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MORPHOLOGY AND DISTRIBUTION OF HETEROTROPHIC PROTISTS ALONG 75°E IN THE SOUTHERN OCEAN

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Abstract: Seawater samples were collected from the 0 and 50 m layers along the transect of 75°E in the Indian sector of the Southern Ocean in the austral summer of 1983-84 during the BIOMASS SIBEX I cruise of the R. V. KAIYO MARU of Japan Fisheries Agency. Distribution and taxonomy of heterotrophic protists were investigated.

Naked amoebae and choanoflagellates were the dominant heterotrophic protists in the Indian sector of the Southern Ocean. The total cell volume of heterotrophic protists was larger at 50 m than at 0 m. The ratio of the cell volume of heterotrophic protists to the total cell volume (heterotrophic and autotrophic protists) was found to be reverse correlation to the total cell volume in the 0m layer. Species of choanoflagellates invested in siliceous loricae (Acanthoecidae) were distributed only in the 0 m layer. Choanoflagellates invested in organic sheaths (Salpingoecidae), naked choanoflagellates (Codonosigidae) and amoebae were distributed in both 0 and 50 m layers. Importances of choanoflagellates and amoebae in the detritus food chain in the pelagic Antarctic ecosystem were suggested.

Three species of choanoflagellates, *Monosiga ovata* KENT, *Pleurasiga cupula* LEADBEATER and *Savillea parva* (ELLIS) LOEBLICH, were firstly reported from the Southern Ocean.

1. Introduction

Recently it has become known that there is abundant stock of heterotrophic protists (nano- and micro-zooplankton including heterotrophic 'phytoplankton') as well as autotrophic protists (autotrophic nano- and micro-phytoplankton) in the pack-ice area of the Antarctic Ocean (BUCK and GARRISON, 1983; HARA and TANOUE, 1984). It has been also suggested that these heterotrophic and autotrophic protists may play important roles in the antarctic ecosystem as food organisms of the antarctic krill, *Euphausia superba*, and other large zooplankton (HARA and TANOUE, 1984; TANOUE and HARA, 1984). Although studies have been conducted concerning the species composition of the heterotrophic protists in the pack-ice area (BUCK, 1981; TAKAHASHI, 1981; BUCK and GARRISON, 1983), there is little information on both quantitative and qualitative

compositions of heterotrophic protist populations in the northern area of the pack-ice area in the Southern Ocean (BRÖCKEL, 1981; HARA and TANOUE, 1984, 1985).

In the present study, qualitative and quantitative distributions as well as taxonomy of the heterotrophic protists along the transect of 75°E in the Indian sector of the Southern Ocean are reported.

2. Materials and Methods

Samples were collected during the cruise of the R. V. KAIYO MARU, Japan Fisheries Agency, from the Indian sector of the Southern Ocean in the austral summer of 1983–84 (BIOMASS SIBEX I cruise). Seawater samples were collected from the 0 and 50 m layers at fifteen stations along the transect of 75°E (Table 1). These seawater samples were frozen to *ca.* −20°C immediately after the sampling and were preserved at *ca.* −40°C until microscopical examination on land.

After thawing the seawater samples at room temperature (*ca.* 20°C), mercury chloride was added to each sample (*ca.* 150 mg of $HgCl_2$ to 500 m*l* of the seawater

Table 1. Standing crops of heterotrophic protist groups in cell volume ($\mu m^3/ml$) along the transect of 75°E in the Southern Ocean, December 1983 – February 1984.

Station	12		15		18		21		30	
Date	4 Dec. 1983		4 Dec.		5 Dec.		6 Dec.		9 Dec.	
Long. (°E)	75-02.1		74-59.0		74-59.0		74-59.6		74-59.4	
Lat. (°S)	45-59.5		47-59.8		49-59.5		52-00.2		56-00.3	
Depth (m)	0	50	0	50	0	50	0	50	0	50
Water temp. (°C)	6.80	5.31	5.60	4.99	3.40	3.20	2.00	1.72	0.30	0.15
Choanoflagellida	20	1340	170	570	40	90	650		9000	630
Amoebida	1100	71000	10	6400	80	16400	2900	19700	1260	13300
Tintinnida		*			*	*				*

