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Phytoplankton community structure at the juncture of the Agulhas Return Front and Subtropical Front in the Indian Ocean sector of Southern Ocean: Bottom-up and top-down control

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ABSTRACT

The juncture of the Agulhas Return Front (ARF) and Subtropical Front (STF) in the Indian Ocean sector of Southern Ocean (SO) is characterized by high mesoscale turbulence, which results in sporadic, short lived phytoplankton proliferation. The biota, mainly the phytoplankton community from such a complex hydrodynamic region and its response to the mesoscale turbulence, are areas of interest for investigation. Hence, during the sixth Indian expedition to SO, a two-day time series was occupied at the ARF and STF merged region (40°S 58°30'E) from 13 to 15 January, 2012. The vertical profiles of phytoplankton (based on pigment indices) indicated variation in the percentage contribution of phytoplankton functional groups (Micro, Nano and Pico). Though the overall community structure was dominated by nanoplankton, as exhibited by pigment indices and CHEMTAX analysis, drastic shifts in the community were observed at 120 m depth at six hourly intervals. The oscillation between Flagellates (nanoplankton) to prokaryotes (picoplankton) and then to diatoms (microplankton) at this depth in three consecutive observations coincided with the significant variations in phosphate and nitrate concentrations, along with increase in abundance of the grazer community (ciliates and heterotrophic dinoflagellates). From the present study, it is evident that the flagellate group is the ideal one to survive in such a complex regime. However, the observed small interval oscillation in the phytoplankton community could be a coupled effect of bottom-up (vertical advection that alters the nutrient flux), and top-down (increased abundance of microzooplankton) factors.

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1. Introduction

Phytoplankton, keystone microscopic algae are important players in aquatic systems due to their role in primary production, biogeochemical cycling of elements and regulation of global carbon budget in oceans through export production. The qualitative and quantitative analyses of phytoplankton are the basic steps towards understanding their community structure in a given region (Holligan, 1992). Phytoplankton community structure may vary from one place to another and also within the same water body (Fogg and Thake, 1987), based on the hydro-biological complexities prevalent in the given region. The knowledge from the marine pelagic system on the species-specific roles of phytoplankton, i.e., resource competition (bottom-up) versus mortality factors (top-down) is very scant (Verity

and Smetacek, 1996). Such factors influence the food chain and biogeochemical cycles (Banse, 1995) by determining the phytoplankton biomass and the fate of produced material. In majority of the research efforts attempting to explain the factors controlling phytoplankton growth rates, mortality factors have been neglected (Smetacek et al., 2004).

The present study area is the juncture of the Agulhas Return Front (ARF) and Subtropical front (STF) in the Indian Ocean sector of Southern Ocean which is the boundary between warm, saline, nutrient-poor, subtropical, surface water and cooler, fresher, nutrient-rich sub-Antarctic surface water. In the Indian Ocean sector of SO, Agulhas return current flows parallel or juxtaposed to the STF (Lutjeharms and Ansorge, 2001). Owing to the presence of Agulhas return current which is dynamically very unstable, the ARF and the STF in the Indian Ocean sector of SO are characterized by high mesoscale turbulence (Ansorge and Lutjeharms, 2005) that results in intermittent and short lived phytoplankton blooms in this region (Llido et al., 2005). It is, therefore, of interest to study

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what kind of phytoplankton community could dominate in such a highly turbulent region and what are the critical factors supporting their dominance.

In view of this, the objective of this time series (48 h at 6 hourly interval) observation was to study the phytoplankton community structure in the merged ARF and STF region of the Indian Ocean sector of SO by characterizing the pigment composition and also to evaluate it in relation to the prevailing physico-chemical variables (growth factors) and microzooplankton community (mortality factor). The information obtained from the present study would be useful for developing biogeochemical models for similar regions.

2. Materials and methods

As part of the sixth Indian Expedition to the Southern Ocean, a two day time series station was occupied at the ARF region (40°S 58°30'E) in the Indian Ocean sector of SO from 13 to 15 January 2012 (Fig. 1). Water samples were collected from standard depths (0, 10, 30, 50, 75, 100 and 120 m) at six hourly intervals (00, 06, 12, 18, 24, 30, 36, 42, 48 h), using Niskin samplers (5 L) mounted on a carousel unit along with the CTD. The collected water samples were used for the analysis of chlorophyll *a*, phytoplankton diagnostic pigments, microzooplankton and macro nutrients. In addition, physical data were collected using different sensors and remote sensing techniques (details under Section 2.1).

