

# Particulate Flux from Sea Ice in Polar Waters

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## 10.1 Introduction

Annually, sea ice extent in polar regions fluctuates greatly, with northern hemisphere sea ice ranging from a minimum of  $8.4 \times 10^6$  km<sup>2</sup> in August to a maximum of  $15 \times 10^6$  km<sup>2</sup> in March, and southern sea ice retreating and advancing from  $4 \times 10^6$  to  $20 \times 10^6$  km<sup>2</sup> between February and September of each year (Squire, 1990; Comiso, Chapter 4). During retreat, melting sea ice can have a tremendous impact on local and regional physical, chemical and biological oceanographic processes. Low salinity melt water floats on top of higher density sea water forming a relatively stable surface layer (Smith & Nelson, 1986; Nelson et al., 1987; Mitchell & Holm-Hansen, 1991), unless disturbed by strong winds (Lancelot et al., 1991a). Nutrients, inorganic and organic particulates, including sea ice algae, contained within the ice, are released to the upper water column, with consequences for all levels of the biological system.

Phytoplankton blooms are commonly associated with the retreating sea ice edge where stable surface layers persist (El-Sayed, 1971; Alexander & Niebauer, 1981; Sakshaug & Holm-Hansen, 1984; Smith & Nelson, 1985; Niebauer & Alexander, 1985; Smith & Nelson, 1986; Nelson et al., 1987; Sullivan et al., 1988; Sakshaug & Skjoldal, 1989; Comiso et al., 1990; Lancelot et al., 1991a,b; Bianchi et al., 1992; Comiso et al., 1993; Schloss & Estrada, 1994). These blooms are thought to be responsible for a considerable proportion of polar productivity. For example, Smith & Nelson (1986) estimated that approximately 50% of annual primary production in the Southern Ocean is associated with the marginal ice zone blooms, while the Legendre et al. (1992) estimate is slightly greater, at about 60%. Clearly these blooms have an impact on successively higher levels of the food web (McRoy et al., 1972; Ainley & Jacobs, 1981; Bradstreet & Cross, 1982; Stretch et al., 1988; Bedo et al., 1990; Runge et al., 1991; Lancelot et al., 1993). Even when ice edge blooms do not occur (Sakshaug, 1989; Lancelot et al., 1991a,b; Veth et al., 1992; Lancelot et al., 1993; Scharek et al., 1994; Boyd et al., 1995), flux of material out of the disintegrat-

ing ice can be a food source for pelagic grazers and plays an important role in linking the surface and deep ocean.

This chapter summarizes the current state of understanding of flux from the sea ice, including data from both the Arctic and the Antarctic. First, the general characteristics of particle flux, in terms of composition, total mass and chemical signature, and the mechanisms of settling, are considered. Following this general review, three major questions are addressed. First, the role of sea ice flux in controlling the taxonomic composition and quality/quantity of primary productivity in the marginal ice zone is considered, by assessing the likelihood that algal cells released from the sea ice seed ice edge communities. Second, the importance of organic carbon released from the sea ice in supporting the pelagic community is evaluated. This is addressed by considering the role of sea ice algae as a food source for pelagic consumers both in the winter and during the late spring to summer. Many researchers have documented active grazing at the under-surface of the ice; a process that likely sustains overwintering pelagic consumers. In addition, the annual release of a large mass of organic particulates to the water column as the annual ice breaks up is very important as a seasonal food source for planktonic grazers. Finally, the role of sea ice flux in determining the structure of the open water food web is reviewed. In particular, the relationship between the sea ice flux and the development of a diatom-based versus microbially based food network (Smetacek et al., 1990) in the upper water column is examined.

## 10.2 General characteristics of particle flux

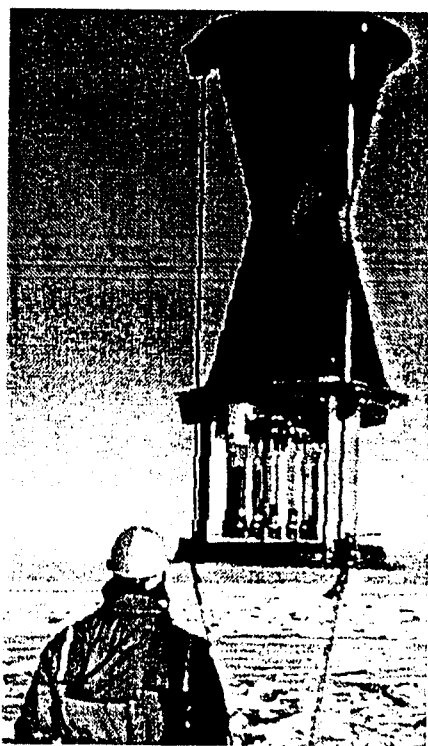
Other papers in this book address the general characteristics and distribution of particulates contained within sea ice (Arrigo, Chapter 5; Lizotte, Chapter 6; Schnack-Schiel, Chapter 7), so this will not be reviewed here. With regard to particle flux, the important thing to consider is that when the ice breaks up each late spring/summer, these constituents, which include variable concentrations of biogenic carbonates and silicates, particulate organic matter and lithogenic debris, are released to the underlying water column, where they play a role in ecosystem processes, both in the water column and at the sea floor. The timing and rate at which particles are released is a function of both their distribution within the ice and the rate at which the ice disintegrates (Leventer et al., 1987). For example, if particles are concentrated in the lower portion of the ice, as is common in Antarctic fast ice and Arctic multi-year ice floes, and that ice breaks up via melting from below, particle flux from the ice may be at a maximum as the ice begins to thin, prior to complete ice breakout (Leventer et al., 1987). If, on the other hand, particles are distributed throughout the ice column, as is more commonly the case in pack ice, particle flux may be distributed over a longer time span, though significant flux may be noted as ice retreat takes place (Fischer et al., 1988).

Honjo (1990) presents an excellent summary of particle flux in polar seas,

including a discussion of the history of particle flux experiments in these waters, an overall characterization and comparison of flux in the southern versus northern polar ocean, and a general description of the mechanisms of settling. Though his article is not focused exclusively on flux from the sea ice, many of his points are very relevant to this discussion and are reviewed below.

### *Particle flux experiments*

The most comprehensive information on flux from the sea ice has been derived from studies that are based primarily on sediment trap deployments (Figs 10.1, 10.2). The primary advantages of sediment trap studies are their ability to collect sub-ice information that is difficult to gain access to any other way, and second, that they can provide long-term and continuous data sets, as opposed to the snapshot view provided by an individual research cruise. These particle interceptor traps may be deployed through the sea ice, where they monitor flux during the later winter



**Fig. 10.1** Sediment trap recovery in the Ross Sea. Note the carousel of collection tubes at the base of the sediment trap. These collection tubes rotate into place on a pre-set schedule.

## Palmer Deep Mooring

Marjorie

(Deployed 23:11Z 3 April 1999)

Location: (64°51.689' S 64°12.34' W)

Design depth = 1040 m (Bathy 2000)

version 3 (as deployed, rbd 4/3/99)

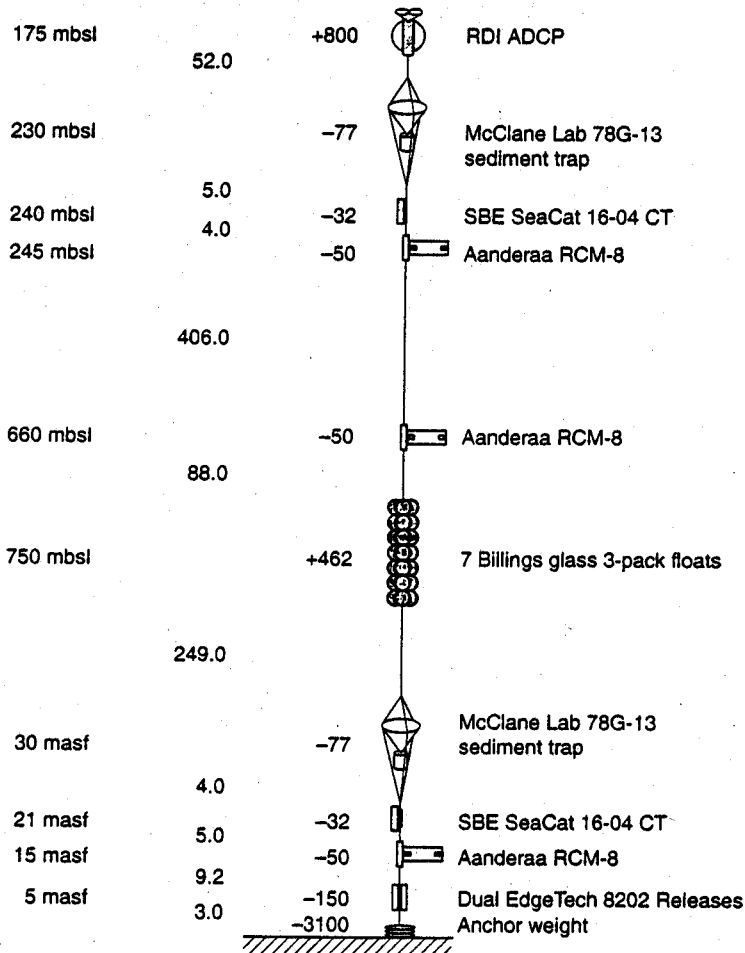
Note: Mooring line =  
12 mm VLS Duron

Fig. 10.2 A schematic describing a typical mooring deployment. Along the mooring line are two sediment traps, as well as several other instruments, including an Acoustic Doppler Current Profiler (ADCP), current meters (Aanderaa RCM-8), and conductivity-temperature recorders (SBE SeaCat 16-04 CT). Flotation to keep the mooring tightly upright is placed at the top of the mooring and along the mooring line. From left to right, vertical columns indicate the estimated metres below sea level (mbsl) of each instrument, the length of line between instruments and the flotation characteristics of each instrument.

through early summer, prior to ice breakout (Carey, 1987; Leventer & Dunbar, 1987; Tremblay et al., 1989; McMinn, 1996; Sakoh et al., 1997; Thomas et al., 2001). The sediment traps are suspended on a line anchored to the overlying sea ice. Traps can be sampled manually, as frequently as necessary, through a hole in the ice, or can be equipped with collection cups that rotate at pre-set intervals. Many of these studies are designed to focus on specific connections between the sea ice and the underlying water column and sea floor. These are discussed in more detail later in this chapter. Investigations range from studies of the role of ice algae in seeding open water blooms (as McMinn, 1996), the source of organic matter enriched in  $^{13}\text{C}$  (Thomas et al., 2001), and the importance of ice algae as a food source for pelagic zooplankton (Michel et al., 1996).

For longer-term and/or year-round information, moored arrays with automatically rotating collection cups (Fig. 10.1) can allow for comparison of flux between ice-covered and ice-free conditions (Hebbeln & Wefer, 1991; Hebbeln, 2000; also see review in Honjo (1990) and Table 10.1). These sediment traps are anchored in place via a mooring line stretched between a bottom weight at the sea floor and buoyancy floats above. Top floats are usually placed deep enough below the sea surface such that drifting icebergs with deep drafts will not catch on the floats and destroy the mooring. The mooring is typically attached to the bottom anchor with an acoustic release, so that the mooring can float free to the surface for recovery, once the acoustic release is opened. A typical mooring design is illustrated in Fig. 10.2.

