

The Contributions of Sea Ice Algae to Antarctic Marine Primary Production¹

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SYNOPSIS. The seasonally ice-covered regions of the Southern Ocean have distinctive ecological systems due to the growth of microalgae in sea ice. Although sea ice microalgal production is exceeded by phytoplankton production on an annual basis in most offshore regions of the Southern Ocean, blooms of sea ice algae differ considerably from the phytoplankton in terms of timing and distribution. Thus sea ice algae provide food resources for higher trophic level organisms in seasons and regions where water column biological production is low or negligible. A flux of biogenic material from sea ice to the water column and benthos follows ice melt, and some of the algal species are known to occur in ensuing phytoplankton blooms. A review of algal species in pack ice and offshore plankton showed that dominance is common for three species: *Phaeocystis antarctica*, *Fragilariopsis cylindrus* and *Fragilariopsis curta*. The degree to which dominance by these species is a product of successional processes in sea ice communities could be an important in determining their biogeochemical contribution to the Southern Ocean and their ability to seed blooms in marginal ice zones.

INTRODUCTION

The presence of sea ice is a defining structural feature for most polar marine ecosystems. Considered as a single ecosystem type, seasonally ice-covered seas cover 35×10^6 km², or 13% of the world surface area (Parkinson and Gloersen, 1993). This is an area larger than most terrestrial biomes (e.g., grasslands, tundra, or deserts). While sea ice in the Northern Hemisphere occurs in several distinct oceanographic regions (including temperate seas), the Southern Ocean is a contiguous polar ecosystem due to circumpolar currents around Antarctica. The annual maximum 20×10^6 km² of sea ice around Antarctica is 50% greater than the area of the continent (Zwally *et al.*, 1983). This sea ice zone covers about 40% of the Southern Ocean.

Antarctic sea ice is inhabited by microbes (bacteria, algae, and protists; e.g., Garrison, 1991), small metazoans (crusta-

ceans, worms; Garrison, 1991; Schnack-Schiel *et al.*, 1998) and large vertebrates (birds and seals; Ainley and DeMaster, 1990). Sea ice is also visited by other mobile grazers from the water column (e.g., fish and zooplankton). Some of the larger grazers and predators might use the sea ice primarily as a physical habitat and feed mostly in the water column, but they might deliver materials to sea ice communities in the form of wastes. The microbes and metazoans associated with this sea ice clearly interact to form an ecological community (Garrison, 1991). These sea ice communities can be supported by materials (both dissolved and particulate) that are allochthonous and autochthonous. Allochthonous materials include those incorporated during ice formation or delivered from the sea via animals, waves, or flooding of ice that has accumulated a lot of snow. Sea ice communities may play a role in transforming allochthonous materials, such as converting dissolved materials (e.g., excreted wastes) into particles (cells and bodies), or degrading particles (detritus, feces) to remineralize nutrients. However, the most common and abundant sea ice communities appear to be supported primarily by the autochthonous production of photosynthetic algae.

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The ecological role of sea ice algae could also be expanded beyond the primary production they conduct in association with sea ice. Priddle *et al.* (1996) called the ice-covered Southern Ocean a "two-phase" ecosystem based on the annual cycle of exchange of materials and organisms between sea ice and the water column. In this context, sea ice could be an important environment for providing refuge to overwintering cells and spores, for natural selection of microalgae during species succession in sea ice (*e.g.*, Gleitz *et al.*, 1998), and for seeding phytoplankton blooms in marginal ice zones (*e.g.*, Smith and Nelson, 1985; Garrison *et al.*, 1987). In this review I will attempt to synthesize our current understanding of primary production and species succession processes in sea ice, and the extent to which these sea ice ecological processes influence phytoplankton dynamics during ice-free periods.

PRIMARY PRODUCTION

There have been several attempts to estimate the contribution of sea ice algae to primary production in the seasonal ice zone (SIZ) of the Southern Ocean. One approach is to compare estimates of annual primary production by phytoplankton and by sea ice algae.

Estimates of primary production of the Southern Ocean have focused primarily on phytoplankton. El Sayed (1967) estimated that primary production for the Southern Ocean was 3,000 Tg C yr⁻¹. However, the available data for these early estimates was primarily for high-productivity waters on the continental shelf. In the 1970s, the estimates dropped about five-fold to ca. 600 Tg C yr⁻¹ as more measurements were made in pelagic waters under non-bloom conditions (Holm-Hansen *et al.*, 1977; El Sayed, 1978). In the last two decades, phytoplankton blooms in the marginal ice zone (MIZ) have been recognized as a major site of primary production in the Southern Ocean. Large-scale annual estimates of primary production have been made based on the assumption that as the sea ice recedes around Antarctica during spring, summer and autumn, conditions leading to phytoplankton blooms persist for weeks and for

hundreds of km away from the ice edge. These conditions might include the formation of a shallow (favorable light) and stable surface mixed layer due to freshening after ice melt (*e.g.*, Smith and Nelson, 1985) and seed populations of algae released from sea ice (*e.g.*, Garrison *et al.*, 1987). The MIZ estimates implied an additional primary production of 300–400 Tg C yr⁻¹ (Smith and Nelson, 1986; Smith *et al.*, 1988). Savidge *et al.* (1996), using a more complex extrapolation scheme, confirmed these estimates. However, the accounting exercise of Legendre *et al.* (1992) came up with less than half the previous estimate (141 Tg C yr⁻¹). Adding 141 to 400 Tg C yr⁻¹ for the MIZ to the previous estimate of 600 Tg C yr⁻¹ yields SIZ total annual production estimates of 741 to 1,000 Tg C yr⁻¹. Recent estimates based on models using satellite-derived phytoplankton pigment concentrations and physiological parameters are somewhat higher: an SIZ total of 1,300 Tg C yr⁻¹, with 420 Tg C yr⁻¹ due to MIZ blooms (Arrigo *et al.*, 1998c). Part of the reason that the most recent estimates are higher may be better representation of the spring blooms that occur in coastal polynyas (*e.g.*, Arrigo and McClain, 1994; Smith and Gordon, 1997; Arrigo *et al.*, 1998a).