2.1. Physico-chemical variables and chlorophyll *a*

During the time series observation, three hourly temperature and salinity profiles were collected using a CTD (Make: SBE 911 plus, with accuracy: temperature ± 0.001 °C, conductivity ± 0.0001 S/m and depth $\pm 0.005\%$ of full scale). The PAR (Photosynthetically Active Radiation) sensor attached with the CTD was Biospherical PAR light sensor: Model no: QSP2300. The Microstructure Profiler (MSS90L) used for the study was manufactured by Sea & Sun Technology (Trappenkamp, Germany) in collaboration with ISW Wassertechnik. It is a loosely tethered system, comprising two PNS06 shear probes; the depth rating given by the manufacturer is 500 m. The details of instrument can be found in Prandke et al. (2000). The Microstructure Profiler (MP) was operated from the starboard side beam of the ship, and the ship was allowed to drift during the operation. The ship thrusters were switched off during the operation. A special winch manufactured by ISW Wassertechnik, Germany was used to deploy the MP. The winch provided sufficient slack in the cable while the instrument was sinking. This reduced the profiler vibrations

transferred from the ship. The microstructure shear data collected were used to infer dissipation rates (ϵ) following a method similar to that of Moum et al. (1995). At each sampling (6 h interval), 3 shear profiles extending to 500 m were collected and the dissipation rates inferred were averaged for the station at 1 m interval. Noise levels of turbulent dissipation rates from the Microstructure Profilers are better than 10^{-9} W/Kg (Prandke and Stips 1998). The euphotic depth was calculated as the depth of 1% of surface PAR. The mixed layer depth was calculated following the 0.03 kg/m^3 density difference criteria from 10 m depth. Apart from the above in situ data, the delayed time Merged Sea Level Anomaly (SLA) obtained from the AVISO live access server (<http://atoll-motu.aviso.oceanobs.com>) and 8 day composite MODIS chlorophyll *a* concentration for the sampling period were also used in this study.

Macro-nutrients – nitrate (NO_3), silicate (SiO_4) and phosphate (PO_4) from the standard depths were estimated using an autoanalyser (SKALAR) following the standard protocol (Grasshoff et al., 1983).

Chlorophyll *a* (Chl *a*): Three litres of seawater collected from the standard depths was filtered through GF/F Whatman filter and the filters were kept frozen (-20 °C) prior to analyses. For total Chl *a* by fluorometry, the frozen samples were placed in 15 ml centrifuge tubes and extracted overnight at 4 °C using 10 ml 90% acetone. The extracted samples were measured fluorometrically using Turner's AU 10 Fluorometer (Turner Designs Inc., USA). Calibration was carried out using standard chlorophyll *a* pigments (DHI, Denmark). Obtained Chl *a* values were correlated with the Chl *a* values obtained from a fluorescence detector attached to CTD and the relationship was found to be statistically significant ($r^2=0.46$, $n=66$, $p \leq 0.0001$). Hence, the merged values (fluorometry and CTD fluorescence) were used to plot the distribution of Chl *a* in the study area. In addition, the satellite MODIS Chl *a* data (weekly composite) for the study period was also downloaded for the study location.

2.2. Phytoplankton pigment analysis

Three litres of water sample were filtered through GF/F (47 mm) glass fiber filters. The filters were stored in liquid nitrogen until analysis. The entire process was carried out in dim light and low temperature to minimize degradation of pigments during the filtration and extraction procedure. The filters were treated with 3 mL 95% acetone for 5 min in an ultrasonic bath filled with ice water and the extracts were stored overnight at -20 °C for HPLC (High Performance Liquid Chromatography) analysis. Chemo-taxonomically similar marker pigments were grouped together based on earlier practice

