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Physical controls on the development and characteristics of Antarctic sea ice biological communities— a review and synthesis

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Abstract—Ice structures found in Antarctic sea ice and related morphological processes are summarized, including: frazil ice growth; the flooded snow layer; pressure ridge induced flooding; thermally driven brine drainage; and platelet-ice formation. The associated colonization, physiological adaptation, and growth of sea ice biota within these structures, to the levels presently identifiable, are also reviewed. A strong interaction exists between the physical processes that form, evolve and deteriorate sea ice, and the biological communities located within sea ice. Variability of ice structure and associated biological communities over small spatial scales necessitated analysis of the biological component in combination with physical and chemical properties of the sea ice. The ice microstructure provides indications of the growth and evolution of the ice properties and initially defines how ice biota colonize the ice. The light, temperature, space and nutrient fields within which ice biota subsequently adapt and grow, are the other key determinants of the biology. While the ice microstructure shapes the localized biological response, relatively large regions of pack ice have characteristic microstructures. Regional patterns of biomass and biological productivity within the Antarctic sea ice zone may therefore be predictable as a result of these physical–biological associations. Examples from the drifting pack ice and fast ice zones of the Weddell and Ross Seas are given.

INTRODUCTION

SEA ice biological communities are a significant component of the polar marine environment. The circumpolar ring of sea ice surrounding the Antarctic continent (varying from 4×10^6 to 20×10^6 km^2 seasonally) is an extensive, seasonally variable habitat for organisms ranging in size from viruses to birds and mammals. Sea ice was once thought to be little more than a relatively minor resting place for algae trapped during ice formation. However, new information (ACKLEY et al., 1979; CLARKE and ACKLEY, 1984; HORNER, 1985; PALMISANO and SULLIVAN, 1985; GARRISON et al., 1986; KOTTMEIER and SULLIVAN, 1990), primarily from ship transects of the Antarctic pack ice and studies near Antarctic coastal stations, has shown the development of the communities is dynamic, and ice communities have major influences at various trophic levels of the oceanic food web. Much of the information, however, is still qualitative, since these sampling programs

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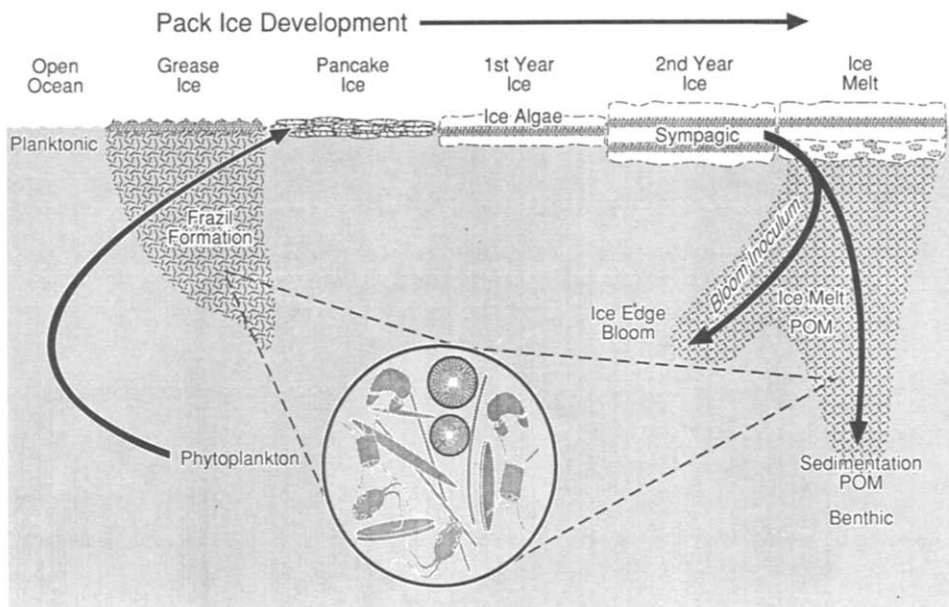
Fig. 1.   Seasonal cycle of polar microalgae and their coupling to pack ice dynamic processes. The diagram shows the hypothesized parallel processes of seasonal sea ice formation and growth and its coupling to colonization of the ice by microalgae and their subsequent growth and accumulation within various pack ice microenvironments. Ice microalgae are comprised of a smaller subset of the phytoplankton that spend a major fraction of their life cycles in association with ice. Species composition differences between ice and water are less in newly formed ice but they may be great in older ice where subsequent *in situ* growth of algae has occurred (LIZOTTE and SULLIVAN, 1991). During periods of ice melt live cells and detritus are released, sometimes as large flocs, to the water column where they may sediment to deeper water or grow again as part of the plankton, possibly seeding ice edge blooms in the upper stabilized water column that results from input of ice meltwater.

(particularly during winter and spring), detailing relationships between physics and biology in ice, are only a recent feature of polar expeditions (e.g. CLARKE and ACKLEY, 1984; LANGE, 1990).

Marked differences exist between the various sea ice communities that develop in physically distinct ice environments, that reflect organismal adaptations to the suite of physicochemical and biological features among the different ice habitats (e.g. DIECKMANN *et al.*, 1991). These communities may influence the development of ice edge blooms in the water column for which the ice microbiota may provide an inoculum or "seed population". A cyclic life history pattern between polar algae and phytoplankton in the seasonal cycle of ice expansion and retreat is shown in Fig. 1.

Foraminifera (DIECKMANN *et al.*, 1990), copepods (HOSHIAI *et al.*, 1987) and krill species have also been associated with particular types of ice communities. KOTTMEIER and SULLIVAN (1987), MARSCHALL (1988) and STRETCH *et al.* (1988) have found that krill (*Euphausia superba*) in the Weddell and Bellingshausen Seas depend on pack ice algae as a winter food source. In the sea ice zone krill are relatively scarce at depth in the water column but are found in high concentrations (1–28×10^3 animals m^{-3}) at the bottom

surface and within interstices in the ice (DALY, 1990; DALY and McCAULEY, 1988). These observations suggest that regional and seasonal variations in sea ice development impact on the overwintering strategy of grazing organisms.