Station	33		36		42		214	209
Date	9 Dec. 1983		10 Dec.		11 Dec.		2 Feb. 1984	2 Feb.
Long. (°E)	74-59.7		74-59.5		75-00.3		75-00.5	75-00.5
Lat. (°S)	57-59.5		60-00.4		62-00.0		62-00.1	63-00.0
Depth (m)	0	50	0	50	0	50	0	0
Water temp. (°C)	−0.70	−0.91	−0.30	−1.09	−0.90	−1.42	1.30	1.10
Choanoflagellida	140	800	310	900	40	40		*
Amoebida	5000	5500	5600	28300	1100	1440	4000	1300
Tintinnida		*						

Station	206	203	200	197	195
Date	1 Feb. 1984	1 Feb.	1 Feb.	31 Jan.	31 Jan.
Long. (°E)	74-58.3	74-59.7	75-00.2	74-58.6	75-00.2
Lat. (°S)	63-57.1	64-59.4	66-00.0	66-57.2	68-00.2
Depth (m)	0	0	0	0	0
Water temp. (°C)	1.10	0.70	0.40	0.50	0.90
Choanoflagellida		*			*
Amoebida	16600	9300	1200	420	15900
Tintinnida					

* Loricae without cytoplasms were observed.

sample) to fix the cells included in the samples. These samples were concentrated by sedimentation to 100 m*l* followed by centrifugation (2100 g, 10 min) to the final volume ranging from 0.5 to 2 m*l*. Cell number and cell volume of each species in an aliquot of the sample were examined by an Olympus inverted microscope (IMT) fitted with a Nomarski interference (objective ×40). The maximum length (*a*), width (*b*) and thickness (*c*) of each cell were measured to estimate the cell volume (*V*). The cell form was approximated as an elliptical disk for diatoms ($V=\pi/4\ abc$), a flat pyramidal form for amoebae ($V=1/6\ abc$) and an ellipsoid for othres ($V=\pi/6\ abc$). Empty loricae without cytoplasm were recorded but not included in the cell volume determination. An analytical electron microscope (JEM-100B) was also used for morphological observation of protists. Samples for electron microscopy were prepared by the ordinary whole mount method which was described by TAKAHASHI and HARA (1984).

3. Results

3.1. Abundance and distribution of heterotrophic protists

Samples were collected from the 0 and 50 m layers at eight stations from Stns. 12 to 42 during the first leg on 4–11 December 1983 (Fig. 1, Table 1). Cell volumes of heterotrophic protists at 0 m ranged from 1.2×10^{2} to $1.0\times10^{4}\mu m^{3}/ml$ and values at 50 m ranged from 1.5×10^{3} to $7.2\times10^{4}\mu m^{3}/ml$ (Fig. 1B). The cell volumes of heterotrophic protists were larger in the 50 m layer than those in the 0 m layer. On the other hand, cell volumes of autotrophic protists at 0 m were always larger than those at 50 m (Fig. 1A). Large ratios of the cell volume of the heterotrophic protists to the total cell volume (hetero- and auto-trophic protists) were obtained in the samples collected from the 50 m layer (2.8% in average), whereas small values (0.23% in average) were calculated in the samples collected from the 0 m layer. These ratios fluctuate inverse-correlatively to the total cell volumes among the samples collected at 0 m (Fig. 1A, C).

Samples were collected from 0 m at seven stations from Stns. 195 to 214 during the second leg on 31 January–2 February, 1984. Cell volumes of the heterotrophic protists ranged from 4.2×10^{2} to $1.7\times10^{4}\mu m^{3}/ml$ (Fig. 1B, Table 1). These values were two times higher in average than the values obtained at 0 m during the first leg. On the other hand, cell volumes of autotrophic protists were determined to be one-tenth lower than the values at 0 m during the first leg. The heterotrophic protists were found to show a spatially and temporally more constant standing stock distribution than autotrophic protists at the 0 m layer. Therefore, the larger values of the ratios of the cell volumes of the heterotrophic protists to the total cell volumes (6.7% in average) were obtained in the samples collected from the 0 m layer during the second leg.

3.2. Morphological observation

The naked forms of amoebae and choanoflagellates were the most dominant heterotrophic protists (Table 1). A few loricae of tintinnids were also observed in the samples collected during the first leg.

