Routledge
Taylor & Francis Group

RESEARCH ARTICLE

Planktonic food web structure at SSTF and PF in the Indian sector of the Southern Ocean during austral summer 2011

H.U.K. Pillai[a,b], N. Anilkumar[a], C.T. Achuthankutty[a], C.R. Mendes [c], P. Sabu[a], K.V. Jayalakshmi[d], C.R. Asha Devi[e], Deepti Dessai[a], Jenson George[a], Sini Pavithran[a], C.K. Hari Devi[d], S.C. Tripathy[a] & N.R. Menon[f]

[a]National Centre for Antarctic and Ocean Research, Vasco Da Gama, India; [b]Zoological Survey of India, Kolkata, India; [c]Institute of Oceanography, Federal University of Rio Grande, Rio Grande, Brazil; [d]National Institute of Oceanography, Regional Centre, Kochi, India; [e]Centre for Marine Living Resources and Ecology, Kochi, India; [f]Nansen Environmental Research Centre, Kochi, India

ABSTRACT

This study aims to describe the planktonic food web structure with respect to phytoplankton biomass (chlorophyll *a*) and prevailing environmental conditions at the South Subtropical Front (SSTF) and the Polar Front (PF) in the Indian sector of the Southern Ocean. Sampling was carried out at each front for 72 hrs, at 6-hr intervals, during the austral summer 2011. Considerable variations were observed in the hydrography between these two fronts. A strong temperature minimum layer was observed at the PF. Although the surface primary production and chlorophyll *a* values showed similar trends at both the fronts, the water column values of these parameters showed major disparities. The phytoplankton composition also revealed marked difference between the fronts. A deep chlorophyll maximum concordant with the upper limit of the temperature minimum layer was prominent at the PF. The microzooplankton abundance at the SSTF was twice as high as at the PF. The mesozooplankton biovolume and population density also showed considerable variations between these fronts. Noticeable diel variations were observed in the surface mesozooplankton biovolumes at both the fronts and the copepod *Pleuromamma gracilis* showed active diel vertical migration at SSTF. Both the grazing and senescence indices showed significant variations between these fronts, suggesting a disparity in the ecological efficiency of the two regions. The variability observed in the plankton community structure with respect to the hydrography and the biological components measured suggests that a multivorous food web at the SSTF and a conventional food web at the PF prevailed during the period of study.

Introduction

The structure of the food web in an aquatic ecosystem is extremely difficult to decipher (Jacob et al. 2006) and is the chief factor that governs the dynamics of these systems (Legendre & Rassoulzadegan 1995; Bradford-Grieve et al. 1999; Froneman et al. 2000). The conventional (herbivorous) food web is believed to dominate the productive regions of the aquatic ecosystems, where energy is channelled through the primary producers (large phytoplankton) to the primary consumers (zooplankton) and then to higher trophic levels. However, many studies have highlighted the dominance of the microbial food web, particularly in oligotrophic waters, in which bacterioplankton/picoplankton and microzooplankton play the major role in energy channelling (Lenz 1992, 2000; Lefevre et al. 1998; Calbet 2008). The multivorous food web is another possibility; here microbial and conventional modes coexist and play a significant part in food-web dynamics (Lefevre 1998). Legendre & Rassoulzadegan (1995) have proposed a continuum of trophic pathways, ranging from herbivorous to multivorous food webs, microbial food web and microbial loop and also suggested that the multivorous and the microbial food webs are more stable than the conventional food web and the microbial loop, the latter two being ephemeral and hence inherently unstable. Sakka et al. (2014) have revisited the planktonic food web and suggested the occurrence of a

phyto-microbial food web in which the microzoo-plankton largely consume the phytoplankton.

The PF and the STF are the two main circum-global zoogeographical frontal boundaries in the SO with enhanced biological activity (Pakhomov et al. 1994). The PF experiences marked seasonality, forms the northern limit of the permanent pack ice during winter and separates the cold Antarctic waters from the sub-Antarctic region. The PF, is characterized by high-nutrient low-chlorophyll waters (Treguer & Bennekom 1991; Laubscher et al. 1993) and experiences seasonal (spring and summer) phytoplankton blooms (Kopczynska et al. 1998; Mengesha et al. 1998). It has been reported that the PF is characterized by high biomass of large-sized zooplankton, ichthyoplankton and myc-tophids compared to the surrounding water masses (Foxton 1956; Hopkins 1971).

The STF, the northern boundary of the Antarctic Circumpolar Current, is formed by the mixing of cool macro-nutrient rich, iron limited sub-Antarctic water with warm low macro-nutrient subtropical water. This is also a region of formation and shedding of eddies (Lutjeharms & Valentine 1988) and experiences year-round elevated chlorophyll and primary production (Sullivan et al. 1993; Van Ballegooyen et al. 1994; Murphy et al. 2001). Thus, though the SO has been regarded as the largest high-nutrient low-chlorophyll water body at a broader scale, this study area falls within the two major productive frontal regions, unique for their physical and biological characteristics.

The planktonic food-web structure of the SO is highly dynamic because of its pronounced seasonal variations. Large-sized diatoms have been considered as the basis of the Antarctic food web (Hart 1934; Guillard & Kilham 1977). However, recent investiga-tions have revealed the significance of nano-and pico-planktonic organisms in the food-web dynamics in different regions of the Antarctic waters (Hanson et al. 1983; Xiuren et al. 1996; Detmer & Bathmann 1997). In an earlier study, LeFevre et al. (1998) pointed out that zooplankton play a critical role in the food-web structure of the SO on account of their feeding versatility with respect to food availability which has been suggested as a successful adaptation for their survival even in this extreme environment. It has been estimated that up to 80% of the net primary production in the SO may be consumed directly by meso- and macrozooplankton (Huntley et al. 1991). Krill is widely recognized as the key species in the Antarctic food web. However, small herbivorous zoo-plankton such as copepods have been estimated to have greater biomass than that of the Antarctic krill and this signifies the importance of other plankton communities in these waters (Takahashi et al. 2010); Although different aspects of the planktonic food web have been addressed from the Indian sector of the SO

(Mayzaud et al. 2002; Fielding et al. 2007; Jasmine et al. 2009; Takahashi et al. 2010; Takahashi et al. 2011), studies of the temporal variations in the plank-tonic food-web structure at the major fronts in rela-tion to the prevailing hydrographic and biological conditions, based on continuous field observations are lacking. Therefore, considering the significance of STF and PF as the two prominent (in terms of production) frontal regions of the SO, this study was designed to describe the planktonic food-web struc-ture at these two fronts with respect to chl *a* and prevailing environmental conditions during the 2011 austral summer. Among the two sections of the STF (south subtropical front and North subtropical front) in the Indian Ocean sector, present study location is positioned in the south subtropical front (SSTF).

Materials and methods

Data and samples were collected at 6-hr intervals for 72 hrs at the SSTF (42° 00'S 47° 00'E; 26/02/2011 – 01/03/2011) and the PF (51° 30'S 57° 30'E; 08/02/2011–11/02/2011) in the Indian sector of the SO (Fig. 1), onboard the ORV *Sagar Nidhi*, an ice-class multidisciplinary research vessel. Oceanic fronts were identified using the charac-teristic property indicators listed by Anilkumar et al. (2006). In this study, the SSTF was identified as the region where the SST ranged between 11 and 17°C and the SSS ranged between 34.05 and 35.35. The PF was identified as the region where the SST ranged between 4 and 5°C (the northern limit of the 2°C isotherm was below 200 m) and the SSS ranged between 33.8 and 33.9. The SST was measured with a bucket thermometer (accuracy ± 0.5°C). A CTD (SBE 911 plus, Sea-Bird Scientific) was used for profiling the temperature (accu-racy ± 0.001°C) and salinity (conductivity ± 0.0001 S/m) of the upper 500 m water column. The salinity values obtained from the CTD were compared with values obtained from the onboard salinometer (Autosal
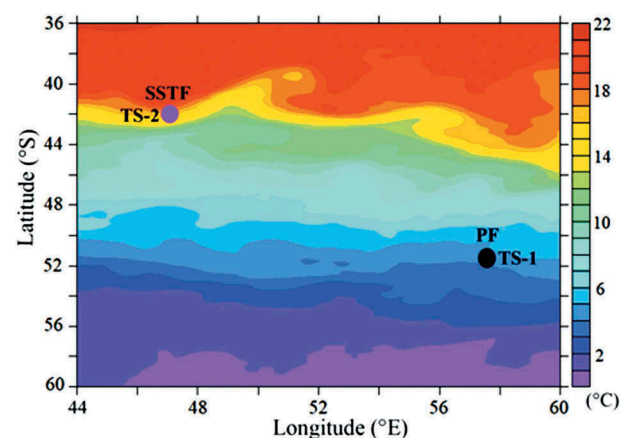
Figure 1. Station locations in the PF (TS-1) and SSTF (TS-2). The background colours represent SSTs (°C) from the Global Group for High Resolution Sea Surface Temperature (1 km × 1 km).

