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Organic carbon partitioning during spring phytoplankton blooms in the Ross Sea polynya and the Sargasso Sea

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Abstract

In this study we evaluate the partitioning of organic carbon between the particulate and dissolved pools during spring phytoplankton blooms in the Ross Sea, Antarctica, and the Sargasso Sea. As part of a multidisciplinary project in the Ross Sea polynya we investigated the dynamics of the dissolved organic carbon (DOC) pool and the role it played in the carbon cycle during the 1994 spring phytoplankton bloom. Phytoplankton biomass during the bloom was dominated by an Antarctic *Phaeocystis* sp. We determined primary productivity (PP; via $H^{14}CO_3^-$ incubations), particulate organic carbon (POC), bacterial productivity (BP; via $[^3H]$ thymidine incorporation), and DOC during two occupations of 76°30'S from 175°W to 168°E. Results from this bloom are compared to blooms observed in the Sargasso Sea in the vicinity of the Bermuda Atlantic Time-Series Study station (BATS). We present data that demonstrate clear differences in the production, biolability, and accumulation of DOC between the two ocean regions. Despite four- to fivefold greater PP in the Ross Sea, almost an order of magnitude less DOC ($mmol\ m^{-2}$) accumulated during the Ross Sea bloom compared to the Sargasso Sea blooms. In the Ross Sea 89% ($\sim 1\ mol\ C\ m^{-2}$) of the total organic carbon (TOC) that accumulated during the bloom was partitioned as POC, with the remaining 11% ($\sim 0.1\ mol\ C\ m^{-2}$) partitioned as DOC. In contrast, a mean of 86% ($0.75\text{--}1.0\ mol\ m^{-2}$) of TOC accumulated as DOC during the 1992, 1993, and 1995 blooms in the Sargasso Sea, with as little as 14% ($0.08\text{--}0.29\ mol\ C\ m^{-2}$) accumulating as POC. Although a relatively small portion of the fixed carbon was produced as DOC in the Ross Sea, the bacterial carbon demand indicated that a qualitatively more labile carbon was produced in the Ross Sea compared to the Sargasso Sea. There are fundamental differences in organic carbon partitioning between the two systems that may be controlled by plankton community structure and food-web dynamics.

The recent resurgence of interest in dissolved organic matter (DOM) in the ocean has resulted in advances in our understanding of the role of this pool in elemental cycling. In ocean regions remote from land, dissolved organic carbon

(DOC) production may originate from several in situ biological processes, but it is ultimately derived from primary production. Significant amounts of newly produced DOC have been shown to accumulate during or after phytoplank-

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ton blooms (Duursma 1963; Parsons et al. 1970; Ittekkot et al. 1981; Eberlein et al. 1985; Cadée 1986; Carlson et al. 1994; and studies cited in Williams 1995). Several studies have demonstrated that DOC is an important component of the "biological pump" in some oceanic environments (Copin-Montégut and Avril 1993; Carlson et al. 1994; Ducklow et al. 1995). Copin-Montégut and Avril (1993) and Carlson et al. (1994) reported that C exported as DOC occurs rapidly as the result of winter-time convective overturn in subtropical and temperate regions. However, as Carlson et al. (1994) pointed out, the DOC export observed in the Sargasso Sea is not considered to be a long-term C-storage mechanism owing to the limited potential for physical transport. The polar environment of the Ross Sea, on the other hand, is a site of bottom-water formation (Gordon 1966; Jacobs et al. 1970). Suspended or dissolved material that is advected to depth during bottom-water formation can be removed from contact with the surface water on the scale of 10^3 years. Thus, the physical conditions favor DOC export and long-term C removal. However, DOC can only be important as an export term if it can be shown to accumulate.

The Ross Sea is a high-latitude, nutrient-rich continental shelf system that exhibits one of the most predictable and spatially extensive phytoplankton blooms in the entire Southern Ocean (Sullivan et al. 1993; Arrigo and McClain 1994). The spring blooms observed in the south-central Ross Sea are dominated by the colonial haptophytes *Phaeocystis* (El-Sayed et al. 1983), with diatoms dominating near the coast (Smith and Nelson 1985; Smith et al. 1996). DOC data from the Ross Sea are scarce, but values ranging from $<100 \mu\text{M C}$ (Lancelot et al. 1989; Tupas et al. 1994; Kähler et al. 1997) to $>1,200 \mu\text{M C}$ (Bölter and Dawson 1982; Davidson and Marchant 1992) have been reported for surface waters from other locations in the Southern Ocean.

One of the objectives of this study was to examine the C dynamics of the Ross Sea system and reference it to another well-studied system. The northwestern Sargasso Sea, the site of the U.S. JGOFS Bermuda Atlantic Time-Series Study (BATS) station ($31^{\circ}50'N$, $64^{\circ}10'W$), is a subtropical, low-nutrient oceanic system that exhibits seasonal patterns of mixing and biological production dominated by spring phytoplankton blooms (Menzel and Ryther 1960; Michaels et al. 1994). Picoplankton dominate the plankton assemblage (Olson et al. 1990; Malone et al. 1993; Caron et al. 1995; Rathbun et al. unpubl.), with haptophytes and diatoms also present (Bidigare et al. 1990; Malone et al. 1993). DOC concentrations can increase by $>0.75 \text{ mol m}^{-2}$ in the surface 250 m through the course of the bloom (Carlson et al. 1994).

In this study we demonstrate clear differences in production, biolability, and accumulation of the bulk DOC pool between the two ocean regions. We determined the cumulative C production, its partitioning between particulate and dissolved pools, and the relative biochemical lability of DOC during bloom events in the two regions. Estimates of bacterial C demand indicated that the DOC produced was more labile in the Ross Sea compared to the Sargasso Sea. There appear to be fundamental differences in the DOM production and cycling mechanisms between the two ocean sites. Our data support the hypothesis of Karl (1993) that dissolved organic substrate production by phytoplankton is limited in

the Southern Ocean. Here, we only discuss the decoupling of phytoplankton and bacterioplankton productivity and biomass in the context of a Ross Sea *Phaeocystis* bloom.

Based on previous studies of primary productivity (PP) and biomass accumulation of these regions (Arrigo and McClain [1994] and Smith and Nelson [1985] for the Ross Sea; Menzel and Ryther [1960] and Michaels et al. [1994] for the Sargasso Sea), we expected to observe significant differences in DOC production and accumulation between the two sites. The Ross Sea is highly productive during the bloom, whereas the Sargasso Sea is not. We did observe significant differences between the two sites; however, contrary to our original hypothesis of large DOC production and accumulation associated with the Ross Sea phytoplankton bloom, we observed only small changes in the DOC. Despite four- to fivefold greater PP in the Ross Sea, almost an order of magnitude less DOC accumulated in the surface waters during the Ross Sea bloom compared to that found in the Sargasso Sea. Differences in mechanisms of DOC production must exert a major control on the amount of DOC made available for potential export from the surface ocean.

