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Ecology of sea ice biota

2. Global significance*

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Summary. The sea ice does not only determine the ecology of ice biota, but it also influences the pelagic systems under the ice cover and at ice edges. In this paper, new estimates of Arctic and Antarctic production of biogenic carbon are derived, and differences as well as similarities between the two oceans are examined. In ice-covered seas, high algal concentrations (blooms) occur in association with several types of conditions. Blooms often lead to high sedimentation of intact cells and faecal pellets. In addition to ice-related blooms, there is progressive accumulation of organic matter in Arctic multi-year ice, whose fate may potentially be similar to that of blooms. A fraction of the carbon fixed by microalgae that grow in sea ice or in relation to it is exported out of the production zone. This includes particulate material sinking out of the euphotic zone, and also material passed on to the food web. Pathways through which ice algal production does reach various components of the pelagic and benthic food webs, and through them such top predators as marine mammals and birds, are discussed. Concerning global climate change and biogeochemical fluxes of carbon, not all export pathways from the euphotic zone result in the sequestration of carbon for periods of hundreds of years or more. This is because various processes, that take place in both the ice and the water column, contribute to mineralize organic carbon into CO_2 before it becomes sequestered. Processes that favour the production and accumulation of biogenic carbon as well as its export to deep waters and sequestration are discussed, together with those that influence mineralization in the upper ice-covered ocean.

Introduction

A fraction of the carbon fixed by algae growing in the ice, or in relation to the ice, is transferred out of the production zone. As in open marine waters (e.g. Legendre and Le Fevre 1991), this includes particulate material sinking out of the euphotic zone, and also material passed on to the food web. Biogenic material may end up being transferred from the production area either horizontally, through passive transport associated with circulation or active migration of large animals, or vertically, again passively, through sedimentation of living or detrital particles, or actively, through vertical migrations.

Within the context of global climate change, two concepts must be distinguished concerning the fate of biogenic carbon in oceans, i.e. export and sequestration. *Export* refers to the flux of biogenic material from surface waters to depth, while *sequestration* concerns the removal of dissolved inorganic CO_2 from the atmosphere and surface waters for periods of interest to global warming (i.e. at least a few hundred years). Export of biogenic carbon and sequestration of carbon are generally not equivalent, since a large fraction of the exported biogenic carbon may sometimes be rapidly respired during its downward transit and recycled back to the atmosphere. For global biogeochemical budgets, the really significant term is not the export but the actual sequestration of carbon. Volk and Hoffert (1985) identified three CO_2 pumps in the oceans, one physical and two biological. The *solubility pump* (physical) is associated with ocean circulation. It is especially active in areas of deep water formation (polar regions), where cooling of the surface water drives a flux of CO 2 from the atmosphere to the ocean, and subsequent sinking of the water ensures sequestration of the dissolved inorganic carbon; this pump will not be discussed here. One biological pump exports carbonate (the *carbonate pump),* and its overall effect on the sequestration of atmospheric CO_2 may be rather complex, as explained below. The other (the *soft-tissue pump,* also known as the *biological* $C0_2$ *pump)* plays an important role in the export of biogenic carbon, of which a fraction may be sequestered, and its activity in polar waters will be examined in relation to sea-ice biological production. The relative importance of biological versus physical pumping of atmospheric CO_2 into oceans is presently under debate (e.g. Broecker 1991; Longhurst 1991). In this paper, vari-

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ous aspects of production export in ice-covered waters are considered, as well as some of the processes involved in carbon sequestration.

Production of biogenic carbon in polar seas

The sea ice does not only determine the ecology of ice biota, but it also influences the pelagic systems since the water column under ice cover differs markedly in its light and temperature regimes from the open ocean under similar irradiance conditions. The freezing and melting of ice that takes place at ice edges affect the vertical stability of the water column, as well as the concentrations of nutrients and the depth of the euphotic zone. They control the physical environment, and create conditions for biological activity that differ from waters removed from the influence of the ice cover. Aside from the uniqueness of ice associated production, one question of interest is: How much biogenic carbon, both absolutely and relatively, is produced at ice edges, in waters under ice, and within the sea ice? Tables 1 and 2 provide some new and perhaps improved estimates of these values for the Antarctic and Arctic respectively.

1 Production of biogenic carbon in the ice-covered Antarctic Ocean

The systems within, under or in the proximity of ice covers have only recently been investigated. Some significant problems exist in estimating large scale quantities such as total production since sampling in the Antarctic ice-covered ocean is not very dense, either seasonally or regionally, and unique measurement problems exist for the ice itself, relative to the water column. Estimates presented here therefore rely heavily on proxy data and inference (detailed below), but they may represent a useful exercise since earlier estimates have ignored the unique processes associated with the ice cover and, therefore, may have also failed to see their potential significance.

Table 1 estimates the carbon production over the 20 x 10^6 km^2 area covered by Antarctic sea ice at its maximum extent. This area roughly corresponds to the ocean between 60°S latitude and the Antarctic continent. The production is partitioned into water column production in ice edge blooms, water column production under ice cover, and production within the sea ice cover. A value that was not computed independently is the water column production that exists away from ice edges once the ice cover has retreated. This value may be inherently low, since production observed along transects is significantly higher in close proximity to retreating ice edges than for the regions where ice has disappeared for some period. Further, the production of deep ocean regions removed from frontal zones or coastal upwelling regions is not usually very high in any case, a condition that applies to most of the waters around Antarctica. A third reason is that many of the organisms in the water column are taken into the ice matrix by advancing ice edges (Ackley 1982; Garrison et al. 1983; Ackley et al. 1987), and may so be

Table 1. Microalgal and bacterial production of biogenic carbon in the ice-covered Antarctic Ocean (south of ca. 60° lat.). Units: carbon uptake rate (mgCrn"^{2} day"^{1}), standing stock (rag Cm"^{2}), area (10^{12} m^{2}), time (days), production (10$^{'4}$ g C year ~^{1})

	Uptake rate (R) or stock (S)	Area	Time	Annual production	Total production
A Water column production in ice edge blooms					
Phytoplankton					
Spring	521 (R)	1.75	121	1.10	
Autumn	126 (R)	1.5	121	0.23	
Winter	32 (R)	2.0	121	0.08	
Bacteria					
Spring	70 (R)	1.75	121	0.15	
Autumn	96 (R)	1.5	121		
Winter	29 (R)	2.0	121		1.8
B Water column				0.17	
production under ice cover *Phytoplankton*				0.07	
Spring	168 (S)	10			
Autumn	168 (S)				
	5			0.017	
Winter	168 (S)			0.0084	
	5		121	0.0084	
Bacteria			121		
Spring	20 (R)	10	121	0.24	
Autumn	19 (R)	5		0.115	
				0.048	
					0.44
Winter	8 (R)	10			
C Production within the sea ice *Ice*		2.5			
		20			
algae		0.265		0.4	
Surface	4000 (S) 8000			0.2	
Freeboard	(S) 80 (S) 6000			0.016	
Interior	32000 (S)			0.016-0.084	0.63-0.70
					2.87-2.94
Total Antarctic production (A + B + C)					
Bottom					

accounted for in section C of Table 1 (production within the sea ice cover). A separate computation for the water column seaward of the ice edge, especially in front of advancing ice edges, might therefore count this production twice if it is accounted for by the ice component.

