

Copepod grazing and their impact on phytoplankton standing stock and production in a tropical coastal water during the different seasons

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ABSTRACT

The grazing rate of copepods on the total and size-fractionated phytoplankton biomass in a coastal environment (off Kochi, Southwest coast of India) were measured during Pre-Monsoon (PRM), Peak Southwest Monsoon (PKSWM), Late Southwest Monsoon (LSWM) and Post-Southwest Monsoon (PSWM). The phytoplankton standing stock (chlorophyll *a* - Chl. *a*) and growth rate (GR) were less during the PRM (Chl. *a* 0.58 mg. m⁻³; GR 0.23 ± 0.02) and PSWM (Chl. *a* 0.89 mg. m⁻³; GR 0.30 ± 0.05) compared to PKSWM (Chl. *a* 6.67 mg. m⁻³; GR 0.43 ± 0.02) and LSWM (Chl. *a* 4.09 mg. m⁻³; GR 0.40 ± 0.04). The microplankton contribution to the total Chl. *a* was significant during the PKSWM (41.83%) and LSWM (45.72%). Copepod density was lesser during the PRM (1354 No.m⁻³) and PSWM (1606 No.m⁻³) than during PKSWM and LSWM (4571 and 3432 No.m⁻³, respectively). Seasonal changes in phytoplankton biomass, phytoplankton size structure and copepod community were closely related to the hydrographical transformations in the study domain. Dominant calanoid copepods in the study region ingested 8.4 to 14.2% of their daily ration from phytoplankton during the PRM and PSWM, which increased to >50 % during the PKSWM and LSWM. The cyclopoid *Oithona similis* was abundant during the PKSWM, ingesting only 21% of their daily ration from phytoplankton. Temporal variation in the phytoplankton biomass and copepod species composition caused differences in community level top-down control. The copepod community ingestion on phytoplankton was high during the LSWM (18583 µg.C.m⁻³), followed by PKSWM (9050 µg.C.m⁻³), PSWM (1813 µg.C.m⁻³) and PRM (946 µg.C.m⁻³). During low Chl. *a* period (PRM and PSWM), dominant calanoid copepods showed a positive selectivity for the micro- and nano-phytoplankton size fractions, whereas during the high Chl. *a* period (PKSWM and LSWM), they showed a positive selection for nano-phytoplankton fractions. Irrespective of the seasons, dominant calanoid copepods showed a negative selection of pico-phytoplankton fraction. Cyclopoid *Oithona similis* and Poecilostomatoid *Corycaeus danae* showed a positive selection of nano - and pico-phytoplankton fractions rather than micro- fraction. The grazing pressure of copepod community ingestion on micro-fraction was less (0.56 % of phytoplankton biomass and 1.06% of phytoplankton production) during the PKSWM. This study provides, for the first time, clear findings on the seasonal variation in the top down control of phytoplankton by copepods in a tropical coastal water ecosystem and discusses its implications on phytoplankton blooming, plankton food web and biogeochemistry.

Keywords - Copepods, Phytoplankton Biomass, Chlorophyll a, ingestion, Tropical waters, grazing pressure.

1. INTRODUCTION

Feeding is the main route of transfer of energy and material from one trophic level to the other in the food web (Bamsteadt et al. 2000). Copepods play a crucial role in transferring the organic carbon from primary to secondary/tertiary trophic levels (Calbet et al. 2000). In addition to the feeding/grazing (top down control) of phytoplankton production, copepods also play a significant role in the vertical carbon export flux by producing rapidly sinking fecal pellets (Banse 1994; Noji 1991; Huskin et al. 2001; Gifford et al. 2007). It was observed earlier that the food availability and its size distribution influence the feeding strategy of copepods (Stoecker and Capuzzo 1990; Froneman 2006).

In the recent decades, considerable amount of scientific information is available on zooplankton composition and distribution ecology in Indian estuarine and marine waters (Madhupratap 1987; Padmavati et al. 1997; Madhupratap et al. 2001; Madhu et al. 2007), whereas, quantification of zooplankton feeding on phytoplankton are limited or almost absent to compare the other parts of the world oceans (Nielsen and Hansen 1995; Pakhomov et al. 1997; Roman and Anne 1997; Calbet and Landry 1999; Calbet 2001; Fileman 2010; Saiz and Calbet 2011; Garrido et al. 2013). Hence, in the present study, efforts have been made to quantify the feeding/grazing of dominant copepods inhabiting in a tropical coastal waters characterized by pronounced seasonality associated with the tropical monsoon. The sampling site selected was off Kochi (25m depth, 10 km far from the coast), located along the southwest coast of India (Fig. 1)

During the Southwest Monsoon (June to September), the study location (off Kochi) receives low saline influx from the adjacent Kochi backwaters (on the surface layer), the largest estuarine system along the west coast of India. During the same period, the subsurface waters of the study area is characterized by cold, nutrient rich upwelled waters making the entire water column of the study area nutrient rich with high amount of phytoplankton stock (Banse 1959; Banse et al. 1996). During the Pre-Monsoon (March-May), water column in the sampling area is characterized by warm and low nutrients. This seasonal hydrographical setting significantly alter the biological properties of the study area (Jyothibabu et al. 2006; Madhu et al. 2007; Sooria et al. 2015) which is expected to make differences in copepods grazing. The objective of the present study was to measure the copepod grazing rate and their impact on the total and size fractionated phytoplankton biomass in the study area during different seasons.

2. MATERIALS AND METHODS

2.1. SEASONAL SAMPLING

Plankton and water samples were collected from the coastal waters off Cochin (Fig. 1) during 2014 in different seasons based on rainfall (Supplementary material 1): Pre-Monsoon (April-2014), Peak Southwest monsoon (July), Late Southwest Monsoon (September) and Post-Southwest Monsoon (November). The

vertical distribution of temperature and salinity in the study area was measured using a Seabird CTD system. Water samples were collected from three different depth layers (surface, middle and bottom) for measuring nutrients and dissolved oxygen. Nutrients (nitrate, phosphate and silicate) and dissolved oxygen were measured using the standard procedures give in Grasshoff et al. (1983).

2.2. ESTIMATION OF TOTAL AND SIZE FRACTIONATED CHLOROPHYLL *a*

In the present study, chlorophyll *a* (hereafter Chl. *a*) was used as an index of the phytoplankton biomass. The total Chl. *a* was measured by concentrating 500 mL of water samples on Whatman GF/F filters (0.2 μ m) and extraction using 10 ml 90% acetone. The extracted Chl. *a* was measured using a Trilogy Turner fluorometer following the standard procedure (UNESCO 1994). The size fractionated Chl. *a* was measured to understand the relative contribution of various size classes of phytoplankton to the total biomass. Taking into account different phytoplankton size fractions such as picoplankton (0.2–2 μ m), nanoplankton (2–20 μ m) and microplankton (>20 μ m), the fractionation of Chl. *a* was carried out following the standard serial filtration method (Iriarte and Purdie 1994; Jyothibabu et al. 2013). The size-based phytoplankton fractions thus separated on suitable filters were estimated following the same analytical procedure mentioned above for measuring the total Chl. *a* concentration.

2.3. ZOOPLANKTON AND COPEPODS COMMUNITY STRUCTURE

For measuring the *in-situ* copepods density and their species composition, zooplankton samples were collected from off Kochi using horizontal tows of WP-2 net (200 μ m mesh) fitted with the hydro bios flow meter. The collected samples were filtered through 200 μ m mesh and excess water was removed using blotting paper. Various zooplankton groups were sorted out and their abundance was measured on the standard procedure of Postel et al. 2000. Among different groups, copepods were further identified down to the species level using the standard literature (Kasturirangan 1983; Sewell 1999).

2.4. GRAZING EXPERIMENTS

For conducting the grazing experiments, live copepods were collected from the study site using horizontal tows of WP-2 net in slow speed. The cod end of the zooplankton net was carefully transferred into 20 liter containers filled with unfiltered *in-situ* seawater and transported to the laboratory. Additionally, unfiltered surface seawater (natural food suspension) was also collected using Niskin samplers and filled in 20 liter carboys and transported to the laboratory. The live zooplankton brought to the laboratory was acclimated in large tanks for one - two hrs and the dominant copepods were separated from the acclimatized tanks. Utmost care was taken while handling the copepods for grazing experiments, individuals without any damages and exhibiting active swimming behavior against the pipette suction were selected for the experiments. Dominant copepods were sorted live and placed in 250 ml beakers filled with GF/F filtered *in-situ* water.

Incubation experiments were conducted using 1litre bottles. All the bottles were acid washed (10% HCL) and cleaned with mild soap (Labolene) solutions and rinsed with large quantity of the distilled water. The number of live copepods added in the experimental bottles varied between 10 and 30, which was determined based on the size and quantifiable amount of Chl. *a* clearances (>20% to <60%) in experimental bottles (after 24 hrs. incubation) compared to the control in trial experiments. Totally, 6-8 sets of experiments were conducted in every field sampling, which include 3-5 separate experiments of dominant calanoid copepods; one separate set of experiments each for Cyclopoids, Harpacticoid and Poecilostomatoids. The large grazers of copepods in the food medium were removed from the experimental bottles by a wide mouth pipette as they aggregate towards the sides the vessel when light passes through it in a dark room. The feeding experiments were conducted using the standard protocol (Bamsteadt et al. 2000). Each set of experiments have designed with initial, control and experimental bottles. Initial and control bottles were filled with only the natural prey assemblages but the experimental bottles with prey assemblages and dominant copepods. Quadruplicates were maintained in all experiments (i.e. 4 initial control, 4 final control, and 4 treatments).

The natural food assemblages (unfiltered seawater) were gently mixed (even distribution) and completely filled to all bottles without air bubbles. Pre-determined numbers of copepods were transferred to the experimental bottles. All the bottles were sealed with the parafilm and capped tightly with the lid. The control and experimental bottles were incubated for 24 hrs in the laboratory at near ambient temperature of the surface seawater and the bottles were gently rotated by hands intermittently to avoid the settling of the particles. Total and size fractionated Chl. *a* concentrations of the samples were measured at time zero for the initial bottles and termination of the incubation for the control and experimental bottles. The measurements of the total Chl. *a* and their size fractions were measured using the procedure explained under the section 2.2.

