

MACROZOOPLANKTON DISTRIBUTION AROUND THE ANTARCTIC
DIVERGENCE OFF WILKES LAND IN THE 1996 AUSTRAL
SUMMER: WITH REFERENCE TO HIGH
ABUNDANCE OF *SALPA THOMPSONI*

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Abstract: Distribution and abundance of macrozooplankton off Wilkes Land, Antarctica in austral summer were studied in relation to environmental features associated with the Antarctic Divergence (AD). A single species of salp, *Salpa thompsoni*, dominated others both numerically and by biomass, occupying 44% of mean total abundance with the maximum density of 29873 inds./1000 m³ (44 mg C/m³). Abundance of Antarctic krill, *Euphausia superba*, was low through the sampling area (max. 41 inds./1000 m³: 2.9 mg C/m³). Total length frequency and stage of maturity of *E. superba* suggested relatively late spawning and low recruitment ratio, respectively. Salps and major copepod species showed a spatially partitioned pattern across the AD, in which the former dominated in areas north and south of the AD while the latter was predominant near the AD. Active reproduction of salps seemed to be ongoing in the areas where mean chl *a* concentration within the euphotic zone was around 0.4–0.6 µg/l, but suppressed where that was higher than 0.6 µg/l. Clogging of mucous nets of salps was considered to be one of the causes of their low abundance at high chl *a* concentration as observed near the AD. The results suggest that the relatively limited phytoplankton growth, particularly in the eastern side of this research area, may have provided the food condition which was optimal for salp reproduction but unfavorable for other phytoplankton consumers, permitting an explosive population growth of salps.

key words: macrozooplankton, distribution, Antarctic Divergence, Wilkes Land, *Salpa thompsoni*

Introduction

Zooplankton are concentrically distributed around Antarctica (BAKER, 1954) with a certain zonation pattern (HEMPEL, 1985) which suggests that the Antarctic Divergence, one of the Antarctic frontal systems, function as a boundary of zooplankton zonation. However, only a little is known about the mechanism at the Antarctic Divergence effecting the distribution patterns.

Distribution and abundance of Antarctic zooplankton are subject to yearly variability (e.g. KAWAMURA, 1986; SIEGEL and PIATKOWSKI, 1990; PARK and WORMUTH, 1993; HOSIE, 1994). Since Antarctic krill (*Euphausia superba*) is broadly recognized as a key species that supports the Antarctic food web, the majority of studies have been

focused on resource variability of this species (reviewed by EVERSON and MILLER, 1994; KNOX, 1994; NICOL, 1994) and ascribed it to diverse oceanographic and/or biological factors (SAHRHAGE, 1988). Recently, however, the ecological importance of other plankton species such as salps and copepods have attracted much scientific attention. Scientists now see a growing need to change the previous perception of a krill-dominated simple and stable Antarctic food web to a more complex and unstable one (NICOL, 1994). In particular, as observed in other oceanic areas, the occasional appearance of salp blooms may significantly influence the structure of the Antarctic ecosystem (HUNTLEY *et al.*, 1989; MARCHANT and MURPHY, 1994; SCHNACK-SCHIEL and MUJICA, 1994; SIEGEL and LOEB, 1995). However, causes of salp blooms and possible ecological interaction between salps and Antarctic krill remain less understood.

A number of integrated oceanographic and/or biological approaches to understanding/variability of distributions and abundances of Antarctic zooplankton have recently been conducted around the Antarctic Peninsula and Weddell Sea region (*e.g.* PIATKOWSKI, 1989; SIEGEL and PIATKOWSKI, 1990; PARK and WORMUTH, 1993; SCHNACK-SCHIEL and MUJICA, 1994). To obtain comprehensive knowledge of the Antarctic zooplankton community in relation to resource variability of *E. superba*, equivalent efforts in other, less studied areas are required. In particular, little knowledge has been accumulated in the area off Wilkes Land (*e.g.* MARUYAMA *et al.*, 1982; KAWAMURA, 1986). In the present study, we observed the distribution and abundance of macrozooplankton off Wilkes Land, and investigated possible environmental factors associated with the Antarctic Divergence which contribute to formation of the observed distribution and abundance pattern, with particular reference to high abundance of salps.

Materials and Methods

Field sampling

Sampling was conducted from January 26 to February 3, 1996, off the Adelie Coast of Wilkes Land in the Antarctic Ocean during the 64th cruise of the R/T Ship UMITAKA-MARU III of Tokyo University of Fisheries. A series of sampling stations were set between 62°S to 65°30'S and 135°E to 145°E to cover the expected area of the Antarctic Divergence (Fig. 1).

Macrozooplankton samples were collected using an ORI net (mesh size: 2 mm, mouth diameter: 1.6 m) equipped with a flow meter and RMD (Digital Memory Depth Meter; Rigosha®). The net was towed obliquely at a ship speed of 3.7 km/h between the approximate depths of 0 and 200 m. Every tow took about 20 to 30 min. When the flow meter did not work, the water volume filtered was determined by multiplying the effective mouth area of the net by distance traveled which was calculated as a function of ship's speed over the period and the maximum depth reached. If the depth meter did not function, the maximum depth was estimated from wire angle at the maximum wire out. When zooplankton sample volumes were very large, mainly due to the large amount of salps, the catch was immediately subdivided on board, and aliquots of the sample which could be placed in one or two 2-l bottles were preserved. All *Euphausia superba* were removed from the catches and kept separately prior to the subdivision.

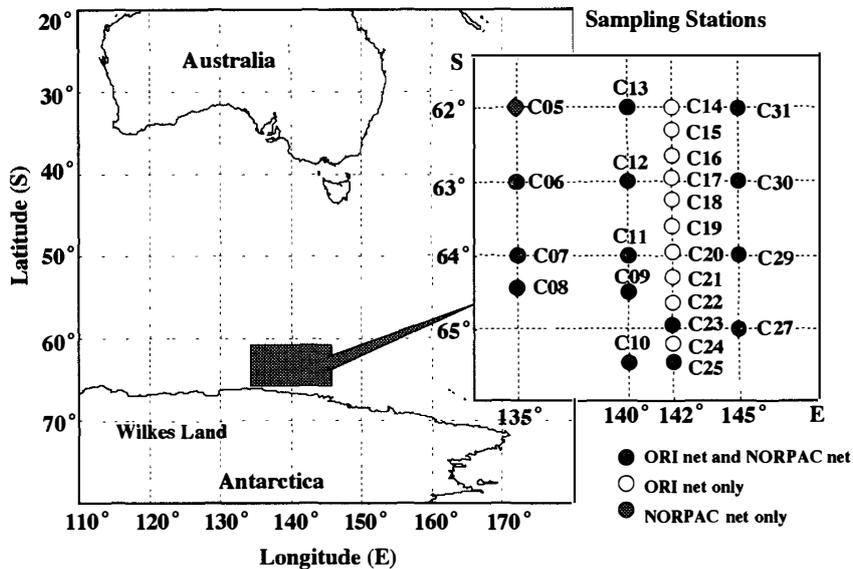


Fig. 1. Survey area and sampling stations. Only an ORI net was towed at Stns C14 to C22, and C24; only a NORPAC net was used at Stn C05. Both the ORI net and NORPAC net were towed at other stations.