In the present study, bacterial carbon uptake is included in estimates of biogenic carbon production, because bacteria are believed to utilize primarily soluble organic compounds derived from phytoplankton, which would otherwise be lost for the particulate phase and then accumulate in the DOM pool. Part of the DOC taken by bacteria is used for metabolic processes and thus respired as CO_2, but part of it is incorporated (packaged) into biogenic particulate matter. Bacterial cells may become part of the microbial food web, from which export is possible (see Export pathways, below).

Water column production in ice edge blooms. Annual production in section A of Table 1 was estimated by taking the seasonal data on production rates and standing crop for phytoplankton and bacteria measured during the AMERIEZ (Antarctic Marine Ecosystem Research at the Ice Edge Zone) program (Nelson et al. 1987, 1989; Cota et al. 1990; Kottmeier and Sullivan 1990; Sullivan et al. 1990) conducted in the Weddell Gyre region for three seasons, i.e. spring, autumn and winter (Table 1). Summer data have not yet been obtained, so that annual estimates are derived by dividing the year equally into the three seasons available. The area of the ice edge bloom is obtained by first taking the area of ice cover for each of the seasons and deriving a perimeter length, essentially the outer circumference of the sea ice area which rings the Antarctic continent. This value is used as the ice edge length for each corresponding season. The ice edge length is then multiplied by the estimated width of an ice edge bloom, i.e. 100 km. The total area over which the ice edge blooms are expected to take place (the sum of the spring, autumn and winter ice edge bloom areas in Table 1) is ca. 5.25 x 10^6 km^2, or roughly one third of the seasonal area of Antarctic pack ice which varies between about 4 and 20xl0^{6}km^2 from minimum to maximum respectively. CZCS data (Comiso and Sullivan 1986; Sullivan et al. 1988; Comiso et al. 1990) indicate considerable variability or patchiness in ice edge blooms, which suggests that considering the full ice area over the seasonal cycle (three times the area actually used) at the measured rates of production may greatly overestimate the carbon contribution. It may however provide an upper bound to the total production, i.e. three times the estimate shown in Table 1. The CZCS studies cited above also determined that the ice edge bloom in which one of these rates was measured from ship stations was not the most intense bloom at that time in the region, suggesting that the rates may not be the maximum nor minimum observable, somewhat rationalizing their use here as typical values. Using a smaller area than the entire seasonal sea ice zone may also be compensated for by the longer times, since the blooms are probably shorter than the 121 days assumed in Table 1, but may be more intense or higher rate events than characterized here. A best guess is that the total estimate of Table 1 is neither the lowest nor the highest possible.

Other measurements of ice edge production, leading to similar estimates of total production, have been made in the region. Marra and Boardman (1984) directly measured phytoplankton production in early spring, at an ice edge location somewhat east of the region where the values used here were obtained (0° longitude), and got 300-400 mg Cm~^{2}day~^{1}. These values are consistent with the spring values obtained during AMERIEZ, but somewhat less than those in Table 1; however they were early spring values at an open ocean area, that would not immediately be an obvious choice for a bloom region. Using an indirect method, similar values for production (200-400 mg Cm"^{2} day"^{1}) were also estimated by Jennings et al. (1984), for an open ocean region in the eastern part of the Weddell Gyre (actually a location corresponding to the direct measurements of Marra and Boardman 1984). These values were estimated from the seasonal depletion of nutrients between winter and end of summer, and are therefore equivalent to an averaging of the spring and autumn values in Table 1. Consequently, they are consistent with the rates used to get annual production in the table, when those rates are averaged. Large uncertainties also exist in this computation concerning the areas and periods over which the estimated production rates are applicable. The AMERIEZ values have an advantage in showing some seasonal dependence, and in also having rates for bacterial production since the latter accounts for nearly 50% of the ice edge total production in autumn and winter. The estimate would be improved by additional production data, but especially by better characterizing the areas and periods over which the ice edge blooms take place.

Water column production under ice cover. In section B of Table 1, the state of water column production is not easy to characterize. Most observations suggest that the levels of chlorophyll *a* concentration beneath the ice cover are generally <0.1 mgm~^{3} (e.g. Marra and Boardman 1984). These low values are consistent with estimates of light penetration through the pack ice which indicate that, over the pack ice regions, the presence of a few 10s cm of ice topped by 10-20 cm of snow reduces the irradiance level, before reaching the bottom of the ice, to < 1 % of the incident radiation at the snow-ice surface. This level of irradiance is generally considered to limit the onset of photosynthetic activity in most ocean waters. Intermittent light penetration can occur because of the opening and closing of the ice cover in leads and polynyas, resulting from the variations in wind and ocean current forcing on the ice cover. Whether this leads to a sustainable level of production in the water column is unknown at this time. In addition, it has been shown that the growth of the algae within the ice cover can prolong the shading of the water column, and thus limit the onset of production there until the ice cover essentially disappears (e.g. Palmisano et al. 1987). It was therefore considered that using rate data for phytoplankton under pack ice would be unrealistic, without reasonable knowledge of the variability in light conditions that may exist there.

First order estimates for phytoplankton production under the ice cover were therefore taken as an extrapolation of the standing stock, in order to obtain a baseline value. The average AMERIEZ standing stock was taken for the three seasons, and applied uniformly across the year. These values were then taken over the appropriate area of pack ice for each season, such that the total pack ice area equaled the 20 x 10^6 km^2 at maximum extent. Such an estimate could be derived differently, and could conceivably raise or lower the value by a factor of two or three. For example, the values of Cota et al. (1990, their Table 1) for chlorophyll *a* and the C: Chi ratio give 672 and 900 mg C m ~ ^{2} for the spring and the autumn respectively while, for the winter, Cota and Smith (1989) report values generally <0.1 mgChlm~^{3} in the top 100 m corresponding to a biomass of ca. 530 mgCm"^{2}; using these values would lead to an upward revision of the annual under-ice phytoplankton production from 0.017 + 0.0084 + 0.0084 = 0.034 x!0^{4}gC (Table 1) to 0.067 + 0.045 + 0.027 = 0.139 x 10^4 gC. However, values in Table 1 show the estimated phytoplankton production to be on the order of 10% of the bacterial production, so that different estimates would have to change the estimated'phytoplankton contribution by one order of magnitude to significantly impact the total production value. Bacterial production, which is based on rate data, shows a seasonal dependence similar to that of ice edge values (Table 1). The rate data used here for bacterial carbon production are methodologically consistent with other estimates for the water column.

The total production for the water column under ice, even though it involves much larger areas, is only about one fourth of that estimated for ice edge blooms. This interpretation is consistent with the harsh under-ice environment, especially in terms of low irradiance, that severely limits water-column production. The low turbidity of ice-covered waters as well as the low observed stocks (e.g. Marra and Boardman 1984) indicate that the overall production should be lower than that generally observed in ice edge blooms.