The Antarctic circumpolar sea ice system is spatially widespread, with differences in physical processes that regionally differentiate the types of communities that develop. In this paper we identify key characteristics of the physical systems that are important for interactions with the biological communities. Physical models of the ice processes can potentially be identified with features that can be sensed remotely (COMISO and SULLIVAN, 1986; SULLIVAN et al., 1988; COMISO et al., 1990). A better estimate of the contribution of the total sea ice biological production to the overall southern ocean production may therefore be possible by linking up the relationship between, on the one hand, ice type and biological communities, as discussed here, and on the other, ice type and remote sensing, as discussed elsewhere (e.g. LYTLE and ACKLEY, 1991; COMISO and SULLIVAN, 1986).

SEA ICE ENVIRONMENTS

(a) *Snow loading and associated surface habitats*

Previous observations in Antarctica (MEGURO, 1962; BURKHOLDER and MANDELLI, 1965) first identified "plankton ice" communities just beneath the snow layer residing on the surface of floes. Figure 2 shows the development of this type of habitat. Only snow covers exceeding one quarter to one half of the ice thickness (depending on the snow
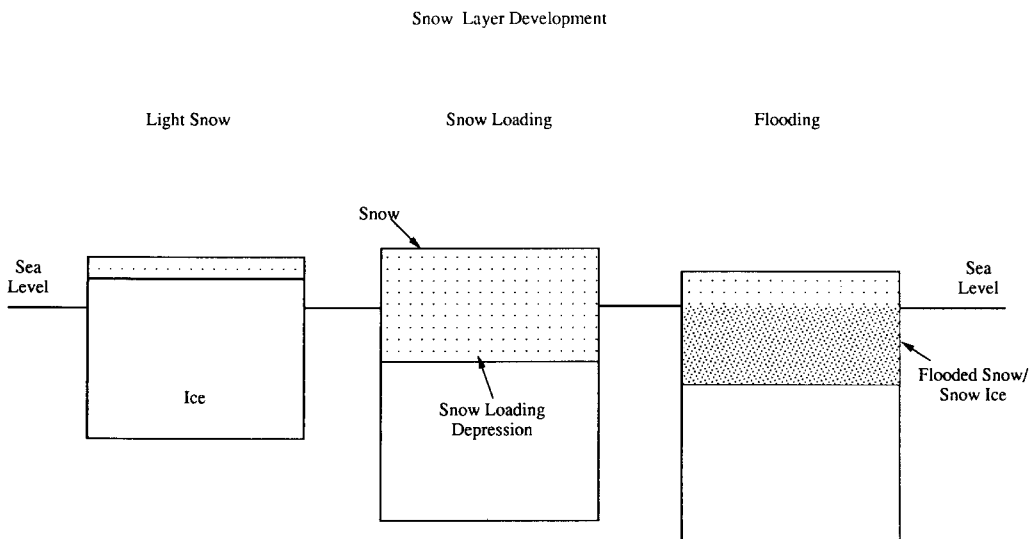
Snow Layer Development

Fig. 2.   The sequence of events showing development of a snow ice community. Development of snow ice communities begins with snow deposition on the surface, loading of the ice surface to just below sea level, and flooding of the surface leading to conditions favorable to growth of a snow ice community.
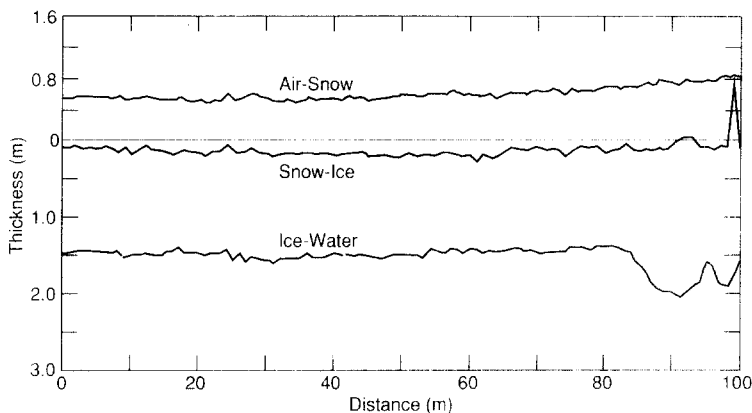
Fig. 3.   Weddell Sea ice flooding. Characteristics of a 100 m long profile line of snow and ice thicknesses obtained from the western Weddell Sea during September 1989, showing portions of the ice surface that are below sea level and flooded.

density) are able to cause the ice surface to be depressed below sea level, and to be flooded by infiltration of surface sea water (ACKLEY et al., 1990). Figure 3 shows such a flooded profile of snow and ice thickness obtained during the 1989 *Polarstern* cruise to the Weddell Sea. ACKLEY et al. (1990) estimated that 50% or more of the sea ice cover in the eastern Weddell Sea region was flooded during the winter period. The combination of thin ice cover and substantial snow, together with the constant redistribution of the snow by high winds, suggests that snow ice can be expected over the majority of the pack ice in the Weddell Sea.

However, the ice cores taken during the winter period show that interior biological communities (rather than the surface communities formed by flooding) dominate in areal extent, despite evidence for flooding throughout the region. The development of the surface community may also require the higher temperature and irradiance of the spring–summer period together with surface flooding. The snow ice community structures may be more concentrated in the northern regions of the Weddell Sea where both temperature and irradiance conditions are more favorable than in the south throughout the year (LIZOTTE et al., 1989).

Depending on the light, temperature, nutrients and seed population of organisms, this layer can develop chlorophyll concentrations of 100–400 mg m^{-3} (MEGURO, 1962; BURKHOLDER and MANDELLI, 1965). KOTTMEIER and SULLIVAN (1990) reported that of the various pack ice microhabitats they examined, the highest concentrations of bacterial cells and biomass, algal biomass and highest rates of primary and secondary microbial productivity, occurred in a flooding regime. LIZOTTE and SULLIVAN (1991) showed that photosynthetic capacity (P^B_{max}) of algae associated with these surface environments was the highest observed, and was similar to that of phytoplankton. High surface irradiance, to which these communities are exposed, and a high nutrient supply from the influx of surface seawater, result in their observed high productivity of 2.4 ± 1.4 g C m^{-2} day^{-1}, observed in the warmer seasons when the temperature, light and exposure to flooding are all optimized. This high productivity may be limited to particular regions and/or seasons. LEGENDRE et al. (1992) have estimated a total annual carbon production from this system,

limited by these seasonal and regional constraints. They estimate, within the limitations imposed by the scarce data, that snow ice communities may be the highest contributor to carbon production of the sea ice communities.