In the Arctic, systematic deployment of sediment traps has focused on the Nordic Seas, including the Greenland, Norwegian and Barents Seas (data summarized by Honjo, 1990; Table 10.1). In the Antarctic, many major research programmes have had a strong sediment trap component:

- Antarctic Peninsula region (Wefer et al., 1982; Dunbar, 1984; Gersonde, 1986; Gersonde & Wefer, 1987; RACER [Research on Antarctic Coastal Ecosystem Rates] – Karl et al., 1991; Leventer, 1991; Palmer LTER [Palmer Long Term Ecological Research] – Ross et al., 1996).
- Weddell Sea (Fischer et al., 1988; Wefer et al., 1990).
- Ross Sea (DeMaster et al., 1992; Dunbar & Leventer, 1987; Dunbar et al., 1987, 1988; Leventer & Dunbar, 1996; Dunbar et al., 1998; Langone et al., 2000); ROAVERS [Research on Ocean-Atmosphere Variability and Ecosystem Response in the Ross Sea], and SOJGOFS [Southern Ocean Joint Global Ocean Flux Study] – Collier et al., 2000; Honjo et al., 2000).

Table 10.1 lists some of the major sediment trap studies that are discussed in this chapter. Both sub-ice deployments and year-round moorings are listed. The year-round trap studies were selected based on their specific reference to seasonal changes in sea ice distribution and its influence on particle flux.

**Table 10.1** Selected references on sediment traps deployed in polar seas, discussed in this chapter. Comments: 1 = sub-ice deployment; 2 = moored array with year-round data.

Reference/Year	Location	Dates	Comments
<b>Arctic</b>			
Bathmann et al., 1990	Norwegian Sea	6/86–10/87	2
Berner & Wefer, 1990	Fram Strait	8/84–8/85; 7/87–6/88	2
Berner & Wefer, 1994	Fram Strait, Norwegian Sea	Summary paper	2
Carey, 1987	Beaufort Sea	4/80–6/80	1
Hebbeln, 2000	Fram Strait	7/87–6/90	2
Hebbeln & Wefer, 1991	Fram Strait	7/88–6/89	2
Kohly, 1998	Greenland–Norwegian Sea	6/91–7/92	2
Michel et al., 1996	Canadian Arctic	4/92–6/92	1
Ramseier et al., 1999	Greenland Sea	8/85–8/96	2
Tremblay et al., 1989	Hudson Bay	4/86–5/86	1
<b>Antarctic</b>			
Abelmann & Gersonde, 1991	Antarctic Peninsula, Weddell Sea	1983–1990 summary data	2
Accomero et al., 1999	Ross Sea	1/95–1/96	2
Collier et al., 2000	Ross Sea	11/96–1/98	2
DeMaster et al., 1992	Ross Sea	1/90–2/91	2
Dunbar et al., 1987	Ross Sea	12/84–12/84; 10/86–2/87	1
Dunbar et al., 1998	Ross Sea	1/90–2/92	2
Fischer et al., 1988	Weddell Sea	1/85–3/86	2
Gersonde, 1986	Antarctic Peninsula	12/83–11/84	2
Gersonde & Wefer, 1987	Antarctic Peninsula, Weddell Sea	3/83–12/83	2
Honjo et al., 2000	Western Pacific sector of Southern Ocean	11/96–1/98	2
Langone et al., 2000	Ross Sea	12/94–1/96	2
Leventer & Dunbar, 1987	Ross Sea	10/84–12/84	1
McMinn, 1996	Ellis Fjord, East Antarctica	11/92–12/92	1
Wefer & Fischer, 1991	Atlantic sector of Southern Ocean	1983	2
Wefer et al., 1990	Antarctic Peninsula, Weddell Sea	12/83–11/87	2

### *Major differences between particle fluxes in the Arctic versus the Antarctic*

One key characteristic distinguishing Arctic and Antarctic sea ice is that Arctic ice is predominantly multi-year as contrasted to the more common single-year ice in Antarctica (Dieckmann & Hellmer, Chapter 1). Consequently, a high percentage of particles contained in Southern Ocean sea ice are released into the water column each spring, as the ice melts. In the Arctic, on the other hand, though particle flux from the ice can be seasonal in nature, there is a greater likelihood that particles will be retained in the ice for multiple years, to be released as the multi-year ice decays.

In addition, as described by Pfirman et al. (1989b), while in new ice, lithogenic particles are likely to be distributed evenly through the ice column (a consequence of particles carried with frazil ice during the formation of sea ice), as ice ages and goes through seasonal melt and freeze cycles, the particles will become concentrated at the surface of the ice floes. Then, individual events, such as the draining of a melt pond on the ice surface, waves washing over the ice, or the overturning of an ice floe, can result in the delivery of a large mass of sediment to the sea floor.

The general composition of particulates in sea ice also varies greatly from the Arctic to the Antarctic. In particular, despite regional variability, both lithogenic and carbonate material are usually more abundant in Arctic sea ice than in Antarctic sea ice. Honjo (1990) describes how the multi-year sea ice that crosses the Arctic from the Siberian side out through the Fram Strait via the Transpolar Drift, is very 'dirty' and contains abundant lithogenic particles, much of which might be wind-blown silt and sand carried from places like Northern Greenland and Svalbard, where exposed rock is subject to strong winds. Pfirman et al. (1989a) also describe, for example, how the surface of approximately half the sea ice encountered on a 1986 cruise to the Arctic (84°86'N), was covered with fine-grained particulate material, mostly lithogenic in origin. This is not to suggest that terrigenous debris is equally distributed over all Arctic sea ice; in particular, ice in regions south of 84°N that are not influenced by the Transpolar Drift, has much lower surface concentrations of debris (Pfirman et al., 1989b).

Much of the Arctic sea ice initially forms in the broad and very shallow continental shelves that rim the Arctic, where the ice is able to incorporate fine-grained material (Pfirman et al., 1990). Sediment is incorporated into the sea ice primarily during the autumn, through frazil ice formation and entrainment of fine-grained sediment from the shallow sea floor (Reimnitz et al., 1993; Eicken et al., 1997). Anchor ice formation may also lift sediment from the sea floor where it will eventually become incorporated into the ice pack. Consequently, lithogenic material entrained in sea ice can comprise a significant portion of the sediment budget in specific regions of the Arctic. For example, Reimnitz et al. (1993), in the Beaufort Sea, estimate a deposition rate of material from the ice of ~ 2 cm/1000 years, a considerable fraction of the entire sediment budget in a region with an estimated sediment accumulation rate of only 2–3 cm/1000 years. Berner & Wefer (1994) summarize particle flux data from the Fram Strait and the Greenland–Norwegian Sea that demonstrates lithogenic fluxes that range between 54 and 78%, and between 23 and 50%, respectively, of the total mass flux each year.

Sediment trap data support these visual observations of a sea ice surface often characterized by high concentrations of lithogenic material that falls to the sea floor as the ice retreats. Data presented from the Fram Strait, between Greenland and Svalbard (Honjo, 1990; Hebbeln & Wefer, 1991), illustrate the early spring flux of sand-sized rock fragments as the overlying sea ice melts. Prior to ice breakout, flux of particles is minimal. However, as melting occurred along the edges of the ice, maximum sedimentation was observed over the sediment trap sites (Hebbeln &

Wefer, 1991). The timing of maximum lithogenic sediment flux can vary regionally however. For example, high winter-time lithogenic flux was described by Hebbeln (2000) in sediment traps from the eastern Fram Strait. This was attributed to the southward movement of drifting ice over the trap site, where it came in contact with waters warm enough to melt the ice and release the entrained lithogenic particles.

In contrast, lithogenic debris comprises only a small fraction of the particulate matter in Antarctic sea ice, for two primary reasons. First, most of the Antarctic continental shelf is remarkably deep, with an average shelf depth of 500 metres (Johnson et al., 1982). Given these water depths, entrainment of lithogenic material from the sea floor via frazil ice formation and/or anchor ice formation, does not occur on any significant scale. Second, the Antarctic continent is 98% covered by ice, so only a limited amount of debris is available to be wind blown. Although aeolian-derived material is visible on the sea ice surface in some areas of the Antarctic (Barrett et al., 1983; MacPherson, 1987), the distribution must be extremely limited, given the very small area of bare rock that is exposed. This is not true in the Arctic, an ocean surrounded by continental rock, much of which is exposed to weathering and can be wind blown onto the sea ice, where it will later melt out and settle to the sea floor.

### *General characteristics of flux – annual particle flux data*

Making generalizations about particle flux can be difficult, given the many differences among particle trap experiments, including different kinds of sediment traps with different trapping efficiencies, different water depths at which traps are placed, different post-collection sample treatment, and temporal differences as related to natural interannual variability. However, significant points can be made with regard to total mass flux in the Arctic and Antarctic.

Several studies in the Arctic have been designed to address differences in particle flux as a function of varying ice cover, from ice free to mainly ice covered. Berner & Wefer (1994) present a comprehensive summary of work comparing sediment data from three distinct regions of the Fram Strait which they define as *polar*, *Arctic-Atlantic*, and *ice-margin* types. Their *polar* setting is characterized by long-term and heavy ice cover, as observed in areas bathed by Polar Surface Water. As a consequence of the lengthy duration of ice cover and cold waters, total flux is low. Biogenic production is inhibited and lithogenic flux from sea ice is limited by the small amount of ice melting that takes place. Total flux is seasonal and determined by the timing of primary production and subsequent biogenic flux. On the other end of the spectrum is the *Arctic-Atlantic* type setting, where seasonal ice cover is restricted and both biogenic and lithogenic fluxes are high. Primary production is higher in the Atlantic waters, and as in the *Polar* setting, a seasonal pattern for phytoplankton flux is observed. Lithogenic flux occurs when sea ice drifts southward and comes in contact with warm Atlantic waters, melting the ice and releasing large amounts of lithogenic material; a process that can take place even in the winter

(Hebbeln, 2000), resulting in a more aseasonal pattern. In both these settings, lithogenic flux makes up more than 60% of the total flux, highlighting the importance of lithogenic flux in the Arctic. In the 'ice-margin' setting, both total and lithogenic fluxes are moderate, and are a function of movement of the ice edge. Hebbeln & Wefer (1991) describe how in this setting, increases in both biogenic and lithogenic flux can be detected as the ice margin moves over sediment traps. Total mass flux ranges from  $< 8 \text{ g m}^{-2} \text{ yr}^{-1}$  in the *Polar* setting, to  $\sim 36.5 \text{ g m}^{-2} \text{ yr}^{-1}$  in the *ice-margin* setting, to  $\gg 36.5 \text{ g m}^{-2} \text{ yr}^{-1}$  in the *Arctic-Atlantic* setting (Berner & Wefer, 1994).

As a comparison to the Fram Strait, where ice cover clearly exerts a strong control on flux, Berner & Wefer (1994) also present a summary of sediment trap data from the Norwegian Sea, from sites that lie outside the average winter ice margin. The data document a total mass flux between  $\sim 15$  and  $30 \text{ g m}^{-2} \text{ yr}^{-1}$ ;  $\sim 20$ – $30\%$  of the flux is lithogenic. In general, flux is seasonal, with higher fluxes in the spring and summer, and lower fluxes as primary productivity decreases in the autumn and winter.

Kohly (1998) presents a similar comparison between the Greenland Sea, with variable ice cover, and the ice-free Norwegian Sea. Kohly's (1998) diatom flux data show that biosiliceous flux occurs as a single large pulse in the Greenland Sea, during the period of open water, with extremely low flux recorded under the ice. In the Norwegian Sea, biogenic flux occurs during both summer and autumn blooms, each characterized by different diatom species. Total downward diatom flux in the Greenland Sea exceeds that in the Norwegian Sea (at 500 m water depth), but this large difference in flux is not translated into the sedimentary record, a consequence of the thinner and more easily dissolved diatom frustules in the Greenland Sea, and perhaps their slower settling rate. Ramseier et al. (1999) also uses sediment trap data from the Greenland Sea to evaluate the effect of sea ice on particle flux. By comparing flux data with satellite imagery of ice cover, they quantitatively define a Biological Marginal Ice Zone that is the site of maximum flux of biogenic particles.

