

Constraints on Carbon Drawdown and Export in the Greenland Sea

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Abstract: Data on the inorganic carbon system, the distribution of oxygen, nitrate, and phosphate, as well as particle sedimentation and plankton biomass collected from winter 1993 to summer 1996 in the central Greenland Sea show that although this area is a sink for atmospheric carbon throughout the year, relatively little of the carbon fixed by photosynthesis into organic compounds in the surface waters is eventually sequestered in deep waters. Rather, due to intensive biological remineralization of organic matter within the winter mixed layer, the bulk of carbon is retained in the upper few hundred meters of the water column. The sequestration of biogenic carbon is constrained by the depth of the winter mixed layer, in that deep winter mixing effectively increases the depth below which true export can occur. There is potential for increased export with increased rates of deep convection. Likewise, a reduction in heterotrophic recycling in near-surface waters may enhance the effectiveness of the biological pump. However, because of our still limited understanding of the interactions between the biological and solubility pumps in this region, the extent to which export may be enhanced is unclear.

Introduction

High-latitude oceans are an important sink for atmospheric carbon. This is particularly true for subpolar seas where deep-water formation is active (e.g. Chen et al. 1990; Broecker and Peng 1992) and biological processes are characterized by high-amplitude seasonal swings in rates of productivity. The physical pumping of carbon to deep water is controlled by the absorption of atmospheric CO₂ into cold surface waters and eventual deep convection; dissolved carbon in convected water masses can be effectively sequestered away from the atmosphere for up to 1000 years (Broecker and Peng 1982). Biological pumping to deep water has traditionally been thought to be relatively effective in these seas, because intensive primary production of short duration, as regulated largely by solar irradiance, may not be matched by concomitant secondary production. This can permit the accumulation of particulate organic matter and its eventual sedimentation.

However, recent research has recognized that we are far from reconciling the role of biology in regulating biogeochemical fluxes of carbon in general, much less in extreme environments such as the subpolar oceans. For example, zooplankton (Longhurst and Harrison 1989; Noji 1991; Silver and Gowing 1991) is now recognized to be an important but complex component influencing the distribution of oceanic carbon. Further, many recent studies have emphasized the importance of the accumulation of dissolved organic carbon (DOC) in surface water (Carlson et al. 1994; Børsheim and Mykkestad 1997; Børsheim submitted), the downward flux of carbon via migrant zooplankton stocks (Dam et al. 1995; Hirche 1997), and the leaching of DOC from sinking fecal pellets (Urban-Rich 1999) and sedimenting particles (Noji et al. 1999b) in controlling carbon export. In addition, physical conditions, such as low winds and a stable surface boundary layer, can also

limit the rate at which carbon assimilated by biota within surface waters can be replaced by exchange with the atmosphere. With the increasing number of relevant variables known to influence biological carbon export, it is increasingly difficult to study them concomitantly in the field.

The importance of understanding these complex biological controls on carbon export has been underscored by models indicating that reasonable variations in the rates of the processes regulating physical and biological carbon drawdown in high-latitude waters may produce changes in atmospheric carbon dioxide concentrations of the same magnitude as those observed in ice cores between glacial and interglacial periods (Knox and McElroy 1984; Sarmiento and Toggweiler 1984; Siegenthaler and Wenk 1984; Sarmiento et al. 1998). However, all of these models have dealt with biological export very simplistically, and the development of high-latitude carbon export models has been severely hampered, not only by a need for consensus on the mechanisms of deep-water formation (Budéus et al. 1998), but also by a lack of the time-resolved (seasonal, annual and decadal) carbon and biological data from deep-water formation regions which would provide an understanding of how biological versus physical processes currently regulate the export of carbon from the ocean's surface.

The Greenland Sea is a high-latitude system characterized by deep-water formation and short, intensive periods of biological production. Greenland Sea Deep Water (GSDW), a source of North Atlantic Deep Water (Aagaard et al. 1985), is thought to be formed in the central Greenland Gyre through a combination of deep convection (Johannessen et al. 1991) and gradual subsurface mixing between a number of Atlantic and Arctic water masses (Carmack and Aagaard 1973). The Greenland Sea is an ideal site for studying interactions between deep-water formation and carbon cycling, because the overall rate of deep-water formation here is extremely variable (Dickson et al. 1996; Bönsch et al. 1997), with apparent replacement times for deep water ranging from 30 to 170 years (Schlosser et al. 1991).

The investigations presented here are part of a large interdisciplinary endeavor which permitted the integrated study of carbon cycling processes, including air-sea exchange of CO_2 , the photosynthetic uptake of nutrients, the release of oxygen and the biological recycling of organic carbon. This paper attempts to synthesize observations from the Greenland Sea. First, we have compared results from different approaches for quantifying the biogenic production of organic carbon in the surface water of the central Greenland

Sea: (1) variations in dissolved inorganic carbon corrected for estimated air-sea CO_2 fluxes; (2) variations in nutrient distributions; (3) and variations in dissolved O_2 distributions corrected for air-sea O_2 fluxes. Direct measurements of dissolved organic carbon, biomass, and particulate carbon export were then used to determine the fate of photosynthetically produced organic carbon. Differences in the frequency and periods of sampling for the field studies presented here necessitate the comparison of individual data sets with caution and restraint from overinterpreting budgets on the oceanic drawdown of carbon, its pelagic cycling and eventual sequestration to the deep ocean or outgassing to the atmosphere. Rather, the processes of key importance for the Greenland Sea carbon cycle have been elucidated and a cycling scenario has been constructed which may be useful for understanding potential changes in carbon flux in response to a changing climate system.

Materials and Methods

The central Greenland Sea (Fig. 1) was visited repeatedly between winter 1993 and summer 1996. The dates of each cruise, a summary of the data collected and sampling details, if not specified below, are presented in Miller et al. (1999), Noji et al. (1999a), Skjelvan et al. (1999) and Børsheim (submitted).

