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Comparison of zooplankton distribution patterns between four seasons in the Indian Ocean sector of the Southern Ocean

Kunio T. Takahashi [a,b,*], Graham W. Hosie [c], John A. Kitchener [c], David J. McLeod [c,d], Tsuneo Odate [a,b], Mitsuo Fukuchi [a,b]

[a] *National Institute of Polar Research, 10-3 Midori-cho, Tachikawa, Tokyo 190-8518, Japan*
[b] *Graduate University for Advanced Studies (SOKENDAI), 10-3 Midori-cho, Tachikawa, Tokyo 190-8518, Japan*
[c] *Australian Government Antarctic Division, Channel Highway, Kingston, Tasmania 7050, Australia*
[d] *Integrated Marine Observing System – AusCPR Survey, CSIRO Marine and Atmospheric Research, Cleveland, Qld 4163, Australia*

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Abstract

We investigated the composition, distribution and abundance of zooplankton in the Indian Ocean sector of the Southern Ocean during the austral summer (December/January) of 2004/05, 2005/06, 2007/08 and 2008/09 using a Continuous Plankton Recorder (CPR). CPR tows were conducted along two transects during voyages south of Cape Town to north of Syowa station and from north of the Mawson station area to south of Fremantle. High zooplankton abundance was recorded on each transect in the Polar Frontal Zone (PFZ) and the northern area of the Antarctic Zone (AZ). Community structure in these zones was dominated by common taxa including the ubiquitous *Oithona similis* and calanoid copepodites, accounting for >50% of total abundance, and *Calanus simillimus*, *Ctenocalanus citer*, *Clausocalanus laticeps* and *Metridia lucens* also occurred in high densities. Appendicularians of the genus *Fritillaria* were the most important component in the Cape Town to Syowa station area in 2008, with 36.9% of total abundance. The average chlorophyll *a* level at this time of year was the lowest (0.32 mg m^{-3}) among all transects. Appendicularians are suited to oceanic oligotrophic waters; therefore, they are suited to low phytoplankton density. Foraminiferans were numerically dominant throughout the Mawson station area to Fremantle transect in 2005. Unlike *Fritillaria* spp., foraminiferans prefer high phytoplankton density. The elevated average chlorophyll *a* biomass in 2005 (0.64 mg m^{-3}) provided favorable conditions for Foraminifera, which were dominant and widespread. CPR surveys provide information on the fine scale structure of the interannual distribution changes in micro- and meso- zooplankton assemblages, and the CPR is one of ideal method to monitor organisms that are indicators of environmental change.

Keywords: Continuous plankton recorder; Copepod; Foraminiferans; Appendicularians

1. Introduction

Antarctica and its surrounding waters are expected to be particularly sensitive and vulnerable to climate change (Zwally, 1994). There are a number of threats to the plankton in the Antarctic and Southern Oceans, e.g. global warming and sea-ice reduction, UV exposure, harvesting impact, invasive species and ocean acidification. Ocean acidification will have a significant impact on calcareous organisms such as pteropods, planktonic foraminiferans and coccolithophorids

* Corresponding author.
E-mail address: takahashi.kunio@nipr.ac.jp (K.T. Takahashi).

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(Riebesell et al., 2000; Orr et al., 2005; Moy et al., 2009). Changes to the plankton will have a dramatic flow-on effect through the food web, resulting in substantial ecological impacts and affecting the survival of higher organisms.

For the last few decades, much of the research in the Antarctic has focused on Antarctic krill (*Euphausia superba*) and higher predators such as fish, birds and mammals. Krill is widely recognized as a key species in the Antarctic food web because of its exceptionally high proportion of biomass as prey for animals at higher tropic levels (Marr, 1962; Hempel, 1985). However, a study by Nicol (1994) noted the importance of the entire plankton including salps and copepods. He suggested that a more complex and unstable food web than previously thought existed in the Southern Ocean. Small herbivorous zooplankton such as copepods are estimated to have greater biomass than that of Antarctic krill (cf. Conover and Huntley, 1991). They are important alternative links in the food web, especially for fish, flying seabirds and squid. They compete for the same food as krill, and consume three to eight times more of the primary production (Conover and Huntley, 1991; Pakhomov et al., 2002).

The Southern Ocean Continuous Plankton Recorder (SO-CPR) Survey commenced in 1991 with the purpose of mapping spatial and temporal variations in zooplankton pattern, and to make use of the sensitivity of plankton to environmental change as an early warning indicator of the health of the Southern Ocean ecosystem (Hosie et al., 2003). The data from CPR surveys have been used to define geographical groupings of plankton taxa and groups of species with similar patterns of seasonal or inter-annual variations in abundance (Reid et al., 2003). The CPR provides sufficient geographic resolution to spatial distribution of zooplankton to identify biogeographic zones in the Southern Ocean and detection of changes to the surface zooplankton community structure (Hosie et al., 2003; Hunt and Hosie, 2003, 2005, 2006a, 2006b; Pinkerton et al., 2010; Takahashi et al., 2002, 2010; Umeda et al., 2002). In particular, micro- and mesozooplankton such as small copepods, foraminiferans and appendicularians have been estimated to have a high abundance (Hunt and Hosie, 2005, 2006a, 2006b). They are closer to the bottom of the food chain, and hence are expected to respond more rapidly to environmental change. They also play a key role in the microbial loop as consumers of bacteria and protists, and are an important food item for krill and larger zooplankton; they play a crucial role as a link between the microbial loop and higher trophic levels. Therefore, the ecological importance of these plankton species has recently attracted attention. Nevertheless, at present we have insufficient information on the role of micro- and mesozooplankton in the Southern Ocean to be able to interpret and predict the consequences of environmental change.

As part of the monitoring program of the Japanese Antarctic Research Expedition, collaborative marine biological studies were conducted in the Indian Ocean sector onboard the RT/V *Umitaka-Maru* of the Tokyo University of Marine Science and Technology over consecutive austral summers (Kasamatsu et al., 2008). This provided an opportunity to conduct CPR tows for four seasons along almost the same cruise track at the same time of year. The objective of the study was to assess the inter-annual variability in micro- and mesozooplankton abundance, species composition and distribution patterns and associated events in the Indian Ocean sector of the Southern Ocean.

2. Materials and methods

Data were collected onboard the RT/V *Umitaka-Maru* on two transects from December to January in 2004/05, 2005/06, 2007/08 and 2008/09 (Table 1). These transects extended south of Cape Town to the Syowa station area (A–D) and north from the Mawson station area to south of Fremantle (E–H) (Fig. 1). Transects A–D (December–January) were used to sample the region between 48°S and 60°S, from 23.4°E in the north to 37.9°E in the south. Transects E–H (January) were used to sample between 50°S and 62°S, from 69.1°E to 98.3°E (Table 1). The CPR had a mouth opening of 1.6 cm^2 and was fitted with 270 μm silk mesh. The CPR was towed horizontally at 6–10 m depth at 15–17 knots towing speed. During sampling, zooplankton captured on the silk were preserved in a formaldehyde bath within the CPR. Following retrieval all zooplankton samples were then preserved in 10% v/v buffered formaldehyde and seawater solution for laboratory analysis. The CPR silks were cut into segments, each representing a five nautical mile (approximately 9.3 km) sampling interval. The estimated length of each segment was calculated from the stop and start position of each, and from 1 min interval GPS positions recorded between these times. A detailed description of the processing technique is presented in Hosie et al. (2003).

Zooplankton were identified to the lowest taxa possible, generally species or genus with a stereomicroscope. Ostracods, decapods and most small hyperiid amphipods were not identified to species.

Table 1
Details of CPR tows conducted on the RT/V *Umitaka-Maru*.