Methods

Study sites—Measurements of DOC, PP, particulate organic carbon (POC), bacterial biomass (BB), and bacterial production (BP) were made (1) during the spring blooms of 1992, 1993, and 1995 in the Sargasso Sea (no spring bloom was observed in 1994 owing to insufficient deep mixing; see Michaels and Knap 1996), and (2) during two occupations along $76^{\circ}30'S$ from $175^{\circ}W$ to $168^{\circ}E$ in the Ross Sea polynya in 1994 (14–17 November and 2–6 December). DOC data collected along the same transect line in the Ross Sea during a subsequent cruise in 1995–1996 (21–29 December and 8–11 January) are also presented to demonstrate trends during later phases of the spring bloom. Sargasso Sea data were collected aboard the RV *Cape Hatteras*, RV *Endeavor*, and the RV *Weatherbird II* at or in the vicinity of the BATS site (nominally $31^{\circ}50'N$, $64^{\circ}10'W$). The Ross Sea data were collected aboard the RV *Nathaniel B. Palmer*.

Sample water for PP was collected via GoFlo bottles on Kevlar hydrowire within the euphotic zone of the Sargasso Sea. All other samples for both sites were collected with a CTD/rosette, holding 24 10- or 12-liter Niskin bottles equipped with epoxy-coated or silicone springs. Ten to 12 depths were sampled for BB, BP, POC, and DOC in the surface 150 m and 250 m in the Ross Sea and Sargasso Sea, respectively. The Sargasso Sea PP and POC data used for this study were obtained from the BATS dataset (<http://www.bbsr.edu>). DOC and bacterioplankton data used in the Sargasso Sea analysis were reported in Carlson et al. (1994, 1996) and were supplemented with BATS data where applicable.

Primary productivity and particulate organic carbon—Details of the sampling scheme, analytical methods, and quality control are available in the BATS methods manual (Knap et al. 1994). Sargasso Sea PP was calculated from net $\text{H}^{14}\text{CO}_3^-$ uptake measurements during dawn-to-dusk in situ incubations at eight depths distributed through the surface 140 m (to $\sim 0.1\%$ light level). POC was collected on pre-

combusted GF/F filters from 12 depths in the surface 250 m. In the Ross Sea, duplicate Niskin bottles were closed at each depth with sample water for POC and PP drawn according to the protocol of Smith and Nelson (1990). Samples for PP were collected from seven isolumes (100, 50, 30, 25, 5, 1, and 0.1% of surface irradiance) and measured by simulated in situ $\text{H}^{14}\text{CO}_3^-$ incubations. POC was sampled from 10 to 12 depths in the surface 150 m and filtered onto combusted GF/F filters. Details of the analytical procedures are given elsewhere (Smith and Nelson 1990).

POC collected on GF/F filters includes phytoplankton, grazers, bacteria, and detritus C. In order to assess the non-bacterial POC, the depth-integrated POC was corrected for bacterial C by determining bacterial biomass that accumulated during the course of each bloom, assuming a 50% filter-retention efficiency (Lee and Fuhrman 1987) and subtracting the resulting values from the observed changes in POC stocks.

Bacterial biomass and productivity—Samples for bacterial abundance and biovolume were preserved with particle-free 25% glutaraldehyde (final concn of 1.0%) and stored at 4°C until slide preparation. Samples were filtered onto 0.2- μm blackened polycarbonate filters and stained with Acridine Orange (final concn of 0.005%) according to Hobbie et al. (1977). BB was determined from bacterial abundance and biovolume estimates. Biovolumes were estimated using a Zeiss Vidas Videoplan image analysis system described in Carlson et al. (1996). Seasonal biovolume estimates (Carlson et al. 1996) were used to obtain BB from the BATS bacterial abundance data.

Bacterial productivity (BP) was estimated with [^3H -methyl]thymidine (^3H -TdR) incorporation. Samples were incubated in the dark at in situ temperatures for 2–4 h and 12 h in the Sargasso Sea and Ross Sea, respectively. Extraction and analytical procedures are detailed elsewhere (Carlson et al. 1996). A median marine ^3H -TdR conversion factor of 2×10^{18} cells mol^{-1} TdR (Ducklow and Carlson 1992) and a C conversion factor of $120 \text{ fg } \mu\text{m}^{-3}$ were used to convert bacterial biovolume and ^3H -TdR into C-based biomass and productivity.

Data for bacterial productivity and biomass in the Sargasso Sea came from Carlson et al. (1996) and were supplemented with data from the BATS dataset. BP data that exist in the BATS dataset do not extend below the euphotic zone; thus, the integrated BP was underestimated. Depth-integrated BP increased by an average of $27 \pm 2\%$ (SE) ($n = 17$ casts) from 140 to 250 m during spring periods (Carlson et al. 1996); thus, this correction factor was applied to the BATS BP in order to compare the two Sargasso Sea datasets.

DOC—All DOC samples were analyzed by a high-temperature combustion (HTC) method using either a modified Dohrmann DC-190 (Carlson and Ducklow 1995) or a homemade high-temperature instrument similar to that described in Hansell et al. (1993). The configuration and operating parameters of the machines were as follows: ultrahigh-purity O_2 was used as a carrier gas and flowed through the machine at 175 ml min^{-1} . One hundred microliters of sample was injected manually through a septumless injection port into a

quartz combustion tube. After passing through the combustion furnace, the carrier gas traveled through several water traps and a final copper halide trap before entering the detector. The resulting CO_2 was detected with a Li-Cor 6252 CO_2 analyzer and the signal was integrated with chromatographic software (Dynamax Macintegrator I version 1.3; Rainin Inst.). The combustion tube dimensions and packing material were the only difference between the homemade and the modified Dohrmann. The quartz combustion tube ($490 \times 13 \text{ mm}$) of the homemade instrument was packed with Pt gauze (Ionics), 7% Pt alumina catalyst (Dymatec), Sulfix (Wako Pure Chemical Industries), and CuO wire (Lee-man Labs) and heated to 740°C. The Pt catalyst, Sulfix, and CuO wire are all separated by a thin layer of quartz wool. Sulfix was used to remove halides and the CuO wire oxidized CO to CO_2 . A two-zone furnace with the top zone heated to 800°C and the bottom zone heated to 600°C was used during the 1995 field season.

Extensive conditioning of the combustion tube with repeated injections of low-carbon water (LCW) and deep seawater was essential to minimize the machine blanks. After conditioning, the system blank was assessed with ampulated LCW that was referenced against blank water provided by Jonathan Sharp in the JGOFS EqPac intercomparison (Sharp et al. 1995). The system response was standardized daily with a 4-point calibration curve of glucose solution in LCW. Deep seawater (>2,000 m) was used as a second reference material. Because deep seawater is very stable, it is valuable in assessing the performance of the machine even though the absolute value is not known. Analyzing LCW water and deep-reference water several times a day allowed us to assess machine stability from run to run and day to day, ensuring confidence in our analyses.

