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Ecology of sea ice biota

1. Habitat, terminology, and methodology*

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Summary. Polar regions are covered by extensive sea ice that is inhabited by a variety of plants and animals. The environments where the organisms live vary depending on the structure and age of the ice. Many terms have been used to describe the habitats and the organisms. We here characterize the habitats and communities and suggest some standard terms for them. We also suggest routine sampling methods and reporting units for measurements of biological and chemical variables.

Introduction

Sea ice is a prominent feature of polar regions where it has profound effects on the plants and animals living in and near the marine environment. At maximum extent sea ice covers some 5% of the Northern Hemisphere and 8% of the Southern Hemisphere; it accounts for about 67% of the earth's permanent ice cover, but only 0.1% of its volume. Sea ice is a thin layer that responds quickly to changes in climate or oceanic heat transport (Maykut 1985). However, sea ice thickness is highly variable due to the age of the ice and is on the average older and thicker in the Arctic than in the Antarctic (Table 1).

In addition to polar regions, sea ice is found seasonally at lower latitudes, including the Baltic, Black, and Okhotsk seas, the Gulf of St. Lawrence, fjords on the west coast of Sweden and in Norway, and salt lakes in northern Japan such as Lake Saroma. In all of these areas, plants and animals live in association with sea ice, either in the ice itself, or closely connected to it in some way, often trophically.

A number of terms have been used in the literature to describe both the organisms and their habitats. Many of the terms have been misused, inadequately defined, or misinterpreted. In addition, experimental studies often report their findings in a variety of units that make it difficult to compare studies (Palmisano and Sullivan 1985a; Horner et al. 1988). Our purpose is to characterize and define the organisms and their habitats and suggest standard terminology for them. We also suggest some standard sampling methods and reporting units for experimental studies.

Geographical distribution

The Arctic Ocean is a deep, permanently ice-covered basin surrounded by broad continental shelves and shallow marginal seas that are seasonally ice-covered (Fig. 1, Table 1). It is breached only through Bering Strait, the North Atlantic, and the Canadian Archipelago. Most of the water and ice exchange is in the North Atlantic with about 10% of the ice drifting out of the Arctic Basin annually, mostly through Fram Strait. Local climate, land mass configuration, and current conditions affect the seasonal ice cover which may extend southward to 44–45°N (Japan) or only to ca 80°N (Spitsbergen). Depending on the season, 50 to 90% of the ice is multi-year ice and greater than 2 m thick. In contrast, Antarctica is a vast, frozen continent occupying most of the area south of 70°S, and surrounded by a seasonally varying ring of ice that extends from about 55 to 70°S (Fig. 2, Table 1). More than 90% of the Antarctic ice is first-year ice less than 2 m thick and melts in summer. For additional discussion, see Maykut (1985).

As a result of these geographical variations, ice conditions in the two polar regions are quite different (Table 1). This has a number of consequences for the organisms that inhabit the ice, such that both the nature of the habitats and the organisms that occupy them vary, although there may be similarities in form and colony shape, e.g., some colonial diatoms.

At lower latitudes, sea ice is present only for short periods of a few weeks to a few months (Grøntved 1950;

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Table 1. Comparison of Arctic and Antarctic sea ice properties (modified from Spindler 1990)

Property	Arctic	Antarctic
Maximum ice cover	14×10^6 km^2	20×10^6 km^2
Minimum ice cover	7×10^6 km^2	4×10^6 km^2
Age of ice	mainly multi-year	mainly one year
Ice thickness	>2 m	<2 m
Ice salinity	low	high
Ice type	mainly columnar	mainly frazil
Space for organisms	low	high
Melting process	at air-ice interface	at water-ice interface
Platelet ice	absent	present
Land fast ice	over shallow water	mainly over deep water

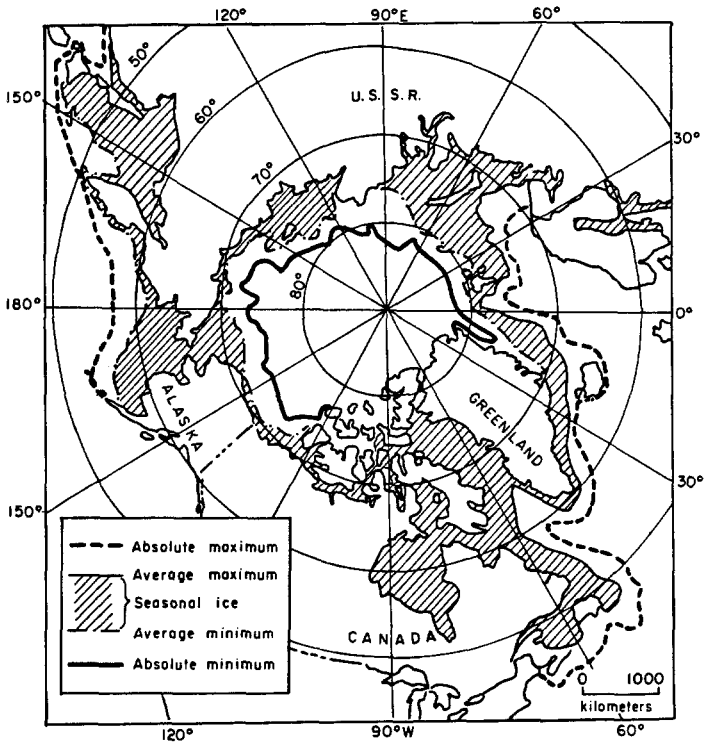

Fig. 1. Sea ice extent in the Northern Hemisphere with greater than 1/8 concentration (from Maykut 1985 with permission)

