THE BIOLOGICAL CO_2 PUMP IN SEASONALLY ICE-COVERED WATERS[*]

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Abstract: Pools of biogenic carbon in oceans have been defined by reference to the time elapsed between the photosynthetic uptake of carbon and its return as carbon dioxide to surface waters or the atmosphere (*i.e.* turnover time). The three pools are: short-lived organic carbon ($< 10^{-2}$ years), long-lived organic carbon (10^{-2} to 10^2 years) and sequestered biogenic carbon ($> 10^2$ years). In seasonally ice-covered waters, as in other aquatic environments, primary production occurs over a large range of sizes, which can be partitioned into three classes, *i.e.* large cells ($> 5 \mu$m), small cells ($< 5 \mu$m), and dissolved organic carbon. In these waters, there is a wide array of pathways that channel the three size classes of primary production into long-lived and sequestered biogenic carbon. Biogenic carbon is often actively transferred from (large) ice algae to large metazoans (long-lived organic carbon). Small biogenic particles can escape the short-lived carbon pool through grazing by microphagous zooplankton such as pteropods, doliolids, appendicularians and Antarctic krill, or through incorporation into organic aggregates (*e.g.* marine snow). In addition, there are direct and indirect sedimentation pathways for ice-related algae. Finally, the alternation between biological pumping of CO_2, during the ice-free season, and algal carbon uptake, during the ice-covered period, creates unique conditions for the potential sequestration of atmospheric CO_2.

1. Turnover of Biogenic Carbon in Oceans

In the oceans, there are various mechanisms that pump CO_2 from the atmosphere into ocean depths. These mechanisms are important for the sequestration of carbon, *i.e.* the removal of CO_2 from the atmosphere and surface waters for periods of interest to global warming (at least a few hundred years). Volk and Hoffert (1985) identified three CO_2 pumps in oceans. The solubility pump (physical) is especially active in areas of deep water formation (*i.e.* polar regions), where cooling of surface water drives a flux of CO_2 from the atmosphere into the ocean, and subsequent sinking of the dense water ensures sequestration of the dissolved inorganic carbon. The two other pumps are of biological nature. The carbonate pump depends on the sedimentation of organisms with calcareous tests. The soft-tissue pump (also known as the biological CO_2 pump) is activated by the photosynthetic incorporation of inorganic carbon into organic molecules by microscopic algae, followed by export to depth; the biologically driven downward flux of carbon causes a proportional flux of CO_2 from the atmosphere into the ocean. The present paper examines the characteristics of the latter two pumps in polar waters, with regards to ice-related biological production.

Table 1.   Typology of biogenic carbon in oceans, as defined by the turnover time of CO_2 (i.e. the period between the photosynthetic uptake of dissolved inorganic carbon and the return of this carbon as CO_2 in surface waters or the atmosphere), and terms used in the literature to characterize the processes the lead to the three pools of biogenic carbon. Adapted from Table 1 of LEGENDRE and LE FÈVRE (1992).

	Turnover time	
$< 10^{-2}$ years	10^{-2} to 10^2 years	$> 10^2$ years
Short-lived organic carbon	Long-lived organic carbon	Sequestered biogenic carbon
Recycling	Export	Sequestration

Biogenic carbon in oceans may be classified by reference to its turnover time, which is defined as the time elapsed between the photosynthetic uptake of carbon and its return as carbon dioxide to surface waters or the atmosphere (LEGENDRE and LE FÈVRE, 1992). These authors proposed a typology based on two break points in the continuum of turnover times, i.e. 10^{-2} and 10^2 years. This defines short-lived organic carbon ($< 10^{-2}$ years), long-lived organic carbon (10^{-2} to 10^2 years) and sequestered biogenic carbon ($> 10^2$ years). Table 1 summarizes the typology, giving in parallel the terms used to characterize the processes that lead to the three pools of biogenic carbon.

