

## **Interactions between trophic levels in upwelling and non-upwelling regions during summer monsoon**

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### **Abstract**

Coastal upwelling is a regular phenomenon occurring along the southwest coast of India during summer monsoon (May-September). We hypothesise that there could be a shift in environmental parameters along with changes in network of interactions between bacteria, phytoplankton, and zooplankton in upwelling and non-upwelling regions. During cruise # 267 on FORV Sagar Sampada, water samples were analysed for environmental and biological parameters from two transects, one upwelling region off Trivandrum (TVM) (8°26'N,76°20'E-8°30'N,76°50'E), and the other non-upwelling region off Calicut (CLT) (11°11'N,75°30'E-11°14'N,74°54'E), about 230 nmi to the north. Meteorological, hydrological, and nutrient profiles confirmed upwelling off TVM. Bacteria, phytoplankton and zooplankton significantly responded. Primary and bacterial productivity enhanced together with increase in the percentage of viable bacteria (TVC). Pearson's correlation analysis pointed out the differences in bacterial interactions with other trophic levels at both transects. TVC played a prominent role in trophic interactions off TVM by depending on phytoplankton for substrate ( $r=0.754$ ). This contrasted with CLT where total counts (TC) played an important role. However, most interrelationships were less pronounced. Principal component analysis (PCA) confirmed the correlation analysis and further showed that the factor loadings of the biotic and abiotic parameters differed in strength and direction in the two regions. More importantly, the processes of mineralization by bacteria and uptake by phytoplankton are obviously more coupled off TVM as evidenced by the clustering of the related parameters in the PCA biplot. Canonical correspondence analysis also complements these findings and demonstrated that the abiotic factors influenced phytoplankton and bacteria, differently – inversely and definite at TVM and more diverse and varied at CLT. The impact on the trophic interrelationships is evident by the close association between all the variables in upwelling waters. Besides, bacteria may represent a more stable element in the food web, TVC for upwelling region and TC for non-upwelling region.

### **Keywords**

upwelling; phytoplankton; zooplankton; bacteria; network of interactions; West coast of India

## 1. Introduction

Physical forcings such as ocean currents, winds and river influx introduce varying complexities in the interlinkages between biotic components and environmental characteristics especially in the coastal waters. Wind-driven coastal upwelling is one such forcing that has been acknowledged to change the associated regional ecology (Chen et al., 2004; Wetz and Wheeler, 2004; Tweddle et al., 2010). Hence, biotic variables such as phytoplankton and bacteria which forms the basis of marine food web (Sherr and Sherr, 1988) are affected. Upwelling of nutrient-rich subsurface waters increases primary producers followed by an increase in metazoan standing stocks (Peterson et al., 1988).

Upwelling, caused by oceanic winds blowing from the southwest during early summer monsoon, is a regular phenomenon occurring between May-September in the Southeast Arabian Sea (SEAS) along the southwest coast of India. The upwelling activity that propagates from southern peninsula of India to the north due to an east boundary current known as West India Coastal Current (WICC) has been well documented (Shetye and Shenoi, 1988; Luis and Kawamura, 2004; Joshi and Rao, 2012; Thomas et al., 2013). Upwelling in SEAS is of moderate intensity and could be graded between the least intense New Zealand and highly intense Benguela and Humboldt Current (Verlecar, 2001; Patti et al., 2008; Carr, 2002; Blanchette et al., 2009). Moreover, upwelling of cold nutrient-rich subsurface waters enhances primary productivity in the area, which otherwise is characterized by nutrient depleted waters and low biological productivity (Packard et al., 1984; Madhupratap et al., 1990; Bhattathiri et al., 1996; Thomas et al., 2013).

Much of the literature on upwelling ecosystems address the cascading effect of physical and chemical processes, and biological responses at different trophic levels, during upwelling (Margalef, 1978; Blasco et al., 1980; Oleg et al., 2003; Lehmann and Myrberg, 2008; Blanchette et al., 2009; Pei, 2009; Schukat et al., 2014), with few publications on the bacterial contribution during the process (Kirchman et al., 2000; Wetz and Wheeler, 2004; Hyun et al., 2009; Capone and Hutchins, 2013). Bacteria play a mediating role in a spectrum of biogeochemical processes that decide the status of an ecosystem (Madsen, 2011). However, the interactions between abiotic and biotic variables and between different trophic levels which form the basis for the maintenance of balance in an upwelling region, is poorly understood.

The primary goal of this study was to discern the interlinkages between the trophic levels in upwelling and non-upwelling regions during summer monsoons. We therefore hypothesise that shift in environmental parameters was accompanied by the changes in “network of interactions” between trophic levels in upwelling and non-upwelling regions especially at the bacterial level. In this study,

the term “network of interactions” refers to the web of statistically significant interlinkages between different biotic variables.

Therefore, in this study, a dataset comprising of biological and environmental parameters from coastal pelagic regions with (Trivandrum) and without (Calicut) signatures of upwelling were examined and the trophic interactions were analyzed. Trivandrum is located towards the southern tip of India at ~8.3°N while Calicut lies approximately 230 nautical miles towards the north at 11.2°N. For the first time, the study highlights how bacteria wield considerable influence on higher trophic levels in upwelling system thus indirectly yet significantly augmenting and sustaining the productivity of upwelling areas.

## **2. Material and methods**

### **2.1 Study area**

Sampling was carried out along the Southwest coast of India in SEAS onboard FORV Sagar Sampada between 30th May – 15th June 2009 (Fig. 1). Two transects were chosen. An upwelling region off Trivandrum (TVM) located towards the southern tip of India at 8°26'N 76°20'E - 8°30'N 76°50'E and a non-upwelling region, off Calicut (CLT) located approximately 230 nautical miles north off TVM at 11°11'N 75°30'E - 11°14'N 74°54'E. Both sites are relatively unaffected by rivers, estuaries or harbours.

### **2.2 Physical forcings**

Wind and meteorology data were collected by the automated weather station, onboard. Salinity and temperature measurements were derived from the Sea Bird CTD attached sensors. The sea surface temperature (SST) was plotted using the blended Tropical Rainfall Measuring Mission (TRMM) Microwave Imager (TMI) and Advanced Microwave Scanning Radiometer (AMSR-E). SST daily dataset was at 0.25° x 0.25° spatial resolution

([http://www.ssmi.com/sst/microwave\\_oi\\_sst\\_data\\_description.html](http://www.ssmi.com/sst/microwave_oi_sst_data_description.html)).

### **2.3 Water sample collection and processing**

Water samples were collected at discrete depths from ten litre Niskin bottles attached to a CTD-rosette system (Fig. 1, Table 1).

#### **2.3.1. Chemical analyses**

The collection bottles for chemical analyses were acid washed (1 M HCl), rinsed thrice with Milli-Q water and completely dried before use. These bottles were also rinsed with sample before

collection. Water samples for dissolved oxygen (DO) were collected in 125 mL stoppered glass bottles without trapping air bubbles, fixed with Winkler's reagents and estimated according to Strickland and Parsons (1965) using a dosimeter (Metrohm 785 DMP Titrino). Samples for nutrient analysis such as nitrate, nitrite, phosphate, silicate and ammonia were collected in 125 mL HDPE bottles. Estimation of nitrate, nitrite, phosphate and silicate was carried out using an autoanalyzer (SKALAR) as described by Wurl (2009). Ammonia was estimated manually according to Grasshoff (1983). For the estimation of particulate organic matter (POM) in the form of particulate organic carbon (POC) and particulate organic nitrogen (PON), one litre sample was filtered on to pre-combusted (450 °C, 4 h) 0.7- $\mu\text{m}$  Whatman GF/F glass fibre filters. The filters were exposed to HCl fumes and dried at 60°C. Analysis was done using a CHN analyzer (Perkin-Elmer 240-C). Total suspended matter (TSM) was determined gravimetrically by filtering the water samples on to pre-weighed Millipore 0.22- $\mu\text{m}$  polycarbonate filters (Krey, 1964).

### 2.3.2 Biological analyses

Water samples for adenosine triphosphate (ATP) were filtered through sterile 0.22- $\mu\text{m}$  polycarbonate filters (Millipore) and extracted in boiling tris-buffer for 5 min. Extracts were measured with luminometer (BMG Labtech Luminometer, Lumistar Optima) using the luciferin-luciferase reaction (Holm-Hansen and Booth, 1966; Parsons et al., 1984). For determining total bacterial counts (TC), 5 mL water sample was immediately fixed with formaldehyde (2.5% final concentration) and stored at 4°C until analysis. For total bacterial viable counts (TVC), samples were processed according to Kogure et al. (1979). Both TC and TVC fixed water samples were stained for 5 min with acridine orange (final concentration 1%) and filtered on 0.2- $\mu\text{m}$  Millipore black nucleopore membrane filters (Hobbie et al., 1977). Cells were counted by epifluorescence microscope (Olympus Fluorescent Microscope Model BX61). Abundance of total heterotrophic bacteria (THB) was estimated from the colony forming units (CFU) retrieved on nutrient agar plate of 0.1% nutrient strength (100% corresponds to 8 g L<sup>-1</sup> nutrient broth with 1.5% agar-agar from Himedia Laboratories Pvt Ltd, Mumbai, India) prepared using 50% aged, pre-filtered seawater (Goltekar et al., 2006). Bacterial productivity (BP) was determined by the incorporation of tritiated thymidine (<sup>3</sup>H-TdR) into bacterial DNA (Fuhrman and Azam, 1982; Smith and Azam, 1992). An aliquot of 1.5 mL sample was collected in Eppendorf tubes in triplicates and incubated under *in situ* conditions in the dark for 1h with 10 nM final concentration of <sup>3</sup>H-TdR (specific activity = 6364 Bq mM, Bhabha Atomic Research Centre, Mumbai). The <sup>3</sup>H-TdR incorporation reaction was stopped by addition of 5% trichloroacetic acid (TCA) and the tubes were incubated for 30 min at 18°C. Tubes were centrifuged at 16,000 rpm for 10 min and the supernatant was discarded. Addition of TCA and centrifugation was repeated twice followed by the addition of 500  $\mu\text{L}$  of scintillation cocktail to the tubes. Radioactivity was measured in a Liquid Scintillation Counter (Beckman Coulter, USA, Model No.

LS6500) with external standards. Experiments carried out to measure the kinetics of uptake showed that isotopic dilution was negligible when using 10 nM thymidine.

BP was calculated in moles of 3H-TdR using the following formula

$$3\text{H-TdR (pM kg}^{-1} \text{ h}^{-1}) = (\text{DPM}/2200) - (1000/V) * (1/\text{SA}) * (60/T)$$

where 3H-TdR is tritiated thymidine, DPM is disintegration per minute of sample/blank, V is the extraction volume (1.5 mL), SA is the specific activity of added 3H-TdR (6364 Bq mM) and T is the incubation time (1 h).

