

Distribution of zooplankton in the Indian sector of the Southern Ocean

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Abstract: The community composition of zooplankton with an emphasis on copepods was assessed in the frontal zones of the Indian sector of the Southern Ocean (SO) during summer 2013. Copepods were the dominant group in both the bongo net and multiple plankton sampler across the entire region. High zooplankton abundance was recorded along each transect in the Polar Front (PF). Community structure in this front was dominated by common taxa, including *Ctenocalanus citer*, *Clausocalanus* spp., *Calanoides acutus*, *Calanus propinquus*, *Calanus australis* and *Rhincalanus gigas*, which together accounted for > 62% of the total abundance. *Calocalanus* spp., *Neocalanus tonsus* and *C. propinquus* were indicator species in the Sub-Tropical Front (STF), Sub-Antarctic Front and PF, respectively. A strong contrast in population structure and biovolume was observed between the PF and the STF. The community structure of smaller copepods was associated with the high-temperature region, whereas communities of larger copepods were associated with the low-temperature region. Thus, it seems probable that physical and biological characteristics of the SO frontal regions are controlling the abundance and distribution of zooplankton community structure by restricting some species to the warmer stratified zones and some species to the well-mixed zone.

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Key words: chlorophyll *a*, copepods, multiple plankton sampler, nutrients, Southern Ocean fronts

Introduction

Zooplankton in the Southern Ocean (SO) are zonally bounded by oceanic fronts, reflecting specific physical requirements that structure their distributions (Atkinson & Sinclair 2000). Studies in the Atlantic and Indian Ocean sectors of the SO have variously identified the Sub-Tropical Front (STF), Sub-Antarctic Front (SAF), Polar Front (PF) and Antarctic Divergence as separating distinct communities (Atkinson & Sinclair 2000). These fronts are recognized as important biogeographic boundaries for zooplankton, based on their temperature and salinity characteristics (Deacon 1982). For example, temperature alters the rates of various biological processes in copepods, such as their growth, productivity and mortality (Hirst & Kiørboe 2002). Differences in environmental factors (physical, chemical and biological) and processes (e.g. stratification, mixing, grazing) define the composition, abundance and productivity of the phytoplankton community (Deppeler & Davidson 2017), and subsequently the zooplankton. Most zooplankton sampling in the SO has been conducted with horizontally

towed nets (Hunt & Hosie 2003, Takahashi *et al.* 2011), facilitating detection of changes to surface zooplankton community structure (Takahashi *et al.* 2010a), seasonal cycles (Hunt & Hosie 2006a) and interannual variation (Takahashi *et al.* 2010b). To date, there has been little study of the horizontal distribution of zooplankton in the Indian sector of the SO, particularly in the region between 47°E and 57°E. Furthermore, there is little information available on the vertical distribution of zooplankton in the permanent open ocean zone of the Indian sector of the SO. To address this shortage of information, zooplankton were collected between 47°E and 57°E in order to understand the seasonal zooplankton abundance in this region, focusing on species composition and distribution patterns.

The objectives of the present study were to investigate the physical and biological mechanisms that mediate the abundance and distribution patterns of zooplankton communities, paying particular attention to the horizontal and vertical biogeographic patterns in zooplankton community structure in the central Indian sector of the SO east of the Kerguelen Plateau.

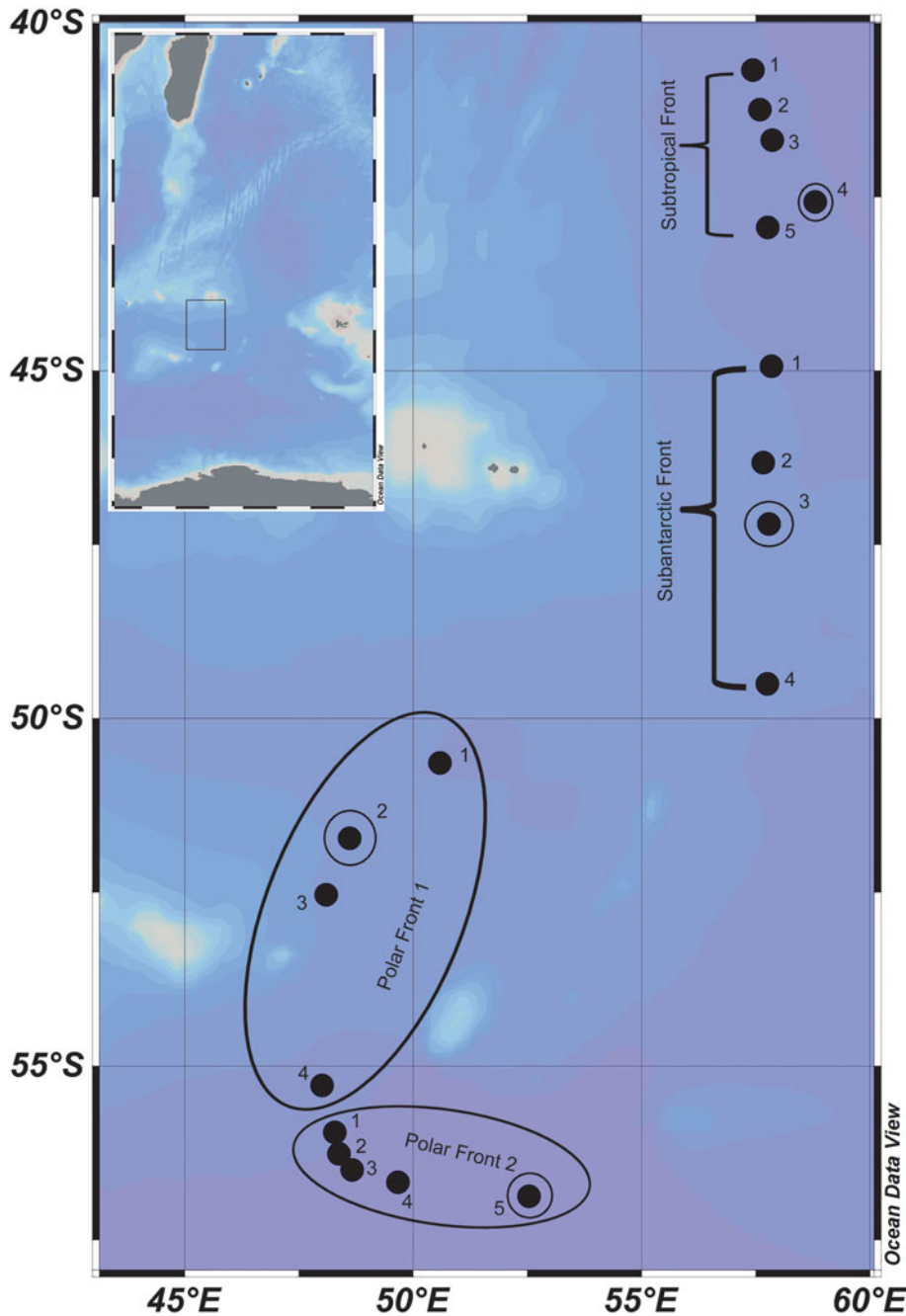


Fig. 1. Study area showing sampling locations (solid dots). The inset image shows a broader map, and the rectangle inside it corresponds to the study area. Small circles indicate vertical sampling points.

