

Spatio-temporal variability of zooplankton community structure off east Antarctica (90 to 160° E)

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ABSTRACT: Spatio-temporal variability of zooplankton community structure off east Antarctica (90 to 160° E) was studied from 1988 to 1996 based on samples collected by the Japanese icebreaker 'Shirase'. Three community groups with distinctive species compositions were obtained by cluster analysis. Group 1 was defined as the 'Subantarctic community' because it appeared exclusively north of the Polar Front, and indicator species of the group included *Eucalanus longiceps* and *Limacina retroversa*, which are typical subantarctic species. Groups 2a and 2b occurred in the Antarctic Circumpolar Current (ACC), and are thus defined as the 'ACC communities'. All indicator species for Group 2b, including large copepods, *Calanoides acutus*, *Calanus propinquus* and *Metridia gerlachei*, were also common indicators for Group 2a. In Group 2a, smaller copepods (small calanoids, cyclopoids and poecilostomatoids) and non-copepod herbivores were also indicators. Total abundance was markedly high in Group 2a, and copepods numerically dominated all 3 groups (>70% in Group 1, >80% in 2a, >90% in 2b). The longitudinal distribution pattern of Groups 2a and 2b varied between years, although they occurred along the same latitude. Multiple-regression analysis on environmental variables and distribution of the groups demonstrated that Group 2a tended to occur in relatively warm water masses with high chlorophyll *a* and low silicate concentrations. While Group 2b occurred in colder areas with low chlorophyll *a* concentrations, the results of this study suggest that the occasional intrusion of northern water further south caused by meandering of the ACC might have been responsible for the observed distribution patterns of the zooplankton community.

KEY WORDS: Zooplankton · Community structure · Multivariate analysis · JARE · Antarctic Ocean · Antarctic Circumpolar Current

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INTRODUCTION

Antarctic regions are areas where the influence of global climate change such as global warming may appear first and be most marked (Zwally 1994). As plankton lifecycles are much shorter than these of animals at higher trophic levels, plankton community structure tends to shift quickly in response to the

changes in ambient environmental conditions. Tanimura et al. (1999) pointed out that zooplankton community structure would be useful as an indicator of environmental variability in the Antarctic Ocean.

In the Antarctic Peninsula/Weddell Sea regions, many systematic approaches have been made to analyze the interaction between zooplankton communities and meso-scale environmental variability, particularly in recent years (Boysen-Ennen & Piatkowski 1988, Piatkowski 1989, Atkinson et al. 1990, Siegel & Piatkowski 1990, Boysen-Ennen et al. 1991, Park & Wor-

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muth 1993, Weeks et al. 1995, Fransz & Gonzalez 1997). Using multivariate analyses, Hosie (1994) and Hosie et al. (1997) studied zooplankton communities from 1981 to 1996 in Prydz Bay, east Antarctica, in relation to environmental variability. On the other hand, only a few zooplankton community studies have been conducted between 90 and 160° E (Maruyama et al. 1982, Kawamura 1986, 1987, Hosie et al. 2000); and with the exception of Hosie et al.'s study, all described community structure without statistical analyses of its interaction with environmental variability.

Monitoring or routine observation is difficult in the remote Antarctic Ocean, where research opportunities are limited both in time and space. However, even in the Antarctic Peninsula/Weddell Sea regions, for which much knowledge has been accumulated, most studies focused on seasonal or local changes, or comparisons between 2 or 3 consecutive years. Multi-year observation is required to detect interactions between zooplankton-environment variability. The Japanese Antarctic Research Expedition (JARE) has routinely conducted oceanographic/biological surveys including plankton-net sampling on the way to (and from) the Japanese Antarctic base off east Antarctica during every austral summer since 1972. Using the zooplankton samples taken during the surveys, Takahashi et al. (1998) reported that zooplankton biomass (wet weight) tended to fluctuate in a 4 to 6 yr cycle. With the same samples, Tanimura et al. (1999) found a positive correlation between plankton biomass and water temperature. These studies, however, were only based on wet

weight data and did not explain the variation in species composition of zooplankton communities. Moreover, since these samples were taken in different months and from various latitudinal locations every year, comparison and interpretation of the results are difficult.

From the 1987/88 to 1995/96 seasons, JARE's plankton surveys were conducted along an east-west transect at approximately the same latitudinal locations in the Antarctic Circumpolar Current (ACC) area off east Antarctica. Taking the opportunity to use the multi-year samples, we conducted multivariate analyses on the spatio-temporal variability of the zooplankton community structure. The goals of this study were to elucidate the characteristics of zooplankton communities in the ACC area off east Antarctica and to clarify how community structure changes in response to changes in meso- and large-scale environmental conditions.

MATERIALS AND METHODS

Sampling and sample processing. Surveys were conducted in March from 1987/88 to 1995/96 during the JARE 29 to 37 cruises by the Japanese icebreaker 'Shirase' along an east-west transect at ca 64° S between 90 and 160° E, and a north-south transect at ca 150° E to 50° S. No observations were made in this area in 1991. The survey area and location of the sampling stations are shown in Fig. 1 (see also Table 8). Sampling was conducted in the daytime for all years. Zooplankton

were collected by a NORPAC net (mesh size: 330 μ m, mouth diameter: 0.45 m) equipped with a flow meter. The net was hauled vertically from an approximate depth of 150 m. The maximum depth reached was estimated from the wire angle and wire paid out. On some occasions, when the flow meter did not work (3 of a total of 44 hauls), the water volume filtered was estimated by multiplying the effective mouth area of the net by the maximum depth reached.

All zooplankton were preserved in 5% neutral formalin within 5 min after collection. Each sample was divided into 2 using a Motoda plankton splitter (Motoda 1959): one-half was used for wet weight measurements (Takahashi et al. 1997), the other for determining for zooplankton species composition (present study). Zooplankton were sorted to species, or lowest possible taxon when species identification was difficult, and counted. Counts of all species were converted into number of individuals (ind.) per m³ for each station. Since not only *Euphausia superba* but also *Salpa thompsoni* are considered important keystone species in the Antarctic marine ecosystem (Nishikawa et

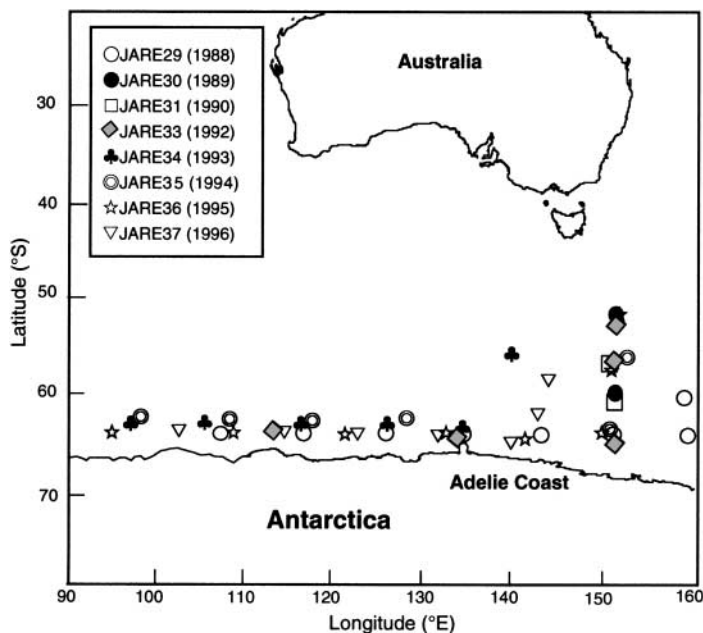


Fig. 1. Location of sampling stations. JARE: Japanese Antarctic Research Expedition

