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Spatio-temporal variability in life cycle strategy of four pelagic Antarctic copepods: *Rhincalanus gigas*, *Calanoides acutus*, *Calanus propinquus* and *Metridia gerlachei*

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Abstract: Spatio-temporal variability in life cycle strategy of four pelagic Antarctic copepods, *Rhincalanus gigas*, *Calanoides acutus*, *Calanus propinquus* and *Metridia gerlachei* was studied, including their copepodite stage composition, using the multi-year samples taken off east Antarctica (90–160°E) in March 1988–1996. Except for *R. gigas*, the rare occurrence of adults indicated that the spawning activities ceased by mid-March in this research area. Younger copepodite stages appeared for *C. propinquus* compared to *C. acutus*, suggesting the late reproduction or slow growth in the former. Multiple regression analysis on the relationship between environmental variables and the copepodite stage composition showed that the population matured earlier in the warmer area for *C. acutus*, *C. propinquus* and *M. gerlachei*. The study demonstrated that the three species flexibly changed timing of the reproduction and development, and shifted their life cycle from one year to two years in the southern Antarctic Circumpolar Current (ACC) area, responding to spatio-temporal environmental change caused by meandering of the ACC.

key words: copepods, life cycle, JARE, Antarctic Ocean, Antarctic Circumpolar Current

Introduction

Ecological importance of Antarctic copepods has been recognized since their biomass was often reported to exceed that of Antarctic krill (*e.g.* Everson, 1984). Because of their higher metabolic rate, copepods could consume as much as eight times the primary production eaten by krill (Conover and Huntley, 1991).

Rhincalanus gigas, *Calanoides acutus*, *Calanus propinquus* and *Metridia gerlachei* are large pelagic copepods which are abundant throughout the Antarctic Circumpolar Current (ACC). They sometimes dominate other zooplankton in krill-absent communities (*e.g.* Kawamura, 1987; Hosie, 1994a; Hosie *et al.*, 1997; Chiba *et al.*, 1998, 2000), and account for up to 90% of total copepod biomass (Hopkins, 1985a; Boysen-Ennen and Piatkowski, 1988; Hopkins and Torres, 1988; Boysen-Ennen *et al.* 1991). These four copepod species are known to graze mainly on diatoms under phytoplankton rich

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conditions (Hopkins *et al.*, 1993a) although the latter two species turns more omnivorous during winter (Hopkins *et al.*, 1993b). Laboratory experiment implied that mass specific grazing rates of these copepod species might be higher than that of krill (Schnack, 1985).

The four copepod species are known to perform more or less seasonal ontogenetic vertical migration (reviewed by Atkinson, 1998). They stay in deeper water in advanced copepodite stages during winter, and become mature and ascend to the surface layer in spring. Reproduction occurs in the surface layer during summer. The summer generation reaches advanced copepodite stages and start descending to deeper water in autumn. Reproductive timing and subsequently, the life cycle of copepods are likely to vary depending on the spatio-temporal environmental condition. For example, both one year and two year life cycles are suggested for all the four species. Both for *C. acutus* and *C. propinquus*, Marin (1988) suggested one year cycle but Drits *et al.* (1993, 1994) reported a two year life cycle. *Metridia gerlachei* perform a one year life cycle in ACC and two year life cycle in Weddell Sea (Kurbjewit, 1993), while several generations may occur within a year at the Gerlachei Strait (Huntley and Escritor, 1991). For *R. gigas*, a one year life cycle is reported in ACC (Voronina *et al.*, 1978; Atkinson, 1991; Bathmann *et al.*, 1993) while other studies suggested a two year life cycle near the Antarctic Peninsula (Marin, 1988) and multi-year life cycle in the Weddell Sea (Bathmann *et al.*, 1993). However, many of these studies were based on seasonal or local changes, or comparison of biomass of certain species for two or three consecutive years, making it difficult to clarify how spatio-temporal environmental variability affects their life cycle strategy.

Zooplankton community structure off east Antarctica (90–160°E) was analyzed by Chiba *et al.* (2001) based on samples taken by Japanese Antarctic Research Expedition (JARE) during 1987/88 to 1995/96 seasons. They concluded that the environmental variability caused by ACC meandering influenced the formation of the observed community structure. Using the same multi-year JARE samples, we investigated whether the observed environmental variability also affect the life cycle strategies of the four major Antarctic copepods.

Materials and methods

Surveys were conducted in March from 1987/88 to 1995/96 seasons during JARE-29 to -37 cruises by the Japanese icebreaker “*Shirase*” along the east-west transect on *ca.* 64°S between 90 and 160°E, and the north-south transect on *ca.* 150°E up to 50°S (Fig. 1). Sampling was conducted during 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 to the surface. All zooplankton were preserved in 5% neutral formalin soon after collection. *Rhincalanus gigas*, *Calanoides acutus*, *Calanus propinquus* and *Metridia gerlachei* were extracted from zooplankton samples to be sorted and counted by each copepodite stage at each station. For *R. gigas* in particular, the nauplius stages were included for the analysis because a number of nauplii were readily observed in the net samples due to its large size. All counts were converted into number of individuals per 1000 m³ for each station.

We applied multivariate analysis as a method best to elucidate the complex

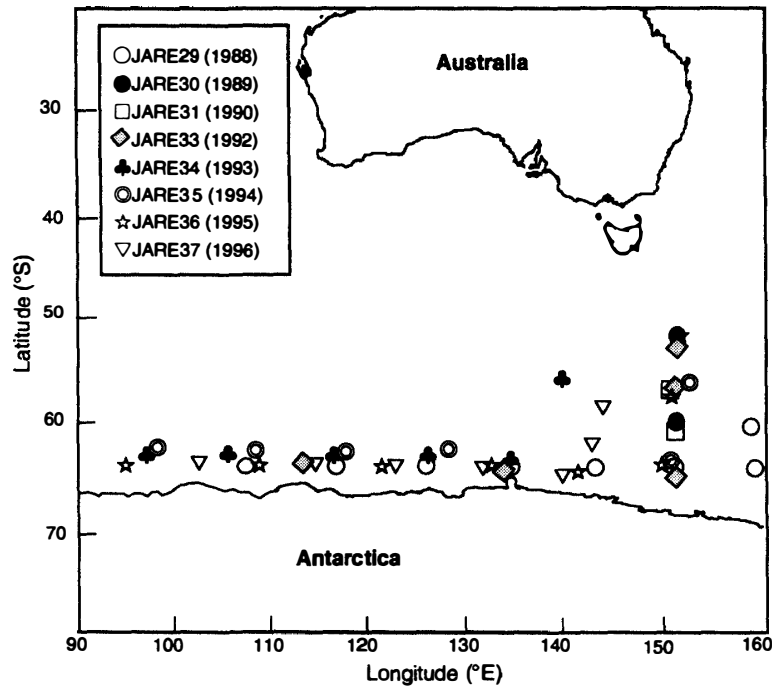


Fig. 1. Research area and sampling stations.