As all animals collected by the ORI net were defined as macrozooplankton in this research, some micronecton species such as *E. superba* and ichthyoplankton were counted into the macrozooplankton. For collection of *E. superba* larvae, a NORPAC net (mesh size: 330 μm , mouth diameter: 45 cm) was towed vertically from 150 m deep at stations except C14 to C22 and C24. Zooplankton were preserved in buffered 5% formalin soon after sampling.

Vertical hydrographic information such as water temperature and salinity of each station was obtained using a CTD. To supplement CTD records, measurement by XBT was conducted every 10' of latitude along each longitudinal sampling line. The location of the Antarctic Divergence was determined based on water temperature profiles. For analyses of chl *a*, sea water samples were collected from six layers between 0 and 145 m at each station using a Rosette Multi-Sampler with Niskin Bottles mounted on a CTD frame, or a Van Dorn Water Sampler.

Sample analyses

After removing large animals such as salps, polychaetes, amphipods, adult euphausiids, and jellyfishes, macrozooplankton were divided using a Motoda plankton splitter (MOTODA, 1959) four times (1/16) at maximum. Animals were sorted and counted for 14 categorical taxa as follows: polychaetes, copepods, decapods, euphausiids, amphipods, ostracods, chaetognaths, cnidarians, thecosomatous pteropods, gymnosomatous pteropods, cephalopods, thaliaceans, appendicularians and fishes. All counts were adjusted to number of individuals per 1000 m^3 . For species identification of salps, we did not conduct minute examination of *Salpa thompsoni* and *Salpa gerlachei* separately, but counted both as *S. thompsoni* since the latter is considered as a clinal form of the former (SOEST, 1974).

Carbon biomass of numerically abundant (>1% of total abundance) categorical

taxa: salps, euphausiids, copepods, amphipods, pteropods and chaetognaths, was estimated from constant wet weight using conversion factors in DAVIS and WIEBE (1985): 8.5% for copepods, 8.2% for euphausiids, 7.9% for amphipods, 3.5% for chaetognaths, and 7.0% for pteropods. Prior to the conversion, possible weight loss of samples after several months preservation was taken into account. The ratio of weight loss was assumed to be 17% for crustacean species and chaetognaths based on the study by AHLSTROM and THRAILKILL (1963). Although the chemical composition of molluscs was thought to be different from that of crustaceans and chaetognaths, the same ratio was adopted for pteropods because there were no equivalent references found on their weight loss. Furthermore, considering that a large portion of the thecosomatous pteropod shell was lost during the preservation, the obtained constant wet weight and carbon biomass of pteropods must be conservative. For salps, wet weight loss was assumed to be 50.2% following the study of REINKE (1987), and their carbon biomass was estimated from the corrected wet weight using the conversion factor described in HUNTLEY *et al.* (1989). All carbon biomass was standardized to mg carbon per m³.

Solitary and aggregate generations of salps were counted separately. Only young and mature stages without embryonic characteristics, such as a placenta and eleoblast, were included as solitary forms. Although FOXTON (1966) reported that an embryo could be released from its parent when its body length reached about 4 to 5 mm, it was difficult to discriminate whether they were naturally released or accidentally expelled during the sampling. Therefore, any size of detached individuals with embryonic characteristics were not counted in solitary forms. In addition, body lengths (oral-atrial distance) of 100 individual aggregate forms which were extracted randomly from each sample were measured to the nearest millimeter to examine the body length distribution at each station.

For *Euphausia superba*, size frequency and stage of maturity were examined. Total length (from the tip of rostrum to the posterior end of telson) of all specimens was measured with an accuracy of 1 mm. Stage of maturity for each post larval individual was determined according to the scheme of MAKAROV and DENYS (1981) as stage I: juveniles, stage II: subadults, and stage III: adults. Adult females were subdivided into IIIA: without spermatophores, IIIB: with spermatophores but ovary not developed, IIIC: with developing ovary, IIID: gravid, and IIIE: recently spawned. Frequency of both total length and stage of maturity at each station was adjusted to number of individuals per 1000 m³ and summed to estimate the size and stage of maturity over the entire sampling area. The recruitment index of *E. superba*, which is the ratio of the first year population to the sum of populations of all age classes, was estimated following the description in SIEGEL and LOEB (1995). Proportion of first year population was determined based on total length frequency.

Euphausia superba larvae obtained by NORPAC net were sorted and counted for each larval stage.

Determination of chlorophyll *a* concentration

Chlorophyll *a* was used as an index of the standing stock of phytoplankton in the present study. After each water sample was filtered with a Whatman GF/F filter, photosynthetic pigments were extracted with dimethyleformamide (SUZUKI and

ISHIMARU, 1990), and the concentration of chl *a* was measured by the fluorometric method (STRICKLAND and PARSONS, 1972) using a Turner Design fluorometer (10R).

Results

Environmental conditions

Figure 2 shows a water temperature profile between 0 and 450 m of a latitudinal sampling line along 142°E. In this study, we used the term “AD” for the approximate location of the Antarctic Divergence where the 1.5°C isotherm rising from the depth was recognized on the profiles. The AD was found between 64°S and 64°30'S through

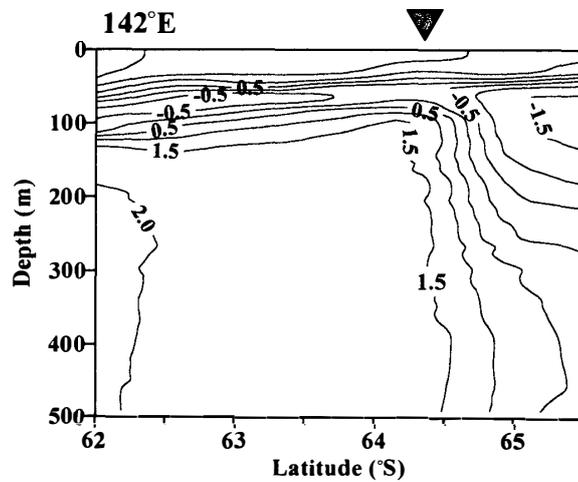


Fig. 2. Water temperature (°C) profile along a longitudinal sampling line (142°E). The black triangle indicates the approximate location of the Antarctic Divergence.