3.2.1. Amoebida

Although genus and species remained unidentified, two types of the naked amoebae, the large (Fig. 2) and the samll (Fig. 3) types, could be characteristic as common

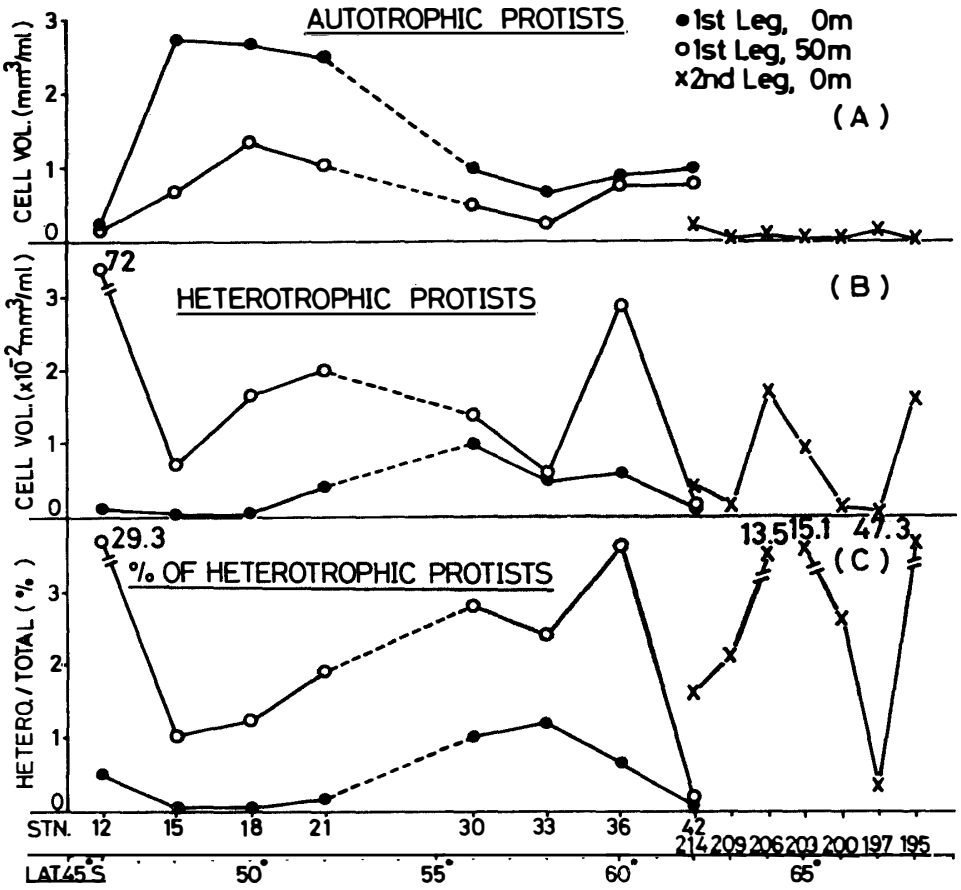

Fig. 1. Distribution of autotrophic and heterotrophic protists along the transect of 75°E in the Southern Ocean, December 1983 - February 1984. A) Total cell volume of autotrophic protists. B) Total cell volume of heterotrophic protists. C) Percentage of the cell volume of the heterotrophic protists to the total cell volume.

members of the heterotrophic protists throughout the whole area examined. The form of the large type, 10–20 μm in diameter and 3–6 μm in thickness, usually has a conspicuous peduncle posteriorly when it creeps actively (Fig. 2). It has some (3–7) slender peduncles when it is floating. The small type, 8–15 μm in diameter, has a semicirculer profile without peduncle when it creeps actively (Fig. 3). These amoebae are usually observed upon the detrital particles, or the inner and outer surfaces of the dead diatom frustules (Figs. 4 and 5).

Amoebae were detected from all of the samples and they constituted 5.6–100% of the heterotrophic protists' cell volumes. Amoebae were more abundant in the 50m layer than in the 0m layer (Table 1).

3.2.2. Choanoflagellida

Monosiga ovata KENT: The cell is ovate or elliptic, broadest posteriorly, 3.5–5.0 μm in length, 2.8–3.2 μm in width. Flagellum 8–11 μm in length. Collar 5.7 μm in length. With or without a short peduncle (Figs. 6 and 7). This species has been identified as *Monosiga ovata* KENT on account of the general shape and the size of the cell and its marine habitat (*cf.* KENT, 1880–1882). This species was the most common and the most dominant choanoflagellate in the area examined (Table 2). This is the

