successful consortia of plankton in coastal waters. The study revealed active epibiosis among the plankton in sub-surface thermal inversion layers in the coastal waters of the western Bay of Bengal under winter-monsoon conditions. Epibiosis was absent or sparse in the surface and deep waters and in areas where thermal inversion was not noticeable.

The coastal waters off Kakinada (i.e., off APK) experience significant hydrographical changes due to the increased freshwater influx and mangrove outwelling during monsoon periods. During summer and winter monsoon, freshwater from river Godavari that flows through the mangroves brings a large flux of nutrients causing significant changes in nutrient and plankton community dynamics in the Kakinada Bay and adjacent coastal waters. The geomorphological changes and breaches in the sand spit that separates the semi-enclosed Bay from the coastal waters mask the winter salinity changes inside the Bay (Prof. A. V. Raman, Andhra University, Visakhapatnam, India- personal communication). Apart from mangrove outwelling, cold-core eddy induced upwelling enriches the coastal waters and causes significant changes in plankton community characteristics off Kakinada in spring inter-monsoon (Rakesh et al., 2008). The effect of eddy pumping on the plankton community is also reported off Visakhapatnam (Bhavanarayana, 1974). Moreover, numerous fertilizer factories, food and oil processing units, and pharmaceutical industries are located along the

coasts of Kakinada and Visakhapatnam (Shaik et al., 2015). These studies suggest that the coastal waters off Andhra Pradesh (correspond to transects APB, APV, and APK) are subjected to different allochthonous and autochthonous fluxes on a seasonal basis. Thus, the exceptional hydrographical settings off Visakhapatnam and Kakinada seem to have promoted the formation of a sub-surface thermal inversion layer in the southern transects, as reported in this study.

The coastal environment of the western BoB, in general, is influenced by freshwater influx from major east draining rivers, causing a lowering of salinity during monsoon periods (Thadathil et al., 2002). From Indian waters, Nanajkar et al. (2019) reported the occurrence of epibiosis under specific environmental conditions at estuarine mouths. In agreement with the observations made by Thadathil et al. (2002), we have documented the formation of a sub-surface thermal inversion layer under winter conditions in the southern areas of the northwestern BoB. Winter surface cooling and salinity stratification are vital drivers in forming and maintaining the thermal inversion layer. Advection of cold, low saline waters over warm, high saline waters can also contribute to developing the thermal inversion layer (Thadathil et al., 2016). As observed in this study, a three-dimensional model simulation by Babu and Rao (2011) suggested thermal inversion at 10–20 m depth in the western BoB.

Chlorophyll *a* concentration was higher in the surface water but showed a marked decrease with depth. In the northern transects where thermal inversion was not apparent, the Chl *a* concentration was higher than that reported from the south where thermal inversion was present. The thermal inversion layer prevents entrainment and vertical mixing of cold, nutrient-rich deeper waters with the nutrient-deficient mixed layer (De Boyer Montégut et al., 2007). Accordingly, we have noticed that the thermal inversion aided sub-surface stratification, and a barrier layer formation limited nutrient supply from the deep to the surface, causing a decrease in Chl *a* levels in the south. A contemporary study by Prasanna Kumar et al. (2010) reported stratification of the water column and diminished wind mixing, causing low Chl *a* and primary productivity in the western BoB.

