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Biomass and production of bacteria and phytoplankton during the spring bloom in the western North Atlantic Ocean

W. K. W. Li,* P. M. Dickie,* W. G. Harrison* and B. D. Irwin*

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Abstract—During the 1989 spring bloom in the western North Atlantic, we estimated the biomass and productivity of bacteria and phytoplankton at two sites (40 and 45°N) representing different water masses. At 40°N, almost all of the phytoplankton carbon could be accounted for by photosynthetic nanoplankton and picoplankton; in contrast, at 45°N, only about half was thus accounted, implying a substantial contribution by photosynthetic microplankton. At both sites, bacterial abundance was quite high (up to 2×10^9 cells l^{-1}), and the rates of bacterial production assessed by incorporation of [^{3}H]thymidine (up to 8 pmol $l^{-1}h^{-1}$) and [^{3}H]leucine (up to 240 pmol $l^{-1}h^{-1}$) were significant. Specific growth rates of bacteria based on [^{3}H]thymidine incorporation were 0.08–0.25 day^{-1}. Taken together, our measurements and assumptions implied a demand for primary production in the order of 16–36% over the euphotic zone or 24–78% over the upper 100 m in the water column. We conclude that ultraphytoplankton and bacteria played significant roles in the flux of carbon during the 1989 North Atlantic spring bloom.

INTRODUCTION

The spring bloom of oceanic phytoplankton in the open North Atlantic covers such a wide geographical extent that it has been called the "largest (remotely-sensed) biological signal on the planet" (Lewis, 1989). The bloom first appears during late March and April in the western Atlantic and soon extends eastwards and northwards, reaching a peak in the following month or two. Although much is known about the plankton ecology of the North Atlantic spring bloom (Colebrook, 1979; Parsons and Lalli, 1988), the information pertains largely to net phytoplankton and metazooplankton. Citing the work of Williams and Robinson at Ocean Weather Station I in the North Atlantic, Parsons and Lalli (1988) described the spring bloom during April to May as consisting of a diverse group of large diatoms such as *Rhizosolenia* spp., *Nitzschia*, *Thalassionema* and *Chaetoceros* spp. With the recent recognition of picoplanktonic cyanobacteria and prochlorophytes as the usual numerical dominants in oceanic phytoplankton communities, there is now a need to evaluate the role of these small cells in the spring bloom. Already, there is evidence of seasonality in abundance (Waterbury *et al.*, 1986) and the display of bloom characteristics following water column stratification in the spring (Olson *et al.*, 1990).

In view of the significance of microbial plankton in pelagic food webs (Pomeroy, 1974; Azam *et al.*, 1983; Sherr and Sherr, 1988) and the fact that the microbial loop has been

*Biological Oceanography Division, Bedford Institute of Oceanography, Dartmouth, Nova Scotia B2Y 4A2, Canada.

little studied in connection with marine spring blooms other than in neritic waters (DUCKLOW and KIRCHMAN, 1983; LANCELOT and BILLEN, 1984; POMEROY and DEIBEL, 1986; BILLEN and FONTIGNY, 1987; NIELSEN and RICHARDSON, 1989), it was a matter of importance that measurements of bacterioplankton biomass and productivity were an integral component of the 1989 North Atlantic Bloom Experiment (NABE) of the Joint Global Ocean Flux Study (JGOFS) (DUCKLOW, 1989). The Canadian effort in this multinational exercise was carried out on the western side of the North Atlantic (40–50°W) and focused on work at two sites (40 and 45°N), each occupied for several days (HARRISON *et al.*, 1993). We report here on the standing stocks and daily rates of production of bacteria and phytoplankton.

During the spring bloom in the western North Atlantic, we found that bacterial standing stocks were substantial, rates of bacterial production were significant, and that the apparent carbon demands exerted by heterotrophic bacteria on primary production were at levels comparable to other (non-bloom) situations. Furthermore, we found that picoplankton and nanoplankton may comprise significant portions of the photosynthetic biomass during the bloom.