interaction between the community structure change and biotic/abiotic factors based on data taken at spatio-temporally various occasions (Field *et al.*, 1982; Ludwig and Reynolds, 1988). The analytical methods described below are based on Hosie (1994b) and Hosie *et al.* (1997), which in turn were modified from Field *et al.* (1982) and Kruskal and Wish (1978). Computer software, BIOSTAT ver. 3.5 (Sigma Soft, California) was employed for the analysis.

Based on the copepodite stage composition, a dissimilarity matrix between stations was constructed using Euclidean distance. Cluster analysis using the unweighted pair group method with arithmetic mean (UPGMA) (Ludwig and Reynolds, 1988) was applied to the matrix to obtain several station groups for each species and their geographical distribution. To verify the cluster analysis, the stations were plotted on a two-dimensional map by non-metric multidimensional scaling (NMDS) method (Ludwig and Reynolds, 1988) based on the same dissimilarity matrix. The goodness of fit of the derived map was verified by the stress value criteria constructed by Kruskal and Carmore (1971 in Domanski, 1984). Multiple regression analysis between NMDS ordination scores of each station and environmental variables (Table 1) were applied to determine which environmental factor could influence the copepodite stage composition. JARE Data Reports were referred to for hydrographic information (Ito and Ishii, 1989; Ikeda and Matsumoto, 1991; Ikeda and Kojima, 1992; Tanaka and Noguchi, 1995; Hashima and Namiki, 1997; Okano and Ogawa, 1998; Yoritake and Namiki, 1999; Oikawa and Miura, 1999). Sea ice information was obtained from satellite sea ice concentration data of 25 km grid from the EOSDIS NSIDC Contributed Active Archive Center, University of Colorado at Boulder (National Snow and Ice Data Center, 1998a, b). The northern sea ice extent for each sampling station was the monthly average value along the longitudinal

Table 1. Environmental variables used for multiple regression analysis.

Variables
Hydrography
Surface Chl <i>a</i> 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
Maximum sea ice extent from coast (October)
Maximum sea ice extent from coast (February)
Distance of ice edge retreat (October to February)
Distance of ice edge retreat (December to February)
Distance of ice formation (February to March)

lines on which JARE sampling stations were located. Areas with more than 15% sea ice concentration were defined as being ice-covered. As sea ice extent usually reaches a maximum in October and minimum in February off east Antarctica (Gloersen *et al.*, 1992), and sea ice retreats most rapidly in December, the data in October, December and February was selected for comparison.

Results

Copepods numerically dominated other zooplankton occupying up to 99% of the total (mean=89%). Abundance of the four species varied from 56 to 87689 inds. 1000 m⁻³ for *Rhincalanus gigas*, 180 to 101567 inds. 1000 m⁻³ for *Calanoides acutus*, 39 to 63571 inds. 1000 m⁻³ for *Calanus propinquus* and 78 to 215133 inds. 1000 m⁻³ for *Metridia gerlachei* (Fig. 2). The four species numerically accounted for up to 77% (mean=22%) of total zooplankton abundance, 79% (mean=25%) of total copepod abundance, and 85% (mean=40%) of total calanoid copepods. On the other hand, non-calanoid copepods (cyclopoid, poecilostomatoid and harpacticoid) accounted for up to 75% (mean=35%) of the total zooplankton abundance and 93% (mean=41%) of the total copepod abundance.

Several groups with distinctive copepodite stage composition were derived for each species by cluster analysis at 89%, 68%, 48% and 67% dissimilarity level for *R. gigas*, *C. acutus*, *C. propinquus* and *M. gerlachei*, respectively (Fig. 3). The characteristics of each group are summarized on Table 2. The stress value for the NMDS two dimensional plots (Fig. 4) was 15.4, 8.4, 11.4 and 8.4 respectively, for *R. gigas*, *C. acutus*, *C. propinquus* and *M. gerlachei*, all of which belong to “Excellent” to “Good” range in the criteria. Thus, the derived two axis ordinations are considered sufficient to explain