Hällfors and Niemi 1974; Dunbar and Acreman 1980; Hoshiai and Fukuchi 1981; Takahashi 1981; Larouche and Galbraith 1989; De Sève and Dunbar 1990). This leads to additional habitat variability, and, in some cases, different species.

Ice formation and structure

The formation of sea ice has been described and figured in detail (Maykut 1985; Lange et al. 1989), and is only briefly reviewed here. Small ice crystals, ca 3–4 mm in diameter, called *frazil* ice, first form on the surface of seawater that is cooled below the freezing point. They may also form below the sea surface in supercooled water and rise to the surface. As freezing continues, the frazil crystals coagulate

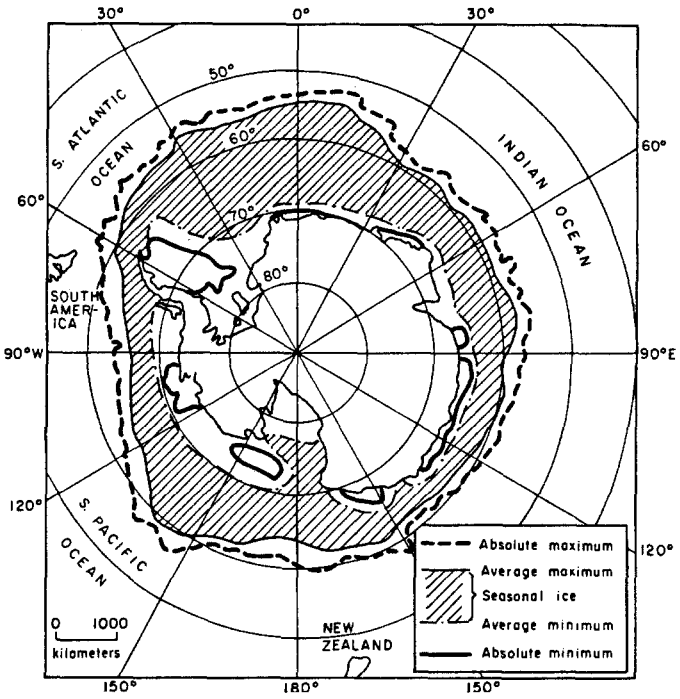

Fig. 2. Sea ice extent in the Southern Hemisphere with greater than 1/8 concentration (from Maykut 1985 with permission)

to form a soupy mixture called *grease* ice (WMO 1970). When no wind or waves are present, the ice crystals quickly freeze together to form *pancakes* and then a solid sheet of ice up to 10 cm thick (Maykut 1985).

Ice growth slows after a solid ice sheet forms or when wave action ceases; loose, frazil crystals no longer form, but long, columnar crystals grow on the underside of the ice producing *congelation* ice (Lange et al. 1989). In some areas frazil ice is found sandwiched between layers of congelation ice, probably a consequence of rafting that occurs when ice sheets collide and ride up onto other ice sheets. This adds to the thickness of the ice.

As the ice forms, brine is trapped in long, narrow channels within the ice lattice. The amount of salt initially trapped depends on the growth rate of the ice and the seawater salinity (Maykut 1985). While the brine initially has the same relative concentration of ions as the seawater from which the ice forms, salts precipitate out of solution as the temperature decreases. The effects of natural temperature variations on ice composition and the sea ice composition literature have been summarized (Reeburgh and Springer-Young 1983). Some biologically active constituents, such as $CaCO_3 \cdot 6H_2O$, apparently precipitate out at temperatures found in sea ice although their chemical behavior is not completely understood (W.S. Reeburgh, personal communication 1990). Further, Meese (1990) has shown that the chemistry of major ions in sea ice is associated with salinity, but nutrient concentrations are independent of salinity and may reflect biological activity. Brine does not remain stationary within the ice, but migrates by brine channel migration, brine expulsion, gravity drainage, and flushing. These mechanisms, but primarily gravity drainage, are responsible for the

salinity changes found in first-year ice. Older ice, e.g., multi-year, is less saline than newly-formed ice, primarily from flushing and drainage processes activated by higher summer temperatures. (For more detailed discussions of the ice environment, see Maykut 1985; Weeks and Ackley 1986; Lange et al. 1989, and references therein.)