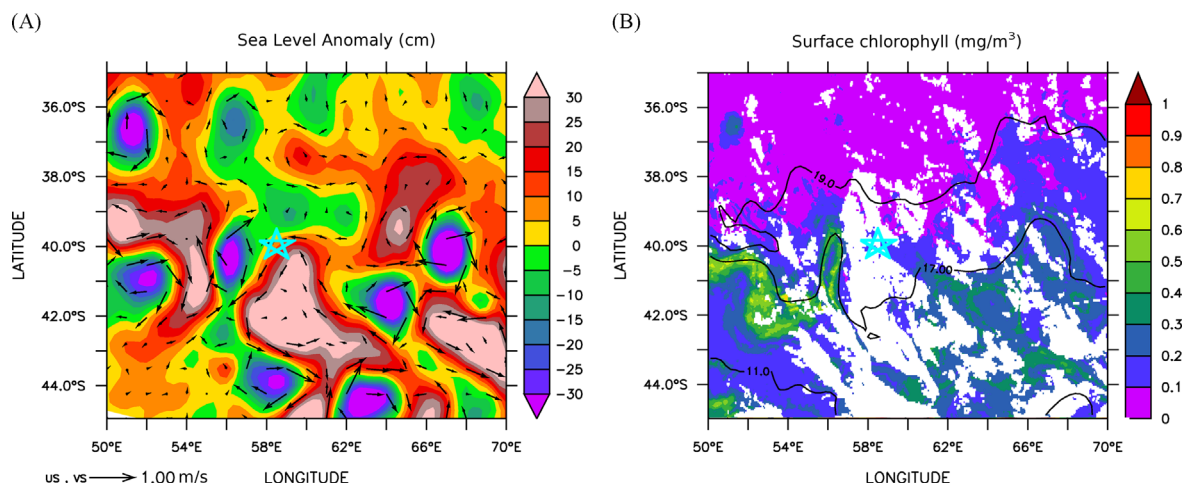


Fig. 1. (a) Study area showing time series station location (marked as star) along with sea level anomaly and (b) chlorophyll distribution at study area (weekly composite from MODIS).

(Naik et al., 2011) and the pigment indices were calculated following the method of Barlow et al. (2007). Diagnostic pigment (DP) index has been used to explain the community structure of the study area after confirming the significant relationship between DP and total Chl *a* by linear regression ($r^2=0.79$, $n=64$, $p \leq 0.0001$).

2.3. CHEMTAX processing

The relative abundance of microalgal groups contributing to total Chl *a* biomass was calculated by pigment concentration data using version 1.95 of CHEMTAX chemical taxonomy software (Mackey et al., 1996; Wright et al., 1996, 2009, 2010). CHEMTAX uses a factor analysis and steepest-descent algorithm to find the best fit of the data on to an initial pigment ratio matrix. The basis for calculations and procedures are fully described in Mackey et al. (1996). Initial pigment ratios for major algal classes were obtained from literature (Mackey et al., 1996; Wright et al., 2000). Based on the diagnostic pigments detected, 4 algal groups were loaded to CHEMTAX: chlorophytes, haptophytes, cyanobacteria and diatoms. The pigments loaded were fucoxanthin, 19'-hexanoyloxyfucoxanthin, zeaxanthin, chlorophyll *b*, and chlorophyll *a*. Because CHEMTAX is sensitive to the feed values in the initial ratio matrix, it needs to be optimized. The CHEMTAX input ratios were optimized based on Wright et al. (2009) and the output with the smallest residual was selected. Ten further pigment ratio tables were generated by multiplying each cell of the initial table by a randomly determined factor, $F = 1 + S(R - 0.5)$, where S is a scaling factor (normally 0.7), and R is a random number between 0 and 1 generated (Wright et al., 2009). Each one of these ratio tables were used as the initial point CHEMTAX optimization. The optimized pigment ratio of the matrix derived by CHEMTAX is presented in Table 1.

2.4. Microzooplankton

For the qualitative and quantitative estimates of MZP, water samples (5 L) collected from standard depths were initially pre-filtered through a 200 μm bolting silk (Hydro-Bios) to eliminate the larger fraction. The filtrate was then carefully collected and fixed in 3–8% of acid Lugol's iodine. These samples were then concentrated by gravity settling and siphoning methods. Prior to microscopic analysis, samples were further concentrated by allowing them to settle for 2 days. The sub samples were analyzed in Sedgwick rafter counting chamber under an inverted microscope, with phase contrast optics (100–400 $\times$ magnification). The organisms present in the samples were identified and categorized in to groups, viz., ciliates (CTS), heterotrophic dinoflagellates (HDS), radiolarians (RAD), Foraminiferans (FORM) and crustacean nauplii (NAUP). CTS were identified to the lowest possible taxonomic level and the RAD, FORMS and HDS were categorized to the group level (Kofoid and

Campbell, 1939; Jorgensen, 1924; Marshall, 1969; Corliss, 1979; Maeda and Carey, 1985; Maeda, 1986; Lynn et al., 1988).

