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The Biota of Antarctic Pack Ice in the Weddell Sea and Antarctic Peninsula Regions

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Summary. Pack ice surrounding Antarctica supports rich and varied populations of microbial organisms. As part of the Antarctic Marine Ecosystem Research in the Ice Edge Zone (AMERIEZ) studies, we have examined this community during the late spring, autumn, and winter. Although organisms are found throughout the ice, the richest concentrations often occur in the surface layer. The ice flora consists of diatoms and flagellates. Chrysophyte cysts (archaeomonads) of unknown affinity and dinoflagellate cysts are abundant and may serve as overwintering stages in ice. The ice fauna includes a variety of heterotrophic flagellates, ciliates, and micrometazoa. The abundance of heterotrophs indicates an active food web within the ice community. Ice may serve as a temporary habitat or refuge for many of the microbial forms and some of these appear to provide an inoculum for planktonic populations when ice melts. Larger consumers, such as copepods and the Antarctic krill, *Euphausia superba* are often found on the underside of ice floes and within weathered floes. The importance of the ice biota as a food resource for these pelagic consumers is unknown.

Introduction

Hooker (1847) observed that diatoms discolored pack ice floes in the Antarctic over 140 years ago. Although subsequent studies have led to the discovery that bacteria (Iizuka et al. 1966; Sullivan and Palmisano 1984), other algae (Burkholder and Mandelli 1965; Mitchell and Silver 1982; McConville and Wetherbee 1983; Garrison et al. 1987), heterotrophic protozoa (Hoshiai and Kato 1961; Fenchel and Lee 1972; Lipps and Krebs 1974; Whitaker 1977; Corliss and Snyder 1986; Spindler and Dieckmann 1986) and metazoa (e.g., Hoshiai 1981; O'Brien 1987; Dahms and Dieckmann 1987; Daly and Macaulay 1988) are also associated with ice, studies of the ice biota in pack ice and their ecology have only recently began.

Detailed studies of the Antarctic ice biota did not commence until the late 1950's and have been restricted largely to land-fast ice near shore-based stations (see Horner 1985a; and Garrison et al. 1986 for recent reviews). Different ice assemblages, which are primarily defined by where algal populations are concentrated in the ice, have been described (Horner 1985a, b; Garrison et al. 1986; Horner et al. 1988). The ice assemblages are still poorly known, so it is probably premature to distinguish distinct communities associated with the various habitats in sea ice. There is, however, increasing evidence of fundamental differences between the deep-water pack ice and near-shore fast ice in the abundance and distribution of ice-associated algae, the structural make up of the ice, and the environmental characteristics of the regions where fast ice and pack ice predominate (e.g., Clarke and Ackley 1984; Garrison et al. 1986). The floristic component of both pack and land-fast ice has been examined (Horner 1985a–c; Grossi and Sullivan 1985; Garrison and Buck 1985; Garrison et al. 1987), but has not been compared. The ice fauna and ice-associated food webs are best known from land-fast ice (e.g., Andriashev 1968; Gruzov et al. 1967; Rakusa-Suszczewski 1972; Richardson and Whitaker 1979). A number of recent reports indicate that the Antarctic krill, *Euphausia superba*, feeds on the undersides and in the interstices of pack ice floes (Hamner et al. 1983, 1989; Garrison et al. 1986; Kottmeier and Sullivan 1987; O'Brien 1987; Marschall 1988; Daly and Macaulay 1988), suggesting that the concentrated biomass in the ice community may be an important food source for pelagic consumers in the deep-water regions.

Sea ice is a prominent feature of the Southern Ocean and covers over 20×10^6 km^2 in late winter. With the seasonal increase in solar radiation in the spring, sea ice melts rapidly and by summer the ice cover is reduced to $< 4 \times 10^6$ km^2. Because of this extensive seasonal melting, most of the drifting pack ice is annual ice, although in some areas (e.g., the Bellingshausen and Weddell Seas) part of the ice persists as multi-year ice (Foster 1984). The processes of the formation and development of ice assemblages are poorly documented. The initial incorporation of cells in ice often involves a physical concentration of

material during frazil ice formation (Garrison et al. 1983). Subsequent development of the ice biota may depend on flooding (Meguro 1962) or other deformational processes (Ackley 1985) or may take place as a result of physical and chemical changes in the ice associated with seasonal melting (Ackley et al. 1979; Garrison et al. 1986). The seasonal melting and decomposition of ice floes may be accelerated by the growth of the ice-algal populations (Buynitskiy 1968).

In this paper, we have focused on the abundance and composition of the microbial community in pack ice, and we discuss some of the more abundant members of this assemblage. Our study is one of the first to determine quantitative relationships among members making up ice-bound populations and to establish trophic relationships among members of the ice community. This type of information is fundamental to understanding the dynamics of the ice community and to begin to predict their role and potential importance in the pelagic system of the Southern Ocean.

Materials and Methods

Samples were collected from pack ice floes in the Weddell Sea during the austral spring (AMERIEZ 83) and autumn (AMERIEZ 86) (Fig. 1). During the austral winter (WINCRUISE), samples were also collected in drifting pack ice near the Antarctic peninsula. Ice cores were collected with a 7.6 cm SIPRE ice-coring auger, cut into ~20 cm vertical sections and allowed to melt in 500–1500 ml of sterile-filtered seawater (Garrison and Buck 1986). We also collected brine from the surface layer of ice floes by removing a short core (~20 cm) from an ice floe and collecting accumulated liquid. No brine was recovered during the winter cruise because of low temperatures resulting in low brine volumes within the surface layer of ice floes.