Different growth processes result in different ice types. The proportions of granular and congelation ice have been discussed elsewhere (Gow et al. 1982; Lange et al. 1989). In the Antarctic, most of the ice is granular ice of frazil origin, while in the Arctic, most of the ice is congelation ice of columnar texture (Spindler 1990).

The main forms of ice that have been studied for ice organisms are fast ice and pack ice. *Fast ice* forms and remains fast along the coast. It may be attached to the shore, an ice wall, an ice front, or to grounded icebergs (WMO 1970) and is formed in situ from seawater or by freezing of pack ice to the shore. *Pack ice* is any area of sea ice, other than fast ice, no matter what form it takes (WMO 1970). Its concentration in a given area is a ratio expressed in tenths or oktas (eighths) and may be compact with no water visible (10/10) or, at the other extreme, very open with $<3/10$ ice. It may extend from a few meters to several hundred kilometers from the coast. Rigorous comparisons of community differences between pack ice and fast ice have not been made, but it appears that pack ice communities are dominated by planktonic forms, while fast ice communities, at least over shallow water, are dominated by benthic forms, including benthic diatoms and larvae of benthic organisms (Carey 1985; Garrison and Buck 1989; Pike and Welch 1989). However, comparison of species found in fast ice at Syowa Station and pack ice in the Weddell Sea suggest that the same species occur in both habitats (Garrison 1991; Garrison and Watanabe, in press).

Sea ice community formation

A number of mechanisms by which organisms are incorporated into sea ice have been proposed (e.g., Ackley 1982; Garrison et al. 1983; Sullivan et al. 1985; Dieckmann et al. 1986; Spindler and Dieckmann 1986; Ackley et al. 1987; Garrison et al. 1989; Shen and Ackermann 1990). Differences in ice growth processes also may lead to differences in how organisms are incorporated into the ice and the amount of space in the ice that is available for colonization. In the Antarctic, it has been suggested that frazil ice crystals rising through the water column harvest or scavenge cells, thus concentrating them in the ice (Ackley 1982; Garrison et al. 1983). This also has been shown in laboratory experiments (Garrison et al. 1989). Another possible mechanism for concentrating cells is by wave fields that pump water through the ice and deposit organisms (Ackley et al. 1987; Shen and Ackermann 1990). It is likely that small-scale circulation features, such as Lang-muir cells, collect organisms suspended in the water column and this may be the best mechanism for concentrating cells in the ice (Garrison et al. 1989). Granular and annual ice may have more space available for organisms, thus Antarctic ice contains more organisms than the surrounding seawater or the columnar and multi-year ice commonly found in the Arctic (Spindler 1990; Spindler et al. 1990; Dieckmann et al. 1991). Further, granular ice contains about twice as much brine as columnar ice (J. Weissenberger, personal communication 1990). Other mechanisms are described below with the discussion of individual habitats.

The organisms

Sea ice biota are organisms, both plants and animals, at all trophic levels that live in, on, or associated with sea ice during all or part of their life cycles. They may be separated into *autochthonous* forms that are regularly found in the ice and spend most of their life cycles there, or *allochthonous* forms that are found only temporarily associated with ice (Gulliksen and Lønne 1989).

Many terms have been used to describe the sea ice biota (Table 2) (Horner et al. 1988). Terms that include plankton are incorrect because they imply a water column existence and, while some of the ice organisms originate in or return to the water column following their release from the ice, this is not always the case. Life in the ice is, in fact, more similar to that in the benthos. A number of other words, including cryophilic, cryophyton, cryobiont, and cryon, that imply association with ice or cold temperatures have been suggested, but have not been widely used (Table 2) (Horner et al. 1988). Sea ice microbial community (SIMCO) was first used by Sullivan and Palmisano (1981). The term was not specifically defined in this paper, but through frequent usage has come to include viruses, bacteria, algae, fungi, and protozoans living in the ice (Sullivan, personal communication 1990). Microbial, however, often refers to bacteria or heterotrophs and may be misinterpreted. Underice (under-ice) has been used in place of bottom ice and is misleading because it could mean organisms living in the water column beneath the ice.

Epontic, meaning "being on", (but sometimes defined as "out of the sea", e.g., Whitaker 1977) has been used in much of the literature since it was first suggested by Bunt and Wood (1963) for attached or nonattached diatoms found in Antarctic sea ice. However, it has also been used for organisms attached to substrates other than ice (Crosby and Wood 1959). Further, it is not a suitable term to describe motile organisms, such as foraminiferans, ciliates, copepods, and amphipods. Because organisms from both the benthos and the plankton live in the ice, descriptive terminology should be very broad (Carey 1985). We therefore strongly suggest that epontic no longer be used for ice organisms. Instead, we propose that *sympagic*, meaning "with ice", be used in the same context as pelagic or benthic. Sympagic has been used previously for both plants (Whitaker 1977) and animals (Carey 1985) living in or associated with sea ice and, at present, is the most appropriate term to include all these organisms (Garrison 1991). Alternatively, the addition of "ice" to taxonomical or ecological categories, e.g., ice algae, ice fauna, is also acceptable.