METHODS

Sampling

All work was performed on cruise 89–003 of C.S.S. *Baffin* from 19 April to 19 May 1989. Details of sampling strategy and water procurement are given in HARRISON *et al.* (1993). For convenience, Table 1 lists the stations for the work reported in the present paper. The spring bloom was studied at two sites: 40°N (Stas 18–36) and 45°N (Stas 50–56). The first of these sites was situated in proximity to the south wall of the Gulf Stream, while the second was clearly influenced by waters originating north from the Labrador shelf (HARRISON *et*

Table 1. Location, sampling date and time of stations

Station number	Latitude (N)	Longitude (W)	Date (1989)	Time (local)	Comment
2	40°24.00′	61°17.00′	April 20	1140	*Transit*
3	37°06.17′	59°06.25′	April 21	1140	*Transit*
18	40°37.40′	47°10.80′	April 28	0830	"40°N site"
23	40°31.94′	47°10.16′	April 29	0903	"40″N site"
27	40°13.22′	47°13.90′	May 01	0730	"40°N site": *Diel sequence*
28	40°11.20′	47°12.60′	May 01	1011	"40°N site": *Diel sequence*
29	40°09.33′	47°13.96′	May 01	1252	"40°N site": *Diel sequence*
31	40°04.40′	47°11.30′	May 02	0827	"40°N site": *Diel sequence*
32	40°04.20′	47°12.40′	May 02	1100	"40°N site": *Diel sequence*
33	40°04.20′	47°10.60′	May 02	1403	"40°N site": *Diel sequence*
34	40°03.50′	47°06.80′	May 02	1727	"40°N site": *Diel sequence*
35	40°01.30′	47°04.30′	May 02	2300	"40°N site": *Diel sequence*
36	39°56.60′	47°04.70′	May 03	0836	"40°N site": *Diel sequence*
47	47°00.10′	39°59.30′	May 07	0832	*Transit*
50	44°59.80′	41°15.10′	May 08	0843	"45°N site"
53	45°01.70′	41°19.30′	May 09	0856	"45°N site"
56	44°48.60′	41°23.30′	May 10	0831	"45°N site"

al., 1992). At 40°N, Stas 27–36 represented a 49 h diel sequence from 1 May, 0730 h to 3 May, 0830 h. Results are also reported for measurements at three other stations sampled in transit (Stas 2, 3 and 47).

Carbon-14 *uptake, chlorophyll and particulate organic carbon*

Primary productivity was measured as ^{14}C uptake by phytoplankton incubated *in situ*. Bulk chlorophyll *a* (Chl *a*) was measured by fluorometry of acetone extracts. Particulate organic carbon (POC) was measured by dry combustion of material collected on glass-fibre filters (Whatman GFF). Details of all these procedures are given in HARRISON *et al.* (1993). We assumed a value of 40 for the ratio of phytoplankton carbon to Chl *a*; this is discussed later.

Cell counts and conversion to carbon biomass

Samples for enumeration of bacterial abundance were drawn from Niskin bottles and immediately preserved in 20 ml glass scintillation vials with 0.2 μm filtered (Millex-GS, Millipore Corp.) formalin (2% final concentration). Preserved samples were stored in the dark, in a refrigerator. Each sample was poured over triplicate polycarbonate membranes (0.2 μm black Nuclepore) underlain by pre-wetted backing filters (Sartorius No. 11306) which aid in distributing cells in an even manner on the Nuclepore surface (PORTER and FEIG, 1980). Cells were stained for 10 min with DAPI (PORTER and FEIG, 1980) at a final concentration of 2 $\mu g\ ml^{-1}$ and then drawn through the filters at a vacuum pressure of about 150 mmHg. The filters were examined by epifluorescence microscopy (Leitz Orthoplan) under ultraviolet excitation from a mercury arc lamp (HBO 100 W). As before (LI *et al.*, 1992), bacterial abundance (cells l^{-1}) was converted to bacterial carbon biomass ($\mu g\ C l^{-1}$) assuming 20 fgC per bacterium (LEE and FUHRMAN, 1987).

Samples for enumeration of cyanobacterial abundance (20–100 ml) were freshly filtered in triplicate onto 0.2 μm black Nuclepore membranes which were underlain by backing filters. The membranes were stored refrigerated after having been covered in a drop of immersion oil. Cyanobacteria were enumerated by epifluorescence microscopy under green excitation (Leitz block N2). As before (Li *et al.*, 1992), cyanobacterial abundance (cells l^{-1}) was converted to cyanobacterial carbon biomass ($\mu g\ C l^{-1}$) assuming 250 fgC per cyanobacterium (KANA and GLIBERT, 1987).