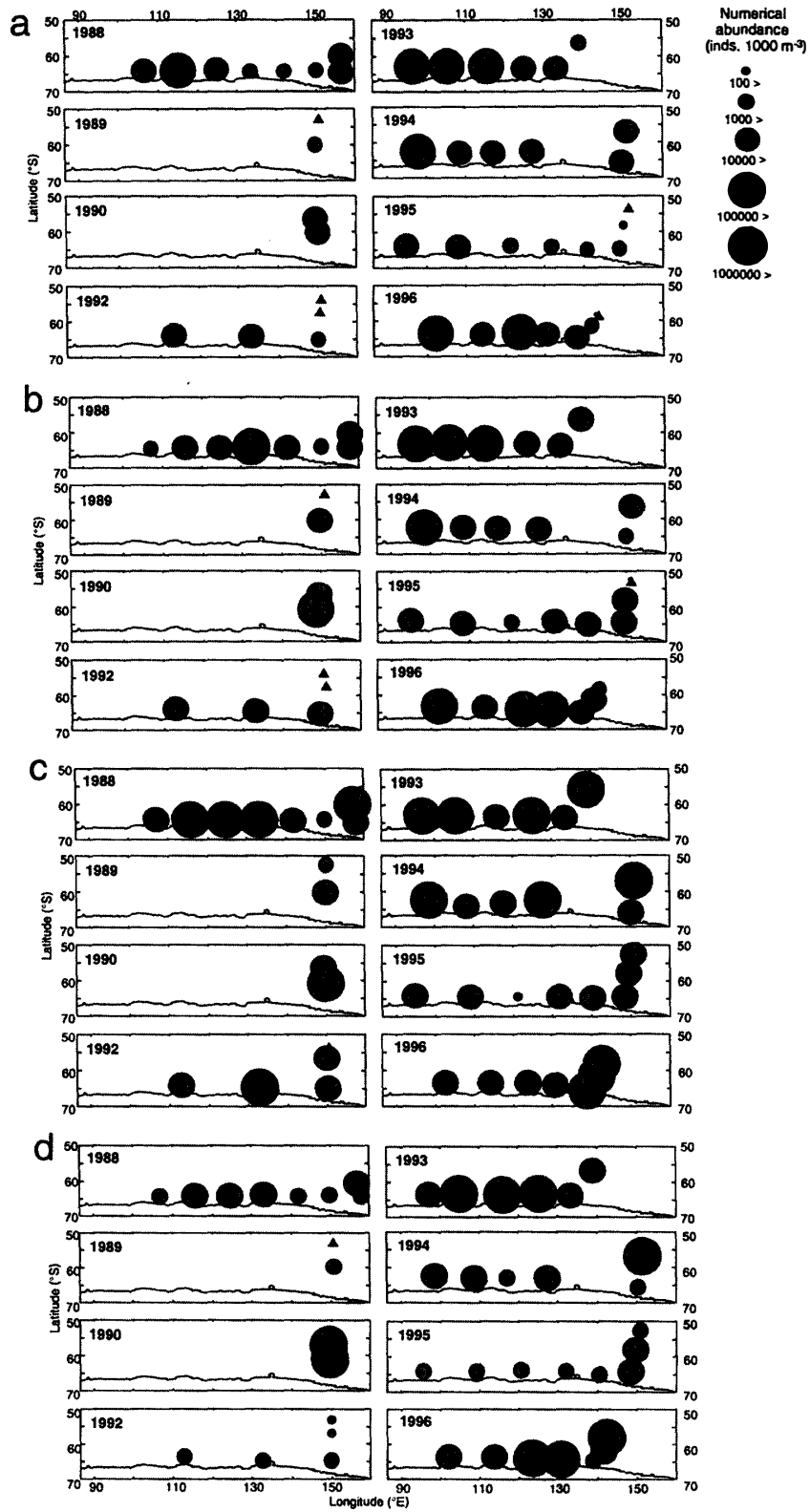


Fig. 2. Numerical abundance (inds. 1000 m^{-3}) for a) *Rhincalanus gigas*, b) *Calanoides acutus*, c) *Calanus propinquus* and d) *Metridia gerlachei*. Black triangle indicates the station at which no individuals were collected.

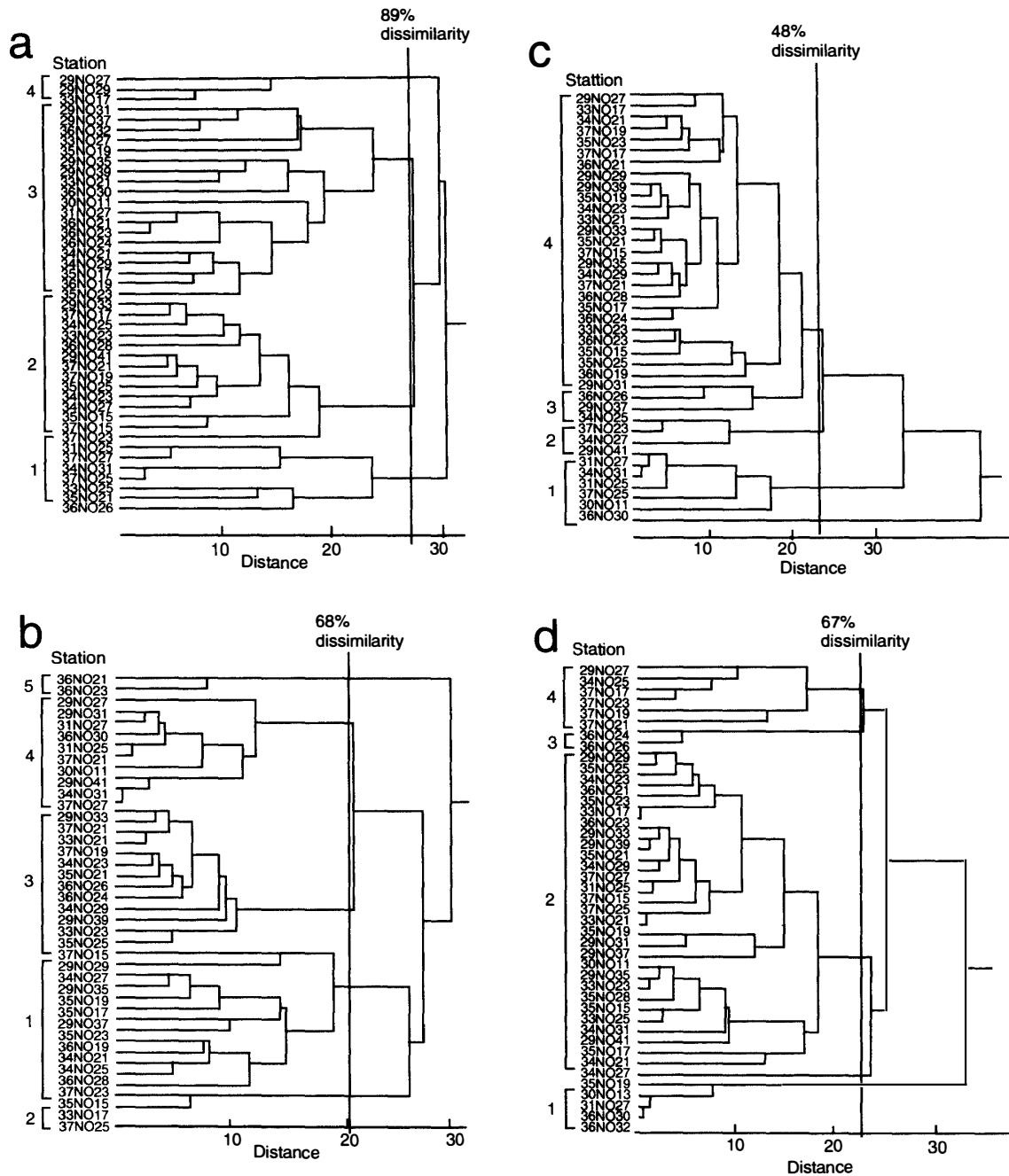


Fig. 3. Cluster diagram of sampling sites obtained based on copepodid stage composition for a) *Rhincalanus gigas*, b) *Calanoides acutus*, c) *Calanus propinquus* and d) *Metridia gerlachei*.

the differences in copepodite stage compositions between groups. Significant multiple regression between environmental variables and the ordination scores (Table 3) were superimposed on the NMDS plots (Fig. 4).