In the Ross Sea, DOC concentrations were determined after removal of POC by filtration, whereas in the Sargasso Sea DOC was estimated by subtracting measured POC values (organic C retained on a GF/F filter) from measured total organic carbon (TOC). In the Sargasso Sea, POC is a small fraction of TOC (mean of 2.7% in 1995 for the surface 250 m during the bloom period). We estimate the maximum error associated with DOC values to be $\sim 3\text{--}4\%$ based on the propagation of error of the TOC and POC measurements. In the Ross Sea, we removed POC from TOC prior to HTC analysis by gravity-filtering the sample through an in-line-combusted GF/F filter attached directly to the spigot of the Niskin bottle. DOC analyses were conducted onboard. Comparisons of TOC and DOC measurements conducted on deep reference water demonstrated no significant contamination resulting from GF/F in-line gravity filtration (data not shown).

No systematic day-to-day variability was observed in integrated DOC stocks during short time-series cruises in the Sargasso Sea (5–10 d) in 1992 and 1993, so that whenever possible a mean of multiple-DOC casts was used from a single cruise in order to minimize the effect of mesoscale patchiness as is often observed in the Sargasso Sea (*see* Carlson et al. 1994).

Data treatment—Ross Sea PP was integrated to the 0.1% light level (ranging from 20 to 150 m). Vertical profiles of

Table 1. Mean surface temperature, depth-integrated primary productivity (PP), bacterial productivity (BP), bacterial biomass (BB), dissolved organic carbon (DOC), and particulate organic carbon (POC) of the Ross Sea. Error values represent standard error. Data in parentheses represent ranges of values.

Period	Surface temp. (°C)	PP*	BP†	BB†	DOC†	POC†
		mmol C m ⁻² d ⁻¹		mmol C m ⁻²		
Transect I—Bloom initiation (14–17 Nov 94)	-1.79±0.02 (-1.86 to -1.66)	44±14 (11–127)	0.4±0.1 (0.04–0.68)	5.6±0.6 (3.7–9.7)	6,530±10 (6,490–6,570)	890±125 (291–1,870)
Transect II—Bloom (2–6 Dec 94)	-1.73±0.02 (-1.59 to -1.80)	260±55 (97–518)	4.3±0.2 (3.8–4.6)	16.4±1.8 (9.8–27.6)	6,650±62 (6,390–6,840)	1,890±248 (708–3,290)

* Values were integrated through the euphotic zone (20–150 m).

† Values were integrated to 150 m in the Ross Sea.

BP, BB, POC, and DOC in the Ross Sea were integrated from the surface to 150 m. The mean mixed-layer depth during the study period was 35 ± 16 m (Smith and Gordon 1997), indicating that the newly produced suspended organic material was not being mixed below 150 m in the Ross Sea. Sargasso Sea PP was integrated to 140 m; however, the surface mixed layer has been shown to reach depths >250 m during convective mixing events (Michaels et al. 1994), resulting in newly produced DOC and POC being mixed to depths deeper than the euphotic zone (~140 m). Because newly produced and entrained organic matter can be consumed at depth, we thought it necessary to account for the potential impact of deep mixing by integrating the DOC, POC stocks, BB, and BP rates to 250 m for a more accurate comparison between prebloom and bloom conditions in the Sargasso Sea.

Arrigo and McClain (1994) used satellite imagery of an intense spring phytoplankton bloom in the Ross Sea to demonstrate the spatial extent of the bloom initiated from the polynya area. They showed the bloom covered ~106,000 km² in the early spring season of 1979. Based on reports of vast spring blooms in the Ross Sea polynya (Sullivan et al. 1993; Arrigo and McClain 1994), we assumed that the reoccupation of the 76°30' transect line nearly 3 weeks later (in 1994) would provide an estimate of temporal change of the study parameters. As in any marine system, mesoscale features may bias temporal comparisons. To reduce the influence of patchiness, we averaged depth-integrated parameters along each transect, which should allow our average transect mean for each parameter to represent an integration of the mesoscale variability within each transect.

The amount of organic C produced via PP (measured as ¹⁴C particles collected on GF/F filters) or consumed via BP (measured as [³H]-thymidine incorporation) over the course of the bloom was defined as cumulative primary productivity (CPP) and cumulative bacterial productivity (CBP). The CPP and CBP were estimated by integrating mean PP and BP estimates over 19 d for the Ross Sea dataset in 1994. Accumulation of BB, DOC, and POC during the bloom was determined as the difference between the transect means of each parameter, here referred to as Δ BB, Δ DOC, and Δ POC. The Sargasso Sea data are from a time-series, so criteria had to be applied to identify the period appropriate for this analysis. The time point immediately prior to elevated PP marked the beginning of the study period, and because one of the objectives of this study was to determine the quantity

of DOC accumulation during a bloom event, the period marked by the maximum DOC accumulation in the spring was used as the endpoint. DOC accumulation was determined as the difference between integrated prebloom estimates and the maximum integrated DOC stocks. Because DOC measurements were not made prior to the Sargasso Sea bloom events of 1992 and 1993, we used average depth-integrated (250 m) autumn estimates (1991 and 1992) reported in Carlson et al. (1994) as prebloom values, and assumed minimal temporal variability in DOC from the autumn to just prior to bloom initiation. By using the criteria described above to define the study period, the CPP and CBP were estimated by integrating PP and BP over 70, 29, and 73 d during Sargasso Sea blooms in 1992, 1993, and 1995, respectively. Δ BB, Δ DOC, and Δ POC were determined as the differences in stocks estimated at the beginning and end of the same bloom periods mentioned above.

Results

Ross Sea—Upon entering the Ross Sea polynya in 1994, strong sustained winds (up to 35 knots) and continuous surface freezing prevailed. Mean PP and POC levels were elevated (Table 1) compared to prebloom conditions, indicating that a phytoplankton bloom had begun. We used the western terminus (76°30'S, 168°30'E) of the first transect as a reference for prebloom conditions (PP was lowest at 11 mmol C m⁻² d⁻¹, and POC was 338 mmol C m⁻²). The colonial haptophyte *Phaeocystis* sp. dominated the phytoplankton assemblage throughout the transect, with significant numbers of diatoms also present. BP rates and DOC concentrations were comparable to 1,000-m-deep water values collected off of the continental shelf (69°37'S, 176°32'W; data not shown), indicating these variables were at background levels (Table 1). DOC concentrations showed a small degree of scatter in the surface 30 m during the first transect, with an amplitude of up to 6 μ M C above the deep-water values. Below 30 m, DOC concentrations were distributed homogeneously down through 150 m (Fig. 1A).