Materials and methods

As part of the seventh Indian expedition to the SO, hydrographic and biological measurements were carried out on board Ocean Research Vessel *Sagar Nidhi* between 40–56°S and 47–57°E (Fig. 1). Sampling occurred between 28 January and 23 February 2013. Temperature and salinity were measured at each station using conductivity-temperature-depth (CTD) profilers (Sea-Bird Electronics, USA). Water samples were collected from

~2–3 m depth using 101 Niskin bottles attached to the CTD rosette. Water samples from the surface (~2–3 m) for nutrients and chlorophyll *a* (chl *a*) were measured following the recommendations of Grasshoff *et al.* (1983) and UNESCO (1994), respectively. The correlation coefficient for NO_3^- , NO_2^- , PO_3^- and SiO_4^{4-} was 0.9999–1.0000 and for NH_4^+ was 0.9996–0.9999, with a precision of ± 0.06 , ± 0.006 , ± 0.01 , ± 0.003 and ± 0.005 μM for NO_3^- , NO_2^- , NH_4^+ , PO_3^- and SiO_4^{4-} , respectively. A total of 51 of surface water was collected for the pigment

analysis. Pigments were separated following slight modifications of the procedure of Van Heukelem (2000), which provides quantitative and qualitative analysis of several phytoplankton pigments. The diagnostic pigment analysis (DPA) was applied to classify phytoplankton types from high-pressure liquid chromatography pigment data (Vidussi *et al.* 2001). Additionally, the Hirata method (Hirata *et al.* 2008) was used to refine the DPA in order to separate picoeukaryotes from nanoeukaryotes. With the Brewin method (Brewin *et al.* 2010), this relationship and the fraction of each size class were quantified, before the method was applied to the chl *a* concentration.

Zooplankton samples were collected from the surface (~2–3 m) by horizontal towing of a bongo net (200 μm mesh; net opening 0.32 m²) at 18 stations in the Indian sector of the SO during daylight hours (Fig. 1 & Table SI). The volume of water filtered by the net was measured with a calibrated flowmeter (General Oceanics, USA) mounted in the mouth of the net and used to calculate zooplankton abundances. Following each surface sample, vertical zooplankton samples were collected from four stations (Table SII) in the upper 1000 m from five discrete depth strata using a multiple plankton sampler (MPS; Hydro-Bios, net opening 0.25 m², mesh size 200 μm) (Weikert & John 1981). Two electronic flowmeters were mounted onto the underwater unit in order to calculate the volume filtered. The depth interval of each top stratum was decided based on CTD profiles as follows: surface to the depth of mixed layer (MLD; MLD varied from 40 to 85 m), MLD to 150 m, 150 to 300 m, 300 to 500 m and 500 to 1000 m. The MLD was computed based on the density difference criteria and was considered as the depth at which potential density increased by 0.03 from the 10 m depth value. The MPS was hauled up at a speed of 0.8 m s⁻¹; upon recovery of the samples, the catch was immediately preserved in a 5% buffered formaldehyde/seawater solution. At each station, total catch of each stratum was taken for quantitative biomass analysis. Zooplankton biomass was measured by the volume displacement method (ICES 2000). Large gelatinous plankton such as salps and jellyfish were removed, and salps were identified to family level. When the sample size was large, as was usually the case in the first, second and third strata, it was split using a Folsoms plankton splitter until ~25% of the sample was available for counting and identification of taxa. Often when the numbers in the deeper layers were low, the entire sample was counted and all organisms identified. Specimens were identified to species level for most taxonomic groups, except for Chaetognatha and Appendicularia, which were counted as one taxon each. In order to test for spatial variability in the environmental parameters, analysis of variance was applied. Multiple regression

Table I. Variability in surface temperature and salinity at various frontal regions of the Indian Ocean sector of the Southern Ocean during summer 2013.

Region	Temperature (°C)		Salinity	
	Range	Average \pm SD	Range	Average \pm SD
STF	11.23–18.97	15.49 \pm 3.36	33.69–35.51	34.63 \pm 0.84
SAF	5.31–9.77	7.97 \pm 1.94	33.70–34.00	33.74 \pm 0.03
PF1	3.23–4.26	3.73 \pm 0.49	33.76–33.89	33.82 \pm 0.06
PF2	1.14–2.75	2.03 \pm 0.65	33.90–33.95	33.93 \pm 0.02

STF = Sub-Tropical Front, SAF = Sub-Antarctic Front, PF = Polar Front.

analysis was performed using zooplankton biovolume and abundance as dependent variables and environmental parameters as predictor variables. In addition, the Shannon diversity index (*H'*) was calculated for the copepod communities.

Results

Variability in temperature and salinity

During the summer of 2013, sea surface temperature varied between 1.14°C and 18.97°C in the study area. Strong temperature gradients occurred between the STF and the PF. Towards the south, a decrease in temperature was noted in PF1 and PF2, while lower temperatures were measured in the PF2 region (Table I). The mean temperatures in the surface waters differed significantly between the frontal regions ($P < 0.0001$). Small salinity changes occurred at the STF, SAF, PF1 and PF2, and the highest mean salinity in surface waters was observed at the STF (Table I). From 42°S southwards, surface salinity decreased; however, the region between 53°S and 56°S exhibited slightly higher salinity (increase in salinity by 0.06 for PF1 and 0.09 for PF2), but the mean values did not show a significant difference among the frontal regions ($P > 0.05$). The water temperature was uniform in the mixed layer (MLD) and decreased below MLD. Depth-integrated temperature differed significantly between frontal regions ($P < 0.001$). The average temperatures within the MLD were 12.20 \pm 0.05°C, 7.79 \pm 0.08°C, 4.03 \pm 0.005°C and 2.43 \pm 0.008°C in the STF, SAF, PF1 and PF2, respectively. In the present study, average MLD was 36 \pm 25 m in the STF, and increased towards the PF, with the average MLD of 50 \pm 18 m in the SAF. In the two most southern sampled areas, the PF1 and PF2 MLD varied between 57 \pm 23 m and 76 \pm 21 m, respectively.

*Nutrients and chl *a* distribution*

A southwards increasing trend in nutrient concentrations was observed, with the maximum dissolved inorganic nitrogen

Table II. Variability in surface water nutrients at various frontal regions of the Indian Ocean sector of the Southern Ocean during summer 2013.