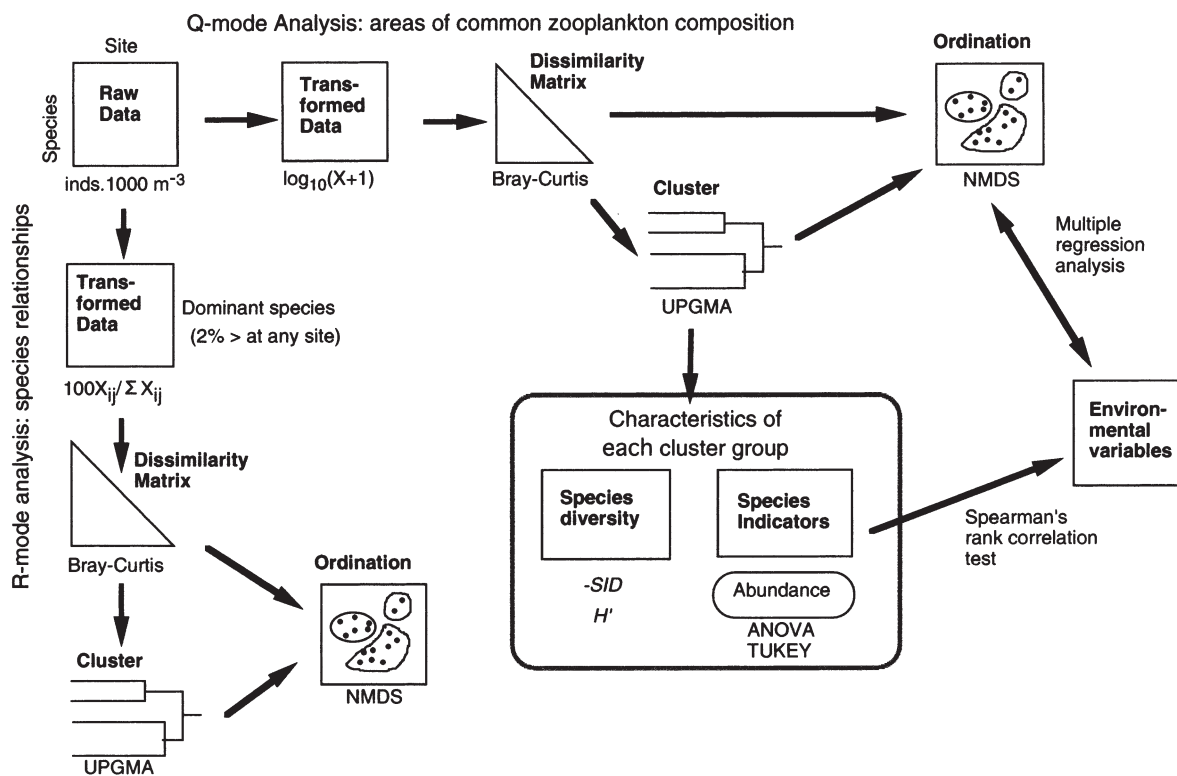


Fig. 2. Diagram of steps used in multivariate analyses. H' , SID : species diversity indices of Shannon & Weaver (1949) and Simpson (1949) respectively

al. 1995, Chiba et al. 2000), abundances (ind. 1000 m^{-3}) were estimated for each maturity stage for the 2 species. We observed many individuals with a dead embryo in their body. Assuming that such embryos had suffered disrupted development, we categorized them as 'Stage X', following the criteria of Chiba et al. (1999).

Data analyses. Multivariate analysis is the perhaps the best method to reveal the complex interactions between community structure changes and biotic/abiotic factors when using data taken on various occasions and thus displaying spatio-temporal variability (Field et al. 1982, Ludwig & Reynolds 1988).

The analytical methods are summarized in Fig. 2, and are based on those in Hosie (1994) and Hosie et al. (1997), which was modified from Field et al. (1982) and Kruskal & Wish (1978). Computer software, BIOSTAT Version 3.5 (Sigma Soft, California) was employed for analyses.

Q-mode (site similarity) analysis: Numerical abundance data were converted into numbers of individuals per 1000 m^{-3} and transformed by $\log_{10}(x+1)$ prior to analysis. A dissimilarity matrix between stations was constructed based on differences in species composition using the Bray-Curtis index (Bray & Curtis 1957). The matrix was analyzed by cluster analysis coupled

with the unweighted pair-group method using arithmetic means (UPGMA) to classify the stations into several groups with similar community composition. The characteristics of each cluster group were examined in terms of composition of major taxa, indicator species, and species diversity indices (Simpson's SID [Simpson 1949] and H' [Shannon & Weaver 1949]). The reciprocal value of SID ($-SID$) was used in this study to simplify comparison with H' . Diversity was calculated from averaged values of the raw data (ind. 1000 m^{-3}) for each group. Indicator species were determined based on differences in their mean abundances between the groups. The difference was tested for each species by ANOVA, using the Tukey multiple-range test, and species significantly abundant in a specific group(s) were defined as indicators of that group(s).

To verify the cluster analyses, stations were plotted on a 2-dimensional map by non-metric multidimensional scaling (NMDS) methods (Ludwig & Reynolds 1988) based on the same dissimilarity matrix. Goodness of fit of the derived map was verified by the stress-value criteria constructed by Kruskal & Carmore (1971, in: Domanski 1984). Both a multiple-regression analysis between the ordination scores for each station and environmental variables and a Spearman's rank-correlation test were

applied to clarify which environmental factors might influence zooplankton community structure. The variables used are listed on Table 1. JARE Data Reports were referred to for hydrographic information (Ito & Ishii 1989, Ikeda & Matsumoto 1991, Ikeda & Kojima 1992, Tanaka & Noguchi 1995, Hashima & Namiki 1997, Okano & Ogawa 1998, Oikawa & Miura 1999, Yoritake & Namiki 1999), and Nimbus-7 SMMR and DMSP SSM/I passive microwave data (National Snow and Ice Data Center, Boulder, Colorado, 1998a,b) were referred to for sea-ice conditions. The northern extent of the sea-ice for each sampling station was a monthly average value along the longitudinal lines on which the JARE sampling stations were located. Areas with more than 15% sea-ice coverage were defined as ice-covered areas. Sea-ice usually reaches its maximum extent in October and its minimum in February off east Antarctica, and its retreat is most rapid in December. Therefore, the extent of the sea-ice in October, December and February was selected for comparison.

R-mode (species association) analysis: Mutual associations between species were investigated by R-mode (inverse type) analysis (Fig. 2) (Field et al. 1982). Only dominant species (more than 2% of total abundance on any one occasion) were examined. Species abundance data were standardized prior to analysis as follows:

$$Y_{ij} = 100X_{ij} / \sum_{j=1}^n X_{ij}$$

Table 1. Environmental variables used for multiple regression analysis and Spearman's rank-correlation test

Hydrography
Source: JARE Data Reports
Surface chlorophyll a concentration
Water temperature (surface)
Water temperature (0–200 m mean)
Salinity (surface)
Salinity (0–200 m mean)
Nitrate concentration (0–100 m mean)
Nitrate concentration (0–200 m mean)
Phosphate concentration (0–100 m mean)
Phosphate concentration (0–200 m mean)
Silicate concentration (surface)
Silicate concentration (0–100 m mean)
Silicate concentration (0–200 m mean)
Depth of mixed layer
Sea ice conditions
Source: Nimbus-7 SMMR and DMSP SSM/I passive microwave data
Maximum sea-ice extent (Oct)
Minimum sea-ice extent (Feb)
Distance of ice-edge retreat (Oct–Feb)
Distance of ice-edge retreat (Dec–Feb)
Distance of ice formation (Feb–Mar)