Sediment trap studies in the Southern Ocean report both highly seasonal variability in flux, as well as very large regional differences in total flux (Table 10.2). In addition, it is important to note that a large proportion of the total mass flux, which is primarily biogenic and not lithogenic, is not sourced directly from the sea ice, but is related to seasonal open water phytoplankton blooms. Winter-time downward fluxes are almost universally low. For example, negligible flux was recorded in traps from the Weddell Sea between July 1984 and January 1985 (Fischer et al., 1988). Measurable, but extremely low, fluxes were similarly observed during the winter-time in the Bransfield Strait (Wefer et al., 1990) and the Ross Sea (Dunbar et al., 1998; Accornero et al., 1999; Collier et al., 2000; Honjo et al., 2000; Langone et al., 2000). In general, flux does not begin to increase until ice retreat has taken place, and there can be a fairly significant time delay between ice retreat and peak flux. Fischer et al. (1988) note a 10-week delay, for example, in the northern Weddell Sea in the spring of 1985, and Dunbar et al. (1998) note that peak particle flux occurred

**Table 10.2** Selected total mass flux data from Antarctica, based on sediment trap samples. \* = average based on carbon and silicon flux data

Reference/Year	Location	Total max flux ( $\text{g m}^{-2} \text{yr}^{-1}$ )
Fischer et al., 1988	Bransfield Strait	107.7
Wefer et al., 1990	Bransfield Strait	60
Fischer et al., 1988	Weddell Sea	0.37
Honjo et al., 2000	Western Pacific sector, ~ 63°S, 170°W	80.6
Honjo et al., 2000	Western Pacific sector, ~ 66°S, 170°W	27.6
Accornero et al., 1999	Ross Sea	6.18
Collier et al., 2000	Ross Sea	17.26–87.6
Dunbar et al., 1998	Ross Sea	35*
Langone et al., 2000	Ross Sea	3.93–30.0

between 2 and 12 weeks after the ice had retreated from sites in the Ross Sea. They attributed this delay to intense wind mixing of the upper water column following ice breakout, and point out that earlier blooms can form if winds are less energetic (Dunbar et al., 1998).

Peak flux is concentrated over a very short time period, and is associated with ice-free as opposed to ice-covered conditions. For example, in the Bransfield Strait, more than 95% total of the annual flux was recorded over a 1–2 month period (Wefer et al., 1990). Abelmann & Gersonde (1991) similarly recorded biosiliceous flux as distinct pulses of 2–9 weeks duration, during the period of open water in the northern Antarctic Peninsula and Weddell Sea. In the Ross Sea, Accornero et al. (1999) measured 93% of total flux between December 1995 and March 1996, and Langone et al. (2000) measured 99% of the annual flux in only 3 months. Given that particle flux in the Antarctic is largely biogenic in origin, seasonal variability is driven by factors that control primary production, including light and nutrient availability. Regionally, total mass flux is extremely variable, with lowest values recorded in the Weddell Sea and values several times higher in all other areas studied (Table 10.2).

### *General characteristics of flux – particle chemistry*

The chemical composition of material incorporated into the ice is significant for several reasons; two of these are addressed here. First, several authors (Martin, 1990; Sedwick & DiTullio, 1997; Collier et al., 2000; Edwards, 2002) have speculated on the role of iron released from sea ice as it melts (the iron may be contained in the overlying snow cover) in driving high primary productivity along the ice-receding ice edge. Sedwick & DiTullio (1997) for example, conducted iron-enrichment

bottle-incubation experiments in the Ross Sea. The experiments were completed first under conditions of melting sea ice and later in ice-free conditions. Their results showed a significant increase in iron concentrations in the presence of melting sea ice and a subsequent increase in algal biomass. The authors suggest that the seasonal release of iron from melting sea ice may be a factor responsible for the occurrence of algal blooms in the marginal ice zone. Similarly, Collier et al. (2000) observed that opal fluxes in their Ross Sea sediment traps were associated with iron export pulses. They state, 'While uncertainties about specific processes that introduce Fe to the Ross Sea ecosystem remain, our observations suggest a connection between opal export, availability of Fe, and the presence of ice. Peak fluxes of opal and iron, as well as fractionated Fe/Al values are associated with partial ice cover.' They suggest that a possible source for the iron is via aeolian material blown onto sea ice and/or its snow cover.

At a greater distance from any continental source, Lescher et al. (1997), working in the Atlantic region of the Antarctic, did not find sea ice to be a source of iron. Extremely low lithogenic fluxes captured by sediment traps deployed in the western Pacific sector of Antarctica (Honjo et al., 2000), suggest the same, that melting sea ice does not supply iron that in turn initiates phytoplankton blooms. In fact, Honjo et al. (2000) suggest that ultimately the strong stratification that results from ice melt may eventually limit production, by preventing upward mixing of iron. The difference between these two findings, the Ross Sea versus the open ocean, may be a function of proximity to a source for wind-blown debris.

While many authors have discussed the critical importance of a relatively fresh meltwater lens in stratifying the water column adjacent to the retreating ice edge, and the role of this physical stratification in driving large phytoplankton blooms (El-Sayed, 1971; Alexander & Niebauer, 1981; Sakshaug & Holm-Hansen, 1984; Niebauer & Alexander, 1985; Smith & Nelson, 1985; Smith & Nelson, 1986; Nelson et al., 1987; Sullivan et al., 1988; Sakshaug & Skjoldal, 1989; Comiso et al., 1990; Lancelot et al., 1991a,b; Bianchi et al., 1992; Schloss & Estrada, 1994), the potential role of released micronutrients, such as iron, cannot be ignored. Clearly the question of iron concentrations in sea ice and its role in driving ice edge blooms deserves additional study. Within this context, regional differences must be considered as well, with continental shelf versus deep-sea sites perhaps quite different from one another based on differences in the sediment load of the sea ice and overlying snow.

Second, the distinctive chemistry of biogenic material released from the sea ice may be a tool that can be used to trace the extent of sea ice over time. While the reconstruction of the history of sea ice extent is addressed in Chapter 11 (Armand & Leventer), the isotopic characteristics of particulate organic carbon in the sea ice is briefly reviewed here. Several researchers have shown an enrichment in the  $^{13}\text{C}$  of particulate organic carbon from the sea ice (Fischer, 1991; Rau et al., 1991; Rogers & Dunbar, 1993; Rogers, 1995; Gibson et al., 1999; Villinski et al., 2000; Kennedy et al. 2002). The degree of enrichment varies, from  $-8\%$  measured in fast ice from McMurdo Sound, Antarctica (Rogers & Dunbar, 1993) and Prydz Bay, Antarctica

(Gibson et al., 1999), to  $-11\%$  in pack ice from the Bellingshausen, Amundsen and Ross Seas (Rogers, 1995), to  $-18\%$  in Antarctic pack ice (Fischer, 1991; Rau et al., 1991). Wada et al. (1987) suggested that this enrichment was a function of high algal growth rates and depletion of dissolved carbon dioxide in the sea ice environment, which can be restricted from rapid exchange with sea water (Kennedy et al. 2002; Thomas & Papadimitriou, Chapter 9). Contrary data are presented by Thomas et al. (2001), who did not observe a significant carbon isotopic enrichment in organic material contained in sea ice from the Weddell Sea. However, they suggest that their data, which are based on measurements of the isotopic composition of sediment trap material, much of which was derived from faecal pellets, may be biased toward organic material that originated at the outer edges of the platelet layer, where conditions are much less restricted, hence the lack of carbon isotopic enrichment. Although more work needs to be done, the potential for tracking sea ice through time as a function of carbon isotopic enrichment in sediments, remains a strong possibility (Gleitz et al. 1995; Gibson et al., 1999; Villinski et al., 2000).

### *Mechanisms of settling*

Biogenic particles released from the sea ice may settle as individual particles, via faecal pellets produced by a variety of pelagic grazers, or as millimetre-sized aggregates, termed 'marine snow'. Repackaging as either pellets or marine snow will greatly increase settling rates (Aldredge & Silver, 1988), increasing the likelihood that biogenic material will reach the sea floor. Honjo (1990) suggests that the formation of amorphous aggregates may be relatively more important in terms of increasing downward flux rates in the Arctic, while pellet production may play a more important role in the Southern Ocean, in particular, in the southern Atlantic sector where dense krill concentrations are often observed. Particles that remain suspended in the upper water column are more likely to be available to serve as a seed population or as food for pelagic grazers.

Grazing by many species of zooplankton and subsequent pellet production has been reported in a number of studies, though a specific link to grazing of material released from the ice is not always apparent. Dunbar et al. (1998) note that faecal pellets and particle aggregates account for 4–70% of mass flux during peak summer events in the Ross Sea, with most of the pellets attributed to grazers other than krill. von Bodungen (1986) observed the production of large, string-shaped krill pellets, averaging  $160\ \mu\text{m}$  in diameter and between 300 and  $1200\ \mu\text{m}$  in length, in the Bransfield Strait, and calculated that 45% of the primary productivity in late November to early December 1983 was lost via grazing. The field area was completely ice free during this time period, hence it is not clear if krill pellet production had a specific and significant impact on algae released from the ice. Similarly, Cadée (1992) discusses the significance of grazing by krill swarms in the downward flux of carbon during ice retreat in the Scotia–Weddell Sea. He suggests that while krill faecal pellets may be directly responsible for the flux of carbon to the sea floor,

some of those pellets will be degraded and/or repackaged before reaching the bottom (von Bodungen et al., 1987; Cadée et al., 1992; Gonzalez, 1992).

Scharek et al. (1994), speculate that krill grazing has a significant impact on ice algae, based on observational data of dense concentrations of krill scraping away at algae on the surface of disintegrating ice floes, during a 1986 cruise in the pack ice covered Weddell Sea. Also, Stretch et al. (1988) and Daly (1990) have observed krill, *Euphausia superba*, feeding on algal cells on the under-surface of sea ice in several areas of the Southern Ocean, including the Weddell and Scotia Seas, and waters off the Antarctic Peninsula. More direct data are reported from the Antarctic by Thomas et al. (2001) who noted that faecal pellets in traps underneath fast ice in the Weddell Sea were composed of diatoms from the platelet ice. However, these authors propose that protozoans were the major producers of the pellets rather than larger metazoan grazers. In the Arctic, many studies demonstrate the presence of ingested ice algae, based on microscopy and the presence of degraded pigments, in zooplankton faecal pellets (Conover et al., 1986; Carey, 1987; Tremblay et al., 1989; Michel et al., 1996).

Similarly, the formation of 'marine snow' has been observed by many researchers (Honjo et al., 1984; Asper & Smith, 1999). Most relevant to this review is Riebesell et al. (1991), who observed that when algae are released from the ice, they tended to form aggregates at a much higher rate than other algae; within the first 2 hours after release from melted ice, aggregates were observed. They suggest that many species of ice algae are 'inherently sticky', producing an extracellular polysaccharide mucilage that permits attachment to the ice substrate (Palmisano & Sullivan, 1985; Thomas & Papadimitriou, Chapter 9) and also increases their aggregation, even within the brine pockets of the ice (Riebesell et al., 1991). Although sinking rates were different for interior ice and infiltration ice assemblages, both groups settled at a rate of between about 200 and 600 m d<sup>-1</sup>. Aggregation rates appear to be species specific, with flagellates and the small pennate diatom, *Fragilariopsis cylindrus*, much less common in aggregates. Riebesell et al. (1991) also noted that cells that were metabolically more active and growing tended to remain unaggregated, thus were more likely to remain suspended. Ice algae that were metabolically less active aggregated to a greater degree, and were thus more likely to flux quickly to deeper waters. This variability in 'stickiness' may play an important role in determining which species of ice algae are most likely to seed a planktonic algal community following ice breakout. For example, the data from Riebesell et al. (1991) may help explain why *F. cylindrus*, a species commonly found in the sea ice and not very 'sticky', is also so successful in exploiting the marginal ice zone (Leventer, 1998).

