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Hydrographic and Biological characteristics along 45°E longitude in the South Western Indian Ocean and Southern Ocean during austral summer 2004

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Abstract

During the austral summer 2004, an intensive multidisciplinary survey was carried out in the Indian Ocean sector of the Southern Ocean to study the main hydrographic features and the associated productivity processes. This sector includes circumpolar zones and fronts with distinct hydrographic and trophic regimes, such as the Subtropical Zone, Subtropical Frontal Zone, Sub Antarctic Zone, Polar Frontal Zone, Northern Subtropical Front , Agulhas Retroflexion Front, Southern Subtropical Front, Subantarctic Front, Surface Polar Front, and SubSurface Polar Front. Seasonal variations in the solar irradiance and day length, stratification, lack of micronutrients like iron and increased grazing pressure are the major factors that influenced or constrained biological production in this region. Even though there are broad differences in these controlling factors in time and space between the zonal regions, the upper 1000 m of the water column of the main zones viz. (STZ, STFZ, SAZ, PFZ) supported almost identical standing stocks of mesozooplankton (0.43, 0.47, 0.45 and 0.49 ml m⁻³, respectively) during the austral summer. This unexpected similarity can be explained either through the functioning of the microbial loop within STZ, STFZ and SAZ or the multivorous foodweb ecology within the PFZ. Dominance of ciliates in the microzooplankton community may be one factor resulting in the maintenance of a high mesozooplankton standing stock in SAZ. In contrast to the zones, frontal regions showed wide differences in hydrography and biological characteristics. The SSTF and SPF were far more biologically productive than that of NSTF and ARF.

Keywords: Fronts, Zones, Microzooplankton, Mesozooplankton, Microbial loop, Southern Ocean

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1. Introduction

The Southern Ocean (SO) plays a major role in regulating the global carbon fluxes and world climate. Tropical regions are characterised by receiving a surplus solar energy whereas the polar regions are in deficit of this not only during winter with either long or continuous nights, but also during summer because of the sun's low angle of incidence. Both atmospheric and oceanic circulations regulate the global carbon budget by exporting the surplus energy from tropical to Polar Regions. Fronts and the water masses of SO have great influence in regulating biological production at the global scale (Abrams 1985a). Huntley et al. (1990) have reported that the air breathing seabirds and mammals may transfer 20-25% of photosynthetically fixed carbon into the atmosphere via respiration by consuming macrozooplankton and micronekton. Therefore, zooplankton occupies an important position in the SO carbon cycle.

The major current system in the Indian Ocean sector of SO is the Antarctic Circumpolar Current (ACC). The principal mechanism determining the different properties within the zones and along the frontal systems is the wind (westerlies) induced transport that drives the uninterrupted eastward flowing ACC. Deacon (1933, 1937) was the first to outline the frontal systems in the SO and suggested that they are circumpolar. The majority of the studies on the Southern Indian fronts were carried out during 1980's (Lutjeharms 1981, Deacon 1982, 1983, Belkin & Gordon 1996, Holliday & Read 1998, Pakhomov et al. 2000, Pollard & Read 2001). Along the 45°E the main features are (from north to south), the existence of North Subtropical Front (NSTF), Agulhas Retroflexion Front (ARF), South Subtropical Front (SSTF), Subantarctic Front (SAF) and Polar Front (PF); the PF has both Surface Polar Front (SPF) and Subsurface Polar Front (SSPF) expressions. These frontal systems subdivide the sector into zones with different biogeochemical characteristics viz., Subtropical Zone (STZ), Subtropical Frontal Zone (STFZ), Subantarctic Zone (SAZ) and Polar Frontal Zone (PFZ) with Surface Polar Zone (SPZ) and Subsurface Polar Zone (SSPZ) at 200 m. The Antarctic Paradox is related to a well-known phenomenon referred to as the High Nutrient Low Chlorophyll (HNLC) condition. i.e. There are regions where nitrogen and phosphorous are in high concentrations throughout the year, but primary productivity is low. Subantarctic zone (SAZ) and Subantarctic front (SAF) exhibit HNLC phenomenon prominently in the SO (El-Sayed 1984). The major hypotheses put forward to explain the paradox are insufficient solar energy for phytoplankton

growth to attain its full potential (Nelson & Smith 1991), deficiency of micronutrients like iron (Martin et al. 1990a & 1990), strong wind stirring resulting in deepening of the mixed layer and convection (Sakshaug et al. 1991), and zooplankton grazing (Dubischar & Bathmann 1997).

The major currents that make this region so dynamic are the Agulhas and ACC. The Agulhas Current (Gordon 1985) is the western boundary current that flows pole ward along the east coast of Africa from 27° to $\approx$ 40°S, and then reverses direction or retroflects eastwards to become the Agulhas Retroflection Current. The retroflection exhibits a quasi-stationary meandering pattern with a wavelength of 500 km between 38° and 40°S (Gordon 1985). The westerlies are largely confined between $\sim$ 40° and $\sim$ 65°S, and drive eastward surface current, initiating a northward Ekman drift that is critical to the formation of Antarctic Intermediate Water mass (AIW), subducted below the subantarctic surface water. The strong circumpolar geostrophic currents and weak stratification result in the isopycnals tilting towards the surface in the southern part of ACC. This tilting brings in deep water upwelling originating from the other oceans and also from the deep Indian Ocean to the surface where they are modified by atmospheric interactions. Another feature that results in the upwelling of nutrient-rich deep water to the surface is the Antarctic Divergence (Jones et al. 1990). The upwelling deep water contains not only high concentrations of dissolved nutrients that support rich biological productivity but also supersaturated with carbon dioxide (CO₂) that is vented to the atmosphere and plays a substantial role in modulating atmospheric CO₂ concentrations. The biological pump is another mechanism whereby atmospheric CO₂ concentrations can be drawn down and transferred into the deep ocean. CO₂ converted into organic matter by photosynthesis is exported to deeper waters from the upper ocean by sedimentation and vertical migrations of organisms. The westerlies have a large impact on SO hydrography, exerting a great influence both on the distribution of sea ice and biological productivity. However, in oceanic waters beyond the influence of landmasses, phytoplankton production of this region is consistently lower than would normally be expected high macronutrient concentrations (Boyd et al. 2000).

The degree of variability in hydrographic and biological characteristics is high between the zones and frontal system (Kostianoy et al. 2003 & 2004). Macro-scale zonation of the epipelagic zooplankton in the SO has been extensively investigated (e.g. Grachev 1991,

Pakhomov & McQuaid 1996, Pakhomov et al. 2000). Although many studies have been conducted in the Pacific and Atlantic sectors, the Indian Ocean sector still remains mostly unexplored. A few studies in the Indian Ocean sector have focused in the vicinity of a major front or zone (Bernard & Froneman 2003, Bernard & Froneman 2005, Froneman et al. 2007) and the waters surrounding the oceanic islands (Fielding et al. 2007). However, an extensive study of the response of biological community from the subtropical to polar region is still lacking. In addition, whether HNLC affects the secondary productivity in the different zones has also not yet been fully understood. The two major objectives of this study were, to describe the response of biological community to different fronts and zones by switching to a food web structure better adapted to the varying environment and to understand the influence of HNLC on the secondary trophic level.

2. Data and Methodology

Hydrographic and biological measurements in the Indian Ocean sector of the SO were carried out onboard FORV *Sagar Kanya* during the austral summer (January - February 2004). Observations were made along 45°E, from 30°S to 55°S (Fig. 1), which passes through the major fronts and zones between the subtropical and polar regions. Hydrographic observations were taken at 1° latitudinal intervals, while the biological samples were collected at 2° intervals. A SBE Seabird 911 plus CTD was used for recording temperature (accuracy $\pm 0.001^\circ\text{C}$) and salinity (conductivity $\pm .0001$ S/m) profiles up to 1000 m depth with a bin size of 1 m. Salinity values from CTD were calibrated against the values obtained from water samples measured using the Autosal (Guildline 8400A) onboard. The sea surface temperature (SST) was measured using a bucket thermometer (accuracy of $\pm 0.2^\circ\text{C}$). AVHRR SST (spatial resolution 4 km and temperature accuracy of about $\pm 0.3^\circ\text{C}$) were recorded over the time span of the cruise and averaged for analysis. Surface meteorological parameters (air temperature, wind speed and direction) were recorded at all stations. Plots of potential temperature versus salinity identified the water masses and frontal structures. QuikSCAT satellite data were used to study the prevailing wind patterns. Data from altimetric sensors mounted on the satellites (TOPEX/POSIDON, JASON-1 and GFO) of NOAA were collected, processed and averaged during the cruise period.

Water samples were collected using rosette sampler from standard depths (0, 10, 20, 30, 50, 75, 100, 150, 200, 300, 500, 750 and 1000 m) and analyzed for nitrate, phosphate and silicate with a Segmented Flow auto-analyzer SKALAR (Model 51001-1) (Grasshoff 1983). Dissolved Oxygen (DO) was estimated by Winkler's method (Carpenter 1965). Water samples from the standard depths were carefully collected in glass bottles (125 ml) without trapping air bubbles. Samples were immediately fixed by adding 0.5 ml of Winkler A (Manganous chloride) and 0.5 ml of Winkler B (Alkaline Potassium iodide) solution and mixed well for precipitation. After acidification by 50% hydrochloric acid, the samples were titrated against standard sodium thiosulphate solution using starch as indicator. The titration was based on iodimetry using a Dosimat. The endpoint was taken as the disappearance of the blue colour with visual end point determination.

CTD data were used to locate the maximum surface gradients in temperature and salinity fields to understand the water masses and frontal systems structures. Sharp gradients in temperature and salinity were observed across the frontal systems; otherwise the temperature and salinity (i.e. water mass structure) remained more or less constant across the hydrographic zones between the fronts.

2.1. *Validation and estimation of the remotely sensed chlorophyll *a* and modeling of primary production with in-situ observation*

For in situ Chlorophyll *a* and primary productivity measurements, water samples were collected from seven discrete depths according to the Joint Global Ocean Flux Study (JGOFS) protocols (UNESCO, 1994). For chlorophyll *a*, two liters of water from each depth were filtered through GF/F filters (pore size 0.7 μm), and extracted with 10 ml of 90% acetone and analyzed spectrophotometrically (Perkin–Elmer UV/Vis). Water samples for primary productivity were collected before sunrise and incubated *in situ* for 12 h after adding 1 ml of $\text{NaH}^{14}\text{CO}_3$ to each sample (5 μCi per 300 ml seawater). After incubation, the samples were filtered through 47 mm GF/F (pore size 0.7 μm) filters under gentle suction, exposed to concentrated HCl fumes to remove excess inorganic carbon and kept in scintillation vials. Scintillation cocktail was added to the vials a day before the analysis, and the activity was counted in a Wallace scintillation counter. The Disintegrations per Minute (DPMs) values were converted into daily production rates ($\text{mg C m}^{-3} \text{ day}^{-1}$) using the formula of Strickland & Parsons (1972). Column chlorophyll *a* (mg m^{-2}) and column primary production ($\text{mg C m}^{-2} \text{ day}^{-1}$) were estimated by integrating the depth values.

In order to understand the primary production and associated biological process that happens in the merged frontal regions and small scale processes, the study requires fine resolution data sets. Such a high resolution *in situ* measurement is not possible because of time constraint during the cruise. The in situ Chlorophyll *a* and primary productivity measurements were done at 2° latitudinal intervals only. Fortunately, remote sensing technique can yield high resolution but less accurate data than in situ on both spatial and temporal scale. But careful analysis and application of the correction for sea surface and atmospheric condition by

incorporating real-time meteorological data will yield highly accurate data. SeaDAS software was used to process the remotely sensed geophysical data with an algorithm for sea surface and atmospheric correction to generate high accuracy output. MODIS-Aqua SST during the night pass was processed to 9 km spatial and 8 day temporal resolution during the cruise period and were used for the present study. The Sea-viewing Wide Field-of-view Sensor (SeaWiFS) is an eight-channel visible light radiometer dedicated to global ocean color measurements which are used to detect and analyze patterns of biological activity in the marine environment. SeaWiFS covers more than 90% of the ocean surface in every two days. The output binned to a spatial resolution of 9 kilometers and temporal resolutions of 8 days were used for the present study. We used chlorophyll *a* concentration and photosynthetically available radiation data from the SeaWiFS and the SST data from aqua-MODIS satellite for the duration of the cruise to derive phytoplankton concentrations and oceanic primary productivity.

SeaWiFS measures the total amount of chlorophyll concentration in the euphotic zone (Z_{eu}). Physical depth of the euphotic zone is defined as the penetration depth of 1% surface irradiance based on the Beer-Lambert's law (Morel & Berthon 1989). Z_{eu} is calculated from C_{sat} following Morel & Berthon (1989). For the comparison and validation of remotely sensed chlorophyll to *in situ*, we have done the integration of *in situ* chlorophyll from surface to euphotic zone (Z_{eu}) by trapezoidal integration.