3. Results

3.1. Physico-chemical variations

The averaged Sea Level Anomaly (SLA) indicates the presence of anticyclonic eddy characterized by ~ 25 cm SLA; the location selected for the time series observation was at the edge of the eddy (Fig. 1a). The weekly composite of surface chlorophyll based on Satellite MODIS data indicates low concentration (~ 0.2 mg/m³) at the time series location. The observed SST (~ 18 °C) and surface salinity (35.6) values (Fig. 2a and b) show that the time series station location was at the Agulhas Return Front (ARF), since the ARF is characterized by SST of 17–19 °C (Anilkumar et al., in press; Fig. 1b). The vertical distribution of potential density and shallow mixed layer depth (< 40 m) indicate a strong stratification at the time series location (Fig. 2c). The *in situ* chlorophyll data showed an oligotrophic pattern of distribution with a deep chlorophyll maximum (DCM) at ~ 50 m depth, having a chlorophyll concentration of ~ 0.3 mg/m³ (Fig. 2d). Very low nitrate values at the surface and presence of DCM close to the thermocline region suggest that nitrate availability was limited at the time series location (Fig. 3a). It can also be noticed that in the mixed layer, only nitrate was limited (< 1 μM), but not silicate and phosphate (Fig. 3c and d). A diurnal pattern of deepening of MLD (~ 40 m) at midnight and shoaling (~ 20 m) by noon was also noticed (Fig. 2c). The eddy dissipation rate below the mixed layer (shown in the figure as a red contour) was generally of the order of 10^{-9} W/kg which is close to the noise level of the microprofiler (Fig. 4a). However, in the mixed layer, the dissipation rates reached up to the order of 10^{-5} W/kg. From the Brunt Vaisala frequency, it can be seen that below the mixed layer, the water column was statically stable in the upper 120 m (Fig. 4b). The weak dissipation rates and the positive Brunt Vaisala frequency below the mixed layer clearly suggest a very weak diapycnal mixing. In the open ocean, away from the shallow bottom topographic features and below MLD, generally the diapycnal mixing is weak (Wunsch and Ferrari, 2004). It is also interesting that no prominent diurnal variability was observed in the chlorophyll distribution (Fig. 2d).

3.2. Pigment indices and community composition based on CHEMTAX analysis

The phytoplankton community structure based on the diagnostic pigment index exhibited short term (6 hourly) variations in Diatom diagnostic pigment (Diat_{DP}), Flagellate diagnostic pigment (Flag_{DP}) and the Prokaryotic diagnostic pigment (Prok_{DP}). The overall community structure for the period of the time series

Table 1

Marker pigment to chlorophyll *a* ratios obtained from literature. Output ratios (after 10 runs) were estimated with the CHEMTAX program. See text for further details.

	Fucoxanthin	19' hexanoyloxyfucoxanthin	Zeaxanthin	Chlorophyll <i>b</i>	Chlorophyll <i>a</i>
Input ratios					
Haptophytes	0.112	0.563	0	0	1
Chlorophytes	0	0	0.02	0.590	1
Cyanobacteria	0	0	0.371	0	1
Diatoms	0.432	0	0	0	1
Output ratios					
Haptophytes	0.257	0.762	0	0	1
Chlorophytes	0	0	0.014	0.728	1
Cyanobacteria	0	0	0.686	0	1
Diatoms	0.761	0	0	0	1