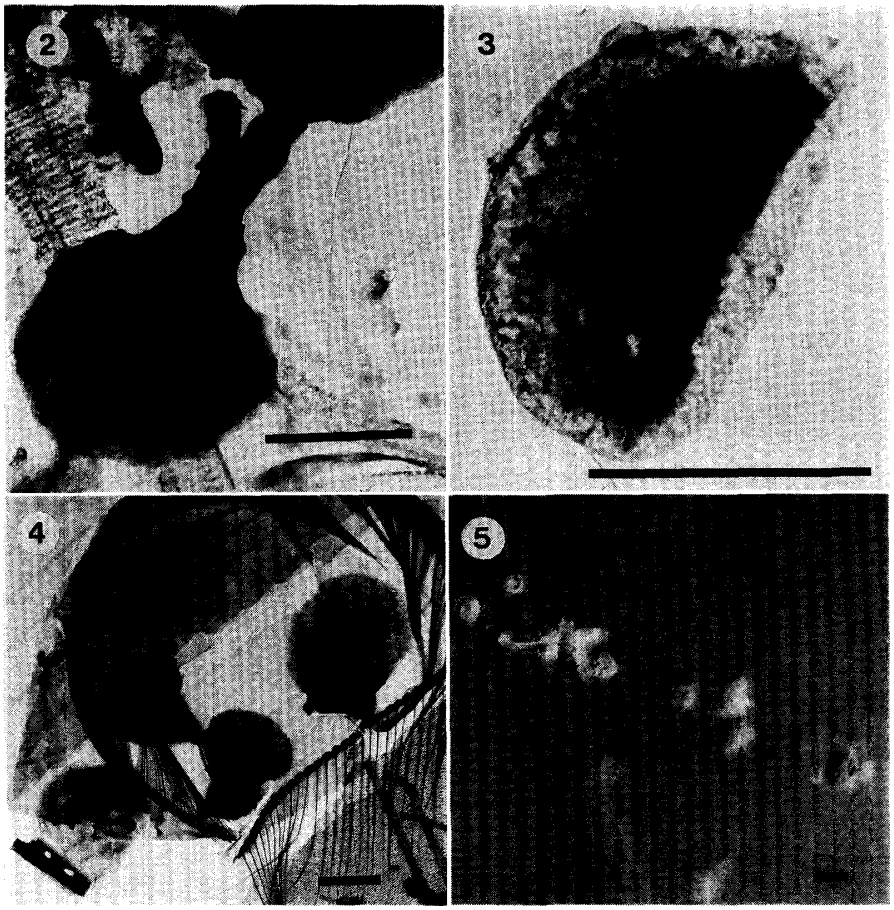

Fig. 2. Large-type amoeba with an obvious long posterior peduncle. Scale: 5 μm.
Fig. 3. Small-type amoeba without posterior peduncle. Scale: 5 μm.
Fig. 4. Four amoebae on a frustule of Corethron criophilum. *Scale: 5 μm.*
Fig. 5. Many amoebae on the outer and inner surfaces of the frustule of Rhizosolenia *sp. Scale: 10 μm.*

Table 2. Distribution of choanoflagellates along the transect of 75° E in the Southern Ocean, December 1983 – February 1984. For data on stations see Table 1.

Station	12		15		18		21		30		33		36		42		214	209	206	203	200	197	195
Depth (m)	0	50	0	50	0	50	0	50	0	50	0	50	0	50	0	50	0	0	0	0	0	0	0
Monosiga ovata	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+							
Salpingoeca sp.		+									+												
Crinolina aperta									+														
Parvicorbicula socialis			+																				
Pleurasiga cupula			+						+		+		+					+		+			+
Savillea parva													+										+

first record of *Monosiga ovata* KENT from the Southern Ocean.

Salpingoeca sp.: This form was common in the area examined (Table 2). The cell body is elliptic or oval, 4–6 μm in length and 3–4 μm in width. Flagellum 7–11 μm in length. Collar 5.7 μm in length. The cell body was invested in a delicate membrane-