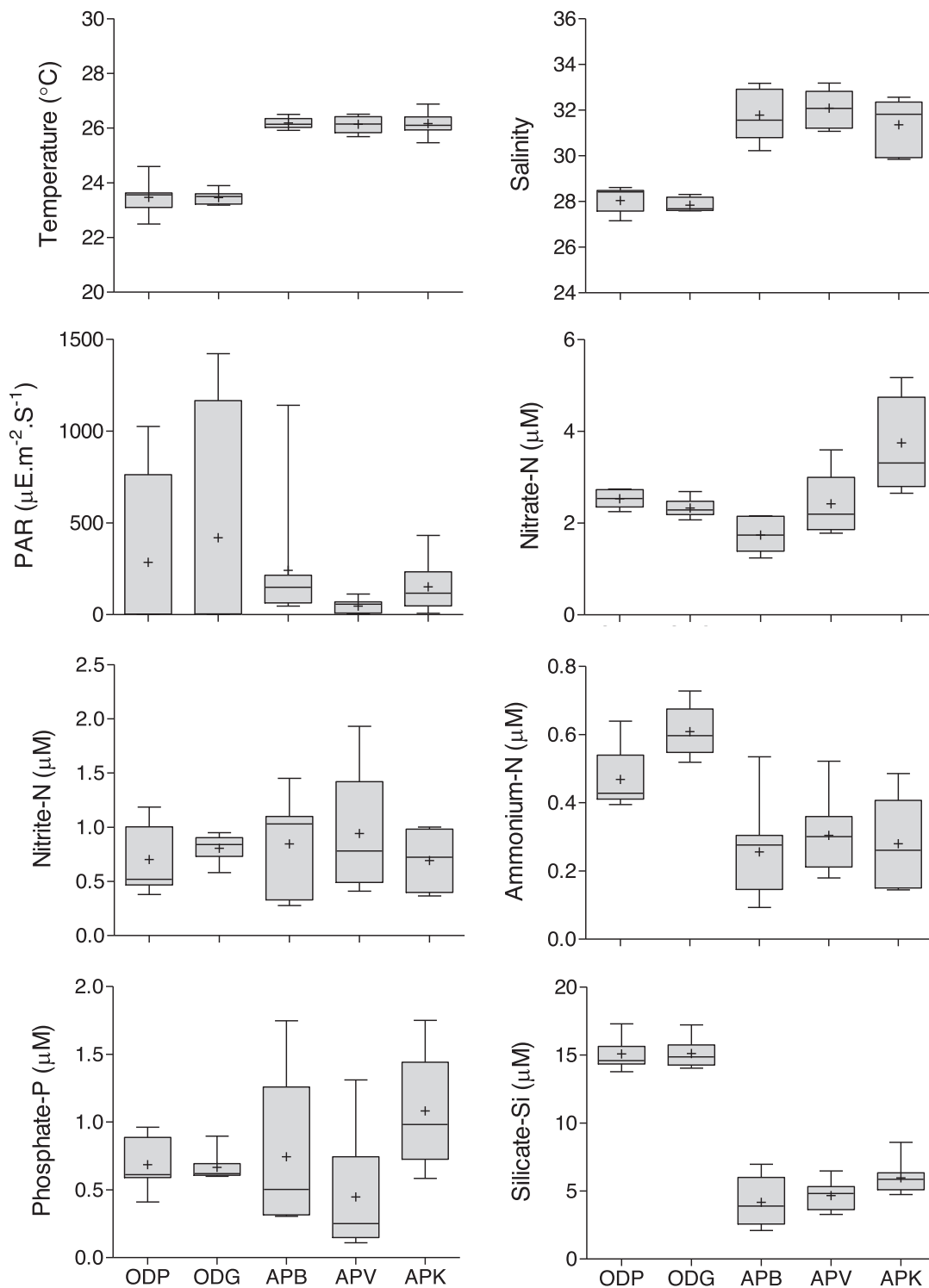
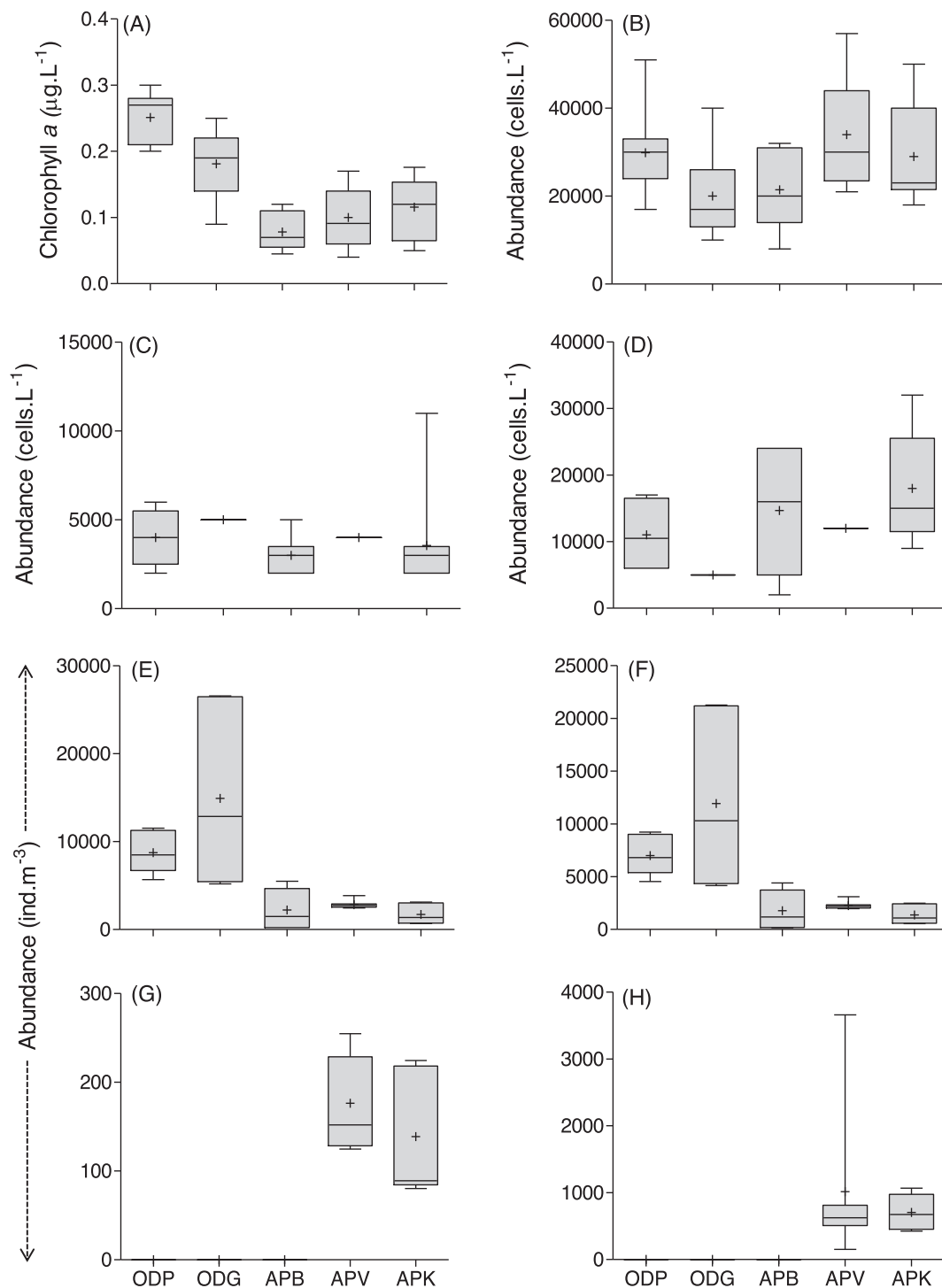


Fig. 5. Distribution of environmental variables across coastal transects sampled during the winter monsoon in the western Bay of Bengal. In the box-whisker plot, the box represents quartile deviation of the values, the horizontal line inside the box represents the 50% value (median), the plus symbol denotes the mean, and the whiskers represent the min-max.

This study has revealed a higher concentration of nitrate, nitrite and phosphate below the thermal inversion layer and deeper layers of southern transects. In contrast, in the north, surface waters were depleted of nutrients. Here, the absence of sub-surface thermal inversion helped the mixing of nutrients, especially silicate and ammonium, from the deep with the mixed layer. Zooplankton can increase the

ammonium levels in the water column (Biggs, 1977). Their biomass and abundance in southern transects were lower than that reported from the north. Higher ammonium levels recorded in the northern transects corroborate well with this observation. Riverine supply and eutrophication also increase the silicate and ammonium levels in coastal waters. High nitrate, nitrite and phosphate levels in the sub-surface layers of





**Fig. 6.** Distribution of biotic variables in the coastal waters. (A) Chlorophyll *a* (B) Phytoplankton density (C) Density of phytoplankton with epibionts (D) Density of epibionts on phytoplankton (E) Total mesozooplankton (F) Copepods density (G) Density of copepods with epibionts (H) Density of epibionts on copepods.

southern waters must have promoted the growth of phytoplankton, including epizoic diatoms. A recent study by Sahu et al. (2015) suggests an increased abundance of epibiotic diatoms in nutrient replete coastal waters.