Behrenfield & Falkowski (1997a) developed a Vertically Generalized Production Model (VGPM), which relates the chlorophyll concentrations to depth integrated euphotic zone primary production.

$$\sum PP = 0.66125 * \left[\frac{E_0}{E_0 + 4.1} \right] * P_{opt}^b * C_{sat} * Z_{eu} * D_{irr} (mgCm^{-2}D^{-1})$$

The core of the VGPM, like other depth-integrated models, which include a measure of depth-integrated phytoplankton biomass, estimates the chlorophyll (C_{sat}) and euphotic depth (Z_{eu}), as well as inclusion of an irradiance dependent function ($f(E_0)$) and a photo adaptive yield term (P_{opt}^b) necessary to convert the estimated biomass into a photosynthetic rate (Behrenfield & Falkowski 1997b). The factor P_{opt}^b , which is the optimal environment for the maximum carbon fixation rate within the water column ($mg\ C\ (mg\ Chl)^{-1}\ h^{-1}$), is the only model parameter that is neither relatable to the chlorophyll, nor possible to measure remotely. We adopted Behrenfield &

Falkowski (1997b) for the computation of the factor, which relates the optimal environment to the SST for the maximum primary production. According to the geographical position and time of year, the amount of the incoming solar irradiance varies, which can be computed from Bird's clear sky spectral irradiance model (1984), with modifications suggested by Sathyendranath & Platt (1988). Day length (D_{irr}) is also included in this model, to scale observational data from hourly incubations to daily rates.

Sampling of zooplankton (both micro- and meso-zooplankton) was carried out at alternate stations. Microzooplankton was sampled by collecting ten liters of water at standard depths (surface, 10, 20, 50, 75, 100 and 120 m). The water samples were initially screened through 200 μm bolting net to remove mesozooplankton, and then filtered through 20 μm bolting silk to retain the microzooplankton. Each microzooplankton sample was then back-washed gently with filtered seawater (20 μm mesh size); volumes made up to 500 ml and preserved by adding 1% acid Lugol's iodine. All samples were further concentrated by siphoning out the excess water through a 20 μm filter. Samples were left to settle for >48 hr. Microzooplankton were enumerated and identified under an Olympus inverted microscope at 100-400X magnifications. Ciliates and dinoflagellates, larval stages of metazoans, radiolarians and foraminiferans were identified upto group level.

Mesozooplankton samples were collected with a Hydrobios Multiple Plankton Net (MPN) (mouth area 0.25 m^2 ; mesh size 200 μm). Vertical hauls divided the upper 1000 m into four depth strata: viz. - 1) 1000-500 m; 500- BT (bottom of thermocline); BT-TT (top of thermocline), TT-surface. Samples were fixed in 5% formaldehyde. Biomass was determined by volume displacement and expressed as ml m^{-3} of water filtered. Major zooplankton taxa were sorted from 25% aliquots. Abundance of individual taxa (ind.m^{-3}) was calculated for the whole sample, and converted to percentage composition. Recent studies suggests (Nielsen et al. 2004, Jaspers et al. 2009) that small fractions of the zooplankters may be drained off while using 200 μm mesh size net in oligotrophic waters. In this study at each station both microzooplankton (20-200 μm) and mesozooplankton(>200 μm) were collected and analysed in order to avoid the underestimation of small fractions of the zooplankters.

3. Results

The maximum sea surface temperature (Fig. 2) of 25.3°C was observed at STZ where the surface salinity was about 35.6, while the minimum of 2°C was recorded at PFZ. The position of the ARF observed was in agreement with that of Lutjeharms & Valentine (1984). SST decreased in ARF by 1.9°C (Fig. 2) from the STFZ value of 18.6°C and the average SSS was 35.6. Across the SSTF, sharp decrease in SST (18.57 to 13.1°C) and Sea Surface Salinity (SSS) (35.61 to 34.16) were noticed. The vertical section of temperature and salinity (Figs. 3a and b) showed that the expression of this front extended down to 900 m. SAZ is a region where temperature stratification was more intense compared to the salinity stratification. Compared to other regions, salinity minimum zone was noticed in the SAZ and it was associated with AAIW. This zone is the limit of the warm and saltier waters, typical of the subtropical regions with a thermostad (Fig. 3a) between 200 and 400 m. The temperature and salinity section (Fig. 3a and b) in the SAF showed a weak gradient at surface between 47° and 48°S, denoting the frontal boundary between Sub Antarctic Surface Water (SASW) and polar surface waters. The mean position of the SPF, according to surface and subsurface expressions, was at around 50°S, where SST (Fig. 2) was 3.8°C and SSS was 33.79. We observed the sub surface polar front between 51° and 55°S with the 2.0°C isotherm clearly demarcating the surface and subsurface expressions of the polar front. The sections of the temperature and salinity (Figs. 3a and b) showed the northward extension of the low temperature (< 2.0°C) and fresher water mass at depths of 100 to 400 m, where salinity (34.2 - 34.6) remained relatively constant.

Strong, zonally prevailed westerly winds forced large, near-surface, northward Ekman transport creating a northward pressure gradient. The ACC is approximately in geostrophic equilibrium, with isopycnals inclined towards the surface layer of polar region. Geostrophic currents (from thermohaline profiles) also showed strong band of eastward flowing current (40 cm s⁻¹) between 41° and 43°S with a vertical extension of 800 m (Fig. 4b).

Surface DO values were relatively low (~225 µM) between 30 and 35°S and increased to 310 µM between 39° and 43°S (Fig. 5a). Further south, DO gradually increased to reach a maximum of 360 µM at 54°S (Fig. 5a). Surface DO was found to be inversely correlated ($r^2 = 0.96$) with SST (Fig. 6a), and positively correlated ($r^2 = 0.324$) with wind speed (Fig. 6b). Surface

macronutrients (Figs. 5b, c and d) were consistently low between 30° and 40°S (nitrate ~1 µM, phosphate ~0.18 µM and silicate 6 µM). However, south of 41°S, nitrate concentrations (Fig. 5b) rose sharply to attain a maximum of 27.5 µM at 51°S, but declined to 10 µM at 55°S. Surface phosphate concentrations (Fig. 5c) rose south of 43°S to a maximum of 1µM, which sustained between 49° and 53°S, but declined to 0.17µM at 55°S.

During the austral summer, the maximum intensity of solar radiation (Fig. 7a) was calculated to be 475 to 400 watt m⁻² between 30° to 55°S and the day length (Fig. 7b) increased southwards from about 14 to 18 hr. The PAR (photosynthetically available radiation) estimated from SeaWiFS showed a zonal pattern, with high radiation (>50 E m⁻² d⁻¹) at 30°S which declined to < 30 E m⁻² d⁻¹ at 55°S. Calculated euphotic zone had a potential depth range of 50 - 70 m between 40° to and 50°S, and increased to 70 - 90 m equator wards. During this period, the average surface chlorophyll a concentration (Fig. 8a) was high (1.0 mg m⁻³) between 41° and 43°S, but was low (0.08 mg m⁻³) in other areas, except at the Polar Front where it reached 0.2 mg m⁻³.

The linear relation between *in situ* and remotely sensed chlorophyll *a* had a correlation (r^2) of 0.43 and yielded a validation relation for remotely sensed chlorophyll *a* as,

$$\text{Corrected remotely sensed chlorophyll} = 1.83 \times \text{in situ Chl} + 0.03$$

This correction was applied to SeaWiFS chlorophyll (Fig. 8b) that showed high chlorophyll *a* concentrations of >7 mg m⁻³ between 41° and 42°S. The linear relation between *in situ* and primary productivity estimated from the Vertically Generalized Production Model (VGPM) showed a correlation (r^2) of 0.41 and yielded a validation relation for modelled primary production as,

$$\text{Corrected primary production (VGPM)} = 22.62 \times \text{in situ PP} + 98.23$$

Results showed a zone of high column productivity of 400 to 1000 mg C m⁻² d⁻¹ between 39° and 43°S with a maximum of 1000 mg C m⁻² d⁻¹ at 42°S (Fig. 9). Primary production rates decreased both northwards to 20°S (to 200 mg C m⁻² d⁻¹) and southwards to 55°S (to 100 mg C m⁻² d⁻¹).

The microzooplankton density in the surface layer increased in the vicinity of the SPF ($139 \times 10^3 \text{ no.m}^{-3}$) and SAF ($80 \times 10^3 \text{ no.m}^{-3}$), and decreased at the PFZ ($2.80 \times 10^3 \text{ no.m}^{-3}$). Frontal regions, north of the subtropical convergence (30° to $42^\circ 30'S$) possessed less microzooplankton than south. Fronts sustained relatively high microzooplankton abundance than the zones except at SAZ where the density was $79.4 \times 10^3 \text{ no.m}^{-3}$. The upper 120 m also showed more or less the same trend as that of the surface layer. Each zone and front was identified and characterised by a unique composition of microzooplankton community (Fig.10a & b). At SPF microzooplankton community was dominated by ciliates (53%), dinoflagellates (16%), and nauplii (26.5%), but at SAF, the composition changed, and the contribution of ciliates fell to 19%, and that of dinoflagellates and nauplii increased to 36.5 and 25%, respectively. North of SSTF, the contribution of ciliates ($>50\%$) to the microzooplankton community was higher than south of SSTF, except at SAZ (84%). The maximum contribution of ciliates (84%) to the microzooplankton community was coinciding with that of SAZ.

Between 30° and $55^\circ S$, high zooplankton biomass in the mixed layer was recorded at PFZ ($50^\circ - 55^\circ S$). Among the fronts, mesozooplankton biomass was high in the mixed layer of SSTF, between $41^\circ 15'$ and $42^\circ 30'S$. However, compared to all other zones and frontal regions, mesozooplankton biomass (Figs. 11a, and b, Table 2) was extremely low (0.010 ml m^{-3}) in the mixed layer and in the upper 1000 m (0.018 ml m^{-3}) of the ARF (Fig. 11a). The major components of mesozooplankton community (Fig. 11b) in ARF were copepods (53.57%), chaetognaths (42.86%), and ostracods (3.57%). An interesting feature observed was that in the upper 1000 m, the mesozooplankton standing stock remained consistent between different zones (STZ, STFZ, SAZ and PFZ), despite the variations in hydrographic conditions and mesozooplankton composition across the fronts (Table 2). The region between SSTF ($41^\circ 15' - 42^\circ 30'S$) and SAZ ($43^\circ - 47^\circ S$) were characterised by high incidence of Euphausiids (68 and 49%, respectively), while in the other regions copepods formed the bulk of the community ($>90\%$).

4. Discussion

In the STZ, surface waters are warm (Fig. 2 and 3a), high saline (Fig. 3b) and nutrient-poor (Fig. 5b, c and d). The subduction of these nutrient-poor surface waters as a result of the

anticlockwise subtropical gyral circulation, results in highly oligotrophic conditions (Karstensen & Quadfasel 2002). The low chlorophyll *a* ($<0.1 \text{ mg m}^{-3}$) (Fig. 8) and low primary production ($< 250 \text{ mg C m}^{-2}$) recorded in this region are clear indications of the oligotrophic nature of the water (Figs. 8 & 9). This is maintained almost throughout the year except during July - September (Fig. 8b). The seasonal variations in the solar irradiance (Figs. 7a and b) of $200 - 450 \text{ W m}^{-2}$ and the day length of 9 to 15 hr indicate that the low primary production was not due to light limitation. The most likely causes for the low primary production in the region may be the combined effect of the low nutrient concentrations in the euphotic zone, the thermocline depth exceeding the compensation depth and high stability due to stratification. Surprisingly, we observed high mesozooplankton standing stock (0.440 ml m^{-3}) in the upper 1000 m (Figs. 11a and b) in this region despite the prevailing oligotrophy and low primary production. Incidentally, the biomass value showed close similarity with those of STZ (0.41), STFZ (0.470 ml m^{-3}), SAZ (0.445 ml m^{-3}) and PFZ (0.50 ml m^{-3}). Microbial food web is known to support high mesozooplankton production in the low-nutrient low chlorophyll systems (Azam 1983 & 1991, Hall et al. 1999), thereby replacing the primary producers (phytoplankton) as the source of nutrition. The occurrence of a relatively high microzooplankton community (Figs. 10a and b), dominated by ciliates ($2203 \times 10^3 \text{ no. m}^{-3}$, 65%), indicates the possibility of strong microbial food web operating in this region. We observed maximum density of ciliates, ($2819 \times 10^3 \text{ no. m}^{-3}$) in STZ, which was in contrast with the minimum density of ciliates ($108 \times 10^3 \text{ m}^{-3}$) in the PFZ. Bradford-Grieve et al. (1997) have reported that significant proportions of the phytoplankton stock were of picoplankton size range, and ciliates were the dominant grazers of both the pico - and nanoplankton. Low phytoplankton density with high abundance of picoplankton has been reported from the subtropical north Pacific (Odate 1994). The flow cytometry data (Detmer & Bathmann 1997) have also shown that autotrophic pico- and nanoplankton may contribute up to 90% of total chlorophyll *a* present in other oligotrophic regions. Under high nitrate condition, large size classes of phytoplankton usually flourish, whereas in nitrate-depleted waters, picoplankton predominates (Taguchi et al. 1992, Calbet et al. 2001) and this population can support substantial amount of secondary (zooplankton) production through the microbial food web. Thus the low availability of the large sized phytoplankton initiated the need for alternating food sources for the mesozooplankton. The trophic role of microzooplankton, in supporting the high mesozooplankton is evident from the high abundance of ciliates. The relatively high

biomass of microzooplankton indicates a very strong coupling between the mesozooplankton and the microbial food web. Satapoomin et al. (2004) also reported the role of microzooplankton in structuring the mesozooplankton community in oligotrophic waters.

