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Sea Ice Microbial Communities in Antarctica

These communities may provide an important food resource in deep-water pelagic systems

David L. Garrison, Cornelius W. Sullivan, and Stephen F. Ackley

Accounts of early naturalists first suggested the richness of Antarctic waters. Along with observations of abundant stocks of great whales, seals, and seabirds came reports of sea ice floes stained and discolored by algae. Although sea ice microbial communities (SIMCOs) have been observed and studied for several decades, fundamental questions about their role remain. Do these communities represent a significant food source for benthic or pelagic food webs in ice-covered oceans? If so, what factors contribute to their productivity? Studies of SIMCOs in the landfast ice at McMurdo Sound and in the pack ice region of the Weddell Sea are part of an ongoing effort to understand the role and importance of sea ice communities in the Antarctic marine ecosystem and the physical and chemical attributes of their habitat.

Sea ice as a habitat

Initially, ice hardly appears to be a

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How much production SIMCOs contribute is an important question that cannot be answered at present

favorable environment for biological activity. Sea ice, however, contains brine inclusions that furnish a habitat for microbial populations. Differing structural characteristics among ice floes and seasonal changes combine to create a unique microenvironment in the ice. Many features of this habitat have been studied only superficially.

Structural characteristics of sea ice are determined by events during ice formation and growth (see Weeks and Ackley 1982). During initial freezing, ice crystals form as small disks, needles, or dendritic stars called frazil ice. Wind and wave action can herd this ice into various forms. Pancake ice, consisting of roughly circular pieces of new ice some 0.5 to several meters wide with upturned edges, forms when frazil ice is subjected to oscillatory wave action. During cold, calm periods with relatively little turbulence, sheet ice forms as a smooth, unbroken surface layer with little horizontal variability. The initial accumulations of frazil, pancake, and sheet ice generally account for the upper 10–12 cm in all sea ice floes. Because they form in a turbulent envi-

ronment, frazil ice crystals are usually randomly oriented.

Once a thin layer covers the sea surface, ice floes thicken either by accumulating more frazil ice from below or by the addition of congelation ice at the ice-water interface. For ice floes to grow from accumulating frazil ice, turbulent mixing requiring open water may be necessary (see Weeks and Ackley 1982). In contrast, congelation ice forms under an established ice sheet. Since congelation ice is added to an existing ice sheet, the ice crystals lose some freedom of growth, resulting in a highly oriented crystal structure.

The history of how ice forms and grows can be determined by examining crystal size and orientation in sections taken from ice cores and examined with polarized light. Such studies suggest that regional differences in environmental conditions may determine whether floes comprise frazil or congelation ice, and this in turn may be fundamental in determining how SIMCOs form and develop. For example, frazil ice crystals appear to be able to harvest and concentrate particles from the surrounding water as they form and float to the sea surface; this may have a profound effect on the initial formation of sea ice microbial populations (Garrison et al. 1983).

Other characteristics of the ice habitat are expected to vary seasonally. In autumn and winter, when sea ice is beginning to grow, ice salinity (measured as melted ice plus trapped brine) is fairly high (10‰). With time, brine is rejected from floes by a

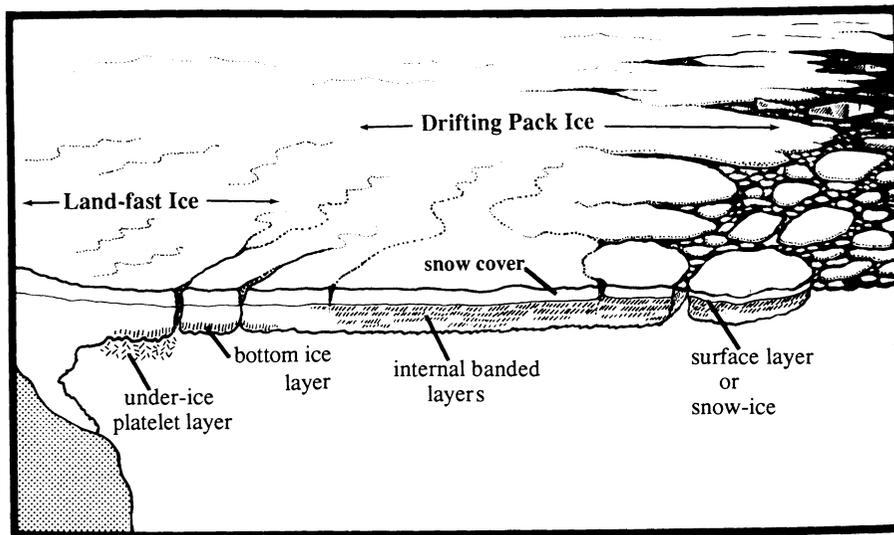


Figure 1. Microbial habitats associated with sea ice. Based on Whitaker (1977) and other sources.