Samples for total alkalinity (A_T), total dissolved inorganic carbon (DIC), fugacity of carbon in both surface water and the atmosphere ($f\text{CO}_2$), nitrate (NO_3), phosphate (PO_4) and dissolved oxygen (O_2) (Skjelvan et al. 1999; Miller et al. 1999), in addition to hydrographic data were collected and analyzed according to standard methods (DOE 1994; WOCE 1994). The "official" terminology for DIC is C_t (DOE 1994), but here the term DIC has been employed in order to minimize confusion when referring to organic carbon. Oxygen data were collected on cruises during May (1993, 1994, 1995), June (1994), July (1996) and August (1993, 1996) from stations located between 73°N and 77°N and west of 6°E and supplemented with September data from the ICES Oceanographic Data Center, Denmark. DOC was sampled and analyzed according to Børsheim and Mykkestad (1997).

Bacteria were counted using an acridine-orange staining method (Hobbie et al. 1977). Macrozooplankton was collected in vertical hauls from 100–0 m using a WP2 net fitted with $180 \mu\text{m}$ mesh. Samples were immediately split on board into aliquots for microscopy and measuring dry weight biomass (Noji et al. 1999a).

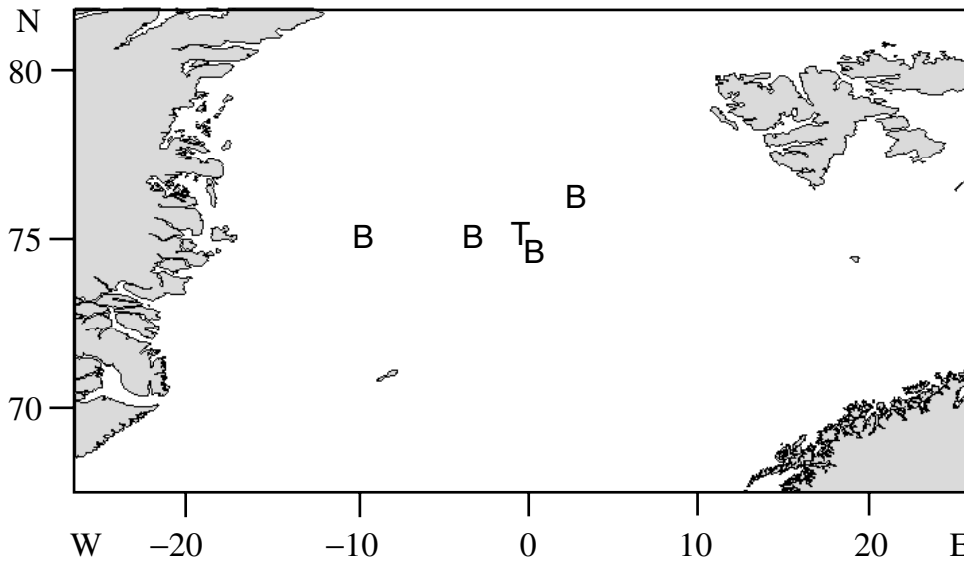


Fig. 1: Sites of the sediment trap (T) and sampling for bacteria (B). N.B. sampling for macrozooplankton during the three years of investigation was between 74.5 and 75° N

A moored sediment trap (Aquatec Meerestechnik, Kiel, Germany) was deployed in the central Greenland Basin (75° N, 0°) at 200 m from August, 1993, to May, 1994, when it was recovered and redeployed at 300 m until June, 1995. Mercuric chloride was used as an in situ biocide (U.S. GOFs 1989). From the particulate fraction of each sample, zooplanktonic “swimmers” were removed using a 180- μm sieve and forceps. The remaining particulate material was split into aliquots and the following parameters were measured in duplicate: total particulate material (TPM) as dry weight, carbonate, particulate organic carbon and nitrogen (POC and PON), and chlorophyll and pheopigments (calculations after Jeffrey and Humphrey 1975) expressed as chlorophyll equivalent (CEQ = chlorophyll a + 1.51·pheopigments; Jeffrey and Welschmeyer 1997). For details see Noji et al. (1999a). POC and TPM data from January 23 to March 20, 1994, and from February 26 to March 16, 1995, are not available.

Biological CO₂ Uptake

CO₂ Consumption

Throughout the entire year, the partial pressure of CO₂ in the sea surface was lower than in the air (Table 1), indicating that the Greenland Sea is an important sink for CO₂ year-round (Skjelvan et al. 1999). Figure 2 shows atmospheric and oceanic $f\text{CO}_2$ during winter and

spring seasons in 1995. During early spring, average underpressure in Greenland Sea surface waters, relative to the atmosphere, was approximately 57 μatm and dropped to approximately 109 μatm in the summer. In the fall, the degree of undersaturation returned to winter values, due to the general breakdown of the near-surface seasonal thermocline and mixing with deeper water. The fluxes of CO₂ into the ocean derived from these observed air-sea $f\text{CO}_2$ gradients (Wanninkhof 1992) varied from 0.36 mol C m⁻² month⁻¹ during spring to 0.59 mol C m⁻² month⁻¹ during fall. For spring and summer, the period of enhanced photosynthetic activity, an average of 0.44 ± 0.1 mol C m⁻² month⁻¹ was absorbed from the atmosphere into the upper ocean in spring and summer, corresponding to a total of approximately 1.3 ± 0.2 mol C m⁻² over the three months of highest biological activity. During the 1993–1995 period, this total estimated drawdown of CO₂ from the atmosphere amounted to approximately 5.9 mol C m⁻² yr⁻¹, a significant quantity.