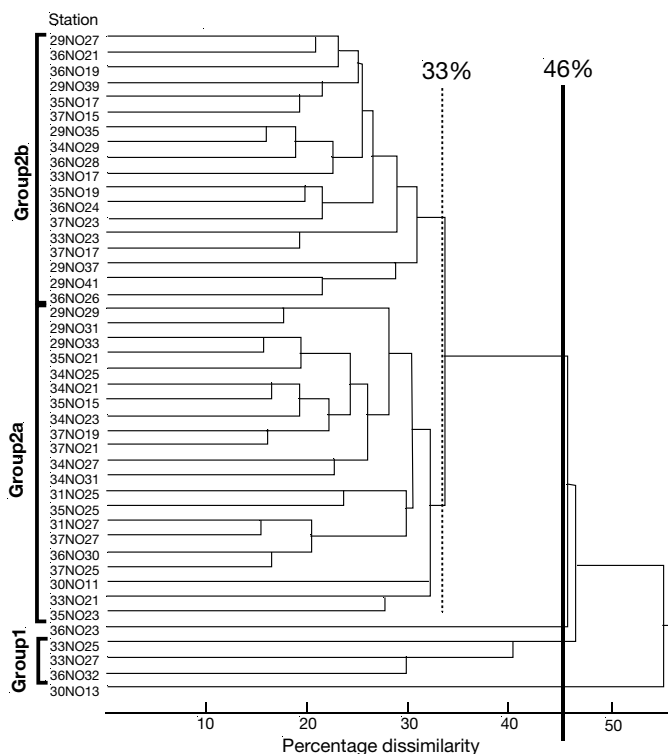


Fig. 3. Cluster diagram of sampling stations based on zooplankton species and revealing 3 zooplankton community groups

where X_{ij} = abundance of the i th species in the j th sample, $\sum_{j=1}^n X_{ij}$ = summed abundance of the i th species over all samples, and Y_{ij} = the corresponding standardized score. Cluster analysis was undertaken to identify similarity in occurrence between species, followed by NMDS ordination using the same procedure as for the Q-mode analysis.

RESULTS

Q-mode (site similarity) analysis

Zooplankton belonging to 41 genera and 53 species were identified. The numerical abundance of the total zooplankton varied from 2 to 3830 ind. m^{-3} (mean \pm SD: 286 ± 615 ind. m^{-3}), and wet weight (Takahashi et al. 1997) ranged from 6 to 3277 mg m^{-3} (mean \pm SD: 214 ± 509 mg m^{-3}).

Zooplankton community groups

Two distinctive zooplankton community groups were identified at the 46% dissimilarity level by cluster analysis (Fig. 3). Group 2 was further divided into 2 subgroups, Groups 2a and 2b, at the 33% dissimilarity level. The respective zooplankton groups formed clusters and did not

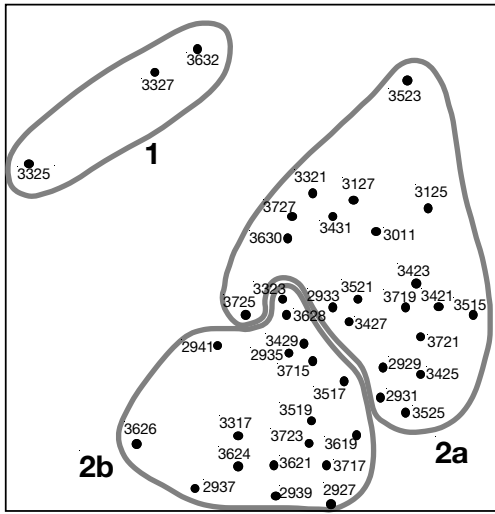


Fig. 4. NMDS ordination of sampling stations with the 3 zooplankton community groups (Fig. 3) derived by cluster analysis superimposed. Numbers are station nos. (e.g. 2927 = 29NO27:27th sampling station of JARE29)

overlap each other on the NMDS 2-dimensional plot (Fig. 4), validating the results of the cluster analysis. The stress value for the NMDS plot was 19% which is 'good' to 'fair' in the criterion range. Thus, the 2-axis ordination obtained is considered sufficient to collectively summarize the similarity (dissimilarity) of zooplankton community structure between the groups.

Group 1, which consists of 3 loosely linked stations, appeared exclusively to the north of 60° S (Fig. 5), whereas Groups 2a and 2b occurred on the same latitudes along the east-west transect, although the former included more stations of lower latitude than the latter. Longitudinal distribution of Groups 2a and 2b varied between years: all stations belonged to Group 2a in 1993, while Group 2b was dominant in 1995.

Abundance and composition of major zooplankton taxa

The numerical abundance of zooplankton was markedly higher in Group 2a than in Groups 1 and 2b

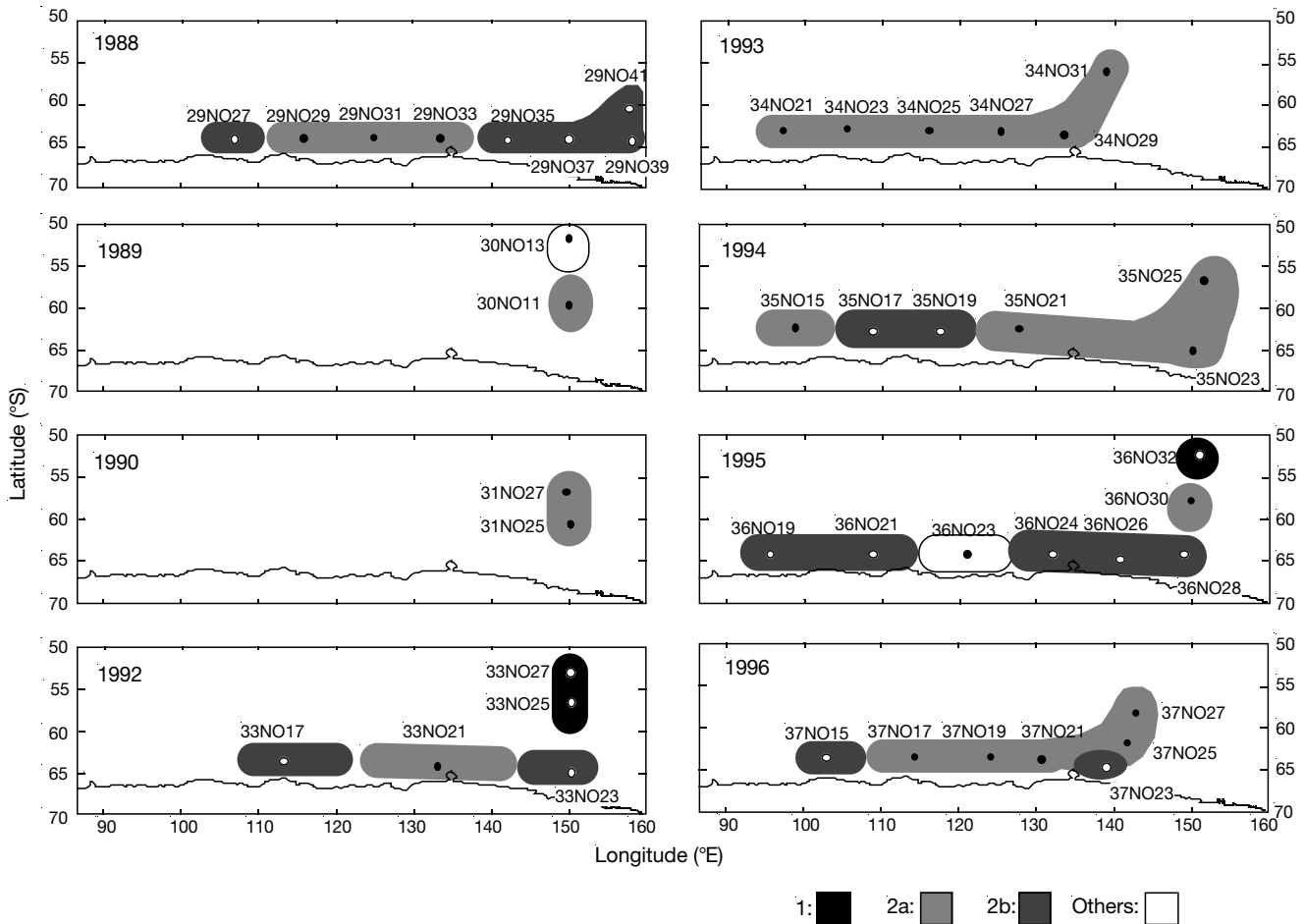


Fig. 5. Geographical distribution of zooplankton community groups derived by cluster analysis