Aliquots (100–500 ml) of diluted ice samples or brine were filtered through Gelman glass fiber filters (GF/F), chlorophyll *a* was extracted in 90% acetone and chlorophyll *a* and phaeopigments were calculated from fluorescence measurements (Parsons et al. 1984a).

Aliquots of the samples were preserved for population analysis with either Karnovsky's solution (Gold 1976) or Lugol's iodine. We examined some samples aboard ship using fluorescence microscopy to distinguish between autotrophic and heterotrophic flagellates. Freshly-collected samples were concentrated on 0.8 μm Nucleopore filters, preserved with glutaraldehyde (~1% final concentration) and mounted in Cargille Type B immersion oil. Some samples were stained with the fluorochrome primulin (Caron 1983). The samples were examined and counted using an Olympus BH microscope with appropriate filters for autofluorescence or primulin.

Preserved samples were stored in the dark and refrigerated during shipping and storage. Sample volumes of 10 to 100 ml were settled and counted using an inverted microscope (Reid 1983). We measured cell dimensions to calculate cell volumes (Kovola and Larrance 1966) and estimated cell carbon from published volume to carbon relationships. For diatoms we used the relationship, Log (Carbon) = 0.76 Log (Cell Volume) − 0.29, and for flagellates we used the relationship, Log (Carbon) = 0.94 Log (Cell Volume) − 0.60, where volume is in ml and carbon is in grams (Eppley et al. 1970). For larger protozoa (ciliates etc.), we assumed a specific gravity of 1.0, a dry/wet weight fraction of 0.20 and we assumed that the carbon was 40% of dry weight (i.e., Carbon = 0.08 × Cell volume; Beers and Stewart 1970).

Results and Discussion

The most extensive record of algal distributions in pack ice are from chlorophyll *a* measurements (Fig. 2). The algae in pack ice are usually distributed throughout ice floes as internal assemblages, which have no particular pattern to their vertical distribution (e.g., Ackley et al. 1979; Garrison et al. 1986; Horner et al. 1988). Although there was considerable variability, chlorophyll *a* concentrations in first-year pack ice averaged < 10 μg chl $a\,l^{-1}$, and these measurements show little evidence of seasonal variation (see Fig. 2). Similar ranges of chlorophyll *a* concentrations were reported in the austral summer by Ackley et al. (1979)

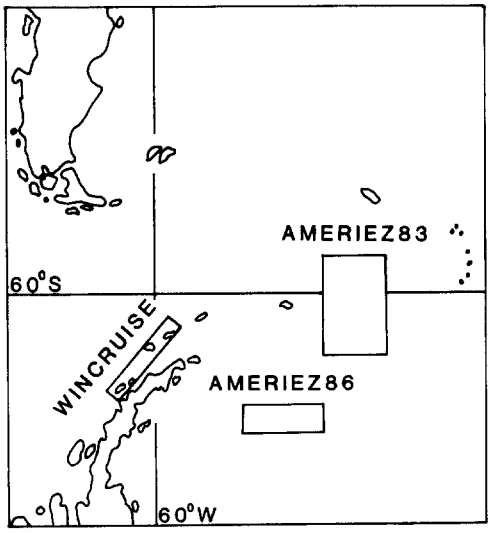

Fig. 1. Locations where ice samples were collected for population analysis. AMERIEZ – Antarctic Marine Ecosystem Research in the Ice Edge Zone. AMERIEZ 83, 5 Nov. – 3 Dec., 1983; AMERIEZ 86, 4 Mar. – 5 Apr., 1986; WINCRUISE (Polar Duke, Winter Cruise II), 7 Jun. – 17 Jul., 1987

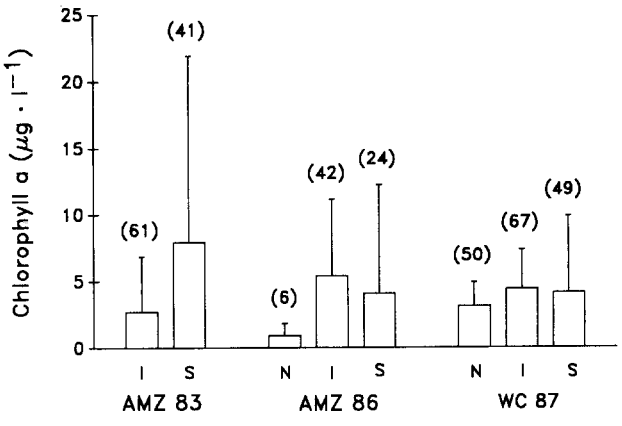

Fig. 2. Chlorophyll *a* concentrations in new- and first-year pack ice. Mean, Standard Deviation and (N) are shown. Cruises: AMZ 83, AMERIEZ 83; AMZ 86, AMERIEZ 86; WC 87, Polar Duke Winter Cruise, 1987. Ice and assemblage types: *N* Newly-forming ice; *I* Internal assemblages (ice core samples) from first year ice; *S* Surface assemblages comprised of brine samples and the upper 20 cm of ice cores from first year ice. Samples in Figs. 3 and 4, identified as surface slush, are included in the brine samples