Measurements of primary production in sea ice are much less common than studies of phytoplankton in the Southern Ocean. Whereas estimates of phytoplankton were initially too high, sea ice primary production estimates were initially too low. One reason may have come from the fact that measurements of primary production before the 1980s were only reported for nearshore sites. Extrapolations from this data led to estimates of annual production that were considered insignificant relative to phytoplankton production; *e.g.*, Bunt (1968) estimated an annual production of less than 0.03 Tg C yr⁻¹. Heywood and Whitaker (1984) extrapolated from the daily primary production rates measured by Burkholder and Mandelli (1965) for the entire SIZ assuming a 100 day growing season to arrive at an estimate of 50 Tg C yr⁻¹. These were considered very generous assumptions, but the estimate is similar to what recent re-

searchers have concluded from more complicated estimation schemes. Based on standing stocks of algae in different types of Antarctic sea ice, Legendre *et al.* (1992) estimated annual primary production at 63 to 70 Tg C yr⁻¹. A model of primary production in the surface communities of pack ice produced an estimate of 36 Tg C yr⁻¹ (Arrigo *et al.*, 1997, 1998b), which was very close to the Legendre *et al.* (1992) estimate of 40 Tg C yr⁻¹ for that type of sea ice.

Thus the most recent and complete estimates for total annual primary production in the Antarctic SIZ stand at 63 to 70 Tg C yr⁻¹ for the sea ice communities and 1,300 Tg C yr⁻¹ for phytoplankton. These estimates mean that annual primary production by sea ice microalgae makes up about 5% of the total for the Antarctic SIZ. However, the ecological importance of primary production by sea ice algae may be underestimated by their contribution to annual primary production for these seas. Variations in the distribution and timing of sea ice around the continent could produce higher or lower contributions from sea ice algae in particular regions and seasons relative to the plankton.

The extent, concentration, timing, and type of sea ice around Antarctica vary spatially, seasonally and interannually. Satellite-based remote sensing based on passive microwave sensors have given us a means of studying these aspects of sea ice since the 1970s. Zwally *et al.* (1983) divided the Southern Ocean into five sea ice sectors based on longitude lines, and Arrigo *et al.* (1997, 1998b, c) have used these same sectors to describe primary production (see Table 1). I will use these sectors to describe regions of the Southern Ocean.

At its maximum extent in September, the northern extent of sea ice varies greatly around the continent; in the Ross and Bellingshausen-Amundsen sectors the sea ice maximum is often south of 65°S, whereas in the Weddell and Indian sectors the sea ice can extend to 55–60°S (Zwally *et al.*, 1983; Parkinson, 1998). These differences in latitude north of the Antarctic Circle can make a great difference in the amount of solar radiation, day length, and length of the

TABLE 1. Percent of total primary production in the Antarctic Seasonal Ice Zone contributed by sea ice algae, based on model estimates for sea ice (Arrigo *et al.*, 1998b) and phytoplankton (Arrigo *et al.* 1998c).

Month	W.					Total
	Weddell	Indian	Pacific	Ross	B-A*	
October	6.1	35.0	6.4	21.7	8.8	10.3
November	11.9	12.0	2.4	8.6	6.5	8.8
December	4.6	2.6	1.4	3.8	2.6	3.4
January	2.1	1.6	1.1	1.2	1.5	1.6
February	1.2	0.8	0.7	0.5	1.4	1.0
March	1.7	0.6	1.2	1.3	1.4	1.3
April	1.0	1.3	2.1	2.0	2.4	1.5

* Bellingshausen-Amundsen.

growing season for algae, all factors that influence primary production (*e.g.*, Smith and Sakshaug, 1990). At the annual minimum for sea ice extent in February, small remnant patches of sea ice hug the Antarctic coast in all sectors, but larger ice-covered regions remain off East Antarctica in the western Weddell Sea, the Bellingshausen-Amundsen Sea and the eastern Ross Sea (Zwally *et al.*, 1983; Parkinson, 1998). The latter regions contain nearly all the multi-year sea ice in the Southern Hemisphere.

The length of the sea ice season can vary from a few days to year-round and generally decreases with distance from the continent, with the exception of coastal polynyas and the large and regular polynya off the Ross Ice Shelf (Parkinson, 1998). Interannual variations in the extent of Antarctic sea ice have been observed (Zwally *et al.*, 1983). Parkinson (1998) noted a clockwise (eastward) rotation in the sequence of years from 1988–1994 for variations in length of the sea ice season, which she linked to the Antarctic circumpolar wave (White and Peterson, 1996). Patterns are emerging for some sectors that show years with higher winter maximum sea ice coverage are followed by lower summer minima, and vice-versa (*e.g.*, Comiso and Gordon, 1998). These interannual variations in sea ice will affect the growing season for sea ice algae as well as for open water phytoplankton blooms.