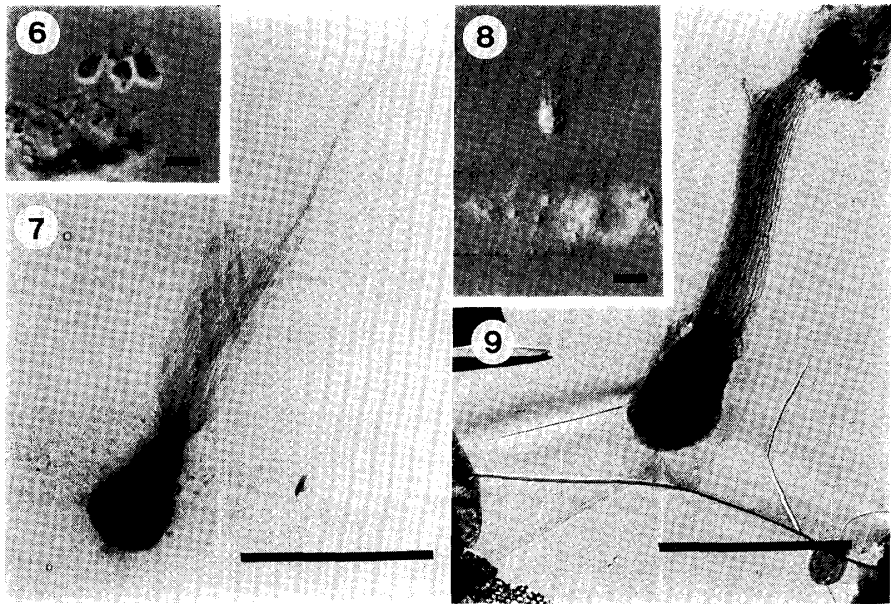

Fig. 6. *Three cells of* Monosiga ovata *attached on a detrital particle. Scale: 5 μm.*
Fig. 7. Monosiga ovata. *The flagellum was lost during preparation. Scale: 5 μm.*
Fig. 8. Salpingoeca *sp. attaching onto a frustule of* Rhizosolenia *sp. by the posterior end of a champagne glass-like shaeth. Scale: 5 μm.*
Fig. 9. Salpingoeca *sp. The protoplast is invested in a delicate membraneous sheath without fibrous structure. Scale: 5 μm.*

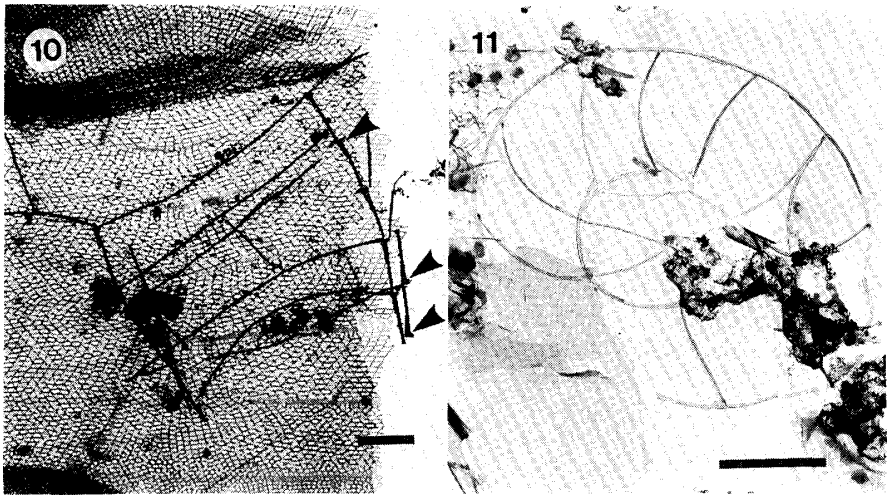

Fig. 10. *A partly damaged lorica of* Crinolina aperta. *Arrowheads indicate the species with characteristic L-shaped ends of transverse costal strips. A net-like structure behind the lorica is a part of a frustule of a diatom,* Rhizosolenia *sp. Scale: 5μm.*
Fig. 11. *A partly damaged lorica of* Parvicorbicula socialis. *Scale: 5μm.*

ous sheath without fibrous structure and this tapered posteriorly to attach the cell to a substratum (Figs. 8 and 9). LEADBEATER (1972a) proposed that the species included in the family Salpingoecidae should have a sheath of horny shape (KENT, 1880–1882) and that should be composed on chitin or cellulose (NORRIS, 1965). The shape of the sheath of *Salpingoeca*, however, was varied from pot-like to champagne glass-like

(KENT, 1880–1882; NORRIS, 1965). At the present time, no evidence has been gained about the material of the sheath. Until more investigations have been made on the composition and the structure of the membraneous sheath of the Salpingoecidae, the authors include tentatively a species with a membraneous sheath into Salpingoecidae. This is the first record of the genus *Salpingoeca* from the Southern Ocean.

Crinolina aperta (MANTON *et al.*) THOMSEN (Syn. *Diaphanoeca aperta* MANTON *et al.*): Only one specimen was collected from the surface water (Table 2). Although the specimen was damaged seriously, the general arrangement of the costal strips and the characteristic L-shaped ends of transverse costal strips (Fig. 10, arrowheads) indicated the propriety of identifying the lorica as that of *Crinolina aperta* (MANTON *et al.*) THOMSEN.