Production within the sea ice cover. This term in the carbon budget has not been considered in detail previously, and data on its major components (i.e. rates or stocks, areal coverage and time of production) are still severely limited. However, lack of data should not be confused with lack of significance, since only recently have the levels of biological production, the location of the production both regionally and vertically within the ice cover, and some of the seasonality of production been quantitatively determined for Antarctic sea ice. Observations of coloured material of biological origin within the ice cover, however, date back to some of the first encounters with the ice cover in early voyages. These incidental observations have taken place consistently during ship transits to the Antarctic, suggesting that the present lack of information is due to lack of quantitative sampling rather than shortage of material to be sampled. Horner et al. (1992) as well as Ackley and Sullivan (ms) have summarized the main characteristics of the various types of sea ice communities involved (i.e. surface, freeboard, interior and bottom) as well as some of the physical processes that are controlling them.

The estimates for carbon shown in Table 1 (section C) are based on stock data for these communities. Estimates are also made of the areas where the physical conditions leading to the development of each particular community are expected to occur. The use of stocks rather than rates in estimating the total production within sea ice may be even more justifiable than for the water column (as done in the previous section). The argument is that the growing microalgae are resident within the ice, until they are released into the water column at the time of ice melt. Because growth takes place within the ice matrix, grazing effects may be relatively low (see Grazing by large herbivores and Microbial food web, below) with a limited downward flux of detrital material. A standing stock value within the ice cover, with some assumptions about whether it is at its maximum, therefore provides a reasonable estimate of the total annual net production within the ice for that particular community, especially for the Antarctic sea ice which forms and melts predominantly on an annual cycle. Values for the standing stock were divided into basically three categories, i.e. surface, interior and bottom, depending on where the community appears in the ice. An additional community, the freeboard type, has also been listed. This community is actually an interior community, but is separable from other interior communities because of its high production and identifiable occurrence.

Surface communities occur primarily through various types of snow and ice loading that deflect the upper surface of the ice below sea level, causing flooding by sea water. Direct measurements show that this type of structure has a standing stock of the order of 4gCm~^{2} (e.g. Burkholder and Mandelli 1965). Its predicted area of occurrence is based on the physical measurements of flooded ice in the Weddell Sea region which, for both first and second year ice types, has been found to affect ca. 50% of the ice covered area (Ackley et al. 1990). By extrapolating this estimate to the total area of sea ice, the area affected by surface comunities is 10 x 10^6 km^2. Because of its relatively widespread occurrence, along with high biomass, this community leads the estimated overall production for sea ice ecosystems in the Antarctic.

Freeboard communities have been observed to occur in ice-covered regions at the end of summer, and possibly in other seasons at the northern ice edge where warm temperature and high irradiance conditions persist. The area where this community occurs is estimated to be ca. 50% of the minimum ice extent, i.e. 2.5 x 10^6 km^2. Although the production in the freeboard layer is somewhat higher than that of the surface communities (Kottmeier and Sullivan 1990), the area of occurrence is smaller, leading to annual production about one half of that estimated for the surface communities.

Interior communities, which are apparently unique to Antarctica, consist in a combination of initial incorporation of biological material as the ice advances in autumn and winter, followed by some subsequent growth of material within the ice during the lifetime of the ice cover. These communities are characterized by low concentrations of biological material, although they may account for a sizable accumulation of the open ocean production during the ice advance over the open ocean. Most ice samples obtained contain low but measurable concentrations of biological material, and the area over which they are expected to occur has been taken as the total area of the ice cover, i.e. 20 x 10^6 km^2. The value used here for the standing stock is typical of end-of-winter values. Some unpublished results of G. S. Dieckmann would suggest a rise in this value by a factor of two or three during spring, which would increase the share of the interior communities to the total sea ice production from this estimate of a few percent to a value near ten percent.

Bottom-ice communities are some of the most productive found in Antarctica (Arrigo et al. 1990). These encompass the communities found in the bottom few centimetres of the ice and the organisms in the subice platelet layer that accumulates in certain regions. While these communities are highly productive, they have been primarily observed in the fast ice, i.e. the portion of the sea ice cover attached to the continent, that accounts for only a small percentage of the total sea ice cover around Antarctica. The area was estimated by taking the approximate circumference of Antarctica, doubling that to estimate the additional coastline of inlets, bays and sounds that make up the continental boundary, and multiplying that value by an estimated average 10 km width of fast ice. The resulting area, 0.265 x 10^6 km^2, is of the order of 1 to 2% of the total area of Antarctic drifting pack ice at maximum extent. The resulting total production is interestingly of the same order as that found in the interior communities for the freely drifting pack ice, even though the production in bottom ice is 100 times higher, because of the difference in growth areas for the two communities.

Partitioning of the carbon production between the different sources. The total Antarctic production of biogenic carbon, defined for the area of ocean that is covered by pack ice at maximum extent, is given at the bottom of Table 1 as ca. 2.9 x 10^{14} gC annually (0.29 Gt year^{-1}). Based on the three sections of the table, this is apportioned as: 60% (plus) for ice edge associated production (mainly phytoplankton), ca. 15-20% for water column under-ice production (dominantly bacterial; the reason why heterotrophic bacterial production has been included in the estimate of primary production is explained above), and 20% (plus) for within sea ice production (dominantly microalgal communities).

Using estimates from water column data only, Walsh (1990) calculated that the Antarctic phytoplankton production (dominated by the ice edge values) ranged between 3 and 66 gCm^{-2} year^{-1}. The areal value from the present study of ca. 15 gCm^{-2} year^{-1} (total annual production of 2.9 x 10^{14} gCm^{-2} divided by maximum sea ice area of 2.0 x 10^{12} m^2; see Table 1) falls within the range of Walsh's estimates. However, the value for phytoplankton production (excluding bacteria) at ice edges only, using data from Table 1, would be ca. 80 gCm^{-2} year^{-1}. This stresses the importance of better understanding ice edge blooms in detail, especially the crucial points of areal coverage and duration as well as production rates, because these blooms are responsible for the largest part of the Antarctic production, their overall production is high (even on an annual average basis), and large errors are probably currently made in estimating their critical parameters. Even the estimate in Table 1 can be rationalized as underestimating the production at ice edges, by the use of only winter and spring values, so that the estimate could potentially be increased when summer ice edge productivity data become available over wider areas.

One issue of some importance to be resolved, concerning the estimation of Antarctic production of biogenic carbon, is the use of bacterial as well as phytoplankton production. In addition, the present study possibly assumed a greater area for bloom activity than Walsh (1990), since he mentions that shelves are the bloom areas where production may be averaged, thus assuming low production for deep ocean areas. This latter point is not, however, very clear in his study. As mentioned above, the production values used here are actually at the low end of those measured for ice edge blooms, i.e. these are spring values that are extrapolated throughout the summer period. So, if a shorter period was used (e.g. 30-60 days as suggested by Walsh instead of 121 days in Table 1), it might also be justified to use higher rates, leaving a net result similar to that of Table 1. More accurate measurements are needed, possibly using calibrated satellite data to estimate the areas and duration of ice edge blooms better than is possible with present data. Another important point when assessing the production of polar waters concerns the fixation of biogenic carbon within the sea ice. As shown here and in the following discussion on the Arctic, production within ice may significantly contribute to the overall carbon production, even in comparison to the open water blooms such as exist at the ice edges.