Rhincalanus gigas

All four groups appeared between 63–65°S along the east-west transect, while all,

Table 2. Mean numerical abundance (inds. 1000 m⁻³) and copepodid stage composition of each subpopulation group obtained by cluster analysis for the four copepod species.

	n	Abundance (inds. 1000 m ⁻³) mean (± std)	Composition (%)						
			N	CI	CII	CIII	CVI	CV	CVI (%female)
<i>Rhincalanus gigas</i>									
Group 1	7	10031 (±22330)	9.5	1.8	12.7	67.2	7.5	1.1	0.2 (47.1)
Group 2	14	12250 (±16296)	67.5	5.7	7.4	5.7	2.0	8.2	3.6 (94.3)
Group 3	19	1962 (±3887)	7.2	1.2	2.8	13.6	32.9	33.4	9.0 (93.2)
Group 4	3	1110 (±1003)	4.8	0.0	1.2	3.6	4.0	26.1	60.3 (37.0)
<i>Calanoides acutus</i>									
Group 1	13	15160 (±27545)	-	14.6	24.6	29.8	21.8	8.7	0.5 (100)
Group 2	2	1820 (±77)	-	1.5	6.3	4.8	78.8	5.2	3.5 (100)
Group 3	13	10615 (±13858)	-	0.5	1.9	8.5	48.2	40.5	0.5 (100)
Group 4	10	8724 (±15305)	-	0.0	0.0	6.2	14.4	78.7	0.6 (100)
Group 5	2	1344 (±1570)	-	1.5	0.0	0.0	4.6	35.4	58.5 (100)
<i>Calanus propinquus</i>									
Group 1	6	1938 (±2381)	-	0.0	0.0	2.6	79.0	18.4	0.0 (100)
Group 2	3	13343 (±9547)	-	56.1	22.5	7.7	11.3	2.3	0.2 (100)
Group 3	3	1923 (±2809)	-	0.0	0.6	63.8	28.1	7.4	0.0 -
Group 4	26	10289 (±16877)	-	13.0	35.9	34.8	12.1	3.8	0.5 (100)
<i>Metridia gerlachei</i>									
Group 1	4	4530 (±3693)	-	0.0	0.2	0.3	13.1	86.3	0.0 -
Group 2	30	19377 (±39282)	-	0.0	3.8	24.5	42.1	28.7	0.8 (100)
Group 3	2	3519 (±1005)	-	0.0	4.9	73.4	11.6	6.7	3.4 (100)
Group 4	6	12015 (±12896)	-	2.6	45.4	33.9	14.3	3.8	0.0 -

N: nauplius, CI-CV: copepodite I to V stage, CVI: adult.

except Group 4, occasionally appeared in the lower latitude, too (Fig. 5a). Group 4 which consisted of three stations was observed only in 1988 and 1992 around 110–120°E. Numerical abundance was markedly high in Groups 1 and 2 (Table 2). Nauplii occupied 68% of the total abundance in Group 2 while copepodite III dominated Group 1. Adults occurred in all population groups and accounted for about 60% in Group 4. More than 90% of adults were females in Groups 2 and 3 while males were most abundant in Group 4. No significant multiple regressions were recognized between ordination of the stations and environmental variables at $P < 0.05$ level (Table 3). Although statistically not significant, F values were highest for “year” and “distance of sea ice retreat from December to February” with $P = 0.068$ and 0.072 levels, respectively.

Calanoides acutus

All five subpopulations appeared along the east-west transect, while Group 4 occasionally occurred in the lower latitude (Fig. 5b). In 1988, the four groups seemed to be distributed at random. No *C. acutus* occurred at some stations located in the north of 55°S. Abundance was high in Groups 1, 3 and 4 but low in Groups 2 and 5 (Table 2). Both young (copepodite I to III) and advanced (copepodite IV and V) stages occurred in Group 1 while only advanced stages were observed in Group 3 and 4. Only small fractions of adults (<1%) were observed in Groups 1, 3 and 4. On the other hand, adults accounted for 4% and 59% of total abundance in Groups 2 and 5, respectively, both of which consist of only two stations. All adults collected were females. Five variables,