Flow cytometric analysis (Becton Dickinson FACS Analyser) was performed on freshly collected samples for enumeration of autofluorescent plankton. Details concerning instrument configuration, sample analysis and counting errors have been described elsewhere (LI, 1990). For the purposes of the present work, the listmode data were analysed to yield abundance estimates for two groups of phytoplankton cells. We call one of these groups the photosynthetic nanoplankton (PNAN): these were red-fluorescing cells with or without phycoerythrin larger than 2 μm equivalent spherical diameter (ESD) but smaller than 10 μm ESD which was the upper bound set by the instrument configuration. We call the other group of autofluorescent bodies the 'very small red-fluorescing cells' (VSRF cells): these were red-fluorescing cells without phycoerythrin and smaller than 1 μm ESD. The taxonomic identity of VSRF cells is not known but pigment analyses by HPLC (E. J. H. HEAD, unpublished data) indicated the presence (amongst many other pigments) of small amounts of zeaxanthin/lutein, chlorophyll *b* and α-carotene, a suite that

occurs in free-living oceanic prochlorophytes (Chisholm *et al.*, 1988). It is also likely that some VSRF cells were small eukaryotic algae (Johnson and Sieburth, 1982). To convert abundance of PNAN (cells l^{-1}) to carbon biomass (μgC l^{-1}), we employed the equation of Strathmann (1967) using the mean ESD of PNAN calculated from the Coulter volume spectra measured on the FACS Analyser. For VSRF cells, we assumed an ESD of 0.8 μm (as if they were prochlorophytes) and followed Booth (1988) in using 220 fgC μm^{-3} for small phytoplankton to yield a factor of 59 fgC $VSRF^{-1}$.

[^{3}H]*thymidine and* [^{3}H]*leucine incorporation*

Water samples were collected between 0830 and 0900 h from nine depths for measurements of [^{3}H]thymidine (Tdr) and [^{3}H]leucine (Leu) incorporation under simulated *in situ* conditions on the deck of the ship. The selection of depths was based on an attempt to match light levels inside the nine differentially light-attenuated deck incubators to light levels *in situ*. The incubators were covered with neutral-density perforated metal screens giving incubation regimes of 96, 46, 25, 9, 5, 3, 1.8, 0.4 and 0.05% of incident surface irradiance. All incubators were temperature-regulated using a flow of near-surface seawater.

Seventy-five millilitres of water sample from each depth were placed into duplicate clear polycarbonate bottles. To one was added [methyl^{3}H]thymidine (70 Ci $mmol^{-1}$, ICN No. 24060) at a final concentration of 5 nM; to the other was added [2, 3, 4, 5-^3H]L-leucine (110 Ci $mmol^{-1}$, ICN No. 20032) at a final concentration of 10 n*M*. Triplicate aliquots (10 ml each) were removed immediately upon radioisotope introduction ("time zero") and at the end of the incubation which lasted for 3 h, a duration over which the incorporation of radioisotopes did not depart greatly from linearity. On occasion, the experiments were initiated with a larger volume of sample so that sufficient water was available for time-course triplicate sampling at 0, 1, 2 and 3 h. The radiolabelled samples were not chemically fixed but immediately filtered onto 0.2 μm Nuclepore membranes, rinsed with freshly filtered seawater, and then stored frozen until analysis. Børsheim (1990) has verified this storage method against others.

Experiments to determine empirical factors needed to convert rates of [^{3}H]Tdr and [^{3}H]Leu incorporation into rates of cell production (Kirchman *et al.*, 1982) were performed as follows. Plankton sample was diluted 1:10 using freshly prepared seawater filtrate (Millipore GS, 0.22 μm). The diluted plankton was incubated under simulated *in situ* conditions. At 6 h intervals over a 24 h period, subsamples were removed for determination of bacterial abundance and for 3 h assays of [^{3}H]Tdr and [^{3}H]Leu incorporation rates as described above. Conversion factors (cells mol^{-1}) were calculated using both the derivative and integrative methods described by Kirchman and Hoch (1988) as well as the cumulative method of Bjørnsen and Kuparinen (1991). As discussed later, only values from the integrative and cumulative methods were used in ensuing calculations.