2 Microalgal production in the Arctic Ocean

While the Arctic and Antarctic seas are contrasted in many ways, a feature of significance concerning the production of biogenic carbon is the presence of broad, shallow continental shelves in the Arctic Basin and its marginal seas. This contrasts with the Antarctic Ocean, where the continental shelves are very deep and the area they occupy is proportionately much smaller than in the Arctic (Walsh, 1990). Since ice cover persists year-round in the deep water regions of the Arctic Ocean, production is somewhat limited there, being characterized by limited under-ice productivity and some algal production within the sea ice itself. The deep water, ice edge ecosystems that are a major contributor to Antarctic production are not found in the Arctic, where they are replaced by water-column production in the shelf area under ice-free conditions. Production in the Arctic Ocean is therefore partitioned into: water column production in shelf areas, water column production in offshore areas (primarily under the ice), and production within the sea ice cover, as shown in sections A, B, and C of Table 2.

Estimates previously made by Subba Rao and Platt (1984) are used in sections A and B of Table 2, with discussion, while an adjustment to their value is proposed tions of biological material, although they may account for a sizable accumulation of the open ocean production during the ice advance over the open ocean. Most ice samples obtained contain low but measurable concentrations of biological material, and the area over which they are expected to occur has been taken as the total area of the ice cover, i.e. 20 x 10^{6} km^{2}. The value used here for the standing stock is typical of end-of-winter values. Some unpublished results of G. S. Dieckmann would suggest a rise in this value by a factor of two or three during spring, which would increase the share of the interior communities to the total sea ice production from this estimate of a few percent to a value near ten percent.

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While the Arctic and Antarctic seas are contrasted in many ways, a feature of significance concerning the production of biogenic carbon is the presence of broad, shallow continental shelves in the Arctic Basin and its marginal seas. This contrasts with the Antarctic Ocean, where the continental shelves are very deep and the area they occupy is proportionately much smaller than in the Arctic (Walsh, 1990). Since ice cover persists year-round in the deep water regions of the Arctic Ocean, production is somewhat limited there, being characterized by limited under-ice productivity and some algal production within the sea ice itself. The deep water, ice edge ecosystems that are a major contributor to Antarctic production are not found in the Arctic, where they are replaced by water-column production in the shelf area under ice-free conditions. Production in the Arctic Ocean is therefore partitioned into: water column production in shelf areas, water column production in offshore areas (primarily under the ice), and production within the sea ice cover, as shown in sections A, B, and C of Table 2.

Estimates previously made by Subba Rao and Platt (1984) are used in sections A and B of Table 2, with discussion, while an adjustment to their value is proposed in multi-year ice, is ca. 200 mg C. Assuming 3-m thick ice, this provides an estimate for annual production of ca. 0.6 gCm~~^{2} which gives, over the 5 x 10^{6} km^{2} of multi-year ice, an annual production of 0.03xl0^{4}gC. This value, although ecologically significant (see Algal blooms, below), may be relatively small compared to first-year ice production, which lies between 0.06 and 0.7xl0^{14}gC year"^{1} according to the area of occurrence used for the calculation. Better estimates of production rates and areas of occurrence are needed for these Arctic communities to further refine the values. The lowest estimate, however, is unlikely given the increased observations of within ice production, and its association with first-year ice of all thickness and not just the young ice of limited area as previously assumed.

Partitioning of the carbon production between the different sources. Summing the water column and ice estimates gives a total Arctic production (bottom of Table 2) of 2.14-2.78 x lO^gCyear"^{1} (0.21-0.28 Gtyear""^{1}). This value differs from that of Subba Rao and Platt (1984) by the additional contribution of sea-ice algal production, which is raised from 3 to 25% of the total Arctic primary production. Using the new estimate, total primary production in Arctic seas is partitioned as: 50% in shelf waters, 25% in offshore waters, and 25% within the sea ice.

Values in Table 2 for total microalgal production in shelf regions (water column + first year ice = 27+10 = 37 g C m ~ ^{2} year ") can be compared to other published estimates for this environment. The value for new primary production over the shelves, derived by Anderson et al. (1990) from a CO_2 budget of the Arctic Ocean, is ca. 45 gCm~^{2}year~^{1}, while the estimates of Wallace et al. (1987), based on apparent oxygen utilization rates in the upper halocline water, range between 18 and 64 gCm~^{2}year~^{1}. Values in Table 2, which were derived from measured rates of carbon uptake or standing stocks are thus consistent with those previously estimated.

Total values in Table 2 cannot be directly compared to those in Table 1, since the former do not include estimates of bacterial production. According to figures from Table 1, the total algal production (i.e. excluding bacteria) for the Antarctic would range between 2.08 and 2.15xl0^{14} gCyear"^{1}. Thus, estimated primary production for the two oceans is similar even though the Arctic production is confined to an area smaller than that taken for the Antarctic (13 versus 20 x 10^{12} m^{2}). This is primarily because of the greater percentage of high production shelf areas in the Arctic Ocean. An interesting feature of the within sea ice production in the two regions is the presence of highly productive bottom ice algal communities, that are assumed to occur over much more extensive regions in the Arctic than in the Antarctic (where it is confined to near-shore locations). Detailed causes for this should be the subject of future research, but two main differences between the Arctic and the Antarctic may be significant in this respect: (1) Columnar ice is present in higher percentages in the Arctic. The presence, at the ice-water boundary, of an interface of the dendritic type (as observed in columnar sea ice) probably provides a substrate for algae to grow on and/or facilitates the contact of growing algae with nutrient-rich sea water. (2) Increased solar radiation in the Arctic removes the snow cover, so that irradiance at the bottom of the first-year ice becomes sufficient to initiate algal blooms. The fact that the snow cover on the Antarctic sea ice remains relatively intact until the ice melts at the northern ice edge may determine to a large degree the type and location of sea ice production and limit the Antarctic bottom-ice communities to develop in the relatively snow free fast-ice regions.

With the additional contribution of the ice communities, the average areal algal production (total carbon uptake divided by the total area) for the two oceans is:

2.8 x 10^{14} gCyear"Vl3 x 10^{12} m^{2}

= ca. 20gCm~^{2} year"^{1} (Arctic) 2.1

x 10^{14} gCyear" V20 x 10^{12} m^{2}

= ca. 10gCm~^{2} year"^{1} (Antarctic, excl. bacteria)

Given the unknown relative importance of bacterial production in the two systems and the numerous simplifying assumptions, these two estimates are surprisingly close. The somewhat higher value for the Arctic algal production primarily reflects the shelf character of these seas, with higher overall productivity than the deep-water ice edge systems in Antarctica. It should be noted, however, that the role of ice is central to the production regimes of both regions, i.e. in the Antarctic, by controlling the structure of the water column at ice edges which are the dominant production system there and, in the Arctic, by exposing or limiting the high-production open shelf waters.