Region	Dissolved inorganic nitrogen (μM)		Dissolved inorganic phosphate (μM)		Dissolved silica (μM)	
	Range	Average \pm SD	Range	Average \pm SD	Range	Average \pm SD
STF	3.34–15.10	10.64 \pm 4.42	0.81–1.54	1.15 \pm 0.29	2.34–3.90	2.98 \pm 0.58
SAF	14.67–23.47	18.52 \pm 4.49	0.96–2.00	1.53 \pm 0.44	3.25–7.66	4.58 \pm 2.06
PF1	14.93–27.78	21.89 \pm 6.49	1.30–2.08	1.80 \pm 0.43	5.33–25.61	14.47 \pm 10.28
PF2	27.54–30.16	29.00 \pm 0.94	1.80–2.18	2.06 \pm 0.15	26.28–36.60	32.10 \pm 3.73

STF = Sub-Tropical Front, SAF = Sub-Antarctic Front, PF = Polar Front.

(DIN), dissolved inorganic phosphate (DIP) and dissolved silica (DSi) observed at PF2 (Table II). The STF and SAF had lower nutrient concentrations compared to the PF. The highest mean DIN concentration in the surface waters was observed in the PF2 and showed significant difference between the frontal regions ($P < 0.001$) (Table II). Relatively low phosphate concentrations were observed in the study area; however, significant variations were observed between the fronts ($P < 0.05$), and the highest concentration was observed in the PF2 (Table II). Regions of higher water temperature coincided with lower silicate concentrations. Furthermore, the mean DSi concentrations were significantly different between the fronts ($P < 0.0001$), and the highest mean value was observed in the PF2 (Table II). The phytoplankton biomass (chl *a*) concentration in the surface ranged from 0.08 mg m⁻³ to its highest values of 0.8 mg m⁻³ on transect #1 in the PF1, followed by the PF2, STF and SAF (Table III). No significant differences were found among the frontal regions ($P = 0.06$) (Table III). Overall, there were no significant correlations between chl *a* and nutrients (DIN, $P > 0.6$; DIP, $P > 0.21$; and DSi, $P > 0.3$) in the study area. During this study, it was observed that diatoms dominated the phytoplankton community structure in the PF1 and PF2 (Fig. 2), where silicate-independent phytoplankton (i.e. small cells) occurred in low numbers. Picoplankton and nanoplankton were dominant in the STF and SAF, respectively (Fig. 2).

Zooplankton biovolume and abundance

Biovolume and abundance varied spatially, and there were significant differences among the frontal regions

($P < 0.05$). The mean zooplankton biovolume in the surface layer was high in the PF2, while the lowest was observed in the SAF (Table III). The maximum zooplankton abundance was observed on transect #4 in the PF1 and the lowest was observed on transect #1 in the SAF. Zooplankton biovolume exhibited a significant positive relationship with abundance ($r^2 = 0.95$; $P < 0.001$). Zooplankton biovolume ($r^2 = 0.52$) and abundance ($r^2 = 0.61$) tended to decrease with increasing temperature. Depth-integrated zooplankton biovolume and abundance in the upper 1000 m at four oceanographic stations ranged from 0.03 to 0.085 ml m⁻³ (Fig. 3) and from 248 to 1068 ind m⁻³, respectively; at station 46°58'S, 57°30'E they varied from 0.03 to 0.15 ml m⁻³ (Fig. 3) and from 156 to 1164 ind m⁻³. Relatively, southwards increasing trends were observed at station 52°25'S, 48°05'E ranging from 0.08 to 0.22 ml m⁻³ (Fig. 3) and from 304 to 1682 ind m⁻³. The highest values were observed at station 56°34'S, 53°39'E ranging from 0.06 to 0.35 ml m⁻³ (Fig. 3) and from 250 to 2684 ind m⁻³.

Major zooplankton community structure and copepod species composition in the surface layer

Zooplankton in the surface layer included Copepoda, Chaetognatha, Appendicularia and Salpida (Table IV). In this study, copepods were the most important group of zooplankton throughout the transect, consisting mainly of Calanoida and Cyclopoida (Table IV). The mean abundances of calanoids ($P < 0.001$) and cyclopoids ($P < 0.001$) in the surface waters differed significantly between the frontal regions. Overall, calanoid copepods were the most abundant group in all

Table III. Average chlorophyll *a* concentration and variability of zooplankton biovolume and abundance of surface water samples from various frontal regions of the Indian Ocean sector of the Southern Ocean during summer 2013.

Region	Chlorophyll <i>a</i> (mg m ⁻³)		Zooplankton biovolume (ml m ⁻³)		Zooplankton abundance (ind m ⁻³)	
	Range	Average \pm SD	Range	Average \pm SD	Range	Average \pm SD
STF	0.13–0.33	0.23 \pm 0.07	0.04–0.05	0.04 \pm 0.005	550–1268	997 \pm 275
SAF	0.13–0.25	0.19 \pm 0.06	0.04–0.25	0.13 \pm 0.108	320–9060	3925 \pm 4042
PF1	0.10–0.82	0.57 \pm 0.32	0.07–0.41	0.20 \pm 0.145	3899–12 452	6868 \pm 3851
PF2	0.08–0.42	0.29 \pm 0.14	0.16–0.39	0.25 \pm 0.085	5192–12 115	8777 \pm 2462

STF = Sub-Tropical Front, SAF = Sub-Antarctic Front, PF = Polar Front.

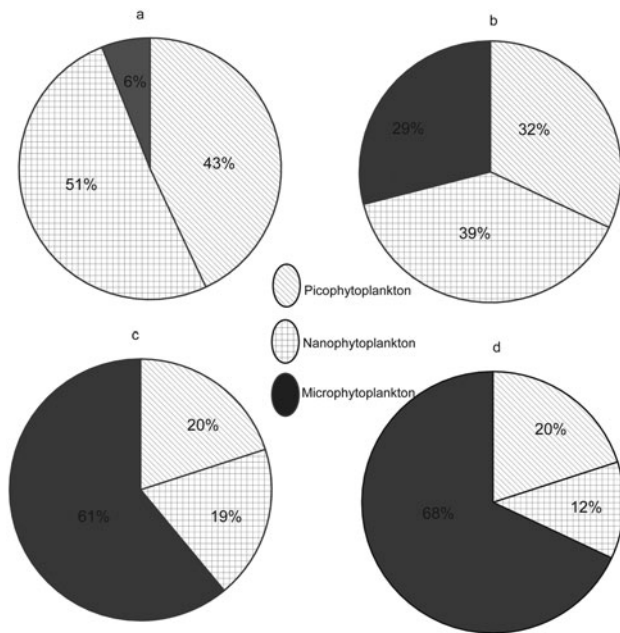


Fig. 2. Surface phytoplankton size distributions presented as average percentage contributions to the phytoplankton community at sampling locations **a.** Sub-Tropical Front, **b.** Sub-Antarctic Front, **c.** Polar Front 1 and **d.** Polar Front 2. The phytoplankton compositions are derived from pigment analysis.

of the regions, followed by cyclopoid copepods (Table IV). The maximum calanoid abundance was recorded at the PF1 followed by the PF2, SAF and STF (Table IV). The maximum cyclopoid abundance was recorded at the PF2 followed by the PF1, SAF and STF (Table IV). Chaetognatha was the next most abundant group after the Copepoda and showed their highest abundance at the SAF followed by the STF and PF (Table IV). Similarly, the maximum abundance of appendicularians