(b) *Pressure ridge loading and surface habitats*

ACKLEY (1986) described an additional surface community associated with pressure ridges (the ice pileups above and below the surface of the ice sheet that result from pack ice deformation). Three distinct processes lead to the development of communities associated with pressure ridges; two result in surface communities and the third causes a submerged community.

The first occurs during the initial ridge formation process. Pressure ridge building causes ice blocks to be loaded onto one of the two overriding ice sheets (Fig. 4). As the sheet is loaded, it cracks at some short distance from the loading and the sheet between the loading and the crack is deflected below sea level leading to surface flooding as shown. If light and temperature conditions allow, as described for the snow ice communities previously, a bloom can take place in the flooded area. ACKLEY (1986) describes an example of this community, with a chl*a* concentration of 43 mg m^{-3}.

The second process associated with ridges occurs in the marginal ice zone as large floes are advected toward the open ocean. As the floes approach the ice edge, floe diameters typically decrease from several kilometers to less than 100 m from wave-induced flexural failure of the parent larger floe. If the floe breakup takes place along or near a ridge, the level surface nearby is placed out of isostatic balance by the weight of the ridge and is deflected below sea level, flooding the surface with sea water. These surface saline ponds (Fig. 5) are distinguishable from snow melt ponds because they are always associated with ridges, they are high salinity (>33 ppt) sea-water intrusions that are at or below sea level (while melt ponds are above sea level, and they consist of fresh water derived from surface melt). Blooms of algae occur, coloring the ice and water green–yellow. These habitats contain a rich diversity of autotrophic and heterotrophic microorganisms and bacteria, as well as small zooplankton (GARRISON and BUCK, 1991; KOTTMEIER and SULLIVAN, 1990). Observed primarily in the northern latitudes of the Weddell Sea, the flooded areas are relatively warm and receive considerable downwelling irradiance when compared to interior pack ice. The surface habitats contain concentrations of algae 10- to 100-times that found in unflooded ice areas or adjacent open ocean (KOTTMEIER and SULLIVAN, 1990).

A third community occurs on the upper surfaces of ice blocks that are submerged beneath the waters' surface by ice ridging. SCUBA divers participating in the AMERIEZ (Antarctic Marine Ecosystem Research in the Ice Edge Zone) 1986 cruise in permanent pack of the western Weddell Sea noted that these ice surfaces are often exposed to a relatively high irradiance field if, for example, they protrude into an adjacent, open lead. Algal mats frequently were observed on their surfaces (Fig. 6) but quantitative collections of biological matter have not been reported from these sources to our knowledge (SYVERTSEN and AARSET, personal communication).

The propensity of a particular region to form ridge-associated microbial communities is related to the spatial ridge frequency (no. km^{-1}). Ridge data (WEEKS *et al.*, 1989; GOVONI *et al.*, 1983; LYTLE and ACKLEY, 1991), suggest eastern Weddell Sea pack ice has similar ridging characteristics to the Ross Sea. The Western Weddell region, based on recent observations, may be more heavily ridged than those other parts of the southern ocean.

The primary observations of surface saline ponds to date have been in the heavier ridged region of the Western Weddell outflow.

(c) *Frazil ice incorporation of biological matter and the development of an interior ice habitat*

Concentrations of algal matter varying from 1 to 50 mg chl*a* m^{-3} are found in the interior of the sea ice in the Weddell Sea region. ACKLEY et al. (1979) first described interior communities of algae in pack ice. The chl*a* distribution was unlike previous observations that reported either bottom or surface ice as the only locations for substantial concentrations of biological matter to occur. Subsequent investigation (Gow et al., 1987) identified the major ice structural type in the Weddell Sea floes as fine-grained frazil ice in contrast to the predominantly columnar ice seen in the Arctic Ocean. The frazil ice structure consists of equiaxed and isotropic grains of millimeter sizes (WEEKS and ACKLEY, 1986) while columnar ice consists of vertically elongate (anisotropic) crystals of centimeter dimensions. Columnar ice also has a characteristic substructure, correlated with the crystal anisotropy, consisting of brine inclusions. The growth of columnar sea ice occurs under quiescent conditions, by the extraction of heat unidirectionally by conduction from the base to the top of the ice. Frazil ice, in contrast, is the product of turbulent motion in the water where small ice crystals are nucleated and are pushed together by wind or wave action, retaining their small sizes and shapes (WADHAMS et al., 1987; LANGE, 1990) in the resulting ice sheet. Gow et al. (1987) and CLARKE and ACKLEY (1984) suggested that the higher concentrations of algal cells were associated with the frazil ice type. Figure 7 (after DIECKMANN et al., 1991) confirms the frazil ice contains higher chl*a* concentrations compared with columnar ice types. Additionally, DIECKMANN et al. (1990), show that the foraminifera *Neogloboquadrina pachyderma* is nearly exclusively found in frazil ice.

ACKLEY (1982) and GARRISON et al. (1983) showed that the initial occurrence of biological matter in frazil ice was a physically controlled process, since high concentrations were found in new ice that could not be accounted for by biological growth. DIECKMANN et al. (1991) have found similar behavior for ice up to about 2 months old. These data on new ice showed that nutrients were distributed conservatively, with respect to salinity, and ratios of nutrients did not change through ice profiles. The observed species similarity index between the water column and ice algal distributions was also not supportive of a biological growth process within the ice. Scavenging of particles by frazil ice crystals, either rising through the water column or being horizontally advected in open water areas, could account for the concentration of biological matter in the sea ice (GARRISON et al., 1983), supported by laboratory experiments where frazil ice rising through a water column was shown to concentrate biological matter (GARRISON et al., 1990). However, field evidence showed that the concentration of biological matter was several times higher than that obtained in laboratory experiments. ACKLEY et al. (1987) and SHEN and ACKERMANN (1990) presented alternative theoretical arguments supported by laboratory tank experiments, that indicate a wave field passing through an unconsolidated frazil ice cover could pump water into the ice layer with each wave passage and deposit particulate matter among the ice crystals. Substantial amounts of particulate matter, more nearly representative of field observed concentration factors, were obtained in wave tank experiments under these conditions. DIECKMANN et al. (1990) observed both chl*a* and foraminifera, at higher concentrations in unconsolidated frazil ice in wave fields in Antarctica than

Fig. 4. Photograph of pressure ridge loading of the ice cover. Deflection of the ice sheet adjacent to the ridge leads to the flooding (grey areas) as shown. Photograph taken in the eastern Weddell Sea, October 1981.