CPR run #	Sample period	Latitude	Longitude	No. of Segments[a]	Night Segments[b]
Transect from Cape Town to Syowa station area					
A	2–5 January 2005	48.0–60.0°S	23.8–30.9°E	153	83
B	7–10 January 2006	48.0–60.0°S	23.4–29.8°E	153	59
C	27–29 December 2007	48.0–60.0°S	23.5–30.7°E	152	72
D	10–12 January 2009	48.0–60.0°S	26.2–37.9°E	168	73
Transect from Mawson station area to Fremantle					
E	15–19 January 2005	50.0–62.0°S	69.1–96.9°E	235	97
F	21–25 January 2006	50.0–62.0°S	72.6–98.3°E	226	70
G	10–13 January 2008	50.0–62.0°S	75.0–97.3°E	207	91
H	27–31 January 2009	52.6–62.0°S	80.3–96.2°E	172	62

[a] Each segment of cut silk corresponds to five nautical miles of towing distance.
[b] Night segments defined as PAR < 100 μmol s^{-1} m^{-2}.

Foraminiferans were assumed to be one species south of the Sub-Antarctic Front *Neoglobigerina pachyderma* according to Scott and Marchant (2005). Ctenophores and Chaetognaths were typically damaged during collection by the CPR, and so their abundance levels refer to each group as a whole. Pteropod shells were usually damaged by the silks and so no attempt was made to differentiate between *Limacina* spp. Copepodite other than adults of calanoid copepods were not identified to species being grouped as calanoid copepodites. Zooplankton abundance was converted to individuals m^{-3}. The volume of water filtered was assumed to be 100% of the volume calculated from the length of each segment and the mouth opening.

Sea surface temperature, salinity and *in vivo* fluorescence (as an indicator of phytoplankton biomass) were continuously recorded by an automated surface-water monitoring system installed on the *Umitaka-Maru*. Fluorescence readings were converted to chlorophyll *a* biomass according to the following formula:

$$y = 1.1364x + 0.0503,$$

where x is the fluorescence value and y is the concentration of chlorophyll *a* (mg m^{-3}) (Lorenzen, 1966). Photosynthetically active radiation (PAR) was measured at 1 min intervals on all transects.

To remove the influence of diel variation, only the night segments defined by PAR <100 μmol s^{-1} m^{-2}

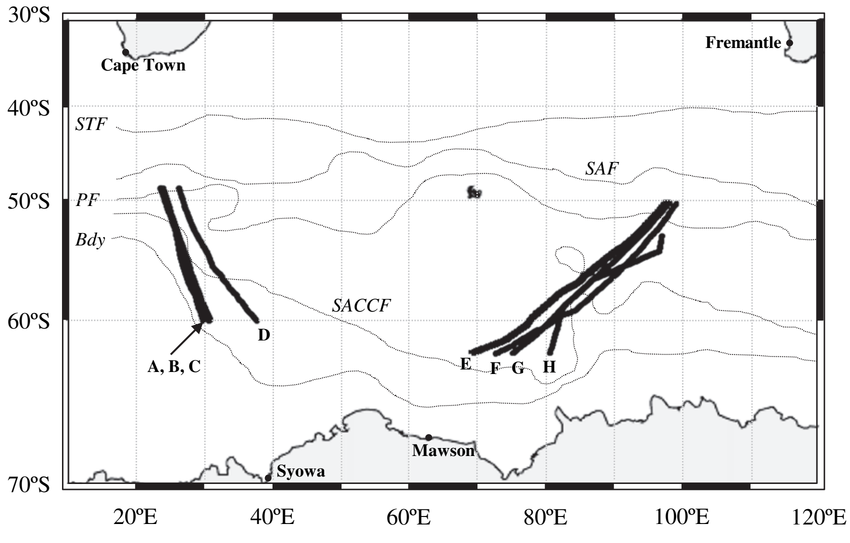

Fig. 1. Map of the study area, indicating the position of the CPR transects A to H. The average positions of the fronts in the study area are the same as those of Orsi et al. (1995). STF: Sub-Tropical Front; SAF: Sub-Antarctic Front; PF: Polar Front; SACCF: Southern ACC Front; Bdy: southern boundary of the ACC.

were used in the data analysis (Table 1). Zooplankton data were further analyzed by cluster analysis using the Bray–Curtis dissimilarity index and Un-Weighted Pair Group Average (UPGMA) linkage to compare species/taxa composition between areas covered by the segments, following the procedures described by Field et al. (1982), Hosie (1994), and Hosie and Cochran (1994). Data were transformed using a $\log_{10}(x + 1)$ function to normalize the high variability in abundances between species caused by patchiness. Indicator value (IndVal) analysis was applied to sample groups at each level of separation in the cluster analysis (Dufrene and Legendre, 1997). An IndVal of $\geq$25% was selected as the cutoff point for indicator species/taxa using this method, which meant that a species/taxa was present in $\geq$50% of samples in a group and that its relative abundance in that group was $\geq$50%. Sample groups with the highest IndVal for a species/taxa were considered to represent the centre of the distribution of that species/taxa. One-way ANOVA was used to test the null hypothesis that the abundance levels of a species/taxa did not differ between sample groups. Newman–Keuls multiple-range tests were performed to identify inter-cluster differences in species/taxa abundance levels. Statistical analyses were carried out using Primer Version 6 and SPSS 10.1 J for Windows.

3. Results

3.1. Oceanography and physical zonation

The Southern Ocean is characterized by circumpolar frontal zones, which separate the different water masses and play an important role in biogeographic zonation (Orsi et al., 1995; Pinkerton et al., 2010). The actual position of the Antarctic Circumpolar Current (ACC) can only be reliably identified by deep oceanographic observations (Orsi et al., 1995); however, surface data collected on the CPR transect showed changes in the water mass (Fig. 2). The Polar Front (PF) is defined by a surface temperature range of 2.5–5.0 °C (Sievers and Emery, 1978; Lutjeharms and Valentine, 1984). At the Cape Town to Syowa station area transects (A–D), the northern (N) branch of the PF were typically located at 49°S–51°S. The southern (S) branch of the PF was moved southward from around 50.50°S in 2005/06 to 52.50°S in 2008/09 (Fig. 2). From the Mawson station area to the Fremantle transects (E–H), the PF-N and PF-S were located at 53°S–54°S and 57°S–58°S, respectively (Fig. 2). In the 2008/09 season, the PF-N had moved southwards to 54.50°S (Fig. 2). We defined the region to the north of PF-N as the Polar Frontal Zone (PFZ), the region between the two branches of the PF as the Inter Polar Frontal Zone (IPFZ) and the region to the south of PF-S as the Antarctic Zone (AZ) (Fig. 2).

3.2. Chlorophyll a concentrations and zooplankton densities

Because of daylight quenching, surface chlorophyll *a* concentration showed a diel cycle at all transects (Fig. 3). Chlorophyll *a* levels varied from 0.05 to 1.41 mg m^{-3} at Transects A–D. Night time level averages at Transects A (ave = 0.64 mg m^{-3}) and D (ave = 0.70 mg m^{-3}) were higher than those at Transects B (ave = 0.42 mg m^{-3}) and C (ave = 0.36 mg m^{-3}) (Table 2). The maximum zooplankton abundance was observed at Transect C with 382.9 ind m^{-3}. It dramatically decreased northward (Fig. 3), and the mean total abundance at Transect C was low (ave = 44.7 ind m^{-3}) compared with that at Transects B (ave = 116.7 ind m^{-3}) and D (ave = 92.4 ind m^{-3}). Similar night time chlorophyll *a* level averages were observed at Transects E to H, ranging from 0.55 to 0.59 mg m^{-3} (Table 2). Mean zooplankton abundance varied from 74.6 ind m^{-3} at Transect G to 187.9 ind m^{-3} at Transect F.