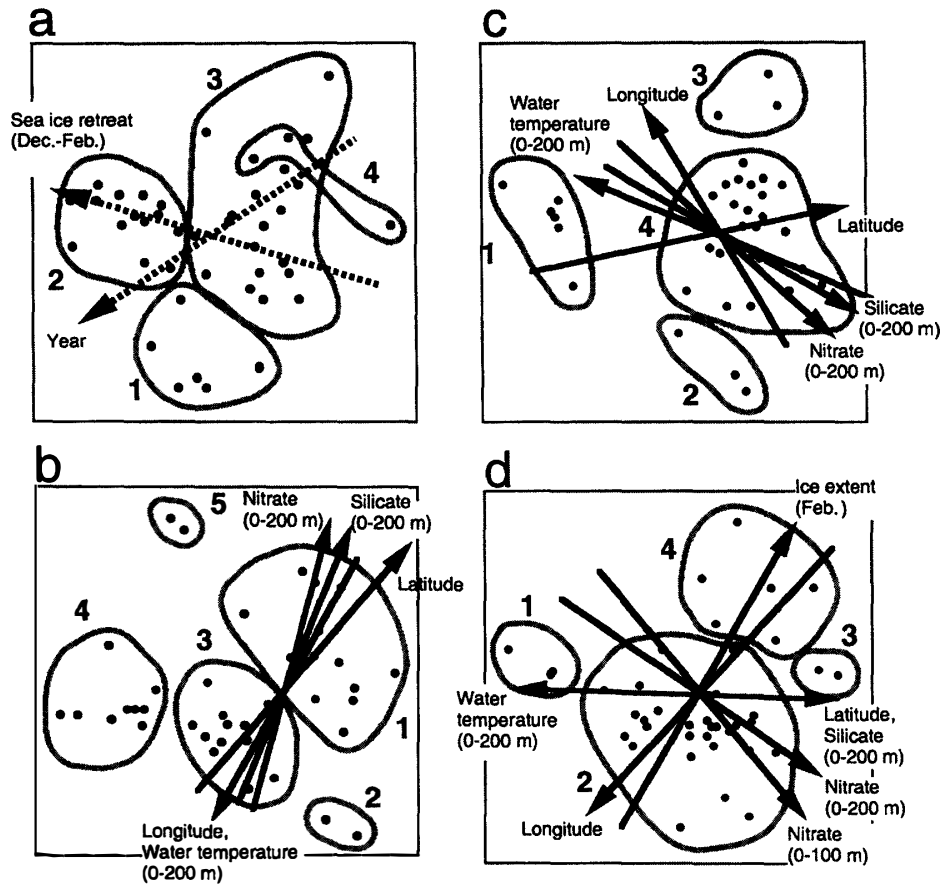


Fig. 4. NMDS ordination plot of sampling sites for a) *Rhinocalanus gigas*, b) *Calanoides acutus*, c) *Calanus propinquus* and d) *Metridia gerlachei*. Each subpopulation group derived by cluster analysis is enclosed in a circle. The stress value for the respective plot is 15.4, 8.4, 11.4 and 8.4 from a) to d). Angle and direction of arrows, which was derived from formula of Kruskal and Wish (1978), indicate significant ($P < 0.05$) multiple regression between the ordination scores and environmental variables (Table 3).

0–200 m mean water temperature, latitude, 0–200 m mean silicate concentration, 0–200 m mean nitrate concentration and longitude had a significant multiple regression with the ordination of the stations (Table 3). Direction of these regressions indicates that Groups 1 and 5 appeared more in high latitude, colder area with higher nitrate and silicate concentration (Fig. 4b) on the western side of the research area. Meanwhile, Groups 2, 3 and 4 occurred in the environmental condition opposite to that mentioned above.

Calanus propinquus

Three of the four groups, Groups 2, 3 and 4 occurred along the east-west transect while Group 1 occurred almost exclusively to the north of 60°S (Fig. 5c). Most stations belonged to Group 4 while either of Group 2 and 3 consisted of only 3 stations. Abundance was high in Group 2 and 4 but low in Group 1 and 3 (Table 2). Younger copepodite stages dominated Groups 2 and 4 while advanced stages were predominant in Group 1 and 3. Adults, all female, were hardly observed in any subpopulations (<1%).

Table 3. Results of multiple regression analysis between environmental variables and NMDS scores on the two-dimensional ordination plot for sampling sites (Fig. 3).

Variable	DF	Direction Cosine		Adjusted R ²	F	P
		X	Y			
<i>Rhincalanus gigas</i>	2, 42					
Year		-0.833	-0.553	0.08	2.879	n.s.
Distance of ice edge retreat (Dec. - Feb.)		-0.939	0.343	0.09	2.832	n.s.
<i>Calanoides acutus</i>	2, 37					
Water temperature (0-200 m mean)		-0.544	-0.839	0.33	10.59	***
Latitude		0.740	0.673	0.29	9.12	***
Silicate concentration (0-200 m mean)		0.448	0.894	0.17	5.04	*
Nitrate concentration (0-200 m mean)		0.318	0.948	0.16	4.74	*
Longitude		-0.557	-0.831	0.13	3.78	*
<i>Calanus propinquus</i>	2, 35					
Latitude		0.973	0.233	0.31	9.43	***
Water temperature (0-200 m mean)		-0.954	0.300	0.18	4.96	*
Silicate concentration (0-200 m mean)		0.901	-0.435	0.18	4.94	*
Nitrate concentration (0-200 m mean)		0.827	-0.562	0.17	4.76	*
Longitude		-0.642	0.766	0.14	3.92	*
<i>Metridia gerlachei</i>	2, 41					
Latitude		0.998	-0.064	0.47	19.05	***
Water temperature (0-200 m mean)		-0.997	0.077	0.45	17.93	***
Silicate concentration (0-200 m mean)		1.000	-0.022	0.38	13.28	***
Sea ice extent from coast (Feb.)		0.601	0.799	0.23	6.36	***
Nitrate concentration (0-200 m mean)		0.862	-0.508	0.19	5.66	**
Longitude		-0.761	-0.649	0.16	5.01	*
Nitrate concentration (0-100 m mean)		0.730	-0.683	0.11	3.48	*

Only significant multiple regressions ($P < 0.05$) are shown for *Calanoides acutus*, *Calanus propinquus* and *Metridia gerlachei* while those of not significant but highest F value are shown for *Rhincalanus gigas*. Among the variables shown on the Table 1, one from a pair which have a simple correlation of > 0.800 (e.g. sea surface temperature and 0–200 m mean water temperature) was excluded prior to the analysis. “Adjusted R²” is the adjusted coefficient of determination which gives the fraction of the variance accounted for by the explanatory variable. For ANOVA between regression and residuals, *** $P < 0.005$, ** $P < 0.01$, * $P < 0.05$.

Five variables, latitude, 0–200 m mean water temperature, 0–200 m mean silicate concentration, 0–200 m mean nitrate concentration and longitude had a significant multiple regression with the ordination of stations (Table 3). Direction of the multiple regressions indicated that Group 4 appeared more in the high latitude, colder area with higher silicate and nitrate concentration while Group 1 appeared in the low latitude, warmer area (Fig. 4c). Group 2 tended to occur in warmer and nutrient rich area in comparison with Group 3.

Metridia gerlachei

Three of the four groups, Groups 2, 3 and 4 occurred along the east-west transect while Group 1 occurred exclusively in the north of 60°S (Fig. 5d). Group 3 which consisted of only two stations appeared only in 1995. Most stations belonged to Group 2. Abundance was high in Groups 2 and 4 but low in Groups 1 and 3 (Table 2).