Table 2. Mean numerical abundance (ind. m⁻³), mean wet weight (mg m⁻³) and composition of major zooplankton taxa (%) for each zooplankton community group derived by cluster analysis. Takahashi et al. (1997) was referred to for wet weight data. -: not collected

	1	Group 2a	2b
(n)	(3)	(21)	(18)
Mean numerical abundance (SD)	66 (±51)	544 (±824)	52 (±38)
Mean wet weight (SD)	56 (±31)	399 (±696)	47 (±57)
Composition of major zooplankton taxa			
Copepods	71.5	83.8	91.0
Poecilostomatoid	(0.9)	(5.9)	(3.3)
Harpacticoid	(0.1)	(1.2)	-
Cyclopoid	(5.6)	(35.5)	(28.8)
Calanoid	(64.9)	(41.2)	(58.9)
Appendicularians	<1.0	1	3.9
Euphausiids	2.8	<1.0	<1.0
Ostracods	13.0	<1.0	<1.0
Pteropods	6.9	10.0	<1.0
Chaetognaths	4.0	<1.0	3.4
Others	1.5	1.7	<1.0

(Table 2). Wet weight showed a similar distribution pattern among the groups. The 6 major taxa comprised nearly 98% of total abundance, with copepods dominating other zooplankton by 70 to 90% of total abundance in all groups. The proportion of smaller copepods such as cyclopoids and poecilostomatoids increased in Groups 2a and 2b, and was particularly large in the former.

Indicator species

Twenty-six zooplankton species were identified as comprising more than 2% of total abundance at any one sampling site, and were thus defined as 'dominant species'; these were examined for indicator species and species associations (Table 3). Three, 15 and 5 indicator species (taxon) were identified for Groups 1, 2a and 2b, respectively (Table 4). Only 2 species and 1 taxon (*Eucalanus longiceps*, *Limacina retroversa* and ostracods) were more abundant and appeared more frequently in Group 1 than the other groups. Indicators for Group 2a were 14 species and a taxon including 4 major pelagic copepods in the ACC area (*Calanoides acutus*, *Calanus propinquus*, *Metridia gerlachei* and *Rhincalanus gigas*), smaller copepods and non-copepod herbivores such as *Clio pyramidata* and *Pelagobia longicirrata*. All 5 indicator species in Group 2b (*C. acutus*, *C. propinquus*, *Eukrohnia hamata*, *Haloptilus oxycephalus*, *M. gerlachei*) were also indicators for Group 2a.

Species diversity

Both species diversity indices, *-SID* and *H'*, varied between groups in a similar manner (Fig. 6). The diversity was lowest and species richness (number of species observed) was poor in Group 1. Group 2b showed higher diversity than Group 2a, although the number of species observed was similarly large in these 2 groups.

NMDS ordination and multiple-regression analysis

As indicated by both the cluster dendrogram (Fig. 3) and the NMDS ordination plot (Fig. 4), Group 1 displayed considerable dissimilarity with Groups 2a and 2b. Since stations belonging to Group 1 were located exclusively at a lower latitude, while Groups 2a and 2b appeared in the high Antarctic Water (Fig. 5), it is no wonder that the zooplankton species in Group 1 differed from those in the other groups.

Table 3. List of dominant zooplankton species (taxa) (>2% of total numerical abundance on any one occasion) and abbreviation used in Table 7 and Figs. 8 & 9

Taxon	Abbreviation
Appendicularians	<i>Ap</i>
<i>Calanoides acutus</i>	<i>Ca</i>
<i>Calanus propinquus</i>	<i>Cp</i>
<i>Calanus simillimus</i>	<i>Cs</i>
<i>Clausocalanus laticeps</i>	<i>Cl</i>
<i>Clio pyramidata</i>	<i>Cy</i>
<i>Ctenocalanus citer</i>	<i>Cc</i>
<i>Eucalanus longiceps</i>	<i>El</i>
<i>Euchaeta antarctica</i>	<i>Ea</i>
<i>Eukrohnia hamata</i>	<i>Eh</i>
<i>Haloptilus oxycephalus</i>	<i>Ho</i>
Harpacticoids	<i>Ha</i>
<i>Limacina helicina</i>	<i>Lh</i>
<i>Limacina retroversa</i>	<i>Lr</i>
<i>Metridia gerlachei</i>	<i>Mg</i>
<i>Microcalanus pygmaeus</i>	<i>Mp</i>
<i>Oithona frigida</i>	<i>Of</i>
<i>Oithona similis</i>	<i>Os</i>
<i>Oncaea antarctica</i>	<i>Oa</i>
Ostracods	<i>Ot</i>
<i>Pelagobia longicirrata</i>	<i>Pl</i>
<i>Rhincalanus gigas</i>	<i>Rg</i>
<i>Sagitta gazellae</i>	<i>Sg</i>
<i>Salpa thompsoni</i>	<i>St</i>
<i>Scolecithricella minor</i>	<i>Sm</i>
<i>Thysanoessa macrura</i>	<i>Tm</i>

Table 4. Mean numerical abundance (ind. 1000 m⁻³) of dominant species in each zooplankton community group, derived by cluster analysis, and results of ANOVA using Tukey multiple-range test. Abundance was transformed by log₁₀(x+1). Species with mean abundance that differed significantly between groups are in **bold** (**p < 0.01). For each species (taxon), cluster group(s) in which its abundance was significantly higher than in other groups was defined by Tukey multiple-range test, and is underlined (p < 0.05)

Species (or taxa)	Abundance in cluster groups			F	p
	1	2a	2b		
Appendicularians	1.58	2.74	2.13	1.45	
<i>Calanoides acutus</i>	0.00	<u>3.75</u>	<u>3.45</u>	53.90	**
<i>Calanus propinquus</i>	0.00	<u>3.43</u>	<u>3.24</u>	20.10	**
<i>Calanus simillimus</i>	3.91	1.97	1.33	2.56	
<i>Clausocalanus laticeps</i>	2.69	2.09	1.53	0.31	
<i>Clio pyramidata</i>	0.00	<u>1.80</u>	0.18	9.87	**
<i>Ctenocalanus citer</i>	3.53	<u>4.63</u>	3.75	8.64	**
<i>Eucalanus longiceps</i>	<u>1.70</u>	0.00	0.00	26.20	**
<i>Euchaeta antarctica</i>	1.83	1.90	1.62	0.25	
<i>Eukrohnia hamata</i>	1.27	<u>3.41</u>	<u>2.94</u>	12.90	**
<i>Haloptilus oxycephalus</i>	0.00	<u>2.46</u>	<u>1.83</u>	11.10	**
Harpacticoids	1.31	1.10	0.20	2.68	
<i>Limacina helicina</i>	0.00	1.59	0.39	3.06	
<i>Limacina retroversa</i>	<u>3.28</u>	1.14	0.00	8.97	**
<i>Metridia gerlachei</i>	2.41	<u>4.10</u>	<u>3.64</u>	8.89	**
<i>Microcalanus pygmaeus</i>	1.05	<u>3.24</u>	2.39	13.90	**
<i>Oithona frigida</i>	3.20	<u>4.16</u>	3.02	20.70	**
<i>Oithona similis</i>	2.77	<u>4.87</u>	3.71	24.50	**
<i>Oncaea antarctica</i>	2.71	<u>4.18</u>	2.45	18.30	**
Ostracods	<u>3.37</u>	<u>2.91</u>	0.88	19.20	**
<i>Pelagobia longicirrata</i>	0.00	<u>2.06</u>	0.70	5.46	**
<i>Rhincalanus gigas</i>	2.23	<u>3.71</u>	2.89	16.70	**
<i>Sagitta gazellae</i>	1.92	1.53	0.98	1.48	
<i>Salpa thompsoni</i>	0.00	0.25	0.35	0.26	
<i>Scolecithricella minor</i>	2.77	<u>3.51</u>	2.99	10.80	**
<i>Thysanoessa macrura</i>	2.13	2.53	1.91	1.84	