3.3. Cape Town to Syowa station area transect

Cluster analysis of night samples from the Cape Town to Syowa station area transect identified four clusters (Fig. 4). Cluster 4 separated at 68.94% dissimilarity and comprised samples from the southern segments in 2005, 2006, and 2008 (Fig. 4). Cluster 4 had the lowest sea surface temperature, average species richness and zooplankton abundance of any of the clusters (Table 3). Surface water in this region was cold (0.71 °C), as demonstrated by the dominance of the euphausiid, *E. superba*, which had the maximum IndVal (51.99) (Fig. 5). Clusters 1 to 3 had samples that shared a number of species/taxa with high IndVals, including the maximum values for copepod nauplii, Foraminiferans and *Oithona similis*, demonstrating their importance across most of the survey transects during each year (Fig. 5).

Cluster 3 separated at 59.75% dissimilarity and comprised samples mostly from 2008 (Fig. 4). Chlorophyll *a* levels were the lowest of any cluster. Appendicularians of the genera *Fritillaria* spp. dominated total abundance and had the maximum IndVal (71.97) (Figs. 4 and 5). Samples from Cluster 1 and 2 had maximum IndVals for calanoid copepodites and *Thysanoessa macrura* (Fig. 5).

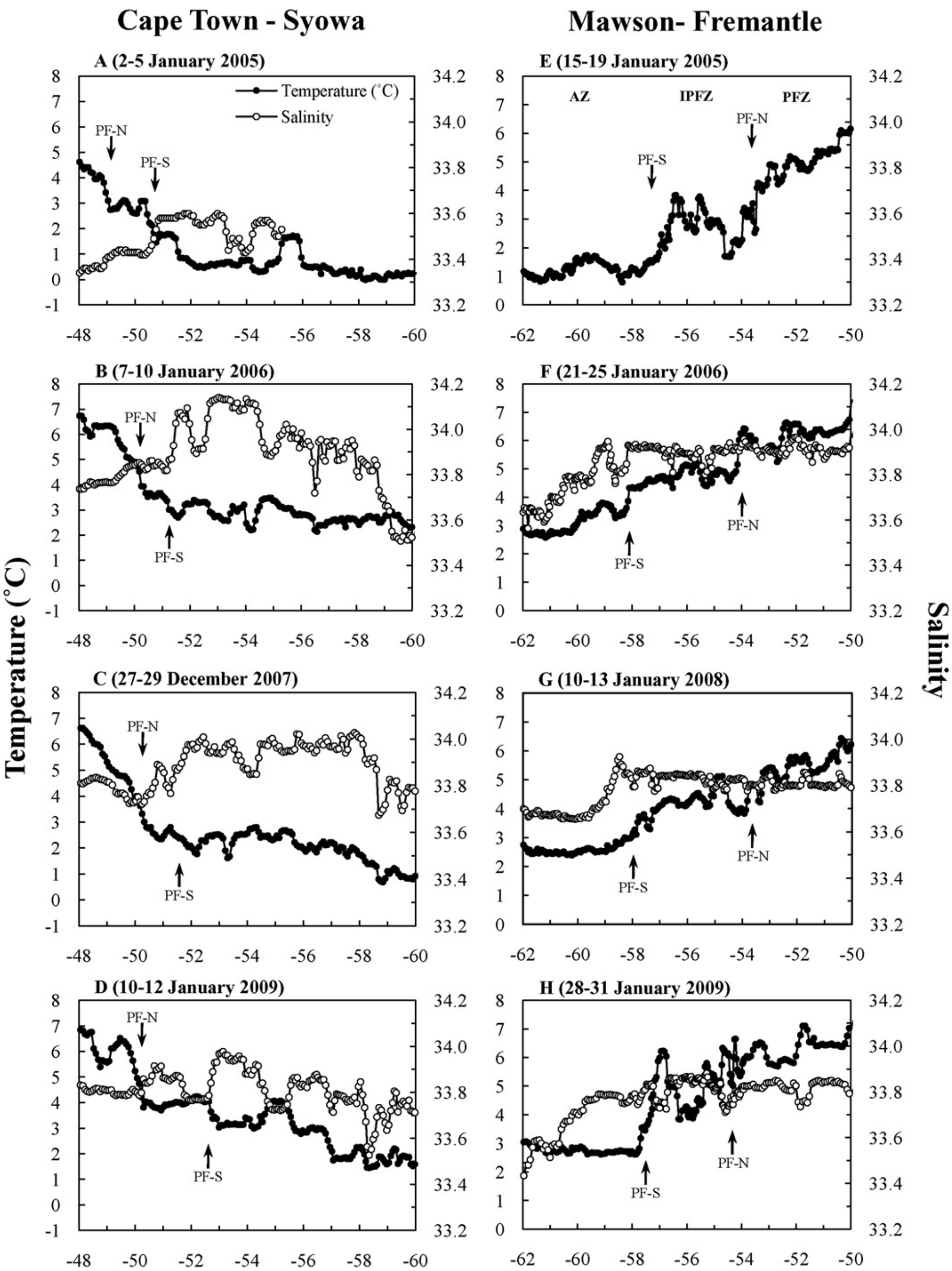

Fig. 2. Sea surface temperature (°C) and surface salinity from the eight CPR transects sampled from January 2005 to January 2009. There were no data for salinity south of 55°S at Transect A and for all of Transect E. The locations of fronts and inter-frontal zones are indicated as follows: PF-N = northern Polar Front; PF-S = southern Polar Front; PFZ = Polar Frontal Zone; IPFZ = Inter Polar Frontal Zone; AZ = Antarctic Zone.

Clusters 1 and 2 separated at 42.33% dissimilarity. Cluster 2 comprised the 103 segments located in the northern area in 2005, 2006, and 2009. Sea surface temperature, chlorophyll *a*, species richness and zooplankton abundance were the highest for any cluster (Table 3). Abundances of 16 species/taxa were significantly higher than those for the other clusters, and seven species/taxa had the maximum IndVal