Recently, it became possible to estimate snow thickness from satellite microwave data (Arrigo *et al.* 1997, 1998b; Markus

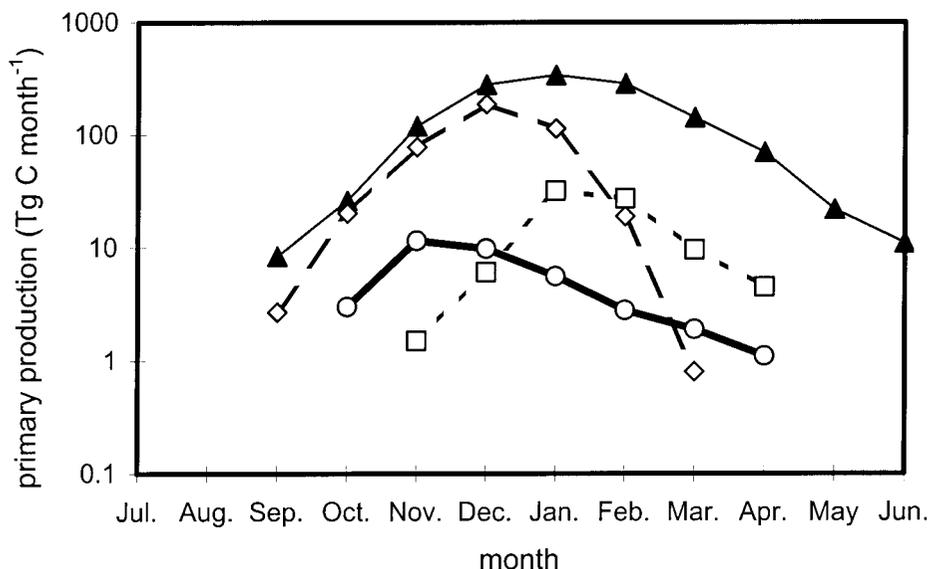


FIG. 1. Primary productivity in the Antarctic sea ice zone (SIZ) by month as modeled by Arrigo *et al.* (1998*b*, *c*). Symbols: SIZ total (triangles); MIZ water (diamonds); shelf water (squares); and sea ice (circles).

and Cavalieri, 1998). The amount of snow on sea ice is relevant for photosynthetic production because snow cover greatly affects light penetration into the sea ice and underlying waters. Snow cover can also have a positive effect on sea ice primary production by depressing the sea ice below sea level and causing flooding of the surface; this delivers algae and nutrients to the sea ice (*e.g.*, Arrigo *et al.*, 1997, 1998*b*). Snow accumulates most on sea ice that has a longer life, such as multi-year ice (Markus and Cavalieri, 1998).

The influence of ice extent and snow cover distributions is apparent in the results from the sea ice primary production model of Arrigo *et al.* (1997, 1998*b*). These results can be contrasted with the results for phytoplankton production by Arrigo *et al.* (1998*c*). The advantage of comparing these two studies is that they are based on the same model structure (with different physiological coefficients for phytoplankton and sea ice algae) and use the same models and climatologies for input of solar radiation and sea ice cover. One weakness is that the sea ice primary production is most likely an underestimate because the model only covers blooms near the ice surface, and the study only considers the months of October

to April. The estimates for total annual sea ice primary production by Legendre *et al.* (1992), which include bottom ice and internal communities, are 50–75% higher than the model total. However, we do not know the geographic or seasonal distribution of algal production in bottom ice or internal communities. However, the following comparison of sea ice versus water column primary production may be instructive to understand the order of magnitude of the importance of sea ice algae to these ecosystems.

The annual cycle for primary production in the sea ice shows a peak earlier than for open waters of the SIZ (Fig. 1). The sea ice peak is in November, the peak month for the MIZ is December, and for the shelf systems and the overall SIZ, the peak is in January. The spring sea ice production is primarily in the annual ice rather than the multi-year ice that is mostly farther south near the continent (Fig. 2). Later in the summer, the production in multiyear ice surpasses that of the annual ice, primarily due to the diminishing amounts of annual ice. The portion of sea ice primary production occurring in annual ice (versus multiyear ice) ranged from 97% in the Weddell sector dur-

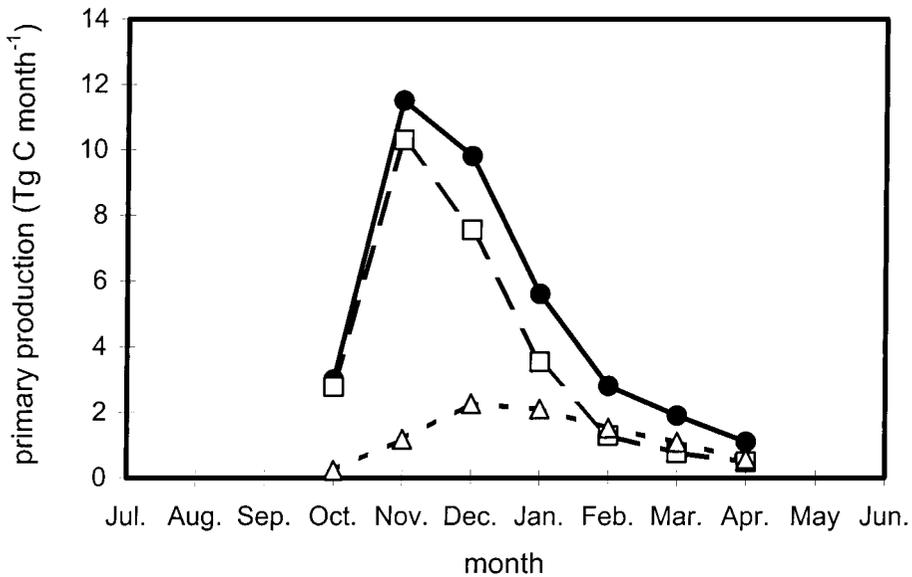


FIG. 2. Primary productivity in the Antarctic sea ice surface communities by month as modeled by Arrigo *et al.* (1998b). Symbols: multi-year ice (triangles); first-year ice (squares); and total sea ice (circles).

ing October to 15% in Bellingshausen-Amundsen sector during April.