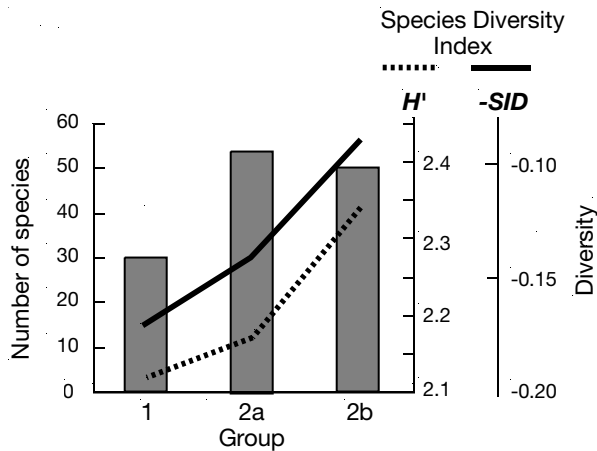


Fig. 6. Number of species observed and species diversity revealed by the 2 diversity indices H' and -SID for each zooplankton community group

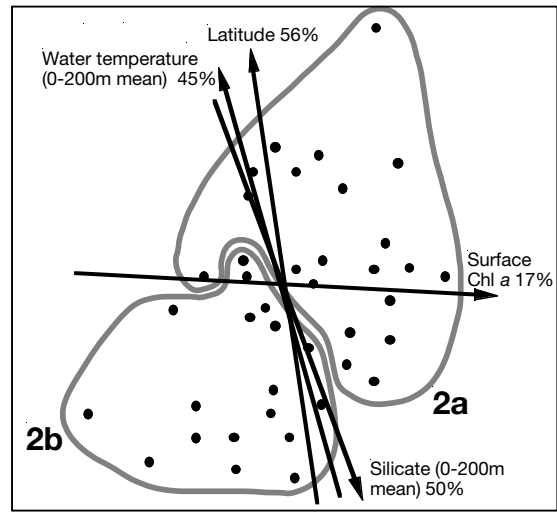


Fig. 7. NMDS ordination of sampling stations with Zooplankton Community Groups, 2a and 2b. Arrows indicate multiple regressions between ordination scores and environmental variables which differ significantly between Groups 2a and 2b

To reveal differences in environmental conditions and zooplankton communities between Group 2a and 2b (which were at the same latitude), Group 1 was excluded from the multiple-regression test.

Eight environmental variables displayed a significant multiple regression with the NMDS ordination scores (Table 5). Among these, 4 variables which actually differentiated Groups 2a and 2b, latitude, silicate concentration (0 to 200 m mean), water temperature (0 to 200 m mean), and surface chlorophyll a concentration, were identified by ANOVA (Table 6); these are indicated by arrows in Fig. 7. The direction of the arrows indicates that Group 2a occurred in lower-latitude areas (that were warmer, and had a lower silicate concentration and higher chlorophyll a concentration) than Group 2b.

Spearman's rank-correlation test

Among the 9 species (taxa) which were indicators for only Group 2a, the abundance of 7 species (*Ctenocalanus citer*, *Scolecithricella minor*, *Oncaea antarctica*, *Oithona frigida*, ostracods, *Rhincalanus gigas* and *Clio pyramidata*) showed a significant positive correlation with water temperature and a negative correlation with silicate concentration (Table 7). The abundances of the other 2 species, *Oithona similis* and *Pelagobia longicirrata*, were also negatively correlated with silicate concentration, but no correlation was observed with water temperature. The abundances of *Calanoides acutus*, *Calanus propinquus* and *Haloptilus oxy-*

Table 5. Results of multiple-regression analysis between environmental variables and NMDS scores on the 2-dimensional ordination plot for sampling stations in Groups 2a and 2b (Fig. 7). Of the environmental variables in Table 1, 1 from a pair that displayed a simple correlation of >0.800 (i.e. sea-surface temperature and 0 to 200 m mean water temperature) was excluded prior to the analysis. *F*: percentage variance in zooplankton community ordination which can be explained by the variable; Adjusted R^2 : adjusted coefficient of determination which gives the fraction of the variance accounted for by the explanatory variable. For ANOVA between regression and residuals: *** $p < 0.005$, ** $p < 0.001$, * $p < 0.05$, ns = not significant (df = 2, 38)

Variable	Direction cosine		Adjusted R^2	<i>F</i>	<i>p</i>
	<i>x</i>	<i>y</i>			
Latitude	-0.193	0.981	0.56	24.93	***
Silicate concentration (0–200 m mean)	0.431	-0.902	0.50	20.07	***
Water temperature (0–200 m mean)	-0.310	0.951	0.45	16.79	***
Distance of sea-ice formation (Feb–Mar)	-0.847	0.531	0.35	11.14	***
Longitude	-0.778	0.629	0.30	9.27	***
Depth of mixed layer	-0.452	0.892	0.21	6.10	**
Surface chlorophyll <i>a</i> concentration	0.995	-0.105	0.17	4.75	*
Salinity (0–200 m mean)	0.388	-0.922	0.12	3.55	*
Nitrate concentration (0–200 m mean)	0.165	-0.986	0.02	1.47	ns
Sea-ice extent from coast (Feb)	-0.777	0.629	0.01	1.18	ns
Nitrate concentration (0–100 m mean)	0.043	-0.999	0.00	1.06	ns
Sea-ice extent from coast (Oct)	0.987	-0.162	0.00	0.96	ns
Sea-ice retreat (Oct–Feb)	-0.967	-0.255	0.00	0.79	ns
Phosphate concentration (0–200 m mean)	-0.770	0.638	0.00	0.75	ns
Sea-ice retreat (Dec–Feb)	0.663	0.749	0.00	0.65	ns
Year	0.349	0.937	0.00	0.07	ns
Salinity (surface)	-0.664	0.747	0.00	0.02	ns

cephalus, which were indicators for both Group 2a and Group 2b, were negatively correlated to the extent of the sea-ice formation from February to March. Only *C. propinquus* showed significant negative correlations with water temperature and extent of the ice-edge retreat from December to February.

R-mode (species association) analysis

Cluster analysis divided 26 dominant zooplankton species (with $>2\%$ of the total abundance at any one sampling site) into 2 groups, A and B, with 3 ungrouped individual species (taxa) at the 77% dissimilarity levels (Fig. 8). The stress value of the NMDS plot (Fig. 9) was 13% which is 'good' to 'fair' in the criterion range (Kruskal & Carmore 1971, in: Domanski 1984). Most of the indicator species of Groups 2a and 2b derived by Q-mode analysis were included in Group A on the plot—further evidence of their close association. In particular, smaller calanoids such as *Ctenocalanus citer*, *Microcalanus pygmaeus* and *Scolecithriclella minor*, cyclopoids and poecilostomatoids formed a tight cluster. Group B consisted of the large chaetognath *Sagitta gazellae*, the carnivorous copepod *Euchaeta antarctica*, and appendicularians. Harpacticoids, *Eucalanus longiceps* and *Salpa thompsoni* showed no close associations with any other species.