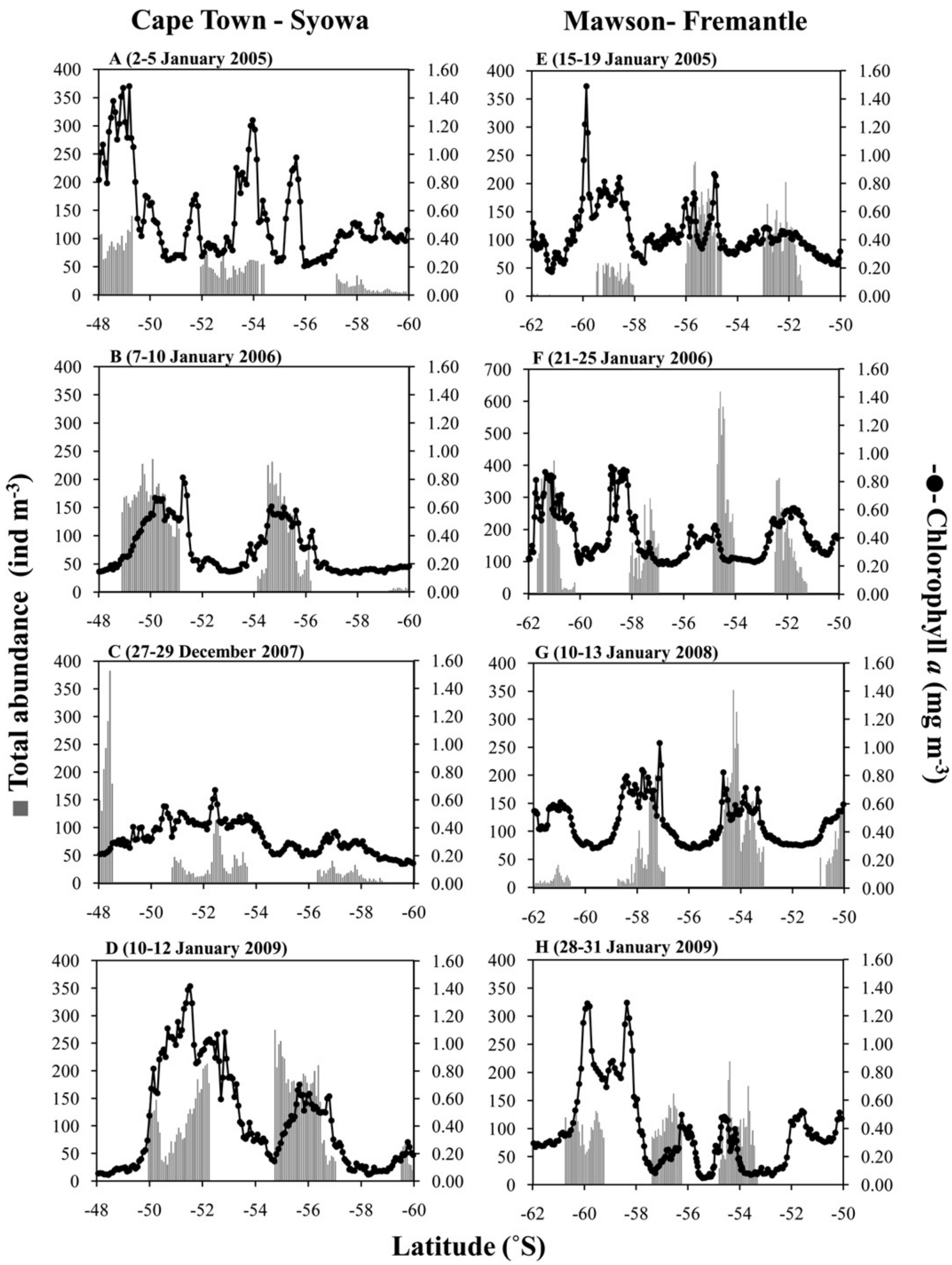

Fig. 3. Chlorophyll *a* concentration determined from fluorescence readings and total zooplankton abundance (individuals m^{-3}) recorded from January 2005 to January 2009.

(Fig. 5 and Table 3). Nine species/taxa were unique to Cluster 2 including the pteropods *Clio pyramidata* and *Spongiobranchaea australis*, the copepods *Metridia lucens*, *Neocalanus tonsus*, *Oncaea* spp., *Pleuromamma borealis* and *Pleuromamma robusta*, the amphipod *Primno macropa* and Decapoda, all of which are species/taxa with typically Sub-Antarctic Zone (SAZ) distributions.

Cluster 1 comprised the segments between 50°S and 57°S in 2005 and 2006. Chlorophyll *a* and species richness were relatively high. The appendicularians, *Oikopleura* spp. and salp *Salpa thompsoni*, had the maximum

Table 2
Average zooplankton abundance and chlorophyll *a* concentration of night samples from the eight CPR transects sampled from January 2005 to January 2009.

CPR run #	Zooplankton abundance (ind m^{-3})		Chlorophyll *a* (mg m^{-3})	
	Average ± SD	Range	Average ± SD	Range
A	43.3 ± 33.2	4.1–140.3	0.64 ± 0.35	0.28–1.38
B	116.7 ± 74.5	3.5–236.4	0.42 ± 0.15	0.16–0.66
C	44.7 ± 66.6	4.1–382.9	0.36 ± 0.11	0.17–0.67
D	92.4 ± 80.1	20.0–274.4	0.70 ± 0.33	0.19–1.41
E	81.0 ± 58.0	0.7–238.4	0.55 ± 0.20	0.33–1.49
F	187.9 ± 143.4	11.1–630.3	0.59 ± 0.16	0.29–0.90
G	74.6 ± 73.3	3.5–351.8	0.58 ± 0.12	0.37–1.03
H	99.5 ± 34.4	14.5–186.6	0.55 ± 0.31	0.23–1.29

IndVal (Fig. 5), while *O. similis*, *Fritillaria* spp. Foraminiferans, copepod nauplii and calanoid copepodites were important contributors to the total abundance (Table 3).

3.4. Mawson station area to Fremantle transect

Six clusters were identified in the segments from the Mawson station area to Fremantle transect (Fig. 6). Cluster 6 separated at 85.33% dissimilarity and comprised the 2005 segments south of 61°S. This cluster had no IndVal indicator species, indicating a low occurrence or abundance of all species/taxa within the corresponding segments (Fig. 7). Foraminiferans and *E.superba* occurred at relatively high abundance. Clusters 1 to 5 had the maximum IndVal for the Foraminiferans, *Fritillaria* spp., *O. similis* and *T. macrura* (Fig. 7).

Cluster 5 separated at 61.37% dissimilarity and comprised segments from the AZ in 2008. Only *Fritillaria* spp. had IndVal ≥25% (Fig. 7). *O. similis* and copepod nauplii were important contributors to total abundance. Cluster 1 to 4 had the maximum IndVal (96.73) for calanoid copepodites (Fig. 7).

Cluster 4 comprised segments from the AZ between 58°S and 60°S in 2005. Chlorophyll *a* concentrations were high, but zooplankton abundance was relatively low. Foraminiferans were important components of this cluster comprising >80% of the total abundance. Clusters 1 to 3 had the maximum IndVal for *Calanus simillimus*, *Clausocalanus brevipes*, *Clausocalanus laticeps* and *Limacina* spp. (Fig. 7).

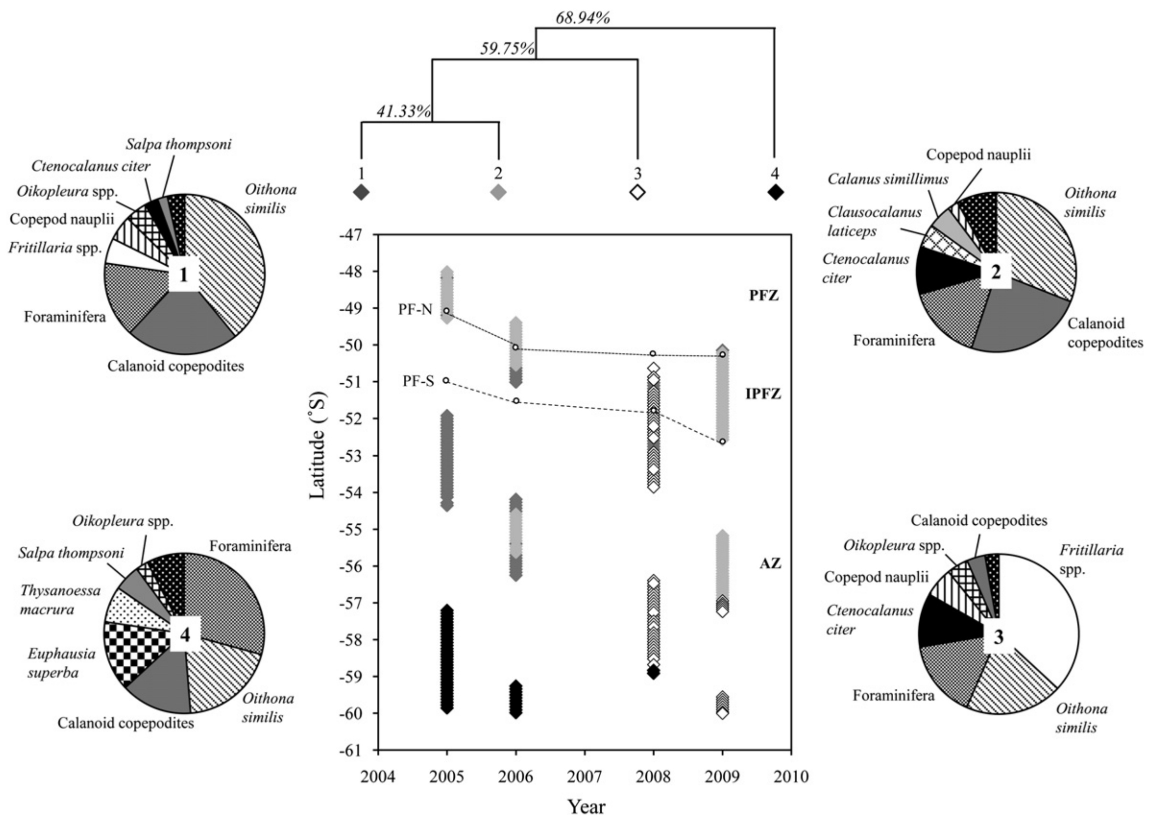

Fig. 4. Results of the cluster analysis for Transects A–D. The upper graph indicates the clusters identified and their level of separation, and the lower panel indicates the spatial and temporal distribution of samples in each cluster. The percentage contribution of major zooplankton groups in each cluster is also shown.