BP incorporated into DNA, was converted into the number of bacterial cells produced by applying a conversion factor ( $1.96 \times 10^{18}$  cells  $\text{M}^{-1}$ ) (Pradeep Ram et al., 2007) and to carbon by using a conversion factor,  $2 \times 10^{-14}$  g C cells $^{-1}$  (Lee and Fuhrman, 1987).

For chlorophyll a (Chl-a) and phaeophytin (phaeo) estimation, 1 l of water sample was filtered using 0.7- $\mu\text{m}$  glass fibre filters (Whatman GF/F). Filters were extracted in 10 mL of 90% acetone for 24 h at 4°C in the dark and centrifuged at 5000 rpm. Concentrations were determined using a Turner Designs 10AU fluorometer (Yentsch and Menzel, 1963). Samples for phytoplankton abundance (PhytoA) were collected in 250 mL bottles, fixed using Lugol's iodine (1% w/v) and formaldehyde (3% final concentration). The sample was concentrated to 20 mL using the settling and siphoning method (Utermohl, 1958). One mL of the aliquot was placed on a Sedgewick-Rafter plankton counting chamber and examined under an inverted microscope (Olympus IX51). Cells were identified according to taxonomic keys (Subrahmanyam, 1946; Tomas, 1997). The Shannon index ( $H'$ ) of diversity was calculated using the Primer 6 software. Primary productivity (PP) was measured following "in situ incubation" of water samples with  $^{14}\text{C}$ -labelled carbon at a fixed station (Station 2) off TVM and off CLT following the JGOFS protocol (JGOFS Report No. 6, 1990) using the light and dark bottle method. Briefly, aliquots of water samples from discrete depths were collected in 300 mL polycarbonate bottles (Nalgene, Germany) in triplicates for light and duplicates for dark incubation. One ampoule of  $\text{NaH}^{14}\text{CO}_3$  (Board of Radiation and Isotope Technology, Mumbai; Specific activity 185 kBq) was injected into each bottle and incubated *in situ* for 12 h from dawn to dusk using a mooring system. After incubation, samples were filtered through glass fibre filters (Whatman GF/F, 0.7  $\mu\text{m}$  pore size) and transferred to scintillation vials. The filters were exposed to 0.5 N HCl fumes overnight in a closed container to remove any inorganic  $^{14}\text{C}$  adhering to samples. Five mL scintillation cocktail (Sisco Research Laboratory, Mumbai) was added to each vial and the radioactivity was measured in a liquid scintillation counter (Beckman Coulter, USA, Model No. LS6500). An internal standard was used for applying appropriate corrections and counts were quench-corrected prior to determination. Integrated PP values were used.

#### **2.4. Mesozooplankton sample collection and estimation**

Mesozooplankton (MZP) samples were collected in a vertical haul from near bottom to the surface at different depth intervals using a Multiple Plankton Closing Net (MPN-Hydro Bios, mouth area 0.25 m<sup>2</sup>, mesh size 200 µm, Table 1b). The number of depths sampled at each station is dependent on the depth of the station ranging from two depths at 30 m station to four depths at 450 m station. MZP biomass was estimated before preservation by the conventional displacement volume method, wherein concentrated samples were blotted on absorbent paper. The displaced volume was then measured in a graduated cylinder and converted to dry weight using a factor of 0.075 g dry wt. mL<sup>-1</sup> and to carbon as 34% of the dry weight. MZP samples for MZP abundance were preserved in 4% buffered seawater-formalin (Madhupratap et al., 1981; Nair et al., 1999). Samples were split using Folsom plankton splitter, and one aliquot was enumerated for qualitative and quantitative analysis of zooplankton groups. Groups were counted using Bogorov counting chamber and stereo zoom microscope (Nikon SMZ1000, 10X magnification) and identified (Kasturirangan 1963; Todd et al., 1966; Conway et al., 2003).

#### **2.5. Benthic fauna collection and analysis**

Sediment samples were collected using a Smith-McIntyre grab operated at the near-shore stations (Station 1, 2, 3). Replicate sub-sampling of >5 was done using a 15x15x10 cm size quadrant and sieved through 300-µm mesh screen (Ingole et al., 2010). Samples were fixed and preserved using neutral formalin-Rose Bengal solution. The fixed samples were re-washed and sorted in the shore laboratory. Specimens were identified up to the lowest possible taxa under a stereo zoom microscope (Nikon SMZ1000, 10X magnification) and biomass was determined by wet weight method after blotting. The average (avg.) number of organisms of the replicate samples was converted to individuals (ind) m<sup>-2</sup> and biomass (shell on) was estimated as wet weight (mg m<sup>-2</sup>).

#### **2.6. Statistical analysis**

Biological data was log(x+1) transformed for statistical analysis. Analysis of variance (ANOVA) was carried out to indicate significant variation between the two study locations. Pearson's rank correlation was done to project one to one relationships that were causal or covaried. Partial correlation in which the effect of depth was removed for each variable was done simultaneously to elucidate the effect of depth on other variables. Correlations between biological and environmental parameters were analyzed using Statistica version 6.0. Flow diagrams representing significant relationships were illustrated using Cytoscape 2.7.0. Since a single factor cannot represent all the factors that contribute to the physicochemical character of a location, multivariate analyses – Principal Component Analysis (PCA) was performed using PRIMER version 6. Combined influence

of parameters (both biotic and abiotic) that group together as components on the region became evident and revealed the extent of similarities and differences between the two locations. Further, Canonical Correspondence Analysis (CCA, Multivariate Statistical Package, Kovacs Computing Services) was done to resolve the effect of each abiotic variable on all the biotic variables. In this analysis, eigen values measured the separation of biotic variable along the linear combination of environmental variables; cumulative constrained percentage gave the total variation explained by the axes; and variable-environment correlation is the total explained variance (Ter Braak, 1987). In the biplot diagram, arrows point in the direction of increasing values of each environmental variable. The length of the arrows indicates the degree of correlation with the represented axes. The independent variables of CCA were temperature, salinity, pH, DO, ammonia, nitrates, nitrites, phosphates, silicates and TSM. The dependent variables considered were POC, PON, TC, TVC, THB, BP, Chl a, phaeo, MZPa, MZPb and ATP ???

### 3.0 Results

#### 3.1. Meteorological, physical, chemical and biological parameters

The environmental parameters measured during the study period are shown in Table 2.

##### 3.1.1 Trivandrum transect

Wind speed and air temperature along the TVM coast ranged between 0.1-8.1 m s<sup>-1</sup> and 23-31.9°C, respectively (data not shown). SST towards the coast at 76°50'E was 25°C and nearly 3°C lower than the offshore waters (Fig. 2b). The concentration of ammonium, nitrate, nitrite, phosphate and silicate ranged between ND (non detectable levels)-0.7, 0.02-37.4, ND-0.8, 0.1-5.6 and 0.7-31.4 µM, respectively (Table 2). The average surface concentration of nitrate, silicate and phosphate off TVM was 3.2, 2.0, 0.5 µM, respectively. The 24 µM nitrate, 2 µM phosphate and 12 µM silicate contour lines noticeably moved towards the surface near the coast (Fig. 3c,i,k). A subsurface peak of 0.7 µM ammonia concentration was evident at around 75 m depth (Fig. 3g). POC and PON ranged between 2.4-76.7 µM and 0.9-11.3 µM, respectively (Table 2). The POC concentration in the euphotic zone at the near-shore stations was nearly 50 µM (fig not shown). The average ATP concentration was 3.2 ± 2.1 ng L<sup>-1</sup>. Average TC was 2.6±0.9 x 10<sup>8</sup> cells L<sup>-1</sup> and decreased with depth (Fig. 4, Table 2). The TVC fraction was 34% of the TC while THB was 7% (Table 2). BP averaged at 3.9 ± 6.1 (pM kg<sup>-1</sup> h<sup>-1</sup>) while PP measured at a near-shore station was 950 mgC m<sup>-2</sup> d<sup>-1</sup>. Average Chl-a, PhytoA and H' was 2.0 µg L<sup>-1</sup>, 1.4 x 10<sup>5</sup> cells L<sup>-1</sup> and 2.954, respectively. Diatoms constituted about 98% of the PhytoA followed by dinoflagellates at 2%. *Nitzschia* and *Chaetoceros* spp. comprised the major genera. MZP abundance and biomass ranged between 1-50 x10<sup>4</sup> individuals 100 m<sup>-3</sup> and 0.3-11.2 mL 100 m<sup>-3</sup>, respectively. *Copepods* dominated MZP population.

Other groups included *Chaetognaths*, *Copepod nauplii* and *Oikopleura*. The average macrofauna abundance and biomass was  $4.3 \times 10^3$  individuals  $m^{-2}$  and  $290 \text{ mg } m^{-2}$  (Table 2). Annelid polychaetes and crustaceans formed the major components of benthic fauna.

### 3.1.2 Calicut transect

Variation in wind speed was lower than off TVM at  $0.2\text{-}7.4 \text{ m s}^{-1}$  but air temperature was higher and ranged between  $23.6\text{-}33.2^\circ\text{C}$ . SST values ranged between  $28\text{-}29^\circ\text{C}$  with no noticeable variation between the near-shore and offshore region (Fig. 2c). Moreover, the vertical structure of the water column showed the  $29^\circ\text{C}$  isotherm extending from the surface to 20 m bss. Generally, the concentrations of ammonium, nitrate, nitrite, phosphate, silicate, POC and PON along with ATP were lower than off TVM (Table 2). TVC fraction was lower than off TVM and formed only 17% of TC (avg.  $4.2 \pm 1.3 \times 10^8$  cells  $L^{-1}$ ) and THB formed 5% (Table 2). Similarly, average BP ( $3.3 \pm 1.8 \text{ pM kg}^{-1} \text{ h}^{-1}$ ), integrated PP ( $62 \text{ mg C } m^{-2} \text{ d}^{-1}$ ), Chl-a (avg.  $0.3 \mu\text{g } L^{-1}$ ) and PhytoA (avg.  $9.8 \times 10^3$  cells  $L^{-1}$ ) were low compared to off TVM. However,  $H'$  was 3.211. Diatoms contributed to 81% of PhytoA followed by cyanobacteria at 13%, dinoflagellates at 2% and others at 4%. The dominant genera included *Chaetoceros*, *Pseudonitzschia*, *Guinardia*, *Nitzschia* and *Navicula*. MZP abundance and biomass ranged between  $0.2\text{-}16.9 \times 10^4$  individuals  $100 \text{ m}^{-3}$  and  $0.08\text{-}3.8 \text{ mL } 100 \text{ m}^{-3}$ , respectively. As in transect off TVM, *Copepods* dominated the MZP population off CLT. Other groups included *Chaetognaths*, *Copepod nauplii* and *Oikopleura*. The average macrofauna abundance and biomass was  $3.0 \times 10^3$  individuals  $m^{-2}$  and  $251 \text{ mg } m^{-2}$  (Table 2).