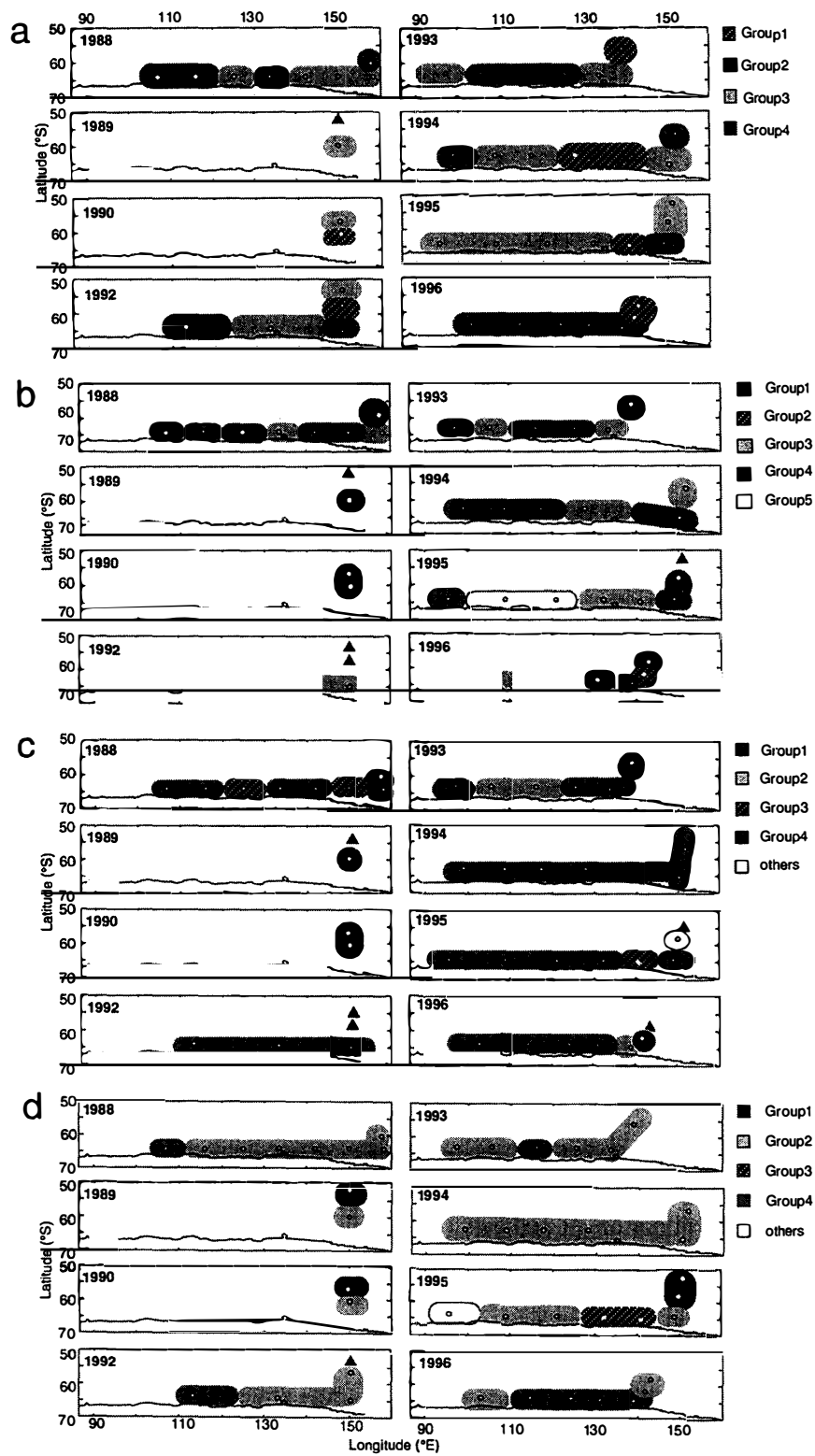


Fig. 5. Geographical distribution of subpopulation groups derived by cluster analysis for a) *Rhincalanus gigas*, b) *Calanoides acutus*, c) *Calanus propinquus* and d) *Metridia gerlachei*. Black triangle indicates the station at which no individuals were collected.

Group 1 showed the most advanced copepodite stage composition in which copepodite V occupied more than 80% of total abundance, then followed by Group 2. Younger stages dominated in Groups 3 and 4. Adults occurred in Group 3 with 3% of the total but were almost absent (<1%) in other groups. All adults collected were females. Six variables, latitude, 0–200 m mean water temperature, 0–200 m mean silicate concentration, 0–200 m mean nitrate concentration, sea ice extent in February, longitude and 0–100 m mean nitrate concentration had significant multiple regressions with ordination scores of the stations (Table 3). The direction of the regressions indicates that Group 2 appeared more where sea ice coverage was less extensive in February on the eastern side of the research area compared with Groups 3 and 4 (Fig. 4d). Groups 2 and 3 tended to occur in the area of higher nitrate concentration compared with Group 1. Group 1 appeared in the warmer, low latitude area while Group 3 appeared in the colder, high latitude area.

Discussion

Abundance and distribution

Rhincalanus gigas, *Calanoides acutus*, *Calanus propinquus* and *Metridia gerlachei* accounted for 25% of the total copepod abundance on average, which is more than 10% less than that of non-calanoid smaller copepods dominated by *Oithona* spp. and *Oncaea antarctica* (Chiba *et al.*, 2001). Also, the mean contribution of the four species to the total calanoid abundance was 40%, the rest of which were dominated by *Ctenocalanus citer* and *Scolecithricella minor* (Chiba *et al.*, 2001). In terms of biomass, however, the four copepods must dominate others since their individual sizes are considerably larger. The adult body lengths are 6–8 mm, 4–5 mm and 3 mm respectively, for *R. gigas*, *C. acutus* and *C. propinquus*, and *M. gerlachei*, while these are about or less than 1 mm for *Oithona*, *Oncaea*, *C. citer* and *S. minor*. Thus, the four copepods were considered keystone species in the observed zooplankton community. Effect of the mesh size (330 μm) used should be considered to evaluate the observed numerical abundance and biomass of the copepods since the mesh size might be too coarse to catch smaller copepod species. However, the four large copepod species dominated in biomass even in the studies in which a fine mesh net (162 μm) was used (Hopkins, 1985a), although relative numerical abundance of smaller copepods much increased.

Rhincalanus gigas was distributed in the wide latitudinal range between 52 and 65°S. Analyzing the data from the Discovery collections in the Scotia Sea, Atkinson (1991) found that *R. gigas* were most abundant in Subantarctic water. However, the results of this study in the Indian Sector agree with Brodskii (1968 in Murano, 1983) who reported that *R. gigas* were widely abundant from the Polar Front area to northern and southern ACC areas. *Calanoides acutus* and *C. propinquus* were distributed throughout the sampling area except at some stations located in the lower latitudes. *Calanus propinquus* are known as a cold water species which are abundant in the southern ACC water (Atkinson, 1991; Bathmann *et al.*, 1993; Chiba *et al.*, 2001). Although water temperature preference was not clear in *C. acutus*, the Polar Front may be the northern limit of distribution of the two species. *Metridia gerlachei* were collected in large numbers at most stations, located over the wide latitudinal range, showing no cold water preference as reported by Boysen-Ennen and Piatkowski (1988) and Hosie *et al.* (1997, 2000).