2.5. CALCULATIONS

Ingestion rates of copepods *I* was calculated using the formula of Frost (1972) considering the Chl. *a* disappearance as the index:

$$I = F \times C$$

F was the clearance rate (copepod. Day⁻¹) and *C* mean concentration of the prey during the incubation.

Clearance rate was calculated by:

$$F = [\ln(C_0 - C_e) - \ln(C_0/C_e)] \times V / (t \times N)$$

*C*₀ represents the initial concentrations of the prey; *C*_e the prey concentration in control and experimental bottles at the end of the experiment. *V* is the volume of the incubation bottle in liter; *N* is the number of copepods added to the incubation bottle and *t* the incubation time.

$$C = C_o [e^{Kt} - 1] / K$$

K represents the growth rate of phytoplankton,

$$K = \ln (C_o/C_e)$$

2.6. CARBON CONVERSION

Chl. *a* was converted into carbon units using the ratio of 50:1 (Carbon: Chl. *a* ratio). Body carbon of copepod was calculated via sequential steps - Estimated Spherical Diameter (ESD) measurements of copepods; Biovolume calculations from the ESD; conversion of the bio volumes to wet weights; wet weight to dry weights and then to carbon conversion.

ESD diameter of copepods was measured through a Flow CAM. The biovolume of copepods were calculated using the formulae $BV (mm^3) = 4/3 \pi (ESD/2)^3$

Biovolume was converted into wet weights assuming that the specific gravity of the animals is 1 and therefore $1mm^3 = 1 mg$ wet mass (Winberg 1971; Omari and Ikeda 1984). Wet mass units were converted into dry matter using standard formulae (Madhupratap et al. 1992; Anjusha et al. 2013), subsequently dry weight was converted into the carbon using the formulae of 34.2% of the dry mass = carbon content (Madhupratap, et al. 1982; Anjusha et al. 2013).

2.7. DAILY RATIONS

Daily C ration in each copepods species/ forms was calculated using the formula

$$DR = (I/B) \times 100$$

Where I is the mass of the Phytoplankton carbon, ingested by copepod per day. B is the body mass of copepod and the DR is expressed as percentage.

2.8. ELECTIVITY INDEX

In addition to the clearances rates of copepods, prey preferences in different size category of phytoplankton was assessed through the Electivity index E^* (Vanderploeg and Scavia 1970 a, b). E^* index is stable and compares the proportion of a particular prey type in the natural assemblages with the proportion of that prey type in the predators diet. The steps involved in the calculation of E^* are presented below.

The consumption of each size categorized prey type (pico/ nano/micro) by the copepod (R_i) in each

experimental vessel was determined as follows $R_i = \frac{(N_{ic} + N_{nc})}{2} - N_{fc}$

Where i was the prey item (Pico/nano/micro), N_{ic} was the mean phytoplankton carbon biomass (Pico/nano/micro) present in the initial bottles, N_{ie} was the mean phytoplankton carbon biomass present in the control bottles at the end of the incubation and the N_{it} was the mean number of Chl. a present in each treatment bottle at the end of the incubation. The proportion of each prey type (pico, nano and micro) in the diet (r_i) and in the available medium (n_i) were calculated as

$$r_i = \frac{R_i}{\sum_{j=1}^m R_j}$$

$$n_i = \frac{N_{ic}}{\sum_{j=1}^m N_{jc}}$$

Where m is the number of prey types and R_i and N_{ic} were described above

E^* for each prey type (pico, nano and Micro) was calculated according to the formula

$$E_i^* = \frac{W_i - \frac{1}{m}}{W_i + \frac{1}{m}}$$

Where W_i was defined by the following equation

$$W_i = \frac{\frac{r_i}{n_i}}{\sum_{j=1}^m \frac{r_j}{n_j}}$$

E^* values range from -1 to 1, 0 indicates neutral selection, positive values represent positive selectivity or preference and the negative values represent negative selectivity or avoidance.

2.9. COPEPODS COMMUNITY INGESTION AND GRAZING PRESSURE (%)

Copepod community ingestion was calculated by multiplying the individual copepod grazing rate by *in-situ* abundance during the each sampling period. In the least abundant forms, appropriate sized dominant copepods species ingestion was used to multiplying that. The grazing pressure (%) of copepod community on phytoplankton standing stock was determined by dividing the community ingestion by the standing stock. Community ingestion and grazing pressure were calculated from the total and size fractionated Chl. a during each sampling periods.

2.10. STATISTICAL ANALYSIS

Differences in the ingestion rate of copepods on total and size fractionated Chl. a biomass during the different sampling periods were compared using Parametric / Nonparametric (Kruskal Wallis) ANOVA on the normal/

clumped distribution of the data (Zar 1999). In case of parametric ANOVA, Tukeys HSD post hoc test was used to pair wise comparisons and Dunn's post hoc test for pair wise comparisons in Non-parametric ANOVA. The tests of normality, parametric and nonparametric ANOVA were carried out in XL stat pro- and SPSS software packages.

3. RESULTS

3.1. HYDROGRAPHICAL PARAMETERS

The temporal variations of hydrographical parameters in the coastal area studied (off Kochi) have been presented (Table 1). Surface salinity was high during the Pre-Monsoon (34.15) and Post-monsoon (34.39) compared to the peak (30.70) and Late (33.85) Southwest Monsoon. On the other hand, the subsurface and bottom salinity was high in the study area during the peak (34.90 in subsurface and 35.89 in bottom) and late Southwest Monsoon (35.58 in subsurface and 35.88 in bottom) than during the Pre-Monsoon (34.33 in subsurface and 34.49 in bottom) and post-Monsoon (34.84 in subsurface and 34.87 in bottom). Surface temperature was high during Pre-Monsoon (31.29 °C) and Post-Monsoon (29.62 °C) compared to the Peak Southwest monsoon (27.77 °C) and Late Southwest Monsoon (28.17 °C). Subsurface and bottom temperature was less during the Peak Southwest Monsoon (26.93 °C in subsurface and 23.01 °C in bottom) and Late Southwest Monsoon (24.85 °C in subsurface and 24.49 °C in bottom) compared to the Pre-Monsoon (30.37 °C in subsurface and 29.15 °C in bottom) and Post Monsoon (28.99 °C in subsurface and 27.81 °C in bottom). In the entire water column, the turbidity was less during the Pre-Monsoon as compared to the Peak and Late Southwest Monsoon.

The surface DO was high during the Peak Southwest monsoon (8.24 ml.L⁻¹) and Late Southwest Monsoon (7.29 ml. L⁻¹) but in the subsurface and bottom layers the DO was high during the Pre-Monsoon (5.03 ml.L⁻¹ in subsurface and 3.98 ml.L⁻¹ in bottom) and post-monsoon (4.03 ml.L⁻¹ in subsurface and 3.26 ml.L⁻¹ in bottom). Nitrate and phosphate concentrations were found <2µM during the Pre-Monsoon and Post-Monsoon in surface and bottom layers. During the Peak and Late Southwest Monsoon, nutrient concentrations significantly increased in the entire water column (Table 1). Pre- Monsoon and Post-Monsoon periods were characterized by warm, well oxygenated and nutrient less water column. On the other hand, the Peak and late Southwest monsoon periods were characterized by cool, poorly oxygenated and high nutrient upwelled waters in the subsurface layer.

3.2. TOTAL AND SIZE FRACTIONATED Chl. *a*

The temporal difference in hydrography setting in the sampling area caused noticeable variations in different size fractions of phytoplankton and community structure of copepods. Chl. *a* was less during the Pre-Monsoon (0.58 µg.L⁻¹) and Post Monsoon (0.89 µg.L⁻¹) as compared to the Peak Southwest Monsoon (6.67 µg.L⁻¹)

and Late Southwest Monsoon (4.09 $\mu\text{g}\cdot\text{L}^{-1}$). The contribution of different size fractions of phytoplankton to the total Chl. *a* varied between seasons. Throughout the observations, the total Chl. *a* was contributed significantly by nanoplankton (52.57% to 70.68%) followed by microplankton (20.69% to 45.72%) and pico plankton (1.05 to 9.93%). The percentage of nanoplankton contributions to the total Chl. *a* was the highest during the Pre-Monsoon (70.68%) and Post-Monsoon (62.92%). The microplankton contribution to the total Chl. *a* in surface was the highest during the Peak Southwest Monsoon (41.83%) and Late Southwest Monsoon (45.72%). The contribution of picoplankton to the total Chl. *a* was high during the Pre-Monsoon (8.63%) and Post-Monsoon periods (13.48%) compared to Peak Southwest Monsoon (1.05%) and Late Southwest Monsoon (1.71%) (Fig. 2a).

The qualitative observations of phytoplankton in the study area showed the dominance of diatoms followed by dinoflagellates and blue green algae. During the Pre-Monsoon, *Coscinodiscus* sp., *Rhizosolenia* sp., *Ditylum* sp., and *Thalassonema* sp., were abundant in micro fractions and *Skeletonema costatum*, *Chaetoceros* sp., *Thalassosira subtilis*, *Asterionellopsis* sp., *Nitzhia*, and *Navicula* sp., were abundant in nano-fractions. During the Peak and Late Southwest Monsoon, *Fragillaria* sp., and *Coscinodiscus* sp., was abundant and they contributed high in the micro-fractions. *Skeletonema costatum*, *Chaetoceros* sp., *Thalassosira subtilis* abundance was high in nano-fractions during the Peak and Late Southwest Monsoon. In Dinoflagellates, *Prorocentrum*, *Dinophysis*, *Ornithoceros*, *Gymnodinium*, *Ceratium*, *Gonylux* and *Protoperidinium* were found in relatively higher abundance throughout the observations.