In the deeper waters of the south, sub-surface Chl *a* maxima (at 20 m depth, Madhu et al., 2006) promoted zooplankton build-up; however, their relationship was not statistically significant ( $P > 0.1$ ). Fernandes and Ramaiah (2009) reported a similar trend, even when zooplankton biomass was five times higher and density eighteen times greater in the sub-surface waters where cold-core eddies existed. Sabu

et al. (2015) also report the influence of cold-core eddy on mesozooplankton community during winter monsoon from the central BoB. Therefore, while cold-core eddies help stimulate plankton production in winter monsoon in the coastal BoB, water column stratification due to sub-surface thermal inversion hinders nutrient induction to the surface layers. Such a scenario would favour tiny phytoplankton in the surface waters that would eventually support a less efficient trophic flow where microzooplankton play a key role (Jyothibabu et al., 2008). Conversely, higher mesozooplankton stock in the thermal inversion layer and deeper waters, where nutrients and Chl *a* were higher,

suggests the dominance of the classical, more efficient phytoplankton-mesozooplankton food chain. Thus, the discrepancy observed between the northern and southern transects in the present study suggests that the sub-surface thermal inversion controls the nutrient dynamics, the plankton distribution patterns, and availability of basibionts, most of which prefer species-specific association with diatoms and copepods.

The present findings on the species-specific association of the peritrichous ciliate *Vorticella oceanica* and the chained centric diatom *Chaetoceros coarctatus* are supported by earlier studies of Karsten (1907); Cupp (1943); Nagasawa and Warren (1996); Gárate-Lizárraga and Muñetón-Gómez (2009); Purushothaman et al. (2020); Gómez (2020). The relationship between *V. oceanica* and *C. coarctatus* is obligatory since *C. coarctatus* provides a favourable substratum for the growth of the ciliate and protects it from predators using diatom setae, forming a cage-like configuration (Gómez, 2020). A tremendous survival advantage has been attributed to the ciliate's association with *C. coarctatus* since the epibiont can rapidly detach and re-attach to the basibiont and attain efficient feeding rates, which is not possible for epibionts adhering to crustaceans (Nanjkar et al., 2019; Gómez, 2020). Such an association is beneficial for the basibiont, as the movement of the attached *V. oceanica* alters the buoyancy of the diatom chain and helps with its horizontal displacement in less turbulent waters (Gómez, 2020). The epibiont-basibiont partnership thus exhibits mutualism rather than commensalism. In this study, the abundance and density of *V. oceanica* on *C. coarctatus* was higher (>5 cells/Cell) at the thermal inversion layer. The reports of *Vorticella* being attached to copepods (Fernandez-Leborans and Tato-Porto, 2000) is restricted to freshwater copepods only.

The dinoflagellate *Tripes furca* was the most dominant phytoplankton taxa throughout the study area, yet without any epibionts. Though *T. furca* is chain-forming phytoplankton, no chains of *T. furca* were observed in this study. The only chained basibiont phytoplankton was *C. coarctatus*; the epibiont *V. oceanica* attached to it in areas where thermal inversion was either present (in greater abundance) or absent (in lesser abundance). Baek et al. (2009) propose that chain-forming phytoplankton showcase diel vertical migration (DVM) between the surface and sub-surface waters to evade strong sunlight and to utilize nutrients efficiently from sub-surface waters at night. Photosynthetic epibionts attached to chain-forming phytoplankton may thus be benefited from such association and hitchhiking.

According to Hiromi et al. (1985), only five species of diatom show epibiosis on marine copepods and the most frequently reported association is between the epizoic diatom *Pseudohimantidium pacificum* and corycaeid copepods. In this study, the association between *P. pacificum* and the corycaeid copepod *D. asiaticus* was observed only in the surface waters where a single basibiont copepod possessed an average of 12 diatoms near their thoracic and urosomal regions. Russell and Norris (1971) reported similar site-specific adherence where these diatoms attached to male copepods' genital and anal segments. They proposed that diatoms are translocated to other copepods during copulatory or non-copulatory entwining. Comparable to our observations, Russell and Norris (1971) reported seven to nine cells of *P. pacificum* per individual of *Corycaeus affinis*. Thus, it can be inferred that *P. pacificum* consorts mainly with a specific family of copepods, Corycaeidae. However, a recent study from the coastal BoB has suggested their association with the copepod family Tachidiidae (Sahu et al., 2015).

Most protozoan epibionts on marine copepods belong to the phylum Ciliophora and are members of the subclasses Suctorina and Peritricha (Carman and Dobbs, 1997). The density of epibionts per copepod ranges from 1 to 8 cells/ind. (Bowman, 1977), which is within the observed density of ciliate infestation per copepod in this study. Ciliates association with copepods depend on gender, developmental stage (Marshall and Orr, 1955), and relative size of the copepod (Weissman et al., 1993). Also, ciliates anchor themselves on specific parts of the copepod exoskeleton like caudal rami and the thoracic region (embedded into the pedigerous somites), as observed in this study. According to Weissman et al. (1993), seasonality contributes to such epibiotic association. In our

study, the epibiotic ciliate *E. plana* flourished in the warmer thermal inversion layer during the winter monsoon. Studies suggest that *E. gemmipara*, a congeneric species, attains peak growth when the water temperature reaches 22–25 °C and becomes dormant when the temperature dwindle to 8–10 °C (Tazioli and Di Camillo, 2013). They also proliferate in high saline waters (for example, *E. gemmipara* at salinity 31; Chen et al., 2008), as reported in this study.