Fig. 5. Photograph of a surface-saline pond. A broken-up floe in the Weddell Sea marginal ice zone is shown with an algae-rich surface saline pond. Photograph taken in the western Weddell Sea during March 1986.
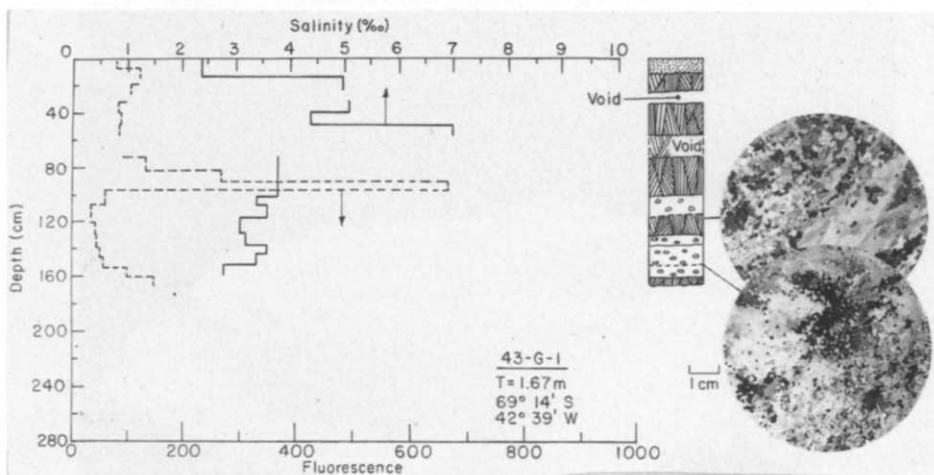
Fig. 6. Underwater photograph of a ridged floe with algal growth on its upper surface. Several similar floes were observed during the AMERIEZ autumn cruise in the persistent pack ice of the western Weddell Sea at 65°30'S latitude, 49°29'W longitude during March 1986.

Fig. 8. Structural profile of a pack ice core obtained in the Weddell Sea showing a void at sea level. High algal biomass (relative fluorescence) was found in the water taken from the hole at the freeborad level. Ice textural characteristics are shown on the right margin.
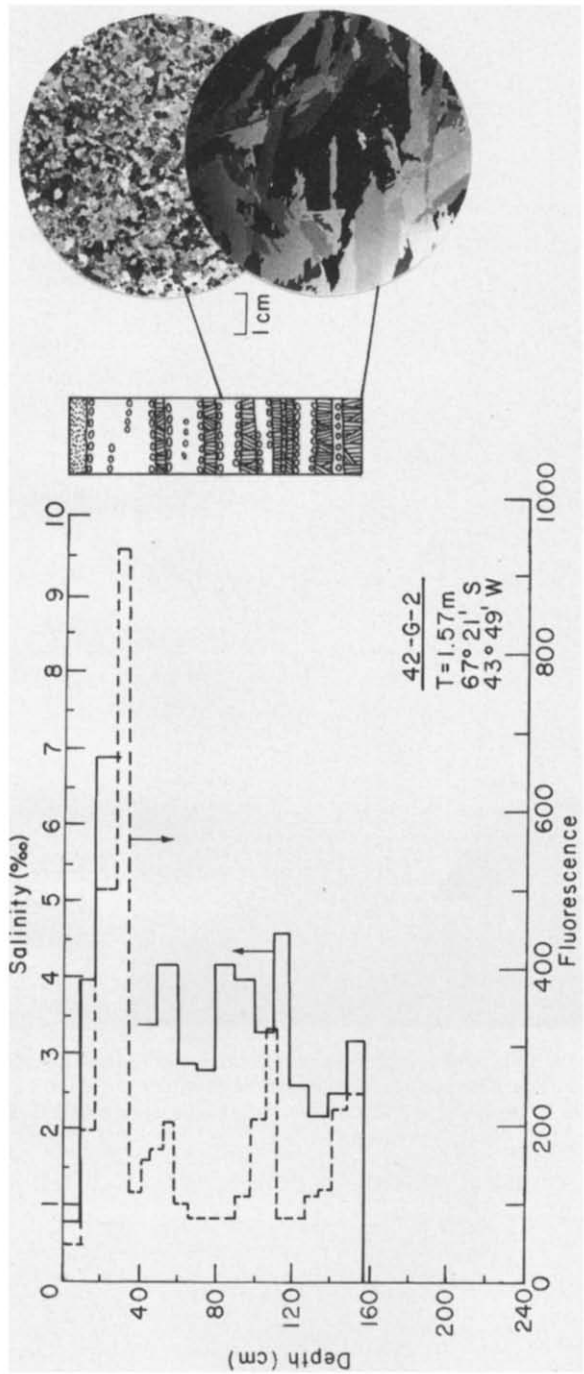
Fig. 9.   Structural profile of a pack ice core obtained in the Weddell Sea showing some desalination of the upper layer. Enhanced salinity and algal biomass (relative fluorescence) was found near the freeboard level. Ice textural characteristics are shown on the right margin.