and Garrison et al. (1982) and in the late winter by Clarke and Ackley (1984). We have measured chlorophyll *a* concentrations of >50 μg chl $a\,l^{-1}$ in multi-year ice, but there have been too few measurements to adequately characterize the seasonal distribution in these older floes. The highest chlorophyll *a* concentrations in pack ice develop in the surface layer near the snow-ice interface (e.g., the brine samples shown in Fig. 2). In some floes during AMERIEZ 83, we found highly-concentrated surface-layer assemblages in 20–30 cm thick, slush-like layers just below the snow-ice interface with chlorophyll concentrations reaching >50 μg chl $a\,l^{-1}$ (Fig. 2). These assemblages appear to develop a seasonal maximum in summer. For example, Meguro (1962) and Burkholder and Mandelli (1965) reported maximum chlorophyll *a* concentrations of 270 and 400 μg chl $a\,l^{-1}$, respectively in the late summer. There is, however, a poor record of both the spatial and temporal occurrence of surface layer assemblages in pack ice.

The ice community is comprised of a variety of microbial organisms including bacteria, diatoms, autotrophic flagellates, dinoflagellates, heterotrophic flagellates, ciliates, other protozoa and metazoans (Table 1; Fig. 3). These organisms vary in size by orders of magnitude (Table 2), so the analysis of community composition should be expressed as biomass rather than abundance. The carbon content of most nano and microorganisms has not been determined directly and is often estimated from cell volume. Carbon : volume relationships for algae have been reported and discussed by Mullin et al. (1966), Strathman (1967) and Booth (1988). The carbon : volume relationships we used to calculate carbon for algae seem to estimate reasonable carbon values for autotrophs based on a comparison with our chlorophyll *a* measurements. For example, total carbon : chlorophyll *a* ratios averaged 140, 51, and 20 for the AMERIEZ 83, AMERIEZ 86 and Wincruise II, respectively, and these ratios are within the range of values reported for both phytoplankton and ice algae (e.g., Bunt and Lee 1972; Parsons et al. 1984b). The carbon : volume relationships for heterotrophs are less well known. The carbon : volume relationship for non-diatom phytoplankton (i.e. Eppley et al. 1970) estimates a range of carbon from 250–210 fgC μm^{-3} for cells ranging from 1–20 μm (diameter), respectively. This conversion factor agrees with values determined for heterotrophic flagellates of a similar size by Fenchel (1982) and Børsheim