### 10.3 Seeding of open water phytoplankton populations by sea ice algae

The question of whether open water and ice edge blooms in polar regions are 'seeded' by algae released from the melting sea ice has been addressed by many

researchers (for example, Horner, 1976; Ackley et al., 1979; Alexander, 1980; Schandelmeier & Alexander, 1981; Garrison et al., 1983; Smith & Nelson, 1986; Wilson et al., 1986; Garrison et al., 1987, 1993). Whether or not these sea ice algae function as a seed population depends on many factors, including the speed at which the particles settle through the water column, the presence of pelagic consumers and the viability of the cells once released from the sea ice.

Critically, if the sea ice algae settle rapidly (Mathot et al., 1991; Riebesell et al., 1991; Michel et al., 1997) or are quickly grazed by pelagic zooplankton and incorporated into rapidly settling pellets (Lancelot et al., 1993; Scharek et al., 1994; Michel et al., 1996), then the released algal cells never have the chance to serve as an inoculum for an open water phytoplankton bloom. Several studies document situations when seeding did not take place. Mathot et al. (1991), for example, observed the development of a flagellate community following the release of a diatom-dominated sea ice community in the Weddell Sea during the period November 1988 to January 1989 (EPOS II – European Polarstern Study). They suggested that either rapid settling and/or grazing of the diatoms may have been responsible for the shift in the assemblage of primary producers. As previously discussed, Riebesell et al. (1991), working on samples from EPOS 2, conducted experimental work that demonstrated the tendency of some species of sea ice diatoms to form aggregates, with settling rates three orders of magnitude higher than non-aggregated cells. They proposed that rapid settling of these aggregates may be responsible for the lack of seeding observed in this study.

Michel et al. (1997) noted that algae released from annual sea ice in Saroma-Ko Lagoon, in the Sea of Okhotsk, rapidly settled to the sea floor, where the organic particulates were an important source of food for benthic organisms. Given rapid transit out of the water column, no seeding was observed. In addition, a pelagic microbial food network, rather than a diatom-based food web, developed in the water column following ice melt since the sea ice diatoms quickly reached the sea floor and were eaten. It is important to point out that the authors note that water depths in this region are very shallow (average 14.5 metres) so processes occurring here may not be directly applicable to the deeper water areas that are characteristic of a large proportion of the ice-covered areas in both the Arctic and the Antarctic.

Michel et al. (1997) suggest that rapid settling and benthic consumption of sedimented ice algae, as observed in the Sea of Okhotsk, may play a similar ecological role to zooplankton grazing at the polar ice edge, in terms of community development within the water column. Specifically, Michel et al. (1997) are referring to the study by Lancelot et al. (1993), who describe the development of a nanophytoplankton bloom in the northwestern Weddell Sea, when high grazing pressure quickly removed sea ice diatoms from the upper water column. Michel et al. (1996), working in the Canadian Arctic, also note that algae may remain suspended in the upper water column, but are then eaten by grazers. The removal of released sea ice diatoms from the system by either rapid settling or grazing, and its effect on the structure of the heterotrophic community, is discussed in more detail later in this chapter.

Under conditions where algae released from the sea ice remain in suspension in the upper water column and are not eaten quickly, the possibility of seeding exists. Garrison et al. (1987) outline several criteria that must be met to make a convincing argument for the importance of seeding. First, they note that if the sea ice community serves as the seed for open water populations, then the sea ice algal and planktonic algal assemblages must be taxonomically similar to one another. Numerous studies from both the Arctic and the Antarctic, including those of Schandelmeier & Alexander (1981), Krebs (1983), Garrison & Buck (1985), Smith & Nelson (1985; 1986), Garrison et al. (1987), Garrison & Buck (1989), Wefer et al., (1990), Kang & Fryxell (1992) and Michel et al. (1993), have demonstrated that this is the case. Haecky et al. (1998) make the excellent point that the taxonomic composition of spring blooms in the Baltic Sea differ depending on whether the winter was ice free or ice covered, an observation that supports the role of seeding by sea ice algae. Garrison (1991; Tables 1 and 2) presents an extremely thorough species list of algae (and other micro-organisms) observed in all types of Antarctic sea ice. Many, though not all, of these species are also important components of the plankton, such as *Fragilariopsis curta* and *F. cylindrus* (Leventer & Dunbar, 1987; Wefer et al., 1990; Kang & Fryxell, 1992).

It is important to note that not all studies demonstrate a remarkable similarity between sea ice and water column algal assemblages, although a connection between the two ecosystems is still evident. In these cases, ice edge blooms may be more strongly influenced by the introduction of phytoplankton from other water masses. For example, Bianchi et al. (1992) note that the dominant species in an ice edge bloom in the Weddell Sea (EPOS I) were *Thalassiosira gravida* and *Chaetoceros neglectum*, neither common in the nearby sea ice. They speculate that these species may have been advected from the Bransfield Strait area. However, small *Nitzschia* were also common in the marginal ice zone; presumably these species could have been seeded from melting ice, since species like *F. cylindrus* are extremely common in annual ice. Saito & Taniguchi (1978) also note a mixed sea ice algal/pelagic diatom community in the northern Bering and Chukchi Seas during and after ice melt, reinforcing the finding that even if seeding by ice algae occurs, algae advected from other areas may be of equal or greater importance.

Second, the planktonic species must be incorporated into the sea ice as it forms in the autumn and winter (Garrison et al., 1987). Many studies have addressed the concentration of algae from the plankton into newly forming sea ice (Bunt, 1968; Bunt & Lee, 1970; Garrison et al., 1983, 1986; Ackley et al., 1987; Watanabe & Satoh, 1987; Lange et al., 1989; Garrison et al., 1989; Grossmann & Gleitz, 1993; Gleitz et al., 1994) and the viability of algal cells incorporated into the ice (Gleitz & Thomas, 1992, 1993). Garrison et al. (1989) performed laboratory experiments that demonstrate the ability of ascending ice crystals to scavenge algal cells from the water, though natural concentration exceeds what they were able to reproduce in the lab. They suggest that this may be due to several factors, including the limited temporal and spatial nature of their experiments, as well as the possibility of other

processes, such as Langmuir circulation, that could act in concert to increase the concentration of algal cells in aggregates of frazil ice. In addition, observations as those made by Gleitz & Thomas (1993), that the concentration of algae in newly formed ice can be 1.5 to 2.5 times greater than their concentration in open water, support the hypothesis that plankton are incorporated into newly forming sea ice.

Smetacek et al. (1992) present another scenario for incorporation of diatoms into sea ice and later seeding of an open water population. They describe a centric algal assemblage, dominated by *Thalassiosira antarctica*, in the Weddell Sea, that was associated with thick platelet ice. They proposed that the ice platelets along with the summer algal bloom cells were incorporated into the seasonal ice cover, and subsequently transported west with the Weddell Sea Gyre. A spring bloom of *T. antarctica* observed in the western Antarctic Peninsula the following spring (von Bodungen, 1986) may have resulted as this advected ice released its incorporated algae to the water column.

Third, the timing of the release of algae in the spring should closely precede the development of the open water bloom (Garrison et al., 1987). As described earlier in this chapter, phytoplankton blooms commonly are associated with the retreating sea ice edge where stable surface layers persist (El-Sayed, 1971; Alexander & Niebauer, 1981; Sakshaug and Holm-Hansen, 1984; Niebauer & Alexander, 1985; Smith & Nelson, 1985, 1986; Nelson et al., 1987; Sullivan et al., 1988; Sakshaug & Skjoldal, 1989; Comiso et al., 1990; Lancelot et al., 1991a,b; Bianchi et al., 1992; Schloss & Estrada, 1994), thus providing a temporal link between the two systems.

Finally, cells released from the ice must be able to survive and grow in open water (Garrison et al., 1987). As stated previously, not all diatom species common in the sea ice are well adapted to life in open water. This topic has been reviewed by Leventer (1998) and is summarized briefly here. Several of the larger diatom species common in congelation ice (a primary component of fast ice), such as *Entomoneis kjellmanii* and *Pleurosigma* sp., for example, do not compete successfully in the ice edge zone, so despite their abundance in sea ice, they do not end up contributing to the phytoplankton community. Several factors may contribute to the inability of some species to survive in an open water setting. First, many of the larger pennate forms found in congelation ice are 'benthic' and may need to remain within or attached to a substrate to survive. Those species with a raphe, such as *Pleurosigma* sp., *Pinnularia quadratarea* and *Navicula glaciei*, may have a competitive advantage within the sea ice, where they are able to move and maintain their position within a favourable environment. This advantage would be lost in the open water environment. Second, many species of ice algae are physiologically 'shade-adapted' (Grossi, 1985; Palmisano & Sullivan, 1985; Grossi et al., 1987; Rivkin & Putt, 1987; Arrigo, Chapter 5), so they may not fare well under the high irradiances of the marginal ice zone. Finally, as Riebesell et al. (1991) have shown, many species of ice algae have a tendency to form sticky aggregates and sink rapidly, taking them quickly out of the photic zone. These factors may help explain why the taxonomic composition of fast ice communities (mostly congelation ice) differs from that characteristic of the

water column, as observed by several studies (Bunt & Wood, 1963; Krebs, 1983; Palmisano & Sullivan, 1983).

Two species in particular, *Fragilariopsis curta* and *F. cylindrus*, are extremely common in both the sea ice and ice edge communities (Garrison & Buck, 1985; Smith & Nelson, 1985; Fryxell, 1986; Fryxell et al., 1987; Garrison et al., 1987; Leventer & Dunbar, 1987; Fryxell et al., 1988, 1989; Garrison & Buck, 1989; Kang & Fryxell, 1991, 1992; Bianchi et al., 1992). Leventer (1998) suggests that these species may succeed not only in the sea ice but also can dominate ice edge blooms, because of their high growth rate and low sinking rate. For example, in Sommer's (1989) work, *F. cylindrus* has the highest growth rate of those species studied. Both species are relatively small (*F. cylindrus* is typically  $< 10 \mu\text{m}$  in length, while *F. curta* is slightly longer, averaging  $28 \mu\text{m}$  in a Ross Sea ice edge bloom – Wilson et al., 1986) and often occur on only short chains (*F. cylindrus* most commonly as doublets – Kang & Fryxell, 1992; *F. curta* from a 1990 ice edge bloom in the Ross Sea, also most commonly as doublets). Consequently, their settling rates are likely to be low (Smayda, 1970). Their size advantage, coupled to *F. cylindrus*'s tendency not to form aggregates (Riebesell et al., 1991), may give these species a competitive advantage in exploiting the stable upper water column associated with melting sea ice.

Experimental work by Kuosa et al. (1992) documents the process of seeding. In their study, the authors added crushed sea ice to seawater aquaria, to evaluate potential seeding of open water by sea ice microbes. Addition of sea ice with high chlorophyll concentrations resulted in rapid growth of algae in the aquaria, though growth was not immediate (average 6 days later). The genus *Nitzschia* dominated the phytoplankton, in particular, the small *Nitzschia* species. *Fragilariopsis cylindrus*, known to be an important component of sea ice and ice edge blooms, was the dominant contributor to the assemblage in the aquaria, while larger forms of *Nitzschia* failed to flourish.