Snow Surface
↑

Granular
Snow

↓
↑
Fresh Ice
↓

Sea
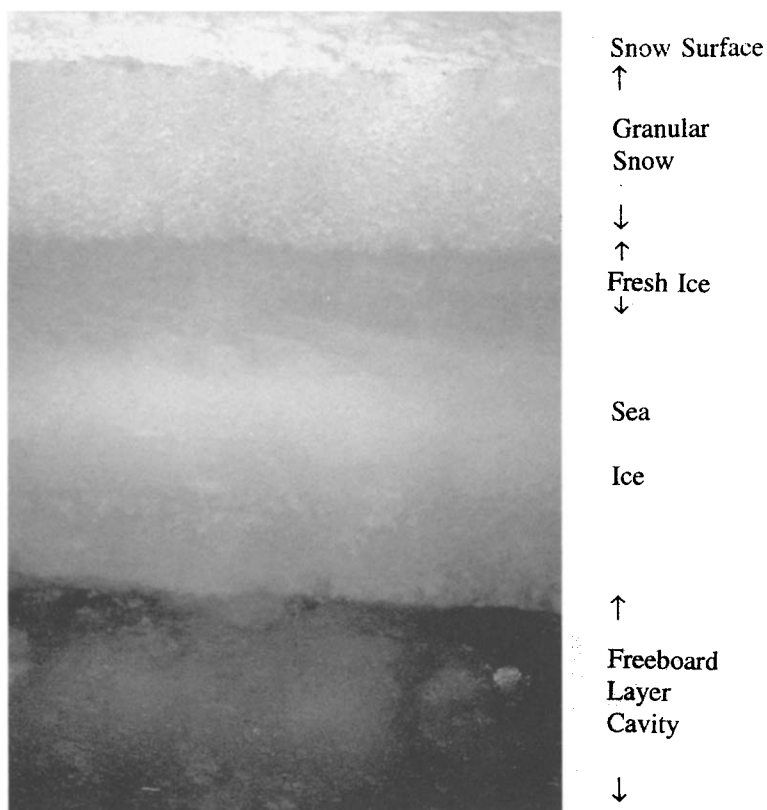
Ice

↑

Freeboard
Layer
Cavity

↓

Fig. 10. Photograph showing profile of the metamorphosed snow, fresh ice and algal-rich freeboard layers from the floe. The floe was located at 61°51'S latitude, 38°08'W longitude in the marginal ice zone of the Weddell Sea and was observed during the spring AMERIEZ cruise on 29 November 1983.

obtained in the water column. Their report provides some field confirmation that pumping by waves incorporates biogenic particulate matter into newly growing frazil ice. PENNY and SULLIVAN (1990) reported enrichment of algae, but not the smaller cell-sized bacteria, in newly formed frazil from the Weddell–Scotia Sea during winter. They suggested that a lower size threshold may exist for particle retention. These observations are consistent with either scavenging or wave-driven processes for harvesting of biological material.

In the western Weddell Sea, recent studies during autumn and winter indicated the photophysiological characteristics of the newly incorporated ice algae were similar to those of the phytoplankton (LIZOTTE and SULLIVAN, 1992). This report strengthens the link between phytoplankton and ice algae (GARRISON and BUCK, 1987), as phytoplankton must be the source of early colonizers of the ice environment (Fig. 1). Yet, after they first colonize the ice, changes in species dominance and photophysiological characteristics apparently take place. For example LIZOTTE and SULLIVAN (1991) have shown that systematic changes in photosynthetic pigments and photosynthetic-irradiance relationships of ice algae occur along gradients of downwelling irradiance through ice profiles, and are evidence for *in situ* metabolism by pack ice algae. The implication is that algal species comprising pack ice communities like those in fast ice (McGRATH-GROSSI *et al.*, 1987), while originating from a water column seed stock, may have a greater propensity for growth under the physical–chemical conditions that prevail in sea ice habitats. The observed differences between algal species composition in the ice and water column (BUNT and LEE, 1970; HORNER and SCHRADER, 1982) are believed to result from the dynamic processes of *in situ* growth, competition for limiting resources (such as the selective draining of specific nutrient pools, DIECKMANN *et al.*, 1991) and species succession (LIZOTTE and SULLIVAN, 1991). Differences may also result from a substantial separation in space or time between incorporation of algae into the ice and later sampling of the ice and underlying water column (GARRISON and BUCK, 1985).

The primary mechanism for frazil ice formation is by wave propagation through an advancing ice field, so the occurrence of waves, frazil ice and interior biological communities are coupled (LANGE *et al.*, 1990; WADHAMS *et al.*, 1987). Since the majority (~16 million km^2) of Antarctic sea ice forms seasonally at the ice edge exposed to the open ocean wave field, the area of resulting frazil ice structure is also extensive. The algal concentration by frazil ice incorporation is however, relatively low compared to some other sea ice communities.

(d) *Freeboard layer and the interior ice habitat*

ACKLEY *et al.* (1979) found that samples from the upper layers of Weddell Sea pack ice showed a decrease in salinity from the top of the ice and an enhanced salinity, along with apparently higher concentrations of biological matter, near the freeboard level (sea level) within the ice. These samples, taken at the end of summer, suggested a brine drainage process may contribute to the development of a biological community at the freeboard or sea level within the ice. BUCK and SULLIVAN (1990) described a similar phenomenon as observed in drift ice in late summer from the southwestern Ross Sea. A cavity or "rotten" ice layer developed at the freeboard level and was associated with higher concentrations of algae (Figs 8 and 9). This layer is in the ice interior and differs from the infiltration layer seen at the very top of the ice cover resulting from surface flooding as discussed earlier [Section (a)]. The proximity of the two layers may however, cause the lower one
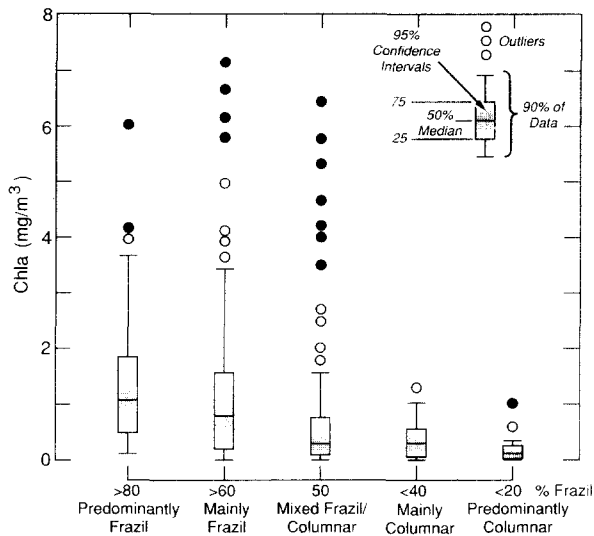
Fig. 7. Variation of chl*a* concentration as a function of pack ice texture based on the Weddell Sea 1986 winter ice core data. Ice texture is >80% frazil to <20% frazil from left to right, respectively. Boxes indicate the 25–75% ranges of the data, while lines with ties contain over 90% of the values. Horizontal lines are the mean values for each ice type.

("freeboard layer") to be mistaken for an "infiltration layer" that results from sea water flooding of the lower snow pack.

The unusual physical aspect of the freeboard layer is the presence of a solid ice layer above and below the cavity and an intact snow cover, usually metamorphosed, above the top solid ice layer (Fig. 10; see also Fig. 2 in Kottmeier and Sullivan, 1990). The question arose as to how an apparently melted ice layer, usually associated with substantial biological matter, could develop in the interior of the ice with intact ice (and snow) above and below this melted layer.