3.3. ZOOPLANKTON, COPEPOD DENSITY AND DOMINANT SPECIES

The zooplankton density in the study area was high during the Peak Southwest Monsoon (4641 $\text{No}\cdot\text{m}^{-3}$) and Late Southwest Monsoon (4156 $\text{No}\cdot\text{m}^{-3}$) compared to the Pre-Monsoon (1626 $\text{No}\cdot\text{m}^{-3}$) and Post-Monsoon (1718 $\text{No}\cdot\text{m}^{-3}$). Copepods contributed 82.58% - 98.49% to the total zooplankton density and their abundance was high during the Peak Southwest Monsoon (4571 $\text{No}\cdot\text{m}^{-3}$) and Late Southwest Monsoon (3432 $\text{No}\cdot\text{m}^{-3}$) compared to the Pre-Monsoon (1354 $\text{No}\cdot\text{m}^{-3}$). During the Pre-Monsoon, 19 species of copepods were recorded wherein 7 species (*Acrocalanus gracilis*, *Paracalanus parvus*, *Acartia danae*, *Acartia erythraea*, *Centropages orsini*, *Oithona similis*, *Corycaeus danae*) were found to be dominant. The dominant copepods during the Peak Southwest Monsoon varied from Pre-Monsoon, consisted of 15 species wherein 8 species (*Oithona similis*, *Paracalanus parvus*, *Acrocalanus gracilis*, *Acartia danae*, *Acartia erythraea*, *Temora turbinata*, *Macrosetella gracilis* and *Corycaeus danae*) were found to be dominant wherein cyclopoid copepod *Oithona similis* alone contributed ~60% of the total copepod density (Table 2). During the Late Southwest Monsoon, *Temora turbinata*, *Pseudodiaptomus serricaudatus*, *Acrocalanus gracilis*, *Paracalanus parvus*, *Acartia danae*, *Acartia erythraea*, *Centropages tenuiremis*, *Euterpina acutifrons*, *Oithona similis* and *Corycaeus danae* were found to be dominant in which calanoid copepods (*Temora turbinata*, *Pseudodiaptomus serricaudatus*, *Acrocalanus gracilis*, *Paracalanus parvus*, *Acartia danae*, *Acartia erythraea*, *Centropages tenuiremis*) together contributed >80% of the total copepod density. During the Post-Monsoon, *Acrocalanus gracilis*,

Paracalanus parvus, *Acartia danae*, *A. erythraea*, *Centropages orsini*, *Euterpina acutifrons*, *Corycaeus danae*, *Oithona similis* were found dominant forms (Table 2).

3.4. GROWTH RATE OF PHYTOPLANKTON

The growth rate of the phytoplankton was calculated based on the differences between the initial and final control bottles (without copepods). The availability of the nutrients alters the growth rate of the phytoplankton biomass between the observations. During the Intermonsoon periods, the growth rate of total phytoplankton was less (Pre-Monsoon 0.23 ± 0.02 and Post-Monsoon 0.30 ± 0.05) compared to the Peak Southwest Monsoon (0.43 ± 0.02) and Late Southwest Monsoon (0.40 ± 0.04). The growth rate of the different size fractions were presented in Fig. 2b. The growth rate of micro and nano phytoplankton fractions was high during the peak (Micro 0.40 ± 0.02 ; Nano 0.46 ± 0.03) and Late Southwest monsoon (Micro 0.32 ± 0.03 ; Nano 0.41 ± 0.01) compared to the Pre-Monsoon (Micro 0.29 ± 0.08 ; Nano 0.32 ± 0.02) and Post-Monsoon (Micro 0.21 ± 0.02 ; Nano 0.35 ± 0.02). The growth rate of picoplankton lack of significant differences between observations and varied from 0.18 to 0.26.

3.5. INGESTION AND DAILY RATIO OF THE DOMINANT COPEPODS

The qualitative representation of phytoplankton intake (red auto fluorescence) by Calanoida, Cyclopoida and Harpacticoid copepods based on laboratory grazing experiments are presented in Fig. 3. *Paracalanus parvus* (*PP*), *Acrocalanus gracilis*, *Acartia danae*, *A. erythraea*, *Oithona similis* and *Corycaeus* sp., were found during the entire sampling period but their phytoplankton carbon ingestion was significantly different during different observations. The mean ESD of *Paracalanus parvus* was 675.12 μm and the individual carbon biomass was 6.61 $\mu\text{g C}$. The *PP* ingestion of phytoplankton carbon ranged from 0.78 to 3.64 $\mu\text{g C. day}^{-1}$ and the ingestion was different during various observations ($P < 0.05$). *PP* ingestion was $< 1 \mu\text{g C. day}^{-1}$ during low Chl. *a* Pre-Monsoon (Av. 0.78 $\mu\text{g C. day}^{-1}$) and Post-monsoon (Av. 0.95 $\mu\text{g C. day}^{-1}$), which was 10.56% and 14.31% of their daily ration. *PP* ingestion was high during the Peak Southwest Monsoon (Av. 3.46 $\mu\text{g C. day}^{-1}$) and Late Southwest Monsoon (Av. 3.64 $\mu\text{g C. day}^{-1}$), sequentially contributing 52.32 and 55.03% of their daily ration (Fig. 4).

The mean ESD and carbon biomass of *Acrocalanus gracilis* (*AG*) were 565.89 μm and 3.87 $\mu\text{g C}$, respectively. Phytoplankton carbon ingestion in *Acrocalanus gracilis* varied significantly during different observations ($P < 0.05$). The *AG* ingestion of phytoplankton biomass was $< 1 \mu\text{g C. day}^{-1}$ during the Pre-Monsoon (Av. 0.46 $\mu\text{g C. day}^{-1}$) and Post-Monsoon (Av. 0.64 $\mu\text{g C. day}^{-1}$), which was 11.89 and 16.41% of their daily ration, respectively. The *AG* carbon ingestion was high during the Peak Southwest Monsoon (Av. 2.46 $\mu\text{g C. day}^{-1}$) and Late Southwest Monsoon (Av. 2.46 $\mu\text{g C. day}^{-1}$) contributing 63.63 and 67.7 % of their daily ration, respectively (Fig. 4).

Acartia danae (AD) and *Acartia erythraea* (AE) were two co-occurring species during the entire observations. The mean ESD of *Acartia danae* and *Acartia erythraea* were 827 μ m and 798.58 μ m, respectively. Individual carbon biomass of the AE and AD was 10.94 and 12.15 μ g C, respectively. The phytoplankton carbon ingestion by *Acartia danae* and *Acartia erythraea* varied significantly during different observations ($P < 0.05$). In both these species, the phytoplankton carbon ingestion was $< 2 \mu\text{g C. day}^{-1}$ during the Pre-Monsoon and Post-Monsoon, and this was 10% of their daily ration. The carbon ingestion of AE and AD increased $> 5 \mu\text{g C. day}^{-1}$ during the Peak Southwest Monsoon (AD Av. 7.25 $\mu\text{g C. day}^{-1}$; AE Av. 6.32 $\mu\text{g C. day}^{-1}$) and Late Southwest Monsoon (AD Av. 6.25 $\mu\text{g C. day}^{-1}$; AE Av. 6.02 $\mu\text{g C. day}^{-1}$), contributing $> 50\%$ of their daily ration (Fig. 4).

Oithona similis (OS) and *Corycaeus danae* (CD) were the two small copepods found during all the observations and their ESD was 496.14 and 475.12 μ m, respectively. The individual carbon biomass of OS was 2.62 μ g C and for CD was 2.30 μ g C. The phytoplankton carbon ingestion by OS ranged from 0.32 - 0.64 $\mu\text{g C. day}^{-1}$ and by CD ranged from 0.28 - 0.67 $\mu\text{g C. day}^{-1}$. The phytoplankton carbon ingestion by OS was $< 0.4 \mu\text{g C. day}^{-1}$ during the Pre-Monsoon and Post-Monsoon, but their ingestion was 0.57 $\mu\text{g C. day}^{-1}$ during the former period and 0.64 $\mu\text{g C. day}^{-1}$ during the latter period. Phytoplankton carbon ingestion by CD was $< 0.3 \mu\text{g C. day}^{-1}$ or $< 12\%$ of their DR during the Pre-Monsoon and Post-Monsoon. Phytoplankton carbon ingestion by CD was 0.47 and 0.67 $\mu\text{g C. day}^{-1}$ during the Peak and Late Southwest Monsoon, respectively, contributing 17 and 25% of their daily ration (Fig. 4).

During the Pre-Monsoon and Post-Monsoon periods, *Centropages orsinii* (CO) was abundant in the study area. The mean ESD of CO was 818.56 μ m and carbon biomass 11.78 μ g C. The phytoplankton carbon ingestion by CO was 1.08 $\mu\text{g C. day}^{-1}$ during Pre-Monsoon and 1.52 $\mu\text{g C. day}^{-1}$ during the Post-Monsoon, contributing $< 15\%$ to their daily ration. During the Peak and Late Southwest Monsoon, *Temora turbinata* (TT) was abundant and their mean ESD diameter and carbon biomass was 824.12 μ m and 12.02 μ g C, respectively. The phytoplankton carbon ingestion of *Temora turbinata* during the Peak Southwest Monsoon and Late Southwest Monsoon were 6.85 μ g C. day^{-1} and 6.46 $\mu\text{g C. day}^{-1}$, respectively contributing 84.02 and 73.58 % of their daily ration (Fig. 4).

Pseudodiaptomus serricaudatus (PS), *Centropages tenuiremis* (CT) dominated during the Late Southwest Monsoon. The mean ESD and carbon biomass of PS was 845.29 μ m and 12.97 μ g C, respectively (Table 3). The mean ESD and individual carbon biomass of CT was comparable with that of PS. The phytoplankton carbon ingestion by PS was 9.53 $\mu\text{g C. day}^{-1}$ and this was 73.58% of their daily ration. Phytoplankton carbon ingestion in CT was 6.46 $\mu\text{g C. day}^{-1}$, which was 49.69% of their daily ration. Harpacticoid copepod *Macrosetella gracilis* (MG) was abundant in the study area during the Peak Southwest Monsoon. The mean ESD and carbon biomass of MG was 696.42 μ m and 7.25 μ g C, respectively. The phytoplankton carbon ingestion in MG was 3.25 $\mu\text{g C. day}^{-1}$ contributing 44.88% of their daily ration. *Euterpina acutifrons* (EA) was abundant during the Late Southwest monsoon and Post-Monsoon periods. The mean ESD and carbon

biomass of *EA* was 468.14 μm and 2.20 $\mu\text{g C}$, respectively. Phytoplankton carbon ingestion in *EA* was 1.19 $\mu\text{g C. day}^{-1}$ during the late Southwest monsoon and 0.98 $\mu\text{g C. day}^{-1}$ during the Post monsoon, contributing 53 and 43% of their daily ration. (Fig. 4).