8400A, Guildline), after calibrating with standard sea-water. The difference found in the salinity values derived from the Autosal and CTD sensor was ± 0.001 to 0.01. The water samples for estimating nutrients (NO_3, PO_4 and SiO_4), DO, chl *a* and phytoplankton pigments were collected from discrete depths (0, 10, 30, 50, 75, 100 and 120 m), using Niskin bottles (5 L) attached to the CTD rosette. The nutrient samples were analysed onboard using an automated continuous flow analyser (Autoanalyzer 51 001–1, Skalar). Winkler's titration method (Carpenter 1965) was followed for estimating DO. For estimating chl *a*, 2 litres of water was filtered through GF/F filters (pore size 0.7 μm), extracted over-night with 10 ml of 90% acetone and measured using a fluorometer (AU-10, Turner Designs), before and after acidification (Strickland & Parsons 1972). The primary productivity experiments were carried out on the third sampling day at both the locations. The water samples for the primary productivity experiments were collected (0, 30, 50, 75 and 120 m) just before sunrise using Niskin samplers (5 L) attached to the CTD rosette. After adding 1 ml of $NaH^{14}CO_3$, (activity 5 μ Ci) in each sample (300 ml Nalgene bottle), it was incubated on the deck for 6 hrs with continuous flow of seawater. Two light and one dark bottles were incubated for each depth with appropriate neutral density filters to compensate for the light intensity. After incubation, the samples were filtered through 47 mm GF/F filters (pore size 0.7 μm), exposed to HCl fumes to remove the excess inorganic carbon and the filters were stored individually in scintillation vials. In the laboratory, the activity was counted in a liquid scin-tillation counter (Wallace), after adding the scintillation cocktail. Using the formula of Strickland & Parsons (1972), the disintegration per minute values were con-verted to daily production rates (mg C m^{-3} d^{-1}). For pigment analysis, the seawater samples (from same depths as that of primary productivity samples) were filtered (0.5–2.5 L) under low vacuum through GF/F filters and immediately frozen in liquid nitrogen for onshore analyses. Pigments were extracted in the dark with 3 ml of 95% cold-buffered methanol (2% ammo-nium acetate) and analysed using a HPLC system equipped with a refrigerated auto-sampler (SIL-20AC), a photodiode array (SPD-M20A) and a fluorescence detector (RF-10AXL), all manufactured by Shimadzu. The gradient elution program used was a slight modifi-cation of that of Zapata et al. (2000). Complete details of the HPLC method followed are described elsewhere (Mendes et al. 2007). To determine the phytoplankton community composition from the HPLC pigment con-centrations, the CHEMTAX matrix factorization soft-ware routine was used (Mackey et al. 1996). The initial pigment ratio matrix was developed primarily from the ratios determined by Schluter et al. (2011), except for the haptophytes ratios, which were determined from Zapata et al. (2004). The basis for calculations and procedures are fully described in Mendes et al. (2015). The HPLC

analysis allowed the separation, identification and quan-tification of three types of chl *a* degradation products: chlide *a*, phytin *a* and phide *a*. The relative content of chlorophyll degradation products can be used as a proxy for the grazing pressure and for the senescence of phy-toplankton cells (Jeffrey 1974). In this way, chl *a* pig-ments derived were used for calculating the grazing index ([phide *a*+ Phytin *a*]/[Total chl *a* + phide *a*+ phytin *a* + chlide *a*]) and the senescence index ([chlide *a*]/[Total chl *a* + phide *a* + phytin *a* + chlide *a*]). For microzoo-plankton analysis, 8 L of surface water was initially fil-tered through 200 μm mesh and subsequently through 20-μm mesh. The concentrated sample was backwashed and transferred to 500 ml filtered seawater and preserved in 1% acid Lugol's iodine. The enumeration and identi-fication were done up to group level under an inverted microscope. A WP-2 net (mesh size 200 μm), attached with a digital flow meter (model 2030, General Oceanic) was towed (ship speed 1 knot/hr) for 10 min (maximum depth 2 m) for surface mesozooplankton sample collec-tion. In addition, vertical mesozooplankton samples from two depth layers (0–50 m and 50–150 m) were also collected using a multiple plankton net (MultiNet, Hydro-Bios, mesh size 200 μm), to estimate the standing stock variation in the water column. The biovolume (after removing large detritus particles) was estimated by displacement volume method (Postel et al. 2000) and the samples were preserved in 5% buffered formal-dehyde–seawater solution. The mesozooplankton com-position and species diversity of copepods were studied only from the surface samples (WP-2 net) as the diel variations were clearly reflected in these samples. Different taxa were sorted out, enumerated and identi-fied from the whole sample or 25% aliquot when the sample volume was > 5 ml. Copepods were identified to species level under a dissecting microscope (CK30, Olympus). Two-way ANOVA (for unequal samples) and three-way ANOVA (for equal samples) were per-formed to comprehend the statistical significance of dif-ferent parameters. PCA was carried out on log transformed and normalized data (Primer 6 software package) to analyse and visualize the overall spatio-tem-poral variations in the environmental and biological parameters across the study area.

Results

Hydrography

Significant spatial variation ($p < 0.001$) was observed in the SST and the SSS between the PF and the SSTF, but the temporal variation at each front was not significant ($p < 0.05$). The highest SST of 16.8°C (SSS of 35.3) was observed at the SSTF, while the lowest SST of 4.57°C (SSS of 33.75) was observed at the PF. In accordance with the higher wind speed (data from a MODIS-Aquaimagery shipboard automatic weather system) observed at the PF
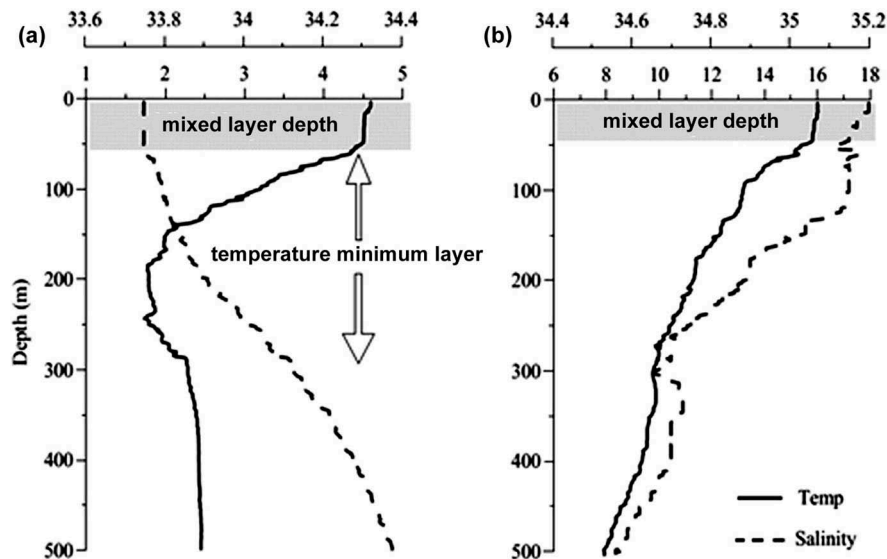
Figure 2. Typical distribution of temperature and salinity at the (a) PF and (b) SSTF.

(10.6 m s^{-1}) compared to that at the SSTF (7.6 m s^{-1}), the mixed layer was also deeper at the PF (60 m) compared to that at the SSTF (45 m), indicating a weaker stratification and deeper vertical mixing at the PF. The vertical temperature profile at the PF showed a temperature minimum layer between 55 and 300 m depth (Fig. 2a) and the lowest temperature of $1.5°C$ was observed at around 220 m depth. However, the vertical distribution of temperature at the SSTF showed a normal pattern (Fig. 2b). The average surface DO concentration was higher at the PF (7.04 ml L^{-1}) compared to that at the SSTF (6.13 ml L^{-1}), but the temporal variability was minimal at both the fronts. Marked variations were observed in the nitrate silicate and phosphate concentrations (NO_3: $p < 0.001$, SiO_4 and PO_4: $p < 0.05$) between the fronts and the NO_3 was around tenfold higher at the PF than at the SSTF (Table 1). The temporal variations of DO and nutrients were not significant ($p < 0.05$) in either of the study areas. The average concentration of DO and nutrients at different depth layers of both the fronts are given in Table 1.

Primary productivity and chl a

Primary productivity in the surface waters did not show any significant change between the fronts (PF: 2.69 mg C m^{-3} d^{-1}, SSTF: 2.87 mg C m^{-3} d^{-1}) while

the water column integrated production showed considerable variation (PF: 211 mg C m^{-2} d^{-1}, SSTF: 152 mg C m^{-2} d^{-1}). In the vertical profile, a sharp increase in primary productivity was observed at 50 m depth (0 m: 2.69, 30 m: 2.12, 50 m: 3.71, 75 m: 0.86 and 120 m: 0.18 mg C m^{-3} d^{-1}) at the PF, which was not evident (0 m: 2.87, 30 m: 1.65, 50 m: 1.14, 75 m: 0.91 and 120 m: 0.46 mg C m^{-3} d^{-1}) at the SSTF. Surface chl a distribution also did not show any marked variation between the PF (average 0.38 ± 0.11 mg m^{-3}) and the SSTF (average 0.34 ± 0.08 mg m^{-3}), but significant variation ($p < 0.001$) was observed in the water column integrated chl a (PF: 65.57 ± 9.06 mg m^{-2}, SSTF: 34.12 ± 6.66 mg m^{-2}). The higher value observed at the PF is explained by the presence of a prominent DCM (chl $a > 1$ mg m^{-3}) at around 75 m depth (Fig. 3a). At the SSTF though DCM was present, it was less prominent (chl $a < 0.7$ mg m^{-3}) and was at a relatively shallower depth (ca. 45 m) compared to that at the PF (Fig. 3b). The satellite imageries (MODIS-Aqua) of surface chl a distribution in the SO (Fig. 4) during the period of study showed a wide band of high chlorophyll area at the PF (south of 50°S), including the present study location (TS-1; Fig. 4a). At the SSTF also a narrow band of high chlorophyll area (south of 40°S), including the present study location (TS-2; Fig. 4b) was seen.

Phytoplankton composition, grazing and senescence indices

The phytoplankton composition (estimated from pigment concentration data using CHEMTAX taxonomic software) revealed marked differences between the two sampling locations. Diatoms comprised the major taxonomic group contributing to the

Table 1. Average DO and nutrient distribution (NO_3, PO_4 and SiO_4) at different depth layers in the study area.