It is important to note that not all studies demonstrate the viability of sea ice algae, including small forms of *Nitzschia*, when released from the sea ice. For example, McMinn's (1996) work in Ellis Fjord showed a negligible contribution of seeding, most likely because a high percentage (often  $> 80\%$ ) of the *F. cylindrus* cells released from the sea ice were dead. In conclusion, although most data support the hypothesis that algal cells released from the sea ice can serve as a seed population for the ice edge community, not all species are equally adept at life in both ecosystems, nor do all cells have an equal opportunity to act as an inoculum.

## 10.4 Food for the pelagic community

In Chapter 7, Schnack-Schiel reviews the macrobiology of sea ice. This section builds upon that introduction and focuses on flux of organic carbon from the sea ice, in the form of algal material, as an important source of food for the pelagic grazing

community. It is important to note that the availability of this food source is not limited to the time of ice break-up in the spring, but is also important prior to ice break-up. Data from both the Arctic and the Antarctic suggest that grazing of sea ice algae is an important component of the overwintering strategies of marine zooplankton, such as amphipods, copepods and euphausiids (Marschall, 1988). For example, Stretch et al. (1988) and Daly (1990) have observed krill, *Euphausia superba*, feeding on algal cells on the under-surface of sea ice in several areas of the Southern Ocean, including the Weddell and Scotia Seas, and waters off the Antarctic Peninsula.

Bradstreet & Cross (1982) observed sea ice algae (mostly pennate diatoms from the genera *Nitzschia* and *Navicula*) in the gut contents of several species of both amphipods and copepods recovered from under fast ice off Baffin Island, prior to ice melt. The importance of this observation is that under-ice grazing may be a significant source of nutrition to zooplankton over the winter (see also Bedo et al., 1990; Conover & Huntley, 1991). Conover et al. (1986) presented data concerning the Arctic copepod, *Pseudocalanus* sp., and noted opportunistic feeding occurs near the ice-water interface, based on the high phaeophorbide concentration in fecal pellets. They are unsure if the copepods are grazing directly on the algae at the bottom of the ice or from material close to the ice-water interface fluxing out of the ice.

Runge et al. (1991) noted a strong link between the timing and magnitude of the ice algal bloom and copepod life cycles. In their southeastern Hudson Bay study, copepod feeding occurred both at the ice-water interface and later continued (and increased) at the time of ice melt, when large quantities of sea ice algae were released into the ocean. They confirmed grazing on sea ice algae by the concentration of phaeopigments in their guts, which increased following night-time migration upward to the ice-water interface. Runge & Ingram (1988, 1991) also observed fragmented ice diatoms in copepod guts and noted that increased egg production of dominant copepod species occurred following ice melt. In addition, Runge & Ingram (1988), observed a ten-fold increase in the concentration of phaeopigments in copepod digestive tracts once the interfacial bloom began.

Once sea ice algae are released from the ice, their value as a food source is at least partially dependent on whether the algae are maintained in the upper water column or sink rapidly to deeper waters and the sea floor. Tremblay et al. (1989), working in the south-eastern Hudson Bay in the Canadian Arctic, observed the retention of sea ice algae in suspension following its flux out of melting sea ice, with generally <2% lost directly to the benthos during the period of their study. Moderate levels of grazing were also noted, based on the flux of phaeopigments and the occurrence of faecal pellets. Michel et al. (1996), also assessing the role of ice algal production as a carbon source for zooplankton in the Canadian Arctic, had similar findings. The sea ice communities were monitored via ice cores, Niskin bottles and sediment traps. They conclude first, that zooplankton actively graze on ice algae prior to their release into the water column, based on the high proportion of phaeopigments in

both suspended and sinking material at a time prior to the presence of algal cells in the water. Second, they conclude that a large proportion (> 65%) of algal material released from the sea ice remains in suspension long enough to serve as a food source for grazers, despite the fact that senescent cells generally sink out of suspension more rapidly than live ones (Smayda, 1970). They speculate on both biological and physical mechanisms that may be responsible for the continued suspension of algal material, including the physiological state of the cells and the presence of a strong pycnocline. Regardless of the mechanism, Michel et al. (1996) demonstrate that the continued suspension of carbon released from the sea ice supplies food for zooplankton. Subsequent faecal pellet production by these herbivores is the primary means through which the algal material eventually is exported to the sea floor (Michel et al., 1996).

In the Antarctic, the life history of the krill, *Euphausia superba*, is clearly tied to the marginal ice zone (Daly & Macaulay, 1991; Schnack-Schiel, Chapter 7). In addition to an overwintering strategy linked to feeding off ice algae scraped from the underside of annual ice (Stretch et al., 1988; Daly, 1990), numerous studies document krill grazing on ice algae at the ice edge (Stretch et al., 1988; Hamner et al., 1989; Daly, 1990; Siegel et al., 1990; Daly & Macaulay, 1991). Although less data are available on other pelagic grazers in the Southern Ocean, several species of copepods appear to have life cycles that are also tied to the sea ice (Conover & Huntley, 1991; Schnack-Schiel, Chapter 7).

## 10.5 Community structure in the marginal ice zone as related to sea ice flux

The role of sedimenting ice algae in structuring the community in the marginal ice zone has been discussed indirectly in previous sections. This larger scale picture connecting the pieces of the ecosystem together is the most critical for continued and future study over the next decade. The links between the downward flux of sea ice algae and the open water ecosystem can be divided broadly into three major categories. First, whether the overall composition of the assemblage at the ice edge is diatom based or microbially based is at least partly a function of the fate of the sea ice algae. Lancelot et al. (1993) propose two scenarios that may partially explain whether diatoms or nanoflagellates dominate the ice edge community. In the Weddell Sea, where large populations of krill overwinter, grazing of sea ice diatoms over the winter by krill might result in limiting the amount of seeding that takes place as the ice retreats; consequently nanoflagellates may dominate the ice edge bloom, resulting in a microbial food web, with correspondingly low phytoplankton concentrations. Where overwintering krill are more sparse, as in the Ross Sea, seeding of the ice edge bloom by algae released from the sea ice may be more common, resulting in high concentrations of phytoplankton, either diatoms or perhaps *Phaeocystis*, that may eventually be grazed by copepods (Lancelot et al., 1993).

Grazing by pelagic zooplankton as the ice retreats is at least as important in limiting the degree of seeding by ice algae. As discussed earlier, if algae released from the ice settle quickly to the sea floor, either as aggregates or in faecal pellets, their role in seeding an open water community may be minimized. For example, during EPOS II, in the north-western Weddell Sea, while the ice assemblages were heterogeneous but dominated by diatoms, the water column was dominated by autotrophic flagellates, always <15% diatoms (Mathot et al., 1991). Although seeding by sea ice diatoms may have occurred, the taxonomic differences between the sea ice and ice edge communities does suggest the possibility that grazing and/or rapid settling removed the diatoms from the upper water column, possibly a case of size selection at work, since krill appear to feed more effectively on larger particles (Meyer and El-Sayed, 1983; Segawa et al., 1983; Boyd et al., 1984). Although the relative importance of grazing, at any time of year, by krill, copepods or microprotozoans (Burkill et al., 1995), pellet formation and the formation of rapidly settling aggregates, in the establishment of an ice edge community dominated by either diatoms or nanoflagellates remains to be determined, it is likely that all contribute to the composition of the community found in the marginal ice zone.

As discussed earlier, flux of organic material from the sea ice, both during the winter and as the ice retreats, provides food for pelagic grazers and has been shown to be an important source of carbon, even during the long periods of darkness when photosynthesis is at a minimum. Runge et al. (1991) explore this link in more detail by presenting a strong case for the critical significance of ice algal production in helping define both zooplankton life cycle strategies and larval fish recruitment in Hudson Bay. For example, under-ice grazing by the copepods *Calanus* sp. and *Pseudocalanus* sp. appears to be related to the timing and magnitude of copepod egg production, and to the growth and development of copepodite stages. In turn, the appearance of fish larvae as the ice breaks out appears to be timed to be coincident with the life cycle of the copepods.

Finally, in the most general sense, the role of flux from the sea ice, and the consequent ice edge bloom that may result, must be considered in terms of the upper portion of the polar ecosystem, a topic that has been addressed by many researchers (Ainley & Jacobs, 1981; Fraser & Ainley, 1986; Sakshaug & Skjoldal, 1989). While this paper has focused on the downward flux of particles from the sea ice, and the role that flux plays in lower levels of the food web, clearly, the processes described have a tremendous impact on higher trophic levels, including seabirds, penguins, seals and whales.

## 10.6 Conclusions

'Particle transport ... controls the transfer of carbon from surface to deep waters, nutrient regeneration, delivery of food to benthic communities, and preservation of sediment records of climate change' (Dunbar et al., 1998). In both the Arctic and the

Antarctic, where seasonal ice cover is an integral component of the ecosystem, particle flux from the sea ice clearly plays an important role. Not only does downward transport of material impact oceanic carbon and silica cycles, flux of materials plays a key role in structuring and shaping the polar ecosystem. As described in this chapter, algae released from the ice can provide a seed community for ice edge and open water blooms, and is a source of food for pelagic grazers. The fate of sedimenting particles also influences community structure of the food web and whether it is diatom or microbially based.

Given the critical role of sediment flux as the connection between different layers of the ocean, particle flux studies in seasonally ice-covered waters are a key ingredient to advancing our understanding of polar oceanic processes. These studies should continue their focus in two directions. First, in order to evaluate the direct impact of particles released from the sea ice on the underlying biological community, there should be an emphasis on more sediment trap studies that sample both the ice and the water column through the period of ice retreat.

Since all ecosystems experience a great deal of interannual variability, continued long-term monitoring of particle flux via moored instruments is necessary. As illustrated in Table 10.1, most studies are just a few years in length, though in selected areas nearly decadal data sets exist. These longer records, with specific reference to the relationship between sea ice and particle flux, will be instrumental in providing the type of information necessary to understand the implications of global change on the polar ecosystem.

## References

- Abelmann, A. & Gersonde, R. (1991) Biosiliceous particle flux in the Southern Ocean. *Marine Chemistry*, **35**, 503–536.
- Accornero, A., Bergamasco, A., Monaco, A. & Tucci, S. (1999) Particle fluxes at the edge of the Ross Ice Shelf: the role of physical forcing. In: *Oceanography of the Ross Sea, Antarctica*, (Eds G. Spezie & G.M.R. Guisepe), pp. 177–195. Springer, Italy.
- Ackley, S.F., Buck, K.R. & Taguchi, S. (1979) Standing crop of algae in the sea ice of the Weddell Sea region. *Deep-Sea Research*, **26**, 269–281.
- Ackley, S.F., Dieckmann, G. & Shen, H. (1987) Algal and foram incorporation into new sea ice. *EOS, Transactions of the American Geophysical Union*, **68**, 1736.
- Ainley, D.G. & Jacobs, S.S. (1981) Sea-bird affinities for ocean and ice boundaries in the Antarctic. *Deep-Sea Research*, **28**, 1173–1185.
- Alexander, V. (1980) Interrelationships between the seasonal sea ice and biological regimes. *Cold Regions Science and Technology Reports*, **2**, 157–178.
- Alexander, V. & Niebauer, H.J. (1981) Oceanography of the Bering Sea ice-edge zone in spring. *Limnology and Oceanography*, **26**, 1111–1125.
- Allredge, A.L. & Silver, M.W. (1988) Characteristics, dynamics, and significance of marine snow. *Progress in Oceanography*, **20**, 41–82.
- Asper, V.L. & Smith, W.O., Jr. (1999) Particle fluxes during austral spring and summer in the southern Ross Sea, Antarctica. *Journal of Geophysical Research*, **104**, 5345–5359.