3.6. Food selectivity

The quality and quantity of the phytoplankton biomass available significantly alters the food selectivity of copepods. *Paracalanus parvus* (*PP*), *Acrocalanus gracilis* (*AG*), *Acartia danae* (*AD*), *Acartia erythraea* (*AE*), showed positive E^* values with micro and nano phytoplankton fraction during the Pre-Monsoon and Post-Monsoon periods. During the Peak and Late Southwest Monsoon, the above species showed a positive E^* values only with nano phytoplankton fraction. Irrespective of seasons, *Oithona similis* and *Corycaeus danae*, showed positive E^* values with nano and pico phytoplankton fractions. All the dominant calanoid copepods of Peak and Late Southwest monsoon periods showed positive E^* values for nano phytoplankton fraction and negative E^* values for micro and pico phytoplankton fractions (Fig. 5).

3.7. Copepod community grazing and their grazing pressure on phytoplankton

The copepod community ingestion significantly varied between the observation, which was related to the copepods density, species composition, ingestion and food preferences of each copepod species. The details about the standing stock and production of the total and different size fractions of phytoplankton are presented in (Figs. 6 & 7a - 7c). The copepods community ingestion of phytoplankton was ranged from 945 to 14047 $\mu\text{g C. m}^{-3}$ showing the large variations between the observations. The copepods community ingestion was high during the Late Southwest Monsoon followed by the Peak Southwest Monsoon and least during the Pre-Monsoon. The copepods community ingestion in different size fractions and their grazing pressure on standing stock also varied significantly between observations ($P < 0.05$).

During the Pre-monsoon, copepods community ingestion was 946 $\mu\text{g C. m}^{-3}$, wherein 25.6% (242.5 $\mu\text{g C. m}^{-3}$) was consumed from micro fraction, 70.2% from nano fraction (663.3 $\mu\text{g C. m}^{-3}$) and 4.2 % from pico fraction. The grazing pressure of copepod community was 3.26% on total phytoplankton standing stock and 11.23% on the phytoplankton production. In micro-phytoplankton fraction, grazing pressure of copepod community was 4.04% of the standing stock and 22.73% of the production. In nano- phytoplankton fraction, grazing pressure was 3.24% of the standing stock and 9.77% of the production. In pico fraction, copepods community ingestion was 1.58% of the standing stock and 7.06% of production (Figs. 6 & 7a - 7c).

During the Peak Southwest Monsoon, copepods community ingestion was 9050 $\mu\text{g C. m}^{-3}$, wherein 8.7 % was from micro-phytoplankton (785 $\mu\text{g C. m}^{-3}$), 88.8% (8038 $\mu\text{g C. m}^{-3}$) from nanoplankton and 2.5% (227 $\mu\text{g C. m}^{-3}$) from pico-plankton fraction. Grazing pressure of copepods community on total phytoplankton standing stock was 2.71% and production was 4.9%. The grazing pressure of copepods on the micro phytoplankton fraction was 0.56% of the standing stock and 1.06% of the production. The grazing pressure of the copepods

on nano phytoplankton fraction was 4.25% of the standing stock and 7.35% of the production. The grazing pressure of the copepods community ingestion on pico plankton fraction was 4.55% of the standing stock and 17.88% of the production (Figs. 6 & 7a - 7c) .

During the Late Southwest Monsoon, copepod community ingestion was 18583 $\mu\text{g C. m}^{-3}$, wherein 16.87% was consumed from micro-fraction (3135 $\mu\text{g C. m}^{-3}$), 81.17% (15084 $\mu\text{g C. m}^{-3}$) from nano fraction and 1.96% (364 $\mu\text{g C. m}^{-3}$) from pico-fraction. The grazing pressure of copepod community on the total phytoplankton was 10.35% of the standing stock and 21.57% of the production. The grazing pressure of copepods community on micro fraction was 8.14% of the standing stock and 18.30% of the production. In nano phytoplankton fraction, the grazing pressure of the copepods community was 10.97% of the standing stock and 22.35% of the production. The grazing pressure of the copepods community on the pico-phytoplankton fraction was 10.4% of the standing stock and 28.61% of the production (Figs. 6 & 7a - 7c).

During the Post-monsoon, copepods community ingestion was 1813 $\mu\text{g C. m}^{-3}$, in which 17.54% (318 $\mu\text{g C. m}^{-3}$) was from the micro fraction, 78.6% (1425 $\mu\text{g C. m}^{-3}$) from nano fraction and 3.86% (70 $\mu\text{g C. m}^{-3}$) from pico fraction. The grazing pressure of copepod community grazing on total phytoplankton standing stock was 4.07% and production was 11.56%. The grazing pressure of copepods community on micro phytoplankton was 3.03% of the standing stock and 12.71% of production. The grazing pressure of copepods community on nano phytoplankton fraction was 5.09% of the standing stock and 12.18% of the production. The grazing pressure of copepods community on pico fraction was 1.17% of the standing stock and 4.69% of the production (Figs. 6 & 7a - 7c).

4.0 DISCUSSION

Earlier studies from elsewhere showed significant seasonal variations in copepod feeding, which was linked with the food concentrations in their surroundings (Gifford and Dagg 1988; Ohman and Runge 1994; Nakamura and Turner 1997; Rollwagen- Bollens and Pentry 2003). The present study area (coastal waters off Kochi) is also characterized by large variations in hydrographical setting and hence the abundances of phytoplankton, microzooplankton and detritus. During the Pre-Monsoon, the present study area is characterized by warm, stratified, low nutrients waters with low phytoplankton biomass and productivity (Jyothibabu et al. 2008; Madhu et al. 2007). This period is also characterized by high microzooplankton abundance (Jyothibabu et al. 2006; 2008). During the Peak and late Southwest monsoon, coastal waters off Kochi is characterized by high estuarine inputs associated and coastal upwelling high nutrient availability in the water column causing high phytoplankton biomass and production (Madhupratap et al. 2001; Jyothibabu et al. 2006; Madhu et al. 2007; Jyothibabu et al. 2008). All these indicate a noticeable difference in the quality and quantity of copepod food items in the study area during different seasons.

All the seasonal characteristics of coastal waters of Kochi explained in the above paragraph was evident in the present study as well. Within the phytoplankton community itself, there were noticeable seasonal changes in the quality and quantity. One feature remained unchanged was the predominance of nanoplankton contribution to the total phytoplankton stock irrespective of seasons (52.57% to 70.68%). The micro fraction contribution to the total Chl. *a* was found significant only during the Peak and later Southwest Monsoon. The growth rate of the total and different size fractions of phytoplankton varied in different observations. The growth rate of phytoplankton was high during the Peak and late Southwest monsoon compared to the Pre-monsoon and Post-monsoon. It was noticed earlier that low nutrient environments decreases the growth of the diatoms and daily production (Campbell et al. 1993; Froneman 2004; Campbell et al. 2009) as in the case of Pre-Monsoon and Post- Monsoon season in the present study.

The copepod community ingestion and grazing pressure on phytoplankton mainly depends upon the density of the copepods and their ingestion rates, food type, quality and quantity, size structure. *Paracalanus parvus*, *Acrocalanus gracilis*, *Acartia danae* and *A. erythraea* were found in the study area throughout the observation but, but their daily ration significantly varied between observations. During the Pre-Monsoon, *Paracalanus parvus*, *Acrocalanus gracilis*, *Acartia danae* and *Acartia erythraea* consumed the very less phytoplankton carbon (<10% of their daily ration) indicating that these species consume large portion of their nutritional requirements from food sources other than phytoplankton (Fessenden and Cowles 1994; Lonsdale et al. 2000; Rollwagen- Bollens and penry 2003). Irigoien and Castel (1995) pointed out that environments with low phytoplankton concentration are incapable to provide all the metabolic requirements of copepods, and in such cases microzooplankton becomes an important food items in the diet of these species. It was clear in the present study that during the Pre-Monsoon and Post-Monsoon (low phytoplankton periods), the ingestion of phytoplankton carbon by *Paracalanus parvus*, *Acrocalanus gracilis*, *Acartia danae* and *A. erythraea* (Fig. 4) was much lesser (<15% of DR) than their normal requirement (>50% of their daily ration). This observation was strongly supported by several earlier researchers and noticed that copepods ingest low amount of phytoplankton stock and large amount of microzooplankton biomass in oligotrophic environments (Fessenden and Cowles 1994; Lonsdale et al. 2000; Rollwagen- Bollens and penry 2003; Verity and paffenhofer 1996; Levinsen et al. 2000; Tang and Taals 2005; Calbet and Saiz 2005).

During the Peak and Late Southwest Monsoon period, phytoplankton carbon ingestion in experiments by *Paracalanus parvus*, *Acrocalanus gracilis*, *Acartia danae*, *Acartia erythraea* was >50% of their daily ration which could be linked to the high standing stock of phytoplankton available in the natural environment (Figs. 2 & 4). Copepods in general ingest phytoplankton in higher rates than other food types during the period of high phytoplankton concentration (Irigoien and Castel 1995; Fronmen 2004; Fronmen 2006). *Oithona similis* and *Corycaeus danae* were the two non calanoid copepods found during entire observations. The ingestion of the phytoplankton carbon biomass by *Oithona similis*, *Corycaeus danae* never exceeds >20% of their daily ration in any of the experiments, strongly suggesting that these two species chiefly consume other food items

(microzooplankton) for their daily ration irrespective of the seasons. *Oithonidae*, and *Corycaidae* are confirmed as primary carnivorous, feeding actively on motile prey (Turner 2004; Atkinson 1996). The phytoplankton carbon ingestion of *Temora turbinata* was found to be >70% of their daily ration. This could be the reason why *Temora turbinata* form swarms along the Southwest coast of India during the Late Southwest monsoon (Madhupratap et al. 2001; Gowsami and Padmavati 1996). Similar was the case of *Pseudodiaptomus serricaudatus* which is abundant along the west coast of India during the Southwest Monsoon (Madhupratap et al. 2001; Gowsami and Padmavati 1996).