Epibiosis was manifested on larger taxa with higher morphological complexity, such as the chain-forming diatom *C. coarctatus* and carnivorous copepods like *L. kroyeri*, *L. bengalensis*, *E. concinna*, *D. asiaticus*, *C. orsinii*, and predominantly herbivorous *C. pauper*. Bigger plankters are easy targets for epibionts as they furnish a larger surface area for anchorage (Regali-Selegim and Godinho, 2004). In this study, the majority of basibiont copepods were predominantly carnivorous. Studies elsewhere suggest an exclusive association of suctorian ciliates with carnivorous (for example, *Pelagacineteta hebensis* with *Paraeuchaeta hebe*; Gregori et al., 2016) and omnivorous copepods (for example, *Tokophrya* sp. with *Limnocalanus* sp.; Evans et al., 1979). Since omnivory is the most preferred feeding habit among planktonic ciliates, they gain nourishment while adhering to carnivorous/omnivorous copepods that prey on smaller zoo- and phytoplankton.

Horikami and Isii (1981) explained how an epibiont ciliate attaches to a basibiont host. On encountering a basibiont, the ciliate immediately attaches to the basibiont. The ciliate secretes a transparent viscous compound that elicits a positive chemotactic response in other ciliates facilitating their adherence on the same basibiont. The stalk of the ciliate retracts in a coiled manner, and they penetrate the ribcage of setae when a crustacean is a host (Gómez et al., 2018). Epibiosis on crustaceans is sparse compared to diatoms since frequent moulting of the crustacean carapace does not allow epibionts to form colonies and force them to find new substratum (Utz and Coats, 2005). Therefore, for an epibiont, the ideal basibiont will be an adult copepod or any other adult crustacean that has completed its moulting stages. In coastal waters, ciliates are the primary grazers of the bacterial community (Sherr and Sherr, 1987). As the death of basibionts seldom affects the existence of epibiotic ciliates (Utz and Coats, 2008), the ciliates become a part of the microzooplankton community and lead a vital role in the biogeochemical cycles in coastal ecosystems (Buitenhuis et al., 2010). Moreover, when compared to their free-living counterparts, epibiotic species have higher feeding efficiency (Fenchel, 1980). Their colony-forming behaviour and a higher rate of bacterivory increase the nutrient remineralization capabilities (Bickel et al., 2012) and generate a subsidiary trophic pathway in the coastal waters (Sherr and Sherr, 1987).

Sawyer et al. (1976) proposed that ciliates are pollution tolerant and can be helpful indicator species. Specific diatom assemblages are indicators of river influx, estuarine state and salt-wedge conditions (Rovira et al. 2012). Jiang et al. (2013) highlighted that pelagic ciliate communities are robust bioindicators of climate change, whereas Wang et al. (2016) considered the body-size spectrum of ciliates as a bio-indicator of ecological changes and global bio-assessment. Ciliates obtained in our study as epibionts were more abundant in the southern transect, which experiences greater coastal eutrophication. Thus, it can be suggested that the epibionts are potential indicators of pollution in the coastal areas since they flourish in nutrient replete waters.

## 5. Conclusion

The present study on winter hydrography and plankton dynamics in the northwestern BoB revealed winter cooling aided shallow mixed layer formation and development of sub-surface thermal inversion layers in the southern coastal waters. The resulting stratification of the water column prevented the infusion of nutrient-rich bottom waters into the surface layers. It resulted in significant spatial disparity in nutrient availability between the southern (thermal inversion region) and northern (non-thermal inversion region) transects. The warmer, high saline waters with moderate nutrient availability promoted both

basibionts and epibionts, leading to active species-specific epibiosis on chained centric diatoms and carnivorous/omnivorous copepods in the thermal inversion layer of the southern transects. Further studies are required to explore the higher frequency of epibiosis in the thermal inversion layer and compare the ecological significance of epibiosis in the mesotrophic-eutrophic coastal waters and the oligotrophic open ocean waters.

### CRedit authorship contribution statement

**Alfisa Siddique:** Conceptualization, Formal analysis, Writing - original draft. **Aishee Bhowal:** Formal analysis, Investigation, Writing - original draft. **Jasmine Purushothaman:** Conceptualization, Funding Acquisition, Project administration, Writing - review & editing. **Rakhesh Madhusoodhanan:** Formal analysis, Software, Writing - review & editing. **Chelladurai Raghunathan:** Methodology, Software. **Kailash Chandra:** Validation, Resources.

### Declaration of Competing Interest

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

### Acknowledgements

The authors are greatly indebted to the Director, Zoological Survey of India, for his kind support and encouragement during this study. The authors (AS, AB, and JP) thank the Department of Science & Technology - Science & Engineering Research Board (DST-SERB) (sanction no. ECR/2007/000087) for the research funding of this work. AS also thanks the Council of Scientific & Industrial Research (CSIR), India, for the research fellowship [sanction letter number 09/1181(0003)/2017-EMR-I]. RM thanks the Kuwait Institute for Scientific Research (KISR), Kuwait, for financial and logistics support.

**Compliance with ethical standards:** On behalf of all authors, the corresponding author declares no conflict of interest, of any financial and academic nature, in this work.