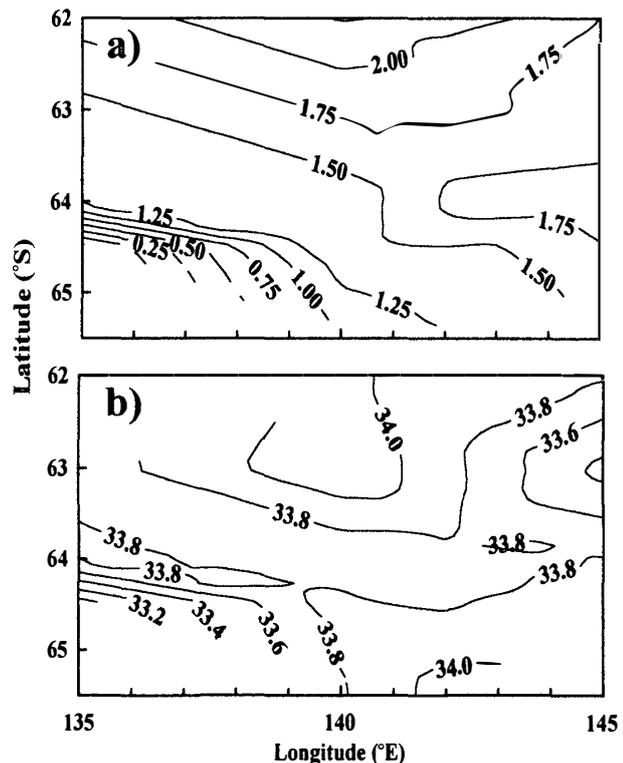


Fig. 3. a) Sea surface temperature (°C), and b) sea surface salinity (PSU) in the sampling area.

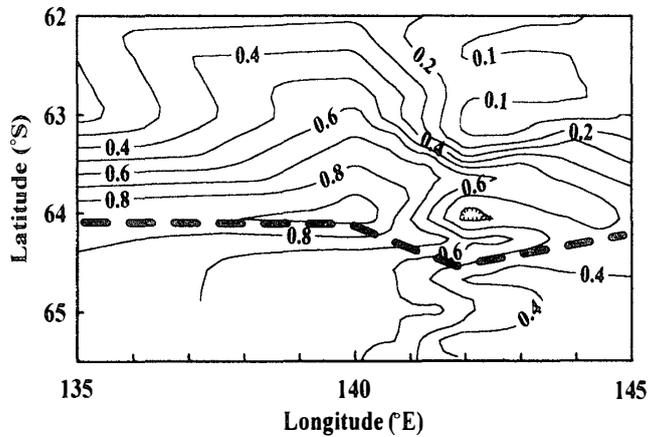


Fig 4. Mean chl *a* concentration ($\mu\text{g/l}$) within the euphotic zone in the sampling area. The dashed line indicates the approximate location of the Antarctic Divergence (AD)

the sampling area. The distribution of surface temperature and surface salinity shows that a relatively warmer and higher salinity water mass extended to the south, particularly in the eastern part of the area (Fig. 3).

The mean chl *a* concentration within the euphotic layer ranged from $0.15 \mu\text{g/l}$ at Stn C31 to $0.97 \mu\text{g/l}$ at Stn C07 (Fig. 4). These values are consistent with those reported in previous studies conducted in similar latitudes off Wilkes Land in austral summer (YAMAGUCHI and SHIBATA, 1982; YAMAGUCHI *et al.*, 1985). Chlorophyll *a* was highly concentrated near the AD, particularly in the western part of the research area.

Macrozooplankton distribution and abundance

A single species of salp, *Salpa thompsoni*, dominated the macrozooplankton both numerically and by biomass. *Salpa thompsoni* accounted for 44% of total macrozooplankton abundance through the sampling area. Copepods followed salps and comprised 40%, among which *Rhincalanus gigas*, *Calanus propinquus*, *Calanoides acutus* and *Metridia gerlachei* occupied more than 90%. The sum of euphausiids, pteropods, chaetognaths and amphipods was only 16%, and other taxa such as polychaetes and cnidarians were less than 1%. Macrozooplankton abundance was markedly high at Stns C21 and C29 (Fig. 5). Salps were most dense ($29873 \text{ inds./}1000 \text{ m}^3$) at Stn C29 while copepods were most abundant at Stn C21 ($29000 \text{ inds./}1000 \text{ m}^3$). Although considerably abundant, salps were not distributed uniformly throughout the sampling area; *i.e.*, they comprised more than 80% of total macrozooplankton abundance at Stns C10, C17, C18, C25 and C29, but less than 5% at Stns C07, C13, C14 and C21 where copepods were more numerous. In particular, the abundance of salps markedly decreased at stations near the AD. Table 1 shows mean carbon biomass of major macrozooplankton taxa. In terms of carbon biomass, salps dominated others, again reaching the mean biomass of 8.15 mg C/m^3 (max.: 44.45 , min.: 0.15). The mean copepod biomass was 1.34 mg C/m^3 (max.: 9.43 , min.: 0.07).

Euphausia superba

Adults, juveniles, and larvae of *Euphausia superba* were collected only at a few stations, the majority of which were located south of the AD (Fig. 6). The maximum abundance of adults and juveniles of $41 \text{ inds./}1000 \text{ m}^3$, 2.9 mg C/m^3 (35 mg/m^3 in wet weight) was recorded at Stn C23 which was the only location where a krill swarm was

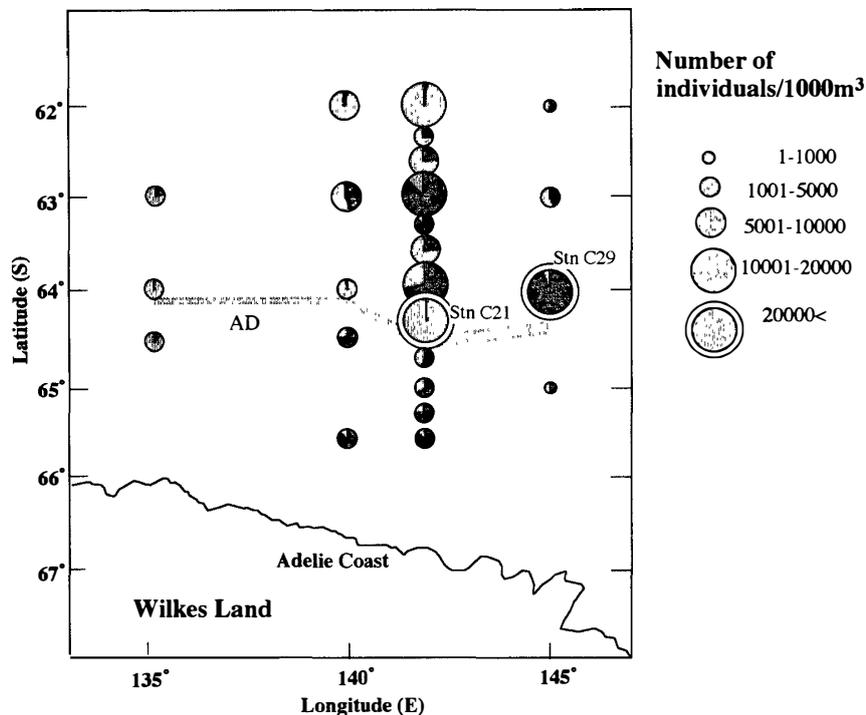


Fig. 5. Distribution and abundance of macrozooplankton (number of individuals per 1000 m³). The black areas in the circles show percentage abundance of *Salpa thompsoni* to the total. The shaded line indicates the approximate location of the Antarctic Divergence (AD).