Table 2. Terms used in the literature to describe sympagic biota (modified from Horner et al. 1988)

Term	Definition	Reference
Ice plankton Cryoplankton	Organisms peculiar to sea ice that develop and form communities in and around ice in summer	Zubov 1945
Brown ice	Defined by color and algal content (diatoms some chrysophytes)	Fukushima 1961
Colored ice	Brown color caused by diatoms	Fukushima 1965
Plankton ice	Formed when seawater freezes; brown color caused by growth of some plankton in sea ice	Matsuda 1961; Meguro 1962; Meguro et al. 1966, 1967
Epontic	Attached and non-attached species especially adapted for life in sea ice	Bunt and Wood 1963
Psychrophilic	Organisms having an optimum temperature for growth below 15°C	Bunt et al. 1966 Round 1971
Cryophilic	Implies association with temporary or permanent ice	Usachev 1949; Round 1971
Epicryotic	Refers to cells living attached to ice crystals	Round 1971
Endocryotic	Refers to cells living within ice crystals	Round 1971
Cryophyton	Algae living in snowfields (snow algae) and ice floes	Round 1981
Cryobiont	Refers to organisms inhabiting snow and ice or algae initially found on the surface of sea ice	Kol 1942; Bursa 1963
Cryon	Sea ice communities	Melnikov 1989
Sympagic	Refers to organisms living with sea ice	Whitaker 1977; Carey 1985
Surface Interior Bottom	Algal communities defined by their location in the ice	Ackley et al. 1979; Horner et al. 1988
SIMCO	Sea ice microbial communities; includes viruses, bacteria, diatoms, fungi, and protozoa	Sullivan and Palmisano 1981
Underice (under-ice)	Refers to organisms living in the bottom of the ice	Cross 1982
Interfacial	Free-floating algae at the ice-water interface	Tremblay et al. 1989

Groups of organisms living in the ice often have been referred to as communities. Horner et al. (1988) suggested assemblage would be a better word because they considered the ice biota to be a group of more or less unrelated organisms and assemblage does not imply interactions either between organisms or between the organisms and their environment. There may be occasional visitors, i.e., those not present as more or less permanent members of the ice biota (allochthonous sympagic organisms), but we now believe that complex interactions do occur between organisms and suggest that *community* is a better term (also see Garrison 1991). Biocoenosis also has been used for ice biota (Melnikov 1989) and is sometimes used interchangeably with both assemblage and community, but has not been as widely used in other sciences related to ice. The concepts of community and biocoenosis in marine ecology have been reviewed by Mills (1969).

The habitats

The organisms occur in special habitats within the ice and the individual communities generally take the habitat name. The primary ice habitats and communities are at the surface, interior, and bottom of the ice (Ackley et al. 1979; Horner et al. 1988) (Fig. 3), each of which can be further divided (Table 3), and a sub-ice habitat/community immediately beneath the ice, but still attached or closely associated with the bottom ice.

Surface

There are three kinds of surface communities. The first is the *infiltration* community that occurs at the snow-ice interface. It was originally described from pack ice in the Antarctic, as a yellow to brown layer, 15–20 cm thick (Meguro 1962). One suggested mechanism for its formation is that the weight of the snow depresses the ice and seawater containing organisms can then infiltrate the snow (Meguro 1962). Burkholder and Mandelli (1965) reported a mixed diatom-flagellate community in layers from 15–100 cm thick. Daily productivity was calculated to be 0.19 $g C m^{-2} day^{-1}$ (Burkholder and Mandelli 1965) and chlorophyll *a* levels may reach >50 $\mu g l^{-1}$. It is often dominated by *Nitzschia cylindrus* (Grun.) Hasle and *N.*

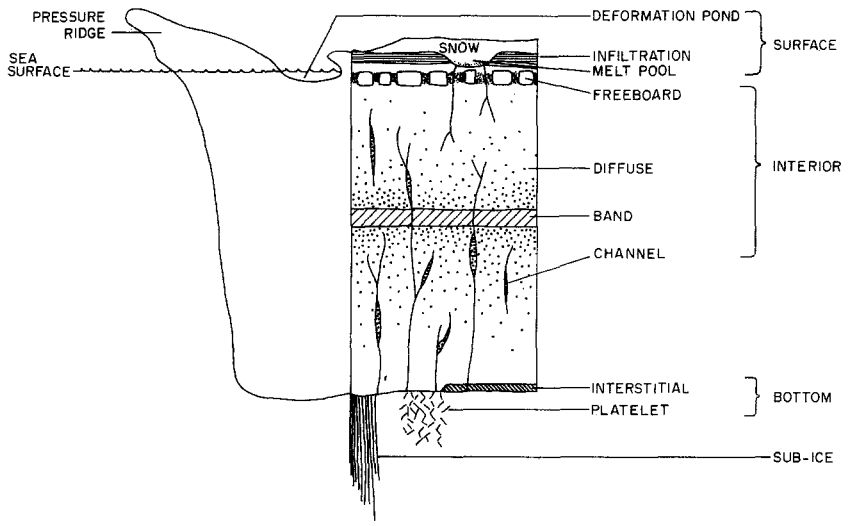

Fig. 3. Schematic representation of biological communities found in sea ice (modified from McConville and Wetherbee 1983; Horner et al. 1988; Kottmeier and Sullivan 1990)