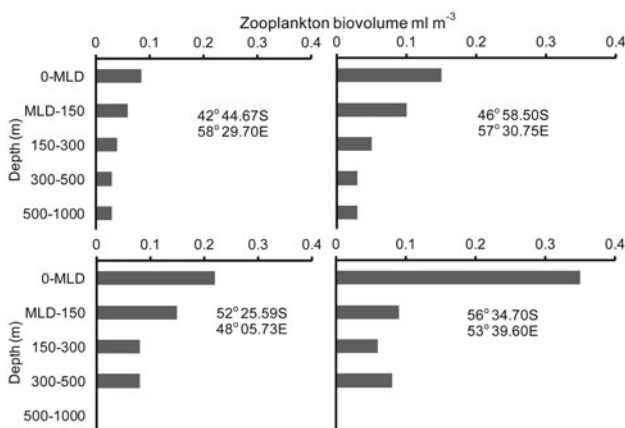


Fig. 3. Vertical variation in zooplankton biovolume at four oceanographic stations. MLD = depth of mixed layer.

was recorded at the SAF followed by the STF and PF (Table IV). In particular, Salpidae demonstrated their importance typically in the STF and SAF (Table IV) across most of the sampling locations, and significant differences were noticed between the frontal regions ($P < 0.0001$). Unlike appendicularians and salps, no significant differences were found in chaetognaths among the frontal regions ($P = 0.3$).

The surface copepod community structure was dominated by a small group of taxa, including *Ctenocalanus* spp., *Clausocalanus* spp., *Calocalanus* spp., *Microcalanus* spp., *Scolecithricella* spp. and *Oithona* spp. (Table V). *Ctenocalanus citer* was more abundant than *Ctenocalanus vanus*, particularly in the PF2. Peak *Clausocalanus* spp. densities mostly occurred in the STF (Table V), while *Calocalanus* spp. and *Microcalanus* spp. ranged from 27 to 111 ind m^{-3} and from 42 to 56 ind m^{-3} , respectively (Table V). *Scolecithricella* spp. occurred at the lowest abundance in the surface layers. *Calanus* spp. and *Calanoides acutus* were major contributors to copepod assemblages of > 2 mm; the abundance of *Calanus* spp. ranged from 27 to 123 ind m^{-3} , and that of *C. acutus* ranged from 24 to 241 ind m^{-3} (Table V). *Neocalanus tonsus* was an important contributor in the SAF (Table V). *Oithona similis* was more abundant than *Oithona frigida* and occurred at almost all stations (Table V). *Oithona similis* was an important member of the surface layer cyclopoid species. The relative percentages of species varied spatially in the surface layer. The Calanoida community represented 51% of the total zooplankton abundance at the STF. Taxa such as *Ctenocalanus* spp. (13%), *Clausocalanus* spp. (10%), *Calocalanus* spp. (8%), *Calanus* spp. (7%), *Eucalanus* spp. (6%), *Microcalanus* spp. (4%) and *Scolecithricella* spp. (3%) were dominant in the STF (Fig. 4). The second major copepod community was Cyclopoida, which represented 33% of the total zooplankton abundance and was dominated by *O. similis* (22%) and *O. frigida* (11%) (Fig. 4). In the SAF, Cyclopoida in the surface layer represented 58% of the total zooplankton abundance, consisting of taxa such as *O. similis* (38%) and *O. frigida* (20%) (Fig. 4). Calanoida represented 31% of the total zooplankton abundance in the surface layer. The dominant species were *N. tonsus* (10%) followed by *Calanus* spp. (5%), *Ctenocalanus* spp. (4%), *Clausocalanus* spp. (3%), *Calocalanus* spp. (2.5%), *Microcalanus* spp. (2.5%), *Eucalanus* spp. (2%) and *Metridia lucens* (2%) (Fig. 4). The results of this study show that there are distinct distribution patterns in the zooplankton communities of the Indian Ocean sector of the SO separated by the frontal regions.

At the PF1 and PF2, Calanoida and Cyclopoida comprised 52% and 45% of the total zooplankton abundance, respectively, while other taxa occurred

Table IV. Variability in abundance of major zooplankton communities of various frontal regions of the Indian Ocean sector of the Southern Ocean during summer 2013.

Region	Calanoida (ind m ⁻³)		Cyclopoida (ind m ⁻³)		Chaetognatha (ind m ⁻³)		Appendicularia (ind m ⁻³)		Salpidae (ind m ⁻³)	
	Range	Average ± SD	Range	Average ± SD	Range	Average ± SD	Range	Average ± SD	Range	Average ± SD
STF	121–937	536–324	437–815	585–163	11–42	25–12	14–25	19–5	19–33	25–7
SAF	229–3150	1614–1326	98–3084	1620–1417	12–64	40–26	33–45	40–6	9–18	12–4
PF1	3860–7416	5076–1630	831–4046	1726–1549	18–33	24–8	11–18	14–3	0	0
PF2	1550–3360	2500–854	3642–6586	5484–1121	9–21	15–6	9–12	9–2	0	0

STF = Sub-Tropical Front, SAF = Sub-Antarctic Front, PF = Polar Front.

in low proportions (appendicularians at 2% and chaetognaths at 1%). The calanoid species that contributed to the total zooplankton abundance were *C. acutus*, *Calanus propinquus*, *Calanus australis*, *Calanus simillimus*, *Rhincalanus gigas*, *Paraeuchaeta* spp., *C. citer*, *Clausocalanus* spp. and *M. lucens* (Fig. 4). Further, *O. similis* and *O. frigida* were also important contributors in the PF (Fig. 4).

The surface copepod species diversity ranged from 0.12 to 1.05 and dominance ranged from 0.10 to 0.88 (Fig. 5). The STF had high diversity but low species numbers, while low diversity and species numbers were recorded in the SAF. In contrast, the surface waters between the PF1 and PF2 had high species numbers, with moderately high diversity. No significant differences were observed in diversity among the frontal regions ($P = 0.8$).

Zooplankton community structure in the upper 1000 m

When comparing between depth zones, it was clear that the greatest abundance was recorded in the 0–MLD stratum. Diversity increased with depth, while abundance decreased. Vertical distributions of zooplankton communities were broadly associated with various depth layers in the present study. Our results indicate that the high zooplankton abundance in the Indian sector of the SO is mostly concentrated within the MLD during the summer.

Copepods were the numerically dominant group at most stations and in most depth strata. *Clausocalanus* spp., *Ctenocalanus* spp., *Calocalanus* spp., *Calanus* spp. and *Oithona* spp. dominated in the upper 150 m at stations STF4 and SAF3 (Table VI). Within the

Table V. Variation in surface layer (~2–3 m) dominant copepods presented as average abundance contributions at various frontal regions of the India Ocean sector of the Southern Ocean during summer 2013.