Export of primary production to ice-related ecosystems

Transfer of biogenic particles to ice-related food webs varies considerably in space and time. Differences are found between the Arctic and Antarctic seas, and changes occur with latitude, season and year. Available data for ice-covered areas are scarce and concern, for the most part, the ice edge.

As explained below in the section on algal blooms, polar seas are characterized by intense seasonal variability in primary production, so that a significant proportion of the annual production may be exported in one or a few short pulses. The quality and quantity of exported particles depend, among other factors, upon the interaction between producers and consumers. This is especially true for the interaction between algae and zooplankton, but may also be observed throughout polar food webs. Despite paucity of data, some general characteristics of the export of primary production to ice-related ecosystems may be derived from the published literature.

1 Zooplankton

Large zooplankters may be found in both polar ice ecosystems. Several metazoans live within the ice, where they use the abundant autotrophs as a food source (e.g. Hamner et al. 1983; Hoshiai and Tanimura 1986; Hoshiai et al. 1987; Kottmeier and Sullivan 1987; Daly and Macaulay 1988; Garrison and Buck 1989). In the Antarctic, krill and zooplankton live in water filled tubes, channels and crevices that permeate the pack ice providing both a foraging environment and a refugium from predators (e.g. Dahms and Dieckmann 1987; Kottmeier and Sullivan 1990). In addition, some species such as the krill, *Euphausia superba* and various copepods graze on algae close to the undersurface of the ice (e.g. Hamner et al. 1983; Carey 1985; Daly and Macaulay 1988; Marschall 1988 and refs. cited therein, Runge and Ingram 1988, 1991; Stretch et al. 1988; Daly 1990). At ice edges in the Canadian High Arctic, the four amphipod and three copepod species studied by Bradstreet and Cross (1982) all consumed algae, especially pennate diatoms of the genera *Nitzschia* and *Navicula.*

Grazing by large zooplankters influences the export of biogenic material out of the euphotic zone, mainly via the production of rapidly sinking faecal pellets. For example, sedimentation in the central Weddell Sea is very low in comparison to other regions in the Antarctic Ocean and also to other oceans (Fischer et al. 1988). Nothig and Bodungen (1989) explain this difference by the low occurrence of krill swarms in the central Weddell Sea (Marr 1962), which would reduce the vertical flux of large faecal pellets. In addition, it has been proposed that diel migrant biota could contribute to the townward transport of biogenic carbon (e.g. Longhurst et al. 1990).

2 Fish

One of the most studied polar fish is the polar cod, *Boreogadus saida* (often called Arctic cod in North America). At ice edges in the Canadian High Arctic, the diet of this species is dominated by amphipods, i.e. *Onisimus glacialis, Gammarus wilkitzkii, Apherusa glacialis* and *Parathemistho libellula,* but it also contains copepods (Bradstreet and Cross 1982). In the western Barents Sea, the diet of polar cod associated with first-year ice mainly consists of copepods (i.e. *Calanus finmarchicus* and *C. glacialis)* and also *P. libellula;* under multi-year ice north of the Svalbard archipelago, their diet is more diverse with *P. libellula* and the sympagic amphipod *A. glacialis* contributing more to the total diet than copepods (L0nne and Gulliksen 1989).

—ft the Arctic, the vernal booming of ice algae extends the period favourable for larval fish feeding, by hastening the reproduction of copepods (Tourangeau and Runge 1991) whose immature stages are the main food of fish larvae (e.g. Last 1980). In southeastern Hudson Bay, Canadian Arctic, Drolet et al. (1991) report that larvae of sand lance *(Ammodytes* sp.) and polar cod experience starvation in the period that follows yolk sac resorption, and that this critical period is synchronized with peak abundance of food. This was hypothesized to be an adaptation to minimize mortality (i.e. critical period hypothesis of Hjort 1914, and match/mismatch hypothesis of Gushing 1972). In addition, most fish larvae are visual predators who require some minimum irradiance to locate and catch their prey (e.g. Blaxter 1975). According to Gilbert et al. (in press), in southeastern Hudson Bay, intensive feeding by sandlance and polar cod larvae only begins after breakup of the ice cover when irradiance in the upper water column no longer limits larval nutrition. It follows that the incidence of larval feeding under first-year ice not only depends on resource availability, but also on light regimes associated with ice-cover conditions and with the seasonal dynamics of under-ice river plumes (advection of turbid continental waters). Recruitment of marine fishes in this environment could be influenced by interannual variations in the timing between the critical period that follows yolk sac resorption and the production of prey, as well as in the timing of ice cover breakup. In the Antarctic, the most conspicuous fish member of the cryopelagic community is *Pagothenia borchgrevinki,* which has a circumantarctic distribution (DeWitt 1971) in surface waters beneath fast and floating ice (Eastman and DeVries 1985). Small *P. borchgrevinki* have been reported to feed actively on such ice zooplankters as copepods and ostracods (e.g. Kottmeier et al. 1985; Hoshiai et al. 1989), indicating that there is a food chain linking small fish of this species to ice algae, which is analogous to that described in the previous paragraph for fish larvae in the Arctic.

3 Marine mammals and seabirds

Even if a large proportion of algal production in polar waters sinks below .the euphotic zone as intact cells, a link back to the surface may be by vertically migrating zooplankton and zooplankton consumers such as pelagic fish (e.g. *Pleuragramma antarcticum,* Hubold 1985), penguins, seals (e.g. *Leptonychotes weddellii,* Plotz 1986), and whales. The magnitude of this upward transport has not yet been quantified. Another such link is by benthos-feeding diving mammals (e.g. walrus, Fay 1981; bearded seal, Burns 1981) and seabirds (e.g. eider ducks, Cramp and Simmons 1977; Bustnes and Erikstad 1988), although this is mostly limited to relatively shallow waters. In the Arctic water column, *Parathemisto libellula,* which has many similarities with *Euphausia superba* in Antarctic waters, plays an important role in under-ice food webs and is an important food item for seabirds and marine mammals (Dunbar 1957; McLaren 1958; Lowry et al. 1980; Finley et al. 1983). Marine birds, mammals, and fish in the Arctic not only feed on invertebrates, but also on fish and especially polar cod which may be a significant fraction of their diet (e.g. Klumov 1937; Andriashev 1954; Quast 1974; Bain and Sekerak 1978; Lowry et al. 1979; Brown 1980; Davis et al. 1980; Lowry and Frost 1981; Bradstreet and Cross 1982; Haug and Gulliksen 1982; Sekerak 1982; Mehlum and Giertz 1984). It is generally accepted that polar cod is a key link towards marine mammals and seabirds in the Arctic (Hognestad 1968; Raas 1968; Bain and Sekerak 1978; Bradstreet and Cross 1982; Craig et al. 1982).

Export and sequestration of biogenic carbon under ice cover

As explained in the Introduction, export of biogenic carbon does not necessarily mean sequestration in sediments or deep waters. The following discussion reviews those processes that favour production/accumulation, export, and sequestration of biogenic carbon as well as those that influence mineralization in the upper ice-covered ocean.