## 3.2 Statistics: Network of interactions functioning in each region

Analysis of variance analysis (ANOVA: single factor) of about 50% of the parameters measured demonstrated significant differences between the upwelling and non-upwelling region ( $p \leq 0.05$ , Table 2).

### 3.2.1 Trivandrum transect

Pearson's correlation showed that distribution of nitrate, silicate and phosphate was depth dependent ( $p \leq 0.001$ , Table 1a Appendix), despite the evidence of upward shoaling of nutrients (Fig. 2). Not surprisingly, the biological parameters varied negatively with depth. DO and macronutrients significantly governed TVC, Chl-a, phytoplankton, and zooplankton parameters ( $p \leq 0.01$ ), but did not correlate with TC. Nitrite, POC and PON related positively to TVC. Salinity, temperature and pH varied positively with Chl-a concentration and PhytoA. These parameters in turn were responsible for the variation in POC and PON concentrations ( $p \leq 0.001$ ). Similarly, TC and TVC followed the trend in Chl-a concentration and PhytoA and corresponded with variation in POC and PON

concentrations. PhytoA and Chl-a strongly related with each other, and Chl-a governed the distribution of THB, and BP. Chl-a, PhytoA and TVC also interacted with the distribution of MZP.

When parallel analysis was done i.e. partial correlation in which the effect of depth was removed for each variables, some new relationships emerged, for example, between salinity and nitrite, PON, Chl-a, phaeo and PhytoA (Table 2a). However, some interrelationships changed, for example, relationship between TVC and PhytoA became stronger. Yet others remained almost same, as with Chl-a and BP, Chl-a and THB, TVC and BP. Fig. 5a illustrates the relationships before and after removing the effect of depth. The latter is shown in parentheses.

While linear regressions were able to delineate the extent of interactions between variables, PCA aggregated the variables into 3 major composite variables with a cumulative variation of ~71%. PC1 explained 48% of the total variance (Table 3). The important variables with negative loadings >0.2 that correlate with PC1 were temperature, pH, DO, PON, POC, Chl-a, Phaeo, PhytoA, MZPa, MZPb and TVC. However, nitrate, silicate and phosphate showed positive loadings (Fig 6a). PC2 explained 13% of the total variance. It correlated positively with salinity, nitrite, TSM, PON, Chl-a, Phaeo, TVC and BP with factor loadings of >0.2 and negatively with MZPb and MZPa (Fig 6a). PC3 correlated negatively with nitrite and ammonia with factor loadings of >0.3 (Fig 6b). Only ATP, THB and BP were positively influenced by this component with factor loadings >0.3. Salinity, Chl-a, phaeo, PON, POC, nitrite, TC, TVC, THB, and BP grouped tightly in quadrant I (QI), phosphate, nitrate and silicate in QII. In QIV, temperature, pH and DO associated with each other closely and distantly with MZP and ammonia (Fig. 6a). In contrast, in fig 6b, tight clustering was noticed only between POC, PON, Chl-a, MZPb and TC in QI. The clustering between phosphate, nitrate and silicate was stronger in fig 6a than 6b. PCA analysis distinctly shows the lack of influence or response of ATP to other variables (Fig 6a, 6b).

In contrast to PCA analysis, CCA delineated the effect of abiotic variables on biotic parameters. The first 2 axis explained 99.8% of the cumulative percentage variance of biotic–environment relation. The first CCA axis (eigen value = 0.011) alone modelled 93.8% of the total explained variance (0.970) (Table 4). CCA ordination diagrams showed that TC and PhytoA clustered on the opposite side of the ordination plot (Fig. 7a). Nitrate, silicate and phosphate was positively associated with TC, TVC and phytoplankton. POC, PON, phaeo, Chl-a, temperature and nitrite related negatively with bacterial and PhytoA parameters.

### **3.2.2 Calicut transect**

Pearson's correlation showed that distribution of most of the parameters was depth dependent ( $p \leq 0.001$ , Table 1a Appendix). Moreover, DO and macronutrients significantly correlated with TC,

Chl-a, phytoplankton, and zooplankton parameters ( $p \leq 0.01$ ) but not with TVC. Ammonia related positively to TC. POC and PON concentrations significantly varied with Chl-a and PhytoA ( $p < 0.001$ ), but not with TC and TVC. However, Chl-a influenced only TC and THB among the bacterial components (Fig. 5b). MZP was strongly associated with Chl-a concentration ( $r > 0.7$ ) (Fig 5b). Partial correlation analysis done after effect of depth was removed showed that the intensity of relationship with salinity and ammonia, nitrate and silicate becomes less strong and therefore less significant (Table 2a appendix). Surprisingly, other relationships between bacteria and higher trophic levels generally disappeared (Fig 5b)

Other statistical analysis like PCA showed that PC1 accounts for 49% of the total variance (Table 3). It showed high positive loadings of  $> 0.2$  on temperature, pH, DO, PON, POC, Chl-a, PhytoA, MZP, and TC. However, nitrate, silicate and phosphate showed negative loadings (Fig 6c). PC2 explained  $\sim 12\%$  of the total variance. The positive loadings were nitrite, TSM, PON, phaeo and BP and negative loadings were DO and TC. Nitrite showed the highest positive loading of 0.531 (Fig 6c). PC3 explained  $\sim 8.5\%$  of the total variance with ammonia showed the highest positive loading of 0.526 and ATP negative at -0.436 (Table 3, Fig 6d). The nutrients phosphate, nitrate and silicate were closely associated in QI (Fig. 6c). In QII, the variables Chl-a, phytoplankton, MZPb, MZPa were closely associated, whereas nitrite, TSM, phaeo, BP, TVC, ammonia, salinity, POC and PON were loosely associated. In Q3, the variables, TC, THB, temperature, pH and DO were loosely associated (Fig 6c). Also, nutrients clustered together in fig 6d. TSM, phaeo, MZPa, Chl-a, THB, MZPb clustered together in QIII and ammonia, BP, salinity, TC, PhytoA, PON, POC, scattered in QII (Fig 6d).

Using CCA plots, the cumulative influence of environmental parameters on biotic variables indicated that the first two axes explained only  $\sim 92\%$  of variance. TC positively influenced silicate and phosphate and negatively ammonia and POC (Fig. 7b). Conversely, TVC positively interacted with ammonia, and negatively with salinity, POC, PON, phosphate, nitrate and silicate. None of the abiotic components wielded any influence on the PhytoA parameters.

#### **4. Discussion**

Upwelling is an important process primed by physical forcing (Luis and Kawamura, 2004). This physical forcing brings about a dynamic change in the chemical properties which favor different responses in phytoplankton and zooplankton. Hence, it is important to understand the interlinkages between the biotic variables in upwelling regions. Examining non-upwelling regions as a reference could elucidate the extent of influence of this phenomenon. Given these environmental conditions, what would be the bacterial contribution to the network of interactions and maintenance of homeostasis?

#### 4.1. Meteorological, physical, chemical and biological parameters

The meteorological variables suggested the arrival of the SWM off TVM but were untraceable off CLT. The near-shore SST off TVM was 2 °C lower than the off CLT waters and there was notable shoaling of the isotherms towards the TVM coast. Such discernible differences were not evident off CLT. Previous studies have recorded that the shoaling of isotherms indicated the presence of coastal upwelling (Shetye et al., 1990; Muraleedharan and Kumar, 1996; Naidu et al., 1999; Luis and Kawamura, 2003). For the current study period, the occurrence of upwelling off TVM has already been reported (Thomas et al., 2013).

The average values of chemical parameters such as nitrate, phosphate, silicate, PON and POC off TVM were ~19, 38, 50, 50 and 160 % higher than those off CLT (Table 2). Such high nutrient and POM concentration in upwelled waters is consistent with earlier reports (Barange et al., 1991; de Souza et al., 1996; Kumar et al., 2000; Luis and Kawamura, 2004). In response to the physical signatures and shifts in the chemical concentrations, the biological responses were quite evident. As expected, the ATP concentration was 60% higher in the upwelling region off TVM than off CLT. Besides, the average BP was twice higher off TVM than off CLT. However, at both locations, the average TC, TVC and THB were in the order of  $10^8$  cells

$L^{-1}$ ,  $10^7$  cells  $L^{-1}$ , and  $10^7$  cells  $L^{-1}$ , respectively (Table 2). The total bacterial abundance observed in this study is in the range previously reported in upwelling waters (Barbosa et al., 2001; Gauns et al., 2005). The fraction of TVC to TC was 34% off TVM and 17% off CLT, while the fraction of THB to TC was 7% off TVM and 5% off CLT (Table 2). This high retrievability could be linked to the ambient TOC concentration especially off TVM. Furthermore, Amann et al. (1995) have compiled data on culturability which suggested that ambient concentration of organic carbon could decide the extent of culturability. The higher count of heterotrophic bacteria in the upwelling region could be due to the higher PhytoA (avg.  $136 \times 10^3$  cells  $L^{-1}$ ) and higher availability of POC (avg.  $\sim 22 \mu M$ ). In upwelling areas, bacterioplankton generally respond to augmented primary production demonstrating the dependence of bacterioplankton on phytoplankton-derived organic carbon (Kirchman et al., 1995; Tenore et al., 1995; Wiebinga et al., 1997; Hyun et al., 2009). Such dependence has been noticed in the present study, particularly off TVM.

Chl-a and PP was ~60x (x=times) and 150x higher off TVM again corroborating with the physical and chemical signatures. Off TVM, Chl-a concentration averaged at  $2.0 \mu g L^{-1}$ . Comparison of this estimated Chl-a concentration of WICC along with other upwelling regions, worldwide, showed that Chl-a concentration off TVM was low compared to the upwelling region of Benguela current off southwest Africa ( $3.4 \mu g L^{-1}$ ), equal to the Humboldt current off southwest Peru ( $2.0 \mu g L^{-1}$ ) but higher than region of Canary off northwest Africa ( $1.4 \mu g L^{-1}$ ) and California current ( $1.2 \mu g L^{-1}$ )

(Carr, 2002; Patti et al., 2008). However, the extent of high productivity could not be complemented using remote sensing data as the satellite imageries of SST and Chl-a during the same period showed gaps in coverage over the Indian Ocean due to large cloud cover (<http://oceancolor.gsfc.nasa.gov>).