For certain sectors and months, the contribution of sea ice algae to total primary production can also greatly exceed the overall average of 5% calculated above (Table 1). During early spring, sea ice primary production may be highly significant in the Ross and Indian sectors. The comparison between model results for sea ice and phytoplankton did not include the winter months, but during that season the light environment in ice-covered waters could heavily favor algae in the sea ice over those in the water column. The Arrigo *et al.*

(1998b) model is for surface ice communities, which may be limited during winter due to low air and ice-surface temperatures and the accompanying high salinities in the brine. However, algae at ice-seawater interfaces should have favorable temperatures for growth (if light is sufficient). Thus it is possible, even probable, that sea ice algal production exceeds phytoplankton production during the winter. There are few direct measurements to compare for the Antarctic SIZ during winter (Table 2). Daily production measured in the sea ice averaged as high or higher than rates measured for the waters column on an areal (m⁻²) basis. In

TABLE 2. Winter (June–August) primary production rates in the Antarctic Seasonal Ice Zone.

median productivity (range; n) in mg C m ⁻² d ⁻¹		
Seawater	Sea ice*	Reference
1.3 (ca. 0 to 1,100; 8)	12 (ca. 0 to 60; 8)	WINCRUISE 85 (Kottmeier and Sullivan, 1987)
4.9 (2.7 to 11; 9)	F: 27 (6 to 370; 10) N: 0.2 (0.2 to 1.0; 5)	WINCRUISE 87 (water, Brightman and Smith, 1989; ice, Lizotte and Sullivan, 1992)
29 (10 to 86; 28)	F: 41 (6 to 300; 10) N: 0.5 (0.03 to 13; 10)	AMERIEZ 88 (water, Cota <i>et al.</i> , 1992; ice, Lizotte and Sullivan, 1992)

* F refers to floes; N refers to new ice such as grease ice, nilas and thin (<8 cm) pancake ice.

TABLE 3. Winter (April–October) biomass of microalgae in the Antarctic Seasonal Ice Zone.

median [mean] (range; n) in mg chlorophyll m ⁻³		
Seawater (0 to 100 m)	Sea ice*	Reference
0.12 [0.13] (0.02 to 0.26; 27)		ELTANIN-38 (Holm-Hansen <i>et al.</i> , 1977; unpublished data from S.Z. El Sayed)
0.08 [0.25] (0.02 to 1.3; 20)	10 [13] (1.2 to 30; 38)	WINCRUISE 85 (Kottmeier and Sullivan, 1987)
[0.18] (0.04 to 0.3; 11)	F: 3.2 [26] (0.8 to 260; 21) N: 1.4 [1.6] (1.2 to 2.4; 5)	WINCRUISE 87 (water, Brightman and Smith, 1989; ice, Lizotte and Sullivan, 1992)
[0.12] (<0.05 to 0.33)	F: 7.0 [17] (0.1 to 91; 53) N: 1.1 [2.2] (0.22 to 18; 43)	AMERIEZ 88 (water, Cota <i>et al.</i> , 1992; ice, Lizotte and Sullivan, 1992)
(0.03 to 0.45)	6.0 [11] (2 to 46; 21)	ICE STATION WEDDELL (Melnikov, 1998)
		WINTER WEDDELL GYRE (Spironov <i>et al.</i> , 1996)
(<0.01 to 0.02)	[1.9] (0.04 to 15; 79) [3.6] (0.40 to 78; 41)	ANT V/2 (Dieckmann <i>et al.</i> , 1998)
		ANT VIII/2 (water, Nothig <i>et al.</i> , 1991a; ice, Dieckmann <i>et al.</i> , 1998)
[0.22]	[1.9] (0.06 to 16; 48)	ANT X/4 (Dieckmann <i>et al.</i> , 1998)
		PALMER LTER R. Smith <i>et al.</i> , (1998)

* F refers to floes; N refers to new ice such as grease ice, nilas and thin (<8 cm) pancake ice.

comparison, Arrigo *et al.* (1998c) estimated minimum rates of about 80 mg C m⁻² day⁻¹ for open waters north of the SIZ during winter.

FATE OF SEA ICE PRIMARY PRODUCTION

The ecosystems to which sea ice algal production contributes are known to have strong seasonal cycles and major differences in food webs depending on ice conditions (*e.g.*, Garrison *et al.*, 1986; Legendre *et al.*, 1992; Garrison and Mathot, 1996). The winter could be the time when sea ice production is most important for local grazers. Numerous authors have reviewed the importance of winter sea ice algae as a food source at key points in zooplankton life cycles (*e.g.*, see the review by Quetin *et al.*, 1996 and by Ross and Quetin, 2001). The food resources available in sea ice will include remnant biomass in multiyear ice, water column products incorporated into new sea ice, and any subsequent primary production. In winter, the most outstanding food-related feature of the sea ice might be the concentration rather than the production rates of algae. This will be particularly im-

portant for grazers when food concentrations in the water column go below the minimum needed to make feeding worthwhile (positive net energy received for a given amount of foraging effort). Chlorophyll concentrations (a measure of algal biomass) under sea ice are usually less than 0.1 mg m⁻³, far less than typically found in winter sea ice (Table 3). Sea ice frequently has concentrations of algae exceeding 1 mg m⁻³ (a commonly used definition for a bloom in Antarctic waters) even during the winter, and concentrations of tens and hundreds of mg m⁻³ have been measured. Thus sea ice may be the only suitably concentrated food source for grazers during the winter in ice-covered seas.

How do grazers gain access to sea ice algae? The algae and grazers (protists and animals) that are incorporated into the ice during formation and grow over the winter can constitute a closed system until ice breakup or melting. However, the physical growth of sea ice includes the development of brine drainage channels open to the sea (Eicken, 1992; Fritsen *et al.*, 1998). Some grazers from the water column are small

enough to enter the brine channels and gain access to the sea ice organisms. Melnikov (1998) proposed that brine drainage over the winter delivers algae and particulate matter to the underlying water column; the algal species he observed in winter sea ice were also observed in copepods collected under the ice (Pasternak, 1995).