Depth (m)	SSTF				PF			
	DO (ml/l)	NO$_3$ (µm)	SiO$_4$ (µm)	PO$_4$ (µm)	DO (ml/l)	NO$_3$ (µm)	SiO$_4$ (µm)	PO$_4$ (µm)
0	5.9	1.3	3.5	1.5	6.97	14.7	4.7	1.8
10	6.0	1.7	3.5	1.1	7.01	13.2	4.5	1.7
30	5.8	0.9	4.2	1.3	6.72	13.7	4.7	1.9
50	5.8	1.6	4.9	1.2	6.99	15.3	6.1	1.9
75	5.2	2.4	3.4	1.4	6.94	13.2	6.2	1.8
100	5.6	4.3	3.1	1.3	6.89	14.3	8	1.7
120	5.6	5.5	4.5	1.7	6.95	15.1	11.5	1.7
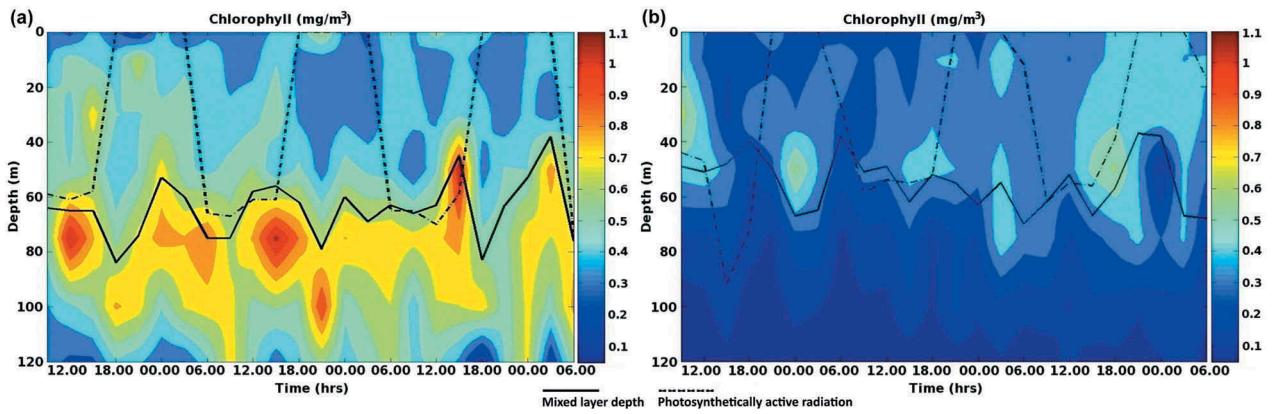
Figure 3. Vertical profile of chl *a* at the (a) PF and (b) SSTF.
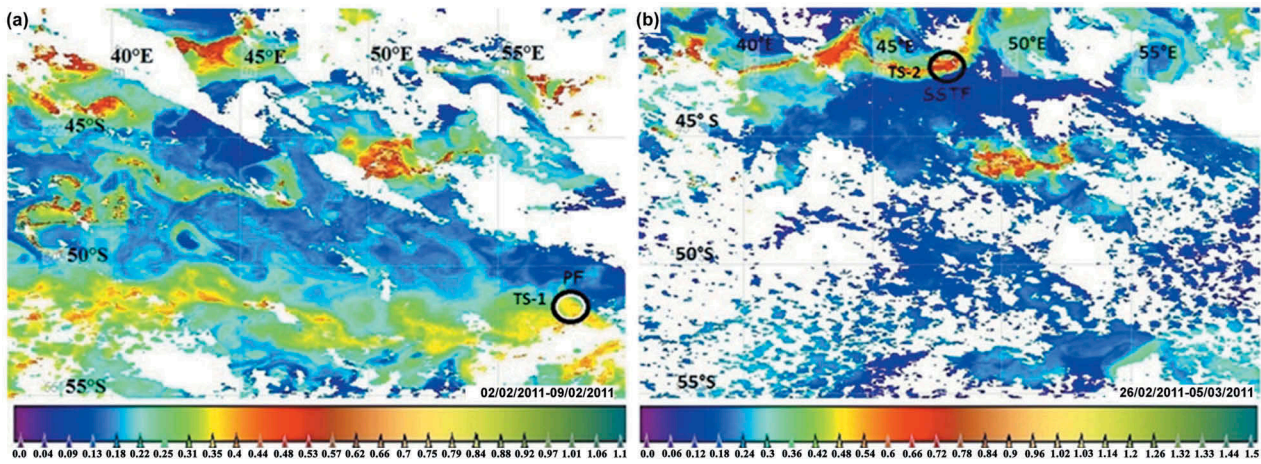
Figure 4. Chl *a* (mg m^{-3}) concentration (MODIS-Aquaimagery) during the study period at the (a) PF and (b) SSTF. Study areas encircled.
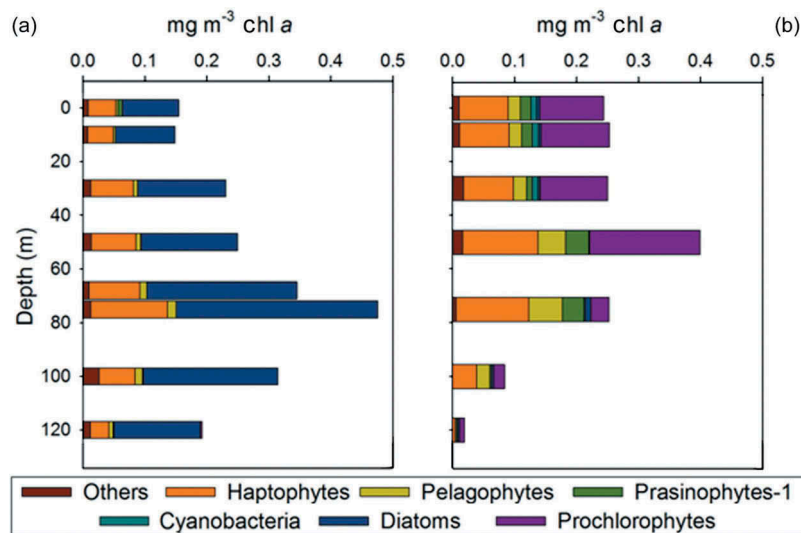
Figure 5. Depth distribution of phytoplankton groups biomass (as chl *a* concentration) calculated using the CHEMTAX programme at the (a) PF and (b) SSTF. The category 'others' comprises cryptophytes, peridinin-containing dinoflagellates and prasinoxanthin-containing prasinophytes. Prasinophytes-1 are prasinophytes without prasinoxanthin.

phytoplankton biomass at the PF (Fig. 5a) whereas prochlorophytes dominated at the SSTF (Fig. 5b). Haptophytes were a dominant component at both

the fronts. The grazing and senescence indices were observed to be higher at the PF (Fig. 6a) compared to the SSTF (Fig. 6b). The vertical profile of grazing
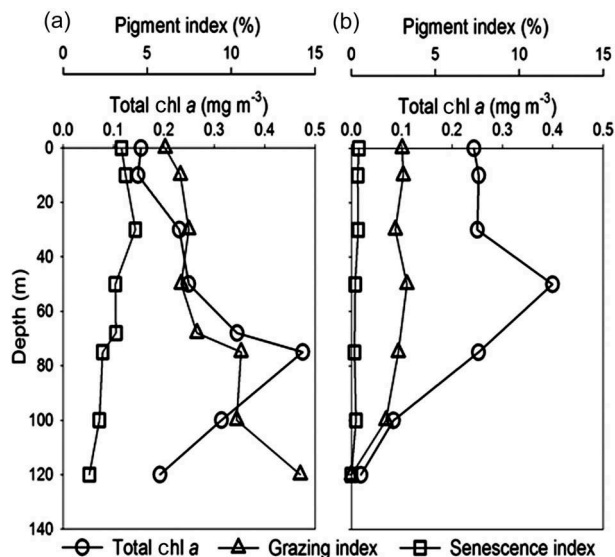
Figure 6. Vertical profiles of Total chl *a* (Total chl *a*; mono-vinyl + divinyl chl *a*), Grazing Index ([phide *a*+ phytin *a*]/[Total chl *a* + phide *a*+ phytin *a* + chlide *a*]) and Senescence Index ([chlide *a*]/[Total chl *a* + phide *a* + phytin *a* + chlide *a*]) at the (a) PF and (b) SSTF.

index at the PF showed a comparatively high value at 75 m, which was well correlated with the DCM depth. At the SSTF, grazing pressure was also relatively high at the DCM depth, but was not as intense as at the PF. The senescence index was also moderately high at the PF (Fig. 6a), but was negligible at the SSTF (Fig. 6b). Therefore, the concentrations of all degradation products were observed as significantly higher ($p < 0.001$) at the PF (10.1% for grazing and 3.4% for senescence) than at the SSTF (4.3% for grazing and 0.3% for senescence).

Microzooplankton density and diversity

The average microzooplankton density was around two-fold higher at the SSTF (1403 ± 1694 no m^{-3})

than at the PF (789 ± 777 no m^{-3}). Ciliates dominated the community at both regions (PF: 57.9%, SSTF: 79.7%), but was nearly twice as high at the SSTF compared to the PF: average densities were 1833 ± 1135 no m^{-3} and 3354 ± 2912 no m^{-3} at the PF and the SSTF, respectively. The dinoflagellates density marginally varied between the regions (PF: 438 ± 784 no m^{-3}, SSTF: 542 ± 775 no m^{-3}). The average density of copepod nauplii was significantly higher ($p < 0.05$) at the PF (875 ± 272 no m^{-3}) compared to the SSTF (313 ± 428 no m^{-3}). Radiolarians were negligible as this group was observed only once at the PF (250 no m^{-3}) during the study period. The microzooplankton community did not show any diel pattern at either front (Fig. 7).