Euphausia superba and *Salpa thompsoni*

Both *Euphausia superba* and *Salpa thompsoni* were observed at only a few stations, and at only 1 station together (Table 8). Larval *E. superba* appeared at 6 stations, with a maximum abundance of 513 ind. 1000 m^{-3} in 1996, while no adults were collected. All individuals collected were Calyptopsis I stage, except at Stns 35NO25 and 37NO21, which had Furcilia at the former and ca 30% Calyptopsis II individuals at the latter.

Salpa thompsoni occurred at 5 stations, with a maximum abundance of 1206 ind. 1000 m^{-3} in 1992. All individuals were aggregate forms of Maturity Stage X (Chiba et al. 1999), which possessed a dead embryo. *S. thompsoni* appeared exclusively east of 130°E .

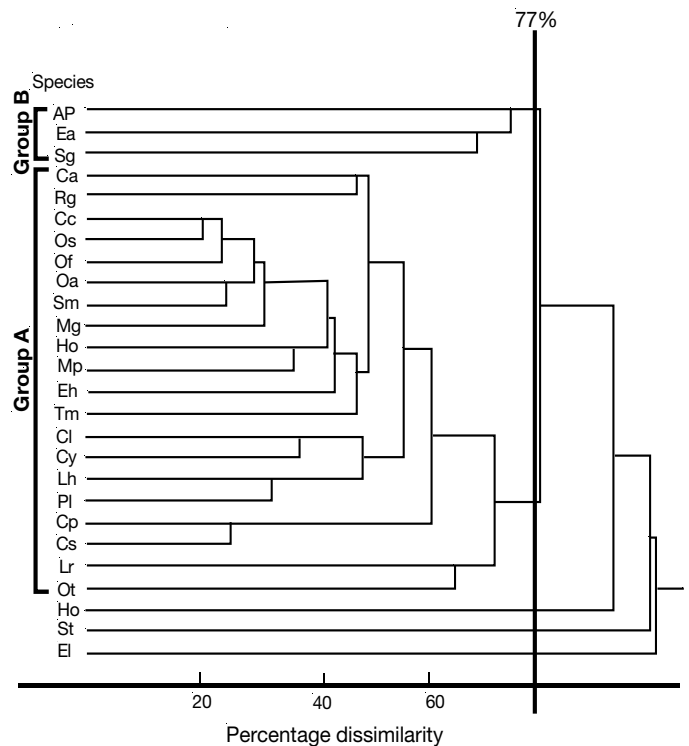


Fig. 8. Cluster diagram of dominant species ($>2\%$ of total numerical abundance on any one occasion) based on association of their occurrence. Species abbreviations as in Table 3

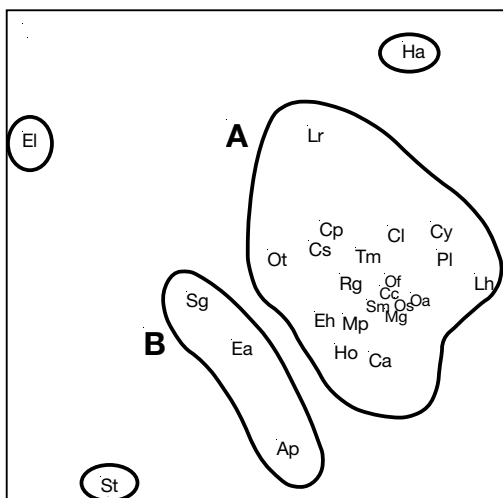


Fig. 9. NMDS ordination of dominant zooplankton species. Species groups (A and B) derived by cluster analysis (Fig. 8) are superimposed. Species abbreviations as in Table 3

DISCUSSION

Characteristics of zooplankton community

Water mass structure and community distribution

We observed 2 zooplankton community groups with distinctive species composition and geographical distribution: Groups 1 and 2. The polar front is usually located around 56° S along 150° E (Belkin & Gordon 1996), and subantarctic water is well characterized by a sharp decline in silicate concentration (Ishino 1981). Comparing the latitudinal location of stations belonging to Group 1 (Fig. 5) with the plots of sea-surface temperature and silicate concentration (Fig. 10), these stations are obviously located in the north of the Polar Front zone. Also, the indicator species for Group 1, *Euca-*

lanus longiceps and *Limacina retroversa*, are known to be distinctive in the subantarctic waters (Chen 1965, Razouls 1994). Thus, we designated Group 1 as the 'Subantarctic community.' Group 2 appeared in the ACC area of south of the Polar Front, and was thus designated the 'ACC community'. Superimposing the geographical distribution of each community group on the zonation for Antarctic zooplankton (Hempel 1985), the Subantarctic community was distributed within the ice-free zone, and the ACC community within the seasonal pack-ice zone. The ACC community was further divided into 2 sub-groups, 2a and b. Multiple-regression analysis and ANOVA revealed that Group 2a occurred in areas of higher water temperature and lower silicate concentration than Group 2b (Fig. 7, Table 6). Since water temperature increases and silicate concentration decreases in northern ACC waters, we designated the former the 'Northern ACC community' and the latter the 'Southern ACC community', although both sub-groups appeared on the same latitude along the east-west transects.

Species composition of Northern and Southern ACC communities

The characteristic that best differentiates the Northern ACC community from the Southern ACC community is the dominance of smaller copepods and non-copepod herbivores in the former (Table 4). Species diversity was lower in the Northern ACC community than in the Southern ACC community (Fig. 6), despite the fact that the number of species observed was similar between the 2 groups and more indicator species appeared in the former. However, this was due substantially to high abundances of the small copepods *Ctenocalanus citer*, *Oithona frigida*, *Oithona similis* and *Oncaea antarctica*, which were 1 to 2 orders of magnitude more abundant than other indicator species. An NMDS ordination plot of species association revealed a tight association between the distribution patterns of these smaller copepods, suggesting that they share a common, favorable, environment. Spearman's rank correlation revealed that most smaller copepods and non-copepod herbivores prefer warmer waters with a low silicate concentration (Table 7), resulting in much higher total zooplankton abundance in the Northern ACC community than in the Southern community. Despite the fact that surface chlorophyll *a* concentration was significantly higher in the Northern ACC community, only 2 of its indicator species, *Oithona frigida* and ostracods, showed a pos-

Table 6. ANOVA (*F*) of environmental variables showing difference between Groups 2a and 2b. Only those variables which produced a significant multiple regression with NMDS scores on the ordination plot are shown. Significance levels as in legend to Table 5

Variable	<i>F</i>	<i>p</i>	Difference
Latitude	8.95	***	2a > 2b
Longitude	0.25	ns	
Silicate concentration (0–200 m mean)	5.54	*	2b > 2a
Water temperature (0–200 m mean)	7.58	**	2a > 2b
Surface chlorophyll <i>a</i> concentration	4.60	*	2a > 2b
Depth of mixed layer	1.14	ns	
Salinity (0–200 m mean)	1.54	ns	
Extent of sea-ice formation (Feb–Mar)	0.41	ns	

itive correlation to this variable. Although high abundance and thus ecological importance of smaller copepods as phytoplankton grazers has been pointed out in recent years (Hopkins 1985a,b, Schnack et al. 1985, Fransz 1988, Atkinson 1998), the distribution of these species within the ACC have not been fully understood, in comparison to larger copepods and euphausiids. 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. It is possible that phytoplankton availability is an important factor in spring and summer, but less important in autumn when many copepods species start changing their feeding strategy from herbivorous to omnivorous or fasting.