Table 1. Mean carbon biomass (mg C/m³) of numerically abundant macrozooplankton taxa.

	Salpa	Euphausiacea	Copepoda	Amphipoda	Pteropoda	Chaetognatha
Mean + SD	8.15 + 13.21	1.07 + 1.07	1.34 + 1.88	0.79 + 0.96	0.41 + 0.38	0.14 + 0.13
Maximum	44.45	3.85	9.43	3.61	1.32	0.60
Minimum	0.15	0.02	0.07	0.10	0.02	0.01

seen on an echo sounder (frequency: 120 kHz). As for larvae, a small quantity of calyptopis I and calyptopis II stages (max. 204 inds./1000 m³) were collected while no calyptopis III and furciliae were caught. Although neither stages of nauplius nor metanauplius were examined, they are known to live deeper than the sampling depth of 150 m (MARR, 1962).

Total length frequency in all samples plotted with 2 mm intervals showed a smaller mode at 29–30 mm and a larger mode at 47–49 mm length (Fig. 7). The mean total length of first year class individuals was assumed to be 25 to 32 mm. With this assumption, the recruitment index was estimated to be 0.024. Figure 8 shows the stage of maturity of females in which advanced stages, 3C and 3D, were most abundant.

Salpa thompsoni

Figure 9 shows the distribution and abundance of *Salpa thompsoni* with the ratio of solitary individuals. Solitary individuals were mainly collected at stations located

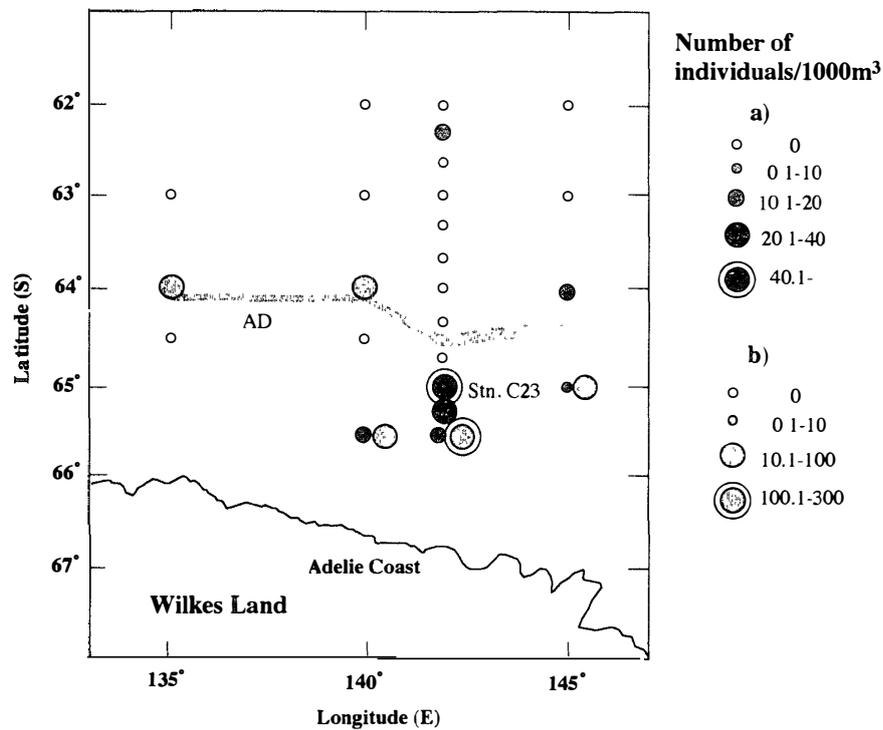


Fig. 6. Distribution and abundance of *Euphausia superba* for a) adults and juveniles, and b) larvae (number of individuals per 1000 m³). The shaded line indicates the approximate location of the Antarctic Divergence (AD).

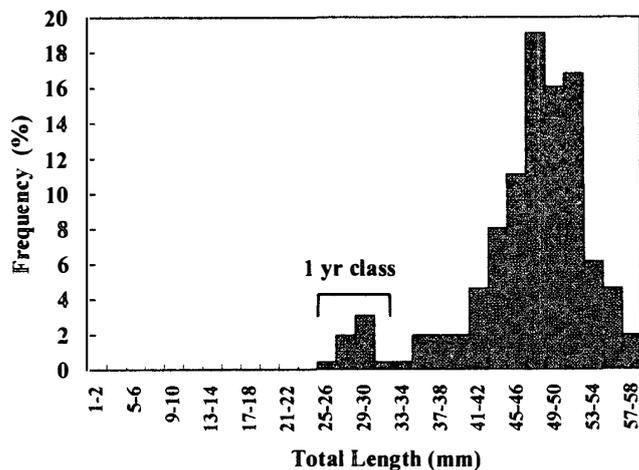


Fig. 7. Total length frequency of adult and juvenile *Euphausia superba* plotted at 2 mm intervals. The smaller mode of frequency at total length of 25 to 32 mm is assumed to be composed of first year class individuals.

north of the AD while they were hardly observed south of the AD. Both the body length composition and the mean body length of aggregate forms varied among stations, ranging from 14.0 mm at Stn C09 to 38.6 mm at Stn C11. Particularly larger individuals were dominant at Stns C07 and C11 located near the AD (Fig. 10).