Extraction of radiolabelled macromolecules from cells collected on Nuclepore membranes was performed as follows. Samples were allowed to thaw in clean dry test tubes and then received 5 ml of ice-cold 5% trichloroacetic acid (TCA). After a 20 min extraction period on ice, samples (including the Nuclepore membrane) were filtered onto glass-fibre filters (Whatman GFF) and first rinsed twice with aliquots of ice-cold 5% TCA and then with 95% ethanol. Kennell (1967) noted that the acid or alcohol precipitates of nucleic

acids or proteins are retained by membranes of 0.80 μm pore size and recommended the use of glass-fibre filters. After having been rinsed, the filters were allowed to dry in air for 10 min before being placed into glass scintillation vials. Following KOBAYASHI (1980), samples were then digested in 1 ml of Protosol (New England Nuclear) by heating at 55°C for 10 min. When cooled, the samples received 50 μl of glacial acetic acid followed by 10 ml of scintillation fluor. Liquid scintillation counts obtained on a Beckman LS-3133T spectrometer were corrected for quenching by the external standards ratio method. CHIN-LEO and KIRCHMAN (1988) reported no significant difference in the amount of ^{3}H recovered between hot and cold TCA extractions of various natural marine plankton assemblages incubated in [^{3}H]Leu. WICKS and ROBARTS (1988) confirmed this and suggested that cold TCA can replace hot TCA for precipitation of labelled proteins in studies of aquatic bacterial production.

RESULTS

Depth profiles

Depth profiles of biomass are shown for the first site in transit through the Gulf Stream (Sta. 2, Fig. 1) and then for the spring bloom sites at 40°N (Sta. 18, Fig. 2) and at 45°N (Sta. 53, Fig. 3). The spring bloom sites were distinguished not only by the high stocks of phytoplankton (surface Chl a>2 mg Chl a m^{-3}) but also by the great abundance of bacteria (surface concentrations between 1.5 and 2 × 10^9 cells l^{-1}). Profiles of temperature, σ_t, and nitrate at these stations are given by HARRISON *et al.* (1993).

Areal biomass

At each station, we compared the water-column integrated values (0–100 m) of carbon biomass for (i) POC, (ii) the bacteria, (iii) the cyanobacteria, (iv) the VSRF cells, (v) the PNAN, (vi) the sum of (iii) to (v) which we call ultraphytoplankton, and (vii) the total phytoplankton which is based on a conversion from bulk Chl a (Fig. 4). In this paper, we refer to the last named category as "Chl-carbon". Here, we do not mean the carbon content of Chl a; rather we mean the estimate of phytoplankton carbon calculated from the measured Chl a concentration and the assumed C:Chl a ratio of 40. We use this terminology to emphasize that total phytoplankton carbon was estimated in a way completely different from the cell-counting method for cyanobacteria, VSRF cells and PNAN.

With one exception (Sta. 36 which we describe in the next paragraph), PNAN was the major carbon component of ultraphytoplankton. Even though cyanobacteria and VSRF cells were many times more abundant than PNAN, the much larger cell size of the latter accounted for their dominance of the ultraphytoplankton carbon pool. In comparing ultraphytoplankton carbon with total phytoplankton Chl-carbon, we found the values to be generally similar, except at the 45°N site (Stas 53 and 56). In other words, at 40°N, we could account for much of the Chl-carbon by summing up the ultraphytoplankton contributions; but at 45°N, ultraphytoplankton carbon was only about 50% of estimated total Chl-carbon.

While on station at 40°N, we encountered a change in water mass between 0830 and 1100 h on 2 May (between sampling Stas 31 and 32). A diel sequence of observations