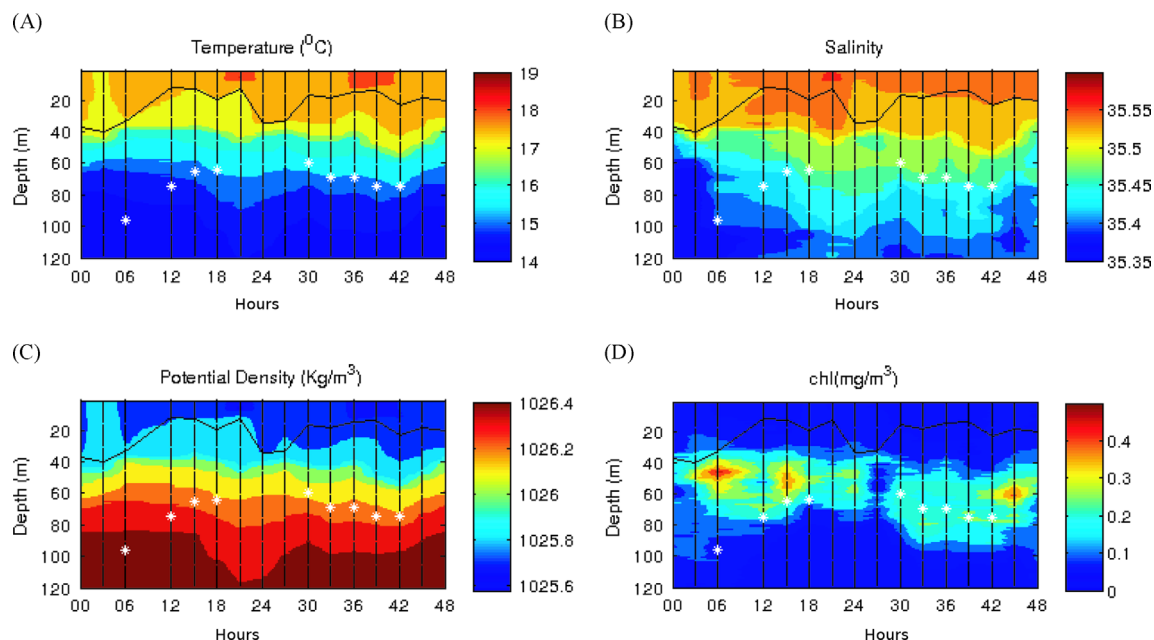


Fig. 2. Time series (six hour time interval) data observation from study area on (a) temperature, (b) salinity, (c) potential density and (d) chlorophyll *a*. The horizontal line represents the mixed layer depth and the asterisk symbols over vertical lines represent the photic depths. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

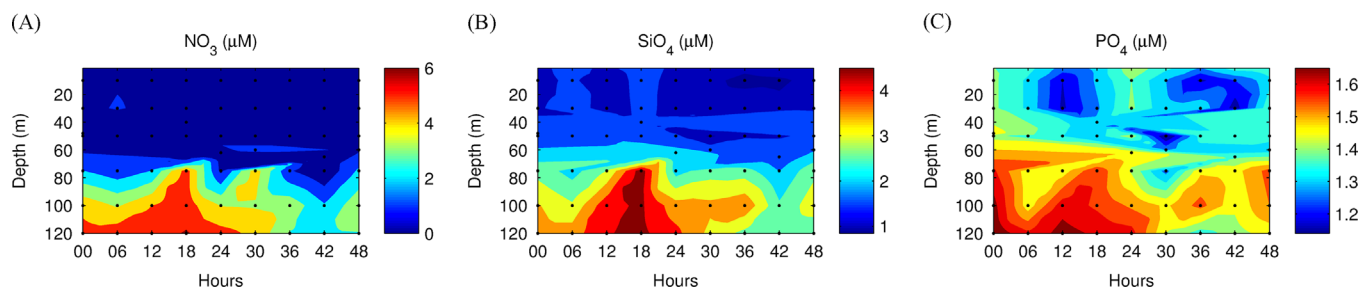


Fig. 3. Observed nutrient distribution at time series location, (a) nitrate, (b) silicate and (c) phosphate. The asterisk over vertical lines represents the photic depths.