Mesozooplankton biovolume and numerical abundance

Significant spatial difference ($p < 0.001$) between the PF and the SSTF was observed in the mesozooplankton biovolume and population density distribution (Fig. 8). The average biovolume as well as population density distribution in the surface was three times higher at the PF (biovolume: 0.42 ± 0.19 ml m^{-3}, population density: 1252 ± 584 no m^{-3}) than at the SSTF (biovolume: 0.14 ± 0.13 ml m^{-3}, population density: 410 ± 594 no m^{-3}). Temporal variations were clearly reflected in the surface biovolume distribution as it increased during the night hours at both the frontal regions, but was more evident at the SSTF (Fig. 8a, b). However, the diel variation was not clearly seen in the population density distribution in the surface water (Fig. 8c, d). In the vertical distribution, 0–50 m depth in the water column supported higher average biovolume (PF: 0.65 ± 0.43 ml
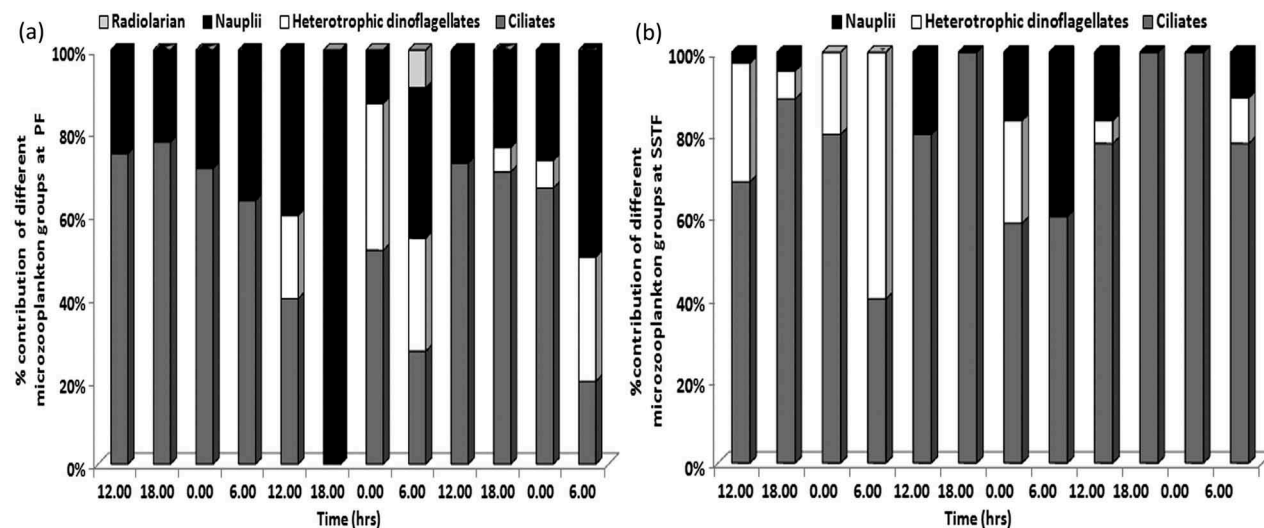
Figure 7. Diel pattern of major components of microzooplankton at the (a) PF and (b) SSTF.
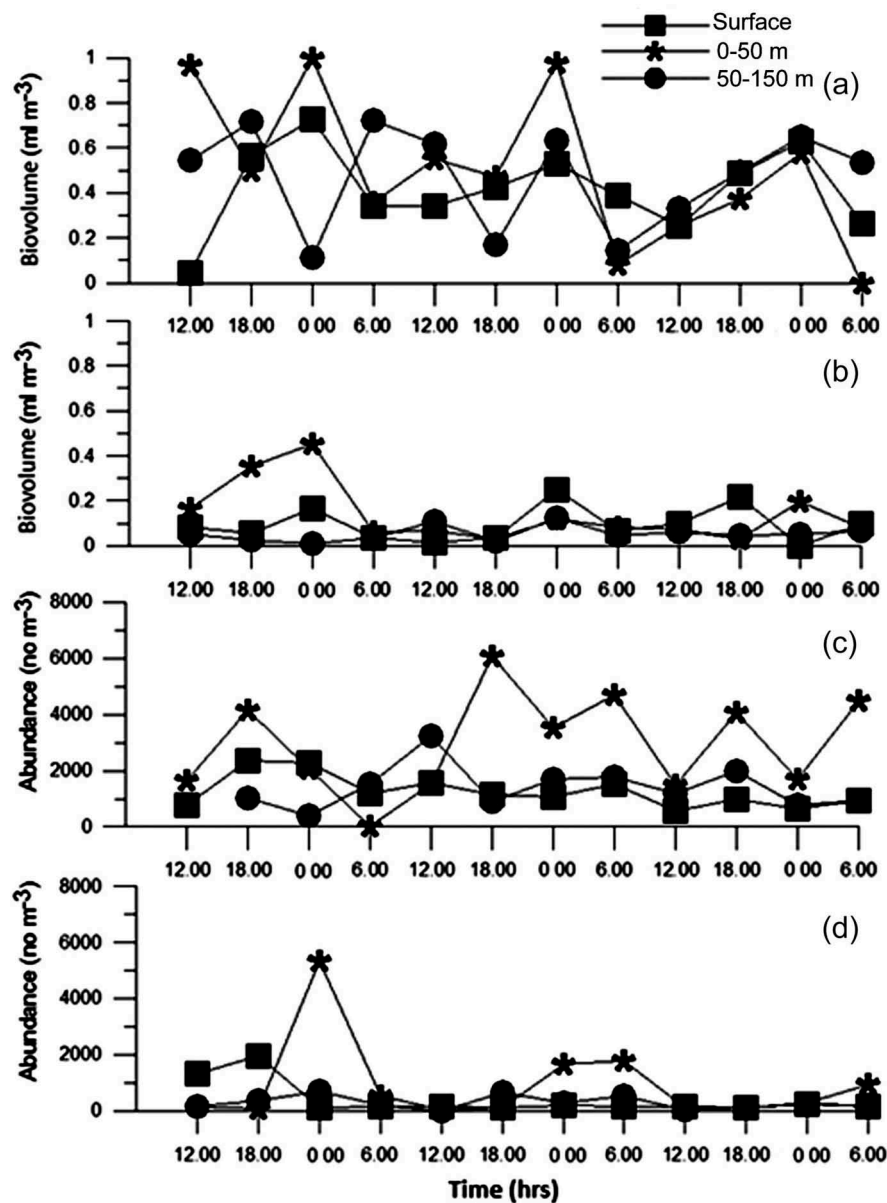
Figure 8. Diel pattern of mesozooplankton biovolume and population density in different depth layers at the (a, c) PF and (b, d) SSTF.

m^{-3}, SSTF: 0.10 ± 0.08 ml m^{-3}) as well as population density (PF: 2952 ± 1785 no m^{-3}, SSTF: 935 ± 1517 no m^{-3}) compared to 50–150 m depth in the water column (PF biovolume: 0.47 ± 0.23 ml m^{-3}, population density: 1397 ± 770 no m^{-3}; SSTF biovolume: 0.05 ± 0.03 ml m^{-3}, population density: 296 ± 230 no m^{-3}). It is also worth noticing that at the PF the average biovolume at 50–150 m depth in the water column (0.47 ± 0.23 ml m^{-3}) was also moderately high and almost comparable with that of 0–50 m depth in the water column value (0.65 ± 0.43 ml m^{-3}).

Mesozooplankton community (surface)

Eighteen taxa were encountered at the SSTF and the temporal variations of the different taxa are given in Table 2. In general, Copepoda formed the predominant taxon with an average contribution of 95%, followed by

Chaetognatha (2.21%), Salpa (1.69%) and Appendicularia (0.64%). Considerable temporal variation was seen in the composition, which also followed a diel pattern. During the first two observations (12:00 and 18:00), the blue-tinged neustonic clausocalanid copepods were dominant (99%). However, during the next observation (00:00) their density sharply reduced (43%) and the abundnce of euphausiids (23%), chaetognaths (21%) and pteropods (8%) markedly increased. Other large grazers and carnivores such as salps (0.28%), myctophids (0.58%), cephalopod larvae (0.02%) and hydromedusae (0.04%) were also encountered, though in small numbers. The abundance of copepods (76.3%) and appendicularians (18.05%) increased considerably during the fourth sampling (06:00). This was followed by (12:00) an increase in the abundance of salps (58.66%) and a decrease in copepods (31.71%). Copepods again dominated the community during the next two observations (00:00: 94%; 06.00: 92%) and this was followed again by a

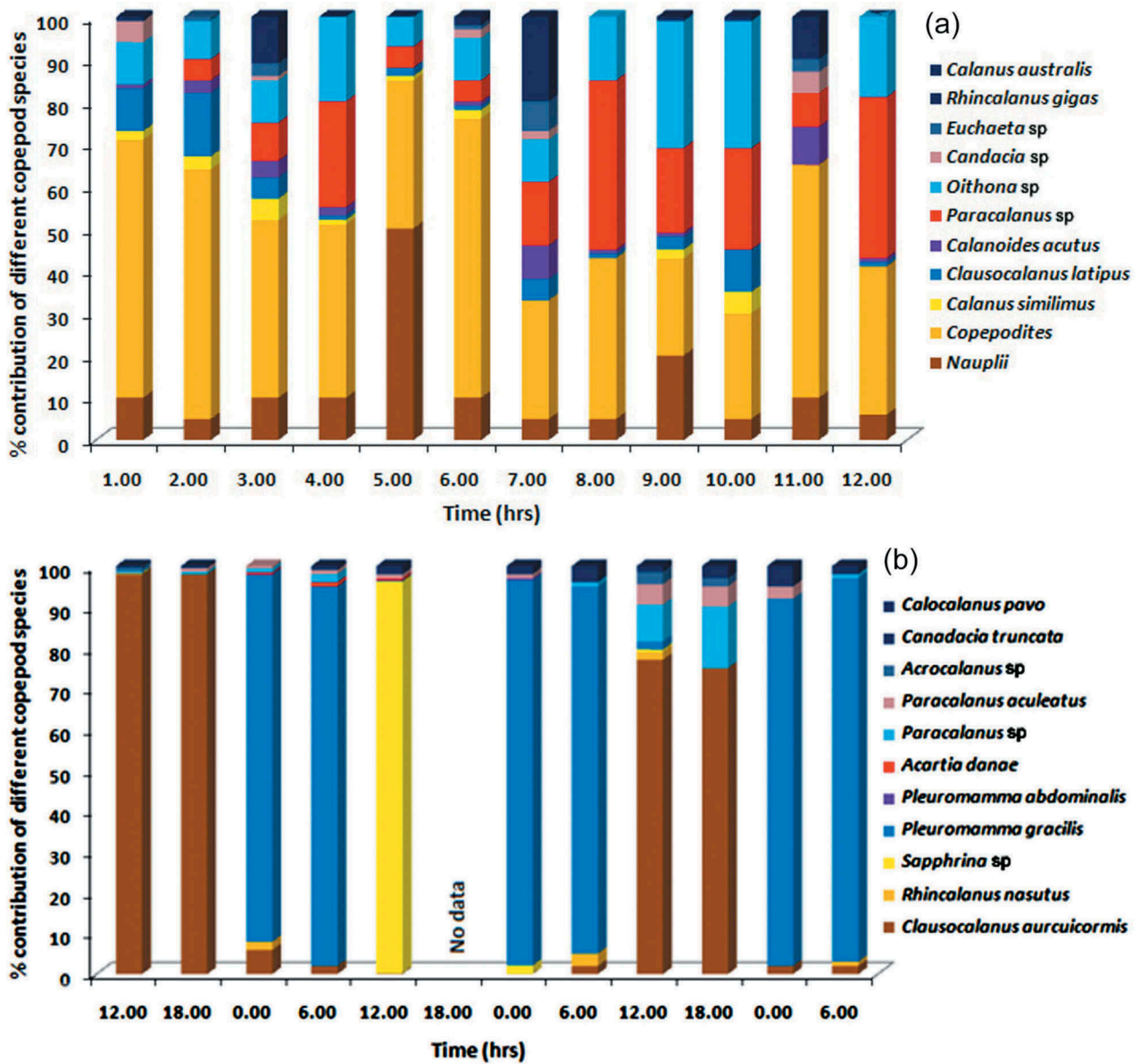**Table 2.** Diurnal pattern in percentage contribution of various mesozooplankton groups in surface waters at the SSTF.