Nearly 3 weeks later, *Phaeocystis* sp. continued to dominate the phytoplankton assemblage, with maximum PP rates in excess of 500 mmol C m⁻² d⁻¹. Mean surface temperatures were not significantly different ($P > 0.01$) between the two transects (Table 1). Considerable spatial heterogeneity was observed for most of the parameters during both tran-

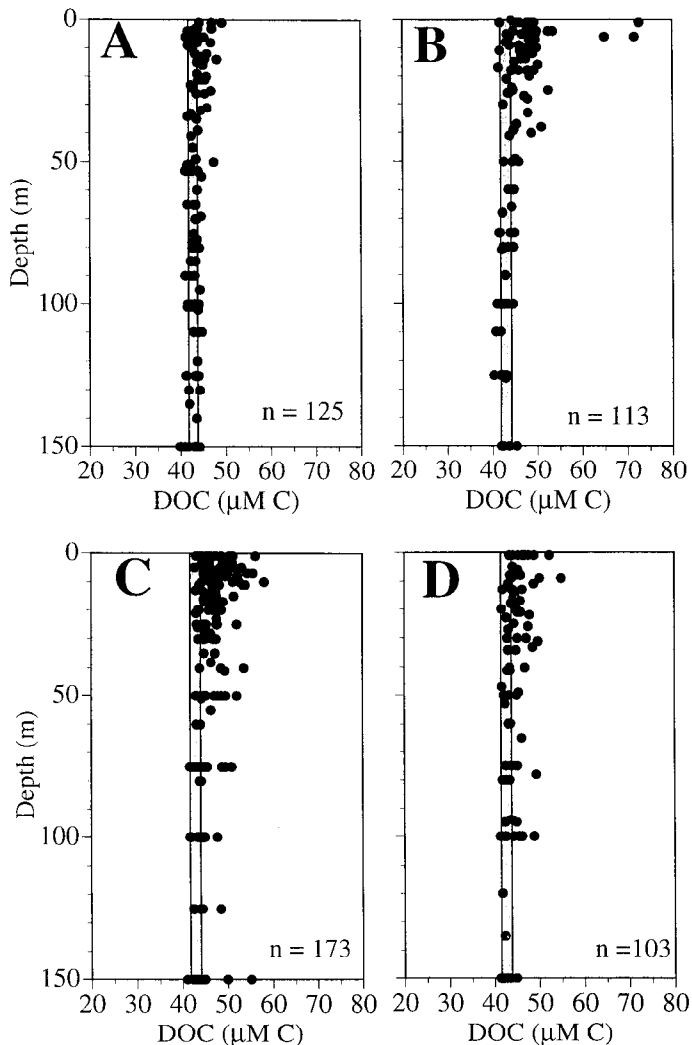


Fig. 1. Vertical distributions within the upper 150 m in the Ross Sea along 76°30'S. A. DOC values collected during 14–17 November 1994. B. DOC values collected during 2–6 December 1994. C. D. DOC values collected during two transects conducted in 1995–1996 (21–29 December 1995 and 8–11 January 1996). The grey bars in each panel represent the range of deep-water values collected off the continental shelf in >1,000 m and >200 m on the continental shelf. This deep-water DOC is very old and refractory DOC and is used as a benchmark to emphasize the production of relatively new DOC (i.e. <50 m).

sects (Fig. 2). Mean transect values for PP, BP, BB, and POC increased 2- to 10-fold (Table 1). Conversely, there was a very small (2%) increase in DOC stocks (Table 1). The vertical distribution of DOC showed elevated concentrations in the surface waters, ranging from 41 to 72 $\mu\text{M C}$, with a transect mean of $48 \pm 6 \mu\text{M C}$ in the surface 50 m (Fig. 1B). The mean surface mixed layer depths for transects I and II were 35 ± 13 m and 34 ± 10 m, respectively, indicating that surface DOC concentrations were not kept low by deep mixing during the study period.

Bacterioplankton productivity increased by an order of magnitude, with a threefold rise in biomass during the study

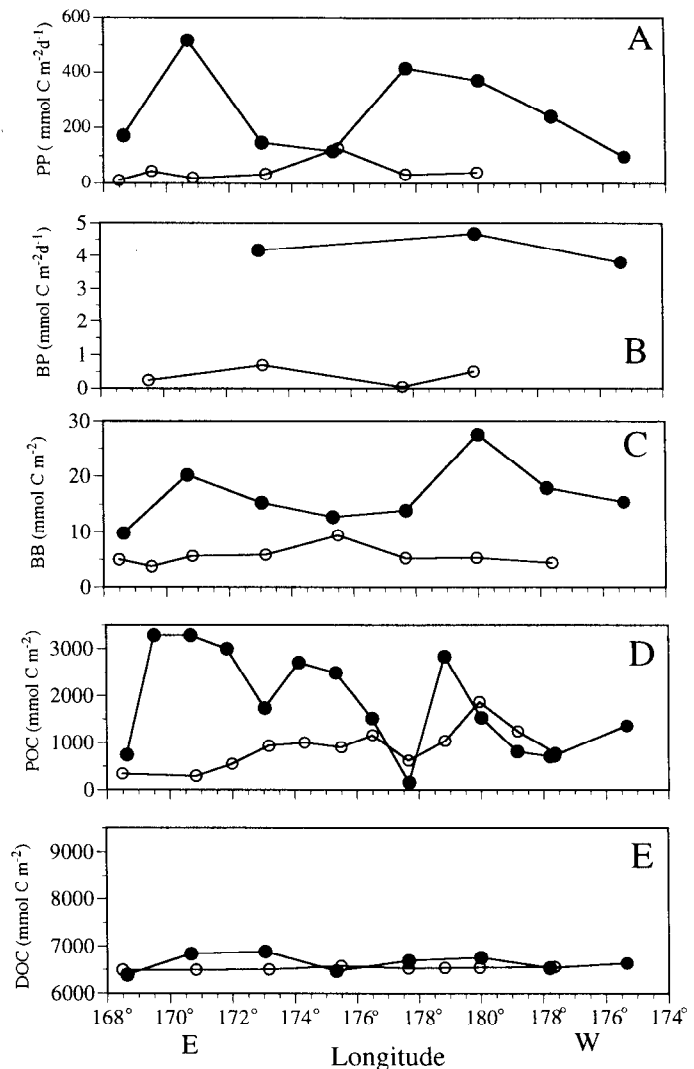


Fig. 2. Observations of (A) primary productivity (PP), (B) bacterial productivity (BP), (C) bacterial biomass (BB), (D) particulate organic carbon (POC), and (E) dissolved organic carbon (DOC) along 76°30'S between 168°E and 175°W in the Ross Sea. Open symbols represent depth-integrated variables measured during the first occupation of the transect from 14 to 17 November 1994. Solid symbols characterize the second occupation of the same transect from 2 to 6 December 1994. PP was integrated to the 0.1% light level (range from 20 to 150 m). All other variables were integrated to 150 m.

period. This increase in bacterial activity, despite no significant change in temperature (Table 1), indicated that bacterial assemblages were responding to supply of labile substrate rather than to change in temperature.

The 1995–1996 Ross Sea cruise was conducted during the austral summer months of December and January. The polynya had opened considerably, and the majority of the stations were ice-free. The phytoplankton community displayed considerable variability, with diatoms (primarily *Pseudonitzschia* sp.) and *Phaeocystis* sp. dominating the phytoplankton assemblages. Qualitative observation showed that *Phaeocystis* mucilage was colonized by attached bacterioplankton, in-

dicating that *Phaeocystis* was senescing. During the first transect (21–29 December 1995), DOC was enhanced by up to $14 \mu\text{M C}$ in the surface 50 m, with some casts having elevated concentrations throughout the surface 150 m (Fig. 1C). The mean integrated concentrations were 3% greater than in December 1994 ($6,650 \pm 60 \text{ mmol C m}^{-2}$ in 1995–1996 vs. $6,540 \pm 60 \text{ mmol C m}^{-2}$ in 1994). During the last occupation of the $76^{\circ}30'S$ transect line (8–11 January 1996), the integrated stocks of DOC had decreased to concentrations of $6,570 \pm 60 \text{ mmol C m}^{-2}$ and were not significantly different from 1994 means. Bacterial productivity rates were similar to the rates observed during the second transect in 1994 (mean of $3.5 \text{ mmol C m}^{-2} \text{ d}^{-1}$; range of $1\text{--}6 \text{ mmol C m}^{-2} \text{ d}^{-1}$). Although these data were collected during a subsequent year, it appears that neither DOM accumulation nor bacterial productivity increased during later phases of a bloom event in the Ross Sea at least through January 1996.