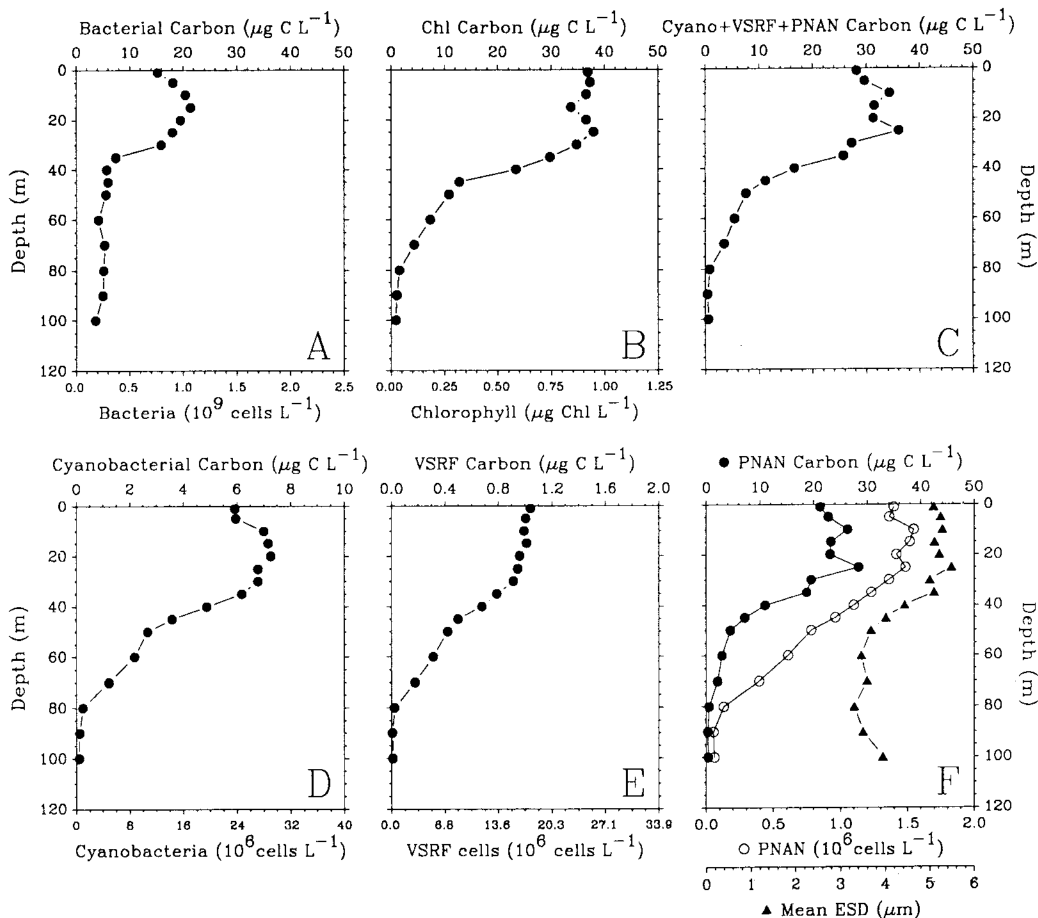

Fig. 1. Biomass profiles at a transit station in the Gulf Stream (Sta. 2). (A) Bacteria, assuming 20 fgC cell^{-1}. (B) Chlorophyll, assuming carbon: Chl *a* ratio of 40. (C) Sum of D,E, and F. (D) Cyanobacteria, assuming 250 fgC cell^{-1}. (E) VSRF cells, assuming 59 fgC cell^{-1}. (F) PNAN cells [○] converted to PNAN carbon [●] using PNAN mean ESD [▲] and STRATHMANN (1967).

was fortuitously centred about the change and indicated the following shifts in the upper 40 m (Fig. 5): a temperature drop from 15.34 to 14.94°C; a salinity drop from 35.82 to 35.69 ppt; a 3-fold increase in cyanobacteria from 33 to 99 × 10^6 cells l^{-1}; a 1.3-fold increase in VSRF cells from 26 to 33 × 10^6 cells l^{-1}; and a 2-fold decrease in PNAN from 2.0 to 1.0 × 10^6 cells l^{-1}. Thus, the early phase (Stas 18 and 23, Fig. 4) was a period of relatively low picoplankton (cyanobacteria + VSRF cells) abundance but relatively high PNAN abundance; on the other hand, the later phase (Sta. 36, Fig. 4) was marked by high picoplankton and low PNAN abundance.

In summary, at 40°N (during the early phase), mean ultraphytoplankton biomass (3.8 gC m^{-2}) was the same as mean Chl-carbon biomass (3.9 gC m^{-2}); and both were double the mean bacterial biomass (1.9 gC m^{-2}). At 45°N, mean bacterial biomass (2.4 gC m^{-2}) was about the same as mean ultraphytoplankton biomass (2.2 gC m^{-2}), but only