Comparison of the quality of Chl-a at both locations, showed that phaeo:Chl-a ratio off TVM was lower at 0.52 than off CLT (0.66) indicating that the PhytoA were in a more active physiological state off TVM. However, off TVM, the higher concentration of phaeo ( $1.04 \mu\text{g L}^{-1}$ ) compared to off CLT ( $0.2 \mu\text{g L}^{-1}$ ) suggests higher degradation due to bacterial activity leading to lower ambient oxygen concentration. Like Chl-a, PhytoA was also 20x higher off TVM but the Shannon diversity index was ~ 1.5x lower than off CLT. The lower plankton diversity is a characteristic feature of upwelling regions where one/few species dominate and outgrow others in a competitive environment (Blasco et al., 1980; Gromiszi and Szymelfenig 2005). Evidently, the percentage of diatoms in the upwelling waters off TVM was 98 and was higher than off CLT at 81. *Nitzschia* and *Chaetoceros* species dominated the diatom fraction off TVM and *Chaetoceros*, *Pseudonitzschia*, *Guinardi*, *Nitzschia* and *Navicula* off CLT. Off CLT, the dinoflagellates formed 2% while cyanobacteria 13% of the total phytoplankton community. Nitrogen-fixing cyanobacteria is a common feature in the west coast of India (Krishnan et al., 2007; Prasanna Kumar et al., 2010). The relatively higher SST off CLT could have possibly favored the proliferation of this group. It is established that cyanobacteria require higher temperature for growth than other phytoplankton and this parameter has been considered the most important factor governing their abundance (Suvapepun, 1992; Sellner, 1997).

Compared to CLT, MZPb and MZPa off TVM was 2 and 5x higher, respectively. These values are in agreement with the values reported in the Arabian Sea during summer monsoon (Gauns et al., 2005; Nair, 2010). The higher MZPb in the upwelling region could be in response to higher primary productivity resulting from increased nutrient availability near-shore (Madhupratap et al., 1990). The macrofaunal abundance and biomass was 3.5x and 1.5x higher in the upwelling transect off TVM than off CLT. Macrofaunal diversity was marginally higher off TVM. Annelid polychaetes and crustaceans formed the major component of benthic fauna. The higher values of primary consumers suggest that the upwelling stage has also stimulated an increase in the zooplankton of the water column and to a certain extent in the benthic fauna of the sediment below.

Thus, the relatively higher concentration of macronutrients off TVM, Chl-a ( $>2.0 \mu\text{g L}^{-1}$ ), primary production and nearly 98% contribution of diatoms to PhytoA indicated a mesotrophic environment off TVM. Such observations have been previously recorded during upwelling off the NW Iberian margin (Barbosa et al., 2001). Moreover, in CLT, low nutrient concentrations, low Chl-a ( $0.3 \mu\text{g L}^{-1}$ ), increased percentage of cyanobacteria (13%) and lower percentage of diatoms (81%) indicated an oligotrophic environment. Joint et al. (2001) also aver that relatively high contribution from

picoplankton to primary production and the virtual absence of diatoms suggested the prevalence of oligotrophy.

## 4.2 Statistical analysis

Both biological parameters and nutrients show that their levels off TVM were higher than off CLT. This difference is attributed to the upwelling waters which are richer in nutrients off TVM. The variation between the two stations has been statistically confirmed by ANOVA (Table 2). Phytoplankton parameters like Chl-a ( $p \leq 0.027$ ) and PhytoA ( $p \leq 0.005$ ) were significantly higher confirming the influence of inorganic nutrients on the phytoplankton community. The average bacterial abundance was significantly low ( $p < 0.001$ ) than that off CLT possibly due to grazing by MZP whose abundance was notably high off TVM. However, the absence of significant difference in benthic fauna between upwelling and non-upwelling region, despite their higher abundance off TVM, suggested that pelagic-benthic coupling was yet to build up in the upwelling region.

Pearson's correlation analysis between the biotic variables and the environmental parameters revealed significant relationships at both sites. At both locations, the ambient concentrations of DO and macronutrients were modulated by PhytoA and MZP variables (Table 1a Appendix). The particulate organic pool was contributed by both PhytoA and MZP. However, the influence of PhytoA and MZP on POM was more pronounced off TVM than off CLT. The interrelationships also suggest that the influence of PhytoA was higher than MZP and their contribution to the variation of PON was higher than POC. The most obvious feature among these interrelationships was that DO and macronutrients closely coupled with TVC off TVM and with TC off CLT ( $p < 0.05$ ) indicating that the viable fraction was the prominent governing factor in the upwelling system. The bacterial parameters correlated positively with POC and PON suggesting the interdependence of pelagic bacteria on the plankton derived organic matter and active mineralization in upwelling region off TVM. In contrast, the relationship between bacterial variables and POM is weak off CLT, suggesting a less dominant role for bacteria of this sector. Previous studies have reported the dependence of bacterioplankton on plankton-derived organic matter for readily available metabolites wherein phytoplankton fix inorganic carbon to organic carbon and bacterioplankton account for > 50% cycling of the organic carbon through the microbial loop (Azam et al., 1983; Hanson et al., 1986; Sherr and Sherr, 1988; Wiebinga et al., 1997, Grossart et al., 2008). Thus, the correlations between environmental parameters and biological variables reflect similarity in interactions but differences in strength and direction.

Parallel analysis done using partial correlation showed that the interrelationships becomes less strong and therefore less significant suggesting contribution of depth to the changes in the parameters at Calicut. However, off TVM the effect of stratification is less evident than off CLT. At

TVM, the effect is masked by influenced of denser nutrient rich saline waters, thus, suggesting definite signals of upwelling. While, relationship between TVC and PhytoA improved, that between Chl-a and BP, Chl-a and THB, TVC and BP changed very little off TVM, confirming that depth was not a primary driver at this site (Fig. 5a). In contrast, the relationship between nutrients and depth was weakened off CLT. Accordingly, relationships between bacteria and higher trophic levels also weakened. Thus, comparison of relationships before and after removing the effect of depth, the extent of influence of this parameter. It is noted that relationships off TVM have only marginally changed emphasizing the negligible effect of depth off TVM. Relationships become insignificant off CLT suggesting a stronger influence of depth.

The “web of interactions” illustrated using significant interrelationships elucidates the differences between bacteria and other trophic levels (Fig. 5, Table 1a Appendix). Off CLT, the system was influenced by the total bacterial population, while off TVM, the viable component of the bacterial population showed a statistically significant relationship with other biotic variables. It should be noted that TC includes cells from a variety of physiological states, including metabolically active bacteria and less active or dead cells (Barbosa et al., 2001). However, TVC is comprised of metabolically active cells (Kogure et al., 1979). Besides, the interlinkages between bacteria and other trophic levels showed that the bacterial variables related significantly to primary producers suggesting tighter coupling off TVM (Fig. 5a). The viable fraction was associated to Chl-a and MZPa, suggesting that both primary producers and secondary producers contribute to the augmentation of this fraction of bacteria. The network of relationships prevailing between the bacterial abundance and MZP suggests the contribution of viable fraction as a source of food could be more off TVM than off CLT due to its higher percentage of occurrence. Bacterial productivity parallels primary productivity in intensity and is apparently influenced by viable and culturable fraction of bacteria. These observations suggest a much more prominent role of bacteria in the upwelling region. Off CLT, the TVC was delinked from both Chl-a and zooplankton and BP did not relate to any other biological parameters (Fig. 5b). However, THB synchronized with MZP suggesting the contribution of this variable in improving the culturability. The stronger coupling between PhytoA and MZP community and moderate role of bacteria in the non-upwelling region could be suggestive of a trophic system where the consumers are more directly influenced by the primary producers. Such response of the MZP community in the SEAS is known (Madhupratap et al., 1990; Madhupratap and Haridas, 1990).

Pearson’s rank correlation thus highlighted one to one relationships that were causal/covaried. Treatment of data for PCA projected the combined influence of parameters (both biotic and abiotic) pooled into components that influenced the system. This treatment aggregated the variables into 3 major components with a cumulative variation of ~70% at both locations.

Off TVM, the PC1 which explained 48% of the total variance was positively loaded by inorganic nutrients such as nitrate, silicate and phosphate and negatively affected by all other parameters. Therefore this component seems to measure the prevalence of macronutrients over the other parameters, suggesting that the inorganic nutrients wield a stronger influence than all the other variables. This influence could be due to the response of chemical processes to physical signatures. The negative loadings off TVM on pH is suggestive of the relatively more acidic bottom waters than the surface. Capone and Hutchins (2013) have also made such observations in upwelling waters. Besides, biological activities contribute to the pH of a region (Lin et al., 2011). PC2 explained 13 % of the total variance and correlated strongly and positively with salinity, nitrite, TSM, PON, Chl-a, phaeo, TVC and BP with factor loadings of >0.2 and negatively with MZP biomass and abundance (Table 3). This indicates that the resident bacterial community were more associated with the suspended load and particulate fraction which includes phaeo, POC and PON. The clustering of Chl-a, TVC and phaeo in PCA biplot (Fig. 6a) confirmed the inference made from correlation analysis. Bacteria could act on the plankton derived organic matter and get involved in active mineralization in upwelling region off TVM. Off TVM, the region has a relatively higher heterotrophy- dependent microbial load along with higher concentration of POM in the form of POC and PON. This organic load is possibly decomposed microbially, leading to formation of organic acids, CO<sub>2</sub> and ammonia. The increase in nitrite and decrease in pH could be the result of hydrolysis of these acids, dissolution of CO<sub>2</sub> in water column and nitrification process (Kim et al., 2005; Singh et al., 2004; Panda et al., 2006; Vega et al., 1998). The level of nutrients in turn is governed by the resident bacterial community that contribute to the stability of the system. Thus, higher bacterial load mineralizing the organic matter is known to bring about changes in nutrient concentrations (Castillo et al., 2003; Grossart et al., 2008).

PCA analysis distinctly shows the lack of influence or response of ATP to other variables. Parameters like phaeo, POC, PON cluster in Q1 of fig 6a and 6b and Q2 of 6c and Q4 of 6d suggesting a common source of particulate organic matter. As nitrite clusters with this group along with TC and THB in Q1 of fig 6a, it is suggested that nitrite could be more a product of nitrification than denitrification. Likewise, phosphate, silicate and nitrate generally cluster together as in 6a to 6d suggesting a common origin in both transects. Clustering is stronger between phosphate and silicate. In the same biplot, TC associates with THB, nitrite and salinity in QI suggesting their interdependence. THB formed a sizeable a fraction of TC (7%) and could be responsible for the nitrite production through nitrification as PON, phaeo are grouped in QI. Though the concentration of ammonia was low, the clustering of this parameter with MZP in QIV, suggests that it was apparently derived from mesozooplankton activity and excretory products.