Concentrations of DIC in the surface mixed layer (Table 1) were high in winter and early spring, dropped by approximately 80 $\mu\text{mol/kg}$ during the summer and returned to winter levels by November (Miller et al. 1999). A rough estimate of net biological carbon consumption within surface waters can be derived from this observed spring and summer drop in DIC, corrected for flux from the atmosphere and an estimate of vertical diffusion across the seasonal pycnocline (Table 2). A truly rigorous analysis would also correct for hor-

Table 1: Seasonal surface characteristics in the central Greenland Sea from 1993 to 1995. Salinity (S), nitrate (NO₃), phosphate (PO₄) and dissolved inorganic carbon (DIC) concentrations are average values for the mixed layer. Mean $\Delta f\text{CO}_2$ is the air-sea gradient in CO₂ fugacity. Average wind speeds are from Eide et al. (1985). Calculated air-sea CO₂ fluxes are based on the gas transfer relationship from Wanninkhof (1992). Negative signs denote fluxes into the ocean. Modified from Skjelvan et al. (1999) and Miller et al. (1999)

	Winter	Spring	Summer	Fall
S [PSU]	34.813	34.802	34.615	34.872
NO ₃ [$\mu\text{mol kg}^{-1}$]	NA	11.0	0.8	10.0
PO ₄ [$\mu\text{mol kg}^{-1}$]	0.90	0.80	0.23	0.72
DIC [$\mu\text{mol kg}^{-1}$]	2150	2143	2064	2158*
Mean $\Delta f\text{CO}_2$ [μatm]	-36	-57	-109	-58
Wind speed [m s^{-1}]	10.8	8.2	7.2	11.2
Air-sea CO ₂ flux [$\text{mol m}^{-2} \text{month}^{-1}$]	-0.40	-0.36	-0.53	-0.59

* May have been overestimated slightly due to problems with instrumentation. See Miller et al. (1999) for details. NA = Not Available

izontal advection, but our current limited understanding of surface circulation in the Greenland Gyre does not permit a useful estimation of advective effects. Thus, the value of 3.6 mol C m^{-2} gives an estimate of biological uptake of inorganic carbon, assuming horizontal transport is insignificant.

Inorganic Nutrient Cycling

Table 1 lists the average seasonal surface concentrations of nitrate and phosphate (see also Fig. 3) in the surface waters of the central Greenland Gyre. Assuming Redfieldian uptake of nutrients and carbon by phytoplankton (C:N:P = 120:16:1; Takahashi et al. 1985; Anderson and Sarmiento 1994), the observed depletions of nitrate and phosphate between early spring and late summer imply that biological production in the Greenland Sea removed approximately 2.2 mol m^{-2} of inorganic carbon from the surface waters (assuming a mixed layer depth of 30 m) during the photosynthetic season (Miller et al. 1999), thereby increasing the short-term capacity for atmospheric carbon absorption. However, surface nutrient levels increased again as the mixed layer deepened during early fall, indicating that approximately 2.4 mol m^{-2} of inorganic carbon was released back into the water before deep convection could occur. Thus, organic matter formed during the summer and spring was, in effect, recycled and not exported. This dramatic release of nutrients is a direct result of the extreme depth of the winter mixing, which also brings carbon that had been exported below the summer mixed layer back to the surface. Therefore, the nutrient cycle indicates that despite the episodic nature of biological activity in this area, net annual export is more consistent with what is observed in recycling regimes.

Table 2: Biological CO₂ uptake during spring and summer based on observations of the inorganic carbon system. Units are mol C m^{-2} . Negative values indicate decreases in surface DIC levels

1) $\Delta \text{DIC}_{\text{obs}}^1$	-2.0 ± 0.50
2) Air-sea exchange ²	1.4 ± 0.20
3) Vertical diffusion ³	0.2 ± 0.03
Biological CO ₂ uptake = 1) - 2) - 3)	-3.6 ± 0.50

¹ Observed decrease in salinity-normalized DIC assuming a mixed layer depth of 30 m (Miller et al. 1999)

² Flux out of the atmosphere and into the surface ocean. Based on the Wanninkhof (1992) formulation for piston velocity (Skjelvan et al. 1999)

³ Upward diffusion across the seasonal pycnocline into the surface ocean. Based on an average DIC gradient of 1.3 mmol m^{-4} and a vertical diffusion coefficient of $52 \text{ m}^2 \text{ month}^{-1}$ (Denman and Gargett 1983)

Oxygen Production

Oxygen measurements from the surface layer were used to estimate the change in oxygen content with time, oxygen fluxes through the sea surface, and net biological production. All measurements at the surface were averaged to a mean value for each month, and mean saturation concentrations were calculated (Weiss 1970) from temperature and salinity. Net air-sea oxygen fluxes, F_{O_2} ($\text{mol m}^{-2} \text{d}^{-1}$), were calculated from

$$F_{\text{O}_2} = K \cdot ([\text{O}_2] - [\text{O}_2]_s),$$

where K is the piston velocity (from Wanninkhof 1992) using a Schmidt number from Stigebrandt (1991), $[\text{O}_2]$