As explained by LEGENDRE and LE FÈVRE (1992), short-lived organic carbon consists of organisms with high turnover rates and labile dissolved organic compounds. This type of carbon mainly transits through the microbial food web, which comprises small phytoplankton, heterotrophic bacteria and protozoa (flagellates and ciliates). In the microbial food web, small phytoplankters and bacteria are grazed by flagellates, which are in turn prey to ciliates; the activity of flagellated and ciliated protozoa remineralize nutrients, which are used by the small phytoplankton and bacteria. Dissolved organic carbon (DOC) exuded by phytoplankton is used as substrate by bacteria. This differs from the microbial loop, where photoautotrophs are largely absent so that bacteria then use dissolved organic compounds produced by protozoa, who in turn graze upon bacteria, hence a loop (see RASSOULZADEGAN, 1993). Long-lived organic carbon includes renewable marine resources. It flows into long-lived animals, and it also includes microbial heterotrophs involved in the breakdown of organic matter derived from large heterotrophs. Sequestered biogenic carbon comprises organic remains buried in sediments (including oil), inorganic deposits of biological origin (e.g. calcareous ooze, coral reefs, continental limestone), refractory dissolved organic matter, and dissolved CO_2 in deep waters resulting from the oxidation of organic compounds (respiration). Climate changes at various time scales (e.g. glaciations, interglacial oscillations, and the possible ongoing global warming) may be related to (or mediated by) variations in the pool of sequestered carbon.

Primary production may be respired within the euphotic layer, or it may be exported to large heterotrophs or toward the deep ocean. The size of photosynthetic products, i.e. large phytoplankton (>2–5 μm), small phytoplankton (<2–5 μm) and DOC, strongly influences whether biogenic carbon is short-lived, long-lived or sequestered. However, the fate of primary production in oceans is ultimately determined by the trophic pathways through which it is channeled. It must be noted that the size
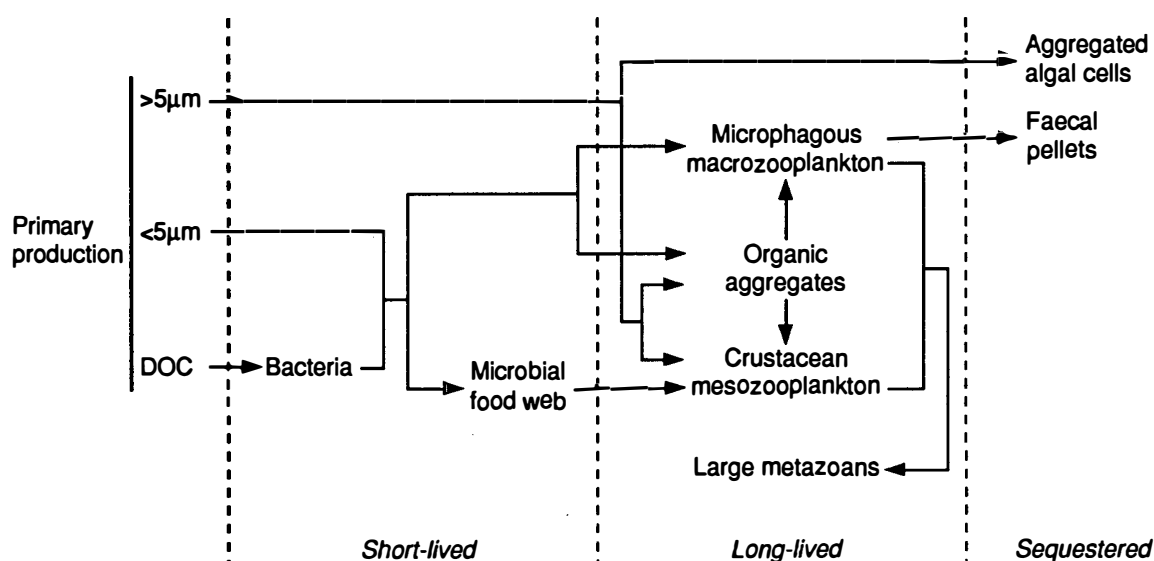
Fig. 1.   Major trophic pathways in marine water, from the three size classes of primary production (i.e. cells >5 μm, cells <5 μm, and dissolved organic carbon) to the three pools of biogenic carbon (i.e. short-lived, long-lived, and sequestered).

spectrum of photosynthetic products is in fact continuous, from the largest phytoplankton down to the smallest exuded organic molecules, so that size limits between the large and the small phytoplankton and DOC are arbitrary.