Sargasso Sea—The BATS site has strong seasonal patterns of mixing and biological production dominated by a spring phytoplankton bloom. Detailed descriptions of the seasonal patterns of PP, POC, DOC, BP, and BB in the surface waters of the Sargasso Sea have been reported elsewhere (Carlson et al. 1994, 1996; Michaels et al. 1994; Michaels and Knap 1996).

Here we briefly describe some of the highlights associated with the bloom periods of 1992, 1993, and 1995. There was significant interannual variability with regard to the duration and the magnitude of the blooms. Maximum PP values ranged from 74 to $94 \text{ mmol C m}^{-2} \text{ d}^{-1}$ and were approximately threefold greater than prebloom estimates for each year (Fig. 3). Maximal DOC stocks and PP rates coincided during 1992 and 1993, indicating that DOC accumulation co-varied with PP increases. In 1995, the DOC maximum occurred after the measured maximum in PP, indicating either a difference in the DOC production mechanisms compared to previous years or that sampling bias existed. It is also possible that we missed the maximal increase in DOC accumulation in 1992 due to low sampling frequency. Newly accumulated DOC (i.e. DOC that accumulated above pre-bloom levels over the course of the bloom period) ranged from 0.75 to 1.1 mol C m^{-2} over the bloom periods and appeared to increase exponentially in 1993 and 1995 (Fig. 3B,C, Table 2). Slight but highly variable increases in POC were observed from prebloom to the end of the bloom period (Fig. 3, Table 2). Bacterioplankton responded to the bloom with a nearly twofold increase in BP, but less than a twofold change in BB was observed (Fig. 3).

Partitioning of organic carbon stocks—Accumulations of total organic C (ΔTOC ; $\Delta\text{TOC eq } \Delta\text{DOC} + \Delta\text{POC}$) during the bloom periods were similar in magnitude at the two sites, with ΔTOC values of $1.1 \pm 0.3 \text{ mol C m}^{-2}$ and a mean of $1.0 \pm 0.2 \text{ mol C m}^{-2}$ for the Ross Sea and Sargasso Sea, respectively (Table 2). However, marked differences in organic C partitioning between the particulate and dissolved pools were evident when the two systems were compared (Fig. 4). For example, in the Ross Sea, 89% (1 mol C m^{-2}) and 11% (0.1 mol C m^{-2}) of the ΔTOC was partitioned into the POC and DOC pools, respectively (Fig. 4B). The Sar-

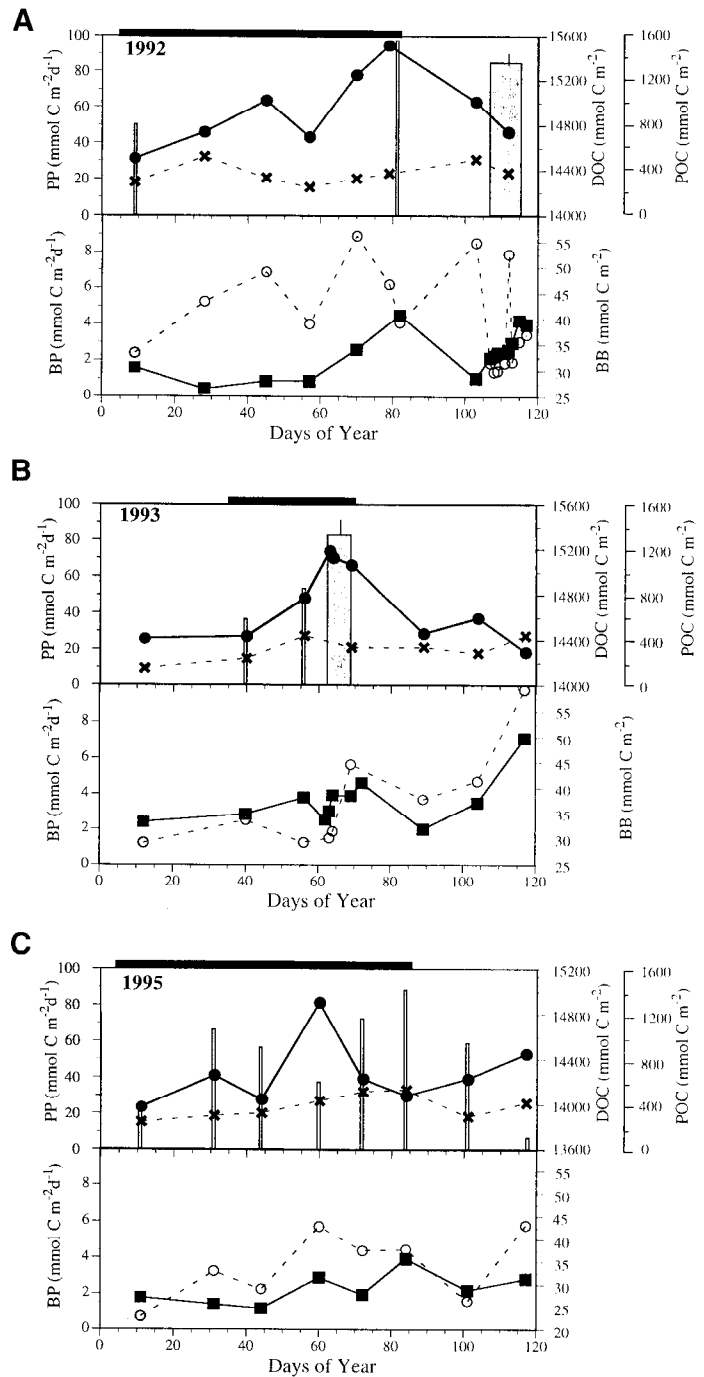


Fig. 3. Variability of depth-integrated organic carbon variables during spring blooms in the Sargasso Sea—(A) 1992, (B) 1993, and (C) 1995. PP (●) was integrated to 140 m; POC (×), BP (■), BB (○) and DOC (bars) were integrated to 250 m. The heights of the DOC columns represent the mean-integrated DOC stock, and the width of the column represents the duration of the sample collection period. The heavy black lines show the bloom period addressed here.

gasso Sea data showed opposite trends in organic C partitioning, with $14 \pm 4\%$ ($\sim 0.1 \text{ mol C m}^{-2}$) and $86 \pm 4\%$ ($\sim 1 \text{ mol C m}^{-2}$) of ΔTOC as ΔPOC and ΔDOC , respectively, for Sargasso Sea spring bloom periods (Fig. 4B).