Size class (mm)	Copepod taxa	STF density (ind m ⁻³) (average ± SD)	SAF density (ind m ⁻³) (average ± SD)	PF1 density (ind m ⁻³) (average ± SD)	PF2 density (ind m ⁻³) (average ± SD)
Smaller size fraction (< 2 mm)	Calanoid				
	<i>Ctenocalanus citer</i>	55 ± 12	35 ± 10	22 ± 5	179 ± 44
	<i>Ctenocalanus vanus</i>	47.28 ± 12.71	31 ± 11	19 ± 13	-
	<i>Clausocalanus laticeps</i>	266 ± 148	177 ± 57	51 ± 22	45 ± 17
	<i>Clausocalanus brevipes</i>	191 ± 22	29 ± 12	19 ± 5	34 ± 16
	<i>Calocalanus</i> spp.	111 ± 41	26.13 ± 12.54	39 ± 11	-
	<i>Microcalanus</i> spp.	56.12 ± 22.56	42 ± 16	-	-
	<i>Scolecithricella</i> spp.	68.15 ± 17.22	-	-	-
Larger size fraction (> 2 mm)	Calanoid				
	<i>Calanus propinquus</i>	-	-	42 ± 11	111 ± 42
	<i>Calanus australis</i>	-	27 ± 7	45 ± 15	109 ± 35
	<i>Calanus simillimus</i>	-	78 ± 21	123 ± 47	37 ± 11
	<i>Calanoides acutus</i>	-	28 ± 18	24 ± 8	241 ± 71
	<i>Neocalanus tonsus</i>	-	143 ± 55	-	-
	<i>Eucalanus longiceps</i>	99 ± 41	11 ± 7	-	-
	<i>Paraeuchaeta</i> spp.	-	-	26 ± 9	51 ± 22
	<i>Metridia lucens</i>	-	11 ± 2	-	42 ± 16
	<i>Rhincalanus gigas</i>	-	-	12 ± 5	85 ± 26
Smaller size fraction (< 2 mm)	Cyclopoid				
	<i>Oithona similis</i>	118 ± 51	353 ± 179	226 ± 93	519 ± 111
	<i>Oithona frigida</i>	68 ± 28	25 ± 11	-	37 ± 10

STF = Sub-Tropical Front, SAF = Sub-Antarctic Front, PF = Polar Front.

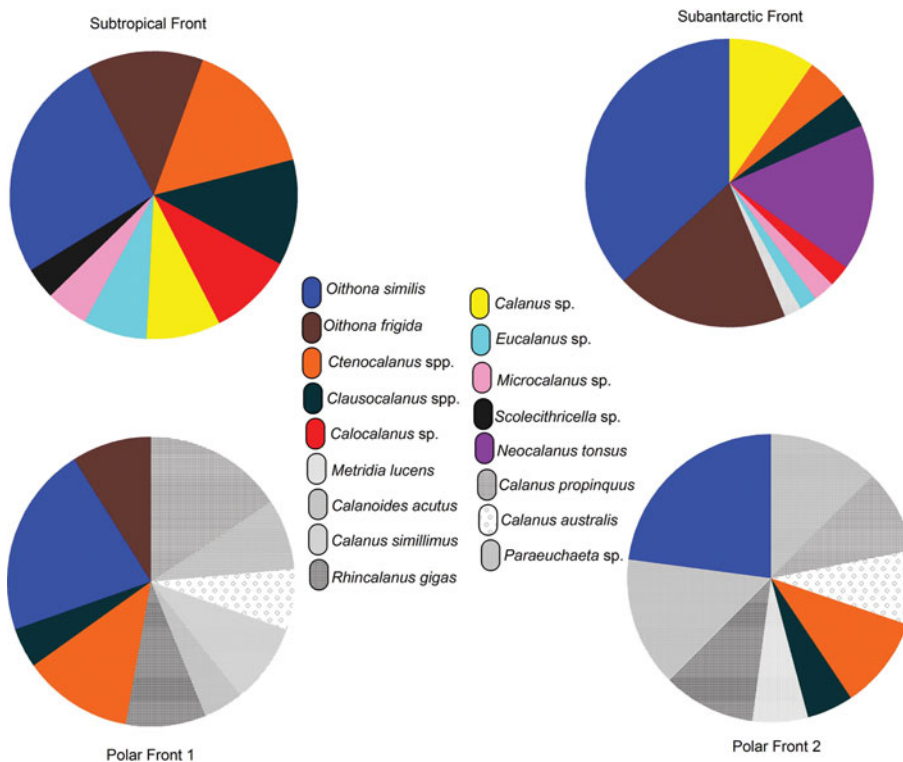


Fig. 4. Relative percentages of copepod species in the surface layer at various frontal regions.

Clausocalanidae, *Clausocalanus laticeps* was largely responsible for the increased abundance in the upper 150 m. Within the Oithonidae, *O. similis* was largely responsible for the extremely high abundances between 0 and the MLD. Relatively, much lower numbers of *Oithona* spp. occurred in the MLD–150 m depth layer. In particular, *Calocalanus* spp. were common at station

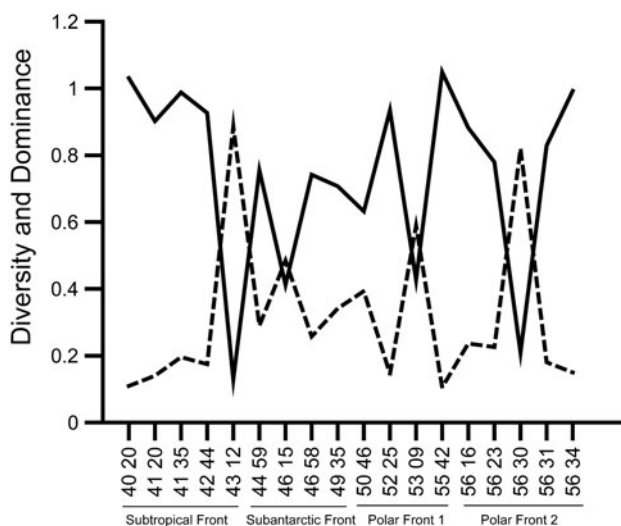


Fig. 5. Spatial variation in zooplankton diversity and dominance (solid line indicates diversity and dashed line indicates dominance).