High abundance of *Macrosetella gracilis* in natural samples was noticeable during the Peak Southwest Monsoon which could be attributed to their high carbon ingestion (>50%) from phytoplankton. *Euterpina acutifrons* is abundant in the study area during the Late Southwest Monsoon and Post-Monsoon. In *Euterpina acutifrons*, the phytoplankton carbon ingestion was > 50% of their daily ration during the Late Southwest monsoon but their phytoplankton ingestion during the Post - monsoon was <20% of the daily ration. This indicate that *Euterpina acutifrons* effectively utilize phytoplankton carbon during the Late Southwest Monsoon and non-phytoplankton carbon (mostly detritus) during the Post Monsoon. Recent culture studies showed that harpacticoid copepods successfully survive on diets of phytoplankton and detritus (Jeyaraj et al. 2014).

Food electivity (E^*) is one of the most important processes in relation to adaptive strategies and competition for food resources between species (Lee et al. 2012). The consumption of phytoplankton by grazers strongly depends on their size structure (Bautista and Harris 1992; Lee et al. 2012). Calanoid copepods showed both positive electivity on micro and nano plankton fractions (Fig.4) during low phytoplankton standing stock periods (Pre-Monsoon and Post-Monsoon), whereas they showed positive E^* values on nano phytoplankton during high phytoplankton standing stocks period (Peak Southwest Monsoon and Late Southwest Monsoon). Agreeing to this, Lee et al. (2012), showed that calanoid copepods are more selective during high concentration of food. Several earlier researchers noticed that calanoid copepods effectively feed on 5 – 25 μm cells (Sautour et al. 2000; Paffenhöfer et al. 1982; Price et al. 1983; Tackx et al. 1989). Calanoid copepods showed a negative selection to picoplankton fractions as noticed earlier elsewhere (Sautour et al. 2000; Paffenhöfer et al. 1982; Price et al. 1983). *Oithona similis* and *Coryceus danae* showed positive E^* values on nano and pico plankton fractions and negative E^* values on micro plankton fraction.

The overall copepod community ingestion was less during the Pre-Monsoon and Post-Monsoon periods and this was related with the low abundance of copepods and very low phytoplankton available for copepods ingestion, the shift in the food preferences of the dominant copepods phytoplankton into non-phytoplankton diets. Even though, copepods density was the highest during the Peak Southwest Monsoon, the highest amount of copepod community ingestion was found during the Late Southwest Monsoon and this was due to the significantly higher abundance of *Oithona similis*. Similar kinds of observation of high copepod abundance with lesser community ingestion was reported by Lee et al. (2012) when a cyclopoid copepod

significantly dominated in the total density. We accept here that as the present experimental studies were carried out in the laboratory, there could be a certain percentage of error in the rate measurements as compared to the field conditions, which is unavoidable in the present experimental approach. However, we tried our best to minimize the error by incubating the experimental bottles in near-field conditions and also by decreasing the particle settling by periodic gentle shaking of the bottles during the incubation period.

Grazing impact by copepods is a key factor in controlling composition and dynamics of phytoplankton communities in marine ecosystems (Sterner 1989; Banse 1994; Banse et al. 1996; Kagami et al. 2002; Pagano et al. 2006). The grazing impacts of copepods on phytoplankton biomass are variable, ranging from <10% to 30% to standing stock (Morales et al. 1991; Bautista and Harris 1992; Dagg 1995; Froneman 2000; Grunewald et al. 2002; Li et al. 2003; Kibirige and Perisinotto 2003). Copepods normally consumed <30% of the daily phytoplankton production (Landry et al. 1994; Rollwagen Bollens and Landry 2000; Bautisa and Harris 1992). The grazing pressure of the copepods ingestion on the phytoplankton standing stock in the present study ranged from 2.71 to 7.83% of the total standing stock and 4.9 to 16.31% of the production (Figs. 5). The high grazing pressure of copepods on phytoplankton standing stock and production was found during the Late Southwest Monsoon (Figs. 5). The grazing pressure of the copepods community ingestion on different size fractionated phytoplankton standing stock and production differed between the observations (Figs. 6 & 7a - 7c); this was mainly due to the size selectivity ingestion of copepods and the species composition in the total copepods density (Bautista and Harris 1992). Kleppel (1993) pointed out copepods effectively consume >5 μm and <20 μm sized phytoplankton cells. Copepods are try to intake of larger phytoplankton cells from their surroundings (Jansen 2008), but they unable to succeed in 100% because of their small mouth size, this leads to the sloppy feeding, this was evident in presented images from experiment and insitu observations (Fig. 8). Nonetheless, it was clear in the present study that the dominant copepods are unable to control the micro phytoplankton blooms due to their grazing preferences towards nano size fraction during the Peak Southwest Monsoon and Late Southwest Monsoon. This observation is particularly significant while considering the fact that larger diatom such as *Fragilaria* and *Coscinodiscus* cause extensive blooms (Fig. 8) along the Southwest coast of India during the Southwest Monsoon.

5. SUMMARY AND CONCLUSION

The copepod grazing on the total and size fractionated phytoplankton biomass in a coastal environment (Off Kochi, Southwest coast of India) were measured during Pre-Monsoon (PRM), Peak Southwest Monsoon (PKSWM), Late Southwest Monsoon (LSWM) and Post -Southwest Monsoon (PSWM). The phytoplankton standing stock (Chlorophyll *a* - Chl. *a*) and growth rate (GR) were found to be less during the PRM (Chl. *a* 0.58 mg. m⁻³; GR 0.23 \pm 0.02) and PSWM (Chl. *a* 0.89 mg. m⁻³; GR 0.30 \pm 0.05) compared to PKSWM (Chl. *a* 6.67 mg. m⁻³; GR 0.43 \pm 0.02) and LSWM (Chl. *a* 4.09 mg. m⁻³; GR 0.40 \pm 0.04). Copepods density was less during the PRM (1354 No.m⁻³) and PSWM (1606 No.m⁻³) than PKSWM and LSWM (4571 and 3432 No.m⁻³, respectively). The dominant calanoid copepods studied ingested 8.4 to 14.2% of their daily ration

from phytoplankton during the PRM and PSWM, which increased to >50 % during the PKSWM and LSWM. The Cyclopoid *Oithona similis* was abundant during the PKSWM, which ingested only 21% of their daily ration from phytoplankton. The copepods community ingestion on phytoplankton was in general high during the LSWM (18583 $\mu\text{g.C.m}^{-3}$) followed by PKSWM (9050 $\mu\text{g.C.m}^{-3}$), PSWM (1813 $\mu\text{g.C.m}^{-3}$) and PRM (946 $\mu\text{g.C.m}^{-3}$). During PRM and PSWM, dominant calanoid copepods showed a positive selectivity on micro- and nano- phytoplankton, whereas during PKSWM and LSWM, they showed a positive selection on nano-phytoplankton fractions. In general, dominant calanoid copepods showed a negative selection on pico-phytoplankton. Cyclopoid *Oithona similis* and Poecilostomatoid *Corycaeus danae* were positive selection on nano - and pico-phytoplankton rather than micro fractions. The grazing of copepods on micro fractions was less (0.56 % of phytoplankton biomass and 1.06% of phytoplankton production) during the PKSWM. This study provide, for the first time, clearly explained the seasonal difference in the top down control of phytoplankton in the coastal waters off Kochi, including phytoplankton bloom formation and structuring the plankton food web.

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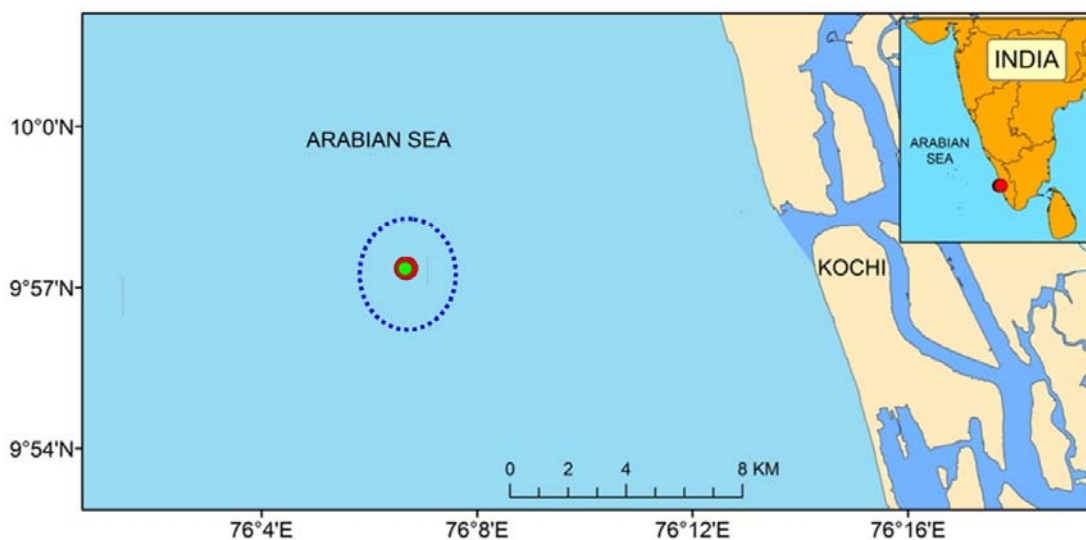


Fig. 1 - The sampling location in the coastal waters off Kochi (blue dotted circle).