	Day 1				Day 2			Day 3			
Time	12:00	18:00	00:00	06:00	12:00	00:00	06.00	12.00	18:00	00:00	06:00
Copepoda	99.37	99.41	43.08	76.29	31.71	94.42	92.36	52.03	39.31	95.91	93.41
Amphipoda	0.01	0.01	0.66	0.20	0.34	0.15	0.00	0.44	0.47	0.05	0.80
Euphausiids	0.01	0.00	23.42	0.95	0.85	0.86	0.92	0.79	2.04	0.62	2.71
Pteropoda	0.21	0.04	8.43	3.81	0.62	1.74	2.31	0.53	1.42	0.93	0.96
Mictophids	0.00	0.00	0.58	0.03	0.00	0.01	0.04	0.00	0.00	0.00	0.02
Apendicuarian	0.01	0.00	1.03	18.05	0.06	1.21	2.18	0.00	8.33	1.11	0.00
Chaetognatha	0.35	0.44	21.34	0.65	7.53	1.39	1.85	45.86	47.17	1.11	2.08
Polychaetea	0.01	0.00	0.00	0.00	0.00	0.03	0.00	0.09	0.00	0.00	0.00
Siphonophora	0.02	0.00	0.00	0.00	0.11	0.06	0.13	0.18	1.10	0.00	0.00
Salpa	0.00	0.10	0.28	0.00	58.66	0.00	0.00	0.00	0.00	0.03	0.00
Fish eggs	0.00	0.00	0.09	0.00	0.06	0.00	0.00	0.00	0.00	0.10	0.00
Fish larvae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.16	0.03	0.00
Heteropoda	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ostracoda	0.00	0.00	0.75	0.00	0.00	0.15	0.20	0.00	0.00	0.08	0.00
Decapodlarvae	0.00	0.00	0.19	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00
Hydromedusae	0.00	0.00	0.04	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.02
Cephalopoda	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Doliolid	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00

sharp decrease in their abundance (12:00: 52%; 18.00: 39%) and a significant increase in the population of chaetognaths (12:00: 46%; 18:00: 47%). The copepod community again showed its predominance during the last two observations (00:00: 96%; 06.00: 93%). Thus, although copepods generally dominated the mesozooplankton community at this front, some conspicuous temporal variations were observed in the community structure and diel variations were also apparent.

Twelve taxa were observed at the PF (Table 3). Copepods, unlike at the SSTF, constituted the major group (average 92%) during all the observations (78.13–97.63%). The other groups, such as amphipods (0.12–16.48%; average 5.56%), pteropods (0.19–5.10%; average 2.28%), and appendicularians (0.15–2.03%; average 0.55%), formed only minor components of the population. Carnivores such as chaetognaths, which formed a significant component at the SSTF, were rare or absent. Euphausiid larvae were present in most of the samples in small numbers and their contribution increased during the night hours. Myctophid larvae, ostracods and polychaetes had relatively minor contributions to the community and were encountered mostly in the midnight samples. Interestingly, a high abundance of large-sized filamentous diatoms (*Thalssiothrix* sp.) was observed in most of the

samples. They occurred as individual filaments during the initial observations, but formed algal mats during the later part of the observation period.

Copepod species composition (surface)

Eleven species belonging to seven families representing the orders Calanoida and Poecilostomatoida were observed at the SSTF, of which calanoids (91%) dominated the community. Among the calanoids, *Pleuromamma gracilis* (50%) and *Clausocalanus arcuicornis* (33%) were the most abundant species. They also exhibited significant day and night variation as *C. arcuicornis* (87%) dominated during the day while *P. gracilis* (92%) dominated during the night. *Sapphirina* sp., belonging to the Order Poecilostomatoida, was the only exception as it dominated (96%) the community during one observation. At the PF, nine species belonging to six families, representing the orders Calanoida and Cyclopoida were present. However, the major fraction of the community was represented by large (> 300 μm) copepodite and nauplii stages not identified to the species. Diel vertical migration was evident in the mesopelagic species *Rhincalanus gigas* as it was seen in the surface layer during the night. *Calanus australis* was another calanoid species observed in the area and other

Table 3. Diurnal pattern in percentage contribution of various mesozooplankton taxa in surface waters at the PF.

	Day 1				Day 2				Day 3			
Time	12:00	18:00	00:00	06:00	12:00	18:00	00:00	06:00	12:00	18:00	00:00	06:00
Copepoda	84.27	92.34	94.01	96.38	97.63	87.67	94.58	82.74	92.76	78.13	94.07	89.11
Amphipoda	11.04	4.62	0.64	2.52	0.12	5.89	3.65	15.23	0.49	16.48	0.33	5.73
Euphausiids	0.40	0.11	0.22	0.06	0.00	0.06	0.47	0.09	0.06	1.58	1.05	0.25
Pteropoda	2.81	2.93	5.10	0.89	0.19	0.76	0.00	1.10	4.02	2.14	3.87	3.50
Mictophids	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Apendicuarian	0.00	0.00	0.00	0.15	2.03	1.06	0.73	0.44	1.48	0.21	0.17	0.32
Chaetognatha	0.00	0.00	0.00	0.00	0.03	0.18	0.36	0.40	0.74	0.94	0.22	0.45
Radiolarian	0.00	0.00	0.00	0.00	0.00	4.38	0.00	0.00	0.43	0.43	0.00	0.64
Ostracoda	1.40	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.04	0.28	0.00
Polychaetea	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00
Foraminifera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00
Salpa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Figure 9. Diel pattern in occurrence of different copepod species at the (a) PF and (b) SSTF.

Table 4. Results of PCA: Eigen values of PCs.

PC	Eigen values	Percentage of variation explained	Cumulative % of variation explained
1	5.19	57.7	57.7
2	1.08	12.0	69.6
3	0.796	8.8	78.5
4	0.678	7.5	86.0
5	0.477	5.3	91.3

Table 5. Results of PCA: Eigen vector values of PC1 and PC2.

Variable	Code	PC1	PC2
Temperature	Temp.	0.421	−0.030
Salinity	Sal.	0.420	0.011
NO_3	Nit.	−0.375	−0.031
SiO_4	Silica.	−0.203	0.542
PO_4	Phos.	−0.143	−0.775
Dissolved oxygen	DO	−0.342	0.068
Chl a	chl a	−0.298	0.248
Zooplankton biovolume	Zoo.BV	−0.340	−0.106
Zooplankton density	Zoo.Den.	−0.350	−0.160

species belonging to the families of Oithonidae and Paracalanidae were fairly abundant throughout the study, without showing any diel vertical migratory pattern. The diel variations of different species at both the frontal regions were illustrated in Fig. 9.

Principal component analysis

PCA was undertaken to analyse and visualize the spatio-temporal variations in the hydrographical and biological parameters in the study regions. The results (Tables 4, 5) revealed that five principal components were able to explain 91% of variance among the observations. Of these PC1 (Eigen value 5.19) and PC2 (Eigen value 1.08), which together explained 70% of the variance among the sites, were used to plot the
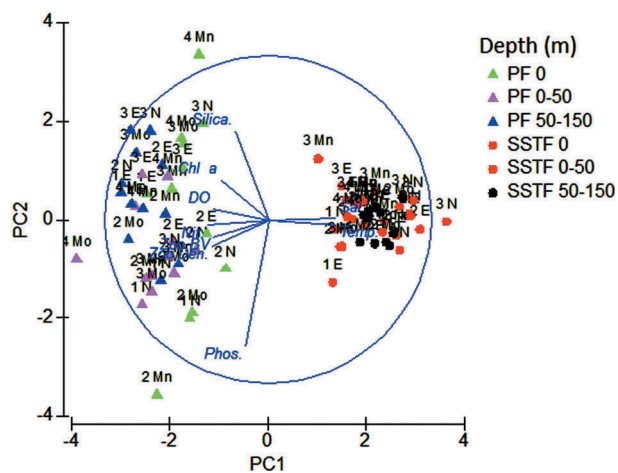
Figure 10. PCA of environmental variables (1, 2 and 3 in the labels indicate observation day 1, 2 and 3, respectively). Mn, Mo, N and E stand for midnight, morning, noon and evening.

PCA ordination (Fig. 10). The PC axis 1 (PC1) separated the stations based on temperature, salinity, NO_3, DO and biological parameters (chl *a*, zooplankton biovolume and density) while PC axis 2 (PC2) separated the stations based on the nutrients SiO_4 and PO_4. In general, temperature and salinity increased along the PC axis 1, while NO_3, DO, chl *a*, zooplankton biovolume and density decreased. Along the PC axis 2, SiO_4 increased while PO_4 decreased. Thus, the observations at the SSTF that were characterized by higher temperature and salinity are ordinated in the right half, while those stations at the PF characterized by high NO_3, DO, chl *a*, zooplankton biovolume and density are positioned in the left half. The PC axis 2 did not separate the samples of SSTF, but clearly separated those of the PF, primarily because of the higher chl *a* in many observations at 50–150 m depth.