- Barrett, P.J., Pyne, A.R. & Ward, B.L. (1983) Modern sedimentation in McMurdo Sound, Antarctica. In: *Antarctic Earth Sciences*, (Eds R.L. Oliver, P.R. James & J.B. Jago), pp. 550–554. Australian Academy of Science, Canberra, Australia.
- Bathmann, U.V., Peinert, R., Noji, T.T. & von Bodungen, B. (1990) Pelagic origin and fate of sedimenting particles in the Norwegian Sea. *Progress in Oceanography*, **24**, 117–125.
- Bedo, A.W., Head, E.J.H., Conover, R.J., Horne, E.P.W. & Harris, L.R. (1990) Physiological adaptation of an under-ice population of *Pseudocalanus* in Barrow strait (NWT) to increasing food supply in the spring. *Polar Biology*, **10**, 561–570.
- Berner, H. & Wefer, G. (1990) Physiographic and biologic factors controlling surface sediment distribution in the Fram Strait, In: *Proceedings of the 1988 NATO Advanced Research Workshop on Geological History of the Polar Oceans; Arctic versus Antarctic NATO ASI Series. Series C: Mathematical and Physical Sciences*, **308**, 317–335.
- Berner, H. & Wefer, G. (1994) Clay-mineral flux in the Fram Strait and Norwegian Sea. *Marine Geology*, **116**, 327–345.
- Bianchi, F., Boldrin, A., Cioce, F., Dieckmann, G., Kuosa, H., Larsson, A.-M., Nöthig, E.-M., Sehlstedt, P.-I., Socal, G. & Syvertsen, E.E. (1992) Phytoplankton distribution in relation to sea ice, hydrography and nutrients in the northwestern Weddell Sea in early spring 1988 during EPOS. *Polar Biology*, **12**, 225–235.
- von Bodungen, B. (1986) Phytoplankton growth and krill grazing during spring in the Bransfield Strait, Antarctica – implications from sediment trap collections. *Polar Biology*, **6**, 153–160.
- von Bodungen, B., Fischer, G., Nöthig, E.M. & Wefer, G. (1987) Sedimentation of krill faeces during spring development of phytoplankton in Bransfield Strait, Antarctica. *Mitteilungen des Geologisch-Paläontologischen Instituts der Universität Hamburg (Sonderband)*, **62**, 243–257.
- Boyd, C.M., Heyraud, M. & Boyd, C.N. (1984) Feeding of the Antarctic krill *Euphausia superba*. *Journal of Crustacean Biology*, **4**, 123–141.
- Boyd, P.W., Robinson, C., Savidge, G. & Williams, P.J.leB. (1995) Water column and sea-ice primary production during Austral spring in the Bellingshausen Sea. *Deep-Sea Research*, **42**, 1177–1200.
- Bradstreet, M.S.W. & Cross, W.E. (1982) Trophic relationships at high Arctic ice edges. *Arctic*, **35**, 1–12.
- Bunt, J.S. (1968) Microalgae of the Antarctic pack ice zone. In: *Symposium on Antarctic Oceanography*, (Ed. R.I. Currie), pp. 198–218. W. Heffer & Sons, Cambridge.
- Bunt, J.S. & Lee, C.C. (1970) Seasonal primary production in Antarctic sea ice at McMurdo Sound in 1967. *Journal of Marine Research*, **28**, 304–320.
- Bunt, J.S. & Wood, E.J.F. (1963) Microalgae and Antarctic sea-ice. *Nature*, **199**, 1254–1255.
- Burkill, P.H., Edwards, E.S. & Sleigh, M.A. (1995) Microzooplankton and their role in controlling phytoplankton growth in the marginal ice zone of the Bellingshausen Sea. *Deep-Sea Research*, **45**, 1277–1290.
- Cadée, G.C. (1992) Organic carbon in the upper layer and its sedimentation during the ice-retreat period in the Scotia-Weddell Sea, 1988. *Polar Biology*, **12**, 253–259.
- Cadée, G.C., Gonzalez, H. & Schnack-Schiel, S. (1992) Diet affects sinking rate of krill faecal strings. *Polar Biology*, **12**, 75–80.
- Carey, A.G., Jr (1987) Particle flux beneath fast ice in the shallow southwestern Beaufort Sea, Arctic Ocean. *Marine Ecology Progress Series*, **40**, 247–257.

- Collier, R., Dymond, J., Honjo, S., Mangonini, S., Francois, R. & Dunbar, R. (2000) The vertical flux of biogenic lithogenic material in the Ross Sea: moored sediment trap observations 1996–1998. *Deep-Sea Research*, **47**, 3491–3520.
- Comiso, J.C., McClain, C.R., Sulllivan, C.W., Ryan, J.P. & Leonard, C.L. (1993) Coastal zone color scanner pigment concentrations in the Southern Ocean and relationships to geophysical surface features. *Journal of Geophysical Research*, **98**, 2419–2451.
- Comiso, J.C., Maynard, N.G., Smith, W.O., Jr & Sulllivan, C.W. (1990) Satellite ocean color studies of Antarctic ice edges in summer/autumn. *Journal of Geophysical Research*, **95**, 9481–9496.
- Conover, R.J., Herman, A.W., Prinsenberg, S.J. & Harris, L.R. (1986) Distribution and feeding by the copepod *Pseudocalanus* under fast ice during the Arctic spring. *Science*, **232**, 1245–1247.
- Conover, R.J. & Huntley, M. (1991) Copepods in ice-covered seas – distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. *Journal of Marine Systems*, **2**, 1–41.
- Daly, K.L. (1990) Overwintering development, growth and feeding of larval *Euphausia superba* in the Antarctic marginal ice zone. *Limnology and Oceanography*, **35**, 1564–1576.
- Daly, K.L. & Macaulay, M.C. (1991) Influence of physical and biological mesoscale dynamics on the seasonal distribution and behavior of *Euphausia superba* in the Antarctic marginal ice zone. *Marine Ecology Progress Series*, **79**, 37–66.
- DeMaster, D.J., Dunbar, R.B., Gordon, L.I., Leventer, A.R., Morrison, J.M., Nelson, D.M., Nittrouer, C.A. & Smith, W.O., Jr (1992) Cycling and accumulation of biogenic silica and organic matter in high-latitude environments: the Ross Sea. *Oceanography*, **5**, 146–153.
- Dunbar, R.B. (1984) Sediment trap experiments on the Antarctic continental margin. *Antarctic Journal of the United States*, **19**, 70–71.
- Dunbar, R.B. & Leventer, A. (1987) Sediment fluxes beneath fast ice: October, 1986 through February, 1987. *Antarctic Journal of the United States*, **22**, 112–114.
- Dunbar, R.B., Leventer, A.R. & Mucciaroni, D.A. (1998) Biogenic sediment fluxes in the Ross Sea, Antarctica: atmospheric and sea ice forcing. *Journal of Geophysical Research*, **103**, 30741–30760.
- Dunbar, R.B., Leventer, A.R. & Stockton, W.L. (1987) Biogenic sedimentation in McMurdo Sound, Antarctica. *Marine Geology*, **85**, 155–179.
- Edwards, R. (2002) The iron content of seasonal sea-ice: a biologically-significant source of iron to the Southern Ocean? Abstract from 2002 *Ocean Sciences Meeting, Honolulu, Hawaii, 11–15 February 2002*. American Geophysical Union, Washington, D.C.
- Eicken, H., Reimnitz, E., Alexandrov, V., Martin, T., Kasser, H. & Vichoff, T. (1997) Sea-ice processes in the Laptev Sea and their importance for sediment export. *Continental Shelf Research*, **17**, 205–233.
- El-Sayed, S. (1971) Observations on phytoplankton bloom in the Weddell Sea. In: *Biology of the Antarctic Seas*, Vol. IV, (Eds G.A. Llano & J.E. Wallen), American Geophysical Union, Washington, D.C. *Antarctic Research Series*, **17**, 310–312.
- Fischer, G. (1991) Stable carbon isotope ratios of plankton carbon and sinking organic matter from the Atlantic sector of the Southern Ocean. *Marine Chemistry*, **35**, 581–596.
- Fischer, G., Futterer, D., Gersonde, R., Honjo, S., Ostermann, D. & Wefer, G. (1988) Seasonal variability of particle flux in the Weddell Sea and its relation to sea ice cover. *Nature*, **335**, 426–428.

- Fraser, W.R. & Ainley, D.G. (1986) Ice edges and seabird occurrence in Antarctica. *BioScience*, **36**, 258–263.
- Fryxell, G.A. (1986) Microalgae at the ice edge in the northern Weddell Sea. *Antarctic Journal of the United States*, **21**, 166–168.
- Fryxell, G.A., Kang, S.-H. & Ashworth, T.K. (1989) AMERIEZ 1988 and ODP Leg 119: Antarctic summer and winter stage indicators. *Antarctic Journal of the United States*, **24**, 156–157.
- Fryxell, G.A., Kang, S.-H. & Reap, M.E. (1987) AMERIZ 1986: Phytoplankton at the Weddell Sea ice edge. *Antarctic Journal of the United States*, **22**, 173–175.
- Fryxell, G.A., Reap, M.E. & Kang, S.-H. (1988) Antarctic phytoplankton dominants, life stages, and indicators. *Antarctic Journal of the United States*, **23**, 129–131.
- Garrison, D.L. (1991) Antarctic sea ice biota. *American Zoologist*, **31**, 17–33.
- Garrison, D.L., Ackley, S.F. & Buck, K.R. (1983) A physical mechanism for establishing algal populations in frazil ice. *Nature*, **306**, 363–365.
- Garrison, D.L. & Buck, K.R. (1985) Sea-ice algal communities in the Weddell Sea: species composition in ice and plankton assemblages. In: *Marine Biology of Polar Regions and Effects of Stress on Marine Organisms*. (Eds J.S. Gray & M.E. Christiansen), pp. 103–122. John Wiley and Sons, New York.
- Garrison, D.L. & Buck, K.R. (1989) The biota of Antarctic pack ice in the Weddell Sea and Antarctic Peninsula regions. *Polar Biology*, **10**, 211–219.
- Garrison, D.L., Buck, K.R. & Fryxell, G.A. (1987) Algal assemblages in Antarctic pack ice and in ice-edge plankton. *Journal of Phycology*, **23**, 564–572.
- Garrison, D.L., Buck, K.R. & Gowing, M.M. (1993) Winter plankton assemblage in the ice edge zone of the Weddell and Scotia Seas: composition, biomass and spatial distributions. *Deep-Sea Research*, **40**, 311–338.
- Garrison, D.L., Close, A.R., & Reimnitz, E. (1989) Algae concentrated by frazil ice: evidence from laboratory experiments and field measurements. *Antarctic Science*, **1**, 313–316.
- Garrison, D.L., Sullivan, C.W. & Ackley, S.F. (1986) Sea ice microbial communities in Antarctica. *BioScience*, **36**, 243–250.
- Gersonde, R. (1986) Biogenic siliceous particle flux in Antarctic waters and its palaeoecological significance. *South African Journal of Science*, **82**, 500–501.
- Gersonde, R. & Wefer, G. (1987) Sedimentation of biogenic siliceous particles in Antarctic waters from the Atlantic sector. *Marine Micropaleontology*, **11**, 311–332.
- Gibson, J.A.E., Trull, T., Nichols, P.D., Summons, R.E. & McMin, A. (1999) Sedimentation of  $^{13}\text{C}$ -rich organic matter from Antarctic sea-ice algae; a potential indicator of past sea-ice extent. *Geology*, **27**(4), 331–334.
- Gleitz, M., Bathmann, U.V. & Lochte, K. (1994) Build-up and decline of summer phytoplankton biomass in the eastern Weddell Sea, Antarctica. *Polar Biology*, **14**, 413–422.
- Gleitz, M., Rutgers van der Loeff, M., Thomas, D.N., Dieckmann, G.S. & Millero, F.J. (1995) Comparison of summer and winter inorganic carbon, oxygen and nutrient concentrations in Antarctic sea ice brine. *Marine Chemistry*, **51**, 81–91.
- Gleitz, M. & Thomas, D.N. (1992) Physiological responses of a small Antarctic diatom (*Chaetoceros* sp.) to simulated environmental constraints associated with sea-ice formation. *Marine Ecology Progress Series*, **88**, 271–278.
- Gleitz, M. & Thomas, D.N. (1993) Variation in phytoplankton standing stock, chemical