variety of mechanisms, and salinities in first-year ice typically range from 3‰ to 8‰. At equilibrium, the salinity within brine inclusions is primarily a function of temperature. During the winter, the portion of ice floes above sea level may be exposed to low atmospheric temperatures. Because brine salinity is expected to increase about 10‰ for each additional degree of temperature below freezing, some organisms living in some portions of ice floes may experience hypersaline and hyperosmotic conditions. During the spring and summer, there may be some freshening as snow cover and ice melt. But since much of an ice floe is submerged, most of the ice habitat should reflect sea surface temperatures and salinities (i.e., $\sim -1.8^{\circ}\text{C}$ and $\sim 34\text{‰}$).

Nutrient concentrations also affect the quality of ice as an algal habitat. Unfortunately, however, there are few published data on nutrient concentrations in Antarctic sea ice (e.g., Garrison and Buck 1982, Clarke and Ackley 1981), and because the brine is diluted by melting ice when samples are collected and processed, determining what concentrations actually occur can present problems.

In the Antarctic, light levels are fundamental in regulating organic production in both the ice and the water column. Without snow cover, sea ice is relatively transparent; a significant portion of the incoming solar radiation (10–50%) may pene-

trate relatively thick (two-meter) sea ice. With even a thin layer of snow, however, albedo (reflection) is dramatically increased, and light penetration through floes may be reduced to less than 1%. In floes with dense microbial populations, absorbance and scattering by SIMCO biomass can also significantly influence both the intensity and spectral composition of the penetrating light (Sullivan et al. 1985). In most ice-covered regions, ice algal populations develop before planktonic ones (e.g., Alexander 1980, Horner 1976). The apparent reason for this is that ice cover blocks the light necessary for production in the underlying water column, whereas sea ice, by virtue of its position at the sea surface, provides an optimal light environment and stable substrate for early seasonal growth of ice-associated algae.

Sea ice algae

Finding rich algal populations in sea ice suggests that ice communities could be important sites of production in the Antarctic. At present, however, uncertainty about production levels in both ice and water permits only tentative comparisons (see Smith and Nelson, p. 251 this issue, for a discussion of pelagic production).

Observations on ice algal communities in the Antarctic span several decades. Hooker's account of diatom populations discoloring icebergs and pack ice floes during the Ross expedi-

tion on H.M. ships *Erebus* and *Terror* (ca. 1841) is the first record of ice algal observations in the Antarctic (Horner 1976). Subsequent studies have also concentrated on the floral component of ice communities, and several more-or-less distinct ice algal associations have now been described (Figure 1).

Pioneering studies on ice algal communities at several locations provide the conceptual base for contemporary work. Meguro (1962) reported that a layer of "plankton ice" developed at the snow-ice interface on floes near Syowa Station in Lutzow-Holm Bay and over extensive areas of the nearby pack ice. Similar surface algal communities—variously labeled snow-ice layer, infiltration ice, slush ice, or melt pond communities—have been widely reported from the Antarctic (Table 1). Bunt (1963), working at McMurdo Sound, described an "epontic" algal community that occurred within the interstices of loosely aggregated underwater platelet ice and in the bottom few centimeters of overlying hard ice. Bottom-layer communities in consolidated ice appear to be widespread in fast-ice regions, and the formation of an under-ice platelet layer has been reported near Mirny Station (Gruzov 1977), although this layer varies in time and location. Whereas most bottom-ice blooms have been reported in the spring, Hoshiai (1977) described how an autumn bloom, which initially formed as a bottom-layer community on the underside of floes near Syowa Station, was covered by new ice during the winter and remained trapped in floes as an internal band. Algal biomass varies markedly among the different ice algal communities; the highest biomass concentrations are usually reported from bottom-ice communities (see Table 1).

The ice biota

Most of the early studies of the ice biota concentrated on diatoms, the most conspicuous component of ice communities, but other algal groups, such as autotrophic flagellates and the prymnesiophyte *Phaeocystis pouchetii*, are often present and abundant (e.g., Horner 1976). A similarity in species composition between ice and ice edge planktonic populations has

suggested to several researchers that the ice is an important source of seed populations for ice edge plankton blooms (Garrison and Buck 1985); this hypothesis is still being tested.