Discussion

The SO is well known as the world's largest high-nutrient low-chlorophyll region (Brzenzinski et al. 2001; Nelson et al. 2002) despite the fact that most of its frontal regions are usually characterized by elevated biological activity during the austral summer (Laubscher et al. 1993; Froneman et al. 1995). Remotely sensed ocean colour data also suggest that elevated chlorophyll concentrations are tightly coupled with the frontal structures (Moore & Abbott 2002). In agreement with this, the satellite images and the in situ observations made during this study showed higher production at both the studied frontal locations. The multivariate analysis clearly separated the two study areas mainly based on their hydrographic and biological properties and also clearly showed the variations that existed in the physical and biological properties in the two study regions. The finding of a strong DCM also confirmed

the significance of the PF in biological production. The constant presence of DCM (ca. 75 m depth) with high primary productivity values also reflected significantly both in the water column production and chl *a* at the PF throughout the period of observation, which is in accordance with an earlier report (Tripathy et al. 2015). Curiously enough, a temperature minimum layer was noticed at the PF in the depth range of 55–300 m. It has been suggested that the temperature minimum layer occurring at the PF is due to the trapped winter water between the warm surface and deeper layers, which could be the remnant of the previous winter Antarctic surface water, capped by seasonal warming and freshening (Park et al. 1998). Several studies (Sharma & Mathew 1985; Park et al. 1998; Anilkumar et al. 2006) have shown the occurrence of temperature minimum layer in the Indian sector of the SO during the austral summer, particularly south of 50°S. Ducklow et al. (2007) have suggested that the Antarctic surface water is a source of iron in these waters; iron is considered the limiting factor for phytoplankton growth in Antarctic waters (Martin, Fitzwater et al. 1990; Martin, Gordon et al. 1990). In accordance with this, the observed DCM coincided with the upper limit of the temperature minimum layer along with high DO levels in deeper waters (Table 1), suggesting the possibility for the proliferation of an active shade-adapted flora in these iron-enriched waters.

In this study, a relatively high-grazing index was noticed at the PF (average 10.1%) compared to the SSTF (average 4.3%), indicating the prevalence of active grazing pressure at the PF. The mesozooplankton biovolume and density were significantly higher at the PF than at the SSTF, further supporting the grazing index pattern noticed. The abundance of copepods, particularly the copepodite stages of large calanoids, which are active grazers, observed during this study indicates the prevalence of an active grazing community in the area. In addition, a steady increase in the grazing index in the deeper waters corresponding with the DCM depth was also noticed. In agreement with this, high mesozooplankton biovolume was observed in most of the 50–150 m depth samples, comparable with that of the 0–50 m layer. This suggests the possibility of the herbivores aggregating in the deep chlorophyll-rich area, which in turn may be the reason for the increased grazing pressure in the deeper waters. Apart from this, a relatively high senescence index was also noticed at the PF (3.4%) as compared to the SSTF (0.3%), which is indicative of the fact that some of the phytoplankton components were still not consumed at the PF. The phytoplankton composition at the PF revealed that diatoms were the major component and also abundance of large-sized diatoms (> 200 μm) were

observed along with mesozooplankton in this region. However, reports are also available (Ohman & Runge 1994; Cowles & Fessenden 1995) on blooming of large diatoms and their non-accessibility (on account of their large size) to most of the zooplankton at the PF.

The significantly higher mesozooplankton biovolume and density at the PF than at the SSTF clearly indicate the prevalence of a favourable environment for the growth of zooplankton in the polar region during the period of observation. The mesozooplankton community structure showed marked disparity between the two fronts. Although Copepoda was the major component at both the fronts, as reported by Pakhomov et al. (2000), most of the other taxa varied significantly. The PF has been reported to be characterized by high biomass of large-sized zooplankton, such as ichthyoplankton and myctophid fishes etc., as compared to the surrounding water masses (Foxton 1956; Hopkins 1971; Maslennikov & Solyankin 1993); however, in this study Copepoda was found to be the predominant taxon, mostly comprising the nauplii and copepodite stages of large calanoids as reported earlier (Conover & Huntley 1991; Froneman et al. 2002), followed by amphipods and pteropods. The relatively low abundance of other taxa could be due to the increased grazing pressure by the copepods or the abundance of large siliceous diatoms in the area, which are generally difficult for grazing and/or unpalatable as opined by Evans & Parslow (1985), Steele & Henderson (1992) and Smetacek et al. (2004). It has also been proposed that the selective grazing pressure of copepods is a major factor shaping the species dominance and biomass of large, tough diatom assemblages when iron limitation is alleviated (Smetacek et al. 2004). Nevertheless, it has also been proposed that the copepods dwelling at the PF are generally omnivores and can satisfy most of their carbon needs by preying upon the microzooplankton (Froneman et al. 1996) and the copepod nauplii are also known to adapt to bacterivory (Turner & Tester 1992; Roff et al. 1995). However, in this study, the microzooplankton density was relatively low in the study area during the observation period and the grazing indices, indicative of grazing on the entire phytoplankton population, were also high. Therefore, it is obvious that a food web channelled through the herbivorous community was dominating at the PF during the time of observation. Atkinson (1994) opined that the ability of metazoans to consume both autotrophic and heterotrophic prey may be a necessary adaptation to the seasonality and patchiness of food distribution in the Antarctic waters. In that case, it is assumed that the dominance of conventional/herbivorous food web observed at the PF during the period of observation may be a seasonal phenomenon.

At the SSTF, chaetognaths, salps and appendicularians collectively brought down the overall copepod dominance during certain observations. The abundance of the blue-tinged neustonic copepod *C. arcuicornis* in the surface during the initial observations (12:00 and 18:00) may be related to the high chl *a* in the region as this species is a typical phytoplankton grazer (Vidal & Smith 1986; Thibault et al. 1994; Gaudy & Youssara 2003). Clausocalanids are small ubiquitous copepods, often dominating the subtropical mesozooplankton community and are considered to be an important link in the pelagic food web (Cornils et al. 2007). The pigment data revealed that pico- and nanoplankton (prochlorophytes and haptophytes, respectively) were the most abundant phytoplankton components at the SSTF during the observation period. Similarly, the fractionated primary production studies carried out from this region by Froneman et al. (1999) have also shown the abundance of nano- and picoplankton. Hence, the higher abundance of smaller fractions of phytoplankton at the SSTF could be the preferred feed for smaller copepods. As time progressed, marked variations occurred in the food-web scenario with changes in the composition and abundance of chaetognaths, hydromedusae, myctophid larvae and filter feeders, including salps and appendicularians. Chaetognaths, hydromedusae and myctophid larvae are potential carnivores (Feigenbaum & Maris 1984; Pakhomov et al. 1996; Gili et al. 1998) and their abundance coinciding with the reduction in density of the copepod *C. arcuicornis* indicates the active upper level grazing since most of the carnivores are opportunistic predators generally consuming the most abundant groups of mesozooplankton (Gibbons et al. 1992; Pakhomov et al. 1999). On the other hand, appendicularians and salps can feed on particles as small as 2 μm (Deibel 1998) and can also efficiently concentrate particulate matter 100–1000 times the ambient concentration (Kremer & Madin 1992; Madin & Purcell 1992; Bedo et al. 1993; Lindsay & Williams 2010). This supports the prevalence of an active mucus web feeding/microphagy dominated community also in this area. Microzooplankton was also abundant in the region throughout the study period (average 4208 no m^{-3}), supporting the existence of an active microbial food web. Gandhi et al. (2012) have reported that among the different frontal regions of the SO, the SSTF was the area which recorded the highest new as well as total regenerated production. Legendre & Rassoulzadegan (1995) have proposed that the herbivorous and microbial trophic modes, though exclusive of each other, can also co-occur in pelagic ecosystems. There is also growing evidence that many copepods can switch their diet from phytoplankton to microzooplankton, thereby facilitating their exploitation of both the herbivorous and the

microbial food resources (Gifford 1993; Ohman & Runge 1994; Cowles & Fessenden 1995). Therefore, even though the trophic relationships are very difficult to decipher in aquatic environments (Jacob et al. 2006), the different feeding strategies observed at the SSTF strongly support the existence of an active multivorous food web in this region. Also, the exclusive abundance of salps and cyclopoid copepod *Sapphirina* sp. during one of the observations clearly indicates the rare predator–prey relationship existing in this area, as reported earlier by Furuhashi (1966) and Heron (1973).

In this study, the mesozooplankton standing stock, both in the surface waters and 0–50 m water column, increased considerably during midnight (24:00) observations, indicating an active diel vertical migration as reported by Pakhomov et al. (1994). Many species of zooplankton exhibit diel vertical migration, and is known to be the largest migration on earth in terms of biomass (Hays 2003). Several hypotheses have been proposed to explain this unique phenomenon (Kerfoot 1985; Lampert 1989). Large predators were seen mostly in the surface waters during the night at the SSTF. The increased abundance of carnivores such as chaetognaths, hydromedusae and myctophid larvae during the night in the surface layer is indicative of feeding migration, as these animals tend to avoid day time to escape from predators and also to avoid light (Johnsen & Jakobsen 1987; Lampert 1989). The active nocturnal migration of the deep water calanoid copepod *Pleuromamma gracilis* to the surface layer may be due to its photo-sensitive nature, as suggested by Buskey et al. (1989). On the other hand, *Clausocalanus arcuicornis*, which was present in high density in the surface layer during the daytime, was considerably less in number during the night, which may be attributed to predation or reverse migration to avoid predators. A unique example of reverse migration was shown by the iridescent copepod *Sapphirina* sp., which was collected during the midday in this study, as reported earlier by Chae & Nishida (1995). As compared to the SSTF, the intensity of migration was low at the PF. However, the adult *Rhincalanus gigas* showed a higher nocturnal abundance in the surface.

It could be deduced from this study that the food-web dynamics at the SSTF and the PF were different from each other during the period of observation. Even though the surface chl *a* concentration and primary productivity did not show any marked variation between these two fronts, the water column values varied considerably. The increased water column integrated chl *a* and primary productivity values observed at the PF were mainly associated with the DCM, which coincided well with the upper limits of the temperature minimum layer. In accordance with the contrasting physical properties and productivity

pattern observed in the two fronts, the phytoplankton composition also showed remarkable variation with the dominance of diatoms at the PF and prochlorophytes at the SSTF. The microzooplankton community showed a higher concentration at the SSTF in contrast to the high mesozooplankton biovolume and abundance at the PF. Further, the mesozooplankton composition and copepod species distribution pattern also varied considerably between the two fronts. These differences were also clearly reflected in grazing/senescence indices which could further help in understanding the role of meso/microplankton grazers on biomass control and energy transfer within the planktonic food web. Even though it is difficult to define the planktonic food web of any aquatic ecosystem, by analysing the structure and composition of different planktonic components vis-à-vis the hydrography of the region, this study observed the predominance of a multivorous food web at the SSTF and a seasonal conventional food web at the PF during the study period. Finally, it is suggested that suitably designed mesocosm experiments and extended time series observations would help to unravel successional patterns in the planktonic food webs, and enhance our understanding of long-term changes, in the SO's dynamic frontal ecosystems.