STF4, while *N. tonsus* was abundant at station SAF3 (Table VI). *Rhincalanus gigas*, *Paraeuchaeta* spp., *Pleuromamma* spp., *Metridia* spp., *Calanus* spp. and *Haloptilus* spp. contributed significantly to zooplankton abundance at depths > 150 m. *Candacia* spp. were restricted to 150–300 m depths, *Eucalanus longiceps* was found only at station STF4 and *Heterorhabdus* spp. were found only at station SAF3 between 150 and 1000 m. Furthermore, small ubiquitous copepods in the genus *Oncaea* were more important at between 150 and 500 m depths at station STF4 and SAF3 (Table VI). *Calanus propinquus*, *C. acutus*, *Clausocalanus* spp., *Ctenocalanus* spp. and *Oithona* spp. were major contributors to the total zooplankton abundance at between 0 and 150 m at stations PF1 #2 and PF2 #5 (Table VI). To a greater or lesser extent, within the *Oithona* spp., *O. frigida* was largely responsible for the increased abundance in the 0–MLD depth, along with the less abundant *O. similis*. *Calanoides acutus* was important at the MLD, while *Microcalanus* spp. were restricted between the MLD and 150 m, and *Candacia* spp. were encountered mostly in the 150–300 m stratum. Between 150 and 500 m, *Pleuromamma* spp., *Metridia gerlachei*, *R. gigas* and *Paraeuchaeta* spp. occurred in large numbers (Table VI). In addition to copepod species, non-copepods were also encountered less frequently. Most of the non-copepod groups, including chaetognaths and appendicularians, were abundant

Table VI. Percentage compositions of dominant copepod groups, chaetognaths and appendicularians sampled throughout the water column at four oceanographic stations.

Depth stratum (m)	Zooplankton taxa	STF4 (%)	SAF3 (%)	PF1 #2 (%)	PF2 #5 (%)	
0–MLD	<i>Clausocalanus</i> spp.	8.9	7.1	4.1	3.6	
	<i>Ctenocalanus</i> spp.	4.2	4.5	5.0	4.0	
	<i>Calanus propinquus</i>	0	0	10.3	11.5	
	<i>Calanoides acutus</i>	0	2	6.4	5.0	
	<i>Calocalanus</i> spp.	2.1	0.5	0	0	
	<i>Neocalanus tonsus</i>	0	6.0	0	0	
	<i>Oithona</i> spp.	5.9	6.1	4.1	5.5	
	Chaetognaths	1.0	0.9	1.1	2.3	
	Appendicularians	0.5	1.0	1.1	0	
MLD–150	<i>Clausocalanus</i> spp.	4.2	4.1	1.3	2.0	
	<i>Ctenocalanus</i> spp.	2.4	2.5	4.1	3.5	
	<i>Calanus propinquus</i>	0	0	3.0	6.1	
	<i>Calanus</i> spp.	2.0	2.1	0	0	
	<i>Calocalanus</i> spp.	0.5	0.5	0	0	
	<i>Microcalanus</i> spp.	0	0	3.3	3.0	
	<i>Oithona</i> spp.	1.2	1.9	2.5	1.5	
	<i>Oncaea</i> spp.	0.5	1.2	1.0	2.4	
	Chaetognaths	1.0	0	0	0.5	
	Appendicularians	0	1.0	0	0	
	150–300	<i>Calanus</i> spp.	3.2	2.2	4.5	5.1
<i>Paraeuchaeta</i> spp.		1.4	0.5	1.0	2.0	
<i>Eucalanus longiceps</i>		1.5	0	0	0	
<i>Heterorhabdus</i> spp.		0	3.5	2.5	1.9	
<i>Haloptilus</i> spp.		2.4	1.5	0	0	
<i>Rhincalanus gigas</i>		3.6	4.4	6.1	6.3	
<i>Candacia</i> spp.		2.2	1.8	2.1	2.7	
<i>Oncaea</i> spp.		1.6	1.5	1.6	1.5	
Chaetognaths		0.25	0.25	0	0.7	
Appendicularians		0.25	0.25	0	0	
300–500		<i>Calanus</i> spp.	2.2	3.7	4.0	4.3
		<i>Paraeuchaeta</i> spp.	4.1	1.6	2.0	1
		<i>Eucalanus longiceps</i>	2.6	0	0	0
	<i>Heterorhabdus</i> spp.	0	2.6	1.5	1.5	
	<i>Haloptilus</i> spp.	2.4	1.8	0	0	
	<i>Metridia gerlachei</i>	3.8	1.2	6.1	4.6	
	<i>Rhincalanus gigas</i>	4.1	4.5	6.5	5.0	
	<i>Pleuromamma borealis</i>	4.0	3.1	7.8	5.5	
	<i>Pleuromamma robusta</i>	4.0	2.7	5.0	6.0	
	<i>Oncaea</i> spp.	1.5	0	1.5	0.5	
	Chaetognaths	0	0	0.25	0.25	
	Appendicularians	0	0	0.25	0.25	
	500–1000	<i>Calanus</i> spp.	2.5	3.6	n/a	n/a
		<i>Eucalanus longiceps</i>	2.0	0	n/a	n/a
<i>Haloptilus</i> spp.		1.4	2.8	n/a	n/a	
<i>Rhincalanus gigas</i>		5.1	5.5	n/a	n/a	
<i>Metridia gerlachei</i>		4.5	4.1	n/a	n/a	
<i>Pleuromamma borealis</i>		3.0	3.0	n/a	n/a	
<i>Pleuromamma robusta</i>		2.0	2.0	n/a	n/a	
<i>Oncaea</i> spp.		0	0	n/a	n/a	
Chaetognaths		0	0.5	n/a	n/a	
Appendicularians		0	0	n/a	n/a	

n/a = data not available, MLD = depth of mixed layer, STF = Sub-Tropical Front, SAF = Sub-Antarctic Front, PF = Polar Front.

typically in the upper 150 m across most of the sampling locations (Table VI). These two groups were important contributors to the total abundance in the study area.

Within the depth range (0–MLD), these two taxa were numerically more dominant at stations PF1 #2 and PF2 #5 than at STF4 and SAF3. In contrast, in the depth range between MLD and 150 m, they were relatively more numerous at stations STF4 and SAF3 (Table VI).

Discussion

Influence of nutrients on chl a distribution

The low nutrient concentrations observed in the STF and SAF, coupled with low chl *a* concentrations and low zooplankton biovolume, may be explained by limiting micronutrients (presumably iron) and/or strong zooplankton grazing. It is well documented that iron limits primary production in high-nutrient, low-chlorophyll regions (e.g. Martin & Fitzwater 1990). In the PF, the high sea level pressure gradients and the low temperatures due to the Southern Annular mode define this region as an upwelling area, which brings nutrient-rich waters to the sea surface. The increase in nutrients triggers the high phytoplankton biomass and eventually promotes a high zooplankton biovolume. Furthermore, iron input from sedimentary sources most probably plays an important role in this region (Moore & Abbott 2002). During the present study, relatively larger phytoplankton cells (diatoms) were found to be dominant at the PF due to the combination of higher silicate and ammonium concentrations than in the STF. Earlier studies reported concentrations of 4 μM in the SO Global Ecosystem Dynamics survey (Serebrennikova & Fanning 2004) and 4 μM in the Ross Sea (Gordon *et al.* 2000) in the summer. In the present study, the concentration was 34.45 μM in the Indian sector of the SO (56°30'S). Moore & Abbott (2002) stated that mesoscale physical processes, including meander-induced upwelling and increased eddy mixing, where the PF encounters large topographic features, probably lead to increased nutrient flux to surface waters over the Keruguelen Plateau. Previous research by Naik *et al.* (2015) showed that higher silicate concentrations in the environment favour the growth and development of larger phytoplankton cell such as diatoms. Sommer (1986) stated that the silicate uptake range is quite high in the PF; therefore, this region is dominated by the bloom forming large-celled or long-chained diatom species (e.g. *Fragilariopsis kerguelensis*, *Corethron criophilum*, *Thalassiothrix* spp.). In this respect, our observations support the notion that the growth condition of the phytoplankton biomass (diatoms) was very favourable as a preferential food source, which strengthens the persistence of larger calanoid copepods and their high abundance in this area. It should also be noted that the species at higher latitudes tend to have larger body sizes. In particular, polar organisms' body sizes are governed by physical, ecological and evolutionary principles (Moran & Woods 2012).