Parvicorbicula socialis (MEUNIER) DEFLANDRE: A few cells have been observed in the surface water samples collected during the first leg (Table 2). The morphology and dimensions of the loricae of these cells were similar to those recorded previously (Fig. 11) (THOMSEN, 1973; BUCK, 1981; HARA, 1984; HARA and TANOUE, 1984). The number of costal strips constituting the longitudinal costa could not been confirmed, because the loricae had been partly destroyed.

Pleurasiga cupula LEADBEATER: This species was fairly common in the surface water samples collected from the whole area examined (Table 2). The form and size of the lorica of the antarctic specimen were similar to those recorded previously (Fig. 12) (LEADBEATER, 1972b; THOMSEN, 1973; HARA, 1984). This is the first record of *Pleurasiga cupula* LEADBEATER from the Southern Ocean.

Savillea parva (ELLIS) LOEBLICH (Syn. *Diaphanoeca parva* ELLIS): This species was common in the surface water samples collected from the whole area examined (Table 2). The morphology and dimensions of the loricae of antarctic specimens were similar to those reported previously (Fig. 13) (ELLIS, 1929; NORRIS, 1965; LEADBEATER, 1972b; THOMSEN, 1973). This is the first record of *Savillea parva* from the Southern Ocean.

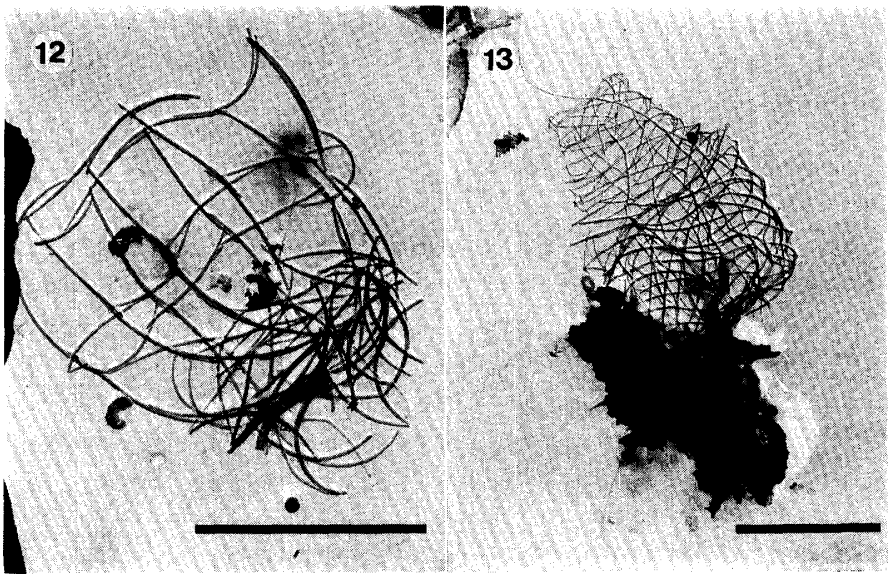

Fig. 12. Pleurasiga cupula. *Scale: 5μm.*
Fig. 13. *A lorica of* Savillea parva *attaced posteriorly on a detrital particle. Scale: 5μm.*

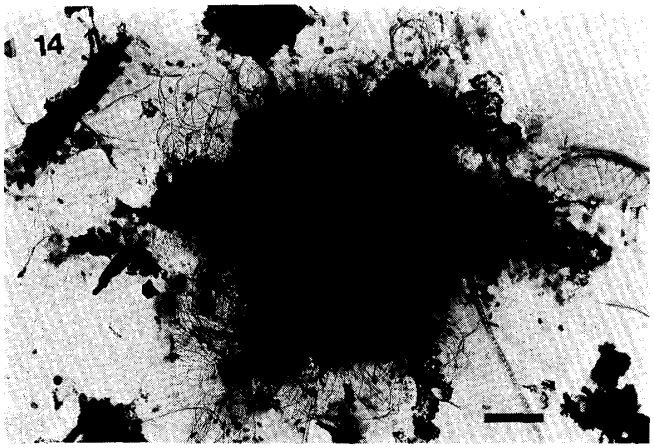

Fig. 14. An aggregation of choanoflagellates (Pleurasiga cupula *and* Savillea parva) *onto a surface of a detrital particle. Scale*: 5*μm*.

This species and *Pleurasiga cupula* were observed in the samples collected during both the first and the second legs. Many organisms of these species were attached at the posterior part of the loricae onto the surface of the detrital particles and formed dense populations (Fig. 14).