We observed the NSTF (Belkin & Gordon 1996) between 34° and 35°S in the southern Indian Ocean where it formed the boundary for warm, saline subtropical water and was well expressed in subsurface features (Figs. 2, 3a and b). Primary productivity and zooplankton biomass and abundance decreased sharply across the front (Figs. 8a, 11a, and b). Compared to other frontal features, the biological production associated with this front was very low. The higher abundance of microzooplankton (Figs. 10a and b) in the NSTF ($3046 \times 10^3 \text{ no.m}^{-2}$) clearly indicates the extreme oligotrophic nature of this front.

The STFZ (Lutjeharms et al. 1993) region is bounded by the NSTF to the north and the ARF to the south. In this region biological production was low, as in the subtropical region despite receiving ample solar irradiance and day length of sufficient duration. But, seasonal chlorophyll *a* concentrations show that it is a low productivity region throughout the year. However, the relatively high abundance of the microzooplankton (Figs. 10a and b) ($2819 \times 10^3 \text{ no.m}^{-2}$) might be sufficient enough to sustain a fairly high mesozooplankton biomass, and it was similar to the biomass values observed in the other zones. Earlier studies have indicated that the low productivity regions were dominated by microbial food web and the major carbon flow was through the microbial food web to the microzooplankton with a very high proportion of the primary production being consumed by the microzooplankton (Azam 1983 & 1991, Hall et al. 1999).

ARF (Lutjeharms & Valentine 1984, Belkin & Gordon 1996) is readily distinguishable by its expression in SST that ranged from 20.7 to 17.2°C (mean 18.4°C) and in the subsurface (upper 100-150 m) thermohaline fields. The Agulhas Retroflection Current has a core width of ~70 km and it transports an estimated $44 \pm 5 \text{ Sv}$ in the upper 1000 m (Boebel et al. 2003). Between 38° and 40°S it develops a quasi-stationary meandering pattern (wavelength 500 km). The upwelled waters along of the southwest African coast are being advected in to the present study area, and this could be identified by their relatively high content of nitrate ($0.28 \mu\text{M}$) (Fig. 5b), chlorophyll *a* (0.13 mg m^{-3}) (Fig. 8a) and primary productivity ($493 \text{ mg C m}^{-2}\text{d}^{-1}$) (Fig. 9).

Both chlorophyll *a* concentrations and primary production within the Agulhas current system exhibited seasonal patterns (Fig. 8b). SeaWiFS data showed high chlorophyll *a* concentrations (0.5 mg m^{-3}) during the austral summer (December) (Fig. 8b). But, instead of a proportionate increase, we observed a drastic decrease (Figs. 11a and b) in the mesozooplankton biomass in this front. On the other hand, microzooplankton was abundant ($12.8 \times 10^3 \text{ no.m}^{-3}$) in the surface layer (Fig. 10a). The integrated abundance of microzooplankton in the upper 120 m (Fig. 10b) was $2434 \times 10^3 \text{ no.m}^{-2}$ and the community was dominated by ciliates (62%). However, elucidating the food web ecology in such complex situations is very difficult. The mixing of the oligotrophic subtropical water with nutrient-rich Atlantic and Subantarctic waters substantially modifies the system. In such a dynamic system, the current velocities (Boebel et al. 1998) are so high ($\approx 200 \text{ cm.s}^{-1}$), that they might deter the stabilization of mesozooplankton population and/or the time may not be sufficient for the population to respond to the nutrient enrichment.

Our observation of the mean position of the SSTF front was consistent with that of Lutjeharms & Valentine (1984). SSTF is the boundary between the warm saline (Figs. 3a and b) subtropical waters and the cool fresh waters of the SO. In the convergence, both chlorophyll *a* and column primary production were high (0.47 mg m^{-3} and $950 \text{ mg C m}^{-2}\text{d}^{-1}$, respectively) and so also the mesozooplankton standing stock (1.46 ml m^{-3}). The isopycnal mixing between the subtropical and subantarctic waters introduces nutrient-rich subthermocline waters into the surface layers, thereby augmenting the primary (Fig. 9) and secondary production (Figs. 11a and b). This also enhanced both the surface (14.4×10^3) and column (Figs. 10a and b) (4459×10^3) microzooplankton biomass. Previous studies have recorded that frontal systems are characterized by increased biological productivity and biomass at all trophic levels of the pelagic eco-system (Lutjeharms et al. 1985, Pakhomov et al. 1994, Pakhomov & McQuaid 1996). The microzooplankton community changes from being totally dominated by ciliates in the subtropical waters to more diverse forms (ciliates 36%, dinoflagellates 38% and nauplii 25%). This change in microzooplankton population could also be due to a change toward larger phytoplankton favouring populations of larger heterotrophic dinoflagellates rather than ciliates. Hansen (1991) reported the ability of heterotrophic dinoflagellates to graze a wider range of prey, from small cyanobacteria to larger diatoms, their diverse feeding mechanisms enable them to survive in a variety of environments. During the winter, productivity is probably light-limited,

and the ciliates dominate in the microzooplankton community, and the energy flow is predominantly via the microbial loop. During the spring and summer, since light is not a limiting factor, large phytoplankton blooms occur (Fig. 8b), which can be sustained by the nutrients supplied by the vertical mixing of water. However, high microzooplankton populations are also maintained at the same time implying that the microbial loop is also active during this period.

The SAZ has an almost uniform SST of 8.3°C (Figs. 2 and 3a) and SSS of 33.8 (Fig. 3b) throughout. There is a clear thermostad (Fig. 3a) at 200 to 400 m depth, which forms in the winter as a result of vertical overturn. This is a HNLC zone. To the north, productivity in the subtropical waters is nutrient-limited, whereas to the south, the Polar zone is light-limited. Within this region solar irradiance is estimated to be 150 W m^{-2} (day length ~9 hr) during the winter and rises to 450 W m^{-2} (day length ~15hr) during summer. Although the macronutrient supplies in the wind mixed layer were sufficient enough to support high productivity, the surface chlorophyll a (Fig. 8a) concentration (0.18 mg m^{-3}) and column primary productivity (374 $\text{mg C m}^{-2} \text{ d}^{-1}$) remained very low (Fig. 9). Two main hypotheses have been proposed to explain why primary production remains suppressed. One hypothesis is that grazing pressure reduces the phytoplankton abundance and the other one is that lack of essential micronutrients, particularly iron limits the primary production (Martin et al. 1990a & 1990). Mesozooplankton standing stocks in this region (Fig. 11a) were similar to those observed in both the subtropical and polar zones (Fig. 11b), but microzooplankton population showed abundance at the surface ($79.4 \times 10^3 \text{ no.m}^{-3}$) and in the upper 120 m column ($5608 \times 10^3 \text{ no.m}^{-2}$) (Figs. 10a and b). This indicates that the primary production in this region is supported by regenerated nutrients and is utilized in the microbial food web. It has also been reported that nano-phytoplankton which supports the microzooplankton community, was the dominant component in the inter frontal regions between the SSTF and SAF during late summer (Laubscher et al. 1993).

SST declined from 9.0 to 5.1°C (Lutjeharms & Valentine 1984) across the SAF, and SSS declined from 34.11 to 33.89 (Allanson et al. 1981). Belkin & Gordon (1996) defined the front as the boundary between the intermediate salinity minimum and Sub Antarctic Mode Water (SAMW) thermostad to the north. Despite the high concentrations of nutrients (Figs. 5b, c and d) (NO_3 , 21.3, PO_4 , 0.96 and SiO_4 , 8.4), the biological production was low. During winter, low solar irradiance (Figs. 7a and b) and the short day lengths were probably the major limiting factors on

productivity. But even during summer, standing stocks of chlorophyll and primary production remained low (Figs. 8a and b) (0.2 mg m^{-2} , $327 \text{ mg C m}^{-2} \text{ d}^{-1}$, respectively) so also the secondary production (0.13 ml m^{-3} , 0.173 ml m^{-3}) (Figs. 11a and b). This finding is in agreement with earlier studies conducted in the SSAF (Bernard & Froneman 2003). Microzooplankton abundance both at the surface ($80 \times 10^3 \text{ no.m}^{-3}$) and in the upper 120 m ($3600 \times 10^3 \text{ no.m}^{-2}$) (Figs. 10a and b) was sufficient to support moderate mesozooplankton standing stocks. The composition of the microzooplankton community (Fig. 10b) changed (ciliates 19%; dinoflagellates 36.5%, and nauplii 25%). This change in microzooplankton population could also be due to a change toward larger phytoplankton favouring populations of larger heterotrophic dinoflagellates rather than ciliates. The reduction in ciliate population was probably related to the development of large diatom blooms, as the diatoms are too large in size for the ciliates to feed on. The other important microzooplankton group the heterotrophic dinoflagellates prefer prey of their own size and the linear size ratio between predators and their optimal prey is 1 : 1 and hence the prey predator size ratio is crucial for the structuring of pelagic food web (Hansen et al. 1994). It has been observed that changes in the environmental conditions influence the abundance and composition of the microzooplankton community (Atkinson, 1996, Hall et al. 1999). A major factor contributing to low biomass of mesozooplankton (Figs. 11a and b) may be the changing environment, i.e. the formation of AAIW and lateral mixing with SAMW, resulting in a sharp drop of 3.0°C in SST. The assemblage of organisms that inhabited the polar region was entirely different from that in the subtropical seas. Even though food resources in the front were potentially high, the sharp shifts in environmental conditions probably inhibited the build up of the standing stocks of zooplankton.

The SPF is a region where SST changes from 6.0° to 2.0°C (mean 3.4°C) and SSS from 33.8 to 33.9. We observed maximum SST gradient (Figs. 2 and 3a) centered at 3.8°C and SSS at 33.79 (Fig. 3b) are in agreement with those reported by Allanson et al. (1981). One effect of the ACC (Fig. 4a) is that it caused the isopycnals to outcrop at the surface, and hence mixing of the high concentration of nutrients occurred from deep water to the surface layers (Sloyan & Rintoul 2001, Pollard et al. 2002). We observed sharp increases in the nutrient concentrations (Figs. 5b, c and d) (NO_3^- 26.7, PO_4^- 0.8 and SiO_4^- 39.4) associated with the frontal region. Seasonal fluctuations in solar irradiance and day length (Figs. 7a and b) showed that there was absence of light during the winter, but during summer, despite the sun's low angle of incidence

sufficient light was available for photosynthesis. However, no concomitant general increase in the chlorophyll *a* (Fig. 8a) and water column production (Fig. 9) were observed. It is now recognized that phytoplankton blooms associated with the seasonal ice retreat contribute substantially to the biochemical cycling (Smith & Nelson, 1986). However, we observed low chlorophyll *a* ($<0.2 \text{ mgm}^{-3}$) and primary production ($<200 \text{ mg C m}^{-2} \text{ d}^{-1}$) (Table.1). Bernard & Froneman (2003) have shown that no enhancement of chlorophyll *a* biomass was recorded in the vicinity of PF. Froneman et al. (2000) and Pakhomov & Froneman (2004) found that zooplankton grazing accounted for up to 89% of daily primary production in the Polar region. Thus, in contrast to the HNLC regions, it appears that high grazing pressure by abundant mesozooplankton standing stock (Figs. 11a and b), and increase of copepod nauplii in the microzooplankton community (Figs. 10a and b) might have limited the build up of chlorophyll *a* concentrations (phytoplankton bloom). The chlorophyll *a* and primary production presented here are substantially lower than those observed in the PF by Allanson et al. (1981) and Lutjeharms et al. (1985). De Baar et al. (1995) correlated high iron concentrations with enhanced primary productivity at PF in the Atlantic sector. They have reported that the high primary productivity was supported by the advection of iron-rich water masses within the frontal jet. Ciliates occurred at maximum densities at the surface at 49°S (Fig. 10a), where the surface chlorophyll was 0.18 mg m^{-3} . The contribution of heterotrophic dinoflagellates appears to be higher in the subsurface layers (Fig. 10b), within the pycnocline as well as at the base of the photic zone. These depth profiles may result from the predator/prey interactions, characteristic for microzooplankton consumers, such as ciliates, which generally feed on particles $< 20 \text{ }\mu\text{m}$. During the spring and summer, diatoms can exploit the eutrophic conditions and develop blooms. We observed the highest microzooplankton (Fig. 10a) abundance both at the surface ($140 \times 10^3 \text{ no.m}^{-3}$) and within the upper 120 m (Fig. 10b) ($8057 \times 10^3 \text{ no.m}^{-2}$). Here the major constituents of the microzooplankton community were ciliates (53%), nauplii (26.5%) and dinoflagellates (16%). In late summer, both chlorophyll *a* (0.125 mgm^{-3}) and primary production ($187 \text{ mg C m}^{-2} \text{ d}^{-1}$) levels declined. Even then the microzooplankton community (8057×10^3) flourished and sustained high mesozooplankton (Figs. 11a and b) standing stock (0.87 ml m^{-3}). Low chlorophyll *a* and low primary production rates with high micro- and mesozooplankton biomass establish that both traditional and microbial loop were active in this front.