Picophytoplankton dominated at the STF and SAF, where lower silicate and ammonium concentrations were found; the growth rate of phytoplankton cells in this region might be limited by low silicate concentrations (Boyd *et al.* 2001). Consequently, the size of the copepods was relatively small, as the smaller zooplankton size fractions feed preferentially on picophytoplankton and nanophytoplankton (Froneman & Perissinotto 1996).

Horizontal distribution of zooplankton communities and species assemblages

In general, the taxa in the surface layer showed broad distributions between fronts. However, they were not vastly different between stations. Most species occurred in adjacent fronts and are considered cosmopolitan, with only few endemic species occurring in particular fronts. The STF community was characterized by low densities of common taxa such as *C. citer* and *Oithona* spp. It is possible that low chl *a* coupled with high temperatures might have led to low zooplankton abundance in the STF. In addition to this, both small copepods *O. similis* and *C. citer* probably have reproductive peaks in early spring, and therefore copepodite stages I–III dominate their populations from December to January (Atkinson 1998). Furthermore, the differences in sampling times will influence growth more than abundance (i.e. development to later stages) (Swadling *et al.* 2011). Small zooplankton, especially copepods, were probably greatly under-sampled, as previously noted by Hunt & Hosie (2006b). The copepodite stages of *O. similis* and *C. citer* might have been missed in the bongo net samples by not being trapped by the 200 µm mesh. Mesozooplankton in the SO are usually sampled with 200 µm mesh nets, although a more suitable size is 100 µm mesh nets, and these will still under-sample juvenile stages of some cyclopoid species (Swadling *et al.* 2011). Therefore, the abundances of many of the copepod species are probably underestimated. Dominant species/taxa showed similar distribution patterns between the STF and SAF. They are also the same species previously observed in the STF (Takahashi *et al.* 2011). In particular, *C. citer* is known to be a strong seasonal migrant able to spawn in early spring, even at low chl *a* concentrations (Atkinson 1998), while *O. similis* is known to be adapted to the low phytoplankton densities of the permanent open ocean zone (Takahashi *et al.* 2010a). Another explanation for this is that the differences in phytoplankton community structure may also have influenced the zooplankton communities, as the occurrence of smaller picophytoplankton and nanophytoplankton and low autotrophic primary production might indicate a microbial-based food web, in which secondary production is observed in the presence of insufficient

autotrophic resources. Several widespread taxa had continuous distributions, being present at the STF and also present in the vicinity of the SAF. *Oithona* spp., *Ctenocalanus* spp. and *Clausocalanus* spp. were all important. *Ctenocalanus citer* was largely responsible for the increased abundance in the surface layers, which was largely due to the presence of younger stages during the summer months. Compared with the other three copepods, *N. tonsus* and *Calanus* spp. were also relatively abundant. A similar SAF community has also been identified in the south Atlantic Ocean and in the Pacific Ocean south of New Zealand (Atkinson & Sinclair 2000). *Neocalanus tonsus* was numerically dominant in the SAF, which is characteristic of this copepod (Letterio & Ianora 1995).

Generally, the PF has been noted as a region of enhanced phytoplankton and zooplankton abundance in the SO (Atkinson & Sinclair 2000). In the present study, enhanced chl *a* was observed in the vicinity of the PF, lending support to the ecological importance of this front. Higher phytoplankton concentrations stimulate grazing, which enhances zooplankton biomass. It is possible that the availability of diatom-dominated phytoplankton biomass in the PF enhanced zooplankton biomass. The usual time lag between phytoplankton blooms and grazer development enabled the high phytoplankton biomass due to high levels of nutrients in the vicinity of the PF. Carloti *et al.* (2008) reported that when the ecosystem structure was dominated by large diatoms, it provided favourable conditions for the large copepods in the Kerguelen Plateau area. This supports our observations that the PF was dominated by larger species, such as *C. propinquus*, *C. acutus*, *C. australis*, *C. simillimus* and *R. gigas*. Increased copepod abundance in response to high phytoplankton biomass has previously been observed at South Georgia Island (Atkinson *et al.* 1996), where copepod life cycles involve reproduction and early larval feeding in summer, with later lipid-rich stages being less active, spending the winter in diapauses or least with reduced activity, and often at depth (Atkinson 1998, Pakhomov *et al.* 2002). Higher population densities of small copepods were also observed, mainly comprising *O. similis* and *C. citer*, apparently contributing significantly to food web dynamics as in the PF. In particular, high chl *a* concentrations in the surface layer may have been the driving force behind the tendency of copepod species to concentrate closer to the surface. If our assumption holds true, these copepods are key elements in the transfer of organic matter to the higher trophic food levels in the open Antarctic Ocean. The small copepods, such as *O. similis* and *C. citer*, have been recognized to be both highly abundant and important in energy flow (Atkinson 1998). In the current study, there was considerable temporal variation in the mean abundance

of the zooplankton assemblages between the months, ranging from 550 ind m⁻³ in late January 2013 to 12 452 ind m⁻³ in late February 2013. Our finding also shows that during the summer, large changes in surface zooplankton community structure were observed, and the average transect abundance of smaller copepods peaked abruptly in early February and then remained high. The high abundance recorded in February may have reflected the overwintering and/or adult reproductive population. Undoubtedly, monthly variations in this survey may also have influenced our observations of zooplankton distributions. Among the mesozooplankton, chaetognaths and appendicularians were often second only to copepods in abundance and biomass, and their population density was low due to their ability to adapt to the prevailing environmental conditions. The predominant taxa were *Mesosagitta* spp., *Sagitta* spp., *Oikopleura* spp. and *Fritillaria* spp. Similar results have been observed near the coastal area east of the Kerguelen Islands in the Indian sector of the SO (Carlotti *et al.* 2015).