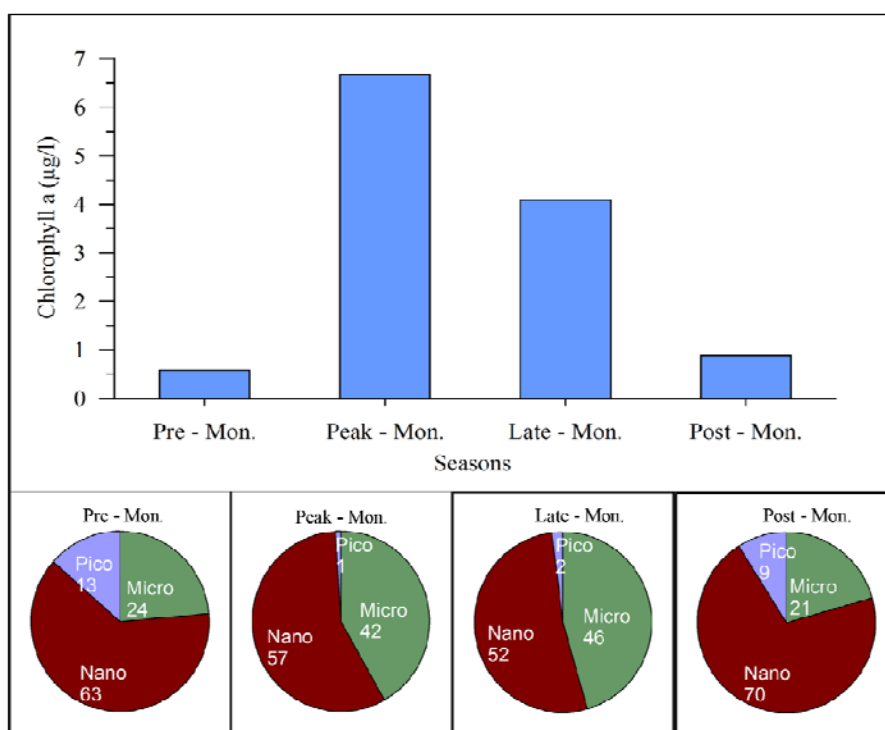


Fig. 2a - Total chlorophyll *a* distribution (Bar chart) and the percentages of micro, nano and pico fractions contribution to the total chlorophyll *a* during the Pre –Monsoon (Pre - Mon.), Peak- Southwest Monsoon (Peak – Mon.), Late – Southwest Monsoon (Late - Mon.) and Post – Southwest Monsoon (Post – Mon.). The contribution of the micro fraction to the total chlorophyll *a* was comparatively high during the peak and late Monsoon than the Pre and Post monsoon periods.

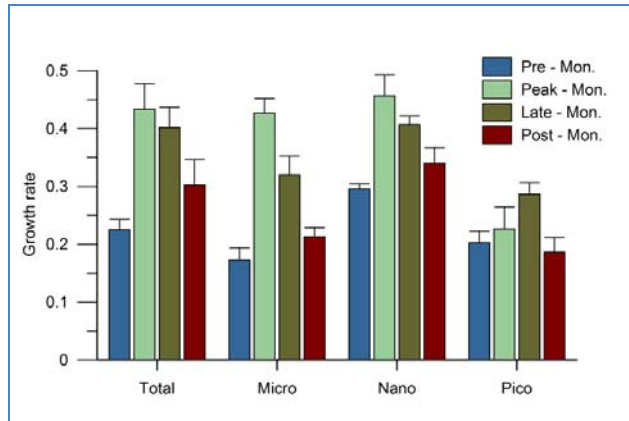


Fig. 2b – Growth rate of the total and size fractionated plankton biomass during the Pre - Monsoon (Pre -Mon.), Peak Southwest Monsoon (Peak - Mon.), Late – Southwest Monsoon (Late - SWM) , Post - Monsoon (Post – Mon.)

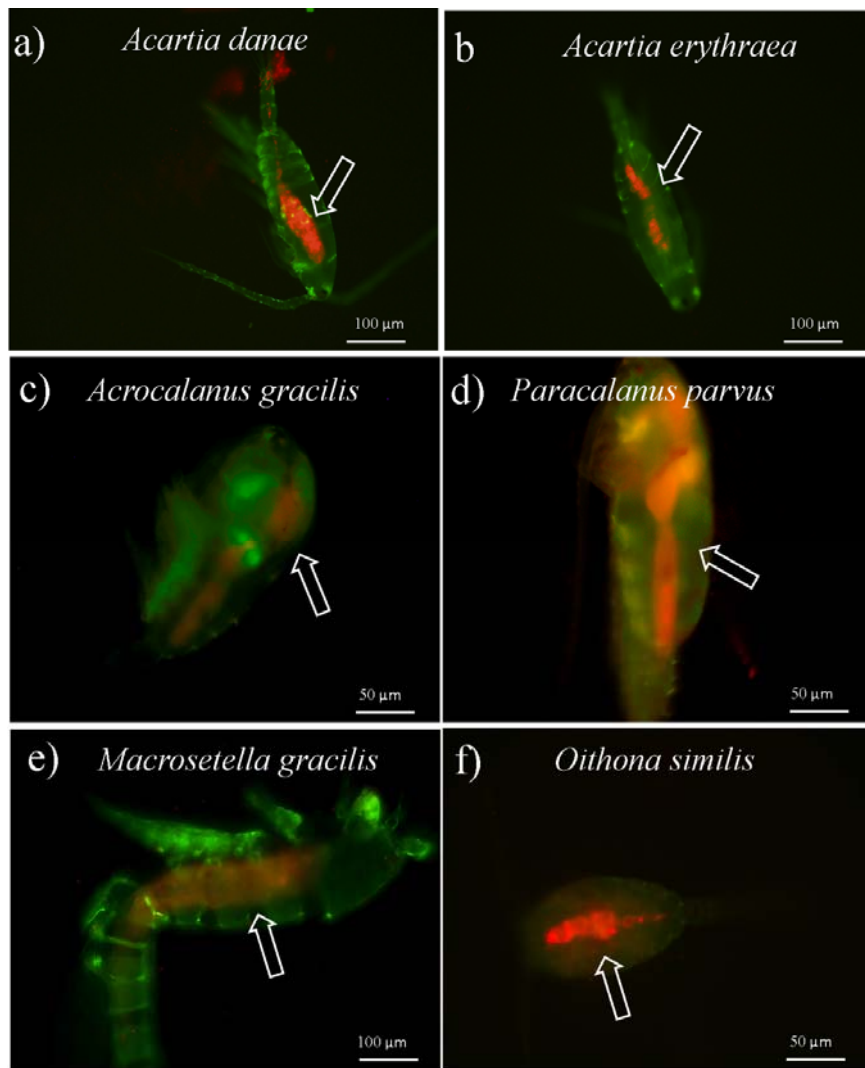


Fig. 3 - The qualitative observational results of some dominant copepod species feeding (a) *Acartia danae*, (b) *Acartia erythraea*, (c) *Acrocalanus gracilis*, (d) *Paracalanus parvus*, (e) *Macrosetella gracilis* and (e) *Oithona similis*. White arrows represents the presence of phytoplankton cells (red auto fluorescence under blue light excitations) inside of the digestive tract.

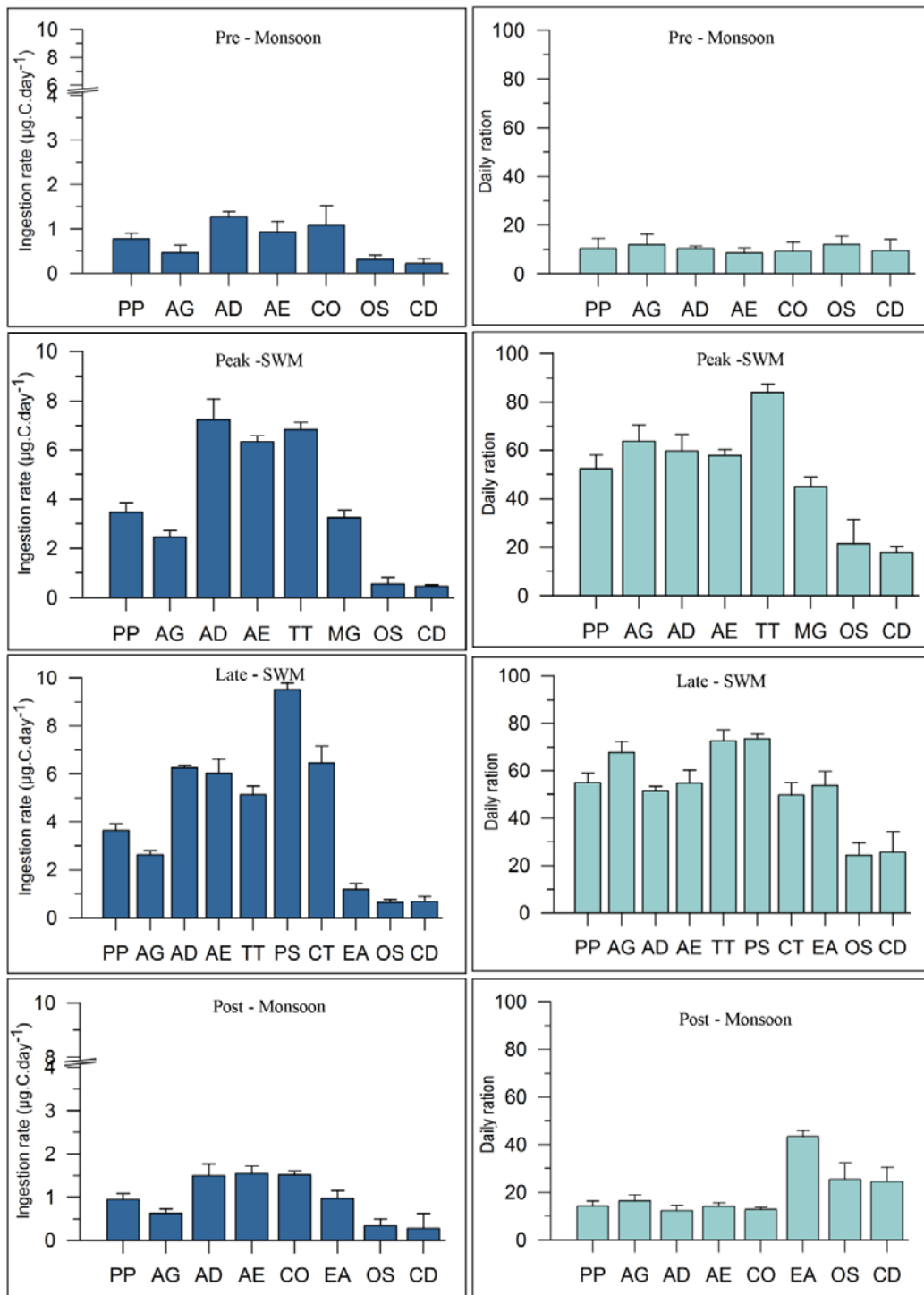


Fig. 4 - Phytoplankton carbon ingestion ($\mu\text{g.C.day}^{-1}$) and their daily ration of the dominant copepods species during the different periods. Abbreviations of the species names are accordance with Table 2.