Table 3. Proposed terms for sea ice biota communities and their occurrence in polar regions (+ = present; − = not yet reported)

Terms	Arctic	Antarctic
Surface		
Infiltration	−	+
Deformation ponds	+	+
Pressure ridge	+	+
Surface saline ponds	−	+
Melt pools	+	+
Interior		
Freeboard	−	+
Brine channels	+	+
Diffuse	+	+
Bands	+	+
Bottom		
Interstitial	+	+
Platelet	?	+
Sub-ice	+	+

closterium (Ehrb.) W. Smith with densities $>10^7$ cells l^{-1} and *Phaeocystis pouchetii* (Har.) Lagerheim with densities up to 5×10^7 cells l^{-1} (Garrison and Buck 1989). *Navicula glaciei* Van Heurck, other microalgae, and microorganisms not specifically identified were found in infiltration ice-slush on the fast ice sheet near the South Orkney Islands (Whittaker 1977). The infiltration community was not found in the Barents Sea during PRO MARE cruises (Syvertsen 1990). To our knowledge, it has not been reported in the Arctic.

Often there are few organisms in the water column when infiltration occurs. Therefore, another possible mechanism for the formation of the infiltration community is that only seawater invades the snow-ice interface, creating a favorable environment for organisms already in the ice. The organisms grow because conditions for growth, e.g., higher temperatures and nutrient availability, improve. The fact that concentrations of cells sometimes increase toward the periphery of ice floes can also reflect the gradient of seawater infiltration.

The second kind of surface community is associated with ice deformation processes, most often pressure ridges. The *deformation* communities include the *pressure ridge infiltration* community, formed during initial pressure ridge formation and the *surface saline pond* community, formed when the ice surface is deflected below sea level and flooded. These communities consist of a variety of both autotrophs and heterotrophs, often with similar groups of organisms (D.L. Garrison, personal communication 1991). Cell concentrations may be 10–100 times those found in the underlying seawater because of the high irradiance characteristics of the ponds.

The third surface community occurs in *melt pools*. These are formed by thawing of surface ice (McConville and Wetherbee 1983), flooding, or a combination of flooding and thawing. Melt pool communities are known from both the Arctic and Antarctic. In the Arctic, they may cover 50–60% of the sea ice; they are observed less often in the Antarctic (Maykut 1985). Some pools formed by surface thawing are above sea level, contain freshwater, and, if organisms are present, they originate in freshwater, possibly being brought to the sea ice by wind or birds. In the Arctic, freshwater, brackish, and saltwater ponds containing a variety of organisms, including freshwater and brackish water species of diatoms, flagellates, and ciliates have been reported (Gran 1904; Nansen 1906). Bursa (1963) found freshwater green algae, chrysophyte flagellates, diatoms, and ciliates in melt pools near Barrow, Alaska. Both freshwater pools containing freshwater green algae and saltwater splash pools containing marine diatoms have been found in the Barents Sea, but few melt pools in that area contained algae (Syvertsen 1990).

In the Antarctic, melt pools, up to 15 cm deep, formed in late spring just below the surface of consolidated snow (McConville and Wetherbee 1983). The community was dominated by small diatoms (especially *Nitzschia* section *Fragilariopsis*), flagellates, and *Phaeocystis* colonies. Large aggregations (2.8×10^6 cells ml^{-1}) with high production rates (363 μg C l^{-1}) formed on the bottom of the pools by mid-January. In the South Orkney Islands,

Whittaker (1977) reported terrestrial and snow algal assemblages in snow-melt pools after meltwater flooding in the coastal tide-crack zone, but no microalgae in snow-melt puddles on the fast ice.

Interior

Interior habitats depend on air temperatures at or slightly below the freezing point to initiate, but not complete, brine drainage (Ackley et al. 1979). The one closest to the upper surface of the ice in the *freeboard* habitat. It apparently occurs when brine drains from the upper layers due to surface warming, algal growth increases, heat is trapped, and the ice melts. The freeboard community occurs 10–30 cm below the upper surface of the ice where the ice is rotting (Kottmeier and Sullivan 1990). Solid ice layers occur above and below the rotten ice and there is an intact snow layer on top of the ice. Chlorophyll *a* levels up to 425 $\mu g\, l^{-1}$ have been reported (Kristiansen and Syvertsen 1990); krill also occur in these cavities, grazing on the algae (Bergstrom et al. 1990).