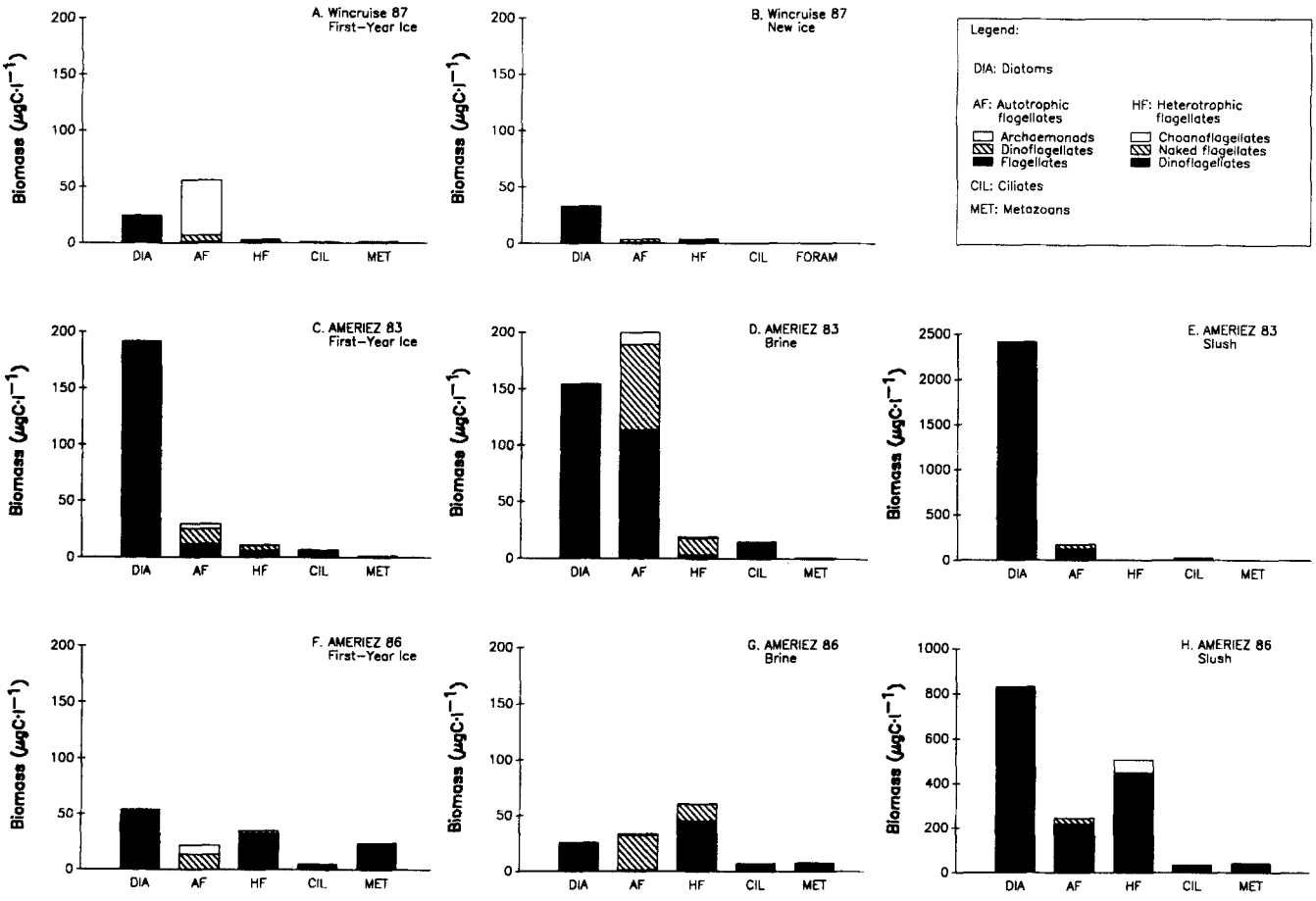

Fig. 3. Average composition of ice assemblages. The number of samples for each ice type (N) is shown in the legend. *A*, *B* Austral Winter, Wincruise 87: New ice (3) and first-year ice (14). *C–E* Spring, AMERIEZ 83: First-year ice (17), brine samples (14), and surface layer slush (2). *F–H* Autumn, AMERIEZ 86: First-year ice (12), brine samples (9), and surface layer slush (4). The legand for the composition of major groups is shown in the inset

Table 1. Species found in pack ice assemblages. (*) Observed only in cultures from ice

Autotrophs

Prymnesiophytes
- *Phaeocystis pouchetii* (Hariot) Lagerheim
- *Chrysochromulina* sp.

Chrysophytes
- *Distephanus speculum* (Ehrenberg) Haeckel
- archaeomonads

Prasinophytes
- *Mantoniella antarctica* Marchant
- *Mantoniella squamata* Manton and Parke

Dinoflagellates
- *Gymnodinium* spp.
- *Prorocentrum* sp.

Cryptophytes

Diatoms
- *Actinocyclus actinochilus* (Ehrenberg) Simonsen
- *Amphiprora kjellmanii* Cleve
- *Amphora* sp.
- *Asteromphalus* spp.
- *Chaetoceros atlanticum* Cleve
- *C. breve* Schütt
- *C. bulbosum* (Ehrenberg) Heiden
- *C. castracanei* Karsten
- *C. convolutum* Castracane
- *C. criophilum* Castracane
- *C. curvisetum* Cleve
- *C. dichaeta* Ehrenberg
- *C. flexuosum* Manguin
- *C. neglectum* Karsten
- *C. neogracilis* Van Landingham
- *C. pendulum* Karsten
- *C. peruvianum* Brightwell
- *Corethron criophilum* Castracane
- *Dactyliosolen antarcticus* Castracane
- *D. tenuijunctus* (Manguin) Priddle and Fryxell
- *Coscinodiscus oculus-iridis* Ehrenberg
- *Eucampia antarctica* (Castracane) Manguin
- *Gyrosigma* sp.
- *Haslea trompii* (Cleve) Simonsen
- *Leptocylindrus mediterraneaus* (H. Peragallo) Hasle
- *Navicula criophila* (Castracane) DeToni
- *Nitzschia angulata* Hasle
- *N. castracanei* Hasle
- *N. closterium* (Ehrenburg) W. Smith
- *N. curta* (Van Heurck) Hasle
- *N. cylindrus* (Grunow) Hasle
- *N. heimii* (Manguin) Hasle
- *N. kerguelensis* (O'Meara) Hasle
- *N. lineata* Hasle
- *N. lineola* Cleve
- *N. neglecta* Hustedt
- *N. obliquecostata* (Van Heurck) Hasle
- *N. prolongatoides* Hasle
- *N. pseudonana* (Hasle) Hasle
- *N. ritscheri* (Hustedt) Hasle
- *N. subcurvata* Hasle
- *N. sublineata* Hasle
- *N. turgiduloides* Hasle
- *N. vanheurckii* (M. Peragallo) Hasle
- *Odontella weissflogii* (Grunow) Janisch
- *Porosira pseudodenticulata* (Hustedt) Lagerheim
- *Rhizosolenia alata* Brightwell
- *R. alata* f. *inermis* (Castracane) Hustedt
- *R. chunii* Karsten
- *R. cylindrus* Cleve
- *R. styliformis* Brightwell
- *R. shrubsolei* (Cleve) Van Heurck
- *Schimperiella antarctica* Karsten
- *Stellarima microtrias* Hasle and Sims
- (*Cosconodiscus furcatus* Karsten)
- *Synedra* sp.
- *Thalassiosira gravida* Cleve
- *T. tumida* (Janisch) Hasle
- *Thalassiosira* spp.
- *Thalassiothrix longissima* Cleve and Grunow
- *Tropidoneis belgicae* (Van Heurck) Heiden
- *T. fusiformis* Manguin
- *T. gaussii* Heiden and Kolbe
- *T. glacialis* Heiden

Heterotrophs

Bodonids
- *Bodo* sp.
- *Rhynchomonas* sp.