- composition and physiology during sea-ice formation in the southeastern Weddell Sea, Antarctica. *Journal of Experimental Marine Biology and Ecology*, **173**, 211–230.
- Gonzalez, H.E. (1992) Distribution and abundance of minipellets around the Antarctic peninsula. Implications for protistan feeding behaviour. *Marine Ecology Progress Series*, **90**, 223–236.
- Grossi, S.M. (1985) *Response of a Sea-Ice Microalgal Community to a Gradient in Under-Ice Irradiance*. PhD dissertation, University of Southern California, Los Angeles.
- Grossi, S.M., Kottmeier, S.T., Moe, R.L., Taylor, G.T. & Sullivan, C.W. (1987) Sea ice microbial communities. VI. Growth and primary production in bottom ice under graded snow cover. *Marine Ecology Progress Series*, **35**, 153–164.
- Grossmann, S. & Gleitz, M. (1993) Microbial responses to experimental sea-ice formation: implications for the establishment of Antarctic sea-ice communities. *Journal of Experimental Marine Biology and Ecology*, **173**, 273–289.
- Haecky, P., Jonsson, S. & Andersson, A. (1998) Influence of sea ice on the composition of the spring phytoplankton bloom in the northern Baltic Sea. *Polar Biology*, **20**, 1–8.
- Hamner, W.M., Hamner, P.P., Obst, B.S. & Carleton, J.H. (1989) Field observations on the ontogeny of schooling *Euphausia superba* furcilliae and its relationship to ice in Antarctic waters. *Limnology and Oceanography*, **34**, 451–456.
- Hebbeln, D. (2000) Flux of ice-rafted detritus from sea-ice in the Fram Strait. *Deep-Sea Research*, **47**, 1773–1790.
- Hebbeln, D. & Wefer, G. (1991) Effects of ice coverage and ice-rafted material on sedimentation in the Fram Strait. *Nature*, **350**, 409–411.
- Honjo, S. (1990) Particle fluxes and modern sedimentation in the polar oceans. In: *Polar Oceanography, Part B, Chemistry, Biology, and Geology*, (Ed. W.O. Smith, Jr), pp. 687–739. Academic Press, San Diego, California.
- Honjo, S., Doherty, K.W., Agrawal, Y.C. & Asper, V.L. (1984) Direct optical assessment of large amorphous aggregates (marine snow) in the deep ocean. *Deep-Sea Research*, **31**, 67–76.
- Honjo, S. Francois, R., Manginini, S., Dymond, J. & Collier, R. (2000) Particle fluxes to the interior of the Southern Ocean in the western Pacific sector along 170°W. *Deep-Sea Research*, **47**, 3521–3548.
- Horner, R. (1976) Sea ice organisms. *Oceanography Marine Biology, An Annual Review*, **14**, 167–182.
- Johnson, G.L., Vanney, J.R. & Hayes, D. (1982) The Antarctic continental shelf – a review paper. In: *Antarctic Geoscience*, (Ed. C. Craddock), pp. 995–1002. University Wisconsin Press, Madison, Wisconsin.
- Kang, S.-H. & Fryxell, G.A. (1991) Most abundant diatom species in water column assemblages from ice ODP Leg 119 drill sites in Prydz Bay, Antarctica: distributional patterns. In: *Proceedings of the Ocean Drilling Program Scientific Reports*, (Eds J. Barron & B. Larsen), pp. 645–666. ODP, College Station, Texas.
- Kang, S.-H. & Fryxell, G.A. (1992) *Fragilariopsis cylindrus* (Grunow) Krieger: the most abundant diatom in water column assemblages of Antarctic marginal ice edge zones. *Polar Biology*, **12**, 609–627.
- Karl, D.M., Tilbrook, B.D. & Tien, G. (1991) Seasonal coupling of organic matter production and particle flux in the western Bransfield Strait, Antarctica. *Deep-Sea Research*, **38**, 1097–1126.

- Kennedy, H., Thomas, D.N., Kattner, G., Haas, C. & Dieckmann, G.S. (2002) Particulate organic carbon in Antarctic summer sea ice: concentration and stable carbon isotopic composition. *Marine Ecology Progress Series*, **238**, 1–13.
- Kohly, A. (1998) Diatom flux and species composition in the Greenland Sea and the Norwegian Sea in 1991–1992. *Marine Geology*, **145**, 293–312.
- Krebs, W.N. (1983) Ecology of neritic marine diatoms, Arthur Harbor, Antarctica. *Micro-paleontology*, **29**, 267–297.
- Kuosa, H., Norrman, B., Kivi, K. & Brandini, F. (1992) Effects of Antarctic sea ice biota on seeding as studied in aquarium experiments. *Polar Biology*, **12**, 333–339.
- Lancelot, C., Billen, G., Veth, C., Mathot, S. & Becquevort, S. (1991a) Modelling carbon cycling through phytoplankton and microbes in the Scotia–Weddell Sea area during sea ice retreat. *Marine Chemistry*, **35**, 305–324.
- Lancelot, C., Mathot, S., Veth, C. & de Baar, H.W.J. (1993) Factors controlling phytoplankton ice-edge blooms in the marginal ice-zone of the north western Weddell Sea during sea ice retreat 1988: field observations and mathematical modeling. *Polar Biology*, **13**, 377–387.
- Lancelot, C., Veth, C. & Mathot, S. (1991b) Modelling ice-edge phytoplankton bloom in the Scotia–Weddell Sea sector of the Southern Ocean during spring 1988. *Journal of Marine Systems*, **2**, 333–346.
- Lange, M.A., Ackley, S.F., Wadhams, P., Dieckmann, G.S. & Eicken, H. (1989) Development of sea ice in the Weddell Sea. *Annals of Glaciology*, **12**, 92–96.
- Langone, L., Frignani, M., Ravaoli, M. & Bianchi, C. (2000) Particle fluxes and biogeochemical processes in an area influenced by seasonal retreat of the ice margin (North-western Ross Sea, Antarctica). *Journal of Marine Systems*, **27**, 221–234.
- Legendre, L., Ackley, S.F., Dieckmann, G.S., Gulliksen, B., Horner, R., Hoshiai, T., Melnikov, I.A., Reeber, W.S., Spindler, M. & Sullivan, C.W. (1992) Ecology of sea ice biota: 2. Global significance. *Polar Biology*, **12**, 429–444.
- Lescher, B.M., de Barr, H.J.W., de Jung, J.T.M., Veth, C. & Dehairs, F. (1997) The distribution of Fe in the Antarctic Circumpolar Current. *Deep-Sea Research*, **44**, 143–187.
- Leventer, A. (1991) Sediment trap diatom assemblages from the northern Antarctic Peninsula region. *Deep-Sea Research*, **38**, 1127–1143.
- Leventer, A. (1998) The fate of Antarctic 'sea ice diatoms' and their use as paleoenvironmental indicators. In: *Antarctic Sea Ice: Biological Processes, Interactions and Variability*, (Eds M.P. Lizotte & K.R. Arrigo), American Geophysical Union, Washington, D.C. *Antarctic Research Series*, **73**, 121–137.
- Leventer, A. & Dunbar, R.B. (1987) Diatom flux in McMurdo Sound, Antarctica. *Marine Micropaleontology*, **12**, 49–64.
- Leventer, A. & Dunbar, R.B. (1996) Factors influencing the distribution of diatoms and other algae in the Ross Sea. *Journal of Geophysical Research*, **101**, 18489–18500.
- Leventer, A., Dunbar, R.B., Allen, M.R. & Wayper, R.Y. (1987) Ice thickness in McMurdo Sound, Antarctica. *Antarctic Journal of the United States*, **22**, 94–96.
- McMinn, A. (1996) Preliminary investigation on the contribution of fast-ice algae to the spring phytoplankton bloom in Ellis Fjord, eastern Antarctica. *Polar Biology*, **16**, 301–307.
- MacPherson, A.J. (1987) *The MacKay Glacier/Granite Harbor system (Ross Dependency, Antarctica) – a study in nearshore glacial marine sedimentation*. PhD Dissertation, Victoria University, New Zealand.

- McRoy, P.C., Goering, J.J. & Shiles, W.E. (1972) Studies of primary production in the eastern Bering Sea. In: *Biological Oceanography of the Northern North Pacific Ocean*, (Ed. A.Y. Takenouti), pp. 199–216. Idemitsu Shoten, Tokyo, Japan.
- Marschall, H.P. (1988) The overwintering strategy of Antarctic krill under the pack ice of the Weddell Sea. *Polar Biology*, **9**, 129–135.
- Martin, J.H. (1990) Glacial-interglacial CO<sub>2</sub> change: the iron hypothesis. *Paleoceanography*, **5**, 1–13.
- Mathot, S., Becquevort, S. & Lancelot, C. (1991) Microbial communities from the sea ice and adjacent water column at the time of ice melting in the northwestern part of the Weddell Sea. In: *Proceedings of the Pro Mare Symposium on Polar Marine Ecology, Trondheim, 12–16 May 1990*, (Eds. E. Sakshaug, C.C.E. Hopkins & N.A. Oritsland), Norwegian Polar Institute, Tromsø, Norway. *Polar Research*, **10**, 267–275.
- Meyer, M.A. & El-Sayed, S. (1983) Grazing of *Euphausia superba* Dana on natural phytoplankton populations. *Polar Biology*, **1**, 193–203.
- Michel, C., Legendre, L., Ingram, R.G., Gosselin, M. & Levasseur, M. (1996) Carbon budget of sea-ice algae in spring: evidence of a significant transfer to zooplankton grazers. *Journal of Geophysical Research*, **101**, 18345–18360.
- Michel, C., Legendre, L. & Taguchi, S. (1997) Coexistence of microalgal sedimentation and water column recycling in a seasonally ice-covered ecosystem (Saroma-ko Lagoon, Sea Okhotsk, Japan). *Journal of Marine Systems*, **11**, 133–148.
- Michel, C., Legendre, L., Therriault, J.-C., Demers, S. & Vandevelde, T. (1993) Springtime coupling between ice algal and phytoplankton assemblages in southeastern Hudson Bay, Canadian Arctic. *Polar Biology*, **13**, 441–449.
- Mitchell, B.G. & Holm-Hansen, O. (1991) Observations and modeling of the phytoplankton crop in relationship to mixing depth. *Deep-Sea Research*, **38**, 981–1008.
- Nelson, D.M., Smith, W.O., Gordon, L.I. & Huber, B.Q. (1987) Spring distribution of density, nutrients and phytoplankton biomass in the ice-edge zone of the Weddell-Scotia Sea. *Journal of Geophysical Research*, **92**, 7181–7190.
- Niebauer, H.J. & Alexander, V. (1985) Oceanographic frontal structuring and biological production at an ice edge. *Continental Shelf Research*, **4**, 367–388.
- Palmisano, A.C. & Sullivan, C.W. (1983) Sea ice microbial communities (SIMCO). I. Distribution, abundance, and primary production of ice microalgae in McMurdo Sound, Antarctica in 1980. *Polar Biology*, **2**, 171–177.
- Palmisano, A.C. & Sullivan, C.W. (1985) Physiological response of micro-algae in the ice platelet to low light conditions. In: *Antarctic Nutrient Cycles and Food Webs*, (Eds W.R. Siegfried, P.R. Condy & R.M. Laws), pp. 84–88. Springer-Verlag, Berlin.
- Pfirman, S., Gascard, J.-C., Wollenburg, I., Mudie, P. & Abelmann, A. (1989a) Particle-laden Eurasian Arctic sea ice: observations from July and August 1987. *Polar Research*, **7**, 59–66.
- Pfirman, S., Lange, M., Wollenburg, I. & Schlosser, P. (1990) Sea ice characteristics and the role of sediment inclusions in deep-sea deposition: Arctic-Antarctic comparisons. In: *Geological History of the Polar Oceans: Arctic versus Antarctic*, (Eds U. Bleil & J. Thiede), NATO ASI Series C, Vol. 308, pp. 187–211. Kluwer Academic Publishers, Dordrecht.
- Pfirman, S., Wollenburg, I., Thiede, J. & Lange, M. (1989b) Lithogenic sedimentation in Arctic pack ice: potential Aeolian flux and contribution to deep sea sediments. In: *Paleoclimatology and Paleometeorology: Modern and Past Patterns of Global Atmospheric Transport*, (Eds M. Samthein & M. Leinen), pp. 463–493. Kluwer, Dordrecht.