Vertical distribution of the zooplankton community dynamics

Zooplankton biomass, abundance and community structure were strongly structured in the vertical plane, and the distributions of a number of species varied between depth zones. The relationship between MLD and zooplankton biomass is complex. For example, deepening of MLD influences the availability of light and nutrient supply, which would determine phytoplankton growth and subsequently cause changes in zooplankton biovolume and community structure; hence, zooplankton biovolume increased with deeper MLD. The zooplankton biovolume and community structure in the Indian sector of the SO would therefore be expected to respond to changes in the mixed layer. Copepods were the greatest contributor to total species abundance in all depth zones. In particular, we observed distinct communities between stations STF4 and SAF3. The numerical dominance of small copepods, such as *Clausocalanus* spp., *Ctenocalanus* spp. and *Oithona* spp., in the upper and mesopelagic zones is similar to that previously reported in the SO (Hunt & Hosie 2006a). *Oithona similis* was the most numerically abundant copepod (Hunt & Hosie 2006a) and is considered to be a key component of the plankton food web of the SO (Atkinson 1998), forming a significant proportion of the zooplankton biomass despite its small size. *Clausocalanus* spp., *Ctenocalanus* spp. and *Oithona* spp. were more numerous in the MLD than the lower layer (MLD–150 m); this small peak in the MLD–150 m layer could be due to the downwards migration of pelagic species in order to avoid predation. South of the PF (stations PF2 and PF5), species such as *C. propinquus*

and *C. acutus* inhabited the low-temperature waters and were distributed widely within the PF. The present study showed that the vertical distributions of zooplankton communities were broadly associated with various depth layers. Copepods were strongly structured in the vertical plane, and the distribution of the number of species varied between depth zones. This was reflected by increased species diversity and decreased dominance with depth. This is probably to be due to smaller gradients in oceanographic properties in the deeper layer compared to those in the epipelagic layer. The depth distribution of *Paraeuchaeta* spp., *R. gigas*, *Metridia* spp. and *Pleuromamma* spp. showed that they were most abundant in the 150–1000 m layer, but this does not account for the disparity in abundance levels. Representatives of various genera that co-occurred in the same depth range generally differed in feeding behaviour and dietary preferences, as evidenced by trophic biomarkers (Laakmann *et al.* 2009). In fact, most calanoid species in the SO are found in deep waters (mesopelagic and bathypelagic layers) (Ward & Shreeve 2001). This indicates that vertical differences in environmental factors are important for determining copepod community structure. In addition to copepods, appendicularians and chaetognaths were relatively important zooplankton contributors to the total zooplankton biomass. Appendicularians are filter-feeders, while chaetognaths are voracious predators of copepods and are generally found at depths coinciding with copepod vertical distribution. Appendicularians are one of the common members of zooplankton communities in all oceans, and they are ideally suited to oceanic oligotrophic conditions (Deibel 1998).

Influence of temperature on variation in the size fraction of common copepod taxa

Size fractionation of the copepod community provides information on what size classes primarily contribute to the various frontal regions. Copepod size is particularly important because it can be an indicator of multiple biological and ecological traits, such as metabolism, feeding strategy (Kjørboe 2011) and trophic links. The present data reveal that larger copepod species (> 2 mm) dominated in cooler regions where temperatures were < 4°C and smaller species (< 2 mm) were dominant in warmer regions where temperatures were > 18°C; thus, it appears that warmer conditions favour the dominance of smaller species (Daufresne *et al.* 2009). This finding demonstrated that the discrepancy in the interspecific temperature–size relationship could be explained by a geographical shift of the thermal niche boundary of these species. We observed a positive relationship between copepod size and water temperature in the SO, with the result being that larger copepods were more

dominant in the cooler waters than warmer waters. The copepod size structure may change further with advection transport and latitudinal shift in water masses, which are driven by oceanic current dynamics. *Clausocalanus* spp., *Ctenocalanus* spp., *Calocalanus* spp., *Microcalanus* spp., *Scolecithricella* spp. and *Oithona* spp. were the major contributors to the < 2 mm group, similarly to an earlier report (Koubbi *et al.* 2011). On the other hand, *C. propinquus*, *C. australis*, *C. simillimus*, *C. acutus*, *N. tonsus*, *E. longiceps*, *Paraeuchaeta* spp. and *R. gigas* were the major contributors to the > 2 mm group. The Kerguelen Plateau was characterized by a greater abundance of large calanoid copepods such as *R. gigas* and *Paraeuchaeta* spp. (Carlotti *et al.* 2015). The success of the numerically dominant species *R. gigas* and *Paraeuchaeta* spp. was probably due to their different life stages (Atkinson 1998). Compared to larger copepod species, smaller warm-water species dominated the surface region of the study area. This pattern was the opposite of the vertical distribution of copepod species. Larger copepod species at station STF4 mostly resided at < 500 m where the temperature was < 4°C; correspondingly, they were present at < 300 m in station SAF3, where the temperature was < 4°C, indicating that a particular temperature was probably serving as the boundary of the thermal niche for the larger copepod species. A question arises as to why the larger fraction of zooplankton occurred at discrete depths. One of the major factors determining the distribution of larger individuals is that they experience greater susceptibility to visual predators, and hence they have a need to descend below the euphotic depth during the day, moving to the surface layers soon after sunset. This behaviour in the large-sized copepods may have caused the strong day/night difference in their distribution pattern. The results of this study demonstrate that water temperature is probably more important than phytoplankton food availability in determining the distribution limit of these species.

Summary and conclusion

The community structure of zooplankton reflected their sensitivity to their surroundings and highlighted their dominance in various frontal regions. Nutrient concentrations were lower in the STF than the PF regions, which led to higher chl *a* concentrations in the latter, corresponding with greater zooplankton abundance. The supply of micronutrients and grazing pressure by zooplankton controlled the onset and duration of the phytoplankton growth period. Lower chl *a* was observed at the SAF and STF, coinciding with low nutrient concentrations and indicating that control of autotrophic production was mainly dependent on the presence of high

levels of nutrients. The highest silicate concentrations were observed in the PF, suggesting the dominance of diatoms and indicating spatial coupling between primary and heterotrophic production in the PF. Chl *a* played a major role in driving the spatial distribution of zooplankton biomass. Similarly to other oceans, copepods numerically dominated the total mesozooplankton in the study region. Calanoida was the dominant zooplankton group in the PF1 region and Cyclopoida was the dominant zooplankton group in the PF2 region. The ecological differences in these communities therefore reflected the physical heterogeneity of the region between the STF, SAF and PF. *Ctenocalanus citer*, *C. laticeps* and *O. similis* were the dominant species during the study period. The taxonomic composition did not show major differences between stations near each front. We found an increase in copepod community size from the STF to the PF because of the increased dominance of large cold-water species due to decreases in temperature. Therefore, environmentally forced changes in the zooplankton community structure may have important implications for ecosystem functioning.

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Author contributions

VV, SCT and NA conceived and designed the study. VV wrote the manuscript, and the final manuscript was improved by KS. Fieldwork and analysis were performed by VV, RKM, AS, SMA, PS, SCT and HUKP. All authors agreed to submit it to *Antarctic Science*.

Supplemental material

Two supplemental tables will be found at <https://doi.org/10.1017/S0954102019000579>.

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