In addition to primary producers, sea ice microbial communities also include microheterotrophs such as bacteria, heterotrophic flagellates, ciliates, and some small metazoans. A variety of larger organisms, including polychaetes, amphipods, copepods, and euphausiids, are sometimes associated with ice, apparently forming part of an ice-based food web (e.g., Andriashev 1968). Until recently, the heterotrophic component of the ice biota has received little attention.

SIMCOs at McMurdo Sound

McMurdo Sound is a shallow, near-shore Antarctic environment. Operating from the US land-based station located here, Sullivan and coworkers have undertaken long-term studies focusing on the seasonal aspects and growth dynamics of SIMCOs associated with the landfast ice (e.g., Grossi and Sullivan 1985, Grossi et al. 1984, Palmisano and Sullivan 1983, Palmisano et al. 1984, 1985, Sullivan and Palmisano 1984, and Sullivan et al. 1985).

Sea ice in McMurdo Sound forms every year and usually persists for 9 to 11 months. Initial freezing occurs in March or April, and by November annual ice throughout the sound is about one and a half to three meters thick. By mid-February or March most of the annual sea ice has melted or broken up. Ice floes here are characteristically composed of congelation ice with numerous brine channels in the bottom 20 cm and ice stalactites extending a meter or more into the water column. The loosely aggregated underwater platelet ice layer that Bunt (1963) reported is not always present. At a study site near Cape Armitage, the ice-water interface consisted primarily of hard congelation ice during the 1980 and 1981 field seasons, but at the same site in 1982, a 0.25- to 1-m thick platelet layer formed on the underside of 2-m thick congelation ice at the same site.

The growth and development of SIMCOs at McMurdo is intimately related to the formation of sea ice. As ice begins to form during the austral

Table 1. Maximum algal biomass measured as chlorophyll *a* from different ice algal communities in the Antarctic. (—), value not given; (–), integrated values not given but could be estimated from ice thickness data. See Figure 1 for community descriptions and Garrison and Siniff, p. 238 this issue for locations cited.

Community and Location	Chlorophyll <i>a</i>		Source
	mg · m ⁻²	mg · m ⁻³	
Surface layer			
Lutzow-Holm Bay	97	670	Meguro 1962
Palmer Peninsula	~122	407	Burkholder and Mandelli 1965
Weddell Sea pack ice			
Late winter	—	43	Clarke and Ackley 1984
Spring	—	54	Garrison, unpubl. obs.
Internal bands			
Weddell Sea pack ice			
Late summer	1.4	4.5	Ackley et al. 1979
Late summer	9.6	9.8	Garrison and Buck 1982
Spring	51.0	77.0	Garrison, unpubl. obs.
Late winter	0.6	3.8	Clarke and Ackley 1984
Young ice			
Weddell Sea			
Late summer	3.9	26.8	Garrison et al. 1983
Bottom ice layer			
McMurdo Sound	309	>656	Palmisano and Sullivan 1983
Syowa Station, fall		829	Hoshiai 1977
Syowa Station, spring		>1000	Hoshiai 1977
Syowa Station, fall	30	944	Hoshiai 1981
Syowa Station, spring	35	5320	Hoshiai 1981
Davis Station	15	—	McConville et al. 1985
Under-ice platelet layer			
McMurdo Sound	~164	132	Bunt and Lee 1969
	~125	250	Bunt 1963, 1968

autumn, algae starts growing on the underside of the forming ice and on ice that has survived summer melting. An autumn algal bloom has only been recorded from a few samples at McMurdo and is not yet well documented. Our observations suggest that the seasonal pattern at McMurdo may be similar to that Hoshiai (1977) reported in fast ice near Syowa Station, although the autumn bloom at Syowa Station developed concentrated populations (see Table 1). The highest levels of algal biomass in SIMCOs at McMurdo Sound develop in late spring as a dense layer in the bottom 20 cm of ice (Table 1 and Figure 2), which may include more than 90% of the chlorophyll *a* in the ice floes. This bloom lasts until ice ablation in late December or January removes it from beneath ice floes.

Because McMurdo Sound has open water one or two months a year at most, in situ phytoplankton production is strongly light limited, and much of the new carbon input into the sound, which supports rich and diverse benthic communities, may be derived from SIMCO production. For example, from average chlorophyll *a*

biomass during the spring bloom, we estimated that SIMCOs could contribute at least 4.1 g C per m² to the pelagic and benthic systems (Palmisano and Sullivan 1983). Although this level would add substantially to local annual production, it is clearly an underestimate because (1) the spring ice algal bloom continued beyond our study; (2) we did not include losses to grazers and secondary production by bacteria; and (3) at McMurdo Sound, a fall bloom may contribute additional production.