Figure 1 shows how the major trophic pathways in marine waters channel the three size classes of phytoplankton production (*i.e.* large and small cells, and DOC) into the three pools of biogenic carbon (*i.e.* short- and long-lived, and sequestered). Short-lived organic carbon mainly results from the oxidation of DOC by heterotrophic bacteria and from respiration within the microbial web. The flux of organic carbon into the long-lived pool is mediated by mesozooplankton (mainly crustaceans) grazing on large cells, on organic aggregates (*e.g.* marine snow) and on microzooplankton, and by microphagous macrozooplankton feeding on small particles and on aggregates. Part of this flux reaches large metazoans such as fish, marine mammals and birds. Finally, sedimentation to deep waters of rapidly sinking aggregated algal cells and fecal pellets (mainly from microphagous macrozooplankton; see below) is a condition for the sequestration of biogenic carbon at depth. As mentioned above, sequestered biogenic carbon is found in both sediments and deep waters, in the latter case as respiratory carbon.

2.   Trophic Pathways in Seasonally Ice-covered Waters

2.1.   Primary and bacterial production

Several of the production processes and export pathways briefly described in the previous section exhibit some special characteristics in seasonally ice-covered waters. These characteristics are discussed by reference to Fig. 1, in order to assess their significance for the partitioning of ice-related primary production among the three pools of biogenic carbon. It will be shown that, in seasonally ice-covered waters, the three size classes of primary production are channeled into long-lived and sequestered biogenic

carbon through a large variety of pathways.

Concerning the production of large photosynthetic cells in seasonally ice-covered waters, algae within the sea ice (which are dominated by pennate diatoms; see the review of HORNER et al., 1992) account for a large proportion of the total annual primary production. In the Southern Ocean (south of 60°S), this proportion is >20% and, in the Arctic Ocean (north of 65°N), it is >25%. Overall, the proportion of the total annual production associated with sea ice (i.e. within the ice, in the under-ice water column, and at ice edges) is >80% in the Southern Ocean, and ca. 35% on the shelves of the Arctic Ocean (see the review of LEGENDRE et al., 1992).

The importance of small primary producers, in polar waters, is poorly documented. A few studies suggest that, in at least some situations, phytoplankton biomass and production could be dominated by the small size fraction. In the Greenland Sea Gyre (75°N; $-0.8 < T < 0.6°C$), for example, phytoplankton $<5 \mu m$ account for 50–70% of the total Chl a, and 35–55% of the total primary production, in June (LEGENDRE et al., 1993). Similarly, in the circumcontinental waters of Antarctica (HEWES et al., 1990), regions with <1 mg Chl a m^{-3} are dominated by nanoplankton ($<20 \mu m$), which typically account for >50% of the autotrophic biomass, in January–February. In contrast, waters containing >2 mg Chl a m^{-3} are dominated by microplankton ($>20 \mu m$). In southeastern Hudson Bay, Canadian Arctic, ROBINEAU et al. (1994) report that ultra-algae (0.4–5 μm) occur primarily at the ice bottom, but that they are also present at the ice-water interface and in the under-ice water column. Concentrations range between 36×10^6 and 63×10^9 cells m^{-3}, and the contribution to total Chl a varies from 9 to 96%, in April–May.

Heterotrophic bacteria are believed to primarily utilize DOC exuded by algal cells (for the significance of this flux, see: AZAM and AMMERMAN, 1984; AZAM and SMITH, 1991; LEGENDRE and RASSOULZADEGAN, 1995). Part of the DOC taken up by bacteria is used for metabolic processes and rapidly respired (short-lived carbon pool), but part is passed on to the food web and may thus become longer-lived. This is why, for example, LEGENDRE et al. (1992) included bacterial carbon uptake in their estimates of total primary production south of 60°S. There, the production of bacteria is, in the under-ice water column, 12 times that of phytoplankton and it is, in the whole Southern Ocean, 25% that of algae. There is no comparable information for the Arctic Ocean.

Thus, according to the environment (i.e. ice matrix, ice-covered waters, or marginal ice zone), there are different proportions of primary production in the small and large cells and in DOC. However, the three size classes play some role in each environment.

2.2. Organic aggregates

In pelagic environments, there are two major types of organic aggrgates. The most frequently cited is marine snow, which continuously forms in the water column and sinks. According to SILVER et al. (1986), sedimentation of small phytoplankton and bacteria occurs mainly through their incorporation into marine snow. The second type of organic aggregates results from particles that accumulate in hydrodynamic traps (e.g. front, pycnocline; see LEGENDRE and LE FÈVRE, 1989). These particles include ungrazed large and small algae and detritus. Contrary to marine snow, trapped organic particles sink little or not. It has been suggested that the accumulated biomass in hydrodynamic

traps may favor the development of a microbial web (accumulation biotope; LE FÈVRE, 1986) and grazing by microphagous macrozooplankton (see below; *e.g.* LE FÈVRE and FRONTIER, 1988). The various types of organic aggregates are also grazed by crustacean mesozooplankton. Since sediment trap studies indicate that the bulk of the deep flux of organic material often consists of sinking fecal pellets (*e.g.* BRULAND and SILVER, 1981; MADIN, 1982, and refs. therein) and not organic aggregates, the latter are not shown, in Fig. 1, as significantly contributing to the sequestration of biogenic carbon.