Table 3
Average within cluster dissimilarity, sea surface temperature, chlorophyll *a*, species richness and abundance levels for the four clusters identified by Cluster Analysis of the transect from Cape Town to the Syowa station area.

	Cluster 1	Cluster 2	Cluster 3	Cluster 4	*F*	*P*-value	
Number of segment	61	103	76	47			
Sea surface temperature (°C)	1.78	3.78	2.02	0.71	No test		
Chlorophyll *a* (mg m^{-3})	**0.55**	**0.78**	0.36	0.38	60.45	<0.001	
Species richness (*r*)	**8.85**	**12.34**	5.91	5.40	185.88	<0.001	
Total abundance (ind m^{-3})	86.54	**213.44**	37.32	16.06	231.05	<0.001	
Species/taxa							
Calanoid copepodites	**19.85**	**51.28**	1.38	2.31	161.49	<0.001	
Calanus simillimus	0.30	**10.16**	0.13	0.06	47.49	<0.001	
Clausocalanus brevipes	0.80	**4.70**	0.04	0.30	92.70	<0.001	
Clausocalanus laticeps	0.80	**10.20**	0.22	0.04	41.95	<0.001	
Copepod nauplii	**4.34**	**4.63**	2.21	0.02	25.66	<0.001	
Ctenocalanus citer	2.33	**20.60**	4.53	0.15	36.58	<0.001	
Euphausia superba	0.26	0.10	0.07	**2.28**	18.68	<0.001	
Foraminifera	**13.20**	**33.01**	5.89	4.70	123.92	<0.001	
Fritillaria spp.	**4.43**	0.81	**13.76**	0.13	71.75	<0.001	
Limacina spp.	0.03	**2.33**	0.03	0.17	17.04	<0.001	
Oikopleura spp.	**3.85**	1.46	1.62	0.40	23.09	<0.001	
Oithona similis	**33.85**	**66.15**	7.36	3.13	115.41	<0.001	
Salpa thompsoni	**1.74**	0.13	0.04	**0.85**	22.97	<0.001	
Themisto gaudichaudi	0.08	0.11	0.01	0.06	1.42	0.236	n.s.
Thysanoessa macrura	1.00	**2.21**	0.14	1.17	15.48	<0.001	
Vibilia antarctica	0.02	0.01	0.01	0.04	0.72	0.540	n.s.
Chaetognath		**0.38**	0.03	0.02	10.91	<0.001	
Calanoides acutus	0.11	**1.61**	0.03		53.37	<0.001	
Euphausia vallentini	0.08	0.05	0.12		1.11	0.347	n.s.
Harpacticoid	0.03	0.08	0.09		1.73	0.160	n.s.
Rhincalanus gigas	0.03	**1.38**	0.01		20.24	<0.001	
Candacia maxima	0.02	0.05			2.20	0.089	n.s.
Hyperiid	0.03	0.06			2.39	0.069	n.s.
Ostracoda	0.02	**0.28**			12.59	<0.001	
Pelagobia longicirrata	0.03	0.05			1.94	0.123	n.s.
Euphausia frigida		**0.34**	0.03		9.02	<0.001	
Euphausia triacantha		0.01	0.01		0.43	0.734	n.s.
Tomopteris sp.		0.06	0.03		1.01	0.356	n.s.
Calanus propinquus		0.06		**0.21**	4.46	0.040	
Ctenophore	0.02				1.23	0.296	n.s.
Clio pyramidata		0.01			0.59	0.620	n.s.
Decapoda		0.01			0.59	0.620	n.s.
Metridia lucens		**1.50**			28.46	<0.001	
Neocalanus tonsus		0.04			2.44	0.064	n.s.
Oncaea spp.		0.02			1.20	0.311	n.s.
Pleuromamma borealis		0.15			3.09	0.028	
Pleuromamma robusta		0.03			1.81	0.145	n.s.
Primno macropa		0.03			1.08	0.360	n.s.
Spongiobranchaea australis		0.01			0.59	0.620	n.s.
Total Species/taxa	25	38	24	18			
Unique Species/taxa	1	9					

Differences between clusters were investigated by one-way ANOVA and Newman-Keuls multiple range test. Significantly higher abundance levels are in bold. The number of unique species/taxa and total species/taxa recorded per cluster are indicated. n.s. = not significant.

Cluster 3 separated at 45.13% dissimilarity and comprised the PFZ and IPFZ in 2005. Chlorophyll *a*, species richness and zooplankton abundance were relatively high. The Foraminiferans, *C. simillimus* and calanoid copepodite abundance levels were significantly higher than those of any other species/taxa. Although 32 species/taxa were identified, only five were unique to Cluster 3, including *Metridia gerlachei*, *M. lucens*, *Paraeuchaeta antarctica*, *Paraeuchaeta exigua* and *Vibilia antarctica*. Clusters 1 and

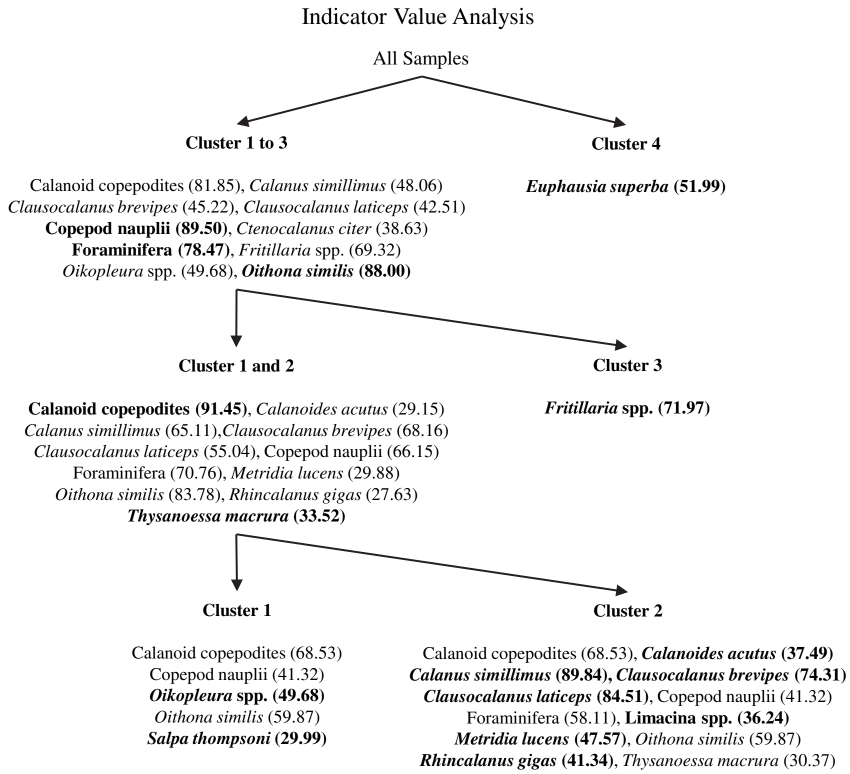

Fig. 5. Results of the Indicator Value (IndVal) analysis for Transects A–D. IndVals were calculated at each level of separation in the cluster analysis (Fig. 4). Only IndVal of ≥25% were used, which meant that a species/taxa was present in ≥50% of samples in a cluster and that its relative abundance in that cluster was ≥50%.