The 4 large pelagic copepods *Rhincalanus gigas*, *Calanoides acutus*, *Calanus propinquus* and *Metridia gerlachei* are known to be very abundant in the ACC (Hopkins 1985a, Hopkins & Torres 1988, Boysen-Ennen et al. 1991, Schnack-Schiel et al. 1991). Among them, only *R. gigas* was not an indicator for the Southern ACC community while the other 3 species were all indicators of both ACC communities. Spearman's rank correlation revealed a strong positive correlation between abundance of *R. gigas* and water temperature. These results are consistent with previous reports that *R. gigas* prefers warmer water than the other 3 species (Beaumont & Hosie, 1997) and is even present in subantarctic waters (Ommanney 1936, Marin 1987,

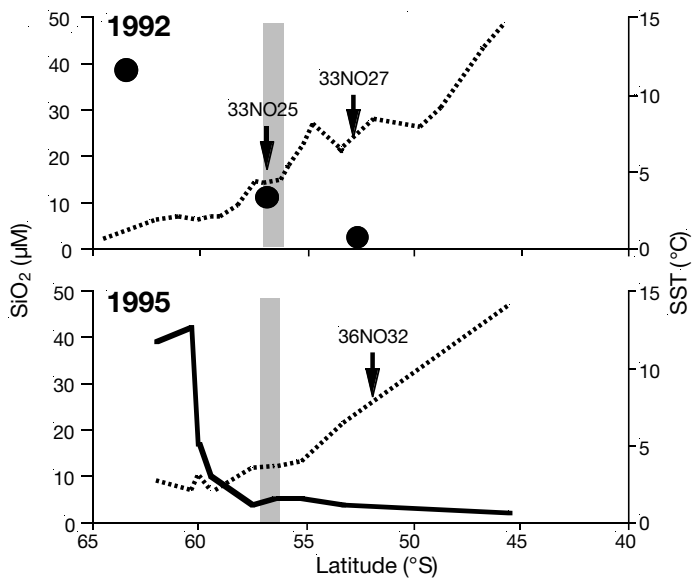


Fig. 10. Surface silicate concentration and sea-surface temperature along north-south transects of ca 150° E in 1992 and 1995. Dotted line: silicate concentration, continuous line and dots: sea-surface temperature (SST); shaded area: approximate location of the Polar Front on 150° E (reported in Belkin & Gordon 1996)

Table 7. Correlation coefficient (r_s) obtained by Spearman's rank-correlation test between environmental variables and indicator species for Groups 2a and 2b. Significant correlations at $p < 0.001$ and 0.05 are indicated by double and single underlining, respectively ($df = 38$). Species (taxon) abbreviations as in Table 3

Variable	Indicator species														
	Rg	Ca	Cp	Mg	Ho	Cc	Mp	Sm	Oa	Os	Of	Ot	Cy	Pl	Eh
Water temperature (surface)	<u>0.640</u>	0.280	-0.082	<u>0.355</u>	-0.058	<u>0.476</u>	<u>0.325</u>	<u>0.452</u>	<u>0.495</u>	0.180	<u>0.408</u>	<u>0.405</u>	0.282	0.245	0.238
Water temperature (0–200 m mean)	<u>0.412</u>	-0.079	-0.375	0.060	-0.025	0.258	0.224	<u>0.406</u>	<u>0.514</u>	0.040	<u>0.369</u>	<u>0.403</u>	0.360	0.051	0.348
Salinity (surface)	-0.189	-0.014	0.140	0.102	-0.004	-0.026	-0.054	-0.067	-0.146	-0.090	-0.160	-0.207	-0.173	-0.308	-0.143
Salinity (0–200 m mean)	-0.185	-0.007	0.154	-0.065	0.135	-0.155	-0.059	-0.161	-0.121	-0.133	-0.100	-0.198	-0.302	-0.249	-0.031
Silicate concentration (surface)	<u>-0.636</u>	<u>-0.316</u>	-0.060	<u>-0.395</u>	0.027	<u>-0.588</u>	<u>-0.308</u>	<u>-0.347</u>	<u>-0.534</u>	<u>-0.413</u>	<u>-0.498</u>	<u>-0.333</u>	<u>-0.316</u>	<u>-0.495</u>	<u>-0.145</u>
Silicate concentration (0–200 m mean)	-0.286	-0.010	0.248	-0.174	0.202	-0.276	-0.075	-0.096	-0.246	-0.110	-0.174	-0.168	-0.214	-0.233	0.160
Phosphate concentration (0–200 m mean)	-0.283	-0.072	-0.168	<u>-0.390</u>	-0.027	-0.244	0.022	-0.238	-0.158	-0.136	-0.226	-0.195	-0.083	-0.150	0.233
Nitrate concentration (0–200 m mean)	-0.254	-0.098	-0.154	<u>-0.404</u>	-0.220	-0.306	-0.184	-0.211	-0.136	-0.022	0.214	-0.239	-0.051	0.011	-0.177
Surface chlorophyll a concentration	-0.080	0.130	0.220	0.023	0.234	0.091	0.161	-0.169	0.138	0.304	0.411	<u>0.346</u>	0.100	0.124	0.070
Depth of mixed layer	0.062	-0.230	-0.296	0.011	-0.187	0.065	-0.093	0.208	0.214	-0.020	-0.249	0.070	0.315	-0.006	-0.141
Maximum sea-ice extent (Oct)	-0.120	-0.041	-0.062	-0.172	0.194	0.069	0.099	-0.014	0.110	0.114	0.055	0.035	0.134	0.071	-0.186
Minimum sea-ice extent (Feb)	0.034	-0.113	<u>-0.343</u>	-0.112	0.011	0.120	0.200	0.182	<u>0.368</u>	0.050	-0.061	0.170	<u>0.324</u>	0.008	-0.076
Extent of ice-edge retreat (Oct–Feb)	-0.001	0.122	0.203	-0.002	0.185	0.077	0.024	-0.135	-0.065	0.138	-0.155	-0.007	0.006	-0.009	0.011
Extent of ice-edge retreat (Dec.–Feb)	0.174	-0.253	-0.385	0.069	0.060	0.119	0.069	0.005	0.006	0.039	0.054	0.053	0.038	0.206	0.170
Extent of ice formation (Feb–Mar)	-0.040	<u>-0.696</u>	<u>-0.445</u>	-0.068	-0.328	-0.151	-0.074	-0.172	-0.051	<u>-0.457</u>	-0.209	0.051	0.182	-0.203	0.043

Atkinson 1991). Although *Calanus propinquus* were more abundant in colder water, sea ice seemed to negatively influence this species, which was more abundant in the areas of low sea-ice extent in summer and slow sea-ice formation in autumn. This is reasonable since *C. propinquus* is reported to be unable to graze on ice algae because it has a low tolerance to the high salinity in brine (Gradinger & Schnack-Schiel 1998). *Calanoides acutus* also showed a preference for slow sea-ice formation in autumn. In this study, *M. gerlachei* was more abundant in warmer waters. This is contrary to previous reports that *M. gerlachei* is cold-water adapted (Boysen-Ennen & Piatkowski 1988, Hosie et al. 1997). In other studies, however, large numbers of this species were observed in Northern ACC water, also (Hopkins & Torres 1989, Hopkins et al. 1993). It is suggested that the distribution of *M. gerlachei* is not water-temperature dependent, but is determined by other factors such as food resources, whose supplies are associated with the icy water present during the summer ice-edge bloom.

Water intrusion and community-structure change

The Northern ACC community occurred in warmer waters with low silicate concentration, while the Southern ACC community was found in colder water with high silicate concentration; they both occurred at the same latitude along the east-west transect. This fact suggests that there may be a sporadic intrusion of northern water to the south, and vice versa. It has been reported that warmer water intrusion causes the east-west environmental gradient and subsequently affects the local trophic structure, including the zooplankton community, off east Antarctica (80 to 150° E; Nicol et al. 2000) and Adelie Land (135 to 145° E; Chiba et al. 2000). In the Antarctic Peninsula area, Atkinson et al. (1990) found the occasional warm-water intrusions caused a change in zooplankton composition by advection. Hosie et al. (1997) also observed that spatio-temporal variation in water temperature determined zooplankton community structure. Indicator species of the Northern and Southern ACC communities overlapped, and abundance was markedly higher in the former. It is reasonable to consider that the difference between the 2 communities derived from advection of the northern ACC species, such as small copepods, into southern ACC waters. Phytoplankton production decreases and

sea ice starts forming in March in the study area. Thus, a community rich in species and abundance might be sustained in those areas where warm-water intrusion occurred, while only species adapted to colder water would remain in the other areas.