Four stages in the process occur (Fig. 11). The surface layer of first year sea ice is generally more saline than the interior (Weeks and Ackley, 1986). As the ice temperature warms in the seasonal progression, the liquid fraction increases such that the total porosity of the top layer is raised and it becomes more permeable. This temperature (frame 2 of Fig. 11) is still below the freezing point of pure water, i.e. below the melting point of the overlying snow cover as observed by Buckley and Trodahl (1987) in McMurdo Sound sea ice. As the brine migrates downward, the temperature is warmer, increasing the brine volume and, apparently, the permeability, so the liquid may flow faster as it moves down through the ice profile. At sea level, the motion may stop, or at least slow down, since the potential (head) for the liquid to move is now zero. The combined increase in salinity, temperature, nutrients and seed population is sufficient, along with the seasonal increase in irradiance, to initiate and sustain algal growth at the freeboard level in the ice (frame 3 of Fig. 11). The increase in pigmented matter causes downwelling radiation to be absorbed almost completely at this level. Since the increase in heat caused by the absorbed radiation must be carried away by conduction, the heat is trapped at this level and causes the ice to melt leading to a cavity or "rotten" ice layer (e.g. Fig. 10).

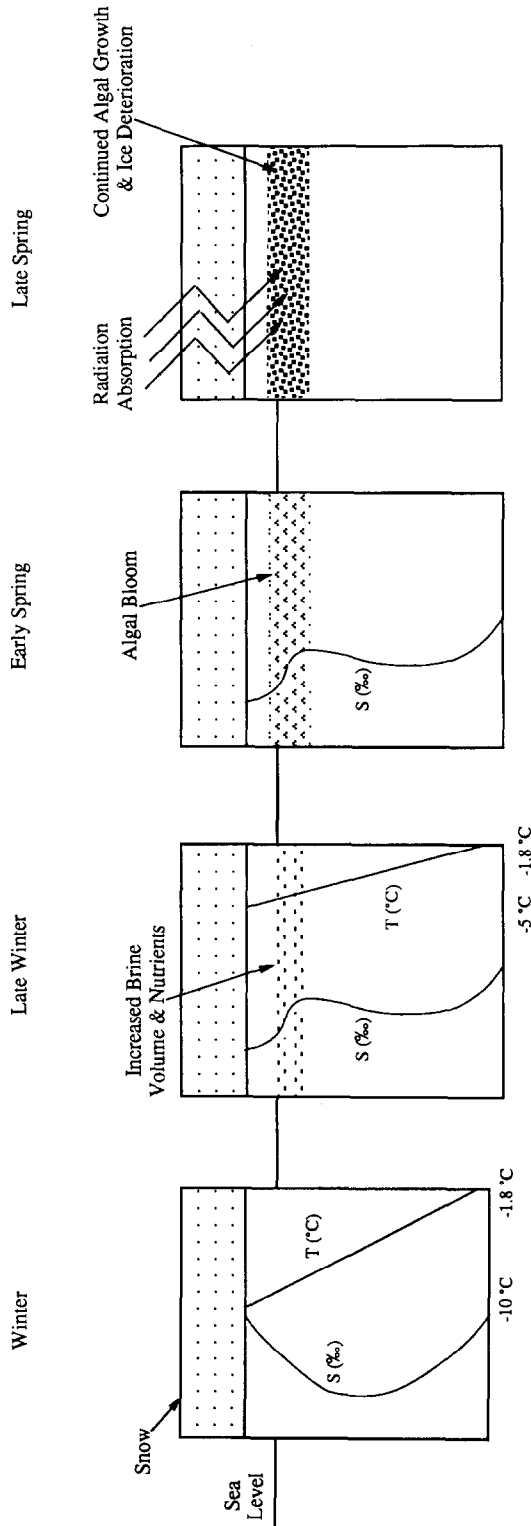Salinity measurements on the freeboard layer pore water retrieved from this porous

Fig. 11. The development of a freeboard layer ice environment. Sequential series of physical and biological events postulated to be necessary to form a freeboard layer microbial community in sea ice.

layer or cavity show that it ranges between 19 and 33 ppt (KOTTMEIER and SULLIVAN, 1990; BUCK and SULLIVAN, 1990; GARRISON and BUCK, 1991). This salinity is that of sea water diluted by ice melt rather than that of melted sea ice (<10 ppt). This observation shows that the cavity is sufficiently opened up to allow the penetration of sea water into the freeboard layer. Observations of juvenile krill feeding in this layer during AMERIEZ cruises in the spring (AINLEY and SULLIVAN, 1984; AINLEY et al., 1986) and autumn (SULLIVAN and AINLEY, 1986) also confirm that the passage to the open ocean is wide enough to allow the migration of centimeter-sized animals. Wave action in the marginal ice zone affects this process by breaking up the floes, thereby decreasing the distance from the perimeter of the floe to its center from kilometers to meters and consequently enhancing nutrient exchange. Waves may also increase sea water exchange in the freeboard layer, as the floes tilt slightly in the wave field, and cause the movement of sea water from side to side in the layer as the floe responds to the wave field. KRISTIANSEN and SYVERTSEN (1990) and GARRISON and BUCK (1991) both report that they observed a horizontal gradient of biological matter, with the higher concentration of algae nearer the edges of the floes. KRISTIANSEN and SYVERTSEN (1990) reported concentrations of algal matter up to 425 mg chl$a$ m^{-3} with the color of the layer observed to be chocolate-like in appearance. KOTTMEIER and SULLIVAN (1990) collected pore water from the freeboard layer of floes during autumn and spring in the Weddell and Scotia Seas and reported it to be the site of high rates of algal (0.38 day^{-1}) and bacterial (1.0 day^{-1}) growth. The bacterial production in pore water exceeded primary production and they suggested this could only be a transient feature or that organic matter must be imported to the system. BUCK and SULLIVAN (1990) and GARRISON and BUCK (1991) provide information on the structure of autotrophic and heterotrophic eucaryotic communities and their interactions. The presence of heterotrophic flagellates and ciliates were found at concentrations of 10^3–10^5 l^{-1}. Diatoms dominated the autotrophic biomass in most samples, although dinoflagellates and the prymnesiophyte *Phaeocystis* were occasionally dominant.

These environments are probably common in the northern parts of the marginal ice zone of the Weddell region throughout the year and in the western Weddell Sea in the summer (Gow et al., 1987).