2 had the maximum IndVal for copepod nauplii and *Ctenocalanus citer*. (Fig. 7).

Clusters 1 and 2 separated at 36.43% dissimilarity. Cluster 2 comprised 101 segments from PFZ and IPFZ in 2006, 2008 and 2009. Species richness and total zooplankton abundance were the highest of any cluster (Table 4). *O. similis*, calanoid copepodites and *C. simillimus* were important contributors to total abundance. Three species/taxa were unique to Cluster 2, including the copepods *Candacia maxima*, *Eucalanus* sp. and *N. tonsus*, all of which are species with typically SAZ distributions.

Cluster 1 comprised the AZ in 2006 and 2009. Only *Tomopteris* sp. had a maximum IndVal value, but the abundance of calanoid copepodites, *Fritillaria* spp. *O. similis*, copepod nauplii, *Oikopleura* spp. and *Limacina* spp. were the highest of any cluster (Table 4).

4. Discussion

High zooplankton abundance in the Southern Ocean was mainly attributable to the cyclopoid copepod, *O. similis* and calanoid copepods. This concurs with previous studies which reported that copepods account for >70% of the total abundance (Atkinson and Sinclair, 2000; Foxton, 1956; Pakhomov et al., 2000; Pakhomov and Froneman, 2004; Yamada and Kawamura, 1986). The permanent open ocean zone (POOZ) is generally considered oligotrophic (Banse, 1996; Fiala et al., 1998). *O. similis* are known to consume diatoms, ciliates and heterotrophic dinoflagellates, and can act as coprophagous filters, preventing feces leaving the surface waters (Gonzalez and Smetacek, 1994). Thus, *O. similis* are ideally suited to the low phytoplankton density of the POOZ and were the dominant taxa from PFZ to the AZ. In January, the average species composition of all data from the SO-CPR project during the past 15 years from the Indian Ocean sector of the Southern Ocean, from 48°S to 62°S, shows that *O. similis* (39.8%) and calanoid copepodites (31.2%) were consistently the most abundant zooplankton species/taxa, followed by Foraminiferans (8.7%), *C. simillimus* (5.8%), *C. citer* (3.2%), *Fritillaria* spp. (2.3%), *Limacina* spp. (1.7%), copepod nauplii (1.4%) and *C. laticeps* (1.2%) (Fig. 8). Therefore, the copepod-dominant community

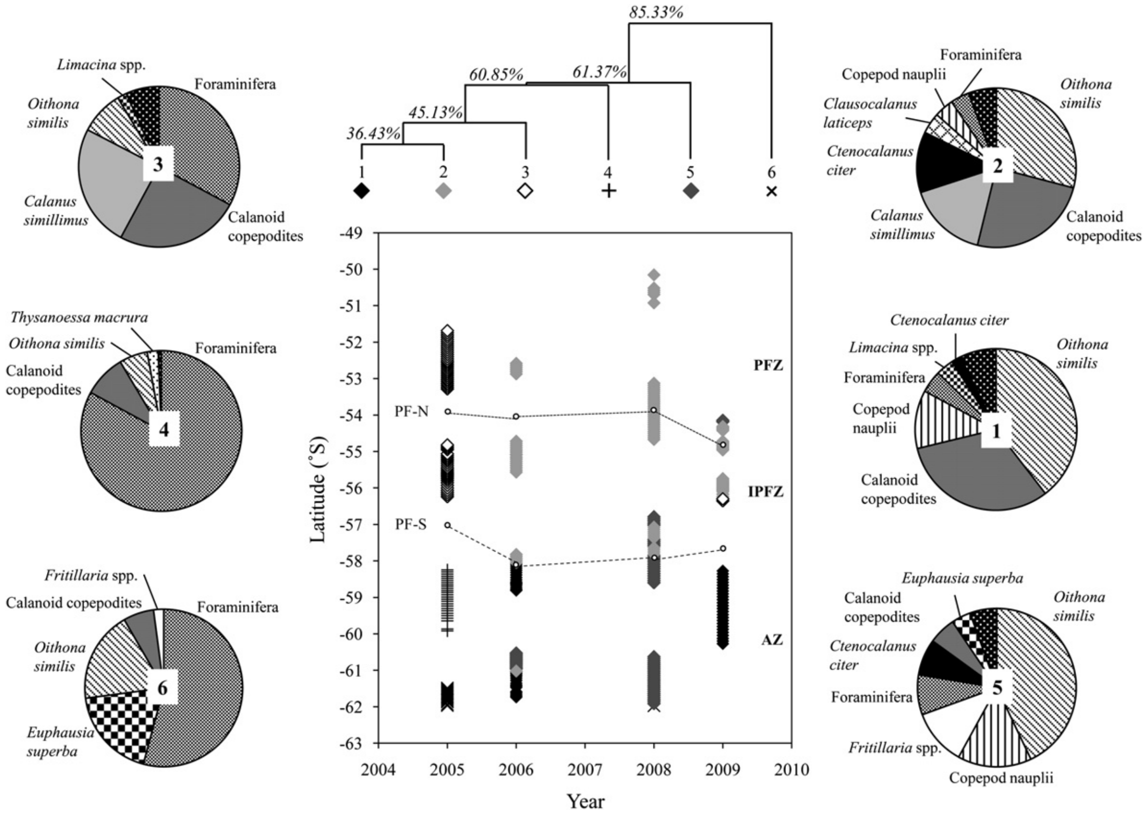

Fig. 6. Results of the cluster analysis for Transects E–H. The upper graph indicates the clusters identified and their level of separation, and the lower panel indicates the spatial and temporal distribution of samples in each cluster. The percentage contribution of major zooplankton groups in each cluster identified from cluster analysis is also shown.

structures observed in the study area were typical of the circumpolar distribution pattern in the permanent open ocean zone of the Southern Ocean.

4.1. Cape Town to Syowa station area transect

Cluster analysis showed that with the exception of the 2008 (Transect C) samples, the PFZ to the northern area of the AZ segments were identified as the same group (Fig. 4). High zooplankton abundance was recorded at the segments near the PF-N in 2005, and north of 57°S in 2006 and 2009 (Cluster 2; Fig. 4). Frontal regions in the Southern Ocean are considered as areas of biological enhancement (Froneman et al., 1995; Lutjeharms et al., 1985; Pakhomov and McQuaid, 1996). The data analysis of all CPR samples collected from the Indian Ocean sector of the Southern Ocean since 1997 shows high zooplankton abundance in the PFZ between the SAF and PF, and in the AZ between the PF and the Southern ACC Front (SACCF) (Hosie et al., 2003). The high zooplankton densities that we observed in the PFZ and AZ are consistent with these previous findings. Zooplankton assemblages in Cluster 2 were dominated by *O. similis* and small copepods species/taxa such as *C. simillimus*, *C. citer*, *C. laticeps* and *M. lucens* and these species/taxa had the maximum IndVal (Fig. 5). In November 1999, the species composition at almost the same transect, from 47°S to 55°S, had a similar species composition (Takahashi et al., 2002). *O. similis* (53.3%) and small calanoid copepods (most likely *Ctenocalanus* spp. and *Clausocalanus* spp.) (15.7%) were consistently the most abundant zooplankton species/taxa, followed by Foraminiferans (10.3%), copepod nauplii (4.9%), *T. macrura* (4.6%), calanoid copepodites (4.2%), *C. simillimus* (2.5%) and appendicularians of genera *Oikopleura* and *Fritillaria* (1.6%).