In Antarctic coastal waters (MARCHANT, 1996), the formation and distribution of marine snow is similar to that observed in other marine waters, and it is possible that krill use these organic aggregates as food. In ice-covered waters, the ice itself is a very effective trap, into which organic matter accumulates over several months (first-year ice) or years (multi-year ice), before being released in the water column (*e.g.* LEGENDRE *et al.*, 1992). Many protozoan and metazoan organisms are known to thrive within the sea ice (SPINDLER, 1996), where they actively graze microalgae and bacteria. In addition, melting of sea ice creates a strong pycnocline, into which sinking particles may accumulate, at least temporarily. Organic particles in such hydrodynamic trap could be grazed by microphagous macrozooplankton (*e.g.* pteropods, doliolids and appendicularians) which are present in the under-ice water column and at ice edges (see below).

2.3. Microbial and herbivorous pathways

Figure 1 shows two major grazing pathways through which primary production is channeled, *i.e.* herbivorous and microbial. The third pathway (microphagy) is discussed in Section 2.4. South of 60°S, phytoplankton blooms at retreating ice edges, in the deep waters that surround Antarctica, account for at least 60% of the total microalgal and bacterial production (see LEGENDRE *et al.*, 1992). The basic mechanism for these ice-edge blooms is the stabilization of the upper water column by melt water, combined with high irradiance. This results in optimal light conditions for cells in the surface mixed layer (refs. in LEGENDRE, 1990). There are two types of production and grazing systems. In the Ross Sea (SMITH and NELSON, 1985; NELSON and TRÉGUER, 1992), blooms (>20 mg Chl *a* m^{-3}) may extend several hundred kilometres seaward from the retreating ice edge. Somewhat lower biomasses are found in Weddell Sea blooms (2–10 mg Chl *a* m^{-3}), which extend over 100–150 km (LANCELOT *et al.*, 1993b) and are dominated by nanoplankton species. In the Weddell Sea, most of the primary production at receding ice edges is processed by the microbial web, which is the main link toward the krill and other mesozooplankton. According to LANCELOT *et al.* (1993a), the role played by krill explains the difference between the two types of ice edges. In the Ross Sea, where overwintering krill is absent or scarce, surface waters at the time of ice melt are seeded by ice diatoms and also *Phaeocystis*, so that there are strong blooms dominated by these taxa. In the Weddell Sea, overwintering krill reduces seeding by ice diatoms of the under-ice water column, so that the ice-edge assemblage is dominated by nanophytoplankton. The development of an efficient microbial food web, which tracks primary production, prevents phytoplankton from reaching high concentrations. Thus, the first type of ice edge is dominated by herbivores, and the second by the microbial food web. In the first, primary production may reach mesozooplankton directly whereas, in the second, it is mainly channeled through the microbial web. Part of the