The mean daily primary productivity in the Ross Sea was

Table 2. Production, demand, and accumulation (mmol C m^{-2}) of organic carbon during spring phytoplankton blooms in the Ross Sea and the Sargasso Sea. Cumulative primary productivity (CPP) and cumulative bacterial productivity (CBP) represent the time-integrated carbon production and consumption during the course of the bloom periods. BCD represents the bacterial carbon demand over each bloom period based on a bacterial growth efficiency (BGE) of 14% (*see text for details*). ΔBB , ΔDOC , and ΔPOC are the differences between prebloom and the end of the study periods (*see text for details*). Error represents standard error during the bloom season.

Study site	Study period (d)	CPP	CBP	BCD	ΔBB	ΔDOC	ΔPOC
Ross Sea (1994)	19	2,890	44	314	11 \pm 2	125 \pm 63	990 \pm 277
Sargasso Sea (1992)	70	3,880	94	673	13	759	76
Sargasso Sea (1993)	29	1,450	97	692	11	752 \pm 147	94
Sargasso Sea (1995)	73	3,100	123	879	9	1,050	286

four to five times greater than in the Sargasso Sea (Figs. 2, 3), yet DOC accumulation was up to 10 times greater in the Sargasso Sea (Fig. 4A). The lack of DOC accumulation could not be explained by rapid microbial removal of DOC in the Ross Sea because the BP rates and BB accumulations were similar in the two systems. The range of volume normalized rates of bacterial productivity were 0.3–30 $\mu\text{M C m}^{-3} \text{ d}^{-1}$ and 3–20 $\mu\text{M C m}^{-3} \text{ d}^{-1}$ for the Ross Sea and Sargasso Sea, respectively. The ranges of integrated BP rates and BB stock are presented in Figs. 2 and 3. These observations indicate that the Ross Sea phytoplankton community, dominated by *Phaeocystis* sp. was extremely efficient in retaining fixed C in particulate form.

DOC flux through bacterioplankton was calculated by di-

viding BP by bacterial growth efficiency (BGE). DOC mineralization experiments (described in Carlson and Ducklow 1996) were performed at each site to determine BGE. Both sites yielded similar BGE values of $\sim 14\%$ (unpubl. data for the Ross Sea; Carlson and Ducklow 1996), which was assumed for estimating bacterial C demand at both sites (Table 2). DOC production was calculated as the sum of bacterial C demand and ΔDOC over the bloom periods (Fig. 5). Less than 0.5 mol C m^{-2} was produced as DOC in the Ross Sea compared to 1.5–2 mol C m^{-2} during the Sargasso Sea bloom periods.

Differences in the partitioning of organic C between the two sites are highlighted when ΔDOC and ΔPOC are placed in the context of CPP (Fig. 6). Total DOC production (ΔDOC plus bacterial C demand) was just 15% of CPP in the Ross Sea compared to a mean of $66 \pm 18\%$ in the Sargasso Sea. The percentage of CPP that resisted rapid microbial degradation and resulted in DOC accumulation was 4% in the Ross Sea and averaged $35 \pm 9\%$ in the Sargasso Sea. POC accumulation accounted for up to 34% in the Ross Sea, but only $6 \pm 2\%$ of the CPP in the Sargasso Sea (Fig. 6).

Discussion

DOC accumulation and the decoupling of phytoplankton productivity from bacterial productivity—Heterotrophic bacterioplankton dominate the oxidation of DOC (Azam and

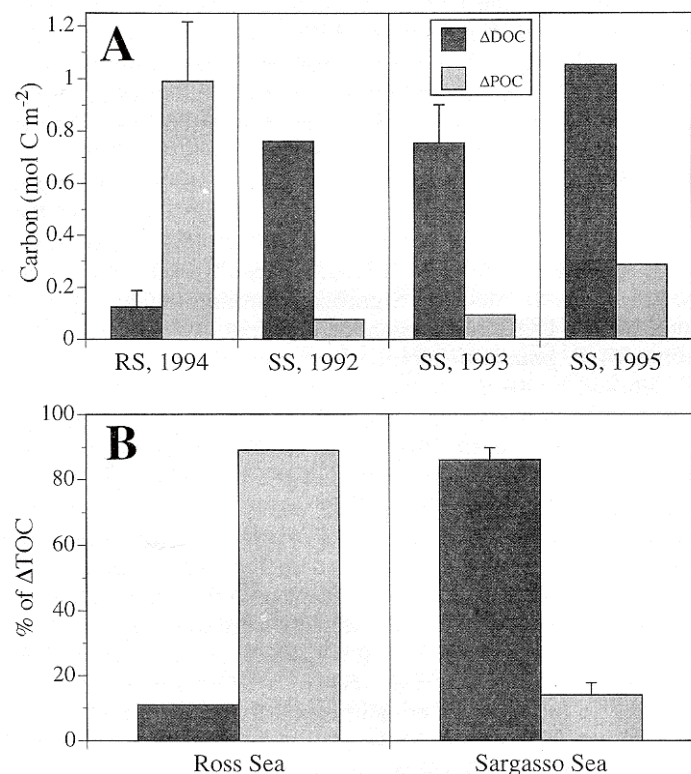


Fig. 4. A. Stocks of DOC and POC that which accumulated during blooms in the Ross Sea (RS) and the Sargasso Sea (SS). B. The percentage of TOC that accumulated as POC and DOC in the Ross Sea and Sargasso Sea. Error bars represent standard error.

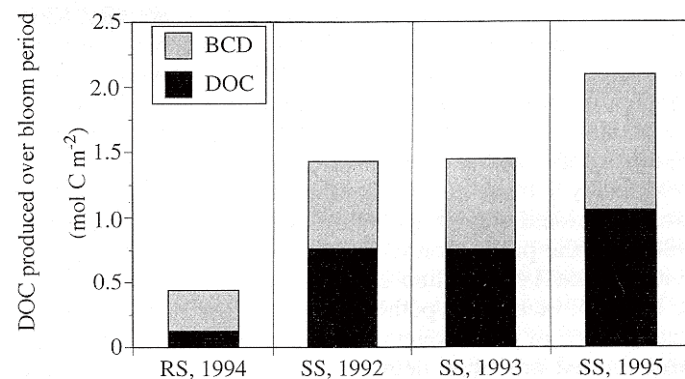


Fig. 5. DOC produced during the bloom periods in the Ross Sea in 1994 and in the Sargasso Sea in 1992, 1993, and 1995. The total DOC production has been partitioned into accumulated DOC (dark bar) and the amount of DOC processed through bacterioplankton (bacterial carbon demand).

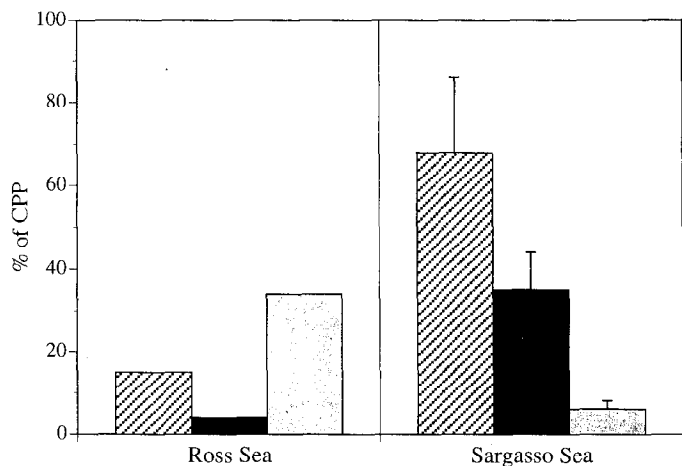


Fig. 6. The percentage of cumulative primary productivity (CPP) resulting in total DOC production (striped column), and accumulated as DOC (dark solid column) or POC (grey column). Error bars represent standard error for the 3 years of analysis in the Sargasso Sea.