### References

- Abelló, P., Pertierra, J.P., Reid, D.G., 1990. Sexual size dimorphism, relative growth and handedness in *Liocarcinus depurator* and *Macropipus tuberculatus* (Brachyura: Portunidae). *Sci. Mar.* 54, 195–202.
- Ansari, K.G.M.T., Bhadury, P., 2017. Occurrence of epibionts associated with meiofaunal basibionts from the world's largest mangrove ecosystem, the Sundarbans. *Mar. Biodiv.* 47 (2), 539–548. <https://doi.org/10.1007/s12526-016-0502-5>.
- Babu, S.V., Rao, A.D., 2011. Mixing in the surface layers in association with internal waves during winter in the northwestern Bay of Bengal. *Nat. Hazard.* 57 (3), 551–562. <https://doi.org/10.1007/s11069-010-9607-5>.
- Baek, S.H., Shimode, S., Shin, K., Han, M.-S., Kikuchi, T., 2009. Growth of dinoflagellates, *Ceratium furca* and *Ceratium fusus* in Sagami Bay, Japan: the role of vertical migration and cell division. *Harmful algae* 8 (6), 843–856. <https://doi.org/10.1016/j.hal.2009.04.001>.
- Bhavanarayana, P.V., 1974. On the vertical distribution of pelagic tunicates in relation to the water masses in the western part of the Bay of Bengal. *Hydrobiologia* 44 (2-3), 209–214. <https://doi.org/10.1007/BF00187270>.
- Bickel, S.L., Tang, K.W., Grossart, H.P., 2012. Ciliate epibionts associated with crustacean zooplankton in German lakes: distribution, motility, and bacterivory. *Front. Microbiol.* 3, 243. <https://doi.org/10.3389/fmicb.2012.00243>.
- Biggs, D.C., 1977. Respiration and ammonium excretion by open ocean gelatinous zooplankton. *Limnol. Oceanogr.* 22, 108–117. <https://doi.org/10.4319/lo.1977.22.1.0108>.
- Bowman, T.E., 1977. *Dendrosomides lucicutiae*, a new species of suctorian from the pelagic calanoid copepod, *Lucicutia*. *Proc. Biol. Soc. Wash.* 89, 695–702.
- Buitenhuis, E.T., Rivkin, R.B., Sailley, S., Le Quéré, C., 2010. Biogeochemical fluxes through microzooplankton. *Global Biogeochem. Cy.* 24 (4), n/a–n/a. <https://doi.org/10.1029/2009GB003601>.
- Carman, K.R., Dobbs, F.C., 1997. Epibiotic microorganisms on copepods and other marine crustaceans. *Microsc. Res. Tech.* 37, 116–135. [https://doi.org/10.1002/\(SICI\)1097-0029\(19970415\)37:2<116::AID-JEMT2>3.0.CO;2-M](https://doi.org/10.1002/(SICI)1097-0029(19970415)37:2<116::AID-JEMT2>3.0.CO;2-M).

- Chen, X., Pan, D., Bai, Y., He, X., Chen, C.T.A., Hao, Z., 2013. Episodic phytoplankton bloom events in the Bay of Bengal triggered by multiple forcings. *Deep Sea Res. Part I: Oceanogr. Res. Pap.* 73, 17–30.
- Chen, X., Song, W., Warren, A., AL-Rasheid, K.A.S., AL-Farraj, S.A., AL-Quraishy, S.A., Gong, J., 2008. Redefinitions of Two Marine Suctorian Ciliates, *Ephelota gemmipara* (Hertwig, 1876) Butschli, 1889 and *E. crustaceorum* Haller, 1880 (Ciliophora, Suctorina), with a Brief Description of the Asexual Reproduction Process in *E. gemmipara*. *Acta Protozool.* 47, 113–124.
- Clarke, K.R., Gorley, R.N., Somerfield, P.J., Warwick, R.M., 2014. *Change in marine communities: an approach to statistical analysis and interpretation*, third ed. Plymouth, Primer-E Ltd, p. 256.
- Cupp, E.E., 1943. Marine plankton diatoms of the west coast of North America. *Bull. Scripps Inst. Oceanogr. Univ. California La Jolla* 5, 1–238. <https://escholarship.org/uc/item/922945w8>.
- De Boyer Montégut, C., Mignot, J., Lazar, A., Cravatte, S., 2007. Control of salinity on the mixed layer depth in the world ocean: 1. General description. *J. Geophys. Res. Oceans* 112, C06011. <https://doi.org/10.1029/2006JC003953>.
- Evans, M.S., Sicko-Goad, L.M., Omair, M., 1979. Seasonal occurrence of *Tokophrya quadripartita* (Suctorina) as epibionts on adult *Limnocalanus macrurus* (Copepoda: Calanoida) in southeastern Lake Michigan. *Trans. Amer. Microsc. Soc.* 98, 102–109. <https://doi.org/10.2307/3225944>.
- Fenchel, Tom, 1980. Relation between particle size selection and clearance in suspension-feeding ciliates. *Limnol. Oceanogr.* 25 (4), 733–738. <https://doi.org/10.4319/lo.1980.25.4.0733>.
- Fernandes, Veronica, Ramaiah, N., 2009. Mesozooplankton community in the Bay of Bengal (India): spatial variability during the summer monsoon. *Aquat. Ecol.* 43 (4), 951–963. <https://doi.org/10.1007/s10452-008-9209-4>.