Dinoflagellates
- *Amphidinium* spp.
- *A. hadai* Balech, 1975
- *Gymnodinium* spp.
- *Gyrodinium* spp.
- *G. lachryma* (Meunier, 1907)
- *Protoperidinium* spp.

Heterotrophic euglenoids
- *Anisonema* sp.
- *Petalomonas* sp.

Incertae sedis
- *Cryothecamonas armgier nom. prov.*

Choanoflagellates
- * *Acanthoeca brevipoda* Ellis 1929
- * *Acanthoecopsis unguiculata* Thomsen, 1973
- *Biscosta antennigera* Moestrup, 1979
- *B. spinifera* (Throndsen, 1970)
- *Calliacantha simplex* Manton and Oates, 1979
- *Cosmoeca ventricosa* Thomsen, 1984
- *Cosmoeca* sp.
- *Crinolina aperta* Leadbeater, 1975
- *Diaphanoeca grandis* Ellis, 1929
- *D. multiannulata* Buck, 1981
- *D. pedicellata* Leadbeater, 1972
- *Kakoeca antarctica nom. prov.*
- *Parvicorbicula quadricostata* Throndsen, 1970
- **Savillea* sp.
- **S. parva* Ellis, 1929
- **Stephanoeca diplocostata* v. *paucicostata* Throndsen, 1969

Ciliates
- *Amphileptus* sp.
- *Aspidisca antarctica* Corliss and Synder, 1986
- *Chilodonella pseudochilodon* Deroux, 1970
- *Chlamydonella* sp.
- *Cohnilembus grassei* Corliss and Synder, 1986
- *Condylostoma* sp.
- *Didinium balbainii* v. *nanum* Kahl, 1930
- *D. gartgantua* Kahl, 1933
- *Euplotes* sp.
- *E. antarctica* Fenchel and Lee, 1972
- *Lacrymaria* spp.
- *Lacrymaria spiralis* Corliss and Synder, 1986
- *Myrionecta rubra* Grain et al., 1982

Table 1 (continued)

Pleuronema glaciale Corliss and Synder, 1986
Scuticociliate spp.
Spiroprorodon spp.
S. garrisoni Corliss and Synder, 1986
Strombidium spp.
S. rhyticollare Corliss and Synder, 1986
Tachysoma parvulum Corliss and Synder, 1986
Trochilia sp.
Uronychia sp.
Codonellopsis gausii Laackmann, 1909
Salpingella spp.

Sarcodines
*Unidentified amoebae
*Unidentified heliozoans
Neogloboquadrina pachyderma Ehrenberg

Metazoa
Stephos longipes
Tisbe racovitzea
Microcalanus pygmaeus
Calanoid naupliar larvae
Euphausia superba

and Bratbak (1987). The relationship that we used to estimate carbon in other microzooplankton (i.e., from Beers and Stewart 1970) assumes a value of 80 fgC μm^{-3}, which is invariate with cell size. This value is similar to conversion values suggested for ciliates by Heinbokel (1978) and Burkill (1982), but lower than the value of 132 fgC m^{-3} determined by Turley et al. (1986). Until carbon determinations are performed on a larger number of organisms, biomass determinations will remain somewhat imprecise. It seems likely, however, that our carbon biomass estimates are conservative, because of the inevitable loss of some cells with sampling, preservation and processing (e.g., see Garrison and Buck 1986).

Integrated biomass in ice floes (excluding bacteria) ranged from <0.01 to >0.4 gC m^{-2}, with the highest concentrations found during the spring (AMERIEZ 83). At the highest concentrations, microbial biomass in ice floes is approximately that found over the upper 100 m of the underlying water column (Garrison and Buck 1989). Overall, autotrophs dominate in the ice assemblage (see Fig. 3). Heterotrophs ranged from <7 to $>57\%$ of the

Table 2. Cell volume and carbon estimates for major groups of organisms comprising the sea ice assemblage. Carbon : volume relationships are discussed in the text