1 Algal production and accumulation of organic matter

Algal blooms. Legendre (1990) defines algal blooms as rapid increases in biomass, caused by locally enhanced primary production and resulting in abnormally high cell concentrations. Algal blooms have a high potential for exporting particulate organic matter from the euphoric zone, becuase they result from low recycling and a large degree of uncoupling between increased primary production and grazing by zooplankton. As a consequence, blooms often lead to high sedimentation of intact cells and faecal pellets (Legendre 1990).

In ice-covered seas, high algal concentrations have been reported in association with several types of blooming conditions (Table 3). In addition to ice-related blooms, there is progressive accumulation of organic matter in sea ice, especially in Arctic multi-year ice, whose fate may potentially be similar to that of blooms, i.e. mass sedimentation. Assuming the multi-year ice to be 3 m thick (as in the above Section on Arctic microalgal production within the sea ice cover), average values of particulate organic carbon (POC) in the ice are ca. 0.7 to 1.3 gCm"^{2} for winter and summer respectively, corresponding to ca. 10-20mg Chi *am*'^{2} (original POC concentrations in multi-year ice from Table 6 in Melnikov 1989, and C:Chl a = 60 from Demers et al. 1989). These values are comparable to many of those listed in Table 3, for first-year ice. This accumulation is especially important since >90% of the primary production in multi-year ice-covered waters occurs in the ice (Melnikov 1989). Biological production in ice-covered environments thus often results in high concentrations of organic matter, within or in association with the ice matrix, which may lead to significant export of biogenic carbon.

Grazing by large herbivores. Legendre (1990) has established that phytoplankton outbrusts are not possible when grazing pressure by large herbivores is high. As a general rule, algal blooms should develop as an inverse function of grazing pressure. Despite the fact that large grazers have been reported to occur within the ice and to actively graze algae close to the undersurface of the ice (see above), high concentrations of ice algae clearly indicate that grazing by large herbivores most often does not track primary production in ice-covered areas. This also seems to be the case in some ice-free polar waters, e.g. the Barents Sea, where herbivorous zooplankton consume only 5-20% of particulate primary production during the spring bloom, resulting in sedimentation of 250 nig Cm"^{2} day"^{1} of phytoplankton with peak values possibly up to 1000 mgCm"^{2} day"^{1} (Eilertsen et al. 1989). Similarly, Wassmann et al. (1990) observed mass sedimentation of *Phaeocystis pouchetii* in the Barents Sea because the zooplankton community was not able to graze the spring phytoplankton bloom.

Microbial food web. Another factor that may affect phytoplankton blooms is consumption and respiration of primary producers, within the euphotic zone, by the microbial food web (which comprises, in addition to small phototrophic cells, heterotrophic bacteria and protozoa; Azam et al. 1983). In warm tropical and subtropical waters, bacterial metabolism and growth are rapid, so that the turnover time of phytoplankton production is of the order of 1 to 3 days; as a consequence, much of the biogenic carbon does not reach the metazoans. In contrast, Pomeroy and Diebel (1986) proposed that reduced activity of the microbial food web, caused by low temperature, could explain the high proportion of the spring bloom that finds its way to metazoan consumers in Newfoundland waters. More generally, Pomeroy and Wiebe (1988) postulated that the microbial food web is often

Table 3. Examples of first-year ice-algal concentrations associated with blooming conditions

Environment	Concentration	References
Freeboard (Antarctic sea ice)	11-80 mg Chi *a* m	Kottmeier and Sullivan (1990) Garrison and Buck (1991)
Interstitial bottom ice (Arctic)	8-23 mg Chi *a* m~^{2} 8-26 mg Chi a m"^{2} 19-130 mg Chi a irT^{2} 2-9 mg Chi am"^{2}	Alexander et al. (1974) Homer and Schrader (1982) Smith et al. (1987, 1989) Dieckmann et al. (1990)
Interstitial bottom ice (Antarctic pack ice)		
Ice platelet layer (Antarctic fast ice)	up to 770 mg Chi a m"	Palmisano and Sullivan (1983), Grossi et al. (1987), Arrigo et al. (1990) Tremblay et al. (1989) Smith et al. (1985) Niebauer et al. (1990) Smith and Nelson (1985) Legendre et al. (1981)
Ice-water interface (Arctic)	<20mg Chi a m~^{2} 10	
Retreating ice edge (Arctic)	mg Chi *a* m~^{3} 27-^1mgChl am"^{3} up to	
Retreating ice edge (Antarctic)	^*6* mg Chi am"^{3}	
Under-ice pycnocline (Arctic)	<1.5mg Chi a m"^{3}	

greatly suppressed at temperatures < 2°C. This could explain the high organic biomasses often observed in ice-covered waters.

It could be argued against the above hypothesis that bacteria are present in the sea ice environment (e.g. Atlas and Griffiths 1984; Sullivan and Palmisano 1984; Grossi et al. 1987; Kottmeier et al. 1987; Bunch and Harland 1990) as well as such protist members of the microbial food web as ciliates and foraminifera (e.g. Homer and Alexander 1972; Grainger et al. 1985; Gradinger et al. (1992), for the Arctic; Fenchel and Lee 1972; Garrison et al. 1986; Spindler and Dieckmann 1986; Garrison and Buck 1989; Agatha et al. 1990, for the Antarctic). Pomeroy and Wiebe (1988) suggested that bacetrial activity at such low temperature might be favoured by the high concentration of substrate provided by the blooming ice algae. On the other hand, Gradinger et al. (1992) report strong development of bacteria and ciliates in sea ice with the snow cover artificially cleared, which did not prevent, however, diatoms from blooming. Thus, the microbial food web may be active in the ice environment, but it does not seem to deeply influence the accumulation of high algal biomasses.

2 Export of bio genie carbon

The accumulated biomass will eventually be exported through sedimentation. In addition to the factors briefly reviewed above, the export of biogenic carbon from the upper ocean is influenced by various ecosystem properties (see Legendre and Le Fevre 1991). These include, for polar waters, the production of plankton organisms with calcareous tests and the various pathways into which production is channeled.

Sedimentation. According to Legendre (1990), when in situ grazing and recycling are moderate, algal blooms often result in high sedimentation of intact cells and faecal pellets. This occurs in ice-covered seas, for example at a retreating ice edge in the western Ross Sea (Antarctic Ocean) where > 50% of the particulate silicon is deposited to the bottom (Smith and Nelson 1986; Nelson and Smith 1986), which is consistent with/-ratios>0.5 (ratio of new to total production, as measured from nitrogen uptake) reported by Olson (1980). Concerning ice algae, some researchers (e.g. Apollonio 1965; Alexander 1980; Leventer and Dunbar 1987, 1988) have suggested that most of them sink to the bottom at the time of ice melt. However, grazing may also be active, as reported for example in Hudson Bay where ca, one third of the sinking material under the sea ice results from grazing by large herbivores (Tremblay et al. 1989). In some other cases, little export was observed. For example, Carey (1987) found that only 1-10% of the ice algal carbon reached the bottom at Narwhal Island, Alaska, and that there was no increased downward flux when the ice melted. Thus, depending on local conditions, the proportion of algal production exported under ice cover may vary quite significantly.