MARINE MAMMALS   FISH

Adults   Larvae

BENTHOS   COPEPODS

Zooplankton

Adults   Larvae   Adults ————► Young

SEDIMENTED   SUSPENDED
ALGAE   ALGAE

Settling   Suspension   Seeding
to bottom   In water   phytoplankton
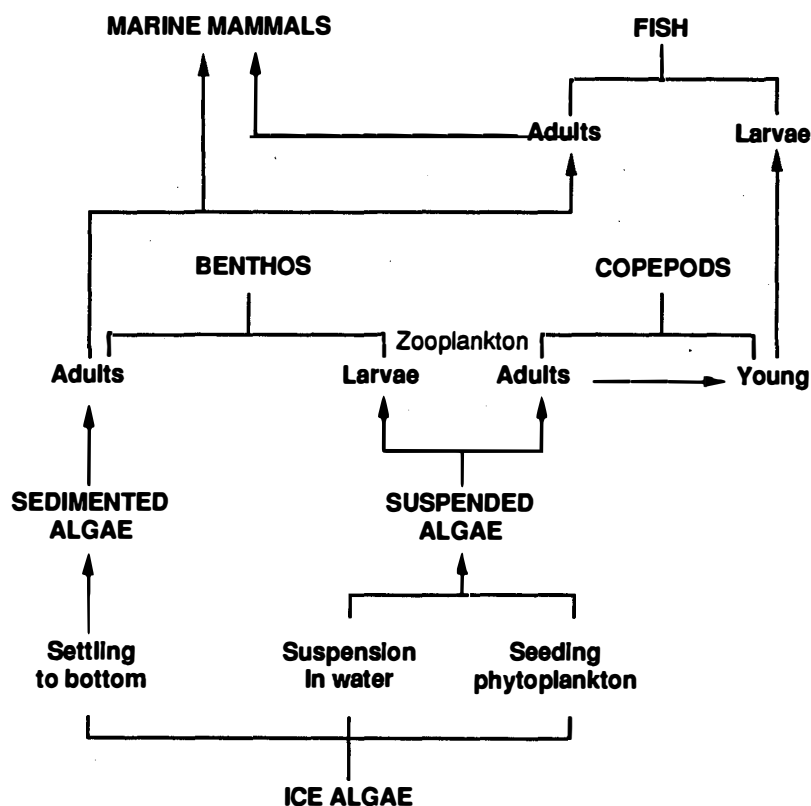
ICE ALGAE

Fig. 2. Fate of ice algae on Arctic continental shelves: food web toward
marine mammals and fish (i.e. marine resources). It must be noted
that ice algae are not the sole primary producers that support
zooplankton, zoobenthos, fish and marine mammals.

biogenic carbon in large zooplankton (including krill) eventually reaches large metazoans.

Polar food webs, in both Arctic and Antarctic waters, often transfer biogenic carbon from ice algae toward large metazoans. Figure 2 illustrates the ice-algal food web on Arctic continental shelves, as seen from the view point of marine resources, i.e. marine mammals and fish. Major determinants of stocks are, for marine mammals, the amount of food (i.e. fish and benthos) and, for fish, the survival of young stages and the amount of food for adults. The survival of young fish (i.e. larvae and juveniles) is very sensitive to the availability of food in early life (often copepod nauplii), and important food items for adult fish are zooplankton and benthos. Thus, overall, benthos and zooplankton are major determinants of mammals and fish.

The abundance of benthos, which are staple food for marine mammals and adult fish, is conditioned by the survival of their larvae. Most larvae of benthic organisms are planktonic, and their survival depends for a large part on the availability of suspended microalgal food. It is likely that ice algae are important food for those larvae of benthic organisms that are present in the under-ice environment. Stocks of adult benthos also depend on the sedimentation of high-quality food particles, of which part is provided by the sedimentation of ice algae at the time of ice melt. Concerning fish larvae, it was already mentioned that the availability of suitable zooplanktonic food is critical for their survival. In Arctic waters, larvae of many fish hatch under the sea ice, and most of these

larvae feed on young copepods. In spring, adult copepods require additional food for egg production in the under-ice water column and, in several instances, this food is provided by algae (diatoms) released from the sea ice. Another important source of food for zooplankton is the spring–summer phytoplankton bloom, which occurs a few weeks after ice break-up and is often seeded by ice algae.

In coastal southeastern Hudson Bay, for example, the timing and the magnitude of copepod egg production are key determinants of both the dynamics of copepod populations in early spring (RUNGE et al., 1991) and the availability of prey to larval fish (FORTIER et al., in press). In the under-ice water column, grazing on small algae may contribute to the early reproduction of small cyclopoid copepods (e.g. Oithona, Oncaea), whose nauplii are dominant before the ice breaks up (FORTIER et al., 1995). At the same time, grazing on larger ice algal cells hastens the maturation of calanoid copepods, thus favoring maximum reproduction at the time of the later phytoplankton bloom (RUNGE et al., 1991). FORTIER et al. (1995) suggest that the early production of larvae of Arctic cod (Boreogadus saida) and sand lance (Amodytes sp.) is a strategy to synchronize first feeding with the early availability of small cyclopoid nauplii. The later emergence of larger larvae of various other fish species, at the time of ice break-up (DROLET et al., 1991; PONTON et al., 1993), would synchronize their first feeding with maximum production of larger calanoid nauplii (FORTIER et al., 1995). Thus, in Arctic shelf ecosystems, ice algae play a major trophic role, at a critical time of the year.