Larger scale ecosystem patterns have been associated with the variation in the extent of sea ice, but a link to sea ice primary production has not been demonstrated. West of the Antarctic Peninsula, zooplankton are dominated by krill (*Euphasia superba*) after winters with high ice extent, and alternately, by salps (*Salpa thompsonii*) after low ice extent years (Siegel and Loeb, 1995; Loeb, *et al.*, 1997). A spatial equivalent has been observed off East Antarctica: krill dominated a region where ice extended farther off the coast, and salps dominated an adjacent region with less ice cover (Nicol *et al.*, 2000). Phytoplankton productivity was noted to be higher in the high ice, krill-dominated systems (Siegel and Loeb, 1995; Nicol *et al.*, 2000). The role of sea ice or sea ice algae has not been explicitly described for these systems.

Assuming that the lack of overlap between krill and salps is habitat separation rather than competition (Nicol *et al.*, 2000), an ecological role for sea ice algae may lie in the positive relationships between ice extent, ecosystem productivity, and krill success. One possibility is that sea ice algae are the stock population for blooms in the marginal ice zone during spring and summer (discussed below). This provides an indirect link from sea ice algae to krill based on the fact that *E. superba* is primarily an herbivore that has reproductive cycles timed to have spawning coincide with or follow spring-summer phytoplankton blooms (Quetin *et al.*, 1996). However it is possible that the survival of these long-lived zooplankton is related more directly to the ephemeral sea ice habitat. Spawning in spring-summer produces overwinter populations of larvae, juveniles, and adults. Field observations imply that one or all stages aggregate near sea ice (*e.g.*, Daly and Macaulay, 1988; Ikeda and Kirkwood, 1989; Daly, 1998). Larvae are observed

most commonly in association with pack ice, while adults are observed more regularly deeper in the water column or benthos (Quetin *et al.*, 1996). Physiological studies of larval krill have shown that growth can be supported by the winter stocks of particles in the sea ice (Daly, 1990) but not by water column stocks (Ross *et al.*, 1987). Without feeding, larvae survive only weeks and would not make it through the entire winter (Quetin *et al.*, 1996). Frazer (1996) determined that sea ice algae were the main food source of larval krill during winter. Juvenile and larval krill feeding on particulate material from sea ice had growth rates similar to those for juveniles feeding on a summer phytoplankton bloom (Daly, 1998). In contrast, overwintering adults do not rely heavily on winter feeding to meet their energy needs, which are satisfied by decreasing metabolic rates, mobilizing body tissues, and opportunistic feeding (Torres *et al.*, 1994). Many of these investigators have also suggested that, in addition to being a source of food, the irregular undersurface of sea ice may be important to krill as a refuge from larger predators. Thus winter sea ice may be as important to krill recruitment as spring-summer MIZ blooms because of habitat separation during winter: sea ice provides an overwinter habitat for larval krill (adequate food resources and protection from predation) while adult krill overwinter at depth, feeding on sea ice algae mostly in early spring to prepare for the reproductive season (Quetin *et al.*, 1996).

Ecological relationships that depend on sea ice have been proposed for larger predators, including penguins, other seabirds, and whales (*e.g.*, Fraser *et al.*, 1992; Smith *et al.*, 1999; Nicol *et al.*, 2000). The explanation is undoubtedly more complicated than food availability from primary production, including physical aspects of sea ice as a platform or a barrier for air-breathing animals. The role of sea ice algae in the population dynamics of higher trophic level organisms will remain speculative until adequate food web descriptions are available and our understanding at all trophic levels allows for sufficiently sophisticated ecosystem models to be built.

Finally, the production of sea ice algae

that is not assimilated or respired by grazers will undergo decomposition in the water column or be exported to the benthos. Biochemical and geochemical tracers for distinguishing sea ice algae from phytoplankton in sediments, microbial loops or food chains are under development (e.g., Kopczyńska *et al.*, 1995; Frazer, 1996). There are reasons to suspect that sea ice algae may contribute a disproportionate amount of the export flux to marine sediments (relative to their contribution to annual primary production in the SIZ). This is an important consideration for assessing their role in the biological pump of the global oceanic carbon cycle or in explaining the heavy deposits of siliceous material in the Southern Ocean. First, sea ice algae may be a preferred food resource for fecal pellet producers, such as copepods (Schnack-Schiel *et al.*, 1998) or krill (e.g., Daly, 1998) and those fecal pellets could rapidly transport sea ice algae to the sediments. Second, algae released from sea ice might be prone to flocculation and mass sedimentation under certain oceanographic conditions (Riebesell *et al.*, 1991). Finally, sea ice communities tend to be more diatom-dominated than SIZ phytoplankton communities, which could translate to a greater contribution to the silicon flux (e.g., Abelmann and Gersonde, 1991) than to the carbon flux.

SPECIES COMPOSITION AND SUCCESSION

The species composition of microalgae in Antarctic sea ice communities is a result of physical processes of ice formation, transformation and destruction, as well as biological processes of colonization, survival, growth, succession, grazing and death. No study has ever documented the full annual cycle for these all these processes, though near-shore, fast ice sites have been studied for some components over shorter periods. The logistical difficulty of long-term studies in the pack ice of Antarctica has left us to construct our understanding from short snapshots of the system.

One example of the problems encountered when we try to understand a complex, cyclical system from singular samples of sea ice is the issue of whether there are algal species that can be designated “sea ice

organisms.” Lists have been compiled for algal species found in Antarctic sea ice samples (e.g., Garrison, 1991; Palmisano and Garrison, 1993), but there is little evidence that this list includes any species that would not be included in a phytoplankton list for these waters (e.g., El Sayed and Fryxell, 1993; Bidigare *et al.*, 1996). The problem is that it is not possible, based only on the species observed in a sample from a single point in time, to distinguish between passive introduction (to water from ice, or to ice from water) and active, *in situ* growth of an algal population.