In the PFZ, weak subsurface salinity and temperature minimum (Fig. 2) were observed that was concordant with the observation of Allanson et al. (1981). During the spring-summer, ice melt and Antarctic divergent water advected from the Antarctic region stabilized the upper water column, especially where the isopycnals outcrop because of the ACC (Fig. 4a). This increased in water column stability with high nutrient and trace metal concentrations play a major role in triggering phytoplankton blooms in the vicinity of the polar front (Dubischar & Bathmann 1997, Perissinotto & Pakhomov 1998). Antarctic polar frontal zones are characterized by patches and bands of high chlorophyll *a* (Laubscher et al. 1993, Dafner & Mordasova, 1994, Bathmann et al. 1997). The growth rates and maximum standing stocks of the large diatom appear to have been regulated by the availability of dissolved silica. Tremblay et al. (2002) reported that along the Polar Front, elevated concentration of chlorophyll *a* and primary production and abundance of microzooplankton (>20-200 μm) coincided with high dominance of large or long chained diatoms. Strong nutrient deficits (Figs. 5b, c and d) were clearly seen in this region. The decrease in the nutrient concentrations (NO_3^- 10 μM) in this region (Figs. 5b, c and d) was generally linked with high diatom blooms; but chlorophyll *a* concentrations (Fig. 8a) and primary production (Fig. 9) did not correlate with these blooms. The high grazing pressure of copepods and salps (Figs. 11b), which were very abundant at the time of our observations, probably reduced the phytoplankton standing crop and productivity. The stable stratification resulting from the advection of fresher, and ice melt water from the ice edge probably prevented vertical mixing of deepwater and replenishment of nutrients. These studies highlight the importance of the PF as a biogeographic boundary for zooplankton distribution, demarcating Subantarctic and Antarctic realms of the SO. The sharp decrease in the microzooplankton abundance in this zone may also be the result of strong grazing pressure by large copepods and carnivorous zooplankton. Copepods were the dominant metazooplankton in the PFZ (Franz & Gonzalaz 1997). The mesozooplankton community was dominated almost entirely by copepods, which is in agreement with a number of previous studies (Pakhomov & Froneman 1999, Bernard & Froneman 2003 & 2005). Within the microzooplankton community, ciliates (25%) were replaced by copepod nauplii (50%), and this probably contributed to the strong grazing pressures. Lugomela et al. (2001) reported that copepod nauplii are an important link between the classical and microbial foodwebs because of their small size and have the ability to feed on pico-sized particles, which are generally unavailable to the later copepodites and adults. The

strong grazing impact of copepods in the PFZ during autumn has been reported (Perissinotto 1992, Bernard & Froneman 2003) and the slightly reduced impact during summer may be attributed to the inability of copepods to consume larger phytoplankton, which dominate total chlorophyll *a* (Fortier et al.1994). The mesozooplankton biomass was 0.5 ml m^{-3} which was almost equal to that observed in the other zones. Although most of the cyclopoids did not significantly ingest small autotrophic and heterotrophic flagellates ($2\text{--}8 \text{ }\mu\text{M}$), large copepods were actively feeding on $>10 \text{ }\mu\text{m}$ particles including autotrophic/ heterotrophic dinoflagellates and ciliates with a clearance rate of $0.03 \text{ to } 0.38 \text{ ml animal}^{-1} \text{ h}^{-1}$ (Nakumura & Turner (1997)). Odate (1994) suggested that top-down control of zooplankton might alter the abundance and size composition of phytoplankton in summer, i.e. net zooplankton grazing may suppress the net phyto- and microzooplankton abundance (Multivorous food web).

Belkin & Gordon (1996) identified the northern boundary of the subsurface minimum layer, bounded by the 2.0°C isotherm, within the depth range of 100 to 300 m. We observed the subsurface polar front between 51° and 55°S ; the 2.0°C isotherm clearly demarcated the polar waters at both the surface and subsurface layers. Our mean path turns southward at the Ob'-Lena Rise (46°E). Seamounts and islands are regions of locally enhanced production through the 'island mass effect' (Genin & Boelhart 1985, Coutis & Middleton 1999), and in HNLC regions by being a source of dissolved iron. The high mesozooplankton abundance (12.8 ml m^{-3}) (Figs. 11a and b, Table 2) found observed in this region may be due to the island mass effect. The major contributors of this high biomass were copepod, salps and medusae.

5. Conclusions

This study revealed that during the austral summer, mesozooplankton-standing stock remained more or less similar in all zones (STZ, STFZ, SAZ and PFZ) of Indian Ocean sector of Southern Ocean crossing 45°E meridian, though chlorophyll *a* and primary production varied in each zone. The similarity in the mesozooplankton standing stock can be attributed to the functioning of alternate food webs like microbial loop and multivorous food web. A chart of solar irradiance and day length showed that light was not a limiting factor for biological productivity in the subtropical region, whereas it was a constraint in the Subantarctic and Polar regions. While nutrient was the major limiting factor for primary production in the photic zone of

Subtropical region, solar irradiance was the cause in the Subantarctic and Polar Frontal zones. Oligotrophic behavior of Subtropical region was due to the combined effect of low nutrient concentration in the surface layers, deep thermocline region that exceeded compensation depth and strong stratifications. Although such a condition existed in this region, microbial food web played a vital role in maintaining the zooplankton standing stock through high ciliate abundance. Thus, the basic metabolic needs of the mesozooplankton were met by grazing microzooplankton. The dominance of the microzooplankton in the subtropical region is supported by the findings of Grieve et al. (1997). In the Agulhas region, availability of sufficient amount of nutrients and primary production made the system eutrophic, but the secondary standing stock was found to be quite low. This may be due to the prevalence of strong currents and dynamic environment, deterring the establishment of mesozooplankton communities. Due to the strong circumpolar current and weak stratification maintained by tilting of isopycnals towards surface in the southern part of ACC, permanent thermocline reached the surface of SSTF and supplied very high amount of nutrients and CO₂ which could be utilized for biological production. High rates of primary and secondary production suggest the prevalence of active traditional food web and high abundance of microzooplankton community indicates the functioning of active microbial foodweb also in this front. Subantarctic zone exhibited HNLC phenomenon, but mesozooplankton abundance in this zone was more or less similar to other zones. This was due to the abundance of microzooplankton which provided the nutritional resources for the mesozooplankton. Polar frontal zone becomes productive during austral summer by a combined effect of advection of ice melt and Antarctic divergent water together with trace metal concentration and stabilized upper water column. However, high grazing pressure exerted by copepods and tunicates decreases the phytoplankton standing stock in the PF, and the prevalence of a multivorous food web maintained a secondary standing stock similar to that of other zones. This was well supported by replacement of ciliates by copepod nauplii in the microzooplankton community. From the study it is understood that the similarity in the mesozooplankton standing stock in all the major zones are supported by microzooplankton community. In the zones, the major share of the primary production could be channelled through the microzooplankton in sustaining the mesozooplankton biomass. This illustrates the importance of the microbial food web as a link for the transfer of carbon fixed by small autotrophs to mesozooplankton. Nonetheless, only long-term observations can clearly show whether

seasonality has any impact on the mesozooplankton standing stock. Further studies in this direction would give a better understanding of the intricate relationship underlying the secondary productivity of the Southern Ocean.

Acknowledgements

We thank the Director, National Institute of Oceanography, Goa and the Director, Centre for Marine Living Resources and Ecology, Kochi and the National centre For Antarctic and Ocean Research, Goa for providing facilities for the study. We are grateful to Dr. K. Banse, School of Oceanography, University of Washington, Seattle, USA and Dr. M.V. Angel, Southampton Oceanographic Centre, UK for critically reading the manuscript. We also thank all the participants of cruise SK 200 of ORV Sagar Kanya for the help rendered in sampling. The anonymous reviewers are greatly acknowledged for their valuable suggestions, which improved the quality and clarity of the manuscript. This investigation was carried out under the pilot expedition to Southern Ocean funded by Ministry of Earth Sciences, Govt. of India, New Delhi.

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FIGURE CAPTIONS

Fig. 1 Map of the study area showing station positions overlaid on bathymetric chart that includes nearby island and seamounts of the area sampled for hydrographic (1°S) and biological studies (2°S) during January – February 2004.

Fig. 2 Sea Surface Temperature from MODIS-aqua is posted with station positions showing strong gradients of temperature in the fronts and less gradients of temperature in the zones.

Fig. 3 Vertical section of (a) temperature and (b) salinity, The frontal feature can be observed where the temperature and salinity exhibit steep meridional gradients (i.e. where the contours are closest together) and less contours in the zonal regions

Fig. 4 Vertical section of (a) dynamic height w.r.t. 1000 m (b) geostrophic current (shaded) overlaid with temperature (°C) contours showing strong flow patterns in the fronts and weak flow patterns in the zonal regions. Strong geostrophic currents were coincided with the temperature gradients at Agulhas Retroflection Front (ARF) and South Subtropical Front (SSTF)

Fig. 5 Vertical section of (a) dissolved oxygen, (b) nitrate, (c) phosphate and (d) silicate contours up to 1000 m showing sharp gradients in their properties in the fronts and uniform concentration in the zonal regions along the 45°E meridian. High concentration of Dissolved Oxygen and nutrients were seen at south of SSTF

Fig. 6 Correlation of Dissolved Oxygen with a) SST and b) wind speed showing that SST has greater influence on dissolved oxygen concentration than wind mixing.

Fig. 7 Seasonal patterns of (a) solar irradiance and (b) Day length showing during the study period (austral summer) light is not a constraint for the biological production in the study area.

Fig. 8 (a) SeaWiFS Chlorophyll *a* (mg m^{-3}) concentration overlaid with AVHRR SST contours during the study period. Maximum chl *a* concentration was seen in the SSTF and minimum was at Subtropical zone. (b) Monthly distribution of SeaWiFS chlorophyll *a* along 45°E from June 2003 to June 2004 showed highest chl *a* concentration was during Nov- Feb.

Fig. 9 Water column primary productivity computed from remotely sensed data by using VGPM model also showed the high primary production rate was at SSTF.

Fig. 10 Variations in the composition of microzooplankton in the (a) surface (b) upper 120 m of different fronts and zones .

Fig. 11 (a) Variations in the mesozooplankton biomass in fronts and zones, Uniform biomass can be observed at different zones (b) Percentage composition of different taxa and total abundances of mesozooplankton. Copepods were the dominant component in all of the zones and fronts except at SSTF and SAZ

Table 1 Surface values of physical (Temperature (°C), Salinity) and chemical (Dissolved oxygen & nutrients) variables measured across the fronts and zones of the 45° E longitude during austral summer 2004. Nutrient levels and dissolved oxygen are expressed in μM .

Table 2 Biological variables measured across the fronts and zones of 45° E longitude during austral summer 2004. Variables such as chlorophyll *a*, Primary productivity, microzooplankton abundance in the surface and in the upper 120 m, mesozooplankton biomass in the mixed layer and in the upper 1000 m are shown. Biomass values shown in bold letters are those which are more or less having same values in different zones.