Rhincalanus gigas

Occurrence of a large proportion of adults, in particular males, in Group 4 (Table 2) suggests the reproduction was about to or just started during the sampling period. In Group 2, adults still appeared and the nauplii dominated, indicating reproduction was actively ongoing, while more advanced stages were dominant in Group 1. It is suggested that the reproduction progressed from Groups 1, 2, to 4 successively. On the other hand, reproductive phase of Group 3 was not clear, because the appearance of adults and nauplii implies ongoing reproduction while the large portion of Copepodite III and IV indicates early reproduction of the season. Voronina (1970) suggested that latitudinal shift of spawning activity of *R. gigas* might occur as the season progresses. Ward *et al.* (1996) reported a strong correlation between its mean population age and water temperature. However, no significant multiple regressions were recognized between environmental variables and NMDS ordination plot of each group. Latitude and latitude dependent variables such as water temperature and silicate concentration did not explain the observed successive reproduction between groups.

Life cycle and reproductive period of *R. gigas* have not been fully understood (Atkinson, 1998). Hagen and Schnack-Schiel (1996) suggested its reproductive period being from December to February. Meanwhile, the occurrence of late summer spawning has been reported (Marin, 1988), as well as late autumn spawning (Marin and Schnack-Schiel, 1993) and winter spawning (Bathmann *et al.*, 1993). The life cycle of *R. gigas* might be one year (Voronina *et al.*, 1978; Atkinson, 1991) or two years (Marin, 1988) depending on the location. Bathmann *et al.* (1993) suggested one year life cycle in ACC but two year life cycle in colder Weddell Gyre. Both Bathmann *et al.* (1993) and Marin (1988) suggested that breeding of *R. gigas* occurred in autumn when they adopt two year life cycles. The observed presence of adults in March in this study indicated that a two year cycle might commonly occur in this research area. Considering that no environmental variables could explain the ordination of groups, cohorts with one year life cycle and two years life cycle might coexist in the same area. Thus, cluster analysis might be less successful in differentiation of the populations of *R. gigas* in time and space.

Calanoides acutus

The results of this study demonstrated that the reproductive timing of *Calanoides acutus* varied depending on water temperature. Most of stations belonged to Groups 1, 3 and 4. Maturity was most advanced in Group 4 which was distributed in warmer, lower latitude than other groups. Advanced stages dominated also in Group 3 which appeared in the warmer areas with lower silicate concentration. Meanwhile, younger stages were predominant in Group 1 which appeared in colder areas with higher silicate concentration. Higher water temperature and lower silicate concentration are characteristics of northern ACC water (Chiba *et al.*, 2001). They reported that occasional intrusion of the northern ACC water to the southern ACC area due to the ACC meandering affected zooplankton community structure off east Antarctica. As we observed Group 1 and 3 appear along the east-west transect on the same latitude, the meandering of the ACC might cause the longitudinal variation of reproductive timing of *C. acutus*.

Adults hardly appeared in those major three groups, indicating reproductive activity

of *C. acutus* generally ceased by mid-March in this research area. This result is consistent with previous studies in the Weddell Sea (Hagen and Schnack-Schiel, 1996). On the other hand, in Groups 2 and 5 both of which consisted of only two stations, adults occupied 4% and even 59%, respectively, indicating reproduction was still ongoing or perhaps only just started. It is thus expected that reproductive timing in Group 5 be delayed in the colder area. No distinctive effects of environmental variables, however, were recognized to explain the late reproduction in Group 2.

Both one year and two years life cycles are known for *C. acutus*. Marin (1988) reported a one year cycle in the Antarctic Peninsula area while Drits *et al.* (1994) found a two year life cycle in the colder Weddell Sea. Atkinson *et al.* (1997) observed that the reproductive season of *C. acutus* started one to three months earlier in the warmer Scotia Sea than in the colder eastern Weddell Sea, but ceased in March in both regions. They thus suggested that *C. acutus* might adopt a two years life cycle in high latitude area where its reproductive period was limited and growth rate was slow due to low summer temperature and a short intense primary production season. Likewise, the observed temperature-dependent variation in copepodite stage composition of *C. acutus* gave us evidence of the variation in their life cycle strategy. Larvae of *C. acutus* which hatched during spring and summer reach copepodite IV or V before they start descending in autumn in a one year cycle (Marin, 1988) while they reached copepodite III or IV in a two year cycle (Drits *et al.*, 1994). Therefore, a two year cycle might be adopted in Group 1 in which copepodite II to IV were predominant, while a one year cycle might exist in Groups 3 and 4 in which copepodite IV and V were predominant.

In Group 5, which had delayed reproductive timing, it is unlikely that new-born larvae could have survived during the next winter. The adults in this group might survive till next reproductive season without spawning as Hagen and Schnack-Schiel (1996) pointed out. It is uncertain if the copepodite IV which dominated in Group 2 consisted of the new generation of that season or survivors from the previous year.

Calanus propinquus

Temperature dependent variation in copepodite stage composition was also recognized in *Calanus propinquus*, although the variation was not as clear as seen in *Calanoides acutus*. Copepodite IV and V occupied more than 90% of total abundance in Group 1 which was distributed exclusively at lower latitudes, and thus in warmer water. On the other hand, Group 4 which was dominated by younger copepodite stages appeared in colder water. As for the two minor groups, Group 2 and 3 consisted of the youngest and advanced stages, respectively. However, environmental variables failed to explain why Groups 2 and 3 occasionally appeared along the same latitude as Group 4.

Adult *C. propinquus* were almost absent from the subpopulations, indicating that their reproductive activity ceased by March, as was the case for *C. acutus*. However, the majority of stations belonged to Group 4 with younger individuals, indicating that the reproductive timing of *C. propinquus* might be delayed by one copepodite stage compared with that of *C. acutus*. The result agrees with Schnack-Schiel *et al.* (1991) and Schnack-Schiel and Hagen (1995) who pointed out that reproductive timing of *C. propinquus* occurred later than *C. acutus* in the Weddell Sea. On the other hand, it disagrees with Hagen and Schnack-Schiel (1996) who concluded that reproductive period was from

October to February in *C. propinquus* and November to March in *C. acutus* in the Weddell Sea. *Calanus propinquus* is known to switch feeding from herbivory to omnivory in autumn (Hopkins, 1985b) and actively feed during winter (Hopkins *et al.*, 1993b; Marin and Schnack-Schiel, 1993). Meanwhile, *C. acutus* are true herbivores which cease feeding during winter (Bathmann *et al.*, 1993; Hopkins *et al.*, 1993b). Considering the difference in feeding adaptation between the two species, the observed later or more prolonged reproductive period of *C. propinquus* than *C. acutus* may be reasonable because a sharp decline in phytoplankton production in autumn might limit the reproduction of *C. acutus*. Contradictory results of past studies mentioned above might be due to spatio-temporal variation in phytoplankton availability.