In the Southern Ocean, a situation somewhat similar to that described for fish on Arctic shelves may exist for Pagothenia borchgrevinki. This fish is the most conspicuous fish member of the cryopelagic community. Its distribution is circumantarctic, and it was shown that young fish actively feed on ice-associated ostracods and copepods (e.g. KOTTMEIER et al., 1985; HOSHIAI et al., 1989), including Paralabidocera antarctica. The latter was shown by HOSHIAI et al. (1987) to feed on ice algae, as also do the krill and various other copepods (refs. in LEGENDRE et al., 1992). It follows that Antarctic food webs often channel ice algal production toward large metazoans.

2.4. Microphagous macrozooplankton

A third trophic pathway through which primary production may be channeled is microphagy, i.e. direct feeding, by large zooplankton, on small particles (e.g. <2–5 μm). Table 2 shows that many salps, pteropods, doliolids and appendicularians can feed on very small particles. These organisms exhibit extremely high size ratios between consumers and food particles (often >5·10³). By reference, the average size ratio consumer/food, in the marine pelagic environment, is ca. 14 (SHELDON et al., 1977). FORTIER et al. (1994) hypothesized that pelagic organisms which package small particles

Table 2. Sizes of various microphagous macrozooplankton organisms and of the smallest food particles they efficiently collect, and ratio between sizes. Summarized from Table 1 of FORTIER et al. (1994).

Taxon	Length (mm)	Food size (μm)	Size ratio
Salps	30–150	1.5–3.4	0.8–4.8 × 10⁴
Pteropods	35–50	1–5	0.7–5.0 × 10⁴
Doliolids	≥7	0.2–5.0	0.1–3.5 × 10⁴
Appendicularians	15–25	2.5–5.0	5.6 × 10³

into larger ones (*i.e.* microphagous macrozooplankton) generally contribute to lengthening biogenic carbon turnover times and even transferring biogenic carbon from a given carbon pool to a longer-lived one. They show that the above four groups of organisms are especially efficient at channeling toward the long-lived (*e.g.* fish) and even sequestered pools part of the biogenic carbon that would have otherwise been shorter lived. Euphausiids also often exhibit consumer/food ratios $>10^3$ but, because they generally feed on particles >5 μm, they were not included by FORTIER *et al.* (1994) in the above list of large microphagous macrozooplankton.

In polar seas, pteropods, doliolids and appendicularians are found under the sea ice, and salps at ice edges (*e.g.* HARBISON, 1988). In addition, Antarctic krill can feed on particles <5 μm, at least when larger food items are absent. This is also true, in polar waters of both hemispheres, of some very large copepod species that consume particles <5 μm (refs. for Antarctic krill and these large copepods are given in FORTIER *et al.*, 1994). Thus, in Antarctic and Arctic waters, small particles can escape the short-lived carbon pool through microphagous grazing, not only by pteropods, doliolids and appendicularians but also by some large planktonic crustaceans.

It is interesting to note that, in the Southern Ocean during summer, there seem to exist two types of mutually exclusive food webs, *i.e.* krill-dominated and salp-dominated (NISHIKAWA *et al.*, 1995). This had already been noted by PIATKOWSKI (1985), who observed that the numbers of salps, in the Atlantic sector of the Southern Ocean, are high when the concentrations of *Euphausia superba* are low. The explanation proposed by NISHIKAWA *et al.* (1995) is that waters dominated by large diatoms are favorable to krill, because these can actively feed on large phytoplankton, but tend to exclude salps, because their feeding apparatus tends to clog at high particle concentrations (refs. and discussion in FORTIER *et al.*, 1994). Conversely, salps thrive in waters dominated by small phytoplankton where they feed on small algae and krill larvae, these conditions excluding krill given their inability to feed on very small cells and also salp predation on the young stages. More observations are needed to test this hypothesis. Presence of these two foods webs is not documented for ice-covered waters or the marginal ice zone.

3. Sedimentation of Biogenic Particles in Seasonally Ice-covered Waters

The production cycle of ice algae and under-ice or ice-edge phytoplankton is often marked by transient export events. These include the release and sedimentation of ice algae at the time of ice melt (*e.g.* SASAKI and HOSHIAI, 1986; TREMBLAY *et al.*, 1989), massive sinking of ice-edge blooms (*e.g.* SMITH and NELSON, 1986; NELSON and SMITH, 1986; WILSON *et al.*, 1986), and sedimentation of algae from the spring-summer phytoplankton bloom (*e.g.* SASAKI and HOSHIAI, 1986; HANDA *et al.*, 1992). Hence, large fluxes of biogenic material toward the sea floor. In the Southern Ocean, this is reflected in bottom deposits of diatomaceous ooze which cover vast areas (*e.g.* BODUNGEN *et al.*, 1986; WILSON *et al.*, 1986). Aggregated algal cells generally sink much faster than single organisms. In the case of algae released from melting sea ice, for example, sinking rates of aggregates are three orders of magnitude higher than those of dispersed cells (RIEBESELL *et al.*, 1991).