Figures

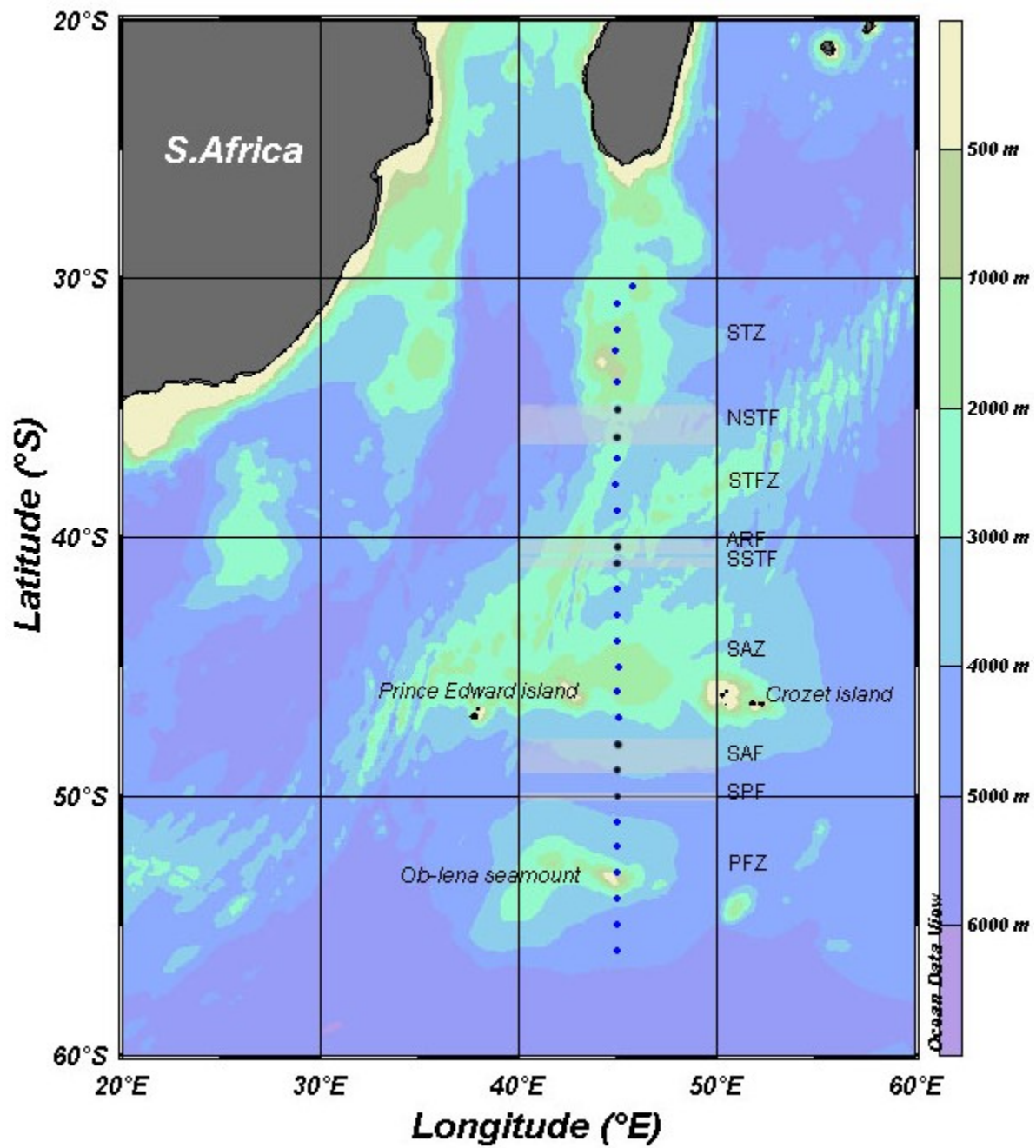


Fig. 1

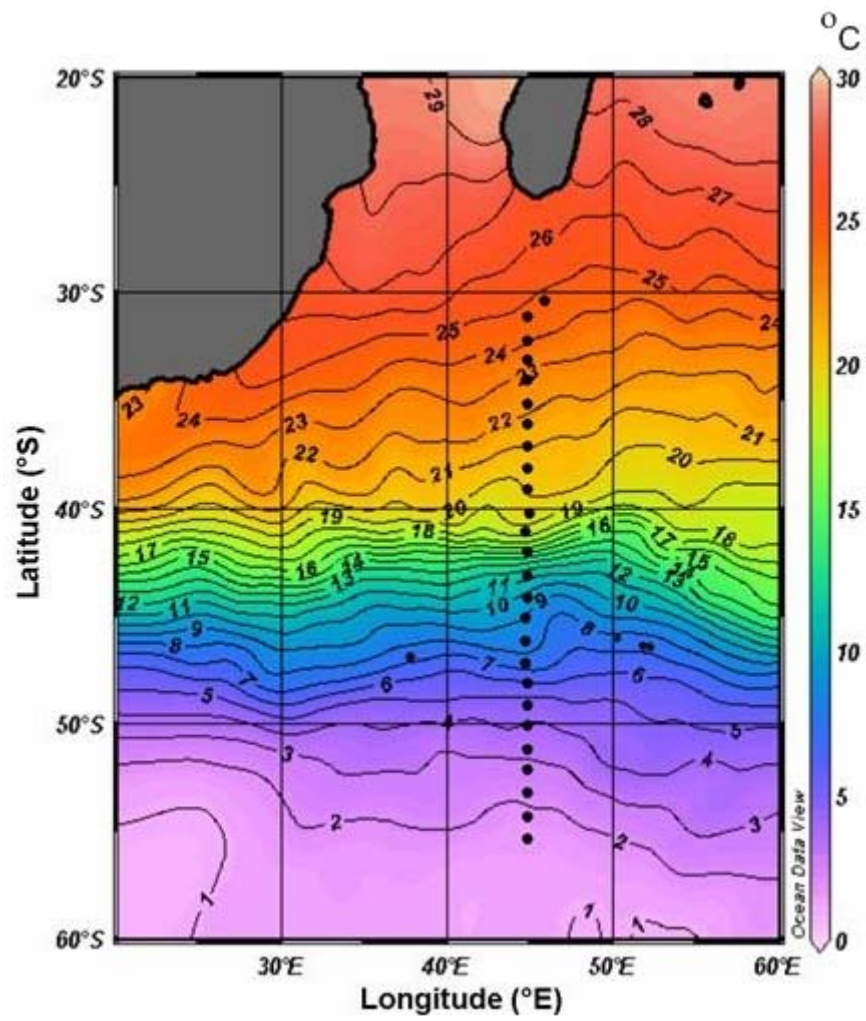
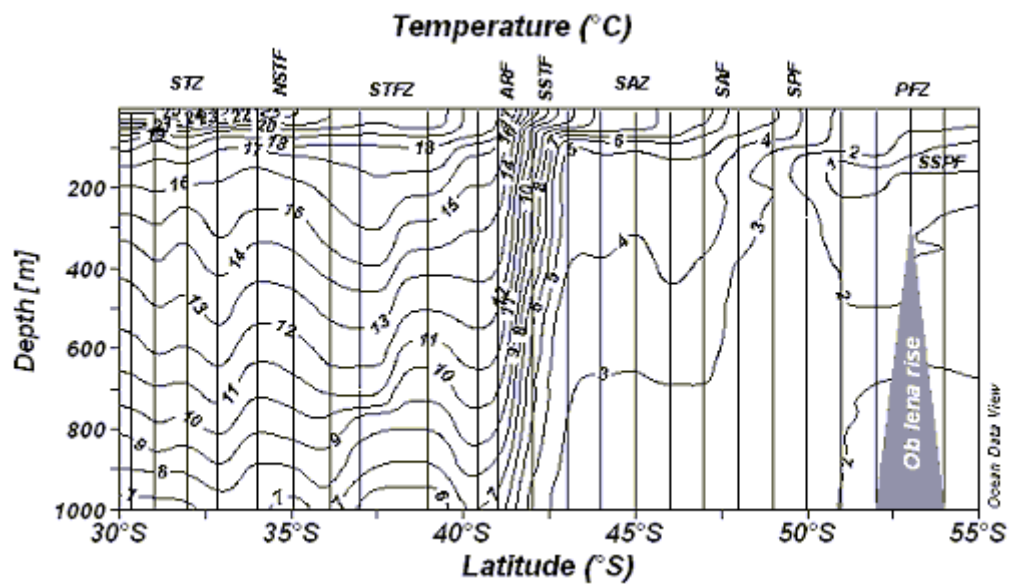
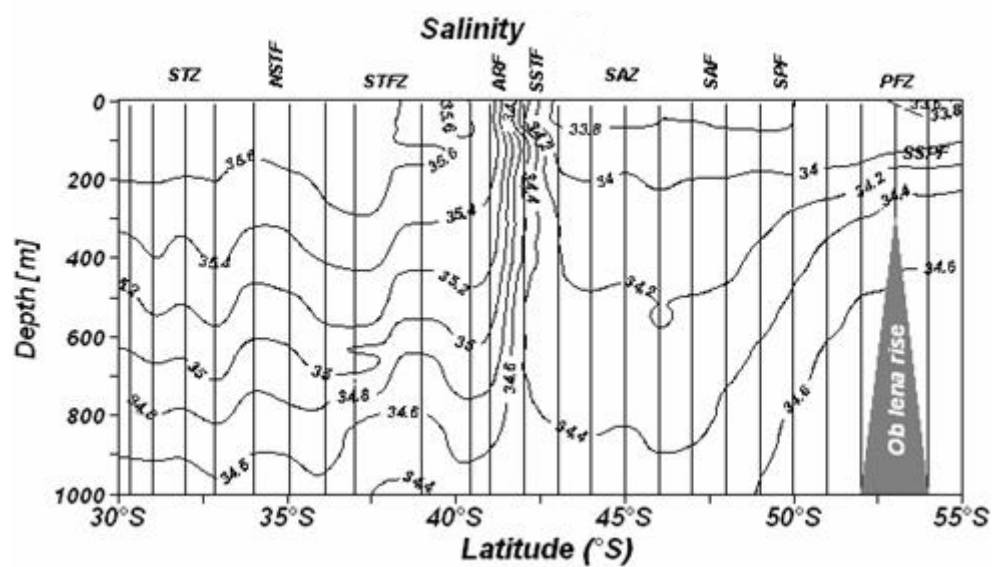


Fig. 2

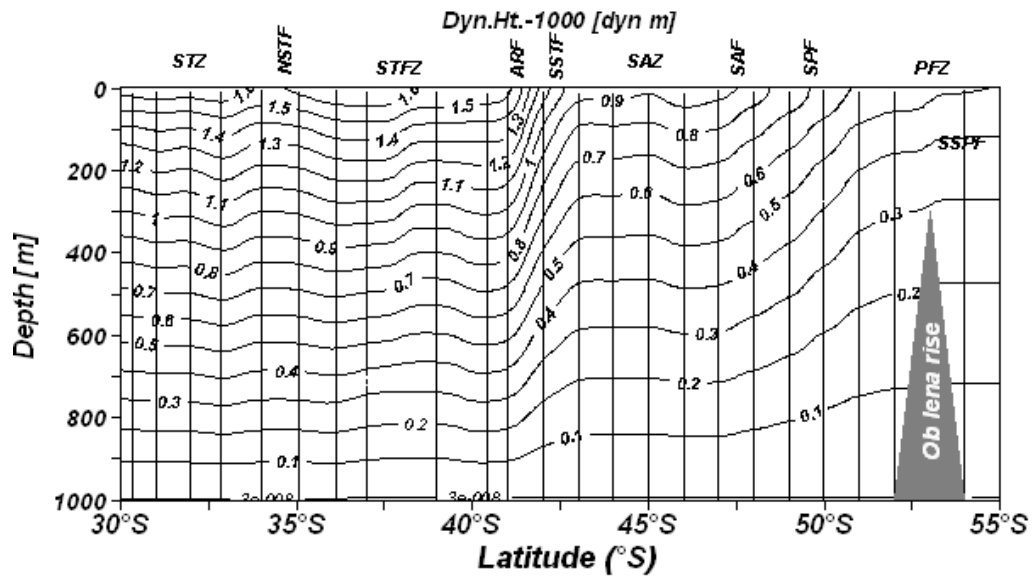


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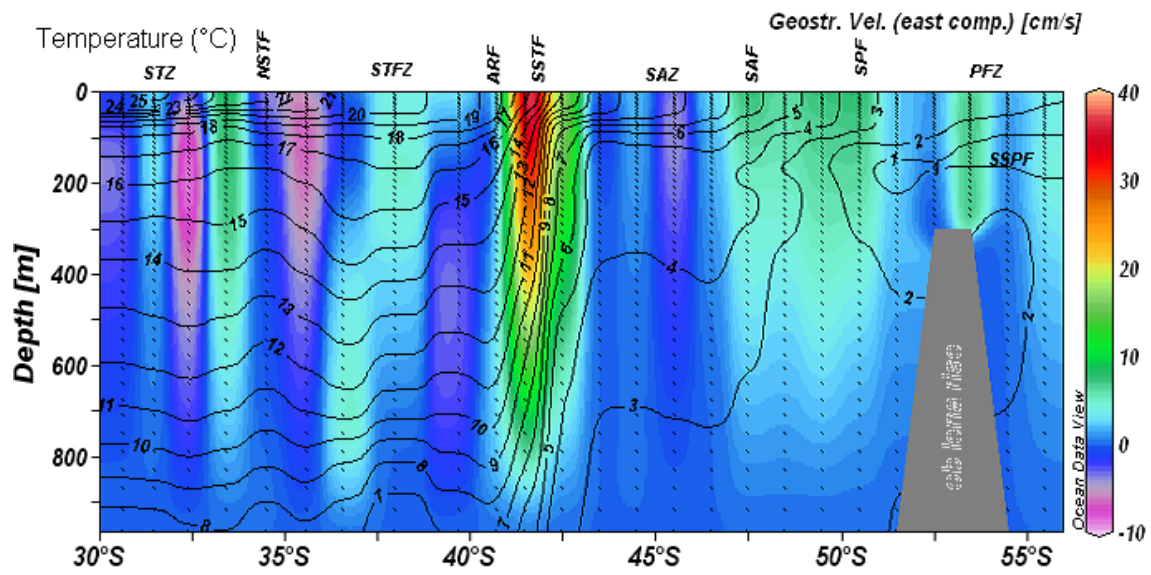


(b)