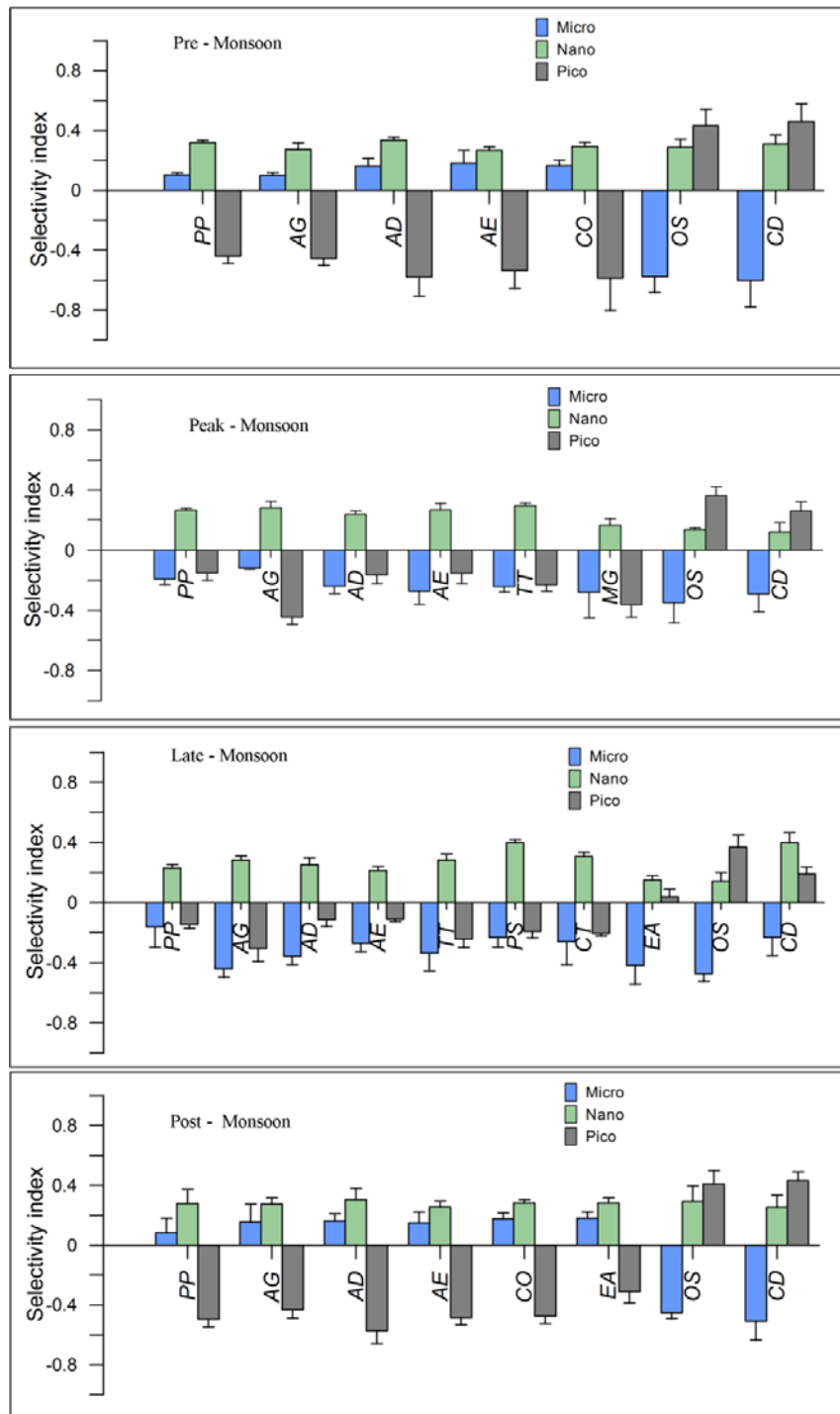


Fig. 5 - Size selectivity index (E^*) of dominant copepod species during the Pre – Southwest Monsoon (Pre -Monsoon), Peak Southwest Monsoon (Peak- Monsoon), late Southwest Monsoon (Late – Monsoon) and Post-Southwest Monsoon (Post - Monsoon). E^* values range from -1 to 1, 0 indicates neutral selection, positive values represent positive selection or preference and the negative values represent negative selection or avoidance. Abbreviations of the species names are accordance with Table 2.

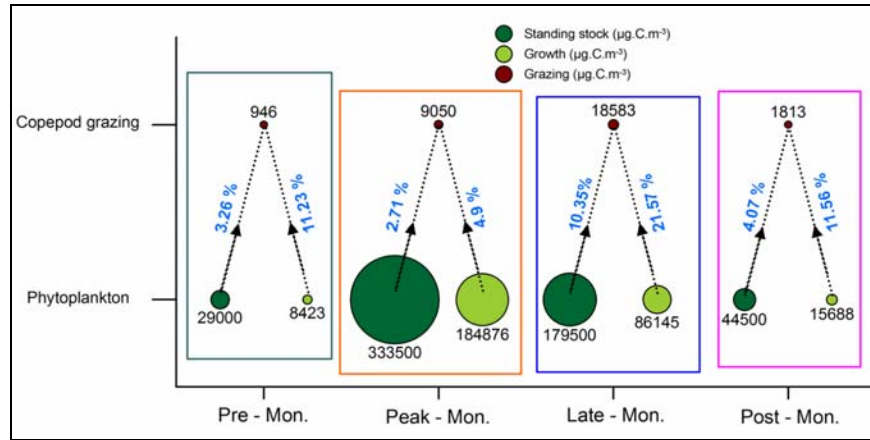


Fig. 6 - Grazing pressure (percentages) of the copepods community ingestion (brown bubbles) in standing stock (dark green bubbles) and production (Light green bubbles) of total phytoplankton biomass during Pre – Southwest Monsoon (Pre -Mon.), Peak – Southwest Monsoon (Peak - Mon.), Late – Southwest Monsoon (Late – Mon.), Post – Southwest Monsoon (Post – Mon.).

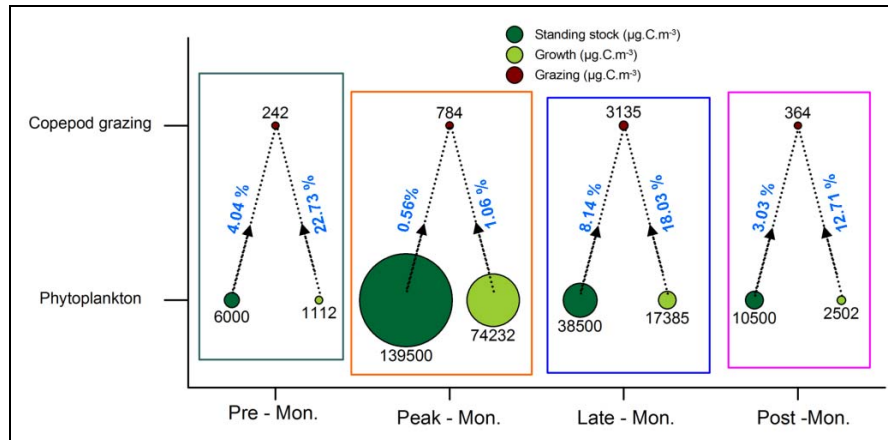


Fig. 7a - Grazing pressure (percentages) of the copepods community ingestion (brown bubbles) in standing stock (dark green bubbles) and production (Light green bubbles) of micro -phytoplankton biomass during different seasons.

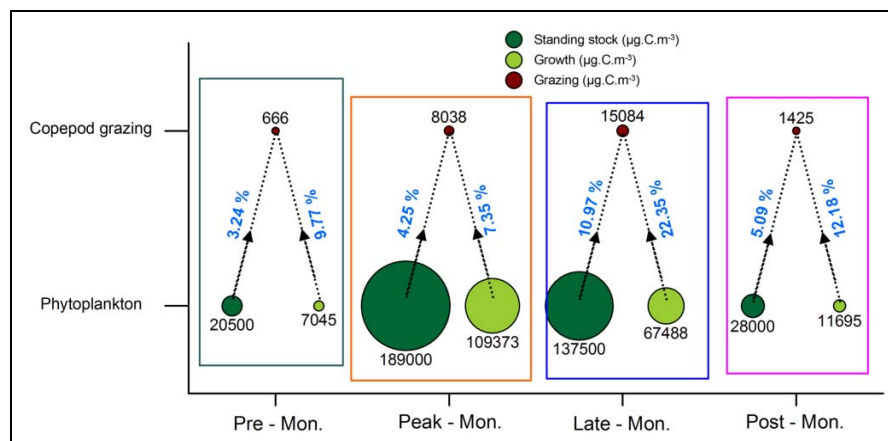


Fig. 7b - Grazing pressure (percentages) of the copepods community ingestion (brown bubbles) in standing stock (dark green bubbles) and production (Light green bubbles) of nano -phytoplankton biomass during different seasons.