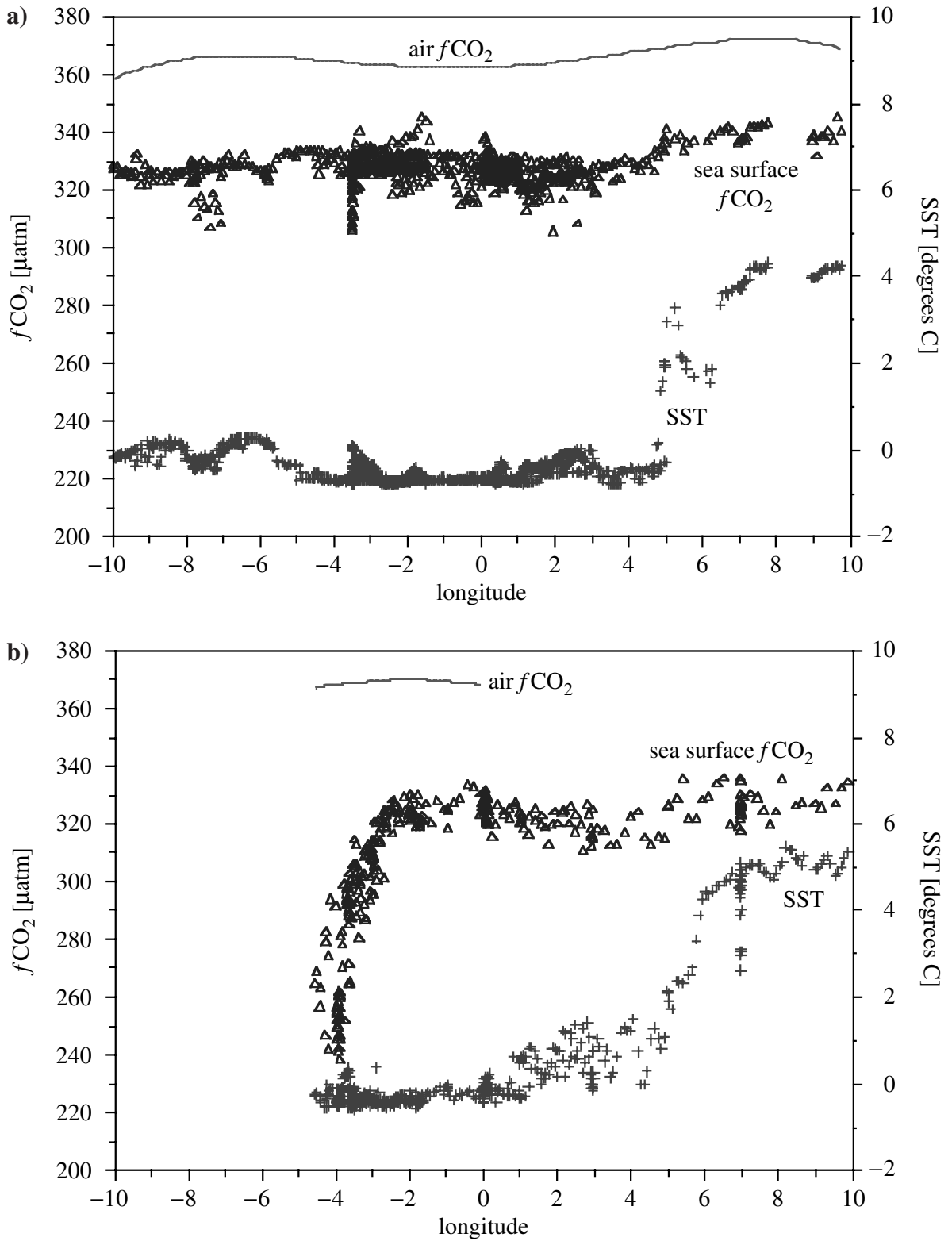


Fig. 2: Air $f\text{CO}_2$, sea surface $f\text{CO}_2$ and surface temperatures (SST) along 75° N in the Greenland Sea during **a)** winter 1995 and **b)** spring 1995. The solid line indicates the mean $f\text{CO}_2$ in air. (from Skjelvan et al. 1999)

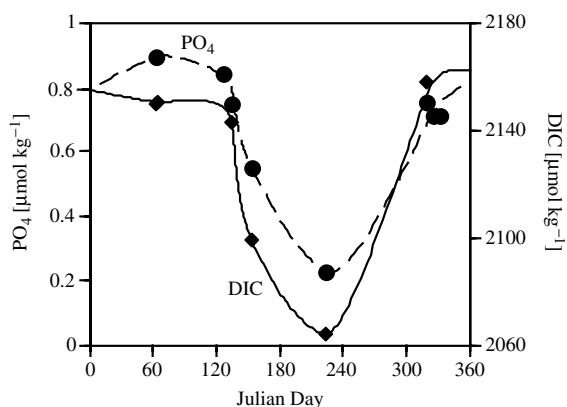


Fig. 3: Seasonal cycles of phosphate (PO_4) and dissolved inorganic carbon (DIC) in surface waters of the Greenland Sea from 1993 through 1995. DIC is represented by filled diamonds and a solid line; PO_4 by filled circles and a dashed line. The lines represent spline curves through the seasonal averages. (modified from Miller et al. 1999)

is oxygen concentration in the surface layer (0–5 m), and $[\text{O}_2]_s$ is the saturation concentration of oxygen (Weiss 1970). A mean monthly wind speed based on pressure field data was used (Eide et al. 1985). The resulting calculated oxygen fluxes were positive in the late spring and summer months, indicating outgassing to the atmosphere (Table 3). (See also Falck and Gade 1999!)

The change in oxygen content (ΔO_2) of the euphotic zone was taken to be the difference in integrated oxygen concentrations over the upper 30 m for each month. Neglecting any horizontal or vertical transport in the water column, a rough estimate of net biological production (B) is provided by

$$B = F_{\text{O}_2} + \Delta\text{O}_2,$$

Table 3: Mean oxygen fluxes and carbon uptake

Month	O_2	$[\text{O}_2]_s$	U	F	E	BO	BC
May	353.1	363.6	7.1	-0.98	0.27	-0.71	
June	375.2	356.4	6.3	1.36	0.23	1.59	1.22
July	347.7	335.6	6.4	1.01	-0.24	0.77	0.59
August	333.1	318.4	7.2	1.62	-0.40	1.22	0.93
September	332.7	335.4	8.3	-0.35	-0.06	-0.41	

O_2 = mean values of all measurements between 0 and 5 m [$\text{mmol O}_2 \text{ m}^{-3}$]

$[\text{O}_2]_s$ = mean saturation values between 0 and 5 m [$\text{mmol O}_2 \text{ m}^{-3}$]

U = mean wind [m s^{-1}]

F = flux of oxygen across the air-sea interface; positive to the atmosphere [$\text{mol O}_2 \text{ m}^{-2} \text{ month}^{-1}$]

E = change in oxygen content in the upper 30 m [$\text{mol O}_2 \text{ m}^{-2} \text{ month}^{-1}$]

BO = net biological production for the upper 30 m [$\text{mol O}_2 \text{ m}^{-2} \text{ month}^{-1}$]

BC = net biological production for the upper 30 m [$\text{mol C m}^{-2} \text{ month}^{-1}$]

where ΔO_2 is the change in oxygen content in the upper 30 m. This biological production of O_2 can then be converted to CO_2 consumption using the ratio from Redfield et al. (1963) for CO_2 uptake: O_2 production of 106:138. Net biological productions for the upper 30 m (BC) for June, July and August were 1.22, 0.6 and $0.94 \text{ mol C m}^{-2} \text{ month}^{-1}$, amounting to $2.7 \pm 2.0 \text{ mol C m}^{-2}$ for the 3-month period.