Calcareous plankters. Many plankton organisms have calcareous skeletal structures, that consist mainly of $CaCO_3$ with small and variable proportions of other substances such as $MgCO_3$. These organisms, which include protozoa (foraminifera) and metazoa (mainly thecosomatous pteropods) export an extra share of carbon when sedimenting to depth. Given their relatively large size and high density, foraminifera and planktonic pteropods sink rapidly, e.g. between 65 and 2500m day"^{1} for foraminiferal and pteropod tests with values >5000mday"^{1} for pteropods ca. 10 mm (Honjo 1980; Takahashi and Be 1984). Although much smaller than many other marine organisms (e.g. vertebrates), calcareous plankters may export significant amounts of $CaCO_3$ because of high turnover rates, e.g. generation times of foraminifera on the order of weeks (Hemleben et al. 1989).

In the Weddell Sea, the pelagic foraminifer *Neogloboquadrina pachyderma* has been reported to occur in large concentrations and actively grow in new and consolidated ice as well as in the underlying water column, averaging >6 x 10^4 forams m~^{2} in both the ice and the underlying 60-m water column (e.g Spindler and Dieckmann 1986; Spindler et al. 1990; Dieckmann et al. 1991). This contrasts with the tropical oligotrophic ocean where foraminifera are found in very low numbers (e.g. Be 1977), and the Arctic sea ice which is practically devoid of foraminifera (Spindler 1990; Dieckmann et al. 1991). The high concentrations of *N. pachyderma* in the ice-covered Weddell Sea, with sinking velocities ca. 500-1000m day"^{1} (derived from the data of Takahashi and Be 1984, and Reynolds and Thunell 1985), suggest that these organisms may play a significant role in the export and sedimentation of carbon in some Antarctic waters.

Pteropods are often present in the under-ice water column (e.g. Kobayashi 1974; Spoel and Boltovskoy 1981; Herman and Andersen 1989). The average molar ratio of carbon to nitrogen in marine plankton is C:N = 6.6 (Redfield 1958; Redfield et al. 1963). Using data from the literature, Legendre and Le Fevre (1991) report C:N for thecosomatous pteropods from 10% to almost 100% above the Redfield ratio. Planktonic pteropods, including those from polar waters, can therefore contribute significantly to the export of biogenic carbon. In fact, it has been estimated that the pelagic aragonite flux (corresponding mainly to pteropod shells) accounts for at least 12% of the worldwide carbonate flux to the deep ocean (Berner and Honjo 1981) and may exceed the calcite flux of planktonic foraminifera by a factor of five (Betzer et al. 1984). Aragonitic shells, however, are 50% more soluble in seawater than calcite (Mucci 1983), so they dissolve during settlement through the water column in >98% of oceanic regions (Berger 1978; Byrne et al. 1984; Farby 1990).

Concerning the biogeochemical cycle of carbon, the production of plankton organisms with calcareous tests leads to rather complex results. Limestone deposits were derived, through biological processes, from atmospheric CO_2 but it has been postulated (e.g. Volk 1989) that, at some geological time scales (e.g. glacial/interglacial oscillations), the precipitation of calcite by marine organisms results in higher atmospheric CO_2 through changes in the carbonate chemistry of surface waters (i.e. lower alkalinity and concentration of total dissolved CO_2). This effect has been described for coccolithophores (e.g. Dymond and Lyle 1985) and also coral reefs (Berger 1982). On the other hand, planktonic organisms with calcareous tests generally sink faster than other organic particles produced in surface waters (see above), thus reducing the amount of carbon respired during their downward transit. In addition, the adsorption of organic matter onto calcite particles (Suess 1973) may contribute to increase the burial of organic carbon sediments. The production and export of biogenic carbon by calcareous organisms may therefore lead to high sequestration of inorganic and organic carbon, but the overall effect of calcite precipitation by organisms could, at least on some time scales, be an increase in atmospheric CO_2. The phenomenon is therefore of major significance for the biogeochemical flux of carbon, on both short and long terms.

Export pathways. Production may be exported through a variety of pathways, which have been reviewed by Legendre and Le Fevre (1989) together with their hydrodynamic control and their significance in terms of particulate organic matter (POM) fallout from the surface layer. Concerning large cells (> *5* ^m), these pathways include sinking of intact algae and grazing by herbivores leading to production of faecal pellets as well as active transport by vertically migrating organisms. Detrital biogenic material accumulated in hydrodynamic traps (e.g. sea ice, pycnoclines, etc.) may be grazed by such microphagous gelatinous feeders as doliolids and appendicularians, which are known to occur in the under-ice water column (e.g. Harbison 1988). Finally, ultraplankton (< 5 *um)* may be incorporated into marine snow or be directly grazed by such microphagous feeders as appendicularians (i.e. "baleen-whale" feeding; Fenchel 1984), which are present in the under-ice water column (e.g. Garrison and Buck 1989, in the Weddell Sea). Although the presence of small phototrophic cells has not been widely recognized in the ice-covered environment, they have been reported for Hudson Bay (Legendre et al. 1987). The presence of heterotrophic members of the microbial food web in this environment is better documented (see Microbial food web, above).

Mass sedimentation of large intact cells, at rates that may exceed 100 m day ~ (Goldman 1988, refs. cited therein), mainly occurs under bloom conditions and, as explained above, is also expected to take place at the time of ice melt. As already mentioned, active grazing by herbivores leads to sedimentation of faecal pellets. These are wrapped in a protective membrane, that somewhat retards degradation during the downward transit. Faecal pellets of copepods generally sink with velocities ca. 100 mday"^{1}, while those of gelatinous zooplankters may sink faster (Alldredge 1984). In addition, gelatinous organisms are instrumental in the production of marine snow, where ultraplankton (which would not normally sink) are aggregated together with other material and thus made available for export to depth. Some export pathways will thus favour rapid transfer of biogenic material to depth, while long and complex food webs will retard transfer and thus increase the amount of organic carbon respired in the upper water column.

Spatio-temporal decoupling. One major effect of the sea ice to decouple production from export in both space and time. In the case of first-year ice, export occurs several weeks, and in some cases months, after biomass has accumulated in the ice matrix (e.g. Leventer and Dunbar 1987; Grossi et al. 1987). Concerning multi-year ice, which is prevalent in the Arctic Ocean, organic matter is accumulated during several years, and the bulk of it is released rapidly at the time of ice melt. In the case of land-fast ice, biogenic material is flushed into the water column at the production site, while the organic load of drifting pack ice may be released far from the production zone. This is especially true of multi-year ice in the Arctic ice pack, which accumulates organic matter over many years in the Beaufort gyre and releases it upon melting in Fram Strait (Melnikov and Pavlov 1978; Larssen et al. 1987; Pfirman et al. 1989). According to Melnikov (1989, p. 62), the sea ice transports 0.4-0.8 x 10^6 tonnes of particulate and 5.6-12.5 x 10^6 tonnes of dissolved organic carbon every year through Fram Strait; similarly, Gulliksen and L0nne (1989) estimate that the yearly loss of sympagic organisms to deeper waters in the Strait may be 0.7 x 10^6 tonnes.