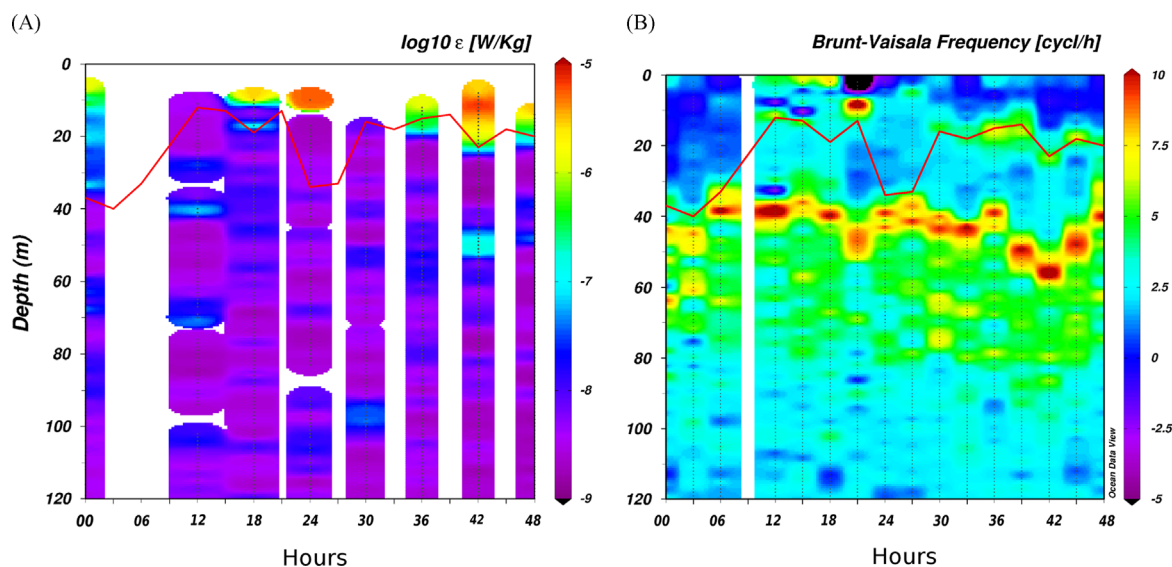


Fig. 4. (a) Eddy dissipation rate (W/Kg) and (b) Brunt-Vaisala frequency (cycle/h) at time series location. The red thick horizontal line represents the mixed layer depth. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

observation was dominated by Flag_{DP} (Fig. 5a–c). However, some patchy variations in the community dominance were observed at the surface water at the 18th hour observation, when the Flag_{DP} was replaced by Diat_{DP} (Fig. 5a and b). Similarly, a change in

community was also observed at 120 m depth at the 18th hour observation with a slight increase in Diat_{DP} (Fig. 5a). In addition to this, marked variations in the community were also observed at 120 m depth, during three consecutive observations (24th, 30th

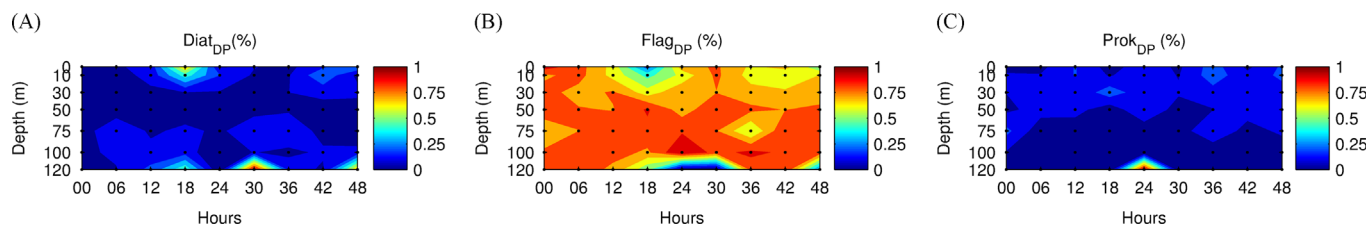


Fig. 5. Pigment indices at time series station: (a) diagnostic indices – Diatom diagnostic pigment (Diat_{DP}), (b) Flagellate diagnostic pigment (Flag_{DP}) and (c) Prokaryotic diagnostic pigment (Prok_{DP}).

and 36th hours). At this depth, the Flag_{DP} dominated water column started showing change in community dominance from Flag_{DP} at 12th hour, to Prok_{DP} at 24th hour, to Diat_{DP} at 30th hour, back to Flag_{DP} at 36th hour (Fig. 5). The relative contribution of various phytoplankton groups to TChl *a*, analyzed by CHEMTAX (Fig. 6), identified four major phytoplankton groups. Haptophytes were more dominant ($\text{av.}=0.108 \mu\text{g l}^{-1}$) and showed strong temporal trends with accumulation at the base of the mixed layer. Chlorophytes ($\text{av.}=0.010 \mu\text{g l}^{-1}$), Cyanobacteria ($\text{av.}=0.002 \mu\text{g l}^{-1}$) and diatoms ($\text{av.}=0.002 \mu\text{g l}^{-1}$) were ubiquitous representing 10–20% of the background population. Overall, the data suggests that surface waters were oligotrophic and major biomass shoaled between top and bottom of the mixed layer at all times.

3.3. Microzooplankton community variation

Microzooplankton analysis indicated the presence of ciliates (CTS), heterotrophic dinoflagellates (HDS), radiolarians (RAD), crustacean nauplii (NAUP) and foraminiferans (FORM). The CTS and HDS were the two dominant groups throughout the observation period (Suppl. Fig. 1). However, in the present work, the emphasis has been given on the observations coinciding with the phytoplankton community fluctuations observed (24th, 30th and 36th hour observations at 120 m depth). The microzooplankton community occurring during these time periods showed variations in abundance and also absence of some groups (Fig. 7). The CTS group exhibited gradual increase in abundance during the three observations, with 10% increase at the 30th hour and 47% at the 36th hour (Fig. 7). The RAD group also showed considerable increase (120%) in abundance at the 30th hour, as compared to that at the 24th hour and this group was totally absent at the 36th hour observation (Fig. 7). In the case of HDS group, an increase in abundance was observed only at the 36th hour observation (Fig. 7).