Hodson 1977); thus, accumulation of DOM depends, at least in part, on the decoupling of microbial consumption from DOC production. This decoupling is a function of the DOC production rate, the biochemical composition of the material produced, and factors that limit bacterial growth. During the study in the Ross Sea there was significant increase of BB and BP, indicating a response of bacterioplankton to PP-derived substrate (Fig. 2B, C, Table 2). However, increases in BB and bacterial C demand were small relative to changes in phytoplankton biomass and productivity, representing only 1% and 11% of the Δ POC and CPP, respectively (Table 2). This small response represents a significant uncoupling of the bacterial and phytoplankton processes. Several studies have demonstrated a lack of correlation between bacterial and phytoplankton parameters in the Southern Ocean (Davidson and Marchant 1987; Cota et al. 1990; Karl et al. 1991; Karl and Bird 1993), seemingly contradicting the cross-ecosystem analyses of Bird and Kalff (1984) and Cole et al. (1988), who showed a strong positive correlation between phytoplankton and bacterial biomass and activity. Karl (1993) suggested that autotrophic-heterotrophic relationships in eutrophic regions of the Southern Ocean are fundamentally different from other habitats.

Lancelot et al. (1989) suggested that the coupling between phytoplankton and bacterioplankton exhibited a lag of approximately 1 month in the Southern Ocean. Low temperatures associated with high latitudes (Pomeroy and Deibel 1986) and the production of high-molecular-weight (HMW) DOC (Billen 1984; Billen and Fontigny 1987; Lancelot et al. 1989) have been hypothesized as factors that limit bacterial growth in polar waters. In *Phaeocystis*-dominated systems, limited microbial degradation of organic material has also been observed (Thingstad and Billen 1994 and references therein). The production of antibiotics such as acrylic acid accompanying *Phaeocystis* blooms (Sieburth 1960; Davidson and Marchant 1992) has been proposed as a potential mechanism to explain low bacterial response; however, re-

cent studies have suggested that acrylic acid concentrations are too low to inhibit bacterial growth (Putt et al. 1994; Slezak et al. 1994). Nutrient limitation has also been hypothesized as a mechanism for limited microbial degradation of *Phaeocystis* sp. (Thingstad and Billen 1994). However, according to the above hypotheses, DOC production and consumption processes should become decoupled and result in a large accumulation of DOC. We found no evidence of a large buildup of DOC within Ross Sea blooms (Table 2). Instead, our data indicate that BP was kept low relative to PP in the Ross Sea not because of temperature, antibiotics, or poor quality DOM, but because the dissolved organic substrate supply was limited. These results support the hypothesis of Karl (1993) which stated that it is the delay or lack of extracellular C production by phytoplankton that limits bacterial response rather than a delay in bacterial utilization of the byproducts in some Southern Ocean environments.

Partitioning of fixed organic C between the dissolved and particulate pools—Spring phytoplankton blooms are net autotrophic events that are initiated by favorable conditions such as sufficient nutrient concentrations or input, solar irradiance, and water-column stratification (Parsons et al. 1970). The result is an accumulation of organic C in the local surface waters. The traditional bloom scenario of the North Atlantic is one of significant increases in DOM concentrations that coincide with progression of the bloom or its later stages (Duursma 1963; Parsons et al. 1970; Ittekkot et al. 1981; Eberlein et al. 1985; Carlson et al. 1994), with accumulation in the DOM pool being greater than or equal to the POM pool (Cadée 1986; Williams 1995 and references therein). Although there are differences in the absolute magnitude and timing among blooms, the accumulation of DOC and POC in the Sargasso Sea was similar to the general trends of other North Atlantic blooms.

There are several reports from the North Sea of large amounts of foam appearing on beaches (Bätje and Michaelis 1986), high mucilage (Lancelot and Mathot 1985), and DOC production (Eberlein et al. 1985), all resulting from *Phaeocystis pouchetii* blooms. Significant production and accumulation of DOC have been demonstrated throughout the course of *P. pouchetii* blooms from initiation to senescence (Billen and Fontigny 1987). As a result of these reports, we expected to observe significant DOC accumulation during the bloom of Antarctic *Phaeocystis* sp. One of the most striking findings of this study was that despite enhanced PP in the Ross Sea only 0.1 mol C m⁻² (4% of the CPP) accumulated in the bulk DOC pool. Net organic C fixation was efficiently channeled and retained in the POC pool of the Ross Sea, making POC the dominant pool in organic C budgets of the surface waters. These results are contrary to those reported by Bölter and Dawson (1982) and Davidson and Marchant (1992) who observed high DOC concentrations (1.2 and up to 8 mM C) coinciding with *Phaeocystis* blooms in the Scotia Sea and Prydz Bay, respectively. We never observed high DOC values associated with the Antarctic *Phaeocystis* sp. blooms and cannot explain the previous observations in the Southern Ocean. Tupas et al. (1994) also reported low accumulation of DOC during diatom blooms in the regions west of the Antarctic Peninsula.

DOC accumulation has been linked to nutrient depletion (Ittekkot et al. 1981). Culture work has demonstrated that large production of extracellular DOC may result from nutrient depletion (Goldman et al. 1992). Nutrient concentrations differ significantly between the Sargasso and Ross Sea, with nonlimiting nutrient concentrations persisting throughout the year in the Ross Sea and oligotrophic conditions dominating in the Sargasso Sea for most of the year. However, seasonal DOC accumulation has also been demonstrated in the presence of measurable nitrate, phosphate, and silicate (Parsons et al. 1970). Other studies have demonstrated increases in DOC that coincide with increases in *Phaeocystis* PP (Billen and Fontigny 1987) and biomass (Eberlein et al. 1985), indicating that DOC accumulated at earlier phases of a bloom when nutrients were not limiting. Thus, nutrient depletion may offer some explanation of the differences between the two sites but it is not likely to be the only factor dictating the accumulation of DOC.

Biological mechanisms responsible for in situ production of DOM in oceanic systems include direct phytoplankton exudation (Lancelot 1979; Lignell 1990), zooplankton sloppy feeding and excretion (Lampert 1978; Banse, 1992; Nagata and Kirchman 1992), particle solubilization (Smith et al. 1992, 1995), and viral lysis (Proctor and Fuhrman 1990). However, the relative contribution and quality of DOC produced by each process are not well understood. Further insights into the biolability of the DOC and potential production mechanisms can be gained by examining bacterial C demand and DOC accumulation.