3 Mineralization of exported biogenic carbon and sequestration

It has been explained in the Introduction that the sequestration of carbon is not necessarily equivalent to the export of biogenic carbon. One important aspect, especially in deep water areas, is the circulation which may either favour the retention of CO_2 at depth for periods of interest to global change or, on the contrary, rapidly bring back the CO_2 toward the atmosphere. In addition to the deep ocean circulation, various processes related to ecosystem properties discussed above may also influence sequestration of the exported biogenic carbon.

Dissolution of calcareous tests. An important aspect of carbonate export to deep waters is the dissolution of calcareous tests with depth. In deep waters, carbonate-carbon is progressively released into the water column, so that its fate (i.e. rapid return to the atmosphere versus sequestration in the deep waters) depends on the interaction between sinking velocity and circulation. On the other hand, in waters shallower than the compensation depths of calcite and aragonite, carbonate sediments may sequester carbon for millions of years. In the Antarctic Ocean, the compensation depth of calcite is quite shallow (e.g. Hemleben et al. 1989, Fig. 11.2) with values in the Weddell Sea varying between 250 and 3700 m (Anderson 1975). Carbonate sediments are known in both the Antarctic and Arctic basins (e.g. Anderson 1975, for the Antarctic; Kennett 1970; Stehman 1972, for the Arctic).

Respiration. Every transfer in the food web is accompanied by mineralization of organic carbon into CO_2 (i.e respiration), with potential rapid return to the atmosphere. It follows that the proportion of biogenic carbon potentially sequestered will be an inverse function of the length and complexity of the food webs (e.g. Legendre and

Le Fevre 1991). Rapid sedimentation of intact cells or other biogenic particles (e.g. some faecal pellets) into deep waters would favour sequestration of carbon, since the amount of organic material respired during the downward transit is largely determined by sinking velocity. At the other extreme, the microbial food web in surface waters will recycle toward the atmosphere most or all of the carbon fixed by the primary producers.

Long-lived dissolved organic matter (DOM). It has been proposed that the concentrations of dissolved organic carbon (DOC) and nitrogen (DON) in oceanic waters are much higher than previously thought (Sugimura and Suzuki 1988). The implication of these new values and the results from a modelling exercise suggest that about half the new phytoplankton production could be exported to depth as long-lived DOM, with a characteristic lifetime of 200 years (Toggweiler 1989). Legendre and Gosselin (1989) have shown that the partitioning of new production into POM (particulate organic matter) and DOM, under the present conditions of global change, may effectively uncouple the export of DOM from that of POM, thus leaving the usually measured/-ratio without much meaning in terms of biogenic export to depth. However, it must be realized that the long-lived DOC could chemically sequester carbon in the surface layer, for periods of interest to global change (i.e. hundreds of years), before this carbon is transferred and released as CO_2 (respired) into the deep waters. For the time being, the status of long-lived DOM in polar waters is not known.

Sequestration of biogenic carbon in Arctic and antarctic waters

Estimates of biogenic carbon production in the Antarctic and Arctic seas were derived earlier in this paper (Tables 1 and 2). Following a parallel approach, it might have been interesting to derive, using the various transfer mechanisms described above and some measured fluxes, a budget for carbon export and sequestration in polar waters. However, the literature on the subject is presently very scarce, and the exercise will have to wait a few years. Nevertheless, some general information may be briefly reviewed.

Arctic Ocean. According to Anderson et al. (1990), the upper layers of the Arctic Ocean are the site of active biological pumping of atmospheric CO_2, for which they provide a sink. However, there would be little penetration of this CO_2 into the deep waters. This does not imply that all the CO_2 dissolved in Arctic sea waters is eventually lost to the atmosphere, since this CO_2 could be sequestered through deep convection in the North Atlantic Ocean (winter time), or fixed back into organic particles by local primary production in waters that leave the Arctic Ocean (mainly through Fram Strait and also the Canadian Archipelago; Moritz et al. 1990) and thus be partly exported to depth. Within that context, major polynyas located in areas where waters flow out of the Arctic Ocean (e.g. the Northeast Water polynya south of Farm Strait, and perhaps the North Water polynya north of Baffin Bay) may play a role in the sequestration of carbon, and also provide a window to observe the various processes involved. In the event of global warming, the prevalence of Arctic polynyas is likely to increase (Manak and Mysak 1989), so that the processes of CO_2 export presently active may then make an even greater contribution to the sequestration of CO_2 in the oceans.

Moritz et al. (1990) report that the Arctic Ocean has been hypothesized to play an important role in the global carbon cycle via the production and vertical flux (and subsequent lateral advection) of organic matter on the shelves and by the incorporation of inorganic carbon into deep water formed during winter in the North Atlantic. They stress that the role of biological processes in sequestering carbon has not yet been investigated on appropriate spatial and temporal scales. Finally, they conclude that, to understand the role of the Arctic in the global carbon cycle, there is need to quantify the magnitude and variations in space and time of the production, cycling and vertical flux of biogenic material from the euphotic zone.

Antarctic Ocean. Indirect evidence suggests that the biological CO_2 pump is active in these waters. For example, Smith and Nelson (1985) and Wilson et al. (1986) describe a large diatom bloom at the receding ice edge in the Ross Sea which probably remained in the water column for only a short time. These authors emphasize that such production events, which may have gone unnoticed in past studies, can be instrumental in the deposition of the large amounts of diatomaceous ooze found in the Southern Ocean. The importance of carbon sequestration would then depend on the deep release of CO_2 from sedimenting algal material. Similarly, in the Atlantic sector of the Antarctic Ocean, Wefer et al. (1990) report that the flux of biogenic particles is often restricted to a short period, during which most of the settling material is incorporated in krill faecal pellets that sink rapidly to the bottom (several hundred metres per day) where the carbon is mineralized.

Model studies have indicated that variations in the efficiency of the biological pump in the Antarctic Ocean could lead to alterations in the concentration of atmospheric CO_2 (e.g. Siegenthaler and Wenk 1984; Sarmiento and Toggweiler 1984; Sarmiento et al. 1988). More recently (e.g. Joos et al. 1991; Peng and Broecker 1991), such exercises were conducted to test the suggestion that fertilizing the Antarctic Ocean with iron (in order to enhance the biological pump) might offset the continuing increase in atmospheric CO_2, to conclude that the only effective and reliable strategy is still the control of anthropogenic emissions. In these models, which are primarily geochemical (phosphorous-based) but also include some basic hydrodynamic features, the downward flux of particles allows to balance the budgets between the surface and deeper layers so as to reproduce the observed chemical properties. Better knowledge of the actual functioning and efficiency of the biologically driven CO_2 pumps (see the Introduction), in Antarctic waters, could therefore improve models of biogeochemical fluxes in the ocean.

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