Diatoms dominate SIMCO biomass at McMurdo. In our recent studies, we found that the same species reported as dominant during 1961–1962 (Bunt and Wood 1963) also dominated in 1982. Although we have found other algae, including *Phaeocystis pouchetii* and various small (10 μm) flagellates, they are never very numerous. Bacteria, heterotrophic flagellates, and ciliates are all present in well-developed SIMCOs.

Bacteria are both particularly important and morphologically diverse at McMurdo Sound (e.g., Grossi et al. 1984, Sullivan and Palmisano 1984). Although present throughout the sea

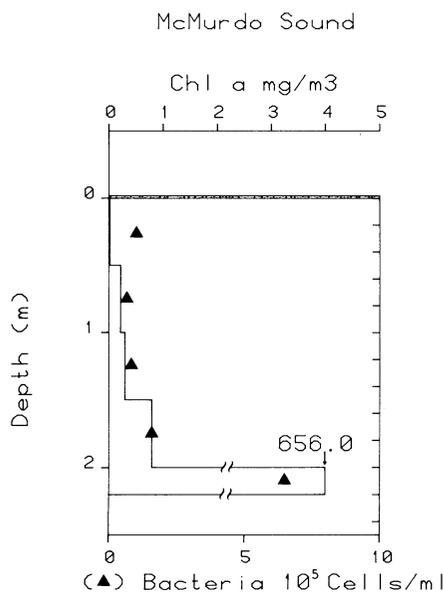


Figure 2. Distribution of chlorophyll *a* and bacteria in landfast ice floes in McMurdo Sound. Chlorophyll *a* values are from Palmisano and Sullivan (1983).

ice, they are most concentrated in the lower 20 cm, along with concentrated ice algal populations (see Figure 2). In comparison with bacterioplankton in the water column, ice bacteria are five- to tenfold larger, often occurring as paired or dividing cells, and are frequently found in chains 10 to 30 cells long.

An intimate relationship apparently exists between bacteria and diatoms in SIMCOs. Epibacteria on diatoms and other particles made up as much as 30% of the total bacterial assemblage in our samples. Using scanning electron microscopy (SEM), for example, we have shown a close physical coupling of bacteria and certain species of ice diatoms, especially the genus *Amphiprora* (Sullivan and Palmisano 1984). These observations have been supported by further experiments.

One of the most important factors regulating production and growth in SIMCOs is solar radiation. We have been able to demonstrate this through large-scale, in situ light perturbation experiments (Palmisano et al. 1984). During spring and summer 1981–1982, we followed the growth and development of SIMCOs in a control quadrat with 1.5–7.0 cm natural snow cover and in an adjacent experimental quadrat that we covered with 70 cm of snow. This design gave us

two different under-ice irradiances, both consistently less than one percent of surface irradiance—a value often used by oceanographers to define the lower limit that will support net photosynthesis by phytoplankton. In the control quadrat, algal cells and chlorophyll *a* concentrations increased more than sixteen- and twentyfold, respectively, during the 44-day experiment. During the same interval, bacteria increased almost sixfold. In contrast, however, neither the algal or bacterial populations in the perturbed quadrat increased significantly.

These corresponding increases in algal and bacterial populations suggested a close link between algal and bacterial production (Sullivan et al. 1985). By using radioactive tracers, we could measure metabolic processes indicating this coupling. During our perturbation experiment, we collected samples from the undersurface of the ice, injected them with radiochemicals, and then incubated them in situ in sealed Plexiglas chambers for 12 to 24 hours. During these experiments, peak primary productivity reached 0.35 mg C per mg chl *a* per h, which about equals algal generation times of 8.1 days. Microautoradiographs showed that the codominant diatoms, *Amphiprora* sp. and *Nitzschia stellata*, were heavily labeled. In other experiments, we have shown that more than 30% of the organic carbon fixed by algae is released as dissolved organic material, which may provide the carbon source for heterotrophic bacterial growth (Palmisano and Sullivan 1985). Microautoradiographic studies using labeled organic substrates indicated that both diatoms and bacteria metabolized a variety of organic compounds, including glucose, amino acids, and thymidine. Bacteria incorporated [³H]thymidine, demonstrating that cell division can take place in the ice.

Ice-associated microbial populations appear physiologically adapted to the ice environment. Ice algae, for instance, are adapted to low light levels. In situ measurements showed that both bacteria and algae grow at temperatures as low as -1.8°C . Algal populations increased in situ at light levels lower than 0.4% of surface irradiance and reached maximum photosynthetic rates at approximate-

ly 1–2% of surface intensities. Some algal cells persist in ice throughout the winter, indicating their ability to survive four months of total darkness. How can these cells do this?