To examine the ecological relationship between salps and other zooplankton in terms of competition for food, distribution patterns across the AD of salps and major copepod species, *Rhincalanus gigas*, *Calanus propinquus*, *Calanoides acutus* and *Metridia gerlachei*, were compared. *Rhincalanus gigas* and *C. acutus* were reported to be generally

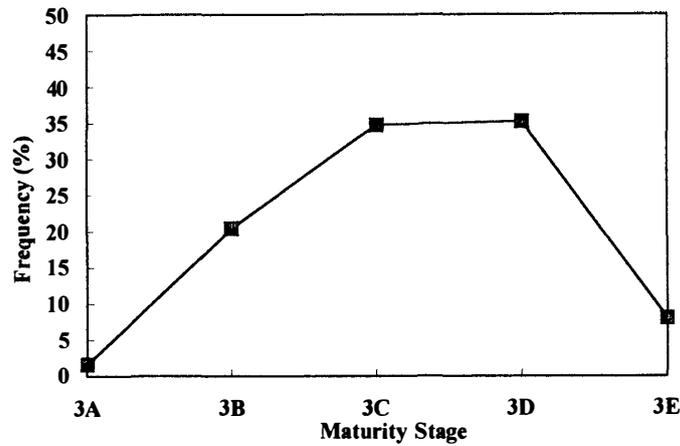


Fig. 8. Stage of maturity of female *Euphausia superba* determined according to the scheme of MAKAROV and DENYS (1981): 3C to 3E are advanced stages (3C: with developing ovaries, 3D: gravid, 3E: recently spawned).

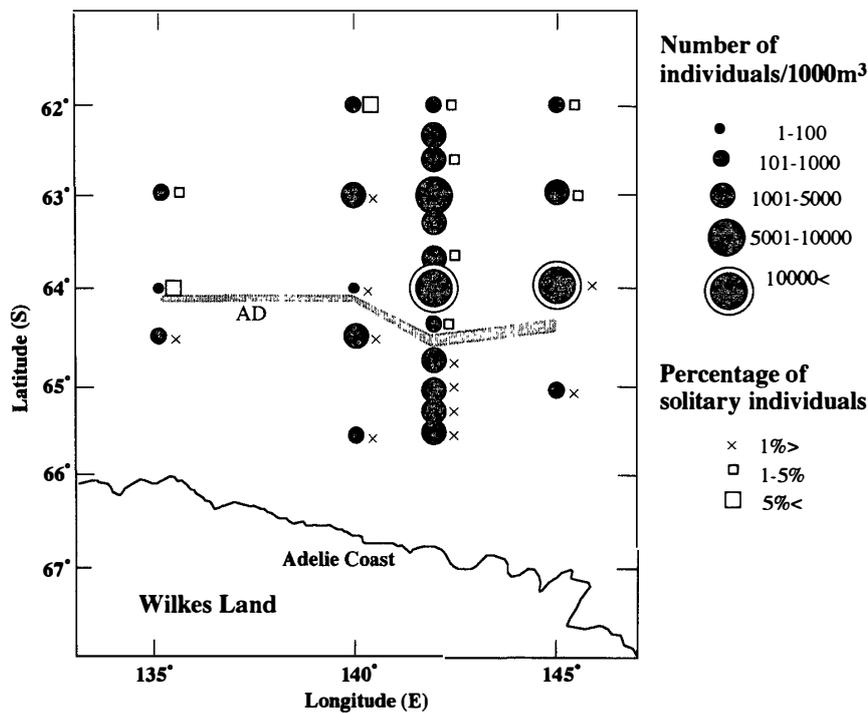


Fig. 9. Distribution and abundance of *Salpa thompsoni* (number of individuals per 1000 m³). Circles show abundance of *S. thompsoni*, and blank squares indicate percentage abundance of solitary individuals to the total. The shaded line indicates the approximate location of the Antarctic Divergence (AD).

herbivorous (HOPKINS *et al.*, 1993). *Calanus propinquus* was recognized to be a phytoplankton eater although they showed some omnivorous features (HOPKINS, 1985). HUNTLEY and ESCRITOR (1992) reported that *M. gerlachei* consumed mainly phytoplankton during summer although the species was known to be omnivorous. Therefore, we considered these four copepod species as possible important phytoplankton

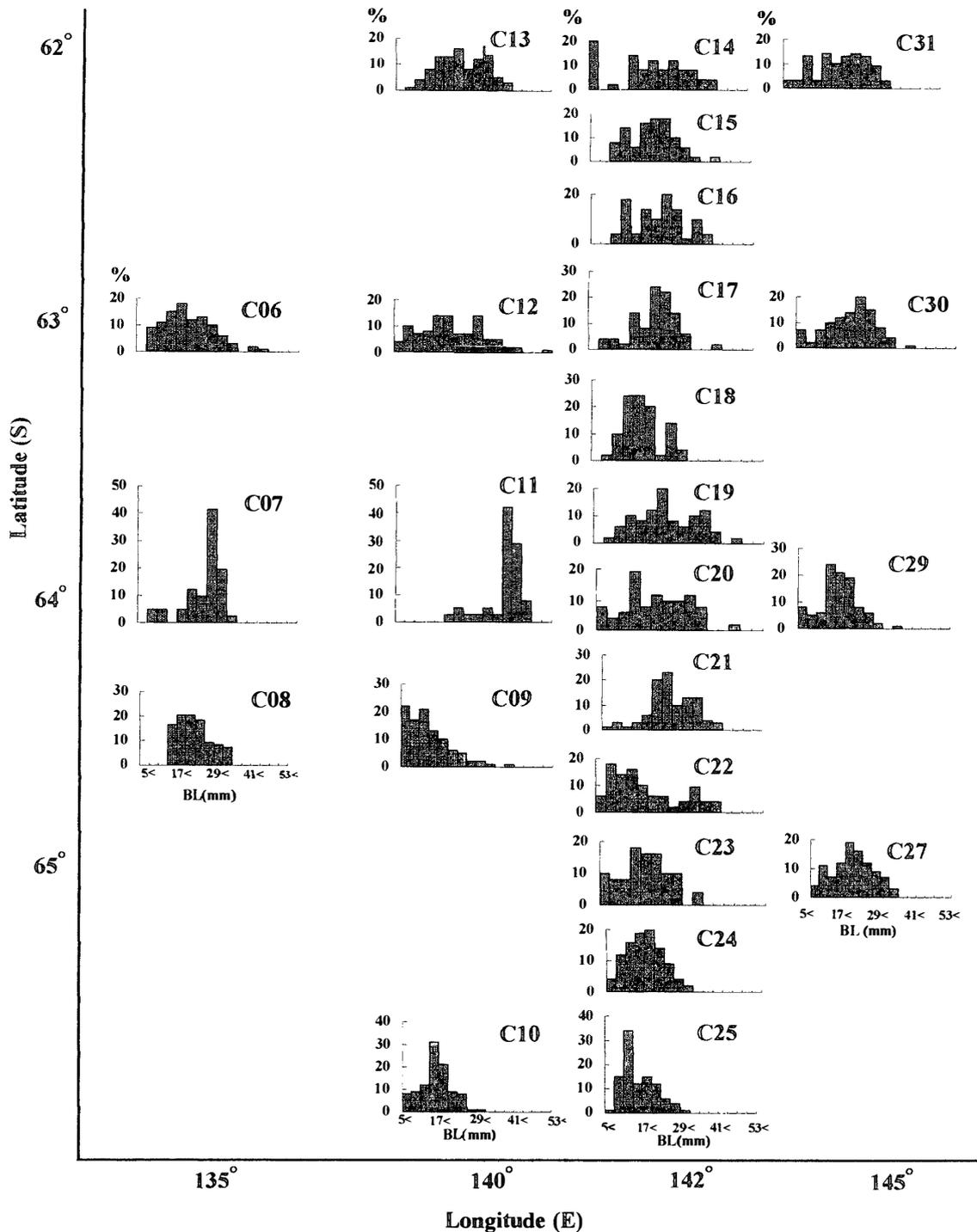


Fig. 10. Body length frequency of aggregate forms of *Salpa thompsoni* plotted at 3 mm intervals for each sampling station