However, perhaps we should suspect that a species that frequently dominates an assemblage is growing and competing effectively in that environment. I reviewed the literature for observations of which algal species dominated offshore sea ice and waters of the Antarctic SIZ in different sectors and different seasons (Table 4). I excluded studies of nearshore fast ice communities (see Garrison, 1991 for a review) and Southern Ocean north of the SIZ (e.g., the polar front). Based on their frequent occurrence as dominant and bloom species, the small pennate diatoms *Fragilariopsis cylindrus* and *Fragilariopsis curta* and the prymnesiophyte *Phaeocystis antarctica* appear to be important in pack ice and the water column of the SIZ. There appears to be more variety in dominants for SIZ phytoplankton. There are no obvious patterns by sector that cannot be explained by our propensity to return to study predictable blooms (e.g., Ross Sea Polynya blooms, Weddell Sea MIZ blooms). A similar observation led Hart (1942) to average his data for species composition in circumpolar belts. He reported that his Intermediate and Southern Regions (approximately equal to the SIZ) were dominated by *Phaeocystis brucei* (= *P. antarctica*?) and *Fragilariopsis antarctica* (= *F. cylindrus*?) and that both species were common in the sea ice and in MIZ blooms.

Time series studies are needed to determine whether species composition changes over time, and whether the changes are due to ecological succession. Such studies are rare for sea ice communities. Fast ice communities near research bases have been the

subjects of time series studies (*e.g.*, Grossi *et al.*, 1984; Grossi and Sullivan, 1985), but the species composition of land-fast ice is different than the species that dominate pack ice from pelagic regions. Melnikov (1995) described species composition changes in newly forming sea ice from the Ice Station Weddell during the autumn–winter transition (March–June, 1992): *F. curta* and *F. cylindrus* dominated the sea ice communities that formed.

Another approach that has been taken is to try and reconstruct a time series by ranking sea ice samples according to age. There are no exact proxies for determining the age of an ice floe, but some assumptions can be made regarding the relatively young age of pancake ice, nilas, or thin floes of consolidated pancake ice. Older floes can be identified by melt features such as erosion at the freeboard level or re-frozen snow-ice on the surface. Using such an approach, Garrison and Buck (1985) showed that the relative abundance of *F. cylindrus* increased from water (25%) to young ice (40%) to ice floes (56%). In contrast, *Phaeocystis* was highest in the water column (>35%) and young ice (53%), but was rarely observed in floes. Melting summer sea ice had “crack pools” that were heavily dominated by *F. cylindrus* (Gleitz *et al.*, 1996a). Gleitz and Thomas (1993) constructed a series of ice age classes with older ice having higher concentrations of particulate organic carbon, chlorophyll, and algal cells, and substantial increases in abundance for *Chaetoceros neogracile*, *F. cylindrus*, and *Nitzschia lecontei*, implying growth of these algae. Other species (*F. kerguelensis*, *Dactyliosolen*) decreased with age of the sea ice, implying they accumulated in ice but were selected against over time. Algal pigment signatures in sea ice also implied that older ice was more diatom-dominated (Lizotte *et al.*, 1998).

With few examples of succession in SIZ algal communities, the factors driving succession remain undetermined. Gleitz *et al.* (1998) found that there was an inverse relationship between the diversity of diatom species and the concentration of diatoms in sea ice (Fig. 3). All ice samples had *F. cylindrus* as a dominant or co-dominant, and

the samples with highest cell concentrations had the lowest diversity because they were nearly monospecific for this species. Gleitz *et al.* (1998) speculated that species succession in Antarctic sea ice is controlled mainly by abiotic factors during the spring–summer growth season which favor certain species such as *F. cylindrus*. The competitive advantages of this species could be related to their physiology (*e.g.*, high growth at anomalous pH, oxygen, or carbon supply levels in sea ice; Gleitz *et al.* 1995, 1996b). One possibility is that some organisms (*e.g.*, *F. cylindrus*) can grow relatively well under the extreme conditions found in sea ice, while other species (possibly *P. antarctica*) dominate sea ice assemblages only when conditions are similar to the water column (*e.g.*, ice surfaces washed by waves or flooded by seawater). We need to beware that some species could “appear” to dominate sea ice when they are merely incorporated from a phytoplankton bloom during ice formation (another subject for time-series study). A competitive advantage for some species could also come from life cycle or generalist strategies that allow them to maintain sufficient populations in the water column or the sea ice depending on seasonal habitat availability. The latter point suggests that algae dominating sea ice communities could play a role in MIZ phytoplankton blooms.

SEEDING PHYTOPLANKTON BLOOMS

Although sea ice algae do not directly contribute a large proportion of the annual carbon fixation in the Southern Ocean, they may indirectly contribute much more via MIZ phytoplankton blooms. A “seeding hypothesis” has been debated that states that the algae released from melting sea ice during the spring and summer are the seed stock for the subsequent blooms often observed in the meltwater stabilized water column of the MIZ. The primary evidence used to support the seeding hypothesis has been circumstantial: the similarity of algal species composition in MIZ phytoplankton and nearby sea ice communities. Garrison *et al.* (1987) found that *Phaeocystis* and *F. cylindrus* dominated both the sea ice and the water column at a receding MIZ in the

TABLE 4. *Species* dominating sea ice and surface waters offshore from Antarctica in the Seasonal Ice Zone. Sectors are defined as in Zwally et al. (1983).*