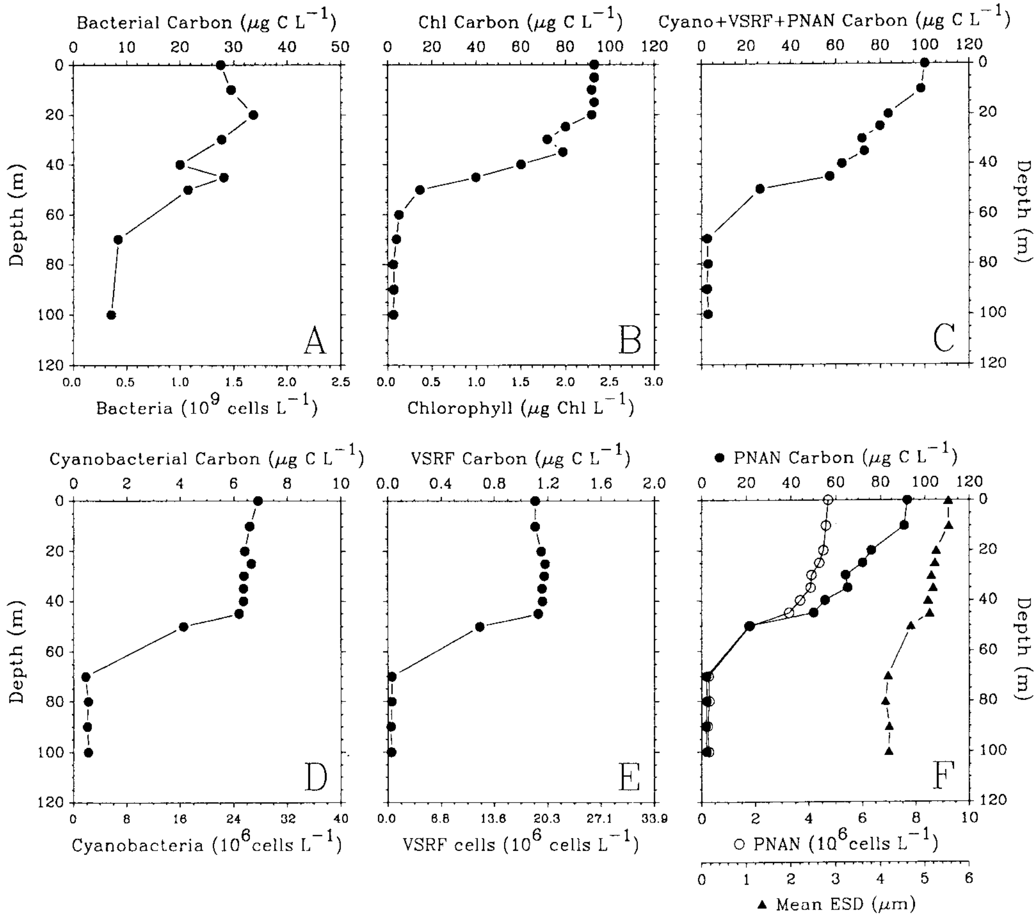

Fig. 2. Biomass profiles at 40°N (Sta. 18). See legend to Fig. 1 for description.

about half of mean Chl-carbon biomass (5.0 gCm^{-2}). In all cases, neither phytoplankton, bacteria, nor even their sum was the majority contributor to POC (Fig. 4).

Ratio of bacterial to phytoplankton carbon

Comparing water-column integrated values of bacterial biomass (B_{bac}) against those of phytoplankton Chl *a* biomass (B_{chl}; Fig. 6A), we found that the ratio B_{bac}:B_{chl} was similar at the two spring bloom sites: namely 0.50 at 40°N (Stas 18 and 23) and 0.46 at 45°N (Stas 53 and 56, Fig. 6B). In no case did B_{bac}:B_{chl} exceed 1 in our study.

We next compared B_{bac} against ultraphytoplankton biomass (B_{ult}; Fig. 6C). In principle, because B_{ult} is a subset of B_{chl}, the ratio B_{bac}:B_{ult} should be greater than B_{bac}:B_{chl}. At 40°N (Stas 18 and 23), B_{bac}:B_{ult} was 0.51 (Fig. 6D), a value not different from B_{bac}:B_{chl} thus indicating the equivalence of B_{ult} and B_{chl}. At 45°N, B_{bac}:B_{ult} decreased from 1.6 (8 May, Sta. 50) to 1.0 (9 May, Sta. 53) to 0.8 (10 May, Sta. 56; Fig. 6D). This ratio decreased progressively because B_{bac} remained the same for the 3 days (2.5, 2.3 and 2.3 gC m^{-2}) while B_{ult} increased (1.6, 2.2 and 2.8 gC m^{-2}). Here, B_{bac}:B_{ult} was substantially greater