consumers as well as salps. Mean carbon biomass of salps and the major copepods at the stations located north of the AD, near the AD, and south of the AD are compared in Fig. 11. Salps were most abundant and predominated over the copepods north of the AD, and also dominated south of the AD although the biomass was smaller than

Fig. 11. Mean carbon biomass (mg C/m³) of *Salpa thompsoni* (light columns) and major copepod species *Rhincalanus gigas*, *Calanus propinquus*, *Calanoides acutus*, and *Metridia gerlachei* (dark columns) at three location categories: north of the AD, near the AD and south of the AD (the AD : approximate location of the Antarctic Divergence). Deviation bars indicate standard deviations.

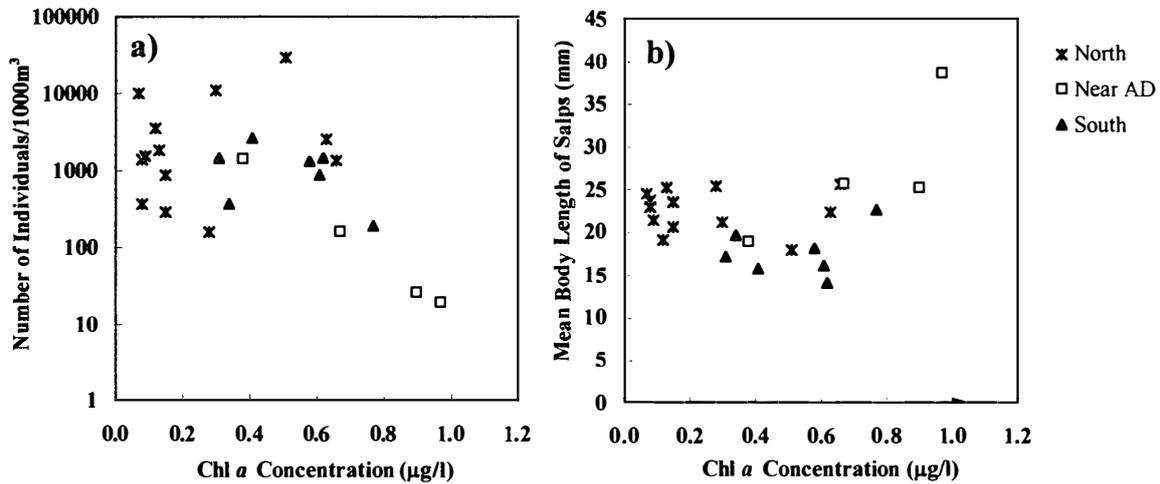
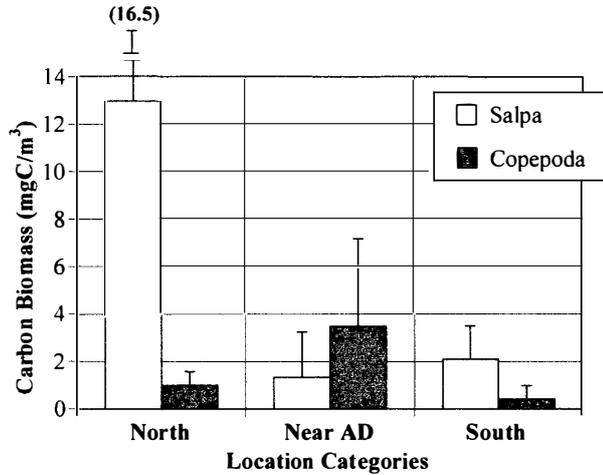


Fig. 12. a) Relationship between mean euphotic zone chl *a* concentration ($\mu\text{g/l}$) and abundance (number of individuals/1000 m³) of *Salpa thompsoni*, and b) relationship between mean euphotic zone chl *a* concentration ($\mu\text{g/l}$) and mean body length of aggregate forms of *S. thompsoni* (mm), for each sampling station. Asterisks, squares and triangles indicate the values at stations located north of the AD, near the AD and south of the AD, respectively (the AD: approximate location of the Antarctic Divergence).

that in the north. On the other hand, copepods showed the inverse distribution pattern to that of salps: their biomass increased greatly and predominated near the AD.

As sampling procedures were conducted continuously night and day during the research period, a bias caused by diel vertical migration (DVM) of the animals on the observed distribution pattern should be considered. Although *S. thompsoni* is known to perform DVM between the surface and 200 to 300 m (CASARETO and NEMOTO, 1986), no statistically significant difference was found between abundance of salps obtained at stations of night sampling and day sampling (Mann-Whitney's U-test, $p > 0.05$, $U = 47$, $n = 6$ for night and 18 for day). Abundance of the major copepods was significantly different in night and day (Mann-Whitney's U-test, $p < 0.05$, $U = 23$, $n = 6$ for night and 18 for day). For both salps and the copepods, however, high standard deviations (salps: mean \pm SD = 7091 ± 11939 for night, 1795 ± 2253 for day; copepods:

mean \pm SD = 7034 \pm 11384 for night, 1264 \pm 1614 for day) suggest that differences between locations may have more significance than DVM.

Since mean chl *a* concentration within the euphotic zone was higher near the AD where salp biomass decreased, the relationship between the distribution pattern of salps and chl *a* concentration was examined for each location category across the AD (Fig. 12a). No simple linear correlations were found between chl *a* concentration and abundance of salps. However, salps were generally abundant north and south of the AD, and their density was over 1000 inds./1000 m³ particularly at stations with moderate chl *a* levels (around 0.4 to 0.6 μ g/l). On the other hand, their abundance dropped at stations near the AD with high chl *a* levels. Chlorophyll *a* concentration and mean body length of aggregate salps were compared in Fig. 12b. Smaller aggregate forms dominated in the south of the AD while their mean body length became larger near the AD. No significant linear correlation was recognized between chl *a* concentration and body length of salps again. However, there was a trend in which smaller individuals dominated where chl *a* was around 0.4 to 0.6 μ g/l while their mean body lengths linearly increased at stations with chl *a* of higher than 0.6 μ g/l. These results suggest that a possible relationship may exist between chl *a* concentration and both abundance and size of salps.