All the three families of the order Choanoflagellida, Codonosigidae (choanoflagellate without a sheath), Salpingoecidae (choanoflagellate with an organic sheath) and Acanthoecidae (choanoflagellate with a lorica composed of siliceous costal strips), were described from the area examined. Codonosigidae and Salpingoecidae are the dominant members of choanoflagellates and they were found in both 0 and 50m layers during the first leg (Table 2). They could not be observed from the samples collected during the second leg (Table 2). The species included in Acanthoecidae are distributed only in the 0m layer. However, they were found during both the first and the second legs. More abundant standing stocks of choanoflagellates in the 50m layer than in the 0m layer was mainly due to the abundant occurrence of *Monosiga ovata* and *Salpingoeca* sp. at 50m (Table 1).

4. Discussion

It is almost impossible to identify and quantitatively estimate live small plankton species at sea (REYNOLDS, 1973). Therefore, preservation or fixation for later examinations is necessary. Samples were preserved by freezing for the present examination. In the process of freezing, cells may change their forms by dehydration and some species seem to retain their morphological deformation after the samples were thawed. In our observation, indeed, some morphological deformation was observed. Some organisms of various species lost their flagella and others changed their external shape. These deformations, however, were not too seriously to identify each species, and most cells observed have retained the form similar to the form previously reported. After thawing, mercury chloride was added to the sample (*ca.* 150mg of $HgCl_2$ to 500m*l* of sea water sample) to stop the biological activity of the protista samples and to repress the

multiplication of bacteria. The effect of mercury chloride on the deformation or on the burst of protista cells in the samples was negregible. Some problems with the method still remain. Freezing may not be an ideal preservative method for protista cells lacking rigid cell coverings. Some naked species seem to burst or others may be damaged to change their form. The quantitative data on the naked heterotrophic as well as autotrophic protists in the present study may be underestimated. The 'naked' species of Prymnesiophyceae and Prasinophyceae, the common members of nanophytoprotista in the Antarctic Ocean (McFADDEN *et al.*, 1982; BUCK and GARRISON, 1983), have characteristic scaly cell coverings and/or other hardy material, such as the thread-like material in *Phaeocystis* species (MOESTRUP, 1979). These materials can retain their forms even after the cells themselves burst out, and these materials can be detected when samples are examined electron microscopically. In our electron microscopic observation, any kinds of these materials isolated from the cells were hardly observed. Although the loss of cells by freezing has not been confirmed, there may be a relatively small total loss of cells.

Relatively high values of the cell volumes of autotrophic protists in the surface water were observed during the first leg (December 1983) as compared with the values observed during the second leg (late January to early February 1984) (Fig. 1). It has been known that surface standing stocks of autotrophic protists in the Southern Ocean fluctuate seasonally and the spring bloom of autotrophic protists occurred during November to December and then tended to decrease with time from January to April (FUKASE, 1962; PLANCKE, 1977). The relatively small cell volumes of autotrophic protists determined during the second leg suggest that this period might have been the post-blooming season. On the other hand, the cell volumes of heterotrophic protists were relatively more constant than those of autotrophic ones between the first and the second leg samples, and more abundant stocks of heterotrophic protists were observed during the second leg (Fig. 1). Then large ratios of the cell volumes of heterotrophic protists to the total cell volumes (47.3% in maximum at Stn. 195) were obtained during the second leg. It is suggested that the heterotrophic protists may be one of the important sources of foods for larger zooplankton such as krill during the subsequent seasons when the bloom of the autotrophic protists was over (HARA and TANOUE, 1984; TANOUE and HARA, 1984).

The species composition (unpublished data) and cell volumes (Fig. 1) of autotrophic protists were quite different between the two legs. It has been suggested that the species composition of autotrophic protists fluctuate seasonally in the Australian sector of the Southern Ocean (HARA and TANOUE, 1985). Species composition of heterotrophic protists examined in the present study was also different between the first and the second legs. Especially *Monosiga ovata* and *Salpingoeca* sp., which were the common heterotrophic protists during the first leg, disappeared during the second leg (Table 2). It is suggested that the seasonal fluctuation of species composition may occur not only in the members of autotrophic protists but also in the members of heterotrophic protists.

Three of the four species of Acanthoecidae examined in the present study had loricae without anterior spines (Figs. 10–13; Table 3). Seventeen species of Acanthoecidae have been described from the Southern Ocean and all the previous faunistic studies of this family have been carried out in ice-covered or ice-fringed regions of the

Table 3. Species of Choanoflagellida recorded from the Southern Ocean.