Group/species	Cell volume (μm^3) Mean	Cell volume (μm^3) Range	Carbon $cell^{-1}$ (pg) Mean
Autotrophic flagellates			
Phaeocystis pouchetii	6.4×10^1	$1.4 \times 10^1 - 8.7 \times 10^2$	13
(motile cells)	1.3×10^1	$1.1 \times 10^1 - 1.9 \times 10^1$	3
archaeomonads	1.6×10^2	$1.8 \times 10^1 - 4.5 \times 10^2$	30
Cryptophytes	3.7×10^2	$7.6 \times 10^1 - 2.1 \times 10^3$	63
Diatoms			
Nitzschia prolongatoides	4.6×10^1	$2.6 \times 10^1 - 1.0 \times 10^2$	9
Chaetoceros neogracilis	6.0×10^1	$3.3 \times 10^1 - 1.4 \times 10^2$	10
Nitzschia cylindrus	1.2×10^2	$3.8 \times 10^1 - 3.1 \times 10^2$	17
N. closterium	2.9×10^2	$8.9 \times 10^2 - 1.4 \times 10^3$	32
Synedra sp.	4.2×10^2	$8.9 \times 10^2 - 1.0 \times 10^3$	43
Nitzschia turgiduloides	4.1×10^2	$2.0 \times 10^2 - 1.1 \times 10^3$	50
N. curta	6.6×10^2	$2.6 \times 10^2 - 9.7 \times 10^2$	61
N. neglecta	2.9×10^3	$1.1 \times 10^3 - 5.9 \times 10^3$	170
Tropidoneis fusiformis	2.9×10^3	$1.3 \times 10^3 - 8.0 \times 10^3$	180
Amphiprora kjellmanii	3.6×10^3	$1.0 \times 10^3 - 2.3 \times 10^4$	220
Corethron criophilum	1.3×10^4	$1.0 \times 10^3 - 5.8 \times 10^4$	600
Rhizosolenia alata	5.0×10^4	$2.4 \times 10^3 - 1.0 \times 10^5$	1600
Thalassiosira spp.	5.9×10^4	$3.6 \times 10^3 - 3.0 \times 10^5$	1700
Dinoflagellates			
Prorocentrum sp.	1.4×10^3	$2.8 \times 10^2 - 2.6 \times 10^3$	220
Protoperidinium spp.	2.0×10^3	$9.6 \times 10^1 - 2.6 \times 10^3$	310
Amphidinium spp.	3.6×10^3	$4.5 \times 10^2 - 1.8 \times 10^4$	540
Gymnodinium spp.	1.1×10^4	$6.6 \times 10^1 - 2.6 \times 10^5$	1400
Gyrodinium spp.	1.4×10^5	$6.5 \times 10^1 - 7.9 \times 10^6$	16545
Heterotrophic flagellates			
Choanoflagellates	5.2×10^1	$1.2 \times 10^1 - 2.1 \times 10^2$	10
Cryothecamonas armiger	2.2×10^3	$1.1 \times 10^2 - 1.4 \times 10^4$	245
Ciliates			
Strombidium spp. (?)	4.0×10^4	$2.3 \times 10^2 - 5.5 \times 10^5$	3178
Myrionecta rubra	7.2×10^4	$7.0 \times 10^2 - 1.8 \times 10^6$	5778
Euplotes sp.	1.2×10^5	$2.1 \times 10^3 - 1.7 \times 10^6$	9740
Didinium sp.	3.2×10^5	$6.0 \times 10^3 - 3.0 \times 10^6$	25901

total microbial biomass over the three cruises. With the variability among samples from any particular cruise, it is difficult to determine if there is a seasonal pattern to community development. Although organisms are found throughout ice floes, the highest concentrations and diversity occurred in a slush-like layer near the snow-ice interface. The highest microbial biomass associated with this layer was over $3\,mgC\,l^{-1}$ (approximately $0.6\,gC\,m^{-2}$). These very highly concentrated populations are patchy in their distribution. The variability among samples from the surface layer in ice is illustrated by the different composition of assemblages shown in Fig. 4.

While we have been able to identify many of the species in ice (Table 1), a considerable amount of systematic work is needed for some microbial groups before the diversity of the ice assemblage is known with certainty. Among the groups present in ice, the diatoms are the most completely known. Although we have recognized over 60 species during our studies (see Table 1), fewer than 15 are regularly present in abundance. The most common forms include several *Nitzschia* species (*N. cylindrus*, *N. closterium*, *N. turgiduloides*, *N. prolongatoides* and *N. curta*), *Chaetoceros neogracile*, *C. neglectum*, *Amphiprora kjellmanii*, *Synedra* sp., and *Tropidoneis fusiformis*. Two species, *N. cylindrus* and *N. closterium*, often dominate in the slush-like surface layers and reached densities $>10^7\,l^{-1}$ (Fig. 4a, b).

Autotrophic dinoflagellates are very abundant in some ice samples (see Fig. 4c). Most of the dinoflagellates that we have found in the ice are 'naked' forms and few have been identified to species. Hypnozygotes of autotrophic dinoflagellates are abundant in some samples (Buck et al., in press).

A variety of autotrophic nanoflagellates including prasinophytes, chrysophytes, cryptophytes and prymnesiophytes are regularly present in ice, and many were not routinely identified to species during our counting. The most abundant autotrophic flagellate in the ice is the prymnesiophyte, *Phaeocystis pouchetii*. Both motile stages and gelatinous colonies were found, and densities reached $5 \times 10^7\,l^{-1}$ in some surface-layer populations (e.g., Fig. 4c). Archaeomonads, which were previously reported as abundant in pack ice by Mitchell and Silver 1982, were found during all seasons at densities of 10^4–$10^6\,l^{-1}$ (see Fig. 4g). Archaeomonads are presumably chrysophyte cysts and we have observed chloroplast fluorescence,