Estimates for Production of Organic Carbon in Summary

These three approaches (Table 4) for estimating biological carbon consumption agree reasonably well, considering the diverse assumptions involved in each. Firstly, both nutrient consumption and oxygen production estimates are dependent upon Redfield-type ratios, which have limited application on small temporal and spatial scales. Secondly, these estimates are based on the assumption that horizontal advection is insignificant, and it is possible that mixing of Atlantic and polar water masses at the surface of the Greenland Sea could influence the observed variations in nutrients, oxygen and inorganic carbon to different extents. Thirdly, uncertainties in gas transfer rates affect the estimates based on inorganic carbon consumption and on oxygen production. For example, application of piston velocity equations from Liss and Merlivat (1986) rather than from Wanninkhof (1992) would reduce the ΔO_2 estimate for the uptake of CO_2 by photosynthesis to approximately 1.4 mol C m^{-2} , while the estimate based directly on CO_2 fluxes (Table 2) would be reduced to approximately 2.9 mol C m^{-2} .

Table 4: Estimates of biological carbon consumption within the upper 30 m from spring to late summer

Proxy	C consumption [mol m^{-2}]
Inorganic carbon consumption (Table 2)	3.6 ± 0.5
Nutrient consumption	2.2 ± 0.4
Oxygen production (Table 3)	2.7 ± 2.0

Fate of Surface Organic Carbon

Particle Sedimentation

With rates of sedimentation of total particulate material (TPM) and particulate organic carbon (POC) (Figs. 4a, b) of approximately 25 to 250 $\text{mg m}^{-2} \text{d}^{-1}$ and 2 to 19 $\text{mg m}^{-2} \text{d}^{-1}$, the magnitude of sedimentation as well as of interannual variation were comparable to those reported from earlier sediment trap deployments in arctic waters of the northern Nordic Seas (Honjo 1990, 1996; Bauerfeind et al. 1993; Bodungen et al. 1995). The increase in sedimentation in June, 1994, corresponds with the occurrence of enhanced phytoplankton growth in the central Greenland Sea. In particular, the annual maximum in sedimentation rates of chlorophyll equivalent (CEQ, Fig. 4c), as well as POC/PON ratios (Fig. 4b) of approximately 7 or 8, indicate that particle flux in this phase was composed of relatively fresh material originating from spring phytoplankton. In contrast, in autumn the sedimentation rate of chlorophyll equivalent was less than one-fifth that recorded in June, and the POC/PON ratios of material sedimenting in September were higher. Sediment-trap material in autumn was characterized by a large contribution of diatom valves, and there was no indication of an unusually large input of zooplanktonic material such as shells from the euthecossomatous pteropod, *Limacina retroversa*, which is also reflected in the low rates of sedimentation of calcium carbonate (see below). These observations indicate that downward particle flux in autumn was probably composed of older phytoplanktonic material. Notably, the annual peak in sedimentation of POC was not in June but in September. Since nutrients were largely depleted in surface waters in late summer (Table 1), the development of a fall phytoplankton bloom was unlikely, and the sedimentation peak presumably had other sources. It has been suggested that enhanced sedimentation in autumn can be caused by a breakdown in pelagic recycling due to the departure of copepod herbivores from surface waters, which descend to depth to overwinter

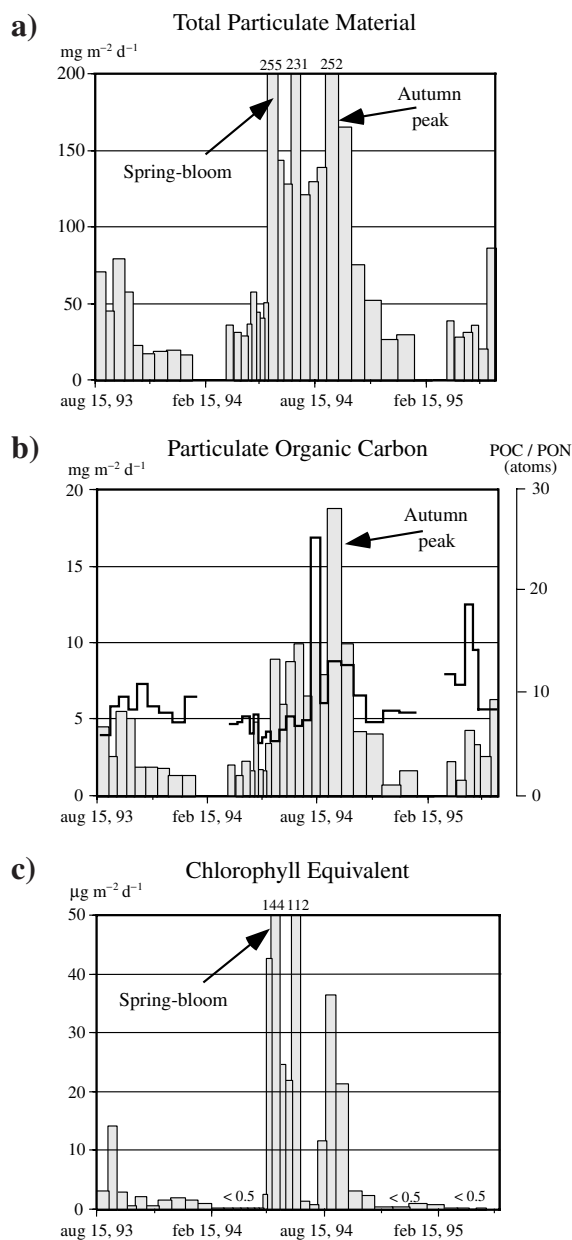


Fig. 4: a) Sedimentation of total particulate material (TPM), b) particulate organic carbon (POC) and c) chlorophyll equivalent (CEQ) in depths of between 200 and 300 m in the central Greenland Sea from August, 1993, to June, 1995. The ratio of particulate organic carbon to particulate organic nitrogen (POC/PON by atoms) is shown in b (bold lines). Absence of columns indicates that data were not available. (from Noji et al. 1999a)

(Peinert et al. 1987). However, the lack of additional evidence precludes further speculation on this subject at this time.