In laboratory studies, we found that sea ice diatoms responded to simulated summer-to-winter changes in light, temperature, and salinity by reducing cellular metabolism and increasing their ability to use reduced organic compounds as an energy source (Palmisano and Sullivan 1982). Thus, viable cells may be maintained throughout the winter via dormant or resting cells, which have lower metabolic requirements and can use organic substrates.

Studies at McMurdo Sound continue. During the 1985–1986 season, we are focusing on the influence of nutrients in sea ice and the uptake kinetics and transport systems of SIMCOs for Si, N, and P to understand the factors influencing SIMCO growth, development, and eventual decline.

SIMCOs in the Weddell Sea

Parts of the remote Weddell Sea region remain heavily ice covered even during the austral summer. Because research here requires icebreaker support, long-term observations such as those conducted at McMurdo Sound have not been possible. Instead we have made observations on several cruises over the past eight years.

In contrast to the nearshore, fast-ice environment of McMurdo Sound, the Weddell Sea is a deep-water oceanic environment. At winter's peak in September, the sea surface is approximately 80% ice covered, but by February much of this ice has melted. Because of the clockwise surface circulation in the Weddell Sea Gyre, drifting pack ice perpetually covers the western Weddell Sea. Ice floes accumulate in this region and may persist for one or more seasons; eventually they are released into the Antarctic Circumpolar Current to the north. Annual ice typically ranges from a few centimeters to about two meters thick, and multiyear floes—those surviving summer melting—may be up to five meters thick.

Shipboard observations of discolored layers in broken and overturned ice floes indicate that sea ice microbial populations occur over vast areas

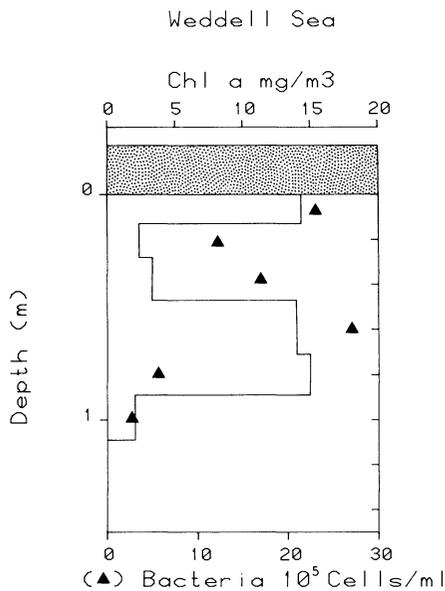


Figure 3. Distribution of chlorophyll *a* and bacteria throughout a pack ice floe from the Weddell Sea.

of the Weddell Sea. Whereas SIMCOs associated with landfast ice, such as those described from McMurdo Sound, occur as bottom-layer or under-ice communities, SIMCOs in the Weddell Sea are found throughout the floes as internal populations, or they occur within a slushlike layer near the snow-ice interface (Figure 3). Since some sea ice persists throughout the year, SIMCOs are a constant feature of this pelagic environment.

The growth of ice floes by incorporation of frazil ice may be fundamental in determining how SIMCOs form in this region. Clarke and Ackley (1981) reported that floes in the Weddell Sea may contain 50–70% frazil ice and suggested that wind action is responsible for maintaining leads (channels) and polynyas (open water). This allows turbulent mixing and apparently results in the unusual amount of frazil ice formation throughout this region. We have proposed a model to explain how frazil ice formation affects SIMCO initiation and development (Garrison et al. 1983). For example, in late summer 1980 we measured chlorophyll *a* concentrations in young sea ice that were up to 50 times the concentrations measured in adjacent water samples. Since algal growth rates could not account for these concentrations, we concluded that dense algal populations had been physically concentrat-

ed during frazil ice formation. Such a mechanism would explain not only how dense populations may be concentrated initially but also why populations may be found throughout floes where frazil ice is continually produced.

Algal biomass in SIMCOs from the Weddell Sea is typically lower than that reported from other ice communities (see Table 1). Even in this region, however, algal concentrations in the ice exceed those in the water column, and standing crops in the ice may equal those found throughout the remainder of an ice-covered water column, suggesting that SIMCOs may

be seasonally important production sites. Although algal biomass, and presumably production as well, is lower in the ice than in ice edge plankton blooms, the water column may be seeded by algae released from SIMCOs (see Smith and Nelson, p. 251 this issue).