DOC production and accumulation—Total DOC production, calculated as accumulated DOC plus bacterial C demand, accounted for $0.44 \text{ mol C m}^{-2}$ (15% of the CPP; CPP measured as particles collected on GF/F filters) in the Ross Sea. This percentage is comparable to the cross-system study by Baines and Pace (1991), who reported that DOC production via extracellular release was ~13% of phytoplankton production. Several additional studies have demonstrated that ~10% of the PP is excreted directly from phytoplankton as DOC (Larsson and Hagström 1982; Sharp 1984; Lignell 1990). Although *Phaeocystis* sp. has been reported to excrete 60% of their fixed C (Guillard and Hellebust 1971; Lancelot 1984), Veldhuis and Admiraal (1985) cautioned that disruption of colonies during filtration may have caused filtration artifacts, thereby overestimating the DOC excretion rates from *Phaeocystis* colonies. They found that when proper care was taken in isolating extracellular DOC from *P. pouchetii*, only 14% of the total photosynthetic production was found.

Smith et al. (1995) proposed that a portion of what is estimated to be direct exudation of DOM is actually enzymatic hydrolysis of phytoplankton surface material by attached bacterioplankton, thus providing a mechanism for an increased flux of labile material to free-living bacterioplankton. During this study we qualitatively observed bacterial colonization of *Phaeocystis* mucilage as the bloom progressed. Suspended POC, dominated by *Phaeocystis* cells and mucilage, represented ~35% of the cumulative fixed C (Fig. 6). The enzymatic breakdown of the mucilage material is a potential mechanism in the flux of labile DOC to free-

living bacterioplankton and may play a dominant role in the DOC production during *Phaeocystis* blooms of the Ross Sea.

Although only a small portion of the fixed C was partitioned into the DOC pool relative to other blooms (cited above and this study), the mechanisms responsible for its production yielded DOC that was available to bacteria. For example, $\sim 0.3 \text{ mol C m}^{-2}$ (72%) of DOC produced was utilized by bacterioplankton over the course of 19 d (Fig. 5), indicating that the newly produced DOC was labile. The supply of DOM, and not the quality, appears to limit bacterial production in the Ross Sea.

In contrast, mean DOC production in the Sargasso Sea accounted for 1.7 mol C m^{-2} ($70 \pm 17\%$) of the CPP. However, half of the newly produced DOC escaped rapid microbial degradation and accumulated as DOC during each bloom season in the Sargasso Sea. These observations indicate that the DOC produced in the Sargasso Sea was somewhat more refractory than in the Ross Sea, and suggest that the mechanisms of DOC production are different than in the Ross Sea. In addition to the direct release of DOC from phytoplankton, other DOC production mechanisms such as grazing interactions and, perhaps, viral lysis may have been important in producing a more refractory DOC. However, the relative contribution to these secondary processes to DOC production and accumulation has not been adequately quantified.

The size structure and composition of the plankton community may be an important factor controlling the DOM production. Karl et al. (1996) stated that picophytoplankton are nearly ubiquitous in the world's oceans, but that Antarctic environments may be an exception. The plankton biomass and production of the Sargasso Sea is dominated by pico- and nanoplankton (Malone et al. 1993; Caron et al. 1995), whereas recent work in Antarctic waters have demonstrated that autotrophic picoplankton contribute as little as 6% of the total phytoplankton biomass (Kang and Lee 1995). Pico- and nanoplankton contribute little to vertical export and are primarily involved in regenerative cycling (Michaels and Silver 1988), but are responsible for supporting a large microheterotrophic biomass relative to the autotrophic biomass (Karl et al. 1996) indicating an active microbial food web. We also observed significant differences in the flux of C through the microbial food web between the two systems, with only 11% of the CPP flowing through the bacterioplankton in the Ross Sea, compared to a mean of 31% in the Sargasso Sea during the bloom periods.

The results of the present study and those mentioned above lend support to the hypothesis of Legendre and Le Fevre (1995), which stated that the microbial food web could serve a significant role in the sequestration of the DOM in the surface water via the production of a refractory DOM. Toggweiler (1989) hypothesized that refractory organic compounds were formed as the result of processing through the microbial food web. Brophy and Carlson (1989) showed that transformation of biologically available C by the microbial community can be an important source of refractory DOC in the oceans. However, low transfer and growth efficiencies associated with microbes and grazer interaction make it difficult to reconcile such a large fraction of the CPP accumulating as refractory material-based secondary processing

of DOM. For example, Brophy and Carlson (1989) demonstrated that microbes can transform glucose into refractory material, but were able to account for only 5% of initial radioactive tracer as transformed refractory material.

Karl et al. (1996) hypothesized that small phytoplankton cells excrete a greater fraction of primary production due to high surface volume ratios. However, the presence of picoplankton alone does not necessarily result in a large accumulation of DOC. During periods of hydrographic stability, heterotrophic and autotrophic processes are tightly coupled with little net DOM production (Hansell and Carlson 1997). Hansell and Carlson (1997) discussed the possibility that deep mixing and associated stresses to the picoplankton community may enhance production and accumulation of DOC observed during the spring in the Sargasso Sea. Further investigation is needed to qualify and quantify the exact mechanisms responsible for the observed buildup, but the fact remains that DOC repeatedly produced and accumulated during the spring bloom events in the Sargasso Sea. These results demonstrate fundamental differences between the two systems in the quality of DOC and the mechanisms by which it is produced.

DOC as potential C export—Export of biogenic C from the euphotic zone is responsible for maintaining the vertical gradient of DIC in the ocean. This process has traditionally been thought to be dominated by the settling of large particles (McCave 1975) from the surface waters. Recent modeling efforts have suggested that downward advective export of DOC may contribute to C export and annual new production (Toggweiler 1989; Najjar et al. 1992). Direct observations of Copin-Montégut and Avril (1993) and Carlson et al. (1994) showed that DOC is exported vertically as a result of deep convective mixing in the late winter. However, this organic C is subsequently remineralized in the deep surface layer (100–250 m) and cannot be considered a long-term storage of C due to ventilation by winter mixing events. In order for DOC to be considered a long-term C-storage pool it must be incorporated into oceanic deep water where it is prevented from ocean-atmosphere transfer for hundreds of years.

The Ross Sea has been identified as a site of bottom-water formation in the Antarctic (Gordon 1966; Jacobs et al. 1970). Water on the continental shelf of the Ross Sea interacts with the atmosphere, sea ice, and glacial ice that alters its salinity, causing it to move back into and under the circumpolar deep water and ventilate to the deep ocean (Trumbore et al. 1991). The advection of suspended C and the potential for long-term C removal is high due to the physics of the system. However, this study demonstrates that the Ross Sea yielded a small but labile portion of PP as DOC (at least through mid-January), so it is unlikely that long-term removal of DOC is an important export term due to the small quantity of DOC that accumulates there. Conversely, the DOC production mechanisms of the Sargasso Sea resulted in the accumulation of a large semilabile-to-refractory DOC pool. However, in regions like the Sargasso Sea, where DOC can accumulate, long-term removal of reduced C to deep water (>1,000 m) is limited by low rates of physical transport. DOC production mechanisms mediated by producer-con-

sumer dynamics, in addition to physical mixing, appear to be major controls on exportable C from the surface ocean.

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