Fig. 3

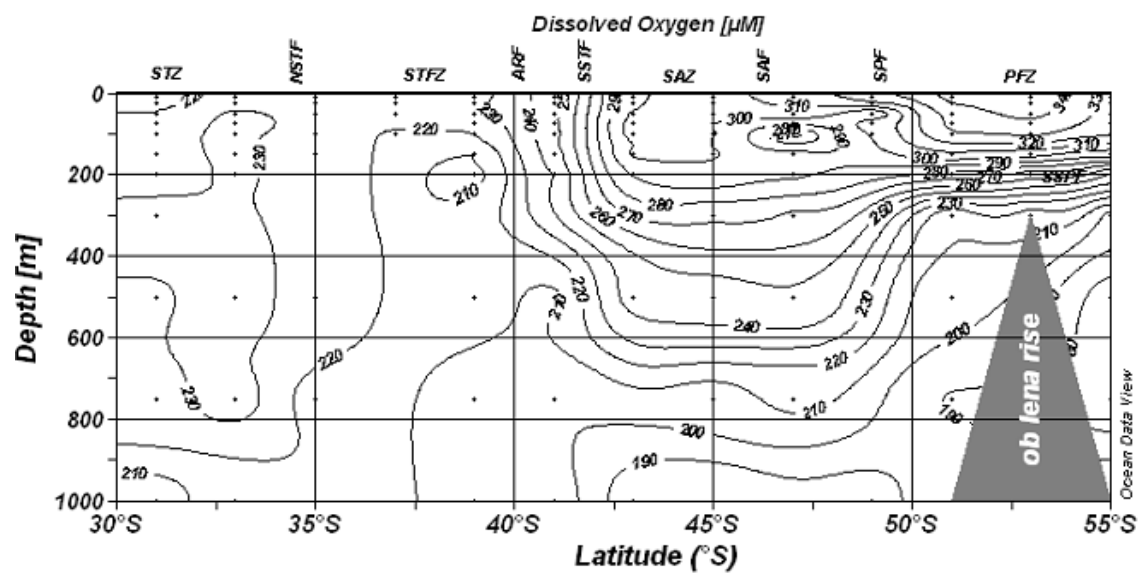


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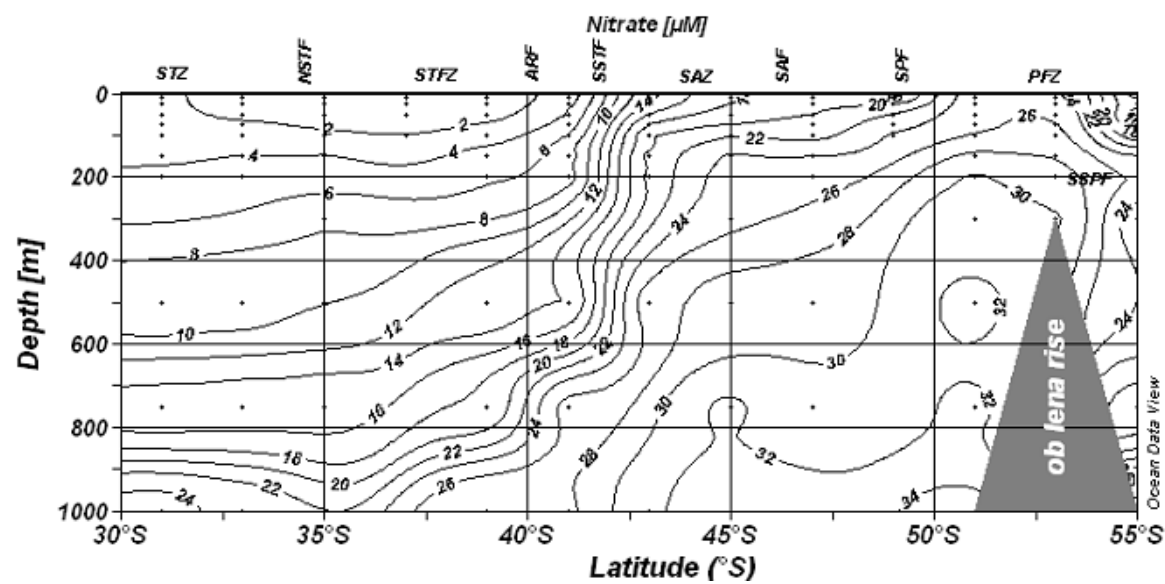


(b)

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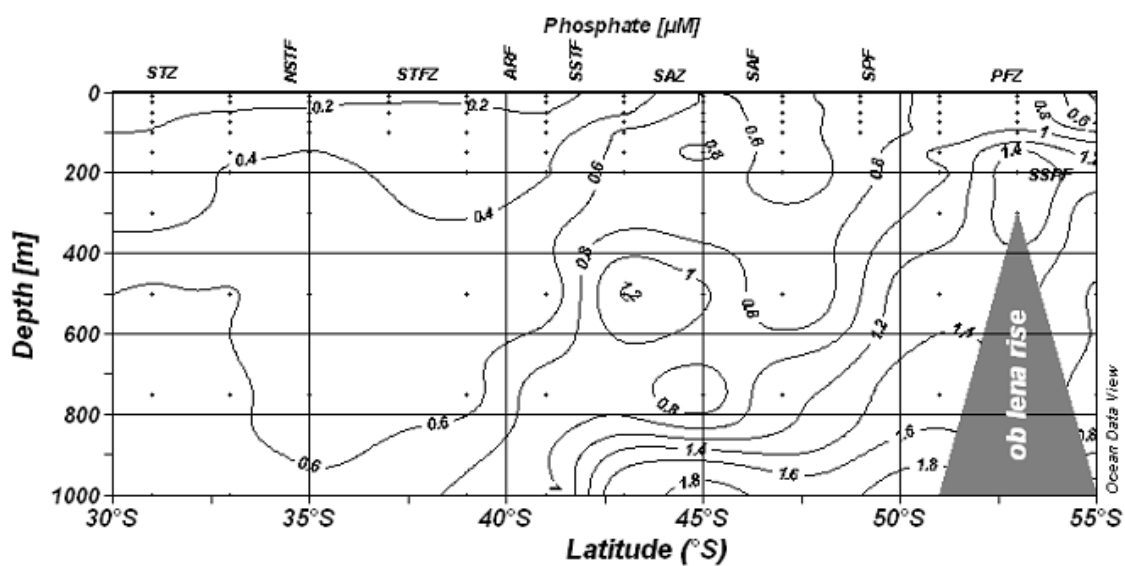


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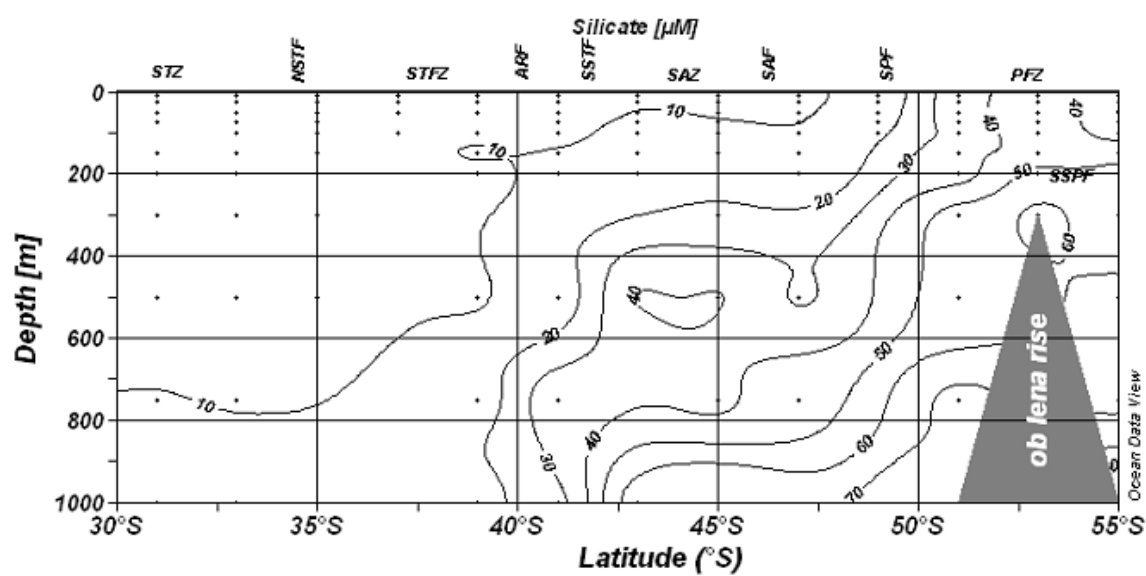


(b)

Fig.

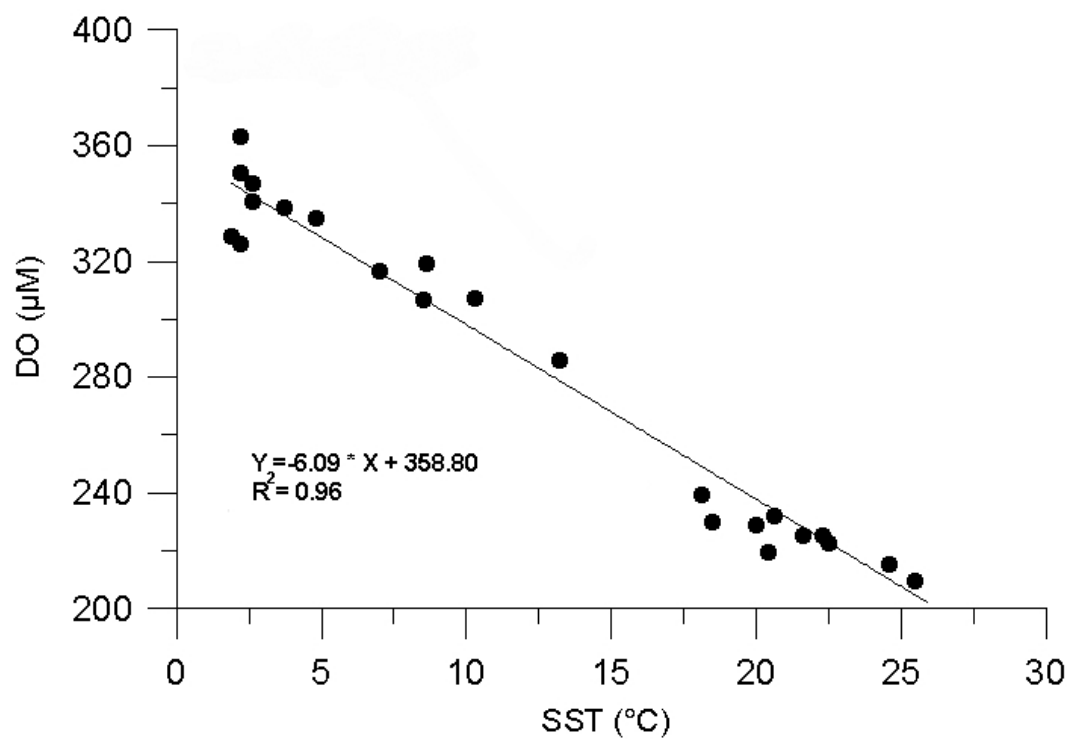


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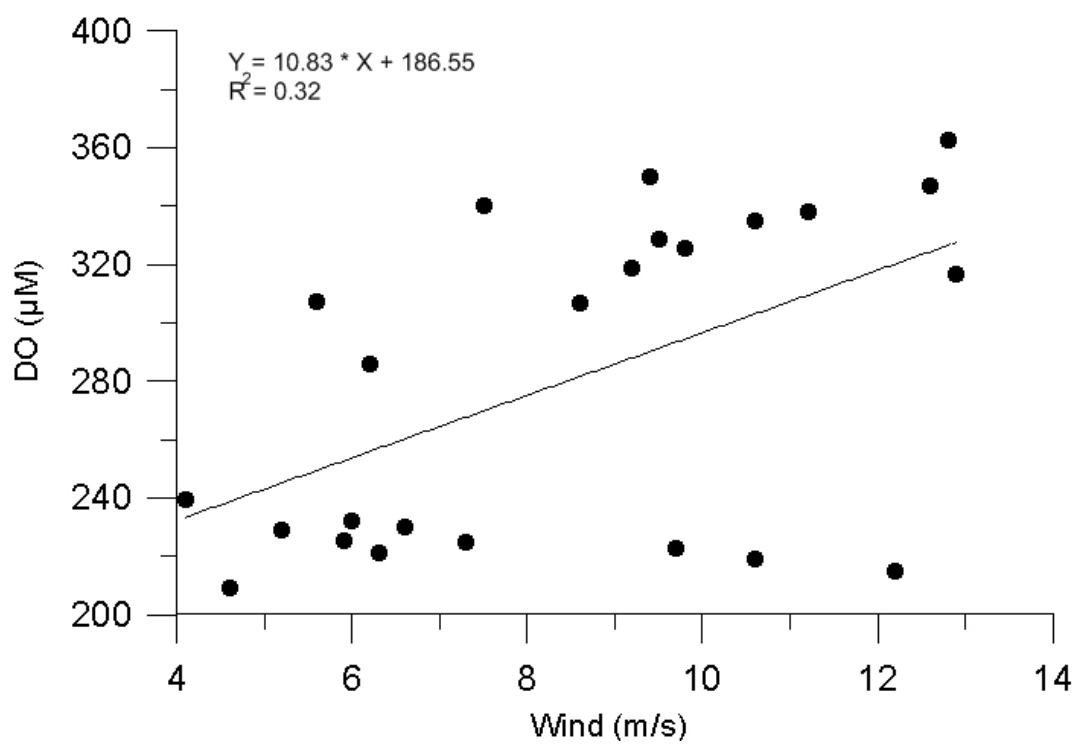