(e) *Bottom and platelet layer habitats*

Bottom and platelet layer communities were among the first characterized in Antarctica (BUNT, 1963), and have been more recently described for the McMurdo Sound region (e.g. SULLIVAN and PALMISANO, 1984; PALMISANO and SULLIVAN, 1985; McGRATH-GROSSI et al., 1987; ARRIGO, 1992). Unlike the drifting pack of the Weddell Sea, where frazil ice structure predominates, the ice attached to the coast in Antarctica (fast ice) is dominated by columnar ice structure, due to the extraction of heat for ice formation by conduction through the existing cover. The lower levels of columnar or congelation ice have high stability, a high probability of colonization and free exchange of nutrients with the underlying sea water. These features, along with increased irradiance, permit algal growth and accumulation of biomass up to 2120 mg chl$a$ m^{-2} (56 g C m^{-2}) to occur (ARRIGO, 1992). Algae accumulate in the bottom 20 cm of the congelation ice during the spring bloom with standing crops of as much as 5 g C m^{-2}. Although congelation ice is seen in up to 50% of the drifting pack ice in the Weddell region, the extent and concentration of chl$a$ in bottom ice communities has not been observed there to the same degree as in coastal

regions (Fig. 7). The lower light level, caused by deeper snow covers in the drifting pack compared to the snow-free and more productive fast ice zones, is the primary factor in producing these differences in algal production between the two systems.

Platelet layers are often observed under nearshore fast ice. These ice layers, seen in most years in the McMurdo Sound region (DAYTON et al., 1969; DAYTON, 1989), are caused by the advection of waters underneath the ice shelves where, by contact with the continental ice, the waters are brought to the pressure freezing point at that depth. As the water masses rise adiabatically at the edges of the shelf, they are supercooled as the pressure decreases without warming (FOLDVIK and KVINGE, 1974). By in situ nucleation, ice crystals form and are brought up as roughly circular platelets underneath the ice cover (DIECKMANN et al., 1986). The platelets are sometimes several centimeters in diameter, 1–3 mm in thickness, and form loose, cloud-like billows under the existing ice cover, sometimes several meters in thickness.

The platelet ice community located below congelation ice can support even more biomass than the congelation ice, presumably because of great stability, more available space, ample opportunity for colonization and a greater capacity for nutrient exchange, than in the skeletal layer and brine channels of congelation ice. The platelet layer is loosely structured and has a 25% ice to 75% seawater composition (BUNT, 1963). Recently ARRIGO et al. (1990) reported a 12 cm thick, biologically active, layer located on the lower side of the congelation/platelet ice interface. It was estimated to contain remarkably high concentrations of 13 g chl$a$ m^{-3} and a standing crop estimated at 60–80 g C m^{-2} under an extensive area of snow-free, second-year ice.

The onset of the bloom in the platelet ice layer is strongly affected by downwelling irradiance, controlled principally by the thickness and properties of the snow cover on the top of the ice (McGRATH-GROSSI et al., 1987; PALMISANO et al., 1987). At the same time the blooms themselves may substantially influence the spectral irradiance regime. ARRIGO et al. (1991) report results of a computer simulation model that reveals how seasonal changes in microalgal concentrations, as well as their photophysiological characteristics, influence both the quantity and quality of downwelled light in sea ice and the upper layers of the ice-covered oceans.

Smetacek and co-workers (SCHNAK-SCHIEL, 1987; SMETACEK et al., 1992) pumped water from a platelet layer in the southern Weddell Sea, which they called the under ice water layer, and found moderately high concentrations (up to 40 mg m^{-3}) of chl$a$, usually as Thalassiosira sp. or Phaeocystis dominated blooms, in late October. The concentration of biological matter caused the waters in the region to be colored reddish-brown when the ice was broken apart. As with the bottom ice community, the platelet ice layer acts as a food source for krill (MARSCHALL, 1988), amphipods (RAKUSA-SUSZCZEWSKI, 1972) and other zooplankton.

In McMurdo Sound the platelet layer community develops during October–December, when the water column is most barren. During the spring bloom, algal biomass in the ice may exceed that in the integrated 500 m deep water column beneath it by 20-fold (ARRIGO et al., 1990; DIECKMANN et al., 1992). By December the approximately 2 m thick ice becomes isothermal, and substantial melting ensues (KOTTMEIER and SULLIVAN, 1988), resulting in an accelerated rate of release of algal cells and flocs from the ice (McGRATH-GROSSI et al., 1987). The flux of diatoms through the upper layers of the water column appears to peak during January at 400–600 mg silica m^{-2} day^{-1} (DUNBAR and LEVENTER, 1987). Yet most of the ice flora, except for Nitzschia curta (Hasle), are not found in the

surficial sediments nor further down core. Sediment trap and sediment core data suggest that a substantial fraction of the sea ice diatom assemblage undergoes preferential dissolution of biogenic opal in the upper 250 m of the water column (Leventer and Dunbar, 1987, 1988).

Strand communities have been described hanging from fast ice (McConville and Wetherbee, 1983; McGrath-Grossi et al., 1987). These are composed of long strands of cells and a complex of colonies attached at one end to the ice but extending tens of centimeters into the water column. Gulliksen (personal communication) photographed several web-like strands approximately 1 m in length during dives in McMurdo Sound during November–December 1984. These strands have been observed to contain *Berkeleya ritulans*, *Amphiprora kufferathi* (Manguin), *Pleurosigma* sp., *Porosira pseudodenticulata* (Hustedt) and *P. glacialis* (Sullivan and Medlin, unpublished). While McConville and Wetherbee suggested these to be unique communities based on single observations, McGrath-Grossi et al. (1987) conducted 3-month time series studies which showed that, rather than strand communities, they actually were derived from remnants of the platelet ice community following platelet melting. Nevertheless these strands, while ephemeral, certainly occupy a strikingly different environment from that of most ice algae, since they are completely bathed in sea water while they remain suspended at constant depth, by virtue of their attachment to the undersurface of the ice. They bear considerable resemblance to the long strands and mats of *Melosira arctica* observed beneath sea ice in the high Arctic (Mel'nikov and Kulikov, 1980).

The platelet ice layer and associated biological community, because of its origins with the lifting of undercooled ice shelf waters, is probably confined to nearshore regions. However, because of its presence in both the southern Weddell and the Ross Sea coastal areas it may be a ubiquitous coastal feature around Antarctica, coinciding with the presence of ice shelves. Eicken and Lange (1989) have shown that platelet ice observed in intact drifting pack ice usually is confined to within 50 km of the Antarctic coast in the Weddell Sea, but accounts for about 30% of the ice in those locations.