ORCID

C.R. Mendes http://orcid.org/0000-0001-6875-8860

References

Anilkumar N., Luis Alvarinho J., Somayajulu Y.K., Ramesh Babu V., Dash M.K., Pednekar S.M., Babu K.N., Sudhakar M. & Pandey P.C. 2006. Fronts, water masses and heat content variability in the Western Indian sector of the Southern Ocean during austral summer 2004. *Journal of Marine Systems 63*, 20–34.

Atkinson A. 1994. Diets and feeding selectivity among the epipelagic copepod community near South Georgia in summer. *Polar Biology* 14, 551–560.

Bedo A.W., Acuna J.L., Robins D. & Harris R.P. 1993. Grazing in the micron and the sub-micron particle size range: the case of Oiklopeuradioica (Appendicularia). *Bulletin of Marine Science* 53, 2–14.

Bradford-Grieve J.M., Boyd P.W., Chang F.H., Chiswell S., Hall J.A., James M.R., Nodder S.D. & Shuskina E.A. 1999. Pelagic ecosystem structure and functioning in the subtropical front region east of New Zealand in austral winter and spring 1993. *Journal of Plankton Research* 21, 405–428.

Brzenzinski M.A., Nelson D.M., Frank V.M. & Sigmon D.E. 2001. Silicon dynamics within an intense open-ocean diatom bloom in the Pacific sector of the Southern Ocean. *Deep-Sea Research Part II: Topical Studies in Oceanography* 48, 3997–4018.

Buskey E.J., Baker K.S., Smith R.C. & Swift E. 1989. Photosensitivity of the oceanic copepods *Pleuromamma gracilis* and *Pleuromamma xiphias* and its relationship to light penetration and daytime depth distribution. *Marine Ecology Progress Series* 55, 207–216.

Calbet A. 2008. The trophic roles of microzooplankton in marine systems. *ICES Journal of Marine Science* 65, 325–331.

Chae J. & Nishida S. 1995. Vertical distribution and diel migration in the iridescent copepods of the family Sapphirinidae: a unique example of reverse migration? *Marine Ecology Progress Series* 119, 111–124.

Conover R.J. & Huntley M. 1991. Copepods in ice-covered seas-distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. *Journal of Marine Systems* 2, 1–41.

Cornils A., Niehoff B., Richter C., Al-Najjar T. & Schnack-Schiel S.B. 2007. Seasonal abundance and reproduction of clausocalanid copepods in the northern Gulf of Aqaba (Red Sea). *Journal of Plankton Research* 29, 57–70.

Cowles T.J. & Fessenden L.M. 1995. Copepod grazing and fine scale distribution patterns during the marine light-mixed layers experiment. *Journal of Geophysical Research—Oceans* 100, 6677–6686.

Deibel D. 1998. Feeding and metabolism of appendicularia. In Q. Bone (ed.): *The biology of pelagic tunicates*. Pp. 139–149. Oxford: Oxford University Press.

Detmer A.E. & Bathmann U.V. 1997. Distribution patterns of autotrophic pico- and nanoplankton and their relative contribution to algal biomass during spring in the Atlantic sector of the Southern Ocean. *Deep-Sea Research II: Topical Studies in Oceanography* 44, 299–320.

Ducklow H.W., Baker K., Martinson D.G., Quetin L.B., Ross R.M., Smith R.C., Stammerjohn S.E., Vernet M. & Fraser W. 2007. Marine pelagic ecosystems: the West Antarctic Peninsula. *Philosophical Transactions of the Royal Society B—Biological Sciences* 362, 67–94.

Evans G.T. & Parslow J.S. 1985. A model of annual plankton cycles. *Biological Oceanography* 3, 327–347.

Feigenbaum D. & Maris R. 1984. Feeding in the chaetognatha. *Oceanography and Marine Biology Annual Review* 22, 343–392.

Fielding S., Peter W., Pollard R.T., Seeyave S., Read J.F., Hughes J.A., Smith T. & Castellani C. 2007. Community structure and grazing impact of mesozooplankton during late spring/early summer 2004/2005 in the vicinity of the Crozet Islands (Southern Ocean). *Deep-Sea Research Part II: Topical Studies in Oceanography* 54, 2106–2125.

Foxton P. 1956. The distribution of the standing crop of zooplankton in the Southern Ocean. *Discovery Reports* 28, 191–236.

Froneman P.W., McQuaid C.D. & Laubscher R.K. 1999. Size-fractionated primary production studies in the vicinity of the Subtropical Front and an adjacent warm-core eddy south of Africa in austral winter. *Journal of Plankton Research* 21, 2019–2035.

Froneman P.W., Pakhomov E.A., Gurney L.J. & Hunt B.P.V. 2002. Predation impact of carnivorous macrozooplankton in the vicinity of the Prince Edward Islands archipelago (Southern Ocean) in austral autumn 1998. *Deep-Sea Research Part I: Oceanographic Research Papers* 29, 3243–3254.

Froneman P.W., Pakhomov E.A., Perissinotto R. & McQuaid C.D. 1996. Role of microplankton in the diet and daily ration of Antarctic zooplankton species during austral summer. *Marine Ecology Progress Series* 143, 15–23.

Froneman P.W., Pakhomov E.A., Perissinotto R. & McQuaid C.D. 2000. Zooplankton structure and grazing in the Atlantic sector of the Southern Ocean in late austral summer 1993. Part 2. Biochemical zonation. *Deep-Sea Research Part I: Oceanographic Research Papers* 47, 1687–1702.

Froneman P.W., Perissinotto R., McQuaid C.D. & Laubscher R.K. 1995. Summer distribution of net phytoplankton in the Atlantic sector of the Southern Ocean. *Polar Biology* 15, 77–84.

Furuhashi K. 1966. Droplets from the plankton net. XXIII. Records of *Sapphirina salpae* Giesbrecht from the north Pacific, with notes on its copepodite stages. *Publications of the Seto Marine Biological Laboratory* 14, 123–127.

Gandhi N., Ramesh R., Laskar A.H., Sheshshaye M.S., Shetye S., Anilkumar N., Patil S.M. & Mohan R. 2012. Zonal variability in primary production and nitrogen uptake rates in the southwestern Indian Ocean and the Southern Ocean. *Deep-Sea Research Part I: Oceanographic Research Papers* 67, 32–43.

Gaudy R. & Youssara F. 2003. Variations of zooplankton metabolism and feeding in the frontal area of the Alboran Sea (western Mediterranean) in winter. *Oceanologica Acta* 26, 179–189.

Gibbons M.J., Stuart V. & Verheye H.M. 1992. Trophic ecology of carnivorous zooplankton in the Benguela. *South African Journal of Antarctic Research* 12, 421–437.

Gifford D.J. 1993. Protozoa in the diets of *Neocalanus* spp. In the oceanic Subarctic Pacific Ocean. *Progress in Oceanography* 32, 223–237.

Gili J.M., Bouillon J., Pages F., Palanques A., Puig P. & Heussner S. 1998. Origin and biogeography of the deep-water Mediterranean Hydromedusae including the description of two new species collected in submarine canyons of northwestern Mediterranean. *Scientia Marina* 62, 113–134.

Guillard R.L.L. & Kilham P. 1977. The ecology of marine planktonic diatoms. In D. Werner (ed.): *The biology of diatoms*. Pp. 372–469. Berkeley: University California Press.

Hanson R.B., Shafeer D., Ryan T., Pope D.H. & Loweryi H.K. 1983. Bacterioplankton in Antarctic ocean waters during austral winter: abundance, frequency of dividing cells, and estimates of production. *Applied Environmental Microbiology* 45, 1622–1632.

Hart T.J. 1934. *On the phytoplankton of the south-west Atlantic and the Bellingshausen Sea, 1929-31. Discovery reports. Vol. 8*. Cambridge: Cambridge University Press.

Hays G.C. 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia 503*, 163–170.

Heron A.C. 1973. A specialized predator–prey relationship between the copepod *Sapphirina angusta* and the pelagic tunicate *Thalia democratica. Journal of the Marine Biological Association of the United Kingdom 53*, 429–435.

Hopkins T.L. 1971. Zooplankton standing crop in the Pacific sector of the Antarctic. *Marine Biology 89*, 197–212.

Huntley M.E., Lopez M.D.G. & Karl D.M. 1991. Top pre-dators in the Southern Ocean: a major leak in the bio-logical carbon pump. *Science 253*, 64–66.

Jacob U., Brey T., Fetzer I., Kaehler S., Mintenbeck K., Dunton K., Beyer K., Struck U., Pakhomov E.A. & Arntz W.E. 2006. Towards the trophic structure of the Bouvet Island marine ecosystem. *Polar Biology 29*, 106–113.

Jasmine P., Muraleedharan K.R., Madhu N.V., Asha Devi C.R., Alagarsamy R., Achuthankutty C.T., Jayan Z., Sanjeevan V.N. & Sahayak S. 2009. Hydrographic & productivity characteristics along 45°E longitude in the south western Indian Ocean and Southern Ocean during austral summer 2004. *Marine Ecology Progress Series 389*, 97–116.

Jeffrey S.W. 1974. Profiles of photosynthetic pigments in the ocean using thin-layer chromatography. *Marine Biology 26*, 101–110.

Johnsen G.H. & Jakobsen P.J. 1987. The effect of food limitation on vertical migration in *Daphnia longispina. Limnology and Oceanography 32*, 873–880.

Kerfoot W.C. 1985. Adaptive value of vertical migration: com-ments on the predation hypothesis and some alternatives. *Contributions in Marine Science 27*, 91–113.

Kopczynska E.E., Fiala M. & Jeandel C. 1998. Annual and interannual variability in phytoplankton at a permanent station off Kerguelen Islands, Southern Ocean. *Polar Biology 20*, 342–351.

Kremer P. & Madin P. 1992. Particle retention efficiency of salps. *Journal of Plankton Research 14*, 1009–1015.

Lampert W. 1989. The adaptive significance of diel vertical migration of zooplankton. *Functional Ecology 3*, 2 l–27.

Laubscher R.K., Perissinotto R. & McQuaid C.D. 1993. Phytoplankton production and biomass at frontal zones in the Atlantic sector of the Southern Ocean. *Polar Biology 13*, 471–481.