The total annual rates of POC sedimentation at approximately 200–300 m varied approximately 0.12 mol

$\text{m}^{-2} \text{yr}^{-1}$. However, the downward transport of carbon via particles was underestimated, as DOC released from particles entering sediment traps was not considered in initial estimates but was proven to be considerable (Noji et al. 1999b). The annual contribution of this DOC associated with sedimenting particles was approximately $0.04 \text{ mol} (0.45 \text{ g}) \text{ m}^{-2}$, or one-third of the total annual POC sedimentation at 200–300 m. Thus, our estimate for particle-mediated carbon sedimentation in this investigation ranges from 0.12 (only POC) to 0.16 (with particle-associated DOC) $\text{mol C m}^{-2} \text{yr}^{-1}$. With rates of approximately $0.8 \text{ mmol C m}^{-2} \text{yr}^{-1}$, the annual sedimentation of calcium carbonate was over two orders of magnitude smaller than for POC, and no significant seasonal pattern was evidenced. These rates of sedimentation for particulate carbonate were similar to those reported for polar waters of the Southern Ocean (Milliman 1993). In comparison, larger carbonate fluxes were reported from sediment-trap investigations near the margins of the Greenland Sea Gyre (e.g. Honjo 1996; Bodungen et al. 1995). We suggest that carbonate-producing organisms, i.e. coccolithophores, pteropods, foraminifers, were scarce in the central Greenland Sea during the period of trap deployment from August, 1993, to June, 1995. This is supported by microscopy of trap samples as well as the lack of evidence for significant alkalinity variations in the Greenland Sea during these investigations (Miller et al. 1999).

Heterotrophic Activity and Dissolved Organic Carbon

Stocks of macrozooplankton near the surface were predominantly herbivorous and, in terms of biomass, were dominated by the copepod *Calanus hyperboreus*, with secondary contributions by *C. finmarchicus* and *C. glacialis*. Prior to the development of the spring phytoplankton bloom, zooplankton biomass (Fig. 5) in May, 1993, in the upper 100 m was approximately $3 \text{ g dry weight m}^{-2}$. When the spring phytoplankton bloom was in early and peak phases of development during May, 1995, and June, 1994, zooplankton biomass was several times larger. This may indicate that zooplankton stocks grew rapidly at the onset of spring bloom and were able to effectively graze spring phytoplankton stocks, however this can only be verified with more data on plankton distribution and hydrography. With values of nearly $2 \cdot 10^6 \text{ cells cm}^{-3}$, bacteria (Fig. 6) in surface waters during phytoplankton bloom in June, 1994, were 3 to 4 times more concentrated than during the early bloom situation of May, 1995. Rapid increases in the abundance of surface bacteria may be related to an initial in-

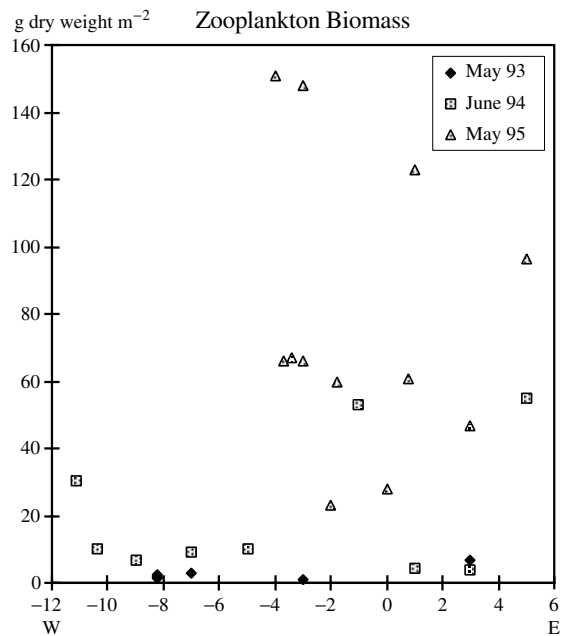


Fig. 5: Zooplankton biomass in the upper 100 m between 74.5° and 75° N in the Greenland Sea in May, 1993, June, 1994, and May, 1995. (from Noji et al. 1999a)

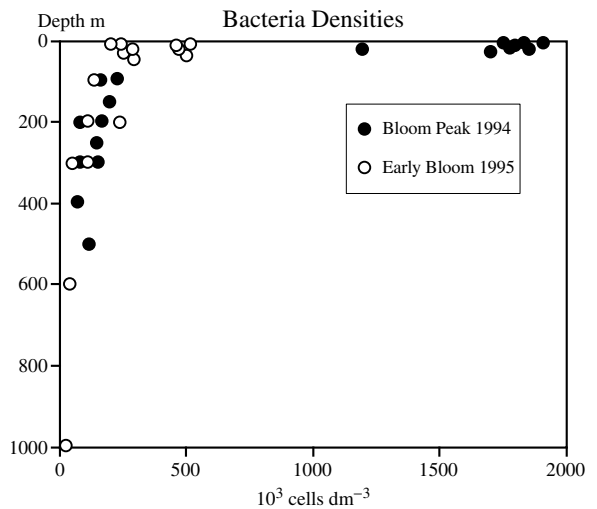


Fig. 6: Vertical distribution of bacteria ($10^3 \text{ cells dm}^{-3}$) during an intensive bloom situation in 1994, and during an early stage of phytoplankton bloom development in 1995. (from Noji et al. 1999a)

crease in zooplankton grazing activity and reflect the bacterial response to increased availability of DOC from zooplankton excretion, sloppy feeding and leaching of DOC from fecal pellets (Urban-Rich 1999) as well as direct exudation by phytoplankton.

Another important aspect of the Greenland Sea carbon cycle is the seasonal migration of herbivorous copepods to deep water, where they overwinter for most of the year. From data collected between 1989 and 1995, Hirche (1997) reports that in the deep Greenland Sea overwintering stocks of the dominant copepod, *Calanus hyperboreus*, exhibited a decrease in specific biomass due to respiration as well as a decrease in abundance due to mortality, and that these processes accounted for roughly $0.33 \text{ mol C m}^{-2}$ in their investigation. This is a significant downward transport of carbon in comparison with the sedimentation of particulate carbon. To our knowledge it is also the only estimate of vertical carbon flux due to seasonal migration and mortality of copepods in the Greenland Sea, and therefore this value is used in Table 6, which provides estimates for the flow of biogenic carbon in the upper 200 m of the central Greenland Sea.