In addition to transferring organic matter toward depth, sedimenting calcareous

plankters export an extra share of carbon in their tests (C_aCO_3). In the Southern Ocean, pelagic foraminifera occur in large concentrations, and they actively grow in new and consolidated ice and in the underlying water column. In contrast, the Arctic sea ice is practically devoid of foraminifera (SPINDLER, 1990), but these are present in the water column (HONJO, 1990; ice edge). Pteropods are often present in the under-ice water column, in both the Arctic and Antarctic. It must be remembered that pteropods are among the large microphages, so that they can feed in waters from which large phytoplankton are absent and also on material accumulated in hydrodynamic traps. They thus contribute to exporting toward depth biogenic material that would otherwise be recycled in the upper water column (see FORTIER et al., 1994). It follows that carbonate sediments are found in both the Antarctic and Arctic basins. For references and a more detailed discussion of the subject, see for example HONJO (1990) and LEGENDRE et al. (1992).

Fast-sinking fecal pellets of some large microphages (i.e. salps) contribute to the deep flux of biogenic carbon from surface waters. In addition, fecal pellets of large microphages and discarded appendicularian houses may reach the deep waters because of extensive vertical migrations (e.g. by salps) and of populations (e.g. salps and appendicularians) that permanently inhabit mesopelagic depths (for a more detailed discussion and references, see FORTIER et al., 1994). There is little information, for seasonally ice-covered waters, concerning the role played by large microphages in the deep flux of organic particles. Crustacean fecal pellets are often invoked when discussing the contribution of biogenic particles to the deep flux of carbon. However, a review of the literature led FORTIER et al. (1994) to conclude that, in general, most fecal pellets of copepods and euphausiids are recycled within the upper few hundred metres of the water column, and thus contribute little to the deep carbon flux (i.e. down to >3000 −4000 m). These authors indicate that the only exception to this rule seems to be the Antarctic krill, whose fecal pellets sometimes dominate the deep flux of biogenic carbon in the Southern Ocean (e.g. BODUNGEN et al., 1986).

Thus, there are several sedimentation pathways for ice-related algae. These include massive sinking of aggregates of large cells, settling of calcareous tests, and fast sedimentation of large fecal pellets produced by the Antarctic krill.

4. Original Trophic Characteristics of Seasonally Ice-covered Waters

The present section brings together several original trophic characteristics of seasonally ice-covered waters, which have been discussed so far. The production cycle of microalgae in these environments is often marked by strong seasonal pulses. At the time of ice melt, ice algae are suddenly released in the water column and, at ice-edges, blooms often sink to depth. Large phytoplankton are not always abundant and, at times, small cells may account for a large proportion of the total biomass and primary production. Finally, in the under-ice water column of the Southern Ocean, the production of heterotrophic bacteria is often much higher than that of phytoplankton.

In the Southern Ocean, krill plays a dominant role in shaping pelagic ecosystems. For example, ice edges may be dominated by large or by small phytoplankton, according to the presence, or not, of overwintering krill. Whatever the trophic system, large

zooplankton remain a major link between primary production and large metazoans. More generally in both Arctic and Antarctic waters, polar food webs often actively transfer biogenic carbon from ice algae toward large metazoans. This is presently better documented for Arctic shelves than for the Southern Ocean. Finally, one special aspect of polar waters is that large microphagous macrozooplankton include, there, some large planktonic crustaceans, *i.e.* the Antarctic krill (in the Southern Ocean) and large copepods (in polar waters of both hemispheres).

The fact that the production cycle of algae in polar waters is marked by strong seasonal pulses often leads to massive, sedimentation of algal material. In addition, contrary to other oceanic environments where most crustacean fecal pellets are rapidly recycled during their downward transit, the dominant crustacean grazer in the Southern Ocean (krill) significantly contributes to the deep flux of biogenic carbon, potentially leading to sequestration.