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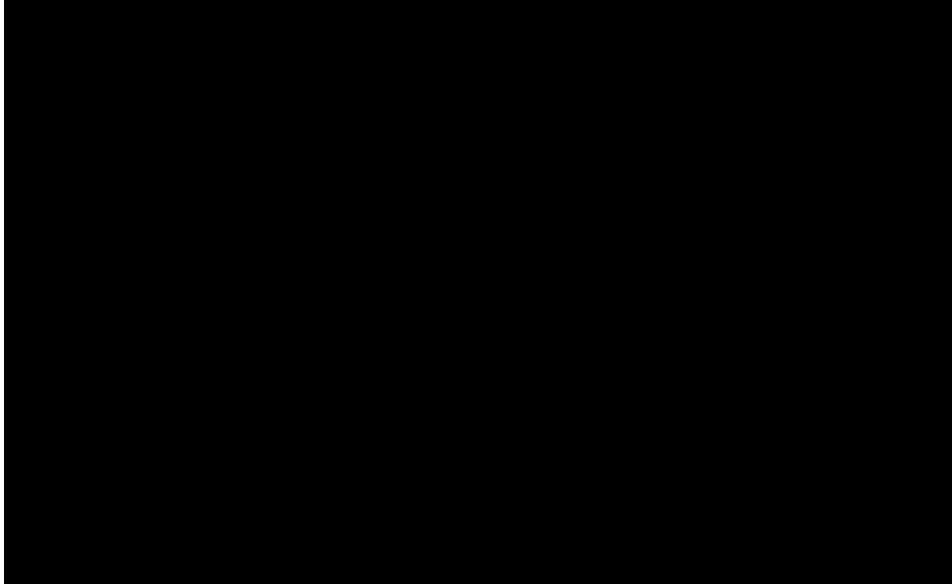
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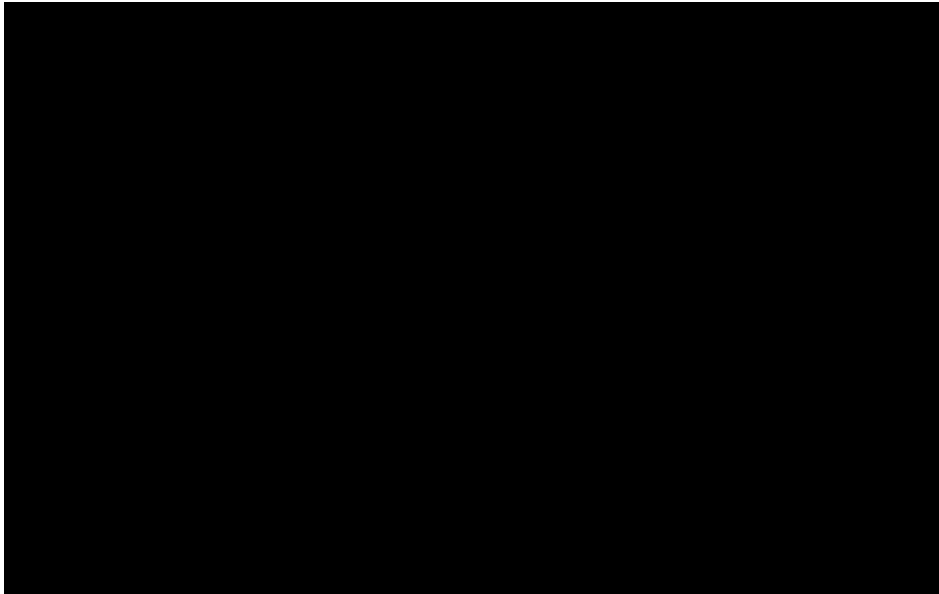
(a)



(b)
Fig. 6

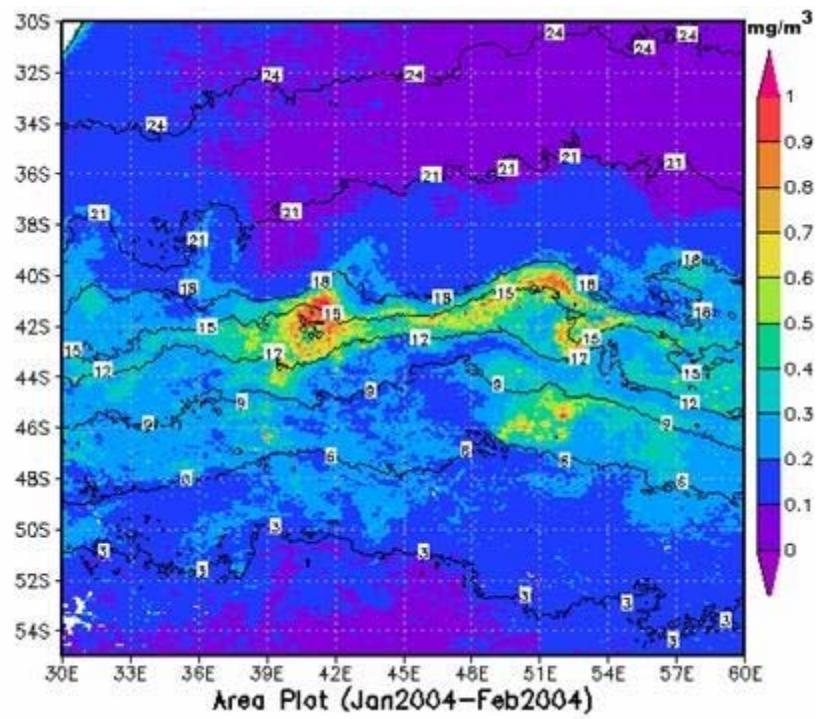


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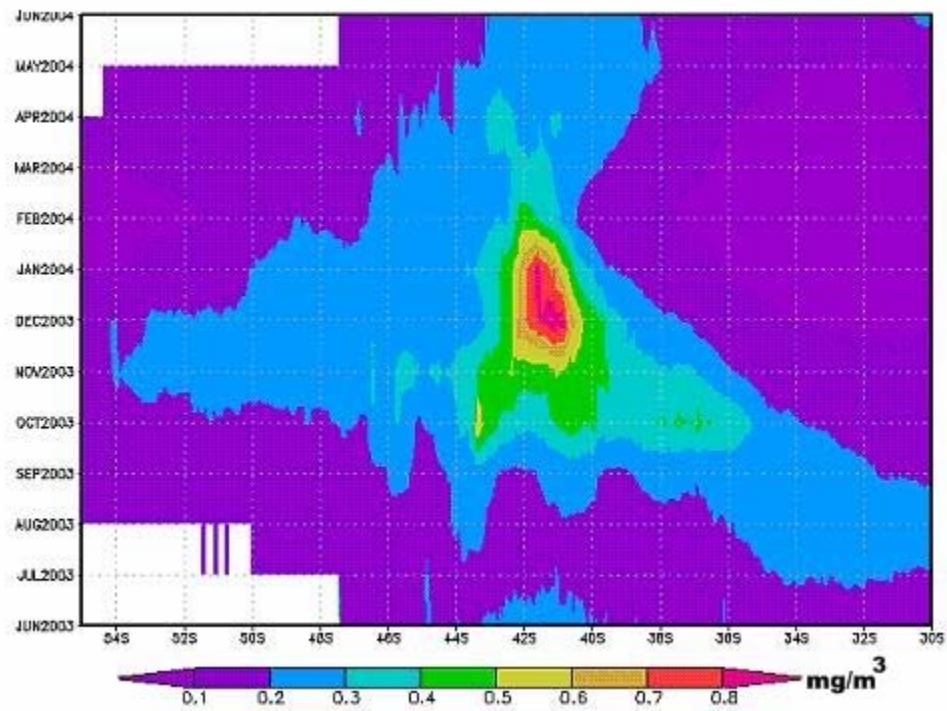


(b)

Fig. 7



(a)



(b)

Fig. 8

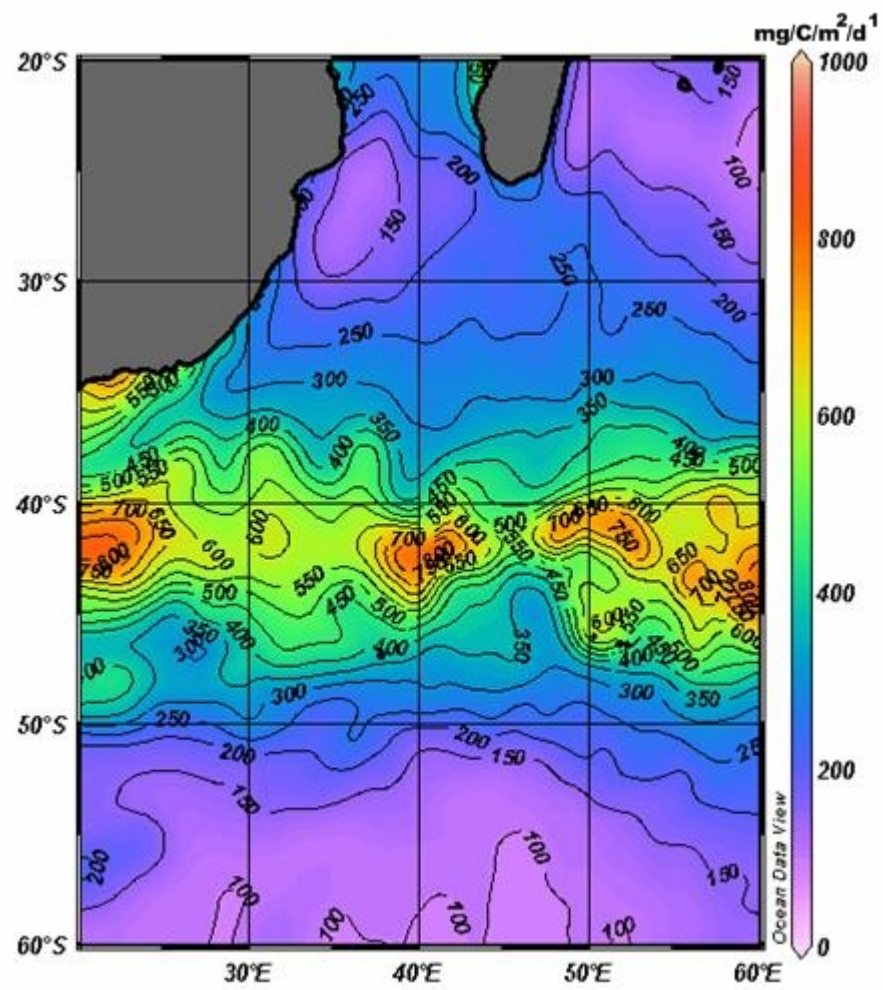
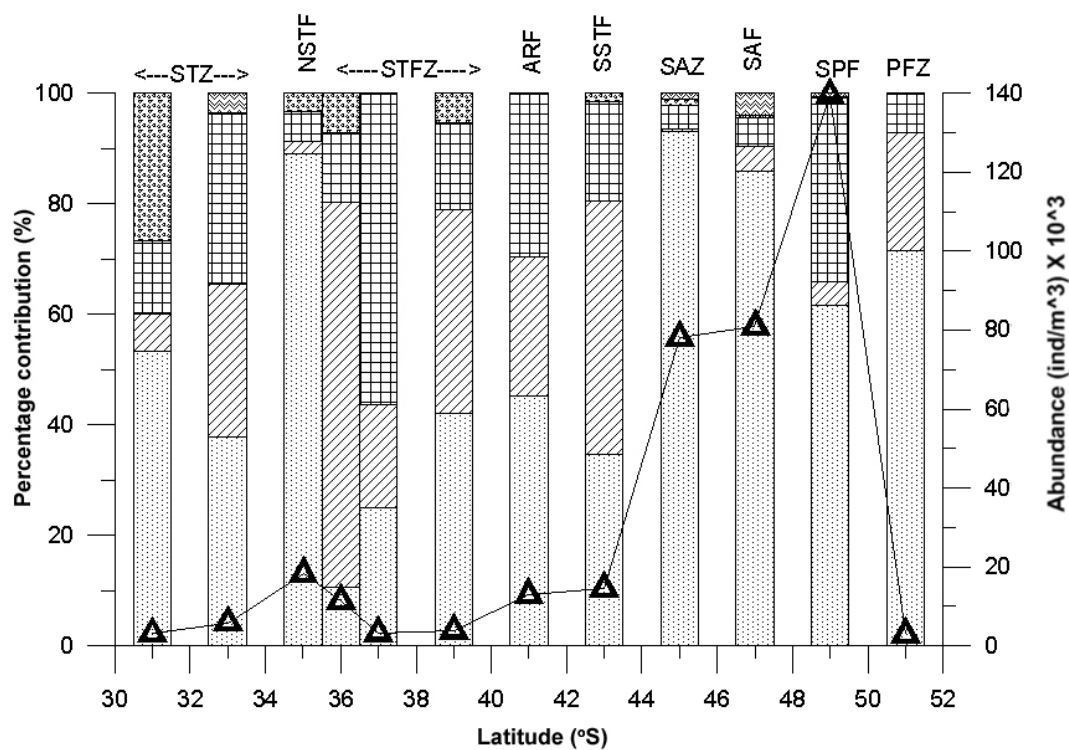
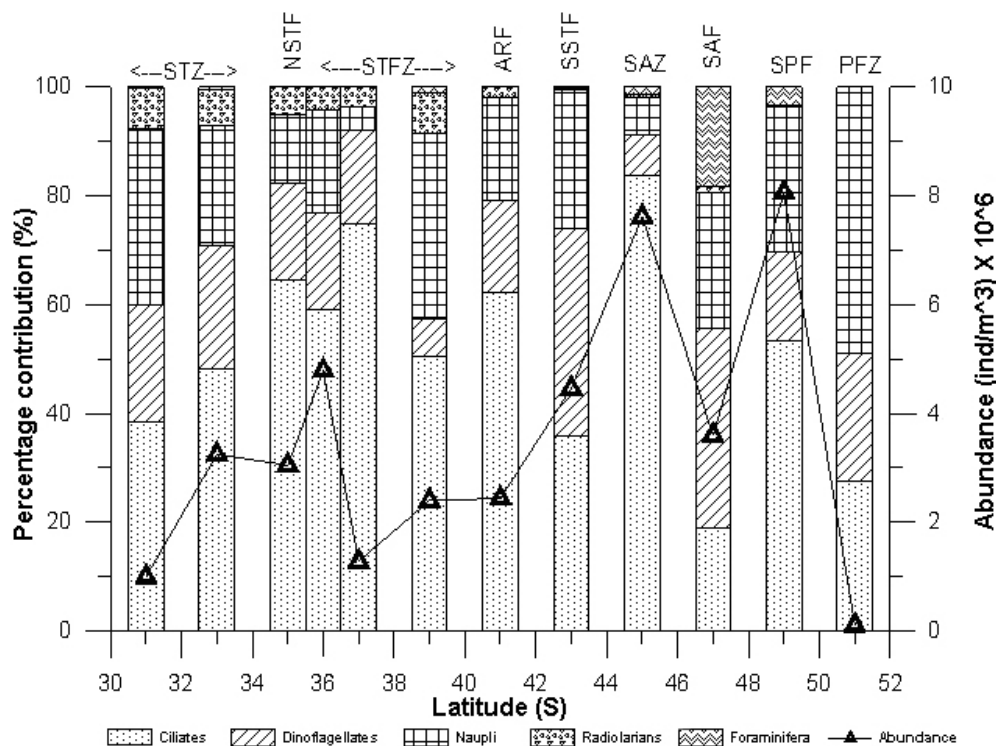