Hence, DO and pH values have negative loadings. The nutrients phosphate, nitrate and silicate cluster together in QII suggesting the common source. Off CLT, PCA analysis showed that PC1 explained 50% of the total variance. Thus, PCA results suggest that the same group of physico-chemical variables regulated the systems at both locations. However, the influence of TC is marked off CLT and TVC off TVM suggesting the prominent contribution of viable bacteria in upwelling systems. Our analysis show that both the systems are bottom-up (nutrients) controlled. However, the top-down influence is much more stronger off TVM as zooplankton is an important variable both in PC1 and PC2.

PC2 explained 12% of the total variance off CLT and correlated strongly and positively with salinity, nitrite, TSM, PON, Chl-a, phaeo, TVC and BP with factor loadings of >0.2 and negatively with MZPb and MZPa (Table 3). This suggests that the resident bacterial community were more associated with the suspended load and particulate fraction which include phaeo, POC and PON. PPC2 correlated positively with nitrite with high factor loadings (>0.5) suggesting this was a mainly nitrite enrichment component. Moreover, TC, BP, phaeo, TSM, PON were influenced by this component. In agreement with this observation, Spinrad et al. (1989) had also suggested that mid-depth maxima in suspended particles were associated with a large bacterial component and high nitrite and low DO in Peruvian waters. Nitrite is an intermediate oxidation state between ammonia and nitrate and can appear as a transient species by the oxidation of ammonia or by the reduction of nitrate (Meeder et al., 2012).

In the PCA biplot, these parameters are loosely associated in QII. However, the clustering of MZP and Chl-a suggest trophic dependence supporting correlation analysis. Also, as nitrite has high loading of 0.531 in PC2, it suggests that this parameter could be an important driver in this region. However, as it is not closely associated with the other parameters in the quadrant, it could have multiple sources – nitrification from ammonia derived from phaeophytin degradation (POC and PON) or excretory products of zooplankton. In QIV, THB, DO, pH and temperature associate. Higher average (23.2°C) temperature at CLT could have a strong influence on THB which in turn could affect the ambient DO and pH. One of the factors which regulate bacterial abundance in aquatic systems is temperature (Barbosa et al., 2001). Off CLT, the nutrients phosphate, nitrate and silicate cluster together in QI suggesting the common source.

The CCA analysis complements the findings obtained from PCA. However, unlike PCA, CCA resolves the effect of each abiotic variable on the biotic variables. Off TVM, CCA ordination diagrams showed that POC, PON, phaeo, Chl-a, temperature and nitrite positively influenced PhytoA variation. Such positive variation in nitrite released during nitrate uptake by phytoplankton in surface waters of upwelling areas has been reported earlier (Collos, 1998). Nitrate, silicate and phosphate were negatively influenced by phytoplankton and positively by bacteria (Fig. 7a). The

parameters i.e POC, PON, phaeo, Chl-a, temperature and nitrite influenced the bacterial variation negatively, but phytoplankton, positively suggesting that the abiotic factors influenced phytoplankton and bacteria, differently – inversely and definite at TVM. In this study, the results corroborate with the established fact that bacteria mineralize the organic matter into inorganic macronutrients. These nutrients are used by phytoplankton for new production, thus confirming the consequence of upwelling off TVM. The processes of mineralization by bacteria and uptake by phytoplankton are obviously more synchronous off Trivandrum. Accordingly, this analysis suggests that the abiotic factors influence phytoplankton and bacteria, differently. TC and TVC being closely placed on the ordination diagram indicated that resident bacterial population were mostly aerobic, heterotrophic and viable. Conversely, off CLT the area tends more towards mineralization. TC correlated positively with silicate and phaeo and negatively with ammonia and POC (Fig. 7b). Further, TVC correlated positively with ammonia, and negatively with POC, PON, salinity, phosphate, nitrate and silicate suggesting multiple roles. Here, the environmental variables had no influence on the phytoplankton components. So, the influence of abiotic factors on phytoplankton and bacteria, was diverse and varied at CLT.

Also, the ordination diagram off CLT demonstrates that the presence of two groups of bacteria within the resident community. The total bacterial community had general propensity towards ammonia oxidation. However, the aerobic viable fraction which forms nearly 5% of the total bacterial community, had a tendency to contribute to ammonification through organic matter degradation. Thus, CCA analysis adds to what PCA elaborates.

## **5. Conclusion**

Significantly higher phytoplankton and zooplankton biomass off Trivandrum, confirms the biological response to the physico-chemical signals of upwelling. Variation in the level of nutrients induced changes in “network of interactions” between trophic levels in upwelling region off Trivandrum and non-upwelling region off Calicut during summer monsoon. These changes were more prominent at the bacterial level. Our results suggest that there is a similarity in the essence of network of interaction restricted to primary producers and secondary producers but not to bacteria. There is a marked difference in the way bacteria particularly the viable fraction influence the ecosystem functioning. PCA showed that the macronutrients influenced at both transects, albeit at reverse directions. Further, CCA complements these findings and demonstrated that the abiotic factors influence phytoplankton and bacteria, differently - inversely and definite at Trivandrum and diverse and varied at Calicut. The process of mineralization by bacteria and uptake by phytoplankton is obviously more synchronous off Trivandrum. These contributions of bacteria in upwelling and non-upwelling regions have been highlighted for the first time. Delineation of the contribution of different

physiological groups of bacteria involved in the cycling of nitrogen, phosphorus and silica would give new perspectives to the contribution of bacteria to the base of the food web in the upwelling region.

### **Acknowledgement**

The authors are grateful to Director, CSIR-National Institute of Oceanography, Goa for the facilities provided. They express their gratitude to Ministry of Earth Sciences for the financial support and to the Director, CMLRE (MoES), Kochi, India for providing FORV Sagar Sampada for sample collection and onboard analysis. The authors also thank the participants of FORV Sagar Sampada cruise # 267. The authors wish to thank I. Suresh, S. Neetu and Parvathi V. for their valuable suggestions and help in drawing the plots. This is NIO contribution no. -----.

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## Figures captions

Fig. 1: Map showing geographical location of the sampling stations

Fig. 2: Region of interest showing (a) SST computed from Tropical Rainfall Measuring Mission (TRMM) Microwave Imager (TMI) and (b) vertical structure of temperature off Trivandrum (TVM) and (c) vertical structure off Calicut (CLT) during the study period. The grey shaded portions at the bottom of (b) and (c) signify land mass.

Fig. 3: Distribution of oxygen concentration, DO (a,b), nitrate (c,d), nitrite (e,f), ammonia (g,h), phosphate (i,j), and silicate (k,l) at the two transects; off Trivandrum (TVM) and off Calicut (CLT). The grey shaded portions at the bottom of the figures signify land mass.

Fig. 4: Distribution of bacterial parameters; total counts- TC (a), total viable counts-TVC (b), total heterotrophic bacteria- THB (c) and bacterial productivity- BP (d) at the two transects; off Trivandrum (TVM) and off Calicut (CLT). Profiles in the panel have been restricted to near shore stations 1-3.

Fig. 5: Comparison of the network of interactions between trophic levels off Trivandrum (TVM, a) and off Calicut (CLT, b). Only the pairwise relationships with a significant correlation coefficient were plotted ( $p \leq 0.05$ ). Three colors were used to represent the different trophic position (red - bacterial parameters, green - primary producers, yellow - primary consumers).

Fig. 6: Comparison of biplots of Principal components analysis (PCA) of the first two axes of the ordination for the two transects; a) off Trivandrum (TVM) and b) off Calicut (CLT).

Fig. 7: Comparison of Canonical correspondence analysis (CCA) plots of the first two axes of the ordination for the two transects; off Trivandrum (TVM) and off Calicut (CLT).

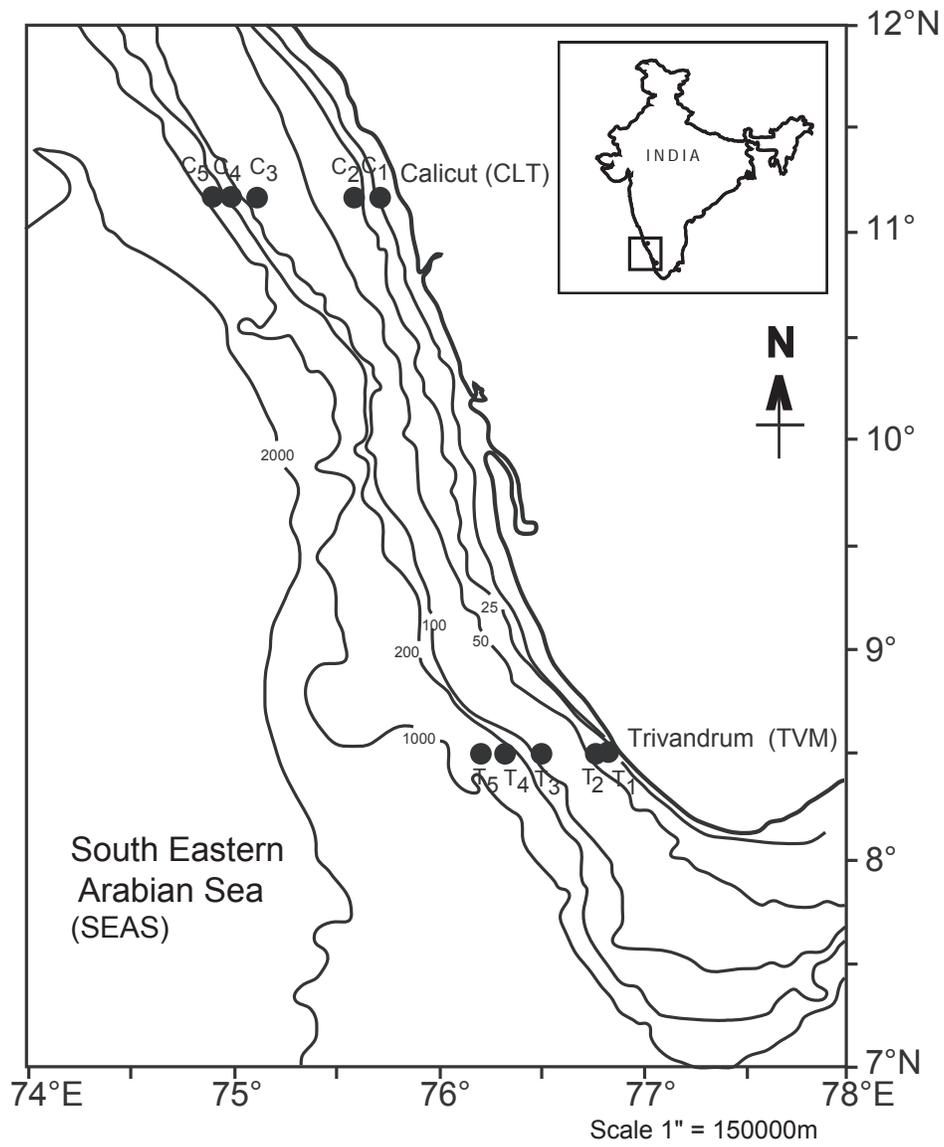
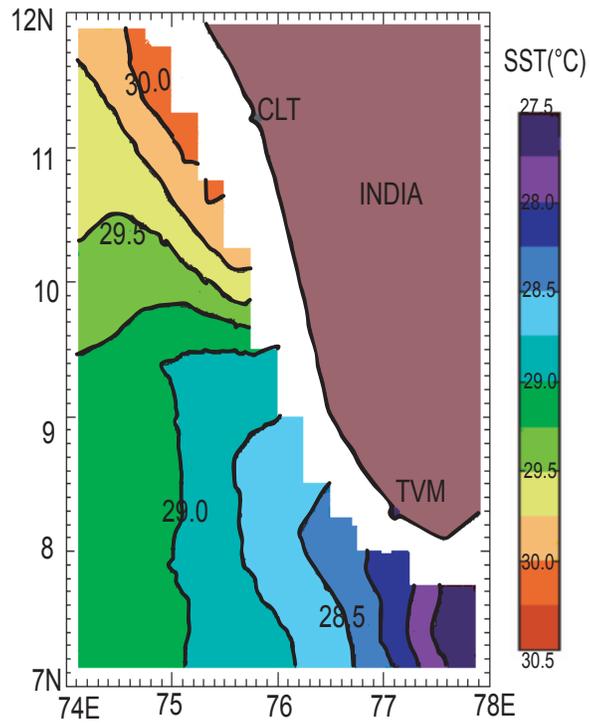
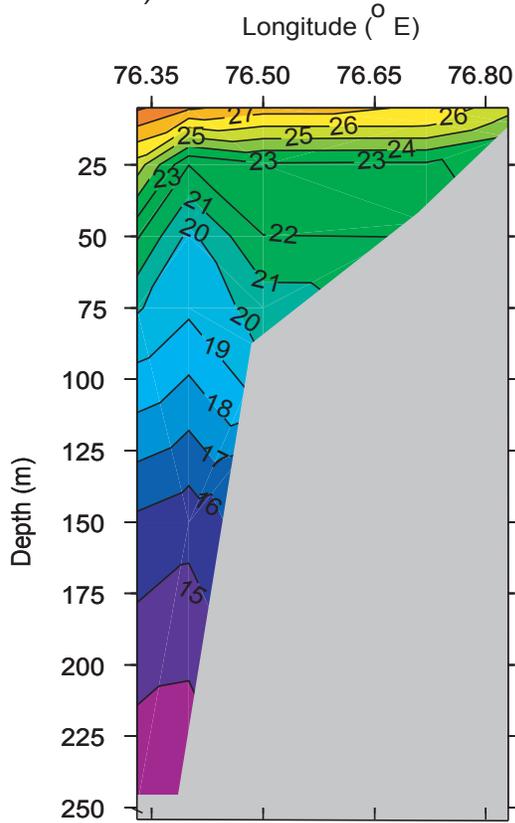