	Terre Adélie (DEFLANDRE, 1960)	Lützow-Holm Bay (TAKAHASHI, 1981)	Weddell Sea (BUCK, 1981)	Weddell Sea (BUCK & GARRISON, 1983)	65°50.6'S: 155°16.0'E (HARA & TANOUE, 1984)	Present study
Codonosigidae						
Monosiga ovata						+
Salpingoecidae						
Salpingoeca sp.						+
Acanthoecidae						
(with anterior spine)						
Acanthoeca brevipoda				+		
Bicosta spinifera		+	+	+		
B. minor				+		
B. antennigera		+	+	+		
Calliacantha natans		+		+		
C. multispina		+	+	+		
C. simplex			+	+		
Crinolina aperta		+	+	+		+
Diaphanoeca pedicellata			+	+		
D. multiannulata		+	+	+		
(without anterior spine)						
Parvicorbicula socialis	+	+	+	+	+	+
P. circularis				+		
P. ongulensis		+				
Pleurasiga minima				+		
P. orculaeformis				+		
P. cupula						+
Saepicula leadbeateri		+				
Savillea parva						+
sp. "N"		+				

Antarctic Ocean (TAKAHASHI, 1981; BUCK, 1981; BUCK and GARRISON, 1983). Ten of the seventeen species described previously possess loricae with anterior spines. Although the functions of these anterior spines and/or posterior stalks have not been elucidated, it has been suggested that the distribution of the species with anterior spines and/or posterior stalks may have a positive correlation with the distribution of the sea ice in the Arctic samples (MANTON *et al.*, 1975) and the Antarctic samples (BUCK, 1981). In addition to the species with anterior spines, TAKAHASHI (1981) and BUCK and GARRISON

(1983) reported seven species of Acanthoecidae without anterior spines in the ice-covered or ice-fringed regions. Our study was carried out in the open water without sea ice and all specimens of Acanthoecidae except one specimen of *Crinolina aperta* were of the species without anterior spines or posterior stalks (Tables 2 and 3). Our results support the previous suggestion that the distribution of the species with anterior spines and/or posterior stalks may have a positive correlation with the distribution of sea ice.

The naked amoebae were the most dominant and the most common members of the heterotrophic protists in the area examined (Table 1). HARA and TANOUE (1985) reported that amoebae as well as colorless dinoflagellates were also the common members of the heterotrophic protists in the surface water of the Australian sector of the Southern Ocean. It is suggested that amoebae may be one of the most widespread heterotrophic protists in the Southern Ocean.

In addition to the choanoflagellates with siliceous loricae (Acanthoecidae), the present study reveals the existence of the choanoflagellates without sheaths (Codonosigidae) and those with organic sheaths (Salpingoecidae) (Tables 2 and 3). Seventeen species of choanoflagellates reported previously from the Southern Ocean were the species belonging to the family Acanthoecidae (TAKAHASHI, 1981; BUCK, 1981; BUCK and GARRISON, 1983) (Table 3). The species of Codonosigidae and Salpingoecidae increase the member of choanoflagellates in the Southern Ocean. The cytoplasm of choanoflagellate is easily damaged in the process of the fixation and preservation, and if the cytoplasm is damaged, it is difficult to detect an evidence of the existence of the species without hardy loricae. They are liable to be overlooked in the faunistic or biomass studies of marine protists even if the samples are examined electron microscopically. These naked and organic sheathed members of choanoflagellates were the dominant forms of choanoflagellates in the present study. BUCK and GARRISON (1983) reported that choanoflagellates with siliceous loricae (Acanthoecidae) were the third most abundant group of protists and outnumbered diatoms and/or prymnesiophycean cells at some stations. The occurrence of naked (Codonosigidae) and organic sheathed (Salpingoecidae) choanoflagellates in the Southern Ocean during the present study suggests that there may be more abundant biomass of choanoflagellates than that reported previously. Species of Codonosigidae and Salpingoecidae may be common members of heterotrophic protists in the Southern Ocean.

HARA and TANOUE (1984, 1985) and the present study suggest that naked amoebae and choanoflagellates were common and dominant members of heterotrophic protists in the Southern Ocean. Amoebae and choanoflagellates are known to be bacteriophagous or coprophagous. HARA and TANOUE (1984) and TANOUE and HARA (1984) suggested that choanoflagellates were one of the important food for the antarctic krill, *Euphausia superba* DANA, and played important roles in the detritus food chain in the Antarctic Ocean. The present study suggests that naked amoebae also may be quantitatively essential members in the detritus food chain in the Southern Ocean.

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