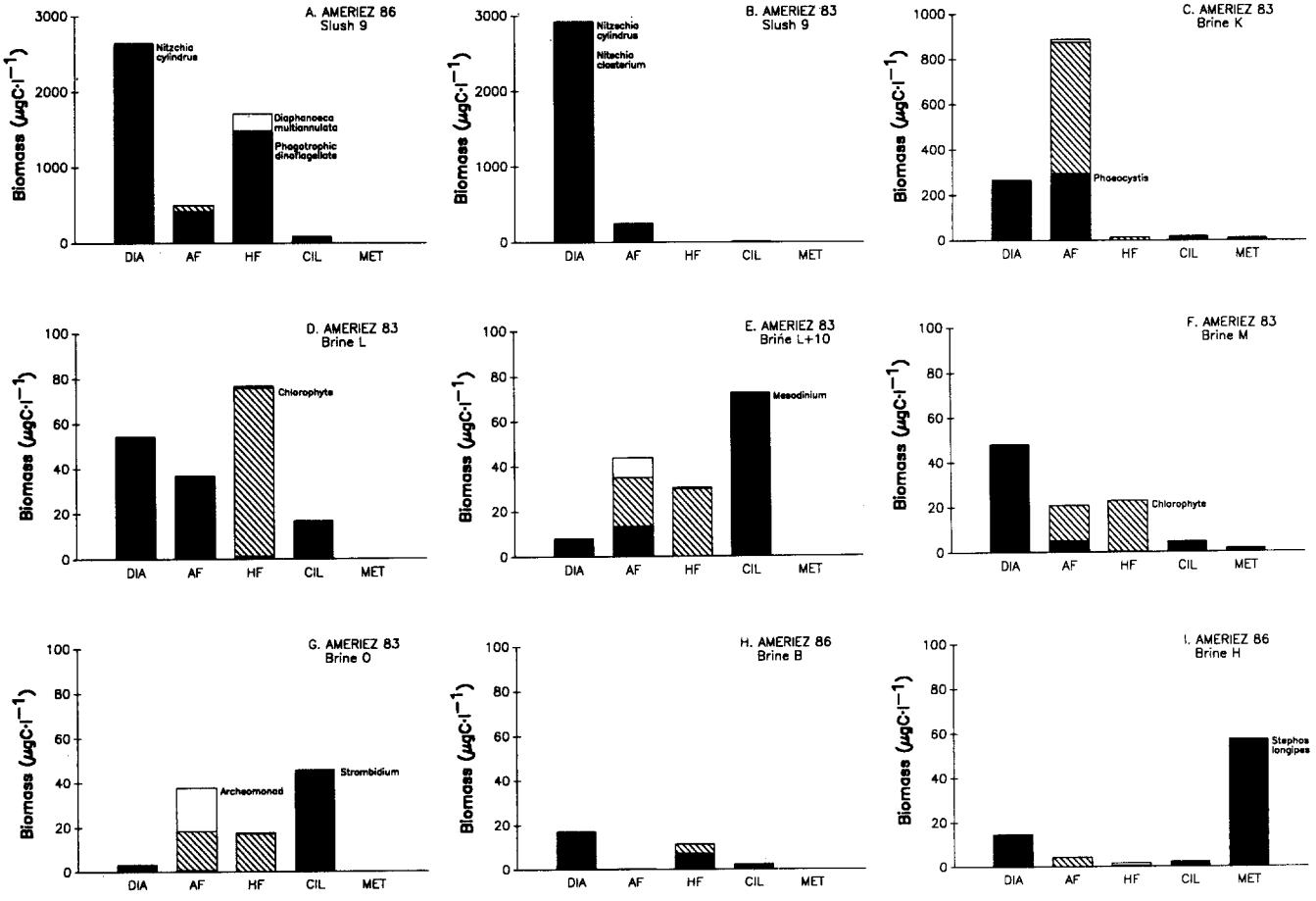

Fig. 4. Composition of individual samples from either brine or slush samples at the surface of ice floes. See Fig. 3 for the legend explaining breakdown among major groups. Dominant species for some groups are noted and are discussed in text

confirming that they are autotrophic forms, but we have never observed germination that would allow us to associate these cysts with the numerous autotrophic flagellates in ice.

Heterotrophic biomass is often dominated by nanoflagellates (Fig. 4d–f). There has been little systematic work on most of the nonloricate (naked) forms (e.g., bodonids). Euglenoids were also present in low numbers. One of the more conspicuous heterotrophic flagellates was a biflagellated form resembling a chlorophyte in external morphology, but its affinity is unknown. This unknown flagellate dominated the biomass in some ice samples during the spring cruise (Fig. 4d).

In contrast to the nonloricate flagellates, choanoflagellates (Acanthoecidae) are relatively well known, with fifteen species of loricate choanoflagellates being identified from ice (Table 1). Most of these species have been reported from ice and water in other regions of the Antarctic (e.g., Takahashi 1981; Buck and Garrison 1983, 1988; Marchant 1985). Choanoflagellates were found in abundances of up to $2.5 \times 10^7\ l^{-1}$ in surface layer assemblages (Fig. 4a). This latter abundance is the highest yet recorded for choanoflagellates in any environment.

A number of the dinoflagellates lacked autofluorescence when freshly-collected samples were examined aboard ship. Most of the heterotrophic forms were naked dinoflagellates (e.g., *Gyrodinium*, *Gymnodimium*, and *Amphidinium*). The most unusual among the heterotrophic dinoflagellates was a large form that was usually found with a vacuole so full of diatoms that it occupied most of the cell volume (Bolt et al. 1988; Buck et al., in press). This form was common in surface-slush layers during the autumn cruise (Fig. 4a) along with discarded fecal pellets similar to those observed within living cells.