The most common interior habitat occurs between ice crystals throughout the interior of the ice (Ackley et al. 1979; Garrison et al. 1983) and is part of the brine channel system (J. Weissenberger, personal communication 1991). The organisms that inhabit it may be scattered between ice crystals throughout the ice with no definite pattern to their vertical distribution (Garrison and Buck 1989) or be concentrated in brine channels or bands. *Brine channels*, formed in response to temperature changes and internal stresses, are long vertical tubes that allow vertical movement of brine through the ice (Maykut 1985). This happens in spring when some melting occurs and the channels become connected to form a network within the ice (Horner et al. 1988). As the channels enlarge, either through growth or melting, there is communication with the underlying water column and the community develops. The brine channel community occurs in brine channels, but also in cracks, and cavities in the ice (Horner et al. 1988). They may contain microalgae common to both the bottom ice and water column communities as observed in east Antarctica (McConville and Wetherbee 1983). Krill are also found grazing in brine channels (Daly 1990; Bergstrom et al. 1990). In the Arctic, the amphipod, *Gammarus wilkitzkii* adapts to a wide range of salinities and is commonly found in brine channels (Aarset and Aunaas 1987).

The *diffuse* community is common in pack ice in the Antarctic where chlorophyll *a* concentrations average $<10\ \mu g\, l^{-1}$ (Ackley et al. 1979; Clarke and Ackley 1984; Garrison and Buck 1989). Organisms present in this community include bacteria, diatoms, dinoflagellates, autotrophic and heterotrophic flagellates, ciliates, foraminiferans, and micrometazoans including copepods. Biomass ranges from <0.01 to $>0.4\ g\, C\, m^{-1}$, with highest concentrations occurring in spring (Garrison and Buck 1989). In the Arctic, diatoms and heterotrophic flagellates are found throughout the ice thickness from the time it forms (Horner 1976), but the diffuse interior community has been little studied and there is only meager information on biomass or cell densities (Poulin et al. 1983; Legendre et al. 1991).

Band communities are formed either by the accretion of new ice under a previously formed bottom ice layer of organisms (Hoshiai 1977; Ackley et al. 1979) or by incorporation of cells at the time of first freezing of surface waters (R. Gersonde, personal communication 1986). They were first described from Syowa Station, Antarctica, (Hoshiai 1969, 1977) and may be remnants of the autumnal ice algal bloom (Ackley et al. 1979) or of the previous year's spring bottom ice bloom (Grossi and Sullivan 1985); they may be a successional stage of a bottom ice community or a senescent or otherwise inactive bottom ice community (D.L. Garrison, personal communication 1991). Diatoms and dinoflagellates are the most abundant organisms in the fall-winter bands (Hoshiai 1977). Band communities apparently occur frequently in the Antarctic, but are infrequent in the Arctic. Bands have been described in Hudson Bay (Poulin et al. 1983) and there is one anecdotal report from the northern Bering Sea in the spring of 1970 (J. Burns, personal communication 1970).

Bottom

The *interstitial* community occurs in the bottom of the ice where ice crystals are generally small. It is usually only a few centimeters thick, consists of a solid, hard layer of congelation ice (Palmisano and Sullivan 1983; Grossi et al. 1987), and is the community most frequently studied. In the Arctic, pennate diatoms usually dominate the fast ice interstitial community, but other organisms, including dinoflagellates, autotrophic and heterotrophic flagellates, ciliates, heliozoans, rotifers, nematodes, harpacticoid and cyclopoid copepods, turbellarians, and polychaete larvae may also be present in varying numbers (Horner 1976; Cross 1982; Carey 1985; Grainger and Hsiao 1990). In pack ice areas, centric diatoms may be more numerous (Booth 1984; Irwin 1990; De Sève and Dunbar 1990). In the Antarctic, pennate diatoms and bacteria are abundant (Grossi et al. 1984; Grossi and Sullivan 1985) in fast ice, and centric diatoms may be abundant in some areas (Watanabe 1982; C.W. Sullivan, personal communication 1990). There is little information on the occurrence of flagellates, protozoans, and other micro- and meiofauna in fast ice except at Syowa Station where a ciliate, calanoid and harpacticoid copepods, and invertebrate larvae were found (Hoshiai and Tanimura 1986; Hoshiai et al. 1987, 1989).