4. Discussion

The SLA and the overlaid geostrophic velocity anomalies (Fig. 1a) indicate high mesoscale activity which is the characteristic feature of this region. The Agulhas return current (which flows from off the tip of South Africa to about 80°E) is dynamically very unstable and characterized by high mesoscale turbulence (Ansorge and Lutjeharms, 2005). In the Indian Ocean sector of SO, the Agulhas return current lies parallel or juxtaposed with the STF (Lutjeharms and Ansorge, 2001); recent studies have shown the merging of the ARF and the STF at some regions in the Indian Ocean sector of SO (Anilkumar et al., 2014). This mesoscale turbulence at the STF results in intermittent and short lived chlorophyll blooms in the region (Llido et al., 2005). However, satellite and *in situ* chlorophyll indicate low phytoplankton biomass within the sampling region covarying with low concentration of nutrients in the upper water column (above 80 m) (Fig. 3a–c). Low phytoplankton proliferation below this photic depth, in spite of nutrient availability, could be related to light attenuation. Since, the uptake of nutrients is an energy demanding

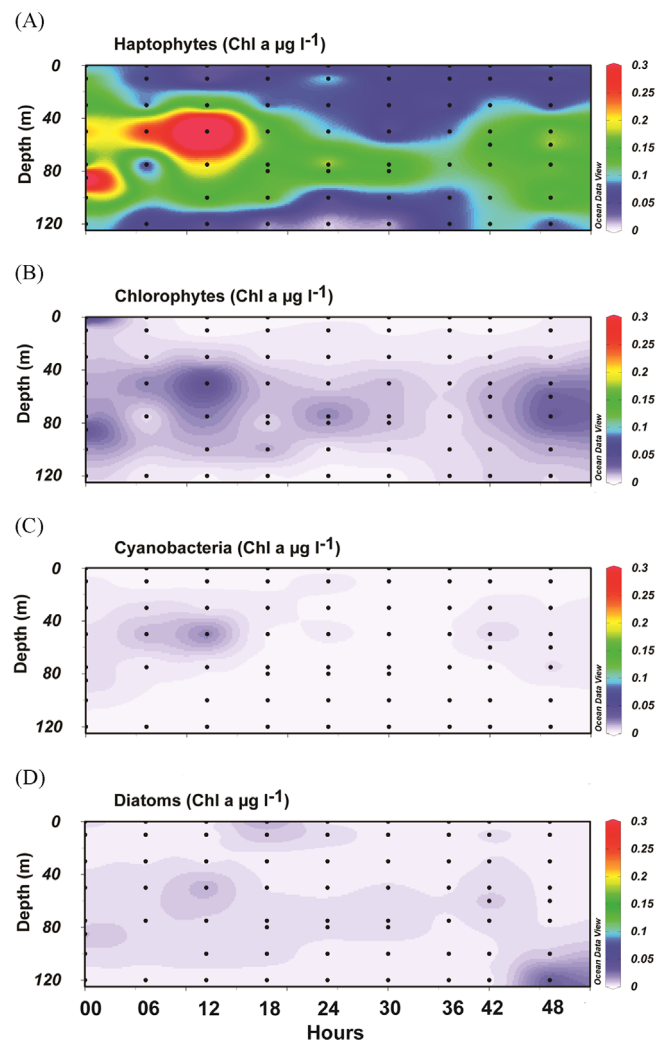


Fig. 6. Depth profiles of CHEMTAX groups for the time series station and its contribution to chlorophyll *a* in $\mu\text{g l}^{-1}$.

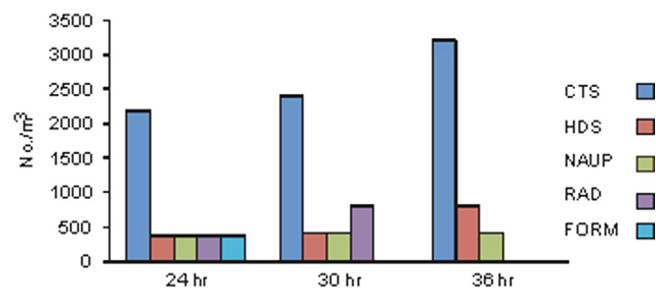


Fig. 7. Microzooplankton community structure observed during 24th, 30th and 36th hour observation at time series station. (CTS – Ciliates, HDS – Heterotrophic dinoflagellates, RAD – Radiolarians, FORM – Foraminiferans and NAUP – Crustacean nauplii).

process, and therefore, is partly light dependent (Kooistra et al., 2007). However, the effect of these factors may vary from one bio-region to another (Longhurst, 1998).