Discussion

The AD and optimal conditions for salp bloom

In the present study, the abundance (max. 29873 inds./1000 m³) of *Salpa thompsoni* was high compared with previous records on swarms of this species around the Antarctic Peninsula: *e.g.* 44–671 inds./1000 m³ (HUNTLEY *et al.*, 1989); 0–1333 inds./1000 m³ (NISHIKAWA *et al.*, 1995); max. 5010 inds./1000 m³ (PARK and WORMUTH, 1993). Salps adopt an opportunistic reproductive strategy in which they can reproduce aggregate forms quickly by budding and attain high density swarms in a short period when the ambient conditions become optimal (*e.g.*, ALLDREDGE and MADIN, 1982; EVERSON, 1984), while they tended to remain at low density most of the year (FOXTON, 1966; EVERSON, 1984). The observed high abundance of salps suggested that environmental conditions were favorable to salp reproduction at the time in the research area.

In this study, salps were numerically abundant at chl *a* levels of 0.4–0.6 μ g/l where smaller aggregate forms dominated. High density and large fraction of smaller, young aggregate forms indicates that asexual reproduction was actively on-going at this chl *a* level. As ALLDREDGE and MADIN (1982) reported, the optimal food supply for most pelagic tunicates appears to be below the maximum bloom density of phytoplankton. Therefore, moderate phytoplankton growth expected from the chl *a* levels of 0.4–0.6 μ g/l was assured to be one of the necessary conditions for occurrence of the observed salp bloom. On the other hand, salp abundance decreased while their mean body length gradually increased at higher chl *a* levels (more than 0.6 μ g/l), implying that reproduction of salps was gradually suppressed as chl *a* concentration increased over a certain level. NISHIKAWA *et al.* (1995) observed salp blooms near the Antarctic Peninsula, and reported that *S. thompsoni* was almost exclusively distributed in areas with chl *a* concentration of 0.5 μ g/l or lower. This relationship between chl *a* concentration and distribution of

salps is generally consistent with our results. It has been reported that mucous net of salps becomes clogged under high concentration of food particles because salps cannot alter the filtration rate responding to the ambient food concentration, with the result that the animals starve to death (MADIN, 1974; HARBISON and GILMER, 1976; HARBISON *et al.*, 1986). This clogging effect might be one of the possible causes of the observed low abundance of salps at high chl *a* levels. Moreover, since *S. thompsoni* were reported as they released young aggregate forms at a shallow depth (CASARETO and NEMOTO, 1986) where phytoplankton are abundant, this behavior could be responsible for further enhancing the clogging of smaller individuals.

In our observations, salps dominated not only north but also south of the AD. CASARETO and NEMOTO (1986) also reported a large catch of this species south of the AD in the vicinity of our study area. Previous studies, however, have reported that *S. thompsoni* is an oceanic species mainly distributed in the warmer ice free zone (FOXTON, 1966; SIEGEL and PIATKOWSKI, 1990; HOSIE, 1994), implying that the AD usually functions as the southern boundary of distribution of the species. We observed solitary forms exclusively north of the AD. Since *S. thompsoni* are known to be sparsely distributed mainly as solitary forms without active reproduction in the Antarctic Ocean during winter (FOXTON, 1966), the absence of solitary forms south of the AD in our survey suggests that salps were originally distributed north of the AD. These facts imply that *S. thompsoni* could occasionally expand their distribution to the south over the AD.

The higher chl *a* concentration (0.8–1.0 $\mu\text{g}/\text{l}$) near the AD, particularly in the western part of the research area, suggests that active nutrients supply by upwelling enhanced phytoplankton growth. On the other hand, phytoplankton growth seemed to be relatively limited near the AD in the eastern part of the research area. In our study, a relatively warm and high salinity surface water mass was observed to extend to the south over the AD. This suggests that upwelling may to some extent weaken in the eastern area, reducing phytoplankton abundance to the optimal level for reproduction of salps at which clogging of their mucous nets did not occur. Such a condition might allow salps to expand their distribution to the south of the AD. Water temperature itself does not seem to limit the distribution of salps since the animals were collected even at the highest latitude in the western part of the research area with sub-zero water (0–100 m depth average).

Causes of the spatial partitioning between salps and major copepods

Carbon biomass of major copepods was highest near the AD with high chl *a* concentration in contrast to that of salps. Previous studies have reported similar spatial partitioning near the Antarctic Peninsula between salps and Antarctic krill (HUNTLEY *et al.*, 1989; NISHIKAWA *et al.*, 1995), and salps and other zooplankton (PARK and WORMUTH, 1993; KAWAMURA *et al.*, 1994). As an explanation of the spatial partitioning observed near the British Island, FRASER (1962) suggested that salp swarms can exclude competitor herbivores from the area by consuming a large portion of phytoplankton food. ALLDREDGE and MADIN (1982) supported FRASER's suggestion, pointing out the large filtration and ingestion rate of salps as well as their quick reproduction. However, our results imply that the ambient food availability presented beforehand could contribute to formation of the distribution pattern rather than direct competition

between salps and other herbivores. Not only food concentration, but also difference in types of food should be considered. Larger diatoms ($> 100 \mu\text{m}$ and $20\text{--}100 \mu\text{m}$) such as *Thalassiothrix antarctica* and *Fragilariopsis kergulensis* were highly concentrated at stations with higher chl *a* while nanoplankton ($5\text{--}20 \mu\text{m}$) were dispersed through the survey area (HORIMOTO, unpublished). Unlike salps which unselectively feed on various types of foods from bacteria to inorganic debris (ALLDREDGE and MADIN, 1982), and are capable of ingesting particles as small as $1 \mu\text{m}$ in diameter efficiently (MADIN, 1974; HARBISON and MCALISTER, 1979), the four major copepod species, *Rhincalanus gigas*, *Calanus propinquus*, *Calanoides acutus* and *Metridia gerlachei* were reported to feed selectively on larger diatoms with enriched food supply (SCHNACK, 1985). Therefore, phytoplankton population composition and availability might have been unfavorable for population growth of these copepods and contributed to observed their low abundance north and south of the AD.

Moreover, direct competition for food between salps and the major copepods is unlikely to occur in terms of differences in their respective reproductive strategies. In contrast to salps which adopt an opportunistic reproductive strategy by taking advantage of temporal and/or local food concentration (EVERSON, 1984), the large copepod species keep their population at relatively constant level through the seasons (MURANO, 1983; KNOX, 1994). Therefore, a possible factor that determines the distribution pattern of salps and copepods might be a change in type of food and timing of its availability, which incidentally provides a condition optimal for salps but unfavorable for selective grazers such as the copepods.