Overall, in both Antarctic and Arctic waters, there is an exceptionally wide array of pathways that channel the three size classes of primary production (*i.e.* large and small cells, and DOC) into the long-lived and, potentially, sequestered biogenic carbon. The latter possibility is examined in the next section.

5. Potential for Sequestration of Biogenic Carbon in Seasonally Ice-covered Waters

Potential sequestration of biogenic carbon in seasonally ice-covered waters is examined within the framework of the "rectification hypothesis" (YAGER *et al.*, 1995). This hypothesis was developed for the annual carbon cycle in polynyas, but it applies to any seasonally ice-covered waters. The hypothesis (Table 3) considers two broad pools of carbon in oceans, *i.e.* total inorganic carbon (C_T) and organic carbon (OC), and fluxes between the atmosphere (A), the surface waters (SW) and the deep waters (DW). In summer, phytoplankton production transfers carbon from the inorganic to the organic pool ($C_T \rightarrow OC$). This leads to decreased CO_2 concentration in surface

Table 3.   *Annual cycle of biological and physical processes affecting the cycling of CO_2 in regions with seasonal sea ice, i.e. "rectification" hypothesis of YAGER et al. (1995). Two pools of carbon in oceans are considered: total inorganic carbon (C_T) and organic carbon (OC). Fluxes are between the atmosphere (A), the surface waters (SW) and the deep waters (DW). Modified from Fig. 6 of YAGER et al. (1995).*

Season	Dominant processes	Carbon pools	Carbon fluxes
Summer	Phytoplankton production	$C_T \rightarrow OC$	OC: SW→DW
Early autumn	Invasion of atmospheric CO_2 in surface waters and deep vertical mixing	$C_T \leftrightarrow OC$	CO_2: A→SW OC: SW→DW C_T: DW→SW
Late autumn and winter	Respiration > primary production	$OC \rightarrow C_T$	None: ice acts as barrier
Spring			
-Before ice melts	Ice algal production	$C_T \rightarrow OC$	None: ice acts as barrier
-Ice melt	Near-surface stratification		Stratification acts as barrier OC: SW→DW

NOTE: At no time during the seasonal cycle is there a flux such that C_T: SW→A. Hence, potential sequestration of carbon by the biological CO_2 pump.

waters. During early autumn, before freezing, there is invasion of atmospheric CO_2 into surface waters, hence a flux of CO_2 from the atmosphere into the ocean. Vertical mixing brings back some deep CO_2 toward the surface (not in the scheme of YAGER *et al.*, 1995). After freezing (late autumn and winter), respiration in the water column exceeds primary production, which results in a transfer of carbon from the organic to the inorganic pool ($OC{\rightarrow}C_T$). However, because the ice provides a barrier to the release of inorganic carbon to atmosphere, there is no transfer of CO_2 back to the atmosphere. During spring, before ice melts, ice algal production causes an initial removal of the CO_2 accumulated in under-ice waters ($C_T{\rightarrow}OC$). The following melting of the ice creates a near-surface highly stratified layer, which isolates the underlying water column from air-sea gas exchange. At the same time, there is often massive sinking of ice algae (not in the scheme of YAGER *et al.*, 1995). References concerning each step are given in YAGER *et al.* (1995), who also discuss the implications of their hypothesis.

In normal (*i.e.* ice-free) oceanic waters, there is a net flux of CO_2 from the atmosphere into the ocean during spring-summer, and a net flux from the ocean toward the atmosphere in autumn-winter. In seasonally ice-covered waters, there is a net flux of CO_2 from the atmosphere into the ocean during early autumn, but at no time during the year can CO_2 escape to the atmosphere. This should result in net sequestration of carbon by the biological CO_2 pump.

6. Summary and Conclusions

In seasonally ice-covered waters, as in other aquatic environments, there is partitioning of primary production among large and small cells and DOC. Biogenic carbon is often actively transferred from ice algae to large metazoans. Small biogenic particles can escape the short-lived carbon pool through grazing by microphagous zooplankton. In addition, there are several sedimentation pathways for ice-related algae. It follows that there is a wide array of pathways that channel primary production into long-lived and sequestered biogenic carbon. Finally, the alternation between biological pumping of CO_2, during the ice-free season, and algal carbon uptake, during the ice-covered period, creates unique conditions for the sequestration of atmospheric CO_2. Thus, primary production in ice-covered waters is significant to both marine ecosystems and the sequestration of biogenic carbon, at least locally and perhaps on large scales.

Acknowledgments

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