Fig.1

a)



b) TVM



c) CLT

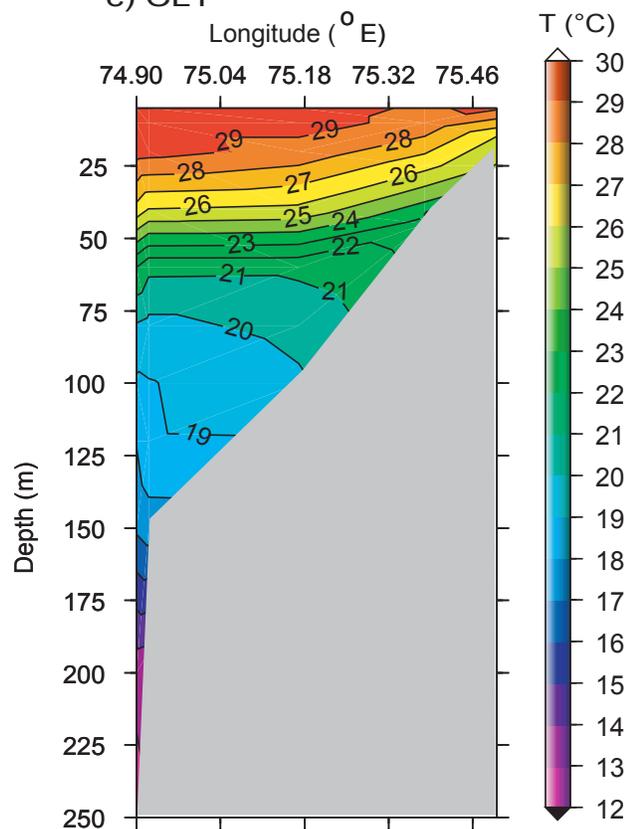


Fig.2

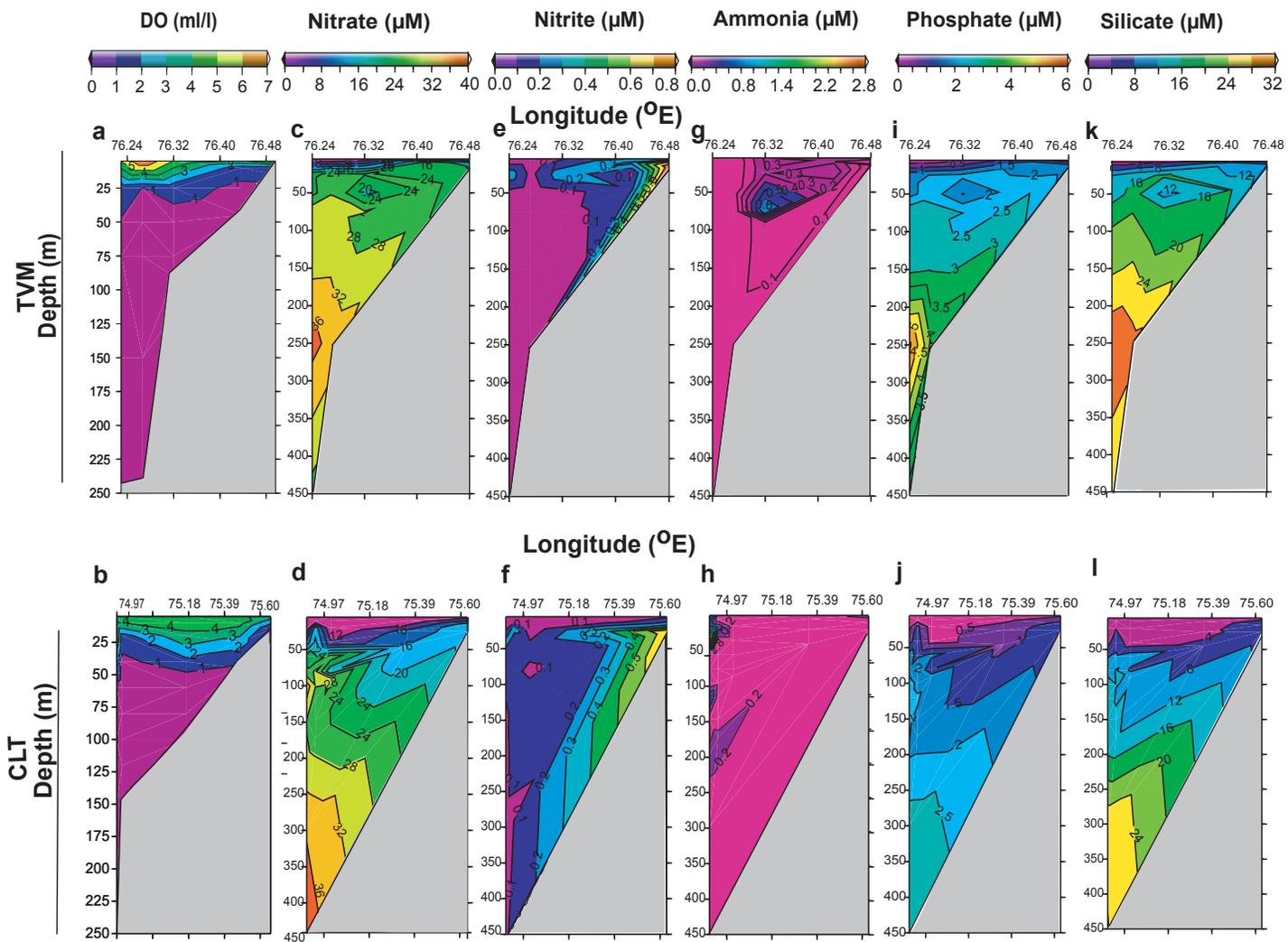


Fig.3

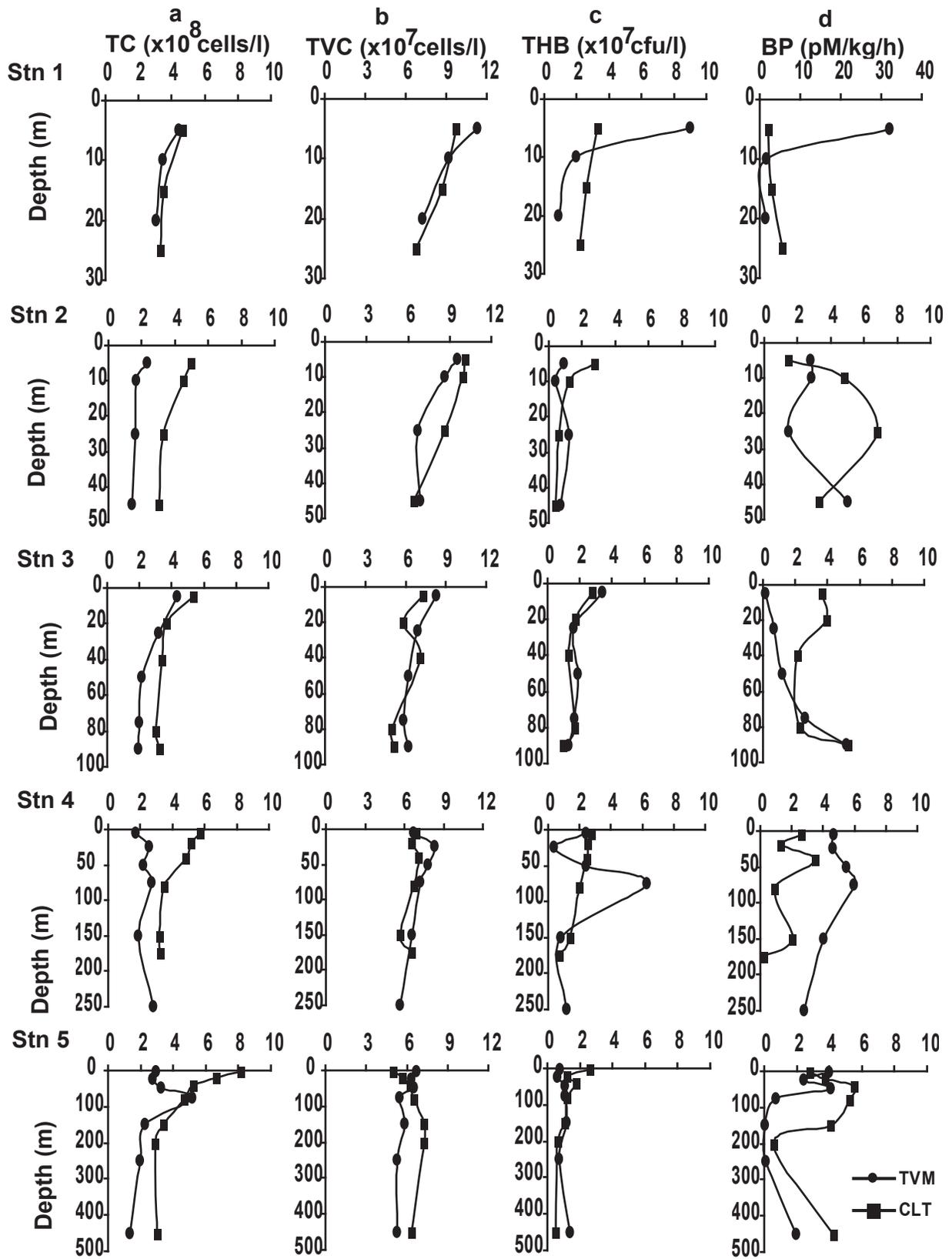
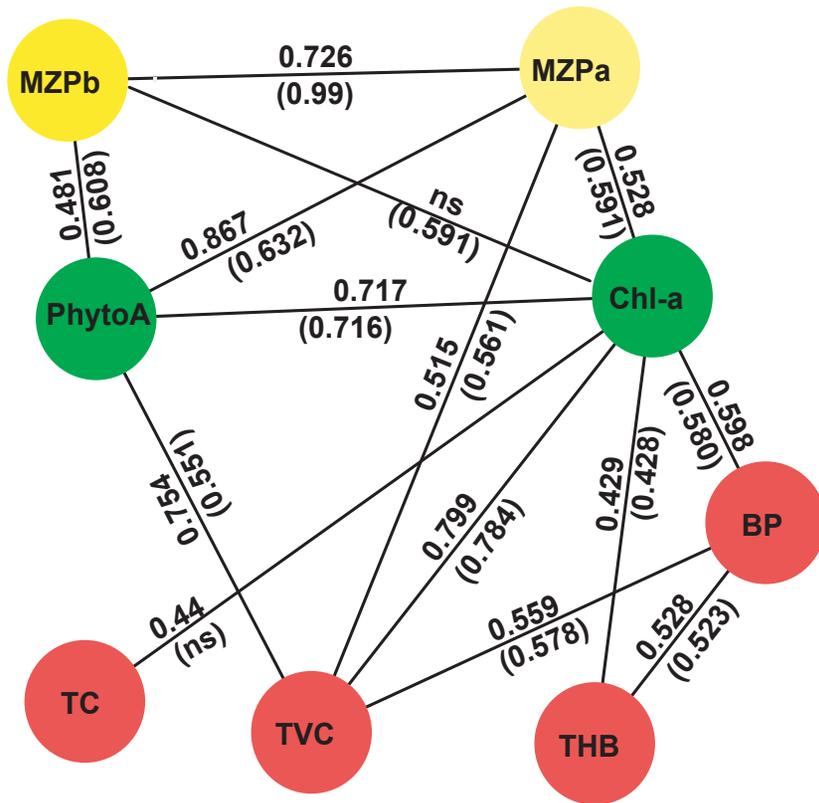
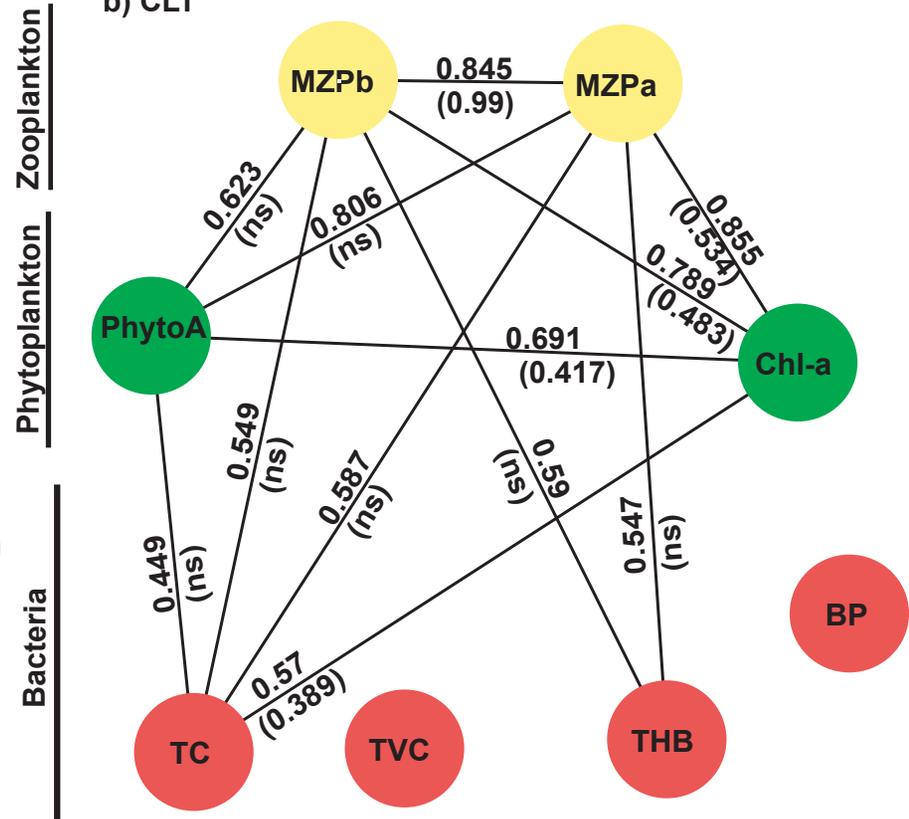


Fig.4

a) TVM



b) CLT