- Fernandez-Leborans, G., 2004. Protozoan epibionts on *Mysis relicta* Loven, 1862 (Crustacea, Mysidacea) from Lake Liūšiai (Lithuania). *Acta Zool. (Stockh)* 85, 101–112. <https://doi.org/10.1111/j.0001-7272.2004.00162.x>.
- Fernandez-Leborans, Gregorio, 2009. A review of recently described epibioses of ciliate Protozoa on Crustacea. *Crustaceana* 82 (2), 167–189. <https://doi.org/10.1163/156854008X367223>.
- Fernandez-Leborans, G., 2011. Epibionts on the krill (*Euphausia pacifica*) from the E coast of Japan. *Acta Zool.* 94, 167–176. <https://doi.org/10.1111/j.1463-6395.2011.00535.x>.
- Fernandez-Leborans, G., Gabilondo, R., 2007. Invertebrate and protozoan epibionts on the velvet swimming crab *Liocarcinus puber* (Linnaeus, 1767) from Scotland. *Acta Zool.* 89, 1–17. <https://doi.org/10.1111/j.1463-6395.2007.00287.x>.
- Fernandez-Leborans, Gregorio, Tato-Porto, Maria Luisa, 2000. A review of the species of protozoan Epibionts on crustaceans. I. Peritrich ciliates. *Crustaceana* 73 (6), 643–683. <https://doi.org/10.1163/156854000504705>.
- Gárate-Lizárraga, I., Muñetón-Gómez, M.S., 2009. Primer registro de la diatomea epibionte *Pseudohimantidium pacificum* y de otras asociaciones simbióticas en el Golfo de California. *Acta Bot. Mex.* 88, 31–45 (in Spanish).
- Ghosh, Moumita, Mandal, Sumit, 2019. Living with Nematode: an Epibiont *Trematosoma rotunda* Associated with Basibiont *Desmodora scaldensis* from Matla Estuary, Sundarbans, India. *Thalassas* 35 (2), 619–624. <https://doi.org/10.1007/s41208-019-00129-3>.
- Gilbert, J.J., Schröder, T., 2003. The ciliate epibiont *Epistylis pygmaea*: selection for zooplankton hosts, reproduction and effect on two rotifers. *Freshw. Biol.* 48, 878–893. <https://doi.org/10.1046/j.1365-2427.2003.01059.x>.
- Gili, J.-M., Abelló, P., Villanueva, R., 1993. Epibionts and intermoult duration in the crab *Bathynectes piperitus*. *Mar. Ecol. Prog. Ser.* 98, 107–113.
- Girishkumar, M.S., Ravichandran, M., McPhaden, M.J., 2013. Temperature inversions and their influence on the mixed layer heat budget during the winters of 2006–2007 and 2007–2008 in the Bay of Bengal. *J. Geophys. Res. Oceans* 118 (5), 2426–2437. <https://doi.org/10.1002/jgrc.20192>.
- Girishkumar, M.S., Ravichandran, M., McPhaden, M.J., Rao, R.R., 2011. Intraseasonal variability in barrier layer thickness in the south central Bay of Bengal. *J. Geophys. Res.* 116, C03009. <https://doi.org/10.1029/2010JC006657>.
- Gómez, Fernando, Wang, Lu, Lin, Senjie, 2018. Morphology and molecular phylogeny of Peritrich ciliate Epibionts on pelagic diatoms: *Vorticella oceanica* and *Pseudovorticella coccinodisci* sp. nov. (Ciliophora, Peritrichia). *Protist* 169 (2), 268–279. <https://doi.org/10.1016/j.protis.2018.03.003>.
- Gómez, F., 2020. Symbioses of Ciliates (Ciliophora) and Diatoms (Bacillariophyceae): taxonomy and host–symbiont interactions. *Oceans* 1 (3), 133–155.
- Grasshoff, Klaus, Kremling, Klaus, Ehrhardt, Manfred (Eds.), 1999. *Methods of Seawater Analysis*. Wiley.
- Green, J.D., Shiel, R.J., 2000. Mobile peritrich riders on Australian calanoid copepods. *Hydrobiologia* 437, 203–221. <https://doi.org/10.1023/A:1026567210125>.
- Gregori, Maria, Fernández-Leborans, Gregorio, Roura, Álvaro, González, Ángel F., Pascual, Santiago, 2016. Description of a new epibiotic relationship (Suctorian–Copepoda) in NE Atlantic waters: from morphological to phylogenetic analyses. *Acta Zool.* 97 (2), 165–176. <https://doi.org/10.1111/azo.2016.97.issue-210.1111/azo.12113>.
- Gutt, Julian, Schickan, Thomas, 1998. Epibiotic relationships in the Antarctic benthos. *Antarct. Sci.* 10 (4), 398–405. <https://doi.org/10.1017/S0954102098000480>.
- Hastenrath, S., Lamb, P.J., 1979. *Climatic Atlas of the Indian Ocean; Part-2*. University of Wisconsin Press, Wisconsin, The Oceanic Heat Budget, p. 104.
- Henebry, M.S., Ridgeway, B.T., 1979. Epizoic Ciliated protozoa of planktonic copepods and cladocerans and their possible use as indicators of organic water pollution. *Trans. Amer. Microsc. Soc.* 98, 495–508. <https://doi.org/10.2307/3225899>.
- Hironi, J., Kadota, S., Takano, H., 1985. Diatom infestation of marine copepods (Review). *Bull. Tokai Reg. Fish. Res. Lab. (Japan)* 117, 37–45.