Calanus propinquus like *C. acutus*, is thought to undergo both one year and two year life cycles. Voronina *et al.* (1978) and Marin (1988) reported a one year cycle, whereas Drits *et al.* (1993) suggested a two year cycle in a small ice free, and thus low primary production area based on results of lipid contents analysis. *Calanus propinquus* starts descending at the copepodite IV or V stages in autumn in the one year model proposed by Marin (1988). However, the observed dominance of younger stages in March implies that a two year life cycle is generally adopted in the southern ACC area off east Antarctica.

Metridia gerlachei

Water temperature influences on copepodite stage composition were clear in *Metridia gerlachei*. Copepodite stages were most advanced in Group 1 which occurred exclusively in warmer, lower latitude areas, followed by Group 2 which included some stations located in lower latitude. On the other hand, younger copepodite stages dominated in Group 3 and 4 appeared in the colder water. Copepodite I was hardly observed through the research period. This is considered due to the mesh size (330 μm) of the plankton net being too coarse to catch small Copepodite I of *M. gerlachei*, as Huntley and Escritor (1992) pointed out. Therefore, it is difficult to compare the reproductive timing of *M. gerlachei* with the other three species.

Only *M. gerlachei* among the four species showed a significant relationship between copepodite stage composition and sea ice-related variables. Advanced stages dominated in Group 2 located in the area with poor sea ice extent in February while younger stages dominated in Group 4 in the area with extensive sea ice coverage. Burghart *et al.* (1999) found reproduction of *M. gerlachei* occurred successively from low latitude open water to high latitude ice edge area as spring and summer went on in the Weddell Sea. Groups 2 and 4 appeared along the east-west transect on the same latitude. Thus, the observed variation of copepodite stage composition between the groups suggested that longitudinal local variation, as well as latitudinal variation of sea ice coverage, influence the reproductive timing of this species.

In the present study, adults of *M. gerlachei* were almost absent except in Group 3, indicating that their reproductive activity had ceased by March in this research area. This result is consistent with past studies conducted in the Weddell Sea region which reported that the reproductive period of *M. gerlachei* was from September to March (Huntley and Escritor, 1992; Kurbjewit, 1993; Hagen and Schnack-Schiel, 1996). The distribution of *M. gerlachei* is deeper and vertically more scattered than that of the other three species

(Schnack-Schiel and Hagen 1995). Because this study was based on samples taken between 0–150 m, copepodite stage composition of this species within a water column might be biased. According to Schnack-Schiel and Hagen (1995), however, even data taken between 0–1000 m in the Weddell Sea shows that adults occupied only a small fraction in autumn, supporting the suggestion that *M. gerlachei* usually cease their reproduction before autumn.

Several life cycle strategies are known for *M. gerlachei*. Kurbjeweit (1993) reported one year life cycle in ACC but a two year life cycle in the colder Weddell Sea. Huntley and Escritor (1991) observed that all developmental stages were present through the year, and suggested that several generations occur during a year in the Gerlache Strait. Huntley and Escritor (1992) also suggested that two to three generations might be produced during a summer in Bransfield Strait. The reproductive period of *M. gerlachei* starts prior to the ice edge bloom, one to three months earlier than the other three species in the Antarctic Peninsula/Weddell Sea regions (Huntley and Escritor, 1991; Kurbjeweit, 1993; Schnack-Schiel and Hagen, 1995; Hagen and Schnack-Schiel, 1996). This early reproduction is not surprising because *M. gerlachei* are known to be omnivorous which feed actively during winter (Hopkins *et al.* 1993b). Thus, if spawning starts in the late winter or early spring also off east Antarctica, more than two generations could occur during a summer. The absence of adults in the surface layer observed in this study indicates that a year-round reproduction is unlikely to occur in this research area.

Regional difference in developmental timing

This study suggests that at least three species of the four copepod species flexibly change developmental timing during austral spring-autumn corresponding to spatio-temporal fluctuation of regional environment.

We observed both latitudinal and longitudinal variation in the developmental timing of the four copepod species. Southward progression of spawning and larval development has been also reported for Antarctic euphausiids, *Euphausia frigida* (Brinton, 1985) and *Thysanoessa macrura* (Hosie, 1991). Hosie (1994b) proposed the three possible direct/indirect environmental factors to cause the southward progression, temperature gradient, sea ice recession and phytoplankton availability associated with the sea ice recession. As for longitudinal variation, we attributed the variation to meandering of the ACC. Nicol *et al.* (2000) also reported that the ocean circulation south of the ACC was responsible for formation of the east-west gradient in the ecosystem structure off east Antarctica. They pointed out the variation in sea ice extent derived by the ACC dynamics might be responsible for the observed ecosystem variation. Our results showed that water temperature was the major factor of variability in the copepod maturity stage compositions, while no sea ice related variables was found to have significant correlations with those except for *M. gerlachei*. Regional variation of the Antarctic sea ice-condition is considerably large (Gloersen *et al.*, 1992), and biological productivity is enhanced in the water when ice edge bloom occurs (*e.g.* Spindler and Dieckmann, 1994). Therefore, it would be no wonder if sea ice condition affected reproductive and developmental timing of the copepod species. The results might be derived because the sampling was done in March, when ice edge bloom was ending.

The spatio-temporal variability in the developmental timing of the copepods species

implied that their life cycle might be shifted from one-year to multi-year. This study is, however, based on the samples taken only one time of the year, and the fate of the observed cohorts is actually unknown. It is difficult to determine their life cycle duration without knowing the maturity stage composition in other seasons. Shift of life cycle strategy of the major copepod species must affect productivity of the higher trophic level animals and off east Antarctica where krill biomass is low. Mechanism of their reproduction and development should be further studied by seasonal and interannual time-series observations.

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