Another bottom ice community is found in *platelet* ice that forms under the congelation ice (Bunt 1963; Bunt and Lee 1970; Palmisano and Sullivan 1985b; Grossi et al. 1987). Platelets accumulate only in close proximity to ice shelves, although in the Weddell Sea, they may be formed at depth and harvest cells as they rise through the water column (Dieckmann et al. 1986). The platelet layer becomes established because of decreased currents and shear near the ice front. The platelet habitat is quite different from the interstitial habitat above it in terms of biospace,

such as crystal structure and orientation, and amount of space between crystals; nutrient exchange potential, i.e., being able to deplete nutrients before they reach the interstitial habitat; and shading where the interstitial community will always shade the platelet community (D.L. Garrison, personal communication 1991). There are strong similarities between platelet layer communities in McMurdo Sound and the Weddell Sea, the two locations where they are best known. Loosely consolidated platelets are areas of high primary production (e.g., Bunt 1964, 1968; Palmisano and Sullivan 1985b) and are also inhabited by other sympagic organisms ranging from protozoans to fish (Andriashev 1968; Tanimura et al. 1984).

Sub-ice

The *sub-ice* habitat is in the seawater immediately under the ice, although organisms, e.g., algal filaments, may be loosely attached to the undersurface of the ice. In the Arctic, this may be a mat of algal cells floating just under the bottom surface of the ice (Cross 1982; Runge and Ingram 1988; Barlow et al. 1988; Michel et al. 1988; Tremblay et al. 1989; Syvertsen 1990; Gosselin et al. 1990; Johnsen and Hegseth 1991) or filaments loosely attached to the bottom surface of the ice (Melnikov and Bondarchuk 1987; Syvertsen 1990). In the Canadian Arctic, *Nitzschia* spp. were dominant in the sub-ice community (Cross 1982; Rochet et al. 1985; Michel et al. 1989; Tremblay et al. 1989), while in both the Barents Sea and the central Arctic Ocean, *Melosira arctica* (Ehr.) Dickie formed huge mats and long strands, especially under multilayer ice (Hasle and Syvertsen 1985; Melnikov and Bondarchuk 1987; Syvertsen 1990).

In the Antarctic, the sub-ice community was called the mat-strand community and consisted of a mat that was suspended under the ice in clumps and strands (McConville and Wetherbee 1983). The dominant species were *Berkeleya* sp., *Entomoneis* spp., and *Nitzschia frigida* (correct identification is *N. stellata* Manguin [Medlin and Hasle 1990]). Cell densities in the strands was 10^6–10^7 cells ml^{-1} (McConville and Wetherbee 1983). At Syowa Station, where the strands begin growing in the hard congelation ice (interstitial habitat), their development depends on calm conditions to keep the colonies from fragmenting. The community consisted of a number of pennate diatoms, including *Amphiprora kufferathii* Mangin, *Berkeleya rutilans* (Trent.) Grunow, *Nitzschia lecointei* Van Heurck, *N. stellata*, N. *turgiduloides* Hasle, *Nitzschia*, spp., and *Navicula glaciei* (Watanabe 1988).

Allochthonous sympagic fauna are also members of the sub-ice community. In the Arctic, these include *Pseudocalanus* sp. and harpacticoid copepods (Runge and Ingram 1988); the amphipods, *Parathemisto libellula* (Gulliksen 1984), *Weyprechtia pinguis*, *Onisimus litoralis*, *Onisimus* spp. juveniles, and *Gammarus setosus* (Pike and Welch 1989); and the polar cod, *Boreogadus saida* (Lønne and Gulliksen 1989). In the Antarctic, the amphipod *Paramoera walkeri* (Gulliksen and Lønne 1989) and the fish *Pagothenia borchgrevinki* (Eastman and DeVries 1985) are common.

Routine sampling strategy

Many methods have been used to sample sea ice for biological investigations (e.g., Horner 1990). There is a lack of consistency both in collection and experimental methods, partly because of differences in ice structure and communities in the Arctic and Antarctic and between fast and pack ice. Comparing results from different investigators is often difficult because of differences in experimental approach. Further, biological studies often have not included investigations of the physical and chemical environment of the sea ice biota. It is now known, however, that the physical and chemical processes associated with ice formation as well as the history of the ice are important for the development of sympagic communities (e.g., Legendre et al. 1991).

When not specifically required for experimental purposes, sea ice samples are usually collected from ice floes that have been selected randomly, but are accessible by ship or helicopter. When working from shore-based stations, sites must be accessible by surface vehicles or helicopter. Before sampling, snow depth and density and other features of the immediate vicinity must be recorded. Cores are obtained with a 10 cm diameter corer (various manufacturers) operated either by hand or a small gasoline engine (Horner 1990). The number of cores collected depends on individual experimental design. One core may be taken for archiving if facilities are available. A second core is placed in an insulated PVC tube and a temperature profile determined by inserting a digital thermometer probe through holes in the PVC tube and holes drilled at 5 cm intervals in the ice (G.S. Dieckmann, personal communication 1990). The core is then placed in an insulated container for transport to the laboratory.

In the cold lab, the core length (ice depth) is measured and the core is placed on a light table so stratigraphy can be discerned. The core may be cut in half lengthwise to facilitate stratigraphic observations. Zones of different structure are determined and the core sectioned horizontally according to the zones. Vertical sections, ca 1 cm thick, are cut for each piece and stored for later, more detailed analysis of the ice structure.