The evidence supporting the seeding hypothesis is most compelling for diatoms, which are abundant in both the ice and planktonic populations. Moreover, diatoms are one group that can be identified and counted with sufficient confidence to make comparisons among assemblages (Table 2). In comparing samples from

Table 2. Summary of diatom species assemblages in the water column, young sea ice, and ice floes. (+) <0.5%. Source: Garrison and Buck 1985.

Species	Relative abundance (%)		
	Water column	Young ice	Ice floes
<i>Nitzschia cylindrus</i>	25	40	56
<i>N. subcurvata</i>	19	1	+
<i>N. curta</i>	16	36	1
<i>N. sublineata</i>	8	2	
<i>Chaetoceros dichæta</i>	6	1	+
<i>C. bulbosum</i>	6	+	
<i>Nitzschia closterium</i>	4	4	7
<i>N. turgiduloides</i>	3	1	4
<i>Chaetoceros neglectum</i>	2		
<i>Rhizosolenia alata</i>	2		
<i>Thalassiosira</i> spp.	1	+	
<i>Odontella weissflogii</i>	1		+
<i>Nitzschia kerguelensis</i>	1	2	
<i>Haslea trompii</i>	1		
<i>Corethron criophilum</i>	1	2	+
<i>Nitzschia angulata</i>	1	1	
<i>Amphiprora kjellmanii</i>	+	1	2
<i>Nitzschia</i> spp.	+	1	6
<i>N. neglecta</i>	+	+	2
<i>Chaetoceros gracile</i>	+	4	15
<i>Dactyliosolen antarcticus</i>	+	1	
<i>Tropidoneis fusiformis</i>	+	1	
<i>T. gausii</i>	+	1	
<i>T. glacialis</i>	+	+	
<i>Nitzschia pseudonana</i>	+	+	
<i>N. obliquecostata</i>	+	+	
<i>Thalassiosira gracilis</i>	+		
<i>Synedra</i> sp.			5
<i>Nitzschia castracanei</i>	+		+
<i>N. lineola</i>			+
<i>N. prolongatoides</i>			+
<i>N. lecointei</i>			+
<i>Coscinodiscus furcatus</i>			+
<i>Tropidoneis antarcticus</i>			+
<i>Eucampia balaustium</i>	+		+
<i>Chaetoceros criophilum</i>	+		+
<i>C. atlanticum</i>	+		
<i>Nitzschia ritscheri</i>	+		
<i>Chaetoceros</i> spp.	+		
<i>C. pendulum</i>	+		
<i>Rhizosolenia styliformis</i>	+		
<i>Asteromphalus parvulus</i>	+		
<i>Thalassiothrix longissima</i>	+		
<i>Tropidoneis belgicae</i>	+		

young ice and the adjacent water, we found no statistical differences among these populations (the average percent similarity among samples was greater than 70%; see Garrison and Buck 1985). This comparison supports our hypothesis that planktonic populations can be nonselectively concentrated during frazil ice formation. We also found a high degree of similarity among assemblages from older ice floes and from planktonic populations (about 46%), indicating that algal species in the Weddell Sea region inhabit both sea ice and water. Such similarity between ice and water assemblages is consistent with seeding, but it is difficult to show unequivocally that populations in ice edge blooms derive from ice populations.

Ice communities have also been suggested as refuges for pelagic forms with overwintering resting stages. Although recognizable diatom resting spores have not been found in abundance, other resting stages, such as archaeomonads (chrysophytelike cysts; Mitchell and Silver 1982), are among the most abundant forms in the ice. Unfortunately, we have not yet succeeded in germinating archaeo-

monads in culture to identify the vegetative stages associated with these cysts, so we do not know if the vegetative stages are common in SIMCOs or plankton. Other siliceous cysts, such as those previously reported by Silver et al. (1980) are also present in ice samples, but in lower abundance. The extent to which ice-associated organisms use resting stages may be difficult to evaluate. As Palmisano and Sullivan (1982) have shown, some ice diatoms show physiological adaptations to overwintering without accompanying morphological changes; such stages may be defined metabolically as resting cells, but do not form morphologically distinct resting spores or cysts. If Palmisano and Sullivan's findings are generally true, many ice diatoms may be overwintering in sea ice as resting cells that we do not recognize as such.