TC:total bacterial count; TVC:total viable count; THB:heterotrophic count; BP:bacterial productivity; PhytoA:phytoplankton abundance; Chl-a: Chlorophyll a; MZPb: mesozooplankton biomass; MZPa: mesozooplankton abundance; ns: not significant

Fig.5

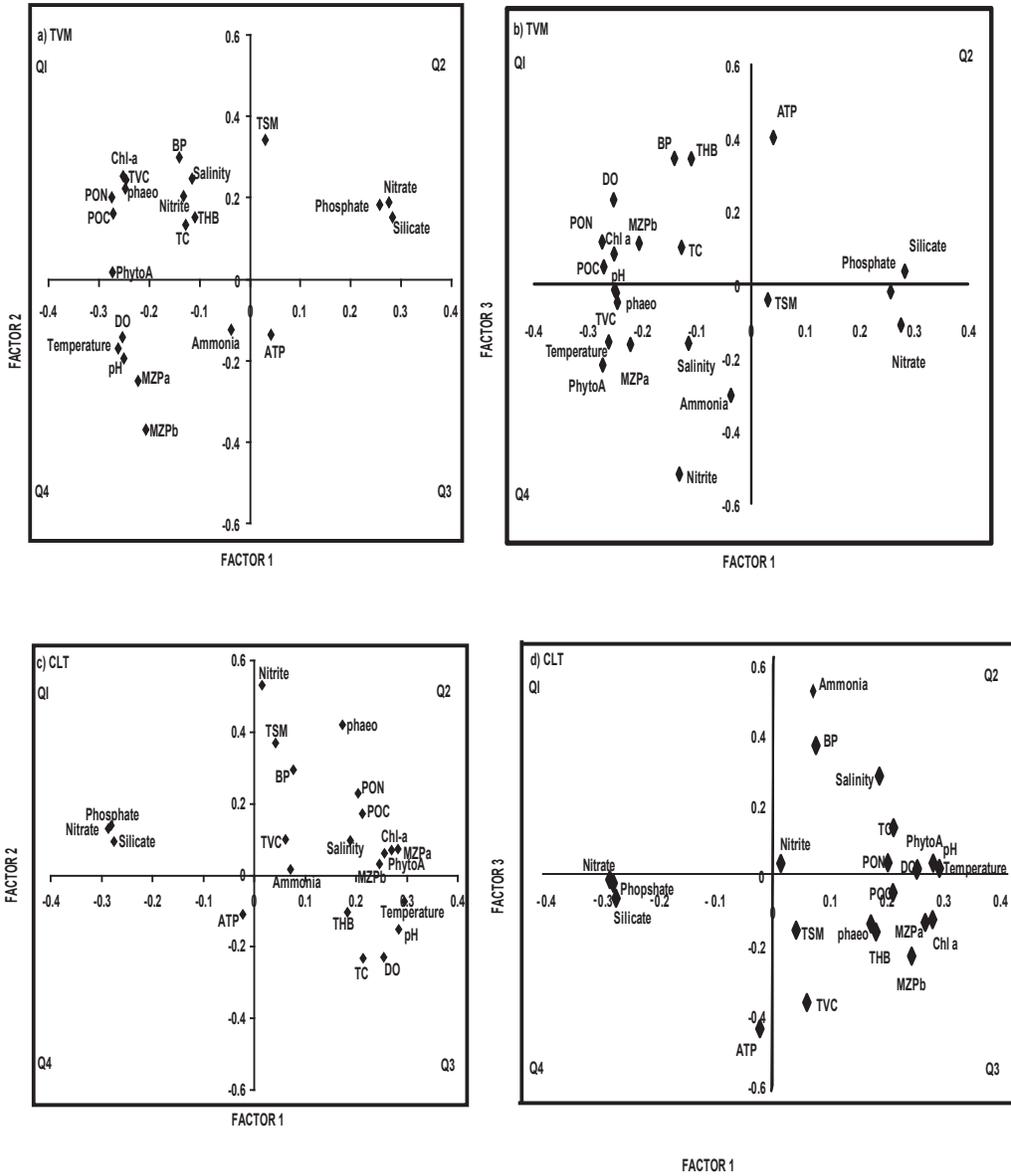
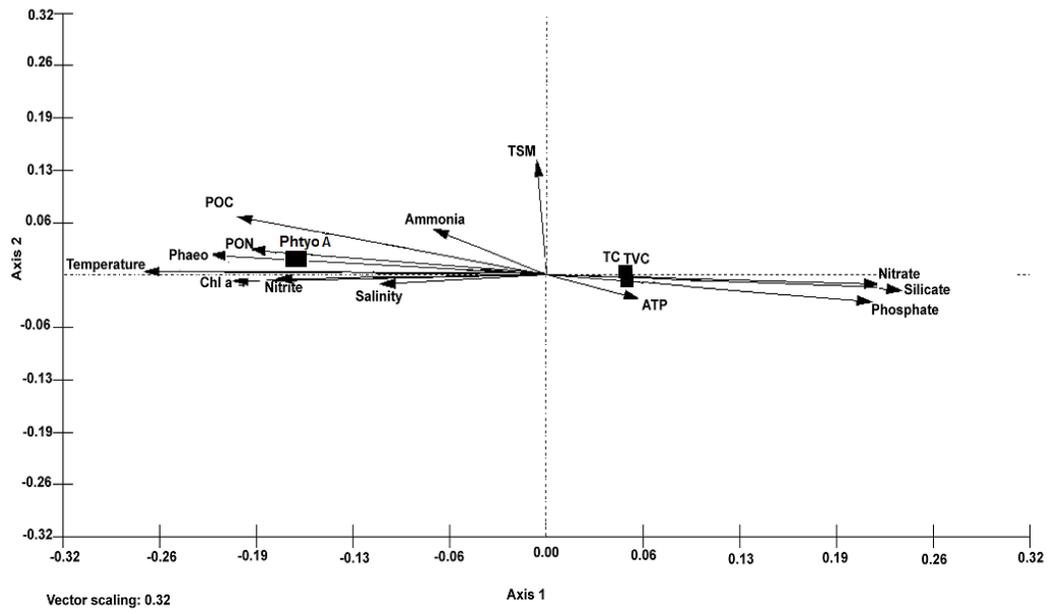