Ecological interaction between *Euphausia superba* and *Salpa thompsoni*

Previous studies have reported that the biomass and/or catch of *Euphausia superba* off Wilkes Land is small in comparison to these in other areas in the Antarctic Ocean (MARR, 1962; MACKINTOSH, 1973, reviewed by NICOL, 1994; KNOX, 1994). Consistent with these records, the density of *E. superba* in this study was quite low, even if we take account of possible underestimation due to limited capacity of the sampling gear and high net avoidance ability of the species. The maximum abundance of 35 mg/m^3 in wet weight (2.9 mgC/m^3) was even lower than that found in other net surveys conducted off Wilkes Land: for example, 1.2 g/m^3 in wet weight (98 mgC/m^3) at minimum in MATUDA *et al.* (1979). NEMOTO and MURANO (1979 quoted in MURANO, 1983) reported that the most frequently observed patch density of *E. superba* in the Antarctic Ocean was about 200 g/m^3 in wet weight (16400 mgC/m^3). The recruitment index (0.024) and stage of maturity we obtained suggest unreproductive conditions and relatively late spawning in comparison to results of the long term study by SIEGEL and LOEB (1995) near the Antarctic Peninsula.

One might attribute low reproduction of *E. superba* to characteristic sea ice conditions in this area, off the Adelie Coast of Wilkes Land, where sea ice compactness and extent have been reported as the least around Antarctica (GLOERSEN *et al.*, 1992). There is accumulating evidence that the sea ice condition can have a crucial influence on phytoplankton growth rate, especially the timing and quantity of the spring bloom in Antarctic Water (SMITH *et al.*, 1988; SPINDLER and DIECKMANN, 1994). Phytoplankton abundance and growth could subsequently affect macrozooplankton biomass, as

well as the recruitment and overwintering success of *E. superba*. Sea ice supports overwintering of *E. superba* not only by providing ice algae food but also providing them with protection from predators (SMETACEK, *et al.*, 1990; DALY and MACAULAY, 1991).

After studying the long term resource variability of *E. superba* near the Antarctic Peninsula, SIEGEL and LOEB (1995) found a significant relationship between sea ice condition, salp abundance, and recruitment success of *E. superba*. They pointed out that increased sea ice extent had a positive effect on *E. superba* recruitment and a negative correlation with salp abundance. According to SIEGEL and LOEB (1995), extensive and prolonged sea ice cover may delay the timing of the spring bloom, providing less optimal condition for filter feeders such as salps which cannot graze ice algae. On the other hand, a thinner and shorter period of ice cover might cause early and limited spring bloom which will provide an optimal condition for salps but an unfavorable situation for active grazers such as *E. superba* and copepods which require rich ice algal food as well as ice-cover protection from predators to survive winter. Besides the influence of weak upwelling, the less extensive ice condition during the previous winter and spring may have partly contributed to the extension of a higher temperature and salinity surface water mass to the south of the AD in our research area. Since the sea ice condition of the area has been consistent for at least 20 years (GLOERSEN *et al.*, 1992), it is possible that the salp bloom and its dominance in the macrozooplankton community might be more or less a regular feature of the area rather than an unusual peculiar incident of that year.

Hypothetical scenario of salp bloom and its subsequent effects

As a summary of the discussion, a hypothetical scenario of salp bloom and its subsequent effects on other phytoplankton consumers off Wilkes Land is constructed (Fig. 13). When the divergence weakens, phytoplankton growth may become limited. Separately, less extensive sea ice condition may control phytoplankton growth, and provide a food concentration optimal for salp reproduction but unfavorable for other large particle grazers including *Euphausia superba*. HERON and BENHAM (1984) and FORTIER *et al.* (1994) suggested that, once rapid population growth of salps is triggered, a salp swarm possibly controls the phytoplankton abundance of the area and keeps particle concentration to the level at which clogging of their mucous net never occurs. Given such a condition, salps may quickly multiply their population by asexual reproduction, resulting in the consumption and removal of a considerable amount of food from the water column with their high filtration and ingestion abilities (reviewed by ALLDREDGE and MADIN, 1982). Consequently, reduced food concentration may suppress reproduction and growth of other phytoplankton consumers. When sufficiently abundant, the salp's direct predation on eggs and larvae of other plankton may significantly restrict their reproduction as HUNTLEY *et al.* (1989) suggested. In summary, once salps dominate the macrozooplankton community, a certain positive feedback system for sustaining a large population of them might be formed.

This study was conducted on a very limited number of samples obtained during a short research period. As the results show, however, the salp bloom may significantly influence the whole Antarctic ecosystem. Further intensive studies on causes and

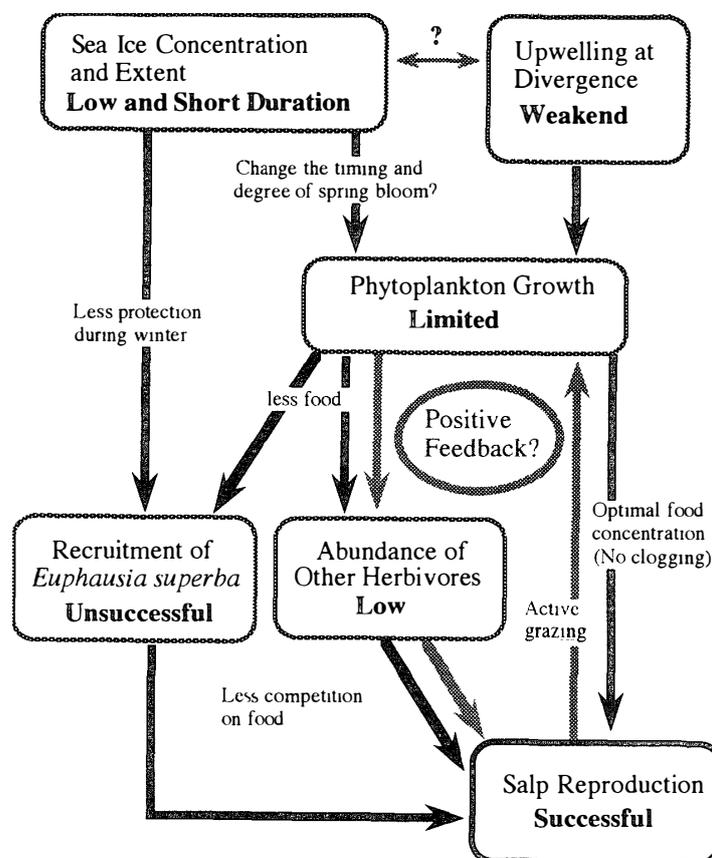


Fig 13 Hypothetical scenario of salp bloom off the Adelie Coast of Wilkes Land

consequences of salp blooms off Wilkes Land are important in understanding the role of salps in the Antarctic marine ecosystem.

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