As reported in Chiba et al. (2000), such a warm-water intrusion is likely to be a result of a meandering of the ACC. Cyclonic eddies keep developing and disappearing along 63 to 65° S off east Antarctica (Wakatsuchi et al. 1994). The Antarctic Divergence is most marked around the center of the eddies, and it is less recognizable between the eddies, where ACC water tends to intrude to the south. How long the observed community structure is sustained is likely to depend on the dynamics of the eddies. This could not be investigated here, however, since annual samples were taken only in March.

The majority of previous studies on the zonation of Antarctic zooplankton focused on latitude-dependence, and thus relatively constant and distinct variations such as oceanic-neritic, or frontal-offshore community structure change (Boysen-Ennen & Piatkowski 1988, Piatkowski 1989, Siegel & Piatkowski 1990, Park & Wormuth 1993, Hosie et al. 1997). However, a result of this study implies that the boundaries of a zooplankton community tend to vary during the relatively short period of a sporadic phenomenon, for example, meandering of the ACC. The abundance of small copepods was the factor differentiating the Northern ACC community from the Southern community. For this reason, the use of a plankton net with fine mesh (330 µm or smaller) at low hauling speed is recommended for detecting subtle spatio-temporal changes in copepod-based zooplankton communities, to avoid undersampling small species and thus 'overlooking' any such change. For example, Marin (1987) did not find any differences in zooplankton communities in different

Table 8. *Euphausia superba* and *Salpa thompsoni*. Distribution and numerical abundance (ind. 1000 m⁻³)

<i>E. superba</i>				<i>S. thompsoni</i>			
Year	Stn	Location	Abundance	Year	Stn	Location	Abundance
1989	30NO11	59°40'S 150°00'E	315	1992	33NO21	63°57'S 133°17'E	1206
1992	33NO21	63°57'S 133°17'E	40		33NO23	64°47'S 150°08'E	828
1993	34NO21	63°06'S 97°02'E	51	1993	34NO29	63°32'S 133°52'E	41
1994	35NO17	62°31'S 98°42'E	78	1994	35NO23	56°21'S 152°48'E	225
	35NO25	56°21'S 152°48'E	79	1995	36NO28	64°07'S 148°45'E	38
1996	37NO21	63°44'S 131°27'E	513				

water mass within the ACC/Weddell Sea water confluence region. However, changes in community structure might have been observed if smaller copepods had been counted as well as larger species.

Euphausia superba

Larval *Euphausia superba* occurred at only a few stations, and its abundance was less than 100 ind. 1000 m⁻³, except at Stns 30NO11 and 37NO21 (Table 8). It is not surprising that no adults were collected, since the mouth area of the NORPAC net used in this study was too small to catch animals with high net-avoidance ability such as *E. superba*. However, the rare appearance of its larvae indicates that reproduction and recruitment of this species were generally unsuccessful in this area. The majority of the larvae collected were Calyptopsis I stage. Assuming that it takes 5 to 6 d and ca 20 d from egg laying to hatching and from hatching to the Calyptopsis I stage (Hofmann et al. 1992), the observed Calyptopsis I individuals are estimated to have originated from eggs laid in late January to early February. According to the criteria of Spiridonov (1995), this suggests that spawning might always occur late in the research area. Although Chiba et al. (2000) observed that the majority of larvae were at Calyptopsis I in January/February 1996 off the Adelie Coast, no advanced stage appeared in March in the same area and year in this study. Ross et al. (1988) reported that larval *E. superba* starved to death before reaching Calyptopsis II when fed with only small flagellates, while they grew well with a diatom mixture food. Thus, the observed prolonged dominance of Calyptopsis I stages in summer to early autumn would suggest that the survival of the larvae was less successful due to poor food availability off east Antarctica. This result may explain the small biomass of this species in the ACC part of the area (e.g. Marr 1962, Nicol 1994).

Salpa thompsoni

As well as larval *Euphausia superba*, *Salpa thompsoni* occurred at only a few stations, and its abundance was much lower than those observed during the RTV 'Umitaka-maru III' survey off Adelie coast in 1996. Because of its small filtration capacity, however, the NORPAC net used in this study is not efficient to catch animals with a patchy distribution, such as *S. thompsoni* (e.g. Casareto & Nemoto 1986). For example, no salps were collected in 1996 in this study, although a considerable number of salps were caught in the same area and periods by an RMT net with large filtration capacity during a survey by the RSV 'Aurora Australis' (Chiba et al. 1999). In addi-

tion, Chiba et al. (1999) reported that a large salp population observed throughout the research area during summer had quickly diminished by March 1996. Taking account of the limited capacity of the sampling gear and the quick population decline of salps in autumn, the appearance of salps in this study is considered to represent remnants of their summer bloom.

It is worth noting that *Salpa thompsoni* appeared exclusively at stations located off the Adelie Coast, where dense salp blooms have been observed (Casareto & Nemoto 1986, Chiba et al. 1998, 1999, 2000, Nicol et al. 2000). This area might constantly present optimal environmental conditions for population growth of *S. thompsoni* during the austral summer. The sea-ice off the Adelie Coast is least extensive around the Antarctica (Gloersen et al. 1992), and negative correlations between yearly salp abundance and sea-ice extent have been reported in the Antarctic Peninsula/Weddell Sea region (Siegel & Loeb 1995, Loeb et al. 1997). Salps are considered to be less adapted to conditions of extensive diatom blooms (Alldredge & Madin 1982), since their feeding nets might malfunction under high concentration of food particles (Harbison et al. 1986). Poor sea-ice conditions off the Adelie Coast might lead to moderate ice-edge blooms in the summer, resulting in the appearance of relatively oligotrophic, offshore-type conditions which might be optimal for small particle-feeders such as salps.

All *Salpa thompsoni* collected in this study were aggregate forms of Stage X (with dead embryo). Observing increased numbers of Stage X in 1996 austral autumn, Chiba et al. (1999) hypothesized that food shortage, resulting from the end of phytoplankton blooms, coupled with decreasing water temperature in surface waters inhibits the growth of salp embryos, leading to an abrupt population decrease in these animals in autumn. The occurrence of Stage X has not previously been reported for any salp species except *S. thompsoni*. However, the result of this study indicates that reduction of capacity for sexual reproduction is one of the major processes responsible for the autumn decline in *S. thompsoni* populations.

CONCLUSION

We observed meso-scale variability in the zooplankton community structure within the ACC. Advection of the northern water to the south caused by meandering of the ACC is considered responsible for the observed community distributions, suggesting that the community structure may vary over a relatively short period. Since the zooplankton community shifted spatio-temporally from a community dominated by small copepods to a community dominated by large copepods, it

is suggested that the dominant trophic structure may change from that of a microbial loop to that of a grazing chain. This may consequently affect the annual zooplankton productivity in the area. This study was based on data limited to the post-bloom season, during which productivity declines. To evaluate to what extent meandering of the ACC affects the annual zooplankton productivity of the area, the dynamics of ACC should be studied together with zooplankton community structure during the spring and summer periods.

Acknowledgements. This study was conducted under the collaboration of the Tokyo University of Fisheries and the National Institute of Polar Research, with financial support of a Sasakawa Scientific Research Grant from the Japan Science Society. We thank very much the officers and crew of the icebreaker 'Shirase' and expedition members of JARE 29-36 for collecting data and zooplankton samples in harsh Antarctic waters.

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Editorial responsibility: Otto Kinne (Editor),
Oldendorf/Luhe, Germany

Submitted: June 6, 2000; Accepted: October 5, 2000
Proofs received from author(s): June 5, 2001