Fig. 9

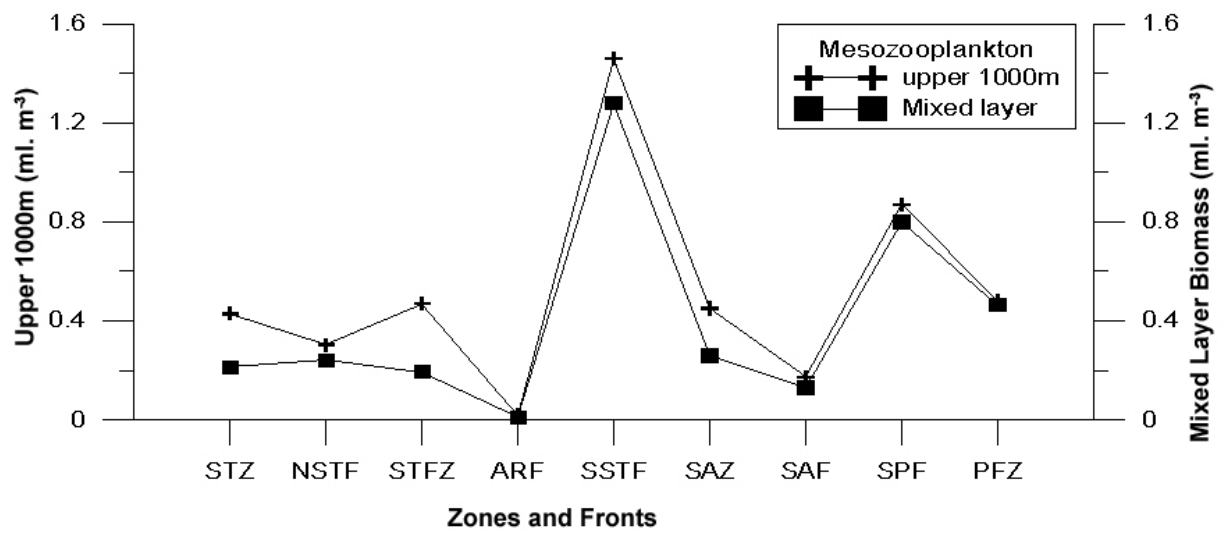


(a)

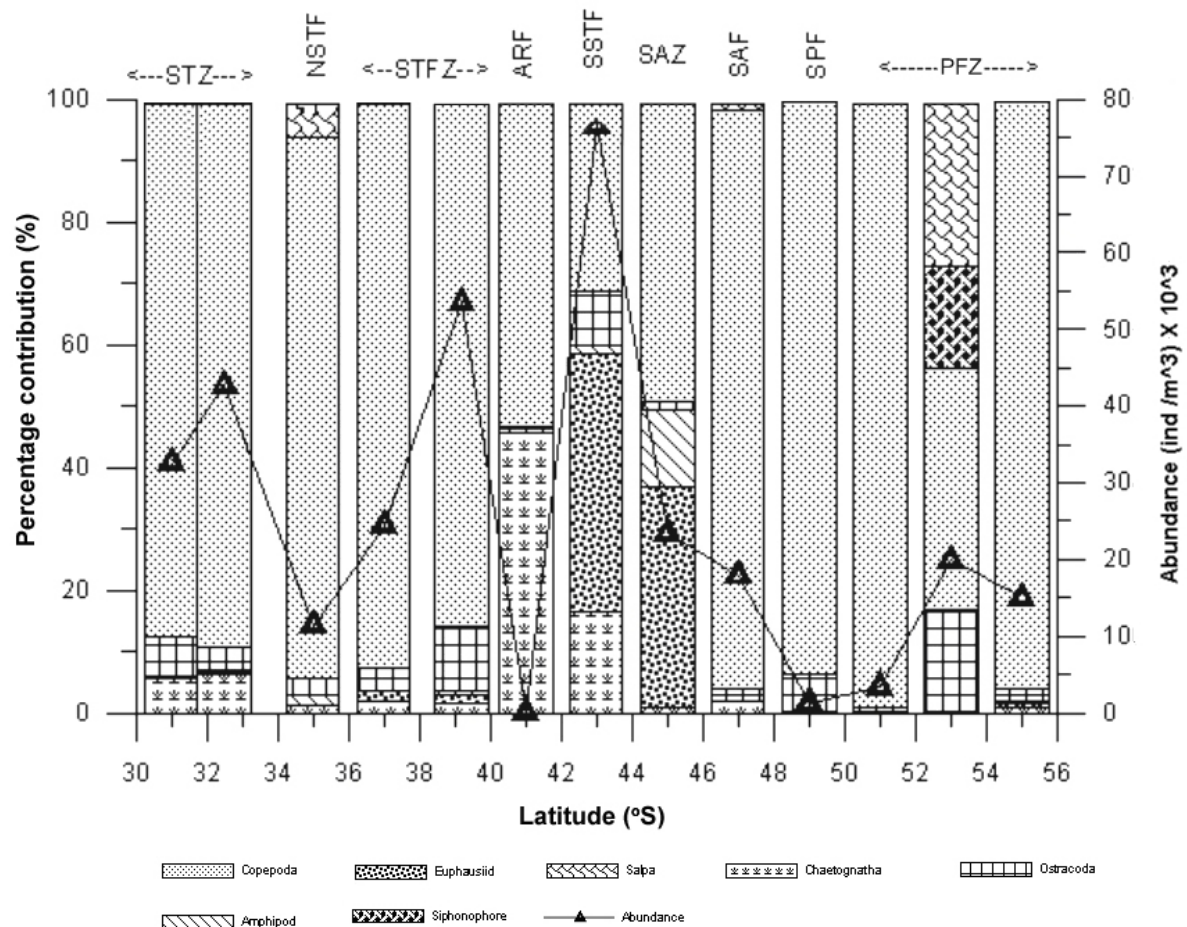


(b)

Fig. 10



(a)



(b)

Fig. 11

Zones and fronts	Lat (°S)	Lon (°E)	Stn. Dep. (m)	Tpot-0 (°C)	Salinity	DO (μM)	NO3 (μM)	PO4 (μM)	SiO4 (μM)
STZ	30.34	45.80	1778	25.31	35.63	221			
	31.01	45.00	2251	25.14	35.66	209	2.66	0.16	6.58
	32.00	45.00	1988	25.00	35.68	215			
	32.84	45.00	1166	23.35	35.69	223	0.66	0.16	5.17
NSTF	34.00	45.00	1100	21.92	35.69	225			
	35.08	45.00	2275	22.22	35.70	225	0.66	0.16	4.39
STFZ	36.14	45.00	2850	21.07	35.68	232			
	36.99	45.00	2979	20.05	35.64	229	0.28	0.16	7.31
	38.01	45.00	3081	20.05	35.62	224			
	39.00	45.00	4004	20.48	35.59	219	0.43	0.16	8.04
ARF	40.43	45.00	3854	18.71	35.60	230			
	41.01	45.00	3256	18.42	35.62	239	0.29	0.10	5.85
SSTF	42.00	45.00	3480	13.06	34.16	286			
SAZ	43.02	45.00	3097	10.23	33.70	307	14.40	0.10	9.50
	44.00	45.00	2205	8.66	33.77	319			
	45.02	45.00	1613	8.43	33.77	307	19.73	0.64	9.50
	46.01	45.00	1897	7.75	33.80	315			
	47.01	45.00	3227	7.24	33.79	317	19.87	0.32	7.31
SAF	47.99	45.00	3927	5.39	33.77	304			
	49.00	45.00	4245	5.23	33.77	335	21.31	0.96	8.04
SPF	49.99	45.00	4383	3.83	33.79	338			
PFZ	51.00	45.00	4051	2.72	33.87	347	26.74	0.80	39.47
	52.00	45.00	3129	2.64	33.88	340			
	53.00	45.00	319	2.35	33.80	350	25.88	0.96	48.97
	54.00	45.00	3876	2.19	33.78	363			
	55.00	45.00	4137	2.24	33.80	326	10.11	0.16	24.12

Table 1

Zones and fronts	Lat (°S)	Lon (°E)	Stn. Dep. (m)	Chl- <i>a</i> (mgm ⁻²)	PP (mgCm ⁻² d ⁻¹)	Micro (S) X 10 ³ (ind.m-3)	Micro (Upper 120) X 10 ³ (ind.m-2)	Meso (MLD) (mlm ⁻³)	Meso (Upper 1000) (mlm ⁻³)
STZ	30.34	45.80	1778	0.085	203.98	4.40	1588	0.21	0.41
	31.01	45.00	2251	0.091	214.68				
	32.00	45.00	1988	0.072	205.58				
	32.84	45.00	1166	0.077	233.90				
NSTF	34.00	45.00	1100	0.077	294.99	18.20	3046	0.24	0.30
	35.08	45.00	2275	0.082	295.19				
STFZ	36.14	45.00	2850	0.079	300.86	3.50	2819	0.25	0.47
	36.99	45.00	2979	0.088	333.99				
	38.01	45.00	3081	0.107	373.23				
	39.00	45.00	4004	0.125	430.15				
ARF	40.43	45.00	3854	0.123	408.75	12.80	2434	0.01	0.01
	41.01	45.00	3256	0.138	493.02				
SSTF	42.00	45.00	3480	0.479	950.13	14.40	4459	1.28	1.46
SAZ	43.02	45.00	3097	0.195	456.38	79.40	5608	0.27	0.45
	44.00	45.00	2205	0.159	348.57				
	45.02	45.00	1613	0.170	335.67				
	46.01	45.00	1897	0.188	365.22				
	47.01	45.00	3227	0.209	367.88				
SAF	47.99	45.00	3927	0.202	338.77	80.80	3600	0.13	0.17
	49.00	45.00	4245	0.224	315.88				
SPF	49.99	45.00	4383	0.125	187.19	139.40	8057	0.80	0.87
PFZ	51.00	45.00	4051	0.091	144.49	2.80	108	0.48 (6.46)	0.50 (6.55)
	52.00	45.00	3129	0.062	108.65				
	53.00	45.00	319	0.072	108.01				
	54.00	45.00	3876	0.069	104.34				
	55.00	45.00	4137	0.109	119.54				

Table2