Ciliated protozoans were also an important heterotrophic group in ice. Although some species from ice were described by Fenchel and Lee (1972), the ciliate assemblage in the Antarctic is poorly known. Corliss and Snyder (1986) examined our ice samples from the AMERIEZ 83 cruise and identified 26 separate taxa of which 7 species were new to science (see Table 1). The most common forms were non-sheathed oligotrichs (e.g., *Strombidium*; see Fig. 4g), which are also present in the plankton (Garrison and Buck 1989). The ciliate, *Myrionecta rubra* (=*Mesodinium rubra*), containing a cryptophyte symbiont, was also present in surface layers in the ice at abundances up to $8.6 \times 10^4\ l^{-1}$ (see Fig. 4e). Most of the taxa described by Corliss and Snyder (1986) are not common in the plankton.

Other protozoa were present in the ice but were only rarely found in our samples. Amoebae and heliozoans developed in culture, but were not found (or recognized) in preserved samples. Foraminifera were present in ice, but were rarely encountered during our routine counting. Maximum abundances were found during the winter (Wincruise 87) with average densities of $200\ l^{-1}$.

The only Metazoa found in pack ice were crustaceans. These included both larvae and adults of copepods and occasionally juveniles of *Euphausia superba* (see Daly and Macaulay 1988). Copepod larvae were the most abundant, numbering up to $800\ l^{-1}$ in some samples. Fecal pellets of copepods were also frequently found, indicating that copepods were regularly present.

Many of the organisms that we have found in pack ice have been reported previously from other ice environments (Carey 1985). The diversity and abundance of delicate forms such as flagellates and ciliates, however, is unusual and may be the result of our sample handling and preservation procedures which are specifically designed to retain these forms (Garrison and Buck 1986). It is not clear why we did not find the abundances of foraminifera that others have reported (e.g., Lipps and Krebs 1974; Spindler and Dieckmann 1986; Dieckmann et al. 1986). Foraminifera, however, are reported to be patchy (Spindler and Dieckmann 1986), and organisms occurring at densities of $10^2\ l^{-1}$ are near the lower limit of resolution of our sampling and counting methods. A detailed comparison between pack ice and land-fast assemblages is premature at this point, but our impressions are that pack ice assemblages are dominated by planktonic forms and that benthic forms (e.g., benthic diatoms and the larvae of benthic organisms) are rare or absent. This is not entirely unexpected, since most of our sampling has been from deep-water regions remote from land.

The seasonally varying composition of autotrophic and heterotrophic biomass suggests a successional change in ice community structure with heterotrophic forms becoming more abundant in the spring and summer (see Figs. 3 and 4), but further studies will be required to confirm this observation. Whereas other studies have emphasized the importance of ice as a site of primary production where algal biomass accumulates (e.g., Fukushima and Meguro 1966; Bunt and Lee 1970; Sullivan et al. 1982), our studies indicate that a well-developed microbial food web is also present. Sullivan and co-workers (Miller et al. 1984; Kottmeier and Sullivan 1987) have also shown that bacterial biomass and production are high. Bacterial production may account for the high densities of heterotrophic flagellates and ciliates. Our finding larger consumers of ice-associated algae (e.g., heterotrophic dinoflagellates and ciliates) also suggests that much of the ice-based production may be consumed in situ. The occurrence of larger metazoan consumers, such as krill, in ice floes, appears to depend on seasonal weathering of the ice or deformation processes to expose the ice biota (e.g., Meguro 1962).

Sea ice has been suggested as a refuge for several organisms. The prevalence of archaeomonads and dinoflagellate cysts suggests ice is an overwintering site for resting or dormant stages. Distinct resting stages of diatoms (i.e., resting spores), which are the most common algae in ice, are rarely found, but Palmisano and Sullivan (1982) have shown that there may be physiological resting cells for ice diatoms. The dense populations of other forms, such as heterotrophic dinoflagellates and ciliates, may result from the concentrations of suitable prey for these

forms in ice or may result from the exclusion of their predators for at least part of the history of ice community development. For many diatoms and *Phaeocystis*, development in ice may be followed by growth in the plankton when seasonal melting releases the ice biota (Garrison et al. 1987). A similar "seeding" may occur for some of the other flagellates and ciliates, since many of the forms in the ice are also present in the underlying and adjacent areas of the water column (Buck and Garrison 1988; Garrison and Buck 1989). The importance of the ice habitat to micrometazoa is unknown. Dahms and Dieckmann (1987) reported that the copepod, *Drescheriella glacialis*, reproduces and grows in ice. The ice habitat, with its concentrated food resources and protected environment, could also be an important temporary habitat for pelagic larvae. For larger consumers, such as krill, concentrated biomass in ice is a potential food source that is present before the onset of significant production in the water column (Holm-Hansen and Huntley 1984).

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Note Added in Proof

The heterotrophic flagellate described throughout the text and in the figures as an unknown chlorophyte (?) is being described as *Cryothecamonas armiger nom. prov. (Incertae sedis)* (H.E. Thomsen, Inst. for Sporeplanter, Univ. Copenhagen, O. Farimagsgade 2D, DK-1353 Copenhagen K, Denmark). A description of the choanoflagellate *Kakoeca antarctica* (Table 1) is also in preparation (K.R. Buck, Institute of Marine Sciences, University of California, Santa Cruz, CA 95064, USA).