Total zooplankton abundance and chlorophyll *a* levels were low at Transect C in 2008 (Cluster 3), and this was reflected in the low number of indicator species identified by IndVal analysis (Fig. 5). Features should be represented by the low densities of copepod species/taxa, such as *O. similis* and calanoid

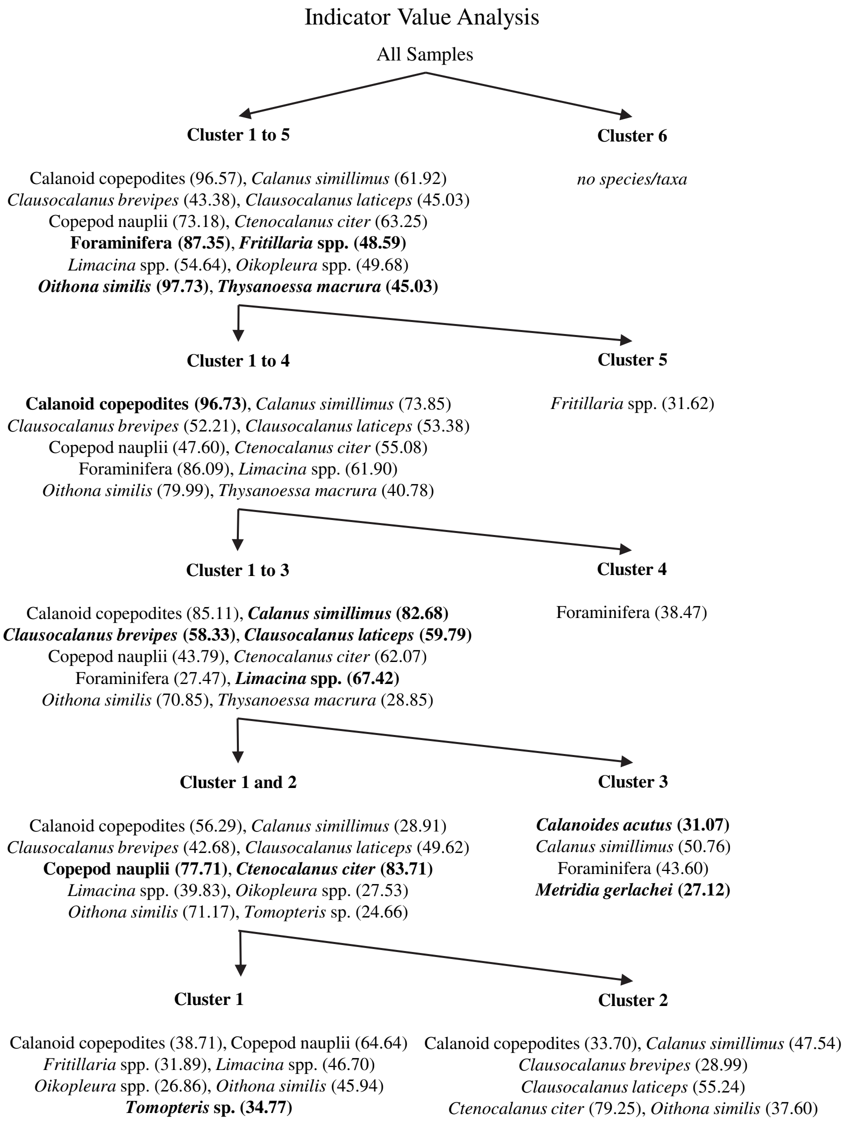

Fig. 7. Results of the Indicator Value (IndVal) analysis of Transects E–H. IndVals were calculated at each level of separation in the cluster analysis (Fig. 6). Only IndVal of ≥25% were used, which meant that a species/taxa was present in ≥50% of samples in a cluster and that its relative abundance in that cluster was ≥50%.

copepodites. In contrast, *Fritillaria* spp. were numerically dominant and they were the only species/taxa with a maximum IndVal (Fig. 5). The high abundance of appendicularians, which was far larger abundance than that of copepods, has been also reported in the Seasonal Ice Zone (SIZ) (Hunt and Hosie, 2005; Tsujimoto et al., 2006). Although appendicularians have been reported from cold waters such as in the southern ACC (Yamada and Kawamura, 1986; Chiba et al., 2001), high abundance in the IPFZ and AZ has not been reported previously. Appendicularians are one of the most abundant members of zooplankton communities in all oceans (Fenaux et al., 1998) and are ideally suited to oceanic oligotrophic conditions (Deibel, 1998). The average of night chlorophyll *a* level was the lowest (0.36 mg m^{-3}) among all transects (Table 2). Therefore, it is not surprising that they were the dominant species/taxa at this time of year.

The samples grouped within Cluster 4 were characterized by the occurrence of *E. superba* and *Calanus propinquus*, which are typical species of Antarctic surface waters (Errhif et al., 1997). Indeed, the average sea surface temperature in Cluster 4 was the lowest (0.71 °C) of any cluster, and zooplankton abundance was also low (ave = 16 ind m^{-3}) (Table 3). Low zooplankton

Table 4
Average within cluster dissimilarity, sea surface temperature, chlorophyll *a*, species richness and abundance levels for the six clusters identified by Cluster Analysis for the transect from the Mawson station area to Fremantle.

	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5	Cluster 6	*F*	*P*-value	
Number of segment	58	101	59	26	58	15			
Sea surface temperature (°C)	2.95	4.58	3.92	1.36	2.98	1.13	No test		
Chlorophyll *a* (mg m^{-3})	0.57	0.51	**0.67**	**0.75**	0.58	0.40	13.08	<0.001	
Species richness (*r*)	**9.91**	**10.59**	**9.24**	3.69	6.03	2.13	145.46	<0.001	
Total abundance (ind m^{-3})	**219.67**	**244.17**	**170.24**	59.50	28.14	3.20	35.46	<0.001	
Species/taxa									
Calanoid copepodites	**69.47**	**60.47**	**42.66**	5.08	1.57	0.20	10.37	<0.001	
Foraminifera	9.69	9.28	**55.93**	**49.35**	2.29	1.73	145.46	<0.001	
Fritillaria spp.	**3.62**	1.54	0.12	0.04	**3.22**	0.07	18.32	<0.001	
Oithona similis	**86.79**	**71.03**	15.03	3.38	12.09	0.60	37.09	<0.001	
Euphausia superba	0.12	0.06	0.03		**1.10**	**0.60**	5.84	<0.001	
Copepod nauplii	**25.60**	**9.58**	0.07	0.12	4.24		97.13	<0.001	
Oikopleura spp.	**2.43**	1.09	0.25	0.08	0.36		9.17	<0.001	
Thysanoessa macrura	0.95	**2.57**	2.08	1.31	0.53		4.32	0.001	
Calanoides acutus	0.33	0.16	**2.07**	0.15			14.47	<0.001	
Calanus simillimus	1.29	**39.47**	**42.14**		0.12		17.27	<0.001	
Clausocalanus brevipes	**3.38**	**3.70**	1.61		0.03		11.25	<0.001	
Clausocalanus laticeps	1.65	**10.43**	1.86		0.07		18.48	<0.001	
Ctenocalanus citer	4.29	**30.17**	0.39		2.09		33.71	<0.001	
Limacina spp.	**7.79**	2.34	3.20		0.19		17.16	<0.001	
Themisto gaudichaudi	0.22	0.26	0.20		0.07		2.20	0.054	n.s.
Tomopteris sp.	**1.59**	0.27	0.02		0.02		14.35	<0.001	
Calanus propinquus	0.07	0.01	0.02				1.53	0.181	n.s.
Euphausia triacantha	0.38	0.07			0.03		5.23	<0.001	
Harpacticoid	0.02	0.10			0.03		2.70	0.021	
Ostracoda	**0.21**	**0.36**			0.05		6.84	<0.001	
Euphausia frigida	0.29		0.29				2.55	0.028	
Rhincalanus gigas	0.70		0.05				1.17	0.324	n.s.
Chaetognath		0.02	0.05				1.47	0.201	n.s.
Euphausia vallentini		0.37	0.51				2.02	0.076	n.s.
Hyperiid		0.06	**0.27**				7.79	<0.001	
Pleuromamma robusta		0.03	0.02				0.59	0.710	n.s.
Salpa thompsoni		0.05	0.10				1.83	0.106	n.s.
Clio pyramidata	0.02				0.02		0.69	0.630	n.s.
Candacia maxima		0.07					2.42	0.036	
Eucalanus sp.		0.02					0.86	0.511	n.s.
Neocalanus tonsus		0.53					3.19	0.008	
Metridia gerlachei			**0.42**				13.96	<0.001	
Metridia lucens			0.05				1.59	0.162	n.s.
Paraeuchaeta antarctica			0.03				1.78	0.117	n.s.
Paraeuchaeta exigua			**0.20**				5.24	<0.001	
Vibilia antarctica			0.02				0.87	0.500	n.s.
Total Species/taxa	20	28	32	8	19	5			
Unique Species/taxa		3	5						