Month/Year	Sea ice	Seawater	Reference
WEDDELL SECTOR (60°W to 20°E)			
2/68		thtu, fr, PHAN	El-Sayed (1971)
2/77–3/77	FRCY, FRCU		Ackley <i>et al.</i> (1978)
12/80–1/81		frke, FRCU	Gersonde and Wefer (1987); Abelmann and Gersonde (1991; sediment traps)
2/80–3/80	PHAN, FRCY, nisu	PHAN, FRCY, nisu	Garrison and Buck (1985)
10/81–11/81	FRCY, nipr		Clarke <i>et al.</i> (1984)
3/83–12/83		FRCY, nips	Gersonde and Wefer (1987); Abelmann and Gersonde (1991; sediment traps)
11/83–12/83	PHAN, FRCY	PHAN, FRCY	Garrison <i>et al.</i> (1987)
1/84–2/84	FRCY, FRCU		Gersonde (1986)
1/85		FRCU	Nothig <i>et al.</i> (1991b)
Summer/85	FRCY, FRCU		Chen and Dieckmann (1991)
1/85–3/86		FRCU, FRCY, thgr	Abelmann and Gersonde (1991; sediment traps)
3/86–4/86	FRCY	PHAN or FRCY	Garrison and Buck (1989); Kang and Fryxell (1993)
7/86–12/86	FRCY, FRCU		Gleitz <i>et al.</i> (1998)
10/86	FRCY	FRCY	Ligowski <i>et al.</i> (1988)
10/86–11/86	than		Smetacek <i>et al.</i> (1992)
1/87–11/87		frke	Abelmann and Gersonde (1991; sediment traps)
12/87–1/88		FRCY or cocr	Figueras <i>et al.</i> (1993)
1/88–2/88	FRCU, FRCY, frsu	cocr	Bathmann <i>et al.</i> (1991; sedi- ment traps)
6/88–8/88	FRCY, chneo		Garrison and Close (1993)
10/88–11/88		thgr, chneg, FRCY, cr	Bianchi <i>et al.</i> (1992); Schloss and Estrada (1994); Socal <i>et al.</i> (1997)
1/88–4/89		frke, FRCY, FRCU	Abelmann and Gersonde (1991; sediment traps)
1/89		da, FRCY	Socal <i>et al.</i> (1997)
1/90–2/90	FRCY	FRCY	Hellum (1992)
1/91–2/91	FRCY	th	Gleitz <i>et al.</i> (1996a)
4/92–5/92	FRCY or chneo	FRCY	Gleitz and Thomas (1993)
3/92–6/92	FRCY, FRCU, cocr	than, FRCY, FRCU, cocr	Melnikov (1995, 1998)
6/92		FRCY, PHAN	Spiridonov <i>et al.</i> (1996)
10/92–11/92		cycl, nipr	Bathmann <i>et al.</i> (1997)
12/92–1/93		PHAN, th, FRCY	Semenah <i>et al.</i> (1998)
12/95–1/96		PHAN	Bracher <i>et al.</i> (1999)
INDIAN SECTOR (20°E to 90°E)			
Summer/65	FRCY		Fukushima and Meguro (1966)
1960's?		FRCU or FRCY	Kozlova (1966; from Fryxell and Kendrick 1988)
2/69		txan	Ligowski (1983)
1/88–2/88		cycl, FRCY	Kang and Fryxell (1991); Kang <i>et al.</i> (1993)
	FRCY		Meguro <i>et al.</i> (1992)
1/91–2/91		FRCU	Kopczynska <i>et al.</i> (1995)
1/91–3/91		FRCU, nian, nisu, th	Semenah <i>et al.</i> (1998)
1/93	PHAN, chneg, FRCY		Kristiansen <i>et al.</i> (1998)
WEST PACIFIC SECTOR (90°E to 160°E)			
1/96–2/96		frke, txan	Chiba <i>et al.</i> (2000)
1/96–3/96		FRCU, Nile, chdi, FRCY	Waters <i>et al.</i> (2000)

TABLE 4. *Continued.*

Month/Year	Sea ice	Seawater	Reference
ROSS SECTOR (160°E to 130°W)			
1/78		PHAN	El Sayed <i>et al.</i> (1983)
1/83–2/83		FRCU	Wilson <i>et al.</i> (1986)
Summer/86	FRCY, FRCU	FRCY, FRCU	Burckle and Humphreys (1986)
1/90		FRCU, FRCY, PHAN, ch	Smith <i>et al.</i> (1996)
2/91		FRCU, FRCY	Leventer and Dunbar (1996; sediment traps)
2/92		PHAN	DiTullio and Smith (1995)
11/94		PHAN	W. Smith <i>et al.</i> (1998)
11/94–12/94		PHAN	Saggiomo <i>et al.</i> (1998)
12/95		PHAN	W. Smith <i>et al.</i> (1998)
12/95		nisu	Sedwick and DiTullio (1997)
12/96		PHAN	Arrigo <i>et al.</i> (1999)
BELLINGSHAUSEN-AMUNDSEN SECTOR (130°W to 60°W)			
2/89–3/89		nihe, rhal, cycl	Hardy <i>et al.</i> (1996)
10/90–11/90		PHAN, FRCY, cycl	Smith <i>et al.</i> (1992); Kang <i>et al.</i> (1993)
11/92–12/92		than or cobo or PHAN	Savage <i>et al.</i> (1995); Robins <i>et al.</i> (1995); Edwards <i>et al.</i> (1998)
2/94	FRCY, FRCU		Thomas <i>et al.</i> (1998)

* Abbreviations: ch = *Chaetoceros spp.*; chdi = *Chaetoceros dicheata*; chneo = *Chaetoceros neogracile*; chneg = *Chaetoceros neglectum*; cocr = *Corethron criophilum*; cobo = *Coscinodiscus bouvet*; cycl = *Cylindrotheca closterium*; cr = cryptomonad; da = *Dactyliosolen sp.*; fr = *Fragilariopsis sp.*; FRCU = *Fragilariopsis curta*; FRCY = *Fragilariopsis cylindrus*; frke = *Fragilariopsis kerguelensis*; frsu = *Fragilariopsis sublinearis*; nian = *Nitzschia antarctica*; nihe = *Nitzschia heimii*; nile = *Nitzschia lecointei*; nipr = *Nitzschia prolongatoides*; nips = *Nitzschia pseudonana*; nisu = *Nitzschia subcurvata*; PHAN = *Phaeocystis antarctica*; rhal = *Rhizosolenia alata*; th = *Thalassiosira sp.*; than = *Thalassiosira antarctica*; thgr = *Thalassiosira gracilis*; thtu = *Thalassiosira tumida*; txan = *Thalassiothrix antarctica*.