To estimate the amount of transient DOC (Kähler et al. 1997) accumulated in the euphotic zone during summer, Børsheim (submitted) compared the vertical distribution of DOC at the end of the biologically productive season in 1996 with winter values in 1995 in the central Greenland Sea. This accumulated, transient DOC was approximately $2.89 \text{ mol C m}^{-2}$ in the upper 200 m (Table 5; Børsheim submitted). This is the only estimate of this phenomenon for the Greenland Sea and is used in Table 6 on estimates of biogenic carbon flow. As in other areas such as the Sargasso Sea, the equatorial Pacific and the Norwegian Sea (Michaels et al. 1994; Carlson and

Ducklow 1995; Børsheim and Mykkestad 1997), DOC in the surface waters of the Greenland Sea can accumulate during summer. Børsheim (submitted) suggested that a large portion of transient DOC is probably remineralized by bacteria. This is supported by our observations, which showed that depleted surface nutrient levels in summer increased as the mixed layer deepened during early fall (see "Inorganic Nutrient Cycling"), suggesting that the large pool of transient DOC fueled nutrient remineralization.

Fate of Organic Carbon in Summary

With an annual sedimentation rate of $0.16 \text{ mol C m}^{-2}$ at depths of approximately 200 m, the fate of most of the newly produced organic carbon (see "Biological CO₂ Uptake") was not attributable to particle flux (Table 6). Further, with $0.33 \text{ mol C m}^{-2}$, the export of carbon by overwintering migrant zooplankton, although twice that of particle sedimentation, was still small. In contrast, the estimated accumulation of transient DOC was approximately $2.89 \pm 1.28 \text{ mol C m}^{-2}$; most of this appears to be remineralized in the upper mixed layer. The sum of these three pools of carbon is approximately $3.39 \text{ mol C m}^{-2}$. The remineralization of organic carbon appears to be promoted by a tight coupling between primary and secondary producers during the period of enhanced biological productivity in spring and summer. Most of the organic material produced in the euphotic zone is consumed, respired and remineralized within

Table 5: Transient DOC (mol C m^{-2}) in the Greenland Sea during autumn of 1996. Transient DOC was calculated by subtracting the average winter value of DOC for the area, which gave a value very similar to the average of deep-water values. The data are reported in Børsheim (submitted)

Date and position	Depth [m]				
	10	30	50	100	200
Jul 22 70°45.04' N 07°00.15' E	0.17	0.57	0.97	1.47	2.30
Jul 22 71°05.19' N 05°49.42' E	0.22	0.74	1.05	1.58	2.63
Jul 23 72°04.68' N 02°14.75' E	0.36	0.92	1.41	2.57	4.64
Jul 23 72°23.80' N 01°08.69' E	0.29	0.77	1.26	2.29	4.51
Jul 24 73°26.21' N 02°13.14' W	0.41	0.90	1.12	1.19	1.99
Jul 25 74°59.54' N 08°13.65' W	0.25	0.49	0.73	0.63	0.21
Jul 26 74°59.90' N 04°58.79' W	0.31	0.82	1.17	1.80	2.57
Jul 26 75°00.12' N 02°57.50' W	0.36	0.85	1.35	2.10	3.49
Jul 26 74°59.99' N 00°08.79' W	0.48	1.17	1.50	2.51	4.54
Jul 31 74°31.03' N 06°57.87' E	0.25	0.77	0.96	1.30	2.91
Aug 1 74°30.07' N 03°55.74' E	0.18	0.80	1.50	2.57	3.28
<i>Average</i>	<i>0.29</i>	<i>0.78</i>	<i>1.15</i>	<i>1.75</i>	<i>2.89</i>
<i>Standard deviation</i>	<i>0.10</i>	<i>0.18</i>	<i>0.25</i>	<i>0.66</i>	<i>1.28</i>
<i>Minimum</i>	<i>0.17</i>	<i>0.47</i>	<i>0.68</i>	<i>0.54</i>	<i>0.21</i>
<i>Maximum</i>	<i>0.47</i>	<i>1.15</i>	<i>1.50</i>	<i>2.57</i>	<i>4.46</i>

Table 6: Estimates for the flow of biogenic carbon in the upper 200 m of the central Greenland Sea. Units in mol C m⁻². Modified from Noji et al. (1999a)

Pool/Mechanism	Time Scale
Particle sedimentation at 200 m	
POC	0.16 ¹ Annual
Carbonate-C	< 0.01 Annual
Migrant zooplankton below 200 m	0.33 ² Fall-Spring
Accumulation of DOC in the upper 200 m	2.89 ³ Summer
<i>Total</i>	3.39

¹ includes 0.04 mol C m⁻² yr⁻¹ from particle-associated DOC (Noji et al. 1999b)
² from Hirche (1997)
³ from Table 5

the upper 200 m of the water column. Thus, the biological sequestration of carbon in the deep ocean through particle sedimentation and the respiration and mortality of migrant zooplankton was small during our investigation.

Deep Release of Nutrients and Inorganic Carbon

An additional estimate of carbon export can be derived from winter surface-to-deep nutrient gradients (Table 7). GSDW renewal rates vary from 0.1 to 0.5 Sv (Schlosser et al. 1991). During 1994 to 1995 the renewal rate was estimated to be 0.17 Sv (Anderson et al. in press). Assuming GSDW has a total volume of 504000 km³, these renewal rates are equivalent to replacement times of 32 to 160 years; 94 years is presently considered to be representative for this study period. From data on the distribution of phosphate and nitrate, it is possible to roughly estimate annual flux rates from the upper ocean to deep water of the Greenland Sea, based on an inventory for the upper 500 m in winter vs. a 1000-m thick stratum of GSDW and a replacement time of 94 years. This exercise results in surface-to-deep-water flux rates for phosphate and nitrate of 0.00105 mol P m⁻² yr⁻¹ and 0.0216 mol N m⁻² yr⁻¹, which are equivalent to 0.126 (range of 0.095 to 0.476) and 0.162 (range of 0.057 to 0.287) mol C m⁻² yr⁻¹, based on the Redfield ratio of C:N:P = 120:16:1. These numbers should probably be considered low estimates, since nitrate and phosphate often appear to be released from decaying organic matter faster than carbon (Lee and Wakeham 1988). The same type of calculation, but based directly on DIC, results in carbon flux rates of 0.0977 mol C m⁻² yr⁻¹ (range of 0.057 to 0.287 mol C m⁻² yr⁻¹); the relatively smaller