LeFevre J., Legendre L. & Rivkin R.B. 1998. Fluxes of biogenic carbon in the Southern Ocean: roles of large microphagous zooplankton. *Journal of Marine Systems 17*, 325–345.

Legendre L. & Rassoulzadegan F. 1995. Plankton and nutrient dynamics in coastal waters. *Ophelia 41*, 153–172.

Lenz J. 1992. Microbial loop, microbial food web and classical food chain: their significance in pelagic marine ecosystems. *Archiv für Hydrobiologie—Beiheft Ergebnisse der Limnologie 37*, 265–278.

Lenz J. 2000. Introduction. In R.P. Harris et al. (eds.): *ICES zooplankton methodology manual.* Pp. 1–32. San Diego: Academic Press.

Lindsay M.C.M. & Williams G.D. 2010. Distribution and abundance of Larvaceans in the Southern Ocean between 30 and 80°E. *Deep-Sea Research Part II: Topical Studies in Oceanography 57*, 905–915.

Lutjeharms J.R.E. & Valentine H.R. 1988. On mesoscale ocean eddies at the Agulhas Plateau. *South African Journal of Science 84*, 194–200.

Mackey M., Mackey D., Higgins H. & Wright S. 1996. CHEMTAX—a program for estimating class abundances from chemical markers: application to HPLC measure-ments of phytoplankton. *Marine Ecology Progress Series 144*, 265–283.

Madin L.P. & Purcell J.E. 1992. Feeding, metabolism, and growth of *Cyclosalpa bakeri* in the Subartic Pacific. *Limnology and Oceanography 37*, 1236–1251.

Martin J.H., Fitzwater S.E. & Gordon R.M. 1990. Iron deficiency limits plankton growth in Antarctic waters. *Global Biogeochemical Cycles 4*, 5–12.

Martin J.H., Gordon R.M. & Fitzwater S.E. 1990. Iron in Antarctic waters. *Nature 345*, 156–158.

Maslennikov V.V. & Solyankin E.V. 1993. Oceanic fronts in the Southern Ocean as the main locations of mycto-phid and krill aggregations. *Antarktika 32*, 86–93.

Mayzaud P., Tirelli V., Errhif A., Labat J.P., Razouls S. & Perissinotto R. 2002. Carbon intake by zooplankton: importance and role of zooplankton grazing in the Indian sector of the Southern Ocean. *Deep-Sea Research Part II: Topical Studies in Oceanography 49*, 3169–3187.

Mendes C.R.B., Cartaxana P. & Brotas V. 2007. Determination of phytoplankton and microphyto-benthos pigments: comparing resolution and sensitivity of a C18 and a C8 method. *Limnology and Oceanography: Methods 5*, 363–370.

Mendes C.R.B., Kerr R., Tavano V.M., Cavalheiro F.A., Garcia C.A.E., Dessai D.R.G.&. & Anilkumar N. 2015. Cross-front phytoplankton pigments and chemotaxo-nomic groups in the Indian sector of the Southern Ocean. *Deep-Sea Research Part II: Topical Studies in Oceanography 118*, 221–232.

Mengesha S., Dehairs F., Fiala M., Elskens M. & Goeyens L. 1998. Seasonal variation of phytoplankton community structure and nitrogen uptake regime in the Indian sector of the Southern Ocean. *Polar Biology 20*, 259–272.

Moore J.K. & Abbott M.R. 2002. Surface chlorophyll con-centrations in relation to the Antarctic Polar Front: seasonal and spatial patterns from satellite observations. *Journal of Marine Systems 37*, 69–86.

Murphy R.J., Pinkerton M.H., Richardson K.M., Bradford-Grieve J.M. & Boyd P.W. 2001. Phytoplankton distribu-tions around New Zealand derived from SeaWiFS remo-tely-sensed ocean colour data. *New Zealand Journal of Marine and Freshwater Research 35*, 343–362.

Nelson D.M., Anderson R.F., Barber R.T., Brzezinski M.A., Buesseller K.O., Chase Z., Collier R.W., Dickson M.L., Francois R., Hiscock M.R., Samroto R.N., Sayles F.L. & Sigmion D.E. 2002. Vertical budgets of organic carbon and biogenic silica in the Pacific sector of the Southern Ocean, 1996–1998. *Deep-Sea Research Part II: Topical Studies in Oceanography 49*, 1645–1674.

Ohman M.D. & Runge J.A. 1994. Sustained fecundity when phytoplankton resources are in short supply: omnivory by *Calanus finmarchicus* in the Gulf of St. Lawrence. *Limnology and Oceanography 39*, 21–36.

Pakhomov A., Perissinotto R. & McQuaid C.D. 1994. Comparative structure of the macrozooplankton/micro-nekton communities of the Subtropical and Antarctic Polar Fronts. *Marine Ecology Progress Series 111*, 155–169.

Pakhomov E.A., Perissinotto R. & Froneman P.W. 1999. Predation impact of carnivorous macrozooplankton and micronekton in the Atlantic sector of the Southern Ocean. *Journal of Marine Systems 19*, 47–64.

Pakhomov E.A., Perissinotto R. & McQuaid C.D. 1996. Prey composition and daily rations of myctophid fishes

in the Southern Ocean. *Marine Ecology Progress Series 134*, 1–14.

Pakhomov E.A., Perissinotto R., McQuaid C.D. & Froneman P.W. 2000. Zooplankton structure and grazing in the Atlantic sector of the Southern Ocean in late austral summer 1993: part 1. Ecological zonation. *Deep Sea Research Part I: Oceanographic Research Papers 47*, 1663–1686.

Park Y.H., Charriaud E. & Fieux M. 1998. Thermohaline structure of Antarctic surface water/winter water in the Indian sector of the Southern Ocean. *Journal of Marine Systems 17*, 5–23.

Postel L., Fock H. & Hagen W. 2000. Biomass and abundance. In R.P. Harris et al. (eds.): *ICES zooplankton methodology manual*. Pp. 83–192. San Diego, CA; Academic Press.

Roff J.C., Turner J.T., Webber M.K. & Hopcroft R.R. 1995. Bacterivory by tropical copepod nauplii: extent and possible significance. *Aquatic Microbial Ecology 9*, 165–175.

Sakka H.A., Nathalie N. & Louis L. 2014. Planktonic food webs revisited: reanalysis of results from the linear inverse approach. *Progress in Oceanography 120*, 216–229.

Schluter L., Henriksen P., Nielsen T.G. & Jakobsen H.H. 2011. Phytoplankton composition and biomass across the Southern Indian Ocean. *Deep-Sea Research Part I: Oceanographic Research Papers 58*, 546–556.

Sharma G.S. & Mathew B. 1985. Hydrography and circulation off the Antarctica in the Indian Ocean region. *Proceedings of the Indian Academic Science (Earth and Planetary Science) 94*, 13–27.

Smetacek V., Assmy P. & Henjes J. 2004. The role of grazing in structuring Southern Ocean pelagic ecosystems and biogeochemical cycles. *Antarctic Science 16*, 541–558.

Steele J.H. & Henderson E.W. 1992. The role of predation in plankton models. *Journal of Plankton Research 14*, 157–172.

Strickland J.D.H. & Parsons T.R. 1972. *A practical hand book of seawater analysis. Fisheries Research Board of Canada Bulletin 167*. Ottawa: Fisheries Research Board of Canada.

Sullivan C.W., Arrigo K.R., McClain C.R., Comiso J.C. & Firestone J. 1993. Distributions of phytoplankton blooms in the Southern Ocean. *Science 262*, 1832–1837.

Takahashi K.T., Hosie G.W., Kitchener J.A., McLeod D.J., Odate T. & Fukuchi M. 2010. Comparison of zooplankton distribution patterns between four seasons in the Indian Ocean sector of the Southern Ocean. *Polar Science 4*, 317–331.

Takahashi K.T., Hosie G.W., McLeod D.J. & Kitchener J.A. 2011. Surface zooplankton distribution patterns during austral summer in the Indian sector of the Southern Ocean, south of Australia. *Polar Science 5*, 134–145.

Thibault D., Gaudy R. & Le Fevre J. 1994. Zooplankton biomass, feeding and metabolism in a geostrophic frontal area (Almeria-Oran Front, western Mediterranean Sea). Significance of pelagic food webs. *Journal of Marine Systems 5*, 297–313.

Treguer P. & Bennekom A.J. 1991. The annual production of biogenic silica in the Antarctic Ocean. *Marine Chemistry 35*, 477–487.

Tripathy S.C., Pavithran S., Sabu P., Pillai H.U.K., Dessai D.R.G., & Anilkumar N. 2015. Deep chlorophyll maximum and primary productivity in the Indian Ocean sector of the Southern Ocean: case study in the Subtropical and Polar Front during austral summer 2011. *Deep-Sea Research Part II: Topical Studies in Oceanography 118*, 240–249.

Turner J.T. & Tester P.A. 1992. Zooplankton feeding ecology: bacterivory by metazoan microzooplankton. *Journal of Experimental Marine Biology and Ecology 160*, 149–167.

Van Ballegooyen R.C., Grundlingh M.L. & Lutjeharms J.R.E. 1994. Eddy fluxes of heat and salt from the southwest Indian Ocean into the southeast Atlantic Ocean: a case study. *Journal of Geophysical Research—Oceans 99*, 14053–14070.

Vidal J. & Smith S.L. 1986. Biomass, growth and development of populations of herbivorous zooplankton in the south eastern Bering Sea during spring. *Deep-Sea Research 33*, 523–556.

Xiuren N., Zilin L., Genhai Z. & Junxian S. 1996. Size fractionated biomass and productivity of phytoplankton and particulate organic carbon in the Southern Ocean. *Polar Biology 16*, 1–11.

Zapata M., Jeffrey S.W., Wright S.W., Rodríguez F., Garrido J.L. & Clementson L. 2004. Photosynthetic pigments in 37 species (65 strains) of Haptophyta, 40 implications for oceanography and chemotaxonomy. *Marine Ecology Progress Series 270*, 83–102.

Zapata M., Rodriguez F. & Garrido J.L. 2000. Separation of chlorophylls and carotenoids from marine phytoplankton: a new HPLC method using a reversed phase C8 column and pyridine-containing mobile phases. *Marine Ecology Progress Series 195*, 29–45.