- Horikami, H., Isii, K., 1981. Cluster inducing factor secreted by *Vorticella* telotroch. In abstract of 6th International Congress on Protozoology, Warsaw. Prog. Protozool. pp. 145.
- Jiang, Y., Yang, E.J., Min, J.O., Kang, S.H., Lee, S., 2013. Using pelagic ciliated microzooplankton communities as an indicator for monitoring environmental condition under impact of summer sea-ice reduction in western Arctic Ocean. Ecol. Indic. 34, 380–390. <https://doi.org/10.1016/j.ecolind.2013.05.026>.
- Jyothibabu, R., Madhu, N.V., Maheswaran, P.A., Jayalakshmy, K.V., Nair, K.K.C., Achuthankutty, C.T., 2008. Seasonal variation of microzooplankton (20–200 µm) and its possible implications on the vertical carbon flux in the western Bay of Bengal. Cont. Shelf Res. 28 (6), 737–755. <https://doi.org/10.1016/j.csr.2007.12.011>.
- Jyothibabu, R., Maheswaran, P.A., Madhu, N.V., Ashraf, T.M., Gerson, V.J., Haridas, P. C., Venugopal, P., Revichandran, C., Nair, K.K.C., Gopalakrishnan, T.C., 2004. Differential response of winter cooling on biological production in the northeastern Arabian Sea and northwestern Bay of Bengal. Curr. Sci. 87, 783–791.
- Kahl, A., 1934. Suctoria. Die Tierwelt der Nord und Ostsee. Lieferung. Teil II c5. 26, 184–226.
- Karsten, G., 1907. Das Indische Phytoplankton nach dem Material der Deutschen Tiefsee-Expedition 1898–1899. Dtsch. Tiefsee-Exped. 1898–1899, 423–548.
- Krasske, G., 1941. Die Kieselalgen des Chilenischen Küstenplanktons. Schweizerbart. Arch. Hydrobiol. 38, 260–287.
- Lukas, R., Lindstrom, E., 1991. The mixed layer of the western equatorial Pacific Ocean. J. Geophys. Res. 96, 3343–3357. <https://doi.org/10.1029/90JC01951>.
- Madhu, N.V., Jyothibabu, R., Maheswaran, P.A., John Gerson, Vijay, Gopalakrishnan, T. C., Nair, K.K.C., 2006. Lack of seasonality in phytoplankton standing stock (chlorophyll a) and production in the western Bay of Bengal. Cont. Shelf Res. 26 (16), 1868–1883. <https://doi.org/10.1016/j.csr.2006.06.004>.
- Madhupratap, M., Gauns, M., Ramaiah, N., Prasanna Kumar, S., Muraleedharan, P.M., de Souza, S.N., Sardesai, S., Muraleedharan, U., 2003. Biogeochemistry of Bay of Bengal: physical, chemical, and primary productivity characteristics of the central and western Bay of Bengal during summer monsoon 2001. Deep Sea Res. Part II 50, 881–886.
- Manca, M., Beltrami, M., Sonvico, D., 1996. On the appearance of epibionts on the crustacean zooplankton of a large subalpine lake undergoing oligotrophication (L. Maggiore, Italy). Mem. Ist. Ital. Idrobiol. 54, 161–172.
- Marshall, S.M., Orr, A.P., 1955. The Biology of a Marine Copepod. Oliver & Boyd, London, p. 195.
- Mignot, J., Lazar, A., Lacarra, M., 2012. On the formation of barrier layers and associated vertical temperature inversions: A focus on the northwestern tropical Atlantic. J. Geophys. Res. 117 (C2), n/a–n/a. <https://doi.org/10.1029/2011JC004735>.
- Mikac, B., Sempucci, F., Guidi, L., Ponti, M., Abbiati, M., Balsamo, M., Dovgal, I., 2019. Newly discovered associations between peritrich ciliates (Ciliophora: Peritrichia) and scale polychaetes (Annelida: Polynoidae and Sigalionidae) with a review of polychaete–peritrich epibiosis. Zool. J. Linn. Soc. zlz111, 20, 1–15. <https://doi.org/10.1093/zoolinnean/zlz111>.
- Mikhailova, Tatiana A., Aristov, Dmitriy A., Naumov, Andrew D., Malavenda, Sergey S., Savchenko, Olga N., Bijagov, Konstantin L., 2019. Diversity and structure of epibenthic communities of the red algae zone in the White Sea. Polar Biol. 42 (5), 953–968. <https://doi.org/10.1007/s00300-019-02488-2>.
- Nagasawa, Sachiko, Warren, Alan, 1996. Redescription of *Vorticella oceanica* Zacharias, 1906 (Ciliophora: Peritrichia) with notes on its host, the marine planktonic diatom *Chaetoceros coarctatum* Lauder, 1864. Hydrobiologia 337 (1–3), 27–36. <https://doi.org/10.1007/BF00028504>.
- Nanjkar, Mandar, Fernandes, Veronica, Bogati, Kalisa, Chatterjee, Tapas, 2019. Gregarious true-colonies of ciliate *Vorticella oceanica* on a chain forming diatom *Chaetoceros coarctatus*: indicating change in the nature of association. Symbiosis 79 (3), 221–229. <https://doi.org/10.1007/s13199-019-00640-4>.
- Noble, A., 1929. Two new species of the protozoan genus *Ephelota* from Monterey Bay California. Univ. Calif. Pub. Zool. 33, 13–26.
- Pane, L., Bonello, G., Mariottini, G.L., 2014. Epibiotic ciliates *Scyphidia* sp. and diatoms on *Tigriopus fulvus* (Copepoda: Harpacticoida) exoskeleton. J. Biol. Res. 87, 66–69.
- Prasanna Kumar, S., Nuncio, M., Narvekar, J., Ramaiah, N., Sardesai, S., Gauns, M., Fernandes, V., Paul, J.T., Jyothibabu, R., Jayaraj, K.A., 2010. Seasonal cycle of physical forcing and biological response in the Bay of Bengal. Indian J. Mar. Sci. 39, 388–405.
- Purushothaman, Jasmine, Bhowal, Aishee, Siddique, Alfisa, Francis, Sanu V., Raghunathan, Chelladurai, 2020. A report on epibionts and new record of two ciliates *Ephelota plana* and *Ephelota gigantea* in the coastal waters of Bay of Bengal, Northern Indian Ocean. Symbiosis 80 (2), 217–230. <https://doi.org/10.1007/s13199-019-00659-7>.
- Rakshesh, M., Raman, A.V., Kalavati, C., Subramanian, B.R., Sharma, V.S., Sunitha Babu, E., Sateesh, Nanduri, 2008. Zooplankton community structure across an eddy-generated upwelling band close to a tropical bay-mangrove ecosystem. Mar. Biol. 154 (6), 953–972. <https://doi.org/10.1007/s00227-008-0991-2>.
- Ramage, C.S., 1971. Monsoon Meteorology. Academic Press, New York, p. 296.
- Rao, R.R., Sivakumar, R., 2003. Seasonal variability of sea surface salinity and salt budget of the mixed layer of the north Indian Ocean. J. Geophys. Res. Oceans. 108, 3009, 9(1–14). <https://doi.org/10.1029/2001JC000907>.