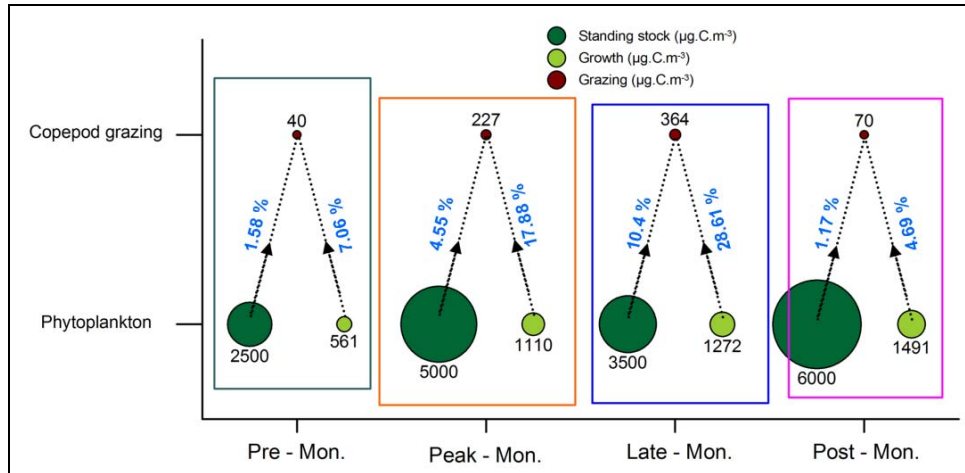


Fig. 7c - Grazing pressure (percentages) of the copepods community ingestion (brown bubbles) in standing stock (dark green bubbles) and production (Light green bubbles) of pico-phytoplankton biomass during different seasons.

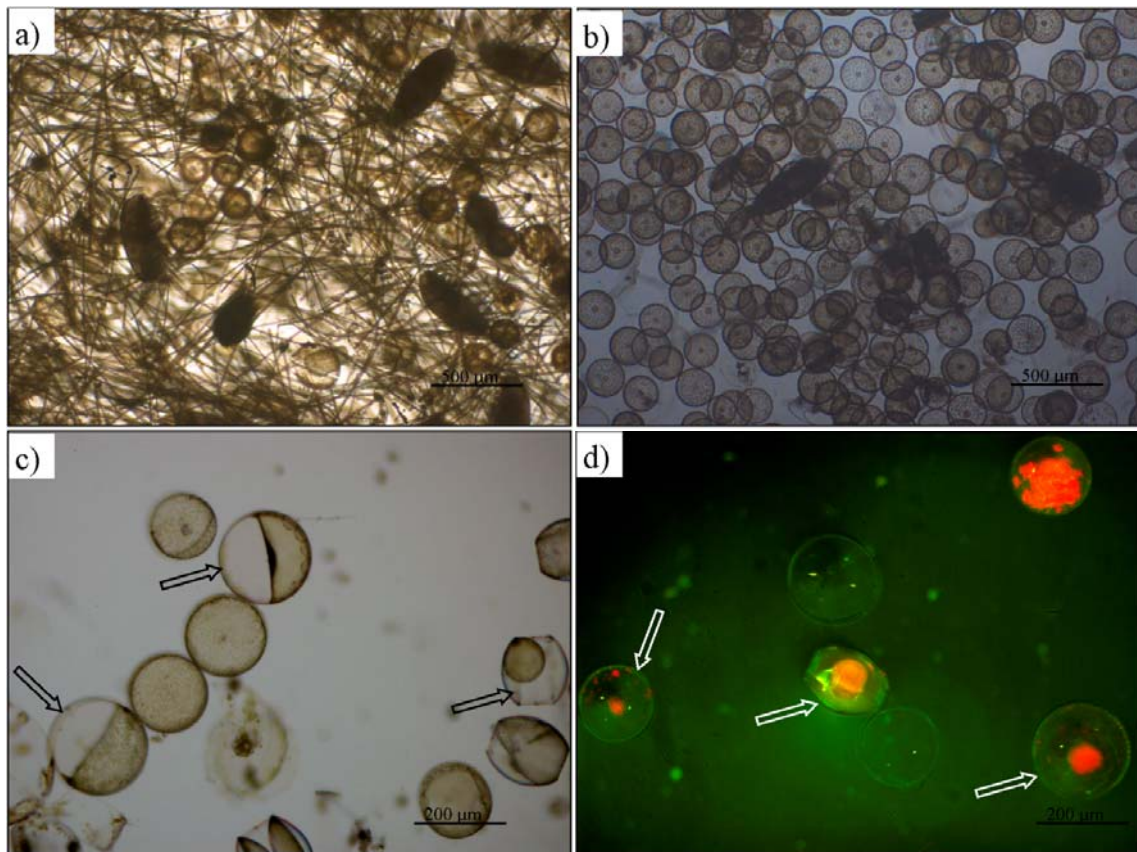


Fig. 8 – Mixed diatoms blooms of *Fragillaria* and *Coscinodiscus* (a and b) was observed in the study domain during the Peak and Late Southwest Monsoon. The partial consumption/Sloppy feeding of larger diatoms by copepods was found in the experiment and *insitu* observations during the peak and Late Southwest Monsoon periods.

Table 1 - Distribution of the physico-chemical and biological parameters during the Pre - Monsoon, Peak Southwest Monsoon (Peak – Monsoon) , Late Southwest Monsoon (Late – Monsoon), Post Southwest Monsoon (Post –Monsoon). S – Surface, M – Subsurface and B – Bottom.

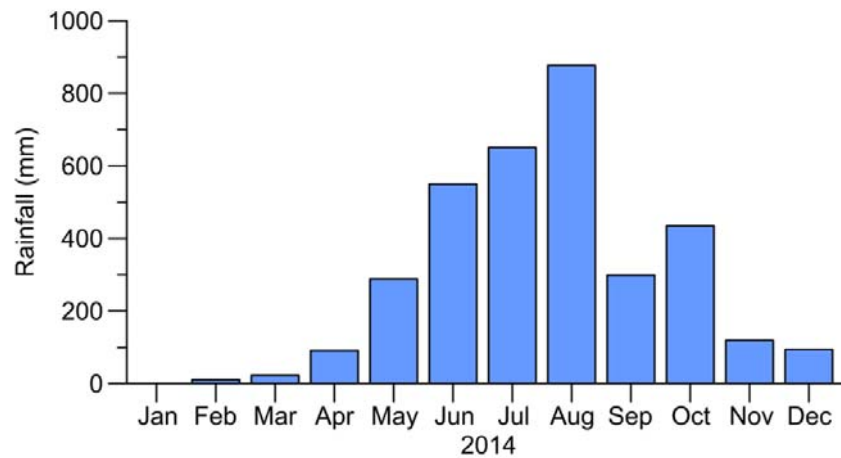
Parameters	Depth	Pre - Monsoon	Peak - Monsoon	Late - Monsoon	Post - monsoon
Salinity	S	34.15	30.70	34.09	34.38
	M	34.33	34.90	35.58	34.84
	B	34.49	35.88	35.88	34.87
Temperature (°C)	S	31.29	27.77	28.16	29.62
	M	30.37	26.93	24.86	28.99
	B	29.14	23.01	23.49	27.80
DO (ml.L ⁻¹)	S	5.47	8.24	7.29	5.93
	M	5.03	3.57	2.82	4.03
	B	3.98	0.56	1.60	3.26
Turbidity (NTU)	S	1.02	3.41	2.14	1.27
	M	1.46	4.30	3.0	1.41
	B	2.14	5.66	4.96	2.24
Nitrate (µM)	S	0.56	7.33	5.30	1.64
	M	0.61	8.95	6.15	1.77
	B	0.82	9.73	8.17	1.63
Phosphate (µM)	S	0.18	1.92	1.22	0.46
	M	0.24	2.02	1.66	0.65
	B	0.31	2.14	1.82	0.90
Zoo. density (No.m ⁻³)	S	1626	4641	4156	1718
Cope. density (No.m ⁻³)	S	1342	4571	3432	1606

Table 2 - List of dominant copepod species (>50 No.m⁻³ in any one of the seasons) and their density (No. m⁻³) during Pre-Monsoon (PRM), Peak Southwest Monsoon (PKSWM), Late Southwest Monsoon (LSWM) and Post Southwest Monsoon (PSWM). – represents absences/less abundance.

	Species	Abbreviations	PRM	PKSWM	LSWM	PSWM
1	<i>Acrocalanus gracilis</i>	AG	136.12	53.25	240.05	225.01
2	<i>Paracalanus parvus</i>	PP	205.82	175.78	470.5	201.72
3	<i>Acartia danae</i>	AD	504.18	85.22	222.34	233.32
4	<i>Acartia erythraea</i>	AE	288.12	83.22	53.51	240.45
5	<i>Pseudodiaptomus serricaudatus</i>	PS	-	-	989.53	-
6	<i>Temora turbinata</i>	TT	-	576.71	685.27	-
7	<i>Centropages orsini</i>	CO	97.56	-	-	214.63
8	<i>Centropages tenuiremis</i>	CT	-	-	139.04	-
9	<i>Euterpina acutifrons</i>	EA	-	-	117.27	129.62
10	<i>Macrosetella gracilis</i>	MG	-	182.52	-	-
11	<i>Oithona similis</i>	OS	52.31	3273.43	333.25	106.32
12	<i>Corycaeus danae</i>	CD	53.21	70.84	140.16	191.86
	Others		16.68	70.03	41.08	63.07

Table 3 - The details about mean ESD diameter, ESD volume, Body length, body width and individual carbon content of the dominant copepod species.

Copepod species	ESD Diameter (μm)	ESD Volume (mm^{-3})	Body Length (μm)	Body Width (μm)	Individual Carbon ($\mu\text{g C}$)
1 <i>Acrocalanus gracilis</i>	565.89	0.09	663.01	298.65	3.87
2 <i>Paracalanus parvus</i>	675.12	0.16	771.71	583.41	6.61
3 <i>Acartia danae</i>	827.14	0.30	955.56	558.84	12.15
4 <i>Acartia erythraea</i>	798.58	0.27	1005.27	485.78	10.94
5 <i>Centropages orsini</i>	818.56	0.29	1065.58	623.52	11.78
6 <i>Centropages tenuremis</i>	846.14	0.32	1089.54	605.52	13.01
7 <i>Temora turbinata</i>	824.12	0.29	910.23	556.54	12.02
8 <i>Pseudodiaptomus serricaudatus</i>	845.29	0.32	1021.46	627.45	12.97
9 <i>Oithona similis</i>	496.14	0.06	610.43	263.41	2.62
10 <i>Macrosetella gracilis</i>	696.42	0.18	906.16	305.46	7.25
11 <i>Euterpina acutifrons</i>	468.14	0.05	864.52	296.52	2.20
12 <i>Corycaeus danae</i>	475.12	0.06	584.14	248.15	2.30



Supplementary information – Monthly total rainfall of Ernakulum district (study area) visualizing the differences in rainfall.