Taxonomic characterization of this low biomass, using HPLC diagnostic pigments, showed the overall dominance of Flag_{DP} (Fig. 5). Nanoflagellates are known to proliferate in regions where the nutrient conditions are intermediate between oligotrophic and nutrient-rich (Falkowski and Oliver, 2007). The results of our investigation also corroborate this. In the present region, the Agulhas return current flows parallel to the STF thereby merging the features of its northern boundary (sub-tropical oligotrophic gyre) and the southern boundary (eddies enriched with nutrients) and thus resulting in a favorable zone for the Flag_{DP}. In addition, the flagellates are also known for their high half-saturation constant of light-dependent growth at low nutrient levels, and their resistance to photoinhibition ability (Nanninga and Tyrrell, 1996). These features allow them to survive better in such dynamically unstable regions compared to other phytoplankton groups. CHEMTAX analysis also highlights dominance of haptophytes with modest contribution of chlorophytes, cyanobacteria and diatoms. An investigation (Wright et al., 2010) from a similar region suggests dominance of *Phaeocystis antarctica* which could presumably be responsible for high abundance of nanoplankton in the region.

The marked temporal variation observed in the phytoplankton community at 120 m depth (Fig. 5) coincides with the variations in growth environment factors like salinity, potential density and nutrient concentrations observed for this depth and time intervals (Figs. 2b, c and 3a–c). Nitrate, silicate and phosphate concentrations showed distinct gradation from 30th to 48th hour observation at 120 m depth (Fig. 3); these changes were reflected in the phytoplankton community at the same time intervals. However, the dominance of Prok_{DP} during high concentration of nutrients and the dominance of Diat_{DP} at relatively low concentration of silicate (Figs. 3 and 5a–c) are unusual to the general pattern, as Prok_{DP} is known to prefer oligotrophic conditions (Aksnes and Egge, 1991), whereas diatoms prefer high concentration of silicate (Schiebel et al., 2004). This discrepancy could be linked to the mortality factors in the environment. Ciliates (CTS) and heterotrophic dinoflagellate (HDS) dominated the microzooplankton grazing community (Fig. 6). The CTS and HDS groups are the major marine phagotrophic protists (Neuer and Cowles, 1995) and play the role of noteworthy grazers in the marine ecosystem (Jonsson, 1986, Stoecker and Capuzzo, 1990, Hansen, 1992, Jeong and Latz, 1994). CTS and HDS biomass can increase substantially with the boosted productivity of the microbial food web (Klaas, 1997, Landry et al., 2002). Their different feeding ecology is reflected in their different growth rates, as CTS grow 2–3 times faster than the HDS (Banse, 1982, Hansen, 1992). This explains the variations observed in the abundance of CTS and HDS at 24th to 36th hour observations (Fig. 6). It has been reported that efficiency in growth rate determines the impact of grazing on prey population and the regeneration efficiency of nutrients (Neuer and Cowles, 1995). The increase in RAD population from 24th to 30th hour could be linked to their preferential food availability during the 24th hour as prokaryotes (Fig. 5c), because RAD are known to feed better on Picoplankton. The increased abundance of HDS at 36th hour could also be linked to the availability of diatoms as prey, since the prey size spectrum of HDS is bigger; it can graze prey equal or larger in size than themselves compared to the CTS (Hansen, 1992).

The weak dissipation rate indicates weak diapycnal mixing. However, the increased nutrients below 60 m depth could be linked to vertical advection. This could be another reason for the fluctuation in community dominance. Since the total phytoplankton biomass itself is in the range of 0–0.4 mg/m³, any grazing pressure on this small biomass can bring in significant difference in the prey population. In other words, the predator size spectrum can change the prey population.

5. Conclusion

The time series occupied area was low in phytoplankton biomass, and was mainly dominated by the dominance of flagellates. The hydrodynamics of the area is influenced by the ARF and that results in an intermittent nutrient zone, favorable for the flagellates. The observed temporal variation in the phytoplankton community was prominent only at 120 m depth and was controlled passively by bottom-up factors due to weak dissipation rate and actively by top-down factors due to presence of ciliates and heterotrophic dinoflagellates. The impact of grazing in altering the community structure is considerable since the total phytoplankton biomass was low.

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Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr.2.2015.01.002>.

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