Differences between clusters were investigated by one-way ANOVA and Newman-Keuls multiple range test. Significantly higher abundance levels are in bold. The number of unique species/taxa and total species/taxa recorded percluster are indicated. n.s. = not significant.

abundances are typically recorded in the sea-ice zone south of the SACCF (Hosie et al., 2003; Hunt and Hosie, 2005). The SACCF closely follows the Southwest Indian Ridge (5°W–20°E), and then it turns gradually to the north around 30°E (Fig. 1). Consequently, several fronts are quite close to each other in this region, and the meanders and eddies are generated from the SACCF in this area (Orsi et al., 1995). The various fronts in the Southern Ocean are detected by deep oceanographic observations, and the SACCF can only be properly defined at depths around 500 m (Orsi et al., 1995). Although we did not detect the position of the SACCF, some of the CPR tows in the present study might have crossed the SACCF. Consequently, the cold water samples within the SACCF were separated from the AZ region by cluster analysis.

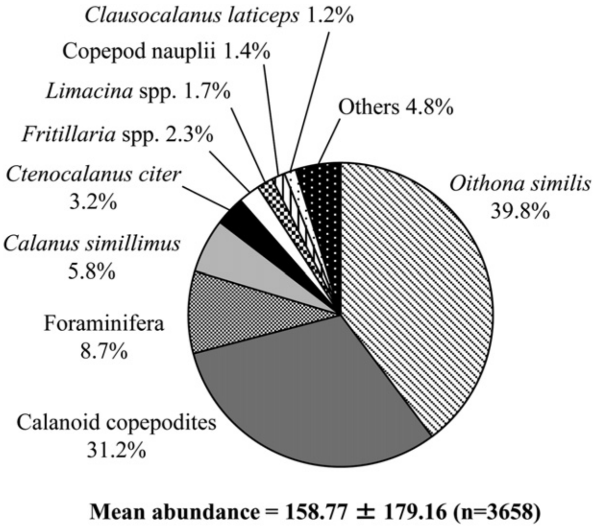

Fig. 8. Average species compositions in January from 48°S to 62°S. The average was calculated using all data from the SO-CPR project in the Indian sector of the Southern Ocean from1997.

4.2. Mawson station area to Fremantle transect

The results from the cluster analysis corresponded with the oceanographic zones in the Cape Town to Syowa station area (Fig. 5). With the exception of the 2005 (Transect E) samples, the PF and IPFZ segments were identified by cluster analysis as the same group (Fig. 6). The similarity of the PFZ/IPFZ assemblages reflected the physical homogeneity of the southern branch of the SAF and the PF-S; the PF-N is a weak biogeographic boundary (Hunt and Hosie, 2005). The PFZ/IPFZ was characterized by the presence of a number of unique species/taxa, including the Sub-Antarctic Zone (SAZ) indicator species, *N. tonsus* (Guglielmo and Ianora, 1995). Zooplankton abundance levels were consistently high and calanoid copepods were important community components (Fig. 6). This finding confirms previous reports that the biomass and abundance of calanoid copepods increase in both the PF area and the PFZ (Atkinson and Sinclair, 2000; Errhif et al., 1997; Pakhomov et al., 2000; Pakhomov and Froneman, 2004; Yamada and Kawamura, 1986). Similar to Cluster 2 in the Cape Town to Syowa station area, with high zooplankton densities, these regions were at the centre of the high abundance of *C. simillimus*, *C. citer* and *C. laticeps* (Fig. 5). *C. simillimus* is an important species in the SAF-PF region because of its high abundance and biomass (Atkinson and Sinclair, 2000; Pakhomov et al., 2000). Small copepods, particularly the Oithonidae and Clausocalanoidae, also dominate zooplankton numbers in the PFZ (Atkinson and Sinclair, 2000; Errhif et al., 1997; Yamada and Kawamura, 1986).

The AZ segments were divided into two groups, one with high zooplankton abundance levels in 2006 and 2009 (Cluster 1) and the other with low densities in 2008 (Cluster 5) (Fig. 6). A feature of Cluster 1 was the high densities of *O. similis*, calanoid copepodites, copepod nauplii, *Limacina* spp. and *Tomopteris* sp. By contrast, Cluster 5 was characterized by low densities of common species/taxa and one indicator species, *Fritillaria* spp. (Fig. 6 and Table 3). There was no difference in chlorophyll *a* levels and sea surface temperature between the two cluster groups (Table 4). It seems that not only the surface environment at the towing time, but also environmental conditions well below the sampling depth of the CPR influenced the zooplankton abundance and community structure at the surface.

Clusters 3, 4, and 6 comprised the 2005 segments; Foraminiferans were numerically dominant, accounting for 32.9, 82.9 and 54.2%, respectively, of total zooplankton abundance in each cluster (Fig. 6). The same trend has been observed in the SAZ and PFZ/IPFZ along 140°E collected in samples from February to March 2002 (Hunt and Hosie, 2006b). The abundance of planktonic Foraminifera is controlled by the fertility of the ocean surface waters (Murray, 1991). They are opportunistic and prey on whatever food organisms they encounter (i.e. omnivorous). Thus, they prefer areas rich in nutrients, phytoplankton and zooplankton. Surface chlorophyll *a* levels were high in 2005 with average of 0.64 mg m^{-3} (Fig. 3).

4.3. Implications

An important observation was the occurrence of two assemblages, one dominated by appendicularians of the genera *Fritillaria* spp. in 2008 (Transect C) and the other with an abundance of Foraminiferans in 2005 (Transect E). We have no evidence to suggest how often these major changes in abundances occur. Whether abundance shifts such as those observed here are cyclical or more sporadic requires further monitoring by the SO-CPR Survey. However, it is likely that changes to appendicularians and foraminiferans abundances will have impacts on food web structure with flow-on effects to higher predators.

Appendicularians play an important role in biogeochemical cycling (Honjo et al., 2000). They can concentrate bacteria, ciliates, flagellates and particulate matter to approximately 100–1000 times the ambient concentration of the delicate filtering mesh of their gelatinous houses (Davoll and Silver, 1986). The discarded houses are platforms for the production of marine snow. Moreover, both the discarded houses and the appendicularians themselves are consumed by carnivorous zooplankton and fish (Gorsky and Fenaux, 1998). They are particularly fragile and are often destroyed or severely damaged when collected in standard plankton nets, and are thus likely to be considerably underestimated (Gorsky and Fenaux, 1998).

Foraminiferans are a large group of protists; they produce a shell made of calcium carbonate. Because calcium carbonate is susceptible to dissolution in acidic conditions, Foraminiferans may be strongly affected by a changing climate and ocean acidification. However, data from the CPR survey of the North Atlantic suggest that certain calcareous taxa including Foraminiferans are increasing in abundance, a trend associated with climate shifts in Northern Hemisphere temperatures (Edwards et al., 2009). On the other hand, evidence from Foraminiferans core records from the Southern Ocean indicates that shell weights are being affected by acidification (Moy et al., 2009).

CPR surveys provide information on the fine structure of surface micro- and mesozooplankton assemblages, and CPR is an ideal method to monitor these vulnerable organisms as part of long-term monitoring programs. Continuation of CPR surveys and accumulation of data will contribute to models being developed to determine the consequences of climate change on the ecosystem and the rate of change.

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