- Rao, Y.R.S., 1999. CS (AR)-2/99-2000: A base line survey of ground water quality in coastal aquifer. Andhra Pradesh, National Institute of Hydrology <http://117.252.14.250:8080/xmlui/handle/123456789/2287>.
- Regali-Selegim, M.H., Godinho, M.J.L., 2004. Peritrich epibiont protozoans in the zooplankton of a subtropical shallow aquatic ecosystem (Monjolino reservoir, São Carlos, Brazil). J. Plankton Res. 26, 501–508. <https://doi.org/10.1093/plankt/fbh055>.
- Rovira, L., Trobajo, R., Ibáñez, C., 2012. The use of diatom assemblages as ecological indicators in highly stratified estuaries and evaluation of existing diatom indices. Mar. Pollut. Bull. 64 (3), 500–511. <https://doi.org/10.1016/j.marpolbul.2012.01.005>.
- Russell, D.J., Norris, R.E., 1971. Ecology and taxonomy of an epizooic diatom. Pacif. Sci. 25, 357–367.
- Sabu, P., Devi, C.A., Lathika, C.T., Sanjeevan, V. N., Gupta, G.V.M., 2015. Characteristics of a cyclonic eddy and its influence on mesozooplankton community in the northern Bay of Bengal during early winter monsoon. Environ. Monit. Assess. 187, 330 (1–19). <https://doi.org/10.1007/s10661-015-4571-x>.
- Sahu, G., Panigrahi, S., Mohanty, A.K., Achary, M.S., Samantara, M.K., Bramha, S.N., Satpathy, K.K., Dovgal, I.V., 2015. New record of an epizooic diatom, *Pseudohimantidium pacificum* on two species of copepods from the Indian Ocean. Indian J. Mar. Sci. 44, 1331–1334.
- Sawyer, Thomas K., MacLean, Sharon A., Ziskowski, John, 1976. A report on *Ephelota* sp. (Ciliata, Suctorida) as an epibiont on the gills of decapod crustaceans. Trans. Amer. Micros. Soc. 95 (4), 712. <https://doi.org/10.2307/3225398>.
- Shaik, A.R., Biswas, H., Babu, N.S., Reddy, N.P.C., Ansari, Z.A., 2017. Investigating the impacts of treated effluent discharge on coastal water health (Visakhapatnam, SW coast of Bay of Bengal, India). Environ. Monit. Assess. 189, 643. <https://doi.org/10.1007/s10661-017-6344-1>.
- Shaik, A.R., Biswas, H., Reddy, N.P.C., Rao, S.V., Bharathi, M.D., Subbaiah, Ch.V., 2015. Time series monitoring of water quality and microalgal diversity in a tropical bay under intense anthropogenic interference (SW coast of the Bay of Bengal, India). Environ. Impact Assess. Rev. 55, 169–181. <https://doi.org/10.1016/j.eiar.2015.08.005>.
- Sherr, Evelyn B., Sherr, Barry F., 1987. High rates of consumption of bacteria by pelagic ciliates. Nature 325 (6106), 710–711.
- Shetye, S.R., Gouveia, D., Shankar, D., Shenoi, S.S.C., Vinayachandran, P.N., Sundar, D., Michael, G.S., Nampoothiri, G., 1996. Hydrography and circulation in the western Bay of Bengal during the northeast monsoon. J. Geophys. Res. Oceans. 101 (C6), 14011–14025. <https://doi.org/10.1029/95JC03307>.
- Strickland, J.D.H., Parsons, T.R., 1972. A practical handbook of seawater analysis. Fish. Res. Board Canada Bulletin. 157, 2nd Ed., 310 pp.
- Sundaray, Sanjay Kumar, Panda, Umesh Chandra, Nayak, Binod Bihari, Bhatta, Dinabandhu, 2006. Multivariate statistical techniques for the evaluation of spatial and temporal variations in water quality of the Mahanadi river–estuarine system (India) – a case study. Environ. Geochem. Health 28 (4), 317–330. <https://doi.org/10.1007/s10653-005-9001-5>.
- Susetiono, P., 2006. Epibiosis *Thecacinetia calix* (Protozoa, Ciliophora) pada meiofauna *Paradesmodora* sp. (Nematoda, Desmodoridae) dari perairan Indonesia. Oceana 31, 41–49.
- Tazioli, Silvia, Di Camillo, Cristina Gioia, 2013. Ecological and morphological characteristics of *Ephelota gemmipara* (Ciliophora, Suctoria), epibiontic on *Eudendrium racemosum* (Cnidaria, Hydrozoa) from the Adriatic Sea. Eur. J. Protistol. 49 (4), 590–599. <https://doi.org/10.1016/j.ejop.2013.04.006>.
- Thadathil, Pankajakshan, Gopalakrishna, V.V., Muraleedharan, P.M., Reddy, G.V., Araligidat, Nilesh, Shenoy, Shrikant, 2002. Surface layer temperature inversion in the Bay of Bengal. Deep Sea Res. Part I: Oceanogr. Res. Pap. 49 (10), 1801–1818. [https://doi.org/10.1016/S0967-0637\(02\)00044-4](https://doi.org/10.1016/S0967-0637(02)00044-4).
- Thadathil, P., Muraleedharan, P.M., Rao, R.R., Somayajulu, Y.K., Reddy, G.V., Revichandran, C., 2007. Observed seasonal variability of barrier layer in the Bay of Bengal. J. Geophys. Res. Oceans. 112, C02009. <https://doi.org/10.1029/2006JC003651>.
- Thadathil, Pankajakshan, Suresh, I., Gautham, S., Prasanna Kumar, S., Lengaigane, Matthieu, Rao, R.R., Neetu, S., Hegde, Akshay, 2016. Surface layer temperature inversion in the Bay of Bengal: main characteristics and related mechanisms. J. Geophys. Res. Oceans. 121 (8), 5682–5696. <https://doi.org/10.1002/2016JC011674>.
- Utz, L.R.P., Coats, D.W., 2005. Spatial and temporal patterns in the occurrence of Peritrich ciliates as Epibionts on Calanoid copepods in the Chesapeake Bay. USA. J. Eukaryot. Microbiol. 52, 236–244. <https://doi.org/10.1111/j.1550-7408.2005.00025.x>.
- Utz, L.R.P., Coats, D.W., 2008. Telotroch formation, survival, and attachment in the epibiotic peritrich *Zoothamnium intermedium* (Ciliophora, Oligohymenophorea). Invertebr. Biol. 127, 237–248. <https://doi.org/10.1111/j.1744-7410.2008.00140.x>.
- Wahl, M., 1989. Marine epibiosis. I. Fouling and antifouling – some basic aspects. Mar. Ecol. Prog. Ser. 58, 175–189.
- Wahl, M., 2009. Epibiosis: ecology, effects and defences. In: Wahl, M., (Ed.), Marine hard bottom communities. Ecol. Stud. Ser. 206. Berlin, Heidelberg: Springer-Verlag, pp. 61–72.
- Wang, Z., Xu, G., Yang, Z., Xu, H., 2016. An approach to determining homogeneity of body-size spectrum of biofilm-dwelling ciliates for colonization surveys. Ecol. Indic. 61, 865–870. <https://doi.org/10.1016/j.ecolind.2015.10.039>.
- Weissman, Penny, Lonsdale, Darcy J., Yen, Jeannette, 1993. The effect of peritrich ciliates on the production of *Acartia hudsonica* in Long Island Sound. Limnol. Oceanogr. 38 (3), 613–622. <https://doi.org/10.4319/lo.1993.38.3.0613>.