The remainder of each section is carefully melted in the dark at ca 4°C and used to obtain bulk parameters such as salinity, nutrient concentrations, chlorophyll *a*, and large protozoan (foraminiferans) and metazoan numbers. Alternatively, the sections may be melted in large volumes of filtered (0.2 μm) seawater to prevent destruction of delicate organisms, e.g., ciliates and flagellates, through osmotic stress (Garrison and Buck 1986). This method could also be used for determining chlorophyll *a*, but care must be taken to exclude all cells from the filtered seawater and to measure volumes accurately. Nutrient and salinity values could be calculated from these samples, but it is better to use another core. It must be remembered, however, that when ice melts, both salinity and nutrient concentrations are diluted, leading to underestimates of their in situ concentrations.

Another, though more time-consuming, method to obtain brine and sea ice biota is by centrifuging intact core sections in a refrigerated centrifuge. The brine retains the

salinity corresponding to the in situ temperature or the temperature during centrifuging, although some ions may remain with the ice because of surface charges (D.L. Garrison, personal communication 1991). This method is not appropriate for quantitative studies. Core squeezers also have been suggested as a quick way to obtain brine from ice cores with minimum change in composition, however, little is apparently known about their use for this purpose. Further, the in situ temperature of the ice would need to be maintained during manipulation to ensure the actual brine composition.

A major source of error in determining salinity, nutrient concentrations, and chlorophyll *a* is introduced when brine is extracted from cores collected using ice corers. The problem is to retain brine and interstitial organisms associated with the bottom of the ice during extraction. No surface sampling technique circumvents this problem, so what is often the most important part of the ice is not sampled adequately. Coring from the bottom of the ice by divers may overcome this problem, but appropriate instrumentation is also needed.

Reporting units

Another problem area with regard to sea ice biota concerns the units used to report biological, chemical, and physical data (Palmisano and Sullivan 1985a; Horner et al. 1988; Irwin 1990). Biological data may be reported per unit volume of ice meltwater or integrated over the depth of the ice column and reported on an areal basis. Unfortunately, the thickness of the ice or algal layer and the diameter of the ice core are often not reported. Production rates may be reported on an hourly, daily, or annual basis. In addition, assimilation numbers (photosynthesis per unit chlorophyll *a* at light saturation) have not been determined for many ice communities or individual species, thus making comparisons of production with other ecosystems difficult. As a result it is nearly impossible to compare values reported in the literature to a common unit.

Unfortunately, there is no general rule for reporting substances in the ice matrix. Sometimes it is better to use the volume, e.g., for dissolved nutrients and for comparing algae to nutrients, while in other instances it may be better to use an areal measurement, e.g., when comparing ice biota populations from different locations, or ice biota densities with water column densities (Table 4). The best solution is always to include information on the thickness of the ice layer or water column. Then others can calculate either volume or areal concentrations for the data.

For sub-ice fauna, the best unit is number (or other measurement) per m^2 or number per volume of ice meltwater or seawater. Units commonly used include number per m^3 or 1000 m^3 (Daly 1990).

Table 4. Variables and suggested units for reporting ice biota data

Variable	Units
Primary productivity	mg C m^{-2}
Chlorophyll	mg chl *a* m^{-2}
Nutrients	μmol l^{-1}, mmol m^{-3}
Ice algae	number m^{-2}
Ice fauna	number m^{-2}
Ice bacteria	number m^{-3}
Irradiance	μE m^{-2} s^{-1}

Further recommendations

We recommend that all papers including names of organisms also cite the authors' names, e.g., *Nitzschia frigida* Grunow. We suggest this for several reasons. First, for algae at least, Article 46 of the Botanical Code of Nomenclature states that authors' names be cited the first time a genus and species name is used in a paper (Greuter 1988). Another way to do this is to include a table of species that includes authors' names. Second, it makes it easier for other investigators to know exactly what organism is being discussed and the name can be verified more easily. Third, lists of species of ice biota sometimes contain synonyms. Moreover, if an organism cannot be identified to species, but is given a provisional name, e.g., *Nitzschia* sp. A or *Nitzschia* cf. *frigida*, that designation should be used for the organism in subsequent investigations and papers until it is correctly identified; a statement should then be made that recognizes the previous provisional identifications. Fourth, algal taxonomy is in a state of flux and names are changed as more information becomes available from new methods and additional study, e.g., Medlin and Round 1986; Medlin 1990; Medlin and Hasle 1990.

Finally, we would encourage all investigators to provide better descriptions of their methods, especially if they are new or modifications of previously used ones. If new instruments are developed, these must be either completely described or a published reference cited. Figures make it easier for others to judge new equipment. A footnote or note added to the references to tell where instruments or other material may be obtained would also be useful. New methods must be developed, but methods must also be compared, both between polar regions and among different ice types and habitats (e.g., McConville et al. 1985; Palmisano and Sullivan 1985a).

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