Fig.6

### a) TVM



### b) CLT

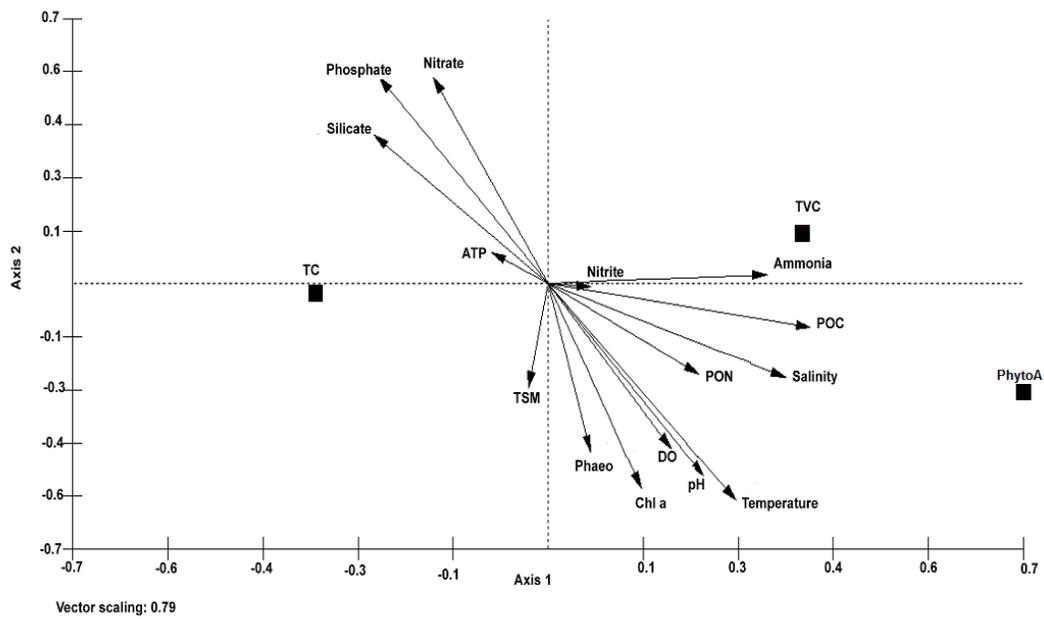


Fig.7

**Table 1: Station and sampling details****a) Water sampling depths**

Station	Co-ordinates	Depths sampled (m)
<b>Trivandrum (TVM)</b>		
1 <sup>#</sup>	8°30'N 76°50'E	5, 10, 20
2 <sup>#</sup>	8°30'N 76°43'E	5, 10, 25, 45
3 <sup>#</sup>	8°28'N 76°30'E	5, 25, 50, 75, 90
4	8°27'N 76°24'E	5, 25, 50, 75, 150, 250
5	8°26'N 76°20'E	5, 25, 50, 75, 150, 250, 450
<b>Calicut (CLT)</b>		
1 <sup>#</sup>	11°11'N 75°30'E	5, 15, 25
2 <sup>#</sup>	11°12'N 75°23'E	5, 10, 25, 45
3 <sup>#</sup>	11°13'N 75°10'E	5, 10, 20, 40, 60, 80, 90
4	11°13'N 74°55'E	5, 10, 20, 40, 60, 80, 100, 120, 150, 175
5	11°14'N 74°54'E	5, 10, 20, 40, 60, 80, 100, 120, 150, 250, 450

\* PP station for in situ primary productivity measurement, # Grab operated for sediments sample collection

**b) Vertical haul for zooplankton sampling**

Water depth	sampling depths (m)
30m	(0-20)m, (20-25)m
50m	(0-7)m, (7-45)m
100m	(0-10)m, (10-90)m
300m	(0-9)m, (9-158)m, (158-255)m
450m	(0-10)m, (10-182)m, (182-300)m, (300-450)m

The number of depths sampled at each station is dependent on the depth of the station ranging from with two depths at 30 m station to four depths at 450 m station

**Table 2: The physico-chemical and biological parameters measure along with range, average and standard deviation off Trivandrum (TVM) and off Calicut (CLT)**

Parameter	TVM		CLT		ANOVA
	Range	(avg±sd)	Range	(avg±sd)	(p value)
Temperature (°C)	10.9-29.2	21.6 ± 4.9	7.4-29.6	23.2 ± 5.6	ns
Salinity (‰)	34.8-35.3	34.97 ± 0.13	34.9-36.1	35.4 ± 0.3	7.48x10 <sup>-7</sup>
pH	7.6-8.5	7.98 ± 0.24	7.6-8.3	8.0 ± 0.2	ns
Dissolved oxygen (ml l <sup>-1</sup> )	0.3-6.9	1.7 ± 1.9	0.03-4.4	1.6 ± 1.58	ns
Ammonia (µM)	NDL-0.7	0.2 ± 0.21	NDL-2.67	0.2 ± 0.4	ns
Nitrate (µM)	0.02-37.4	21.6 ± 10.6	0.02-37.8	18.1 ± 13.2	0.018
Nitrite (µM)	NDL-0.8	0.14 ± 0.2	NDL-0.68	0.1 ± 0.1	ns
Phosphate (µM)	0.1-5.6	2.1 ± 1.9	0.18-4.13	1.4 ± 1.0	6.99x10 <sup>-4</sup>
Silicate (µM)	0.7-31.4	14.3 ± 8.6	0.47-63.3	10.34 ± 12.3	9.66x10 <sup>-4</sup>
Total suspended matter (mg l <sup>-1</sup> )	0.2-18.2	6.6 ± 4.97	0.2-38.4	7.0 ± 7.5	ns
Particulate organic carbon (µM)	2.4-76.7	21.7±22.0	1.9-21.1	8.2±5.1	0.013
Particulate organic nitrogen (µM)	0.9-11.3	3.1±2.6	0.4-5.3	2.0±1.1	ns
Adenosine tri phoshate (ng l <sup>-1</sup> )	0.02-5.5	3.2 ± 2.1	0.03-56.3	2.0 ± 1.6	7.08x10 <sup>-4</sup>

<b>Total counts (x10<sup>8</sup> cells l<sup>-1</sup>)</b>	1.3-5.6	2.6±0.9	2.9-8.2	4.2 ±1.3	8.58 x10 <sup>-7</sup>
<b>Total viable counts (x10<sup>8</sup> cells l<sup>-1</sup>)</b>	0.5-1.2	0.7 ±0.2	0.49-1.0	0.7 ±0.2	ns
<b>Total heterotrophic bacteria (x10<sup>8</sup> cfu l<sup>-1</sup>)</b>	0.04-0.9	0.2 ± 0.19	0.04-0.4	0.2 ± 0.08	ns
<b>Bacterial productivity (pM kg<sup>-1</sup> h<sup>-1</sup>)</b>	0.05-32.0	3.9 ± 6.1	0.1-6.8	3.3 ± 1.8	ns
<b>Chlorophyll a (µg l<sup>-1</sup>)</b>	0.01-14.1	2.0 ± 3.6	NDL-1.1	0.3 ± 0.3	0.027
<b>Phaeopigments (µg l<sup>-1</sup>)</b>	0.04-4.9	1.04 ± 1.6	NDL-0.9	0.2 ± 0.18	0.013
<b>Phytoplankton abundance (x10<sup>3</sup>cells l<sup>-1</sup>)</b>	0.1-879	136 ± 230.3	0-49	9.8 ± 13.5	0.005
<b>Zooplankton abundance (x10<sup>4</sup> ind 100m<sup>-3</sup>)</b>	1.1-50.9	26.6 ± 3.3	0.2-16.9	6.3 ± 7.1	0.03
<b>Zooplankton biomass (ml 100m<sup>-3</sup>)</b>	0.3-11.2	3.3 ± 4.5	0.08-3.8	1.2 ± 1.5	ns
<b>Macrofauna abundance (x10<sup>3</sup> ind m<sup>-2</sup>)</b>	0.36-19.5	4.3±3.1	0.04-10.5	3.2±2.4	ns
<b>Macrofauna benthic biomass (mg m<sup>-2</sup>)</b>	0.1-1502	290.0±510.3	4.6-1000	251.2±316.1	ns

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\* NDL- non detectable level; avg: average; sd: standard deviation; cfu: colony forming units; ind: individuals; ns: not significant. ANOVA was calculated for each parameter between stations.

**Table 3: PCA of the variables at the two locations; off Trivandrum (TVM) and Calicut (CLT)**

Principal component	TVM		CLT	
	Eigen values	%Variation	Eigen values	%Variation
PC				
1	10.6	48.2	10.8	49.3
2	2.93	13.3	2.6	11.8
3	2.08	9.4	1.85	8.4
4	1.34	6.1	1.4	6.4
5	1.17	5.3	1.22	5.6

**Table 4: Comparison of the results of the canonical correspondence analysis (CCA) of the two transects; off Trivandrum (TVM) and Calicut (CLT).**

Transects	TVM		CLT	
	Axis 1	Axis 2	Axis 1	Axis 2
Eigen values	0.138	0.036	0.066	0.008
Cumulative constrained %	74.84	94.63	82.55	93.18
Total variance explained	0.944	0.712	0.467	0.487