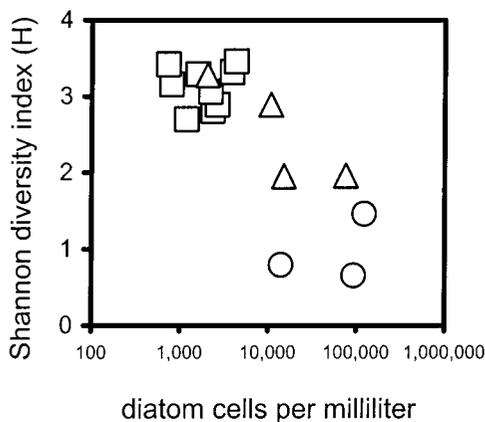


FIG. 3. Diatom diversity versus cell density in pack ice from the Weddell Sea (adapted from Gleitz *et al.* 1998). They clustered samples by species similarity, of which *Fragilariopsis cylindrus* made up: 73–92% (circles); 4–41% (triangles); 9–41% (squares).

Weddell Sea during spring 1983. Percent similarity in species composition, with the same dominant species, was also observed the late summer of 1980 in the same region (Garrison and Buck, 1985). Past reviews have noted that blooms in the MIZ are frequently dominated by *Phaeocystis* (Hart, 1942) or by *F. cylindrus* (Kang *et al.*, 1993), with claims that one or the other is the most important MIZ species.

One limitation of the seeding hypothesis is that it does not consider the role of sea ice ecology in producing a viable seed population. Successional processes and growth of algal populations in ice and the water column may be important parts of a story in which a MIZ phytoplankton bloom is only the most obvious and dramatic stage. The number, species, and physiological condition of the seed population released from melting sea ice will depend on their accumulation or colonization during ice formation, survival and growth over the win-

ter, and the ecological conditions that could limit algal growth during spring/summer sea ice blooms. None of these determinants is well understood at this time.

Numerous external conditions influence the sea ice environment, and thus effect the seed population during its development in the ice. Meteorological conditions (snow accumulation, winds, cloud cover, air temperature; *e.g.*, Eicken, 1992; Ackley and Sullivan, 1994; Worby *et al.*, 1998; Jeffries *et al.*, 1998; Van Woert, 1999) and oceanographic conditions such as heat flux (*e.g.*, Martinson and Iannuzzi, 1998) greatly affect the formation, distribution, and physical structure of sea ice. Nutrient supplies to ice algae can be a function of the type of ice formed (frazil ice with discrete brine inclusions or columnar ice with vertical brine channels open to the sea), convection during brine drainage (Fritsen *et al.*, 1994), tides or storm surges that increase exchange with underlying waters (*e.g.*, Cota and Sullivan, 1991), freeze-thaw cycles (*e.g.*, Fritsen *et al.*, 1998) and uptake by the algae themselves. Salinity also ranges very widely in sea ice as a function of temperature, from hypersaline brines to fresh melt water. Extremes in salinity can diminish algal growth (Kottmeier and Sullivan, 1988) and very low salinities might lead to cell lysis (Garrison and Buck, 1986). The inorganic carbon supply in sea ice can also fluctuate to a much greater extent than in seawater, decreasing substantially with a concomitant increase in pH (Gleitz *et al.*, 1995, 1996a, b). Many of these physical and chemical variables have been incorporated into predictive models of sea ice algae growth and production (*e.g.*, Arrigo and Sullivan, 1994; Arrigo *et al.*, 1998b; Fritsen *et al.*, 1998). However little is known about how these seasonal changes in the sea ice influence species composition and the production of MIZ blooms.

A more thorough seasonal understanding of the linked sea ice and water column ecosystem (Priddle *et al.*, 1996) is needed in order to develop predictive models capable of addressing global change issues. Interpretation of paleoclimate studies based on marine sediments from the Southern Ocean would also benefit. Sediment cores show

that diatom species composition can change significantly. The sea ice diatoms pointed out above, *F. cylindrus* and *F. curta*, show an abrupt decrease at the last glacial maximum (Leventer, 1998). Other studies have shown that the relative amount of *F. cylindrus* increased even during more moderate climate changes (Leventer, 1998). Leventer *et al.* (1993) speculated that these changes were due to an increase in open water for phytoplankton blooms, due to stronger winds during the Little Ice Age and warmer temperatures during the Medieval Warm period. However the possibility exists that climate changes might alter sea ice environments such that conditions favor the development of a large, healthy populations of species capable of seeding MIZ phytoplankton blooms.

In summary, I can suggest several areas of study that could lead to improvements in conceptual and predictive numerical models. A more thorough understanding of the ecology and physiology of key species, particularly *F. cylindrus*, *F. curta*, and *Phaeocystis antarctica*, will be needed to understand their competitive advantage and to parameterize algal growth models. Clones of all three species are available in culture, and have provided us with some valuable insights (*e.g.*, Gleitz *et al.*, 1996b). Some care might be required to distinguish between Arctic and Antarctic clones of *F. cylindrus*; even though this is considered a bipolar species, there could be considerable population differences between the hemispheres. Research needs to continue on the ecological processes that occur in pack ice. Ecological studies to date have documented the great variety of communities and microhabitats, but a grand conceptual model incorporating the complex physical, chemical and biological interactions has yet to be developed. However, any models developed can best, and perhaps only, be validated through comparison with data sets of suitable temporal and spatial detail. Thus finally, and most critically, studies of complete annual cycles in offshore SIZ regions need to be initiated.

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