- Ramseier, R.O., Garrity, C., Bauerfeind, E. & Peinert, R. (1999) Sea-ice impact on long-term particle flux in the Greenland Sea's Odden-Nordbukto region, 1985–1996. *Journal of Geophysical Research*, **104**, 5329–5343.
- Rau, G.H., Sullivan, C.W. & Gordon, L. (1991)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  variations in Weddell Sea particulate organic matter. *Marine Chemistry*, **35**, 355–369.
- Reimnitz, E., Bornes, P.W. & Weber, W.S. (1993) Particulate matter in pack ice of the Beaufort Gyre. *Journal of Glaciology*, **39**, 131, 186–198.
- Riebesell, U., Schloss, I. & Smetacek, V. (1991) Aggregation of algae released from melting sea ice: implications for seeding and sedimentation. *Polar Biology*, **11**, 239–248.
- Rivkin, R.B. & Putt, M. (1987) Photosynthesis and cell division by Antarctic microalgae: comparison of benthic, planktonic and ice algae. *Journal of Phycology*, **23**, 223–229.
- Rogers, J.C. (1995)  $^{13}\text{C}/^{12}\text{C}$  ratios in surface water and sea ice organic matter: variability and contributions to the sediments of the Ross Sea, Antarctic. M.S. thesis, Rice University, Houston, Texas.
- Rogers, J.C. & Dunbar, R.B. (1993) Carbon isotopic composition of particulate organic carbon in Ross Sea surface waters during austral summer. *Antarctic Journal of the United States*, **28**, 81–83.
- Ross, R.M., Hofmann, E.E. & Quetin, L.B. (Eds) (1996) *Foundations for Ecological Research West of the Antarctic Peninsula*, American Geophysical Union, Washington, D.C. *Antarctic Research Series*, **70**, 1–448.
- Runge, J.A. & Ingram, R.G. (1988) Underice grazing by planktonic, calanoid copepods in relation to a bloom of ice microalgae in southeastern Hudson Bay. *Limnology and Oceanography*, **33**, 280–286.
- Runge, J.A. & Ingram, R.G. (1991) Under-ice feeding and diel migration by the planktonic copepods *Calanus glacialis* and *Pseudocalanus minutus* in relation to the ice algal production cycle in southeastern Hudson Bay, Canada. *Marine Biology*, **108**, 217–225.
- Runge, J.A., Theriault, J.-C., Legendre, L., Ingram, R.G. & Demers, S. (1991) Coupling between ice microalgae productivity and the pelagic, metazoan food web in southeastern Hudson Bay: a synthesis of results. In: *Proceedings of the Pro Mare Symposium on Polar Marine Ecology, Trondheim, 12–16 May 1990*, (Eds E. Sakshaug, C.C.E. Hopkins, & N.A. Oritsland). *Polar Research*, **10**, 325–328.
- Saito, K. & Taniguchi, A. (1978) Phytoplankton communities in the Bering Sea and adjacent seas. 2. Spring and summer communities in seasonally ice-covered areas. *Astarte*, **11**, 27–35.
- Sakoh, H., Matsuda, O., Michel, C., Legendre, L., Rajendran, N. & Yamamoto, T. (1997) Temporal variation of chlorophyll-like pigment composition in sinking particles during the ice-covered season in Saroma-ko Lagoon. *Journal of Marine Systems*, **11**, 123–131.
- Sakshaug, E. (1989) The physiological ecology of polar phytoplankton. In: *Proceedings of the 6th Conference of the Comite Artique International*, (Eds W.R. Rey & V. Alexander), pp. 61–89. Leiden, E.J. Brill.
- Sakshaug, E. & Holm-Hansen, O. (1984) Factors governing pelagic production in polar oceans. In: *Marine Phytoplankton and Productivity, Lecture Notes Coastal and Estuarine Studies*, Vol. 8, (Eds O. Holm-Hansen, L. Bolis & R. Gilles), pp. 1–18. Springer, Heidelberg.
- Sakshaug, E. & Skjoldal, H.R. (1989) Life at the ice edge. *Ambio*, **18**, 60–67.
- Schandelmeier, L. & Alexander, V. (1981) An analysis of the influence of ice on spring phytoplankton population structure in the southeastern Bering Sea. *Limnology and Oceanography*, **26**, 935–943.

- Scharek, R., Smetacek, V., Fahrbach, E., Gordon, L.I., Rohardt, G. & Moore, S. (1994) The transition from winter to early spring in the eastern Weddell Sea, Antarctica: plankton biomass and composition in relation to hydrography and nutrients. *Deep-Sea Research*, **41**, 1231–1250.
- Schloss, I. & Estrada, M. (1994) Phytoplankton composition in the Weddell–Scotia Confluence area during austral spring in relation to hydrography. *Polar Biology*, **14**, 77–90.
- Sedwick, P.N. & DiTullio, G.R. (1997) Regulation of algal blooms in Antarctic shelf waters by the release of iron from melting sea ice. *Geophysical Research Letters*, **24**, 2515–2518.
- Segawa, S., Kato, M. & Murano, M. (1983) Growth, moult and filtering rate of krill in laboratory conditions. *Memoires of the National Institute Polar Research, Special Issue*, **27**, 93–103.
- Siegel, V., Bergstron, B., Stromberg, J.O. & Schalk, P.H. (1990) Distribution, size frequencies and maturity stages of krill, *Euphausia superba*, in relation to sea-ice in the northern Weddell Sea. *Polar Biology*, **10**, 549–557.
- Smayda, T.J. (1970) The suspension and sinking of phytoplankton in the sea. *Oceanography and Marine Biology, An Annual Review*, **8**, 353–414.
- Smetacek, V., Scharek, R., Gordon, L.I., Eicken, H., Fahrbach, E., Rohardt, G. & Moore, S. (1992) Early spring phytoplankton blooms in ice platelet layers of the southern Weddell Sea. *Deep-Sea Research*, **39**, 153–168.
- Smetacek, V., Scharek, R. & Nöthig, E.-M. (1990) Seasonal and regional variation in the pelagial and its relationship to the life history of krill. In: *Antarctic Ecosystems. Ecological Change and Conservation*, (Eds K.R. Kerry & G. Hempel), pp. 103–114. Springer-Verlag, Berlin.
- Smith, W.O. & Nelson, D. (1985) Phytoplankton bloom produced by a receding ice edge in the Ross Sea: spatial coherence with the density field. *Science*, **227**, 163–166.
- Smith, W.O. & Nelson, D. (1986) Importance of ice edge phytoplankton production in the Southern Ocean. *BioScience*, **36**, 251–257.
- Sommer, U. (1989) Maximal growth rates of Antarctic phytoplankton: only weak dependence on cell size. *Limnology and Oceanography*, **34**, 1109–1112.
- Squire, V.A. (1990) Sea ice: its formation, distribution and properties. In: *Polar Marine Diatoms*, (Eds L.K. Medlin & J. Priddle), pp. 3–8. British Antarctic Survey, Cambridge.
- Stretch, J.J., Hamner, P.P., Hamner, W.M., Michel, W.C., Cook, J. & Sullivan, C.W. (1988) Foraging behavior of Antarctic krill *Euphausia superba* on sea ice microalgae. *Marine Ecology Progress Series*, **44**, 131–139.
- Sullivan, C.W., McClain, C.R., Comiso, J.C. & Smith, W.O., Jr (1988) Phytoplankton standing crops within an Antarctic ice edge assessed by satellite remote sensing. *Journal of Geophysical Research*, **93**, 12487–12498.
- Thomas, D.N., Kennedy, H., Kattner, G., Gerdes, D., Gough, C. & Dieckmann, G.S. (2001) Biogeochemistry of platelet ice: its influence on particle flux under fast ice in the Weddell Sea, Antarctica. *Polar Biology*, **24**, 486–496.
- Tremblay, C., Runge, J.A. & Legendre, L. (1989) Grazing and sedimentation of ice algae during and immediately after a bloom at the ice–water interface. *Marine Ecology Progress Series*, **56**, 291–300.
- Veth, C., Lancelot, C. & Ober, S. (1992) On processes determining the vertical stability of surface waters in the marginal ice zone of the north-western Weddell Sea and their relationship with phytoplankton bloom development. *Polar Biology*, **12**, 237–243.

- Villinski, J.C., Dunbar, R.B. & Mucciarone, D.M. (2000) Carbon 13/Carbon 12 ratios of sedimentary organic matter from the Ross Sea, Antarctica: a record of phytoplankton bloom dynamics. *Journal of Geophysical Research*, **105**, 14163–14172.
- Wada, E., Terazaki, M., Kabaya, Y. & Nemoto, T. (1987)  $^{15}\text{N}$  and  $^{13}\text{C}$  abundances in the Antarctic Ocean with emphasis on the biogeochemical structure of the food web. *Deep-Sea Research*, **34**, 829–841.
- Watanabe, K. & Satoh, H. (1987) Seasonal variations of ice algal standing crop near Syowa Station, East Antarctica 1983/84. *Bulletin of the Plankton Society of Japan*, **34**, 143–164.
- Wefer, G. & Fischer, G. (1991) Annual primary production and export flux in the Southern Ocean from sediment trap data. *Marine Chemistry*, **35**, 597–613.
- Wefer, G., Fischer, G., Futterer, D.K., Gersonde, R., Honjo, S. & Ostermann, D. (1990) Particle sedimentation and productivity in Antarctic waters of the Atlantic sector. In: *Geological History of the Polar Oceans: Arctic versus Antarctic*, (Eds U. Bleil & J. Thiede), pp. 363–379. Kluwer, Dordrecht, The Netherlands.
- Wefer, G., Suess, E., Balzer, W., Liebezeit, G., Muller, P.J., Ungerer, C.A. & Zenk, W. (1982) Fluxes of biogenic components from sediment trap deployment in circumpolar waters of the Drake Passage. *Nature*, **299**, 145–147.
- Wilson, D.L., Smith, W.O., Jr & Nelson, D.M. (1986) Phytoplankton bloom dynamics of the western Ross Sea ice edge – I. Primary productivity and species-specific production. *Deep-Sea Research*, **33**, 1375–1387.