value is at least partially explained by the flux of DIC from the atmosphere into the surface layer. Interestingly, the estimated export rates shown in Table 7 are comparable to annual sedimentation rates for POC of roughly 0.1 mol C m⁻² yr⁻¹ at approximately 2000 depth (Noji, unpublished data). In addition, our estimate for downward carbon export by migrant zooplankton was approximately 0.33 mol C m⁻² from summer to spring. Because a fraction of the population of migrant zooplankton dies and is remineralized in mesopelagic depths, some unknown fraction of this carbon export may be reflected in the fluxes of phosphate and nitrate; this is dependent upon the depth of overwintering in relation to the depth of winter mixing. Moreover, migrant zooplankton contributes to the pool of dissolved organic nitrogen (and eventually nitrate) via excretion. In summary, estimates of carbon sequestration based on the distribution of phosphate and nitrate are in general agreement with estimates based on biological carbon cycling.

Annual Carbon Fluxes

The sustained undersaturation of CO₂ in surface water, relative to the atmosphere, indicates that the central Greenland Sea is a significant sink for atmospheric carbon throughout the year (with an estimated net annual air-to-sea flux of 5.9 mol C m⁻², Skjelvan et al. 1999). The degree of undersaturation is greatest during the biologically productive spring and summer, when phytoplankton productivity is at a peak and the summer mixed layer is defined by a shallow pycnocline. However, relatively low wind-speeds and warm surface water temperatures during this period limit actual bulk uptake from the atmosphere. During our investigation biological export (totaling 0.49 mol C m⁻² yr⁻¹, Table 6) appeared to play a limited role in the net annual drawdown of carbon. For comparison, the net input of carbon into the surface waters of the Greenland Sea through horizontal advection is estimated to be 26 mol C m⁻² yr⁻¹ (Chierici et al. 1999), while transport into depth with long-term deep-water formation processes is approximately 14 mol C m⁻² yr⁻¹ (based on the average winter surface DIC concentration from Table 1 and an estimated deep-water renewal rate of 0.17 Sv, Anderson et al. in press).

Because of the tight coupling between primary and secondary producers, dissolved and particulate organic carbon were largely recycled in the upper few hundred meters and not exported. The accompanying re-injection of respiratory CO₂ clearly reduced the potential for carbon uptake from the atmosphere as temperatures

Table 7: Estimates of release rates for inorganic nutrients and carbon into deep waters

	NO ₃	PO ₄	DIC
Surface ¹ [mol m ⁻²]	6.2	0.45	1075
GSDW ² [mol m ⁻²]	14.4	1.00	2159
Export ³ [mol m ⁻² yr ⁻¹]	0.021	0.0011	0.10
Carbon export ⁴ [mol C m ⁻² yr ⁻¹]	0.16	0.13	0.10
Range ⁵	0.10–0.48	0.07–0.37	0.06–0.29

¹ Assuming a surface mixed layer of 500 m (Miller et al. 1999)

² For a uniform water mass between 2000 and 3000 m (Miller et al. 1999)

³ Based on a replacement time for GSDW of 94 years (Anderson et al. in press)

⁴ Nutrient-to-carbon conversion from C:N:P = 120:16:1 (Takahashi et al. 1985)

⁵ Based on replacement times for GSDW between 32 and 160 years (Schlosser et al. 1991)

dropped during the autumn. Thus, it is not a priori new production (Dugdale and Goering 1967) which regulates carbon sequestration, rather it is export which is constrained by the depth at which waters are isolated from the surface throughout deepening of the winter mixed layer. The extremely deep winter mixing observed in the Greenland Sea (as deep as 1000 m, even in the absence of deep convection) effectively increases the depth below which true export can occur and paradoxically can decrease net carbon sequestration into the deep water. The combined process of remineralization and deep mixing not only provides a recycled carbon source for biological consumption during the next spring and summer, but it also reduces the winter air-sea $f\text{CO}_2$ gradient and, thereby, the bulk air-sea flux.

Although biological carbon export within the Greenland Sea appeared to be unexceptional during our study period, there is significant potential for increased export. One mechanism may be through decreased vertical mixing during autumn, which would serve to maintain large pools of carbon remineralized below the summer mixed layer until later in the winter, when deep convection is able to permanently transport the dissolved carbon to the deep ocean. In addition, a reduction in heterotrophic recycling in near-surface waters may enhance the effectiveness of the biological pump. Indeed, the mechanisms for reduced recycling exist already as what might be termed exceptional biological phenomena. For example, it has been reported that the Greenland Sea can host massive, rapidly growing phytoplankton blooms (Smith et al. 1991). Such blooms may not be matched by equivalently rapid and large secondary production, the result being sedimentation of organic carbon. Could a changing climate aid such a decoupling of primary and secondary production by, for example, the introduction of planktivorous

fish such as herring to the Greenland Sea, thus adding a top trophic link which is able to reduce the present size of grazing zooplankton stocks? Further, on an annual scale, more extensive and frequent coverage of the Greenland Sea by ice, which was sparse during our investigation (Toudal 1999), may promote carbon export, since enhanced sedimentation can be associated with receding ice in the Greenland Sea (Ramseier et al. 1997), although ice coverage also inhibits CO₂ drawdown from the atmosphere. An accompanying larger input of melt water in spring may influence the taxonomic composition of phytoplankton stocks and promote the dominance of diatoms, which are typically associated with bloom sedimentation, as opposed to flagellate-dominated blooms, which may be more prone to pelagic recycling. If such events become a regular occurrence, then it is not difficult to envision a more effective biological carbon pump. In essence, the lack of scientific consensus presents the best reason for continuing investigations, which attempt to accurately describe the physical and biological processes regulating the transfer of atmospheric carbon to the deep ocean.

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