DISCUSSION

Incorporation of biological matter, especially in frazil ice, leads to a widespread distribution of algae in circumpolar Antarctic sea ice. While these are some of the lowest concentrations (1–50 mg chl$a$ m^{-3}) observed for sea ice communities, they, nevertheless, are generally much greater than chl$a$ concentrations reported in the water column under pack ice throughout the year and in open water regions away from the ice edge (Nelson et al., 1987, 1989; Sullivan et al., 1990). The ice formation processes, particularly the frazil-pancake ice cycle (Lange, 1990), account for the incorporation of biological matter in pack ice. This ice growth, together with other physical characteristics of the Weddell Sea, also permits the use of the algae even in the winter by krill and other grazers. Frazil-pancake ice development generally causes quick growth to 60–80 cm of ice thickness, incorporating algal matter in the process. As the season progresses, ice of this thickness is slowly ablated from below because of the high oceanic heat flux (Gordon et al., 1984; Gordon and Huber, 1990). Slow melting leads to constant exposure of algae throughout the winter period allowing transfer throughout the food web. The interior communities, because of their widespread distribution and continuous availability as the ice erodes from below, may be a critical element in winter feeding and survival of juvenile and adult krill.

The limited observations suggest the snow ice biological communities develop under milder temperature and higher irradiances than are observed in winter in the southerly portions of the Weddell Sea. Therefore we estimate that the full development of snow ice communities occurs either in the late spring or summer in most pack ice regions, where warmer temperatures and higher irradiance are available. They may also be less important as a food source within the ice for higher forms, since they are on the surface and may require extensive deterioration of the ice before the larger zooplankton (krill) can gain access to this layer. However, their utility as a seed population for ice edge blooms, as a food source for grazers near the ice edge, or for sedimentation may be quite high since they will be deposited at their highest concentration into the water column at the ice edge (SULLIVAN et al., 1988; COMISO et al., 1990).

Similar behavior is expected for pressure ridge communities as for snow ice communities, i.e. full development depends on milder temperatures and higher irradiance as well as flooding of the surface near the ridge. Accelerated growth and development of the biological communities takes place as wave breakup events cause the local isostatic imbalance to occur leading to flooding as ponds in the vicinity of the ridges. These processes are prevalent in the outer 200 km of the ice pack. The areal coverage of ridge associated communities is related to the deformational history, resulting in the particular ridge frequency, that the floes undergo prior to their advection into the marginal ice zone. These ponds are commonly observed in the western Weddell outflow region (40 to 60°W longitudes).

Freeboard layer communities also are probably linked seasonally and regionally, with maximum development occurring in the spring–summer periods. Additional acceleration of their development is also tied to wave-induced floe breakup which decreases the distance for water and grazers to migrate from the perimeter of the floe through the honeycomb-like "rotten" ice layer that develops from this process. As deterioration progresses, both the level of primary productivity and the accessibility to higher trophic levels (grazers such as copepods and krill) are expected to increase. These communities therefore may be intermediate between the high availability as a food source of exposed interior communities and the lower availability of snow ice communities. Due to the seasonal requirement, however, their potential as a food source is limited to the spring, summer and, possibly, early autumn in the regions of perennial ice cover such as the western Weddell Sea and the Bellingshausen and Amundsen Seas. The freeboard layer communities, because of access to the open water through labyrinthine channels that permeate deteriorating floes, provide a refugium and rich grazing regime for krill. The preponderance of juvenile krill observed in these floes led KOTTMEIER and SULLIVAN (1987) and DALY (1990) to hypothesize that sea ice may serve as a nursery ground for E. superba.

Bottom and platelet-layer communities have been shown so far to be limited to coastal regions. The enhanced algal growth appears related to the thin snow covers observed over fast ice leading to sufficient irradiance at the base of the ice to support photosynthesis. The ice in these regions occupies only 1–5% of the total ice cover area around Antarctica. Standing crops of algae are at the highest levels observed and are generally three orders of magnitude greater than that reported for interior communities of drifting pack ice. Since the area of fast ice is only two orders of magnitude lower than that of pack ice, the total production from coastal communities may still be commensurate with the carbon produced and contained within the drifting pack. Coastal environments are a major part of the Antarctic marine ecosystem with high densities of birds and mammals. Because they

accumulate such large standing crops, the bottom ice communities may play an important role by providing a substantial fraction of the carbon necessary to support the coastal ecosystem (KNOX, 1990). Early development of the bottom ice community in spring when the water column is particularly barren also is likely to be one of its most important advantages as a source of algae to grazers, including larvae of invertebrates and fish (HOSHIAI *et al.*, 1987). It has been hypothesized that the timing of production in the pelagic system as well as the total production, may be the most important features of the bottom and platelet layer communities to sea ice biological structure and function (SULLIVAN *et al.*, 1985). For example, Ross *et al.* (1987) reported that larval krill stopped development between June and December when water temperature and food levels fell to $-1.3°C$ and $<0.2 \mu g$ chl*a* l^{-1}, respectively; however, when larval krill feeding on sea ice microbiota were examined in the Weddell Sea during winter, they were found to maintain high growth rates typical of summer (DALY, 1990).

The total amount of ice associated production in the circumpolar ice zone that is transported directly to the benthos is unknown. Studies of sedimentation beneath sea ice conducted by Dunbar and colleagues suggest that only robust forms that predominate in ice, such as *Nitzschia curta* and *Nitzschia cylindrus*, contribute substantially to the formation of siliceous sediments in the southwestern Ross Sea, with the remainder being comprised of planktonic forms that develop in open ocean ice edge blooms in the region. LEGENDRE *et al.* (1992) have synthesized data from both polar regions to estimate the potential production. A quantitative understanding of the fraction of this production converted either into higher forms (e.g. krill) or its direct input to the benthos are equally important problems. On the one hand the sea ice algal production may be crucial to the survival of some of the higher trophic forms, while on the other, the input to the benthos, without utilization, sequesters carbon and may be a previously overlooked aspect of the global carbon cycle. At present, the variety, productivity and distribution of sea ice communities suggests at least greater importance to them then previously has been assumed. A more complete understanding of the role of these communities in the marine ecosystem necessitates further field studies in pack ice regions, under ice moorings of both physical and biological fluxes and time series investigations of the ice-related ecological processes through the various seasonal cycles.

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