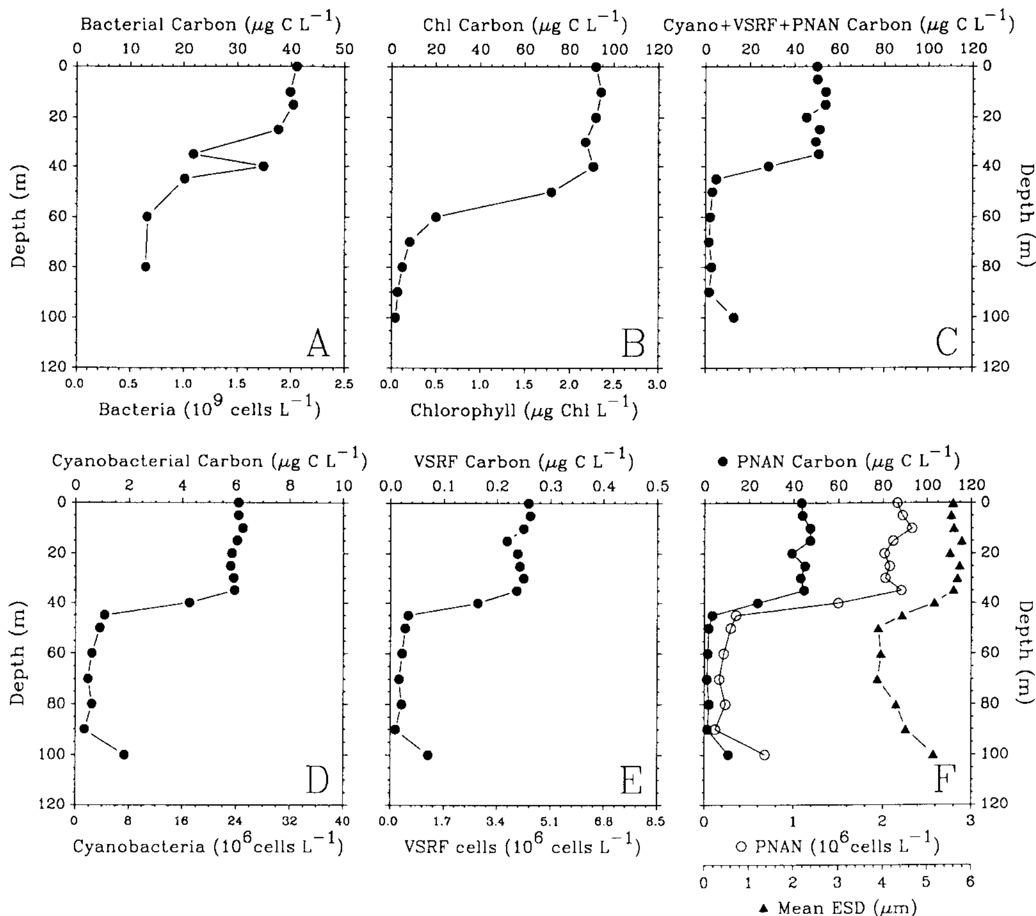

Fig. 3. Biomass profiles at 45°N (Sta. 53). See legend to Fig. 1 for description.

than B_{bac}:B_{chl}, indicating the importance of phytoplankton that were larger than the ultraplankton.

Conversion factors for Tdr and Leu

Empirical factors needed to convert incorporation rates of [^{3}H]Tdr and [^{3}H]Leu into rates of cell production were estimated from measurements made on bacteria growing in diluted seawater (Kirchman *et al.*, 1982). The factors specify the number of cells produced per mole of Tdr or Leu incorporated (cells mol^{-1}). At 40°N, the specific rates of increase in bacterial numbers (cells l^{-1}), [^{3}H]Tdr incorporation rate (pM h^{-1}) and [^{3}H]Leu incorporation rate (pM h^{-1}) were 0.027 ± 0.006, 0.18 ± 0.03 and 0.19 ± 0.07 h^{-1}, respectively. At 45°N, these values were 0.031 ± 0.008, 0.10 ± 0.06 and 0.12 ± 0.06 h^{-1}, respectively. The derivative method for calculating conversion factors (Kirchman and Hoch, 1988) indicated a progressive decline in the factor over the experimental duration. The integrative method (Kirchman and Hoch, 1988) and cumulative method (Bjørnsen and Kuparinen, 1991) yielded similar values which we used to calculate rates of bacterial production: at