SIMCOs in the Weddell Sea comprise a diverse group of microbial forms. Our most recent work, part of the 1983 AMERIEZ (Antarctic Marine Ecosystem Research at the Ice Edge Zone) study, has shown that in addition to diatoms, which are usually considered characteristic of ice

communities, dinoflagellates, small autotrophic and heterotrophic nanoflagellates, bacteria, and ciliates are also regular and abundant components of the ice biota (Figure 4). Naupliar larvae are occasionally present, and crustacean fecal pellets provide additional evidence that small metazoans also inhabit the pack ice. All components of SIMCOs in the Weddell Sea are more concentrated in the ice than in the water, suggesting that these communities support an active food web. Bacteria are both larger and more abundant than those in the water column (Miller et al. 1984), which we would expect if they are growing in an organic-rich environment, and they are most abundant where algae are also most abundant (see Figure 3). From microscopy, we have been able to outline the complexities of the food web associated with SIMCOs in pack ice (Figure 5).

How much production SIMCOs contribute is an important question that cannot be answered with present information. Maximum seasonal biomass has been suggested as an indication of annual production in some ice communities because grazing was thought to be low. By this criterion, SIMCOs in the Weddell Sea would be considerably less productive than bottom-ice-layer communities in near-shore regions (see Table 1). The presence of a well-developed heterotrophic food web, however, argues that algal biomass probably turns over rapidly rather than accumulating in ice floes. The amount of production consumed within the ice floes remains to be determined, but some production in the ice is apparently available to pelagic food webs in the ice edge zone.

The Antarctic krill, *Euphausia superba*, is the most important macrozooplankton consumer in the Antarctic pelagic food web (see Ross and Quetin, p. 264 this issue). Swarms of krill have been observed on upturned ice floes (e.g., Hewes et al. 1983) or in holes in decaying ice floes (Meguro 1962). We also observed this phenomenon during the AMERIEZ 83 Cruise (Ainley and Sullivan 1984); we saw krill on floes upturned by the icebreaker, and divers saw them foraging under floes. Researchers made similar observations during the 1985 winter cruise of the *Polar Duke*. Dur-

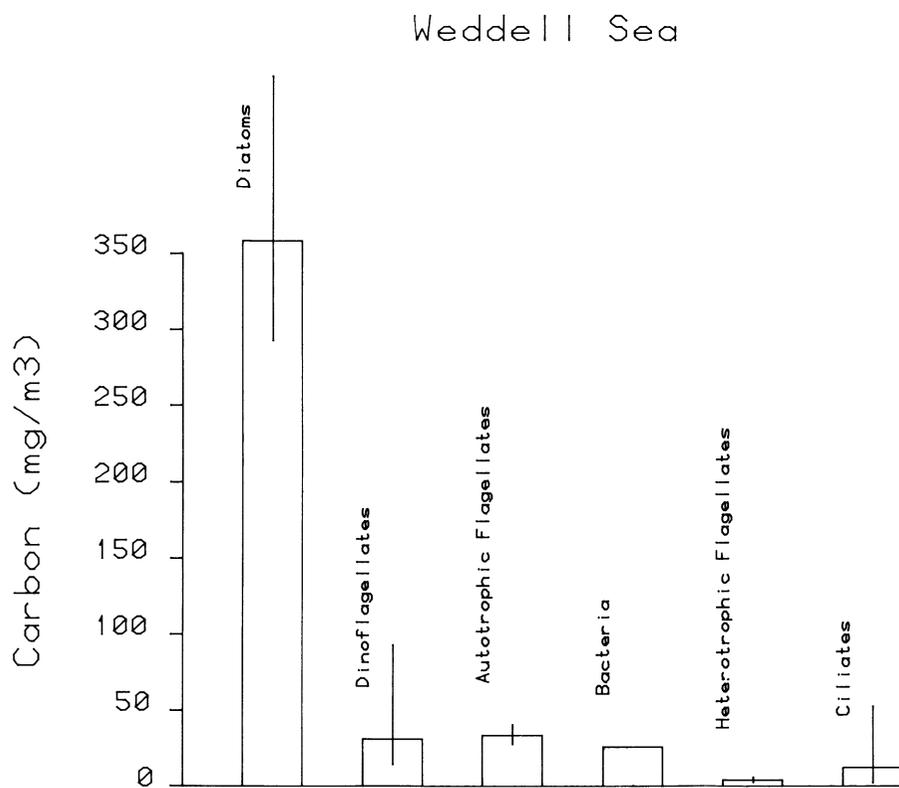


Figure 4. Composition of the ice biota in floes from the Weddell Sea.

ing our 1983 ice-coring operations, some krill were recovered, indicating that these organisms apparently can enter the labyrinth of channels within the ice floes. Many of the collected krill had pigmented material in their foreguts, and we were able to recognize diatoms similar to those we were finding in ice populations. In laboratory experiments, Hamner et al. (1983) have observed krill feeding on ice diatoms, and there is increasing evidence that this happens extensively in nature. Other recent evidence indicates that krill have high levels of digestive enzymes in the late winter, when the most probable source of food would be associated with SIMCOs.

Although many questions about SIMCOs in pack ice regions remain to be answered, evidence is accumulating that they may play an important role in the energetics of deep-water pelagic systems like the Weddell Sea. In the immediate future, these and other questions will be considered by AMERIEZ.

Directions for further studies

Because sea ice microbial dynamics depend heavily on the physical and chemical properties of annual sea ice, future studies should, ideally, be multidisciplinary. Time series, or seasonal observations, are badly needed, particularly in the pack ice regions where data are scarce or nonexistent. Until moored instruments are developed or ships are frozen in drifting pack ice—an approach that is now feasible—we must still rely on shore-based stations for seasonal observations and experiments. Because we are finding considerable differences between SIMCOs in landfast and pack ice, however, this approach is not entirely satisfactory.

Detailed comparisons between landfast and pack ice SIMCOs, although premature, indicate major gaps in our present knowledge. One obvious difference is the prevalence of well-developed bottom-ice communities in landfast ice floes, whereas internal and/or surface snow-ice populations characterize pack ice. In addition, landfast ice, at least at McMurdo Sound, may also have an unconsolidated layer of platelet ice on its undersurface; this layer has not

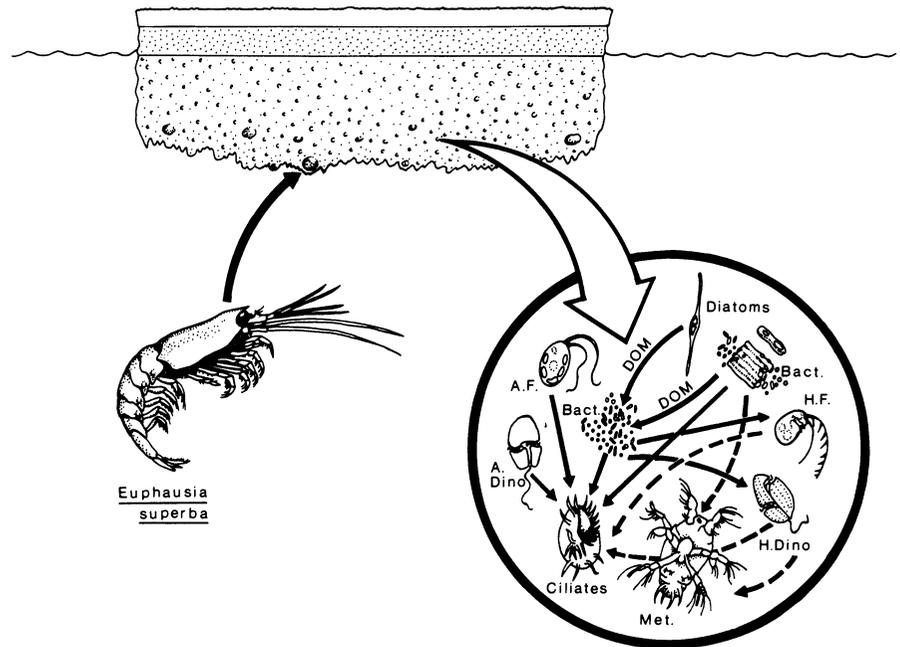


Figure 5. Proposed food web for sea ice microbial communities in pack ice based on microscopy and population studies. Suspected links are indicated as dashed lines. A. F., autotrophic flagellates; H. F., heterotrophic flagellates; A. Dino, autotrophic dinoflagellates; H. Dino, heterotrophic dinoflagellates; Bact, bacteria; DOM, dissolved organic material; Met, small metazoans.

been reported in drifting pack ice. Grossi and Sullivan (1985) have related ice algal distributions at McMurdo Sound to successive seasonal blooms on the underside of a growing ice floe and differential species growth along a vertical physiological gradient in congelation ice. This kind of information is not yet available from pack ice algal communities.

Differing environmental characteristics leading to different types of ice formation may also help explain differences among ice algal communities: landfast ice is predominately congelation ice, whereas pack ice, at least in the Weddell Sea, may be composed mostly of frazil ice. We have described how frazil ice formation may be responsible for establishing ice populations throughout ice floes, but this does not explain why bottom-ice-layer communities do not develop in the pack ice. Clarke and Ackley (1984) have speculated that structural differences in the ice affect nutrient exchange between ice and water and may thus control how ice communities develop in congelation versus frazil ice; this idea needs to be tested. A second likely possibility may be that grazing by pelagic consumers,

such as *Euphausia superba*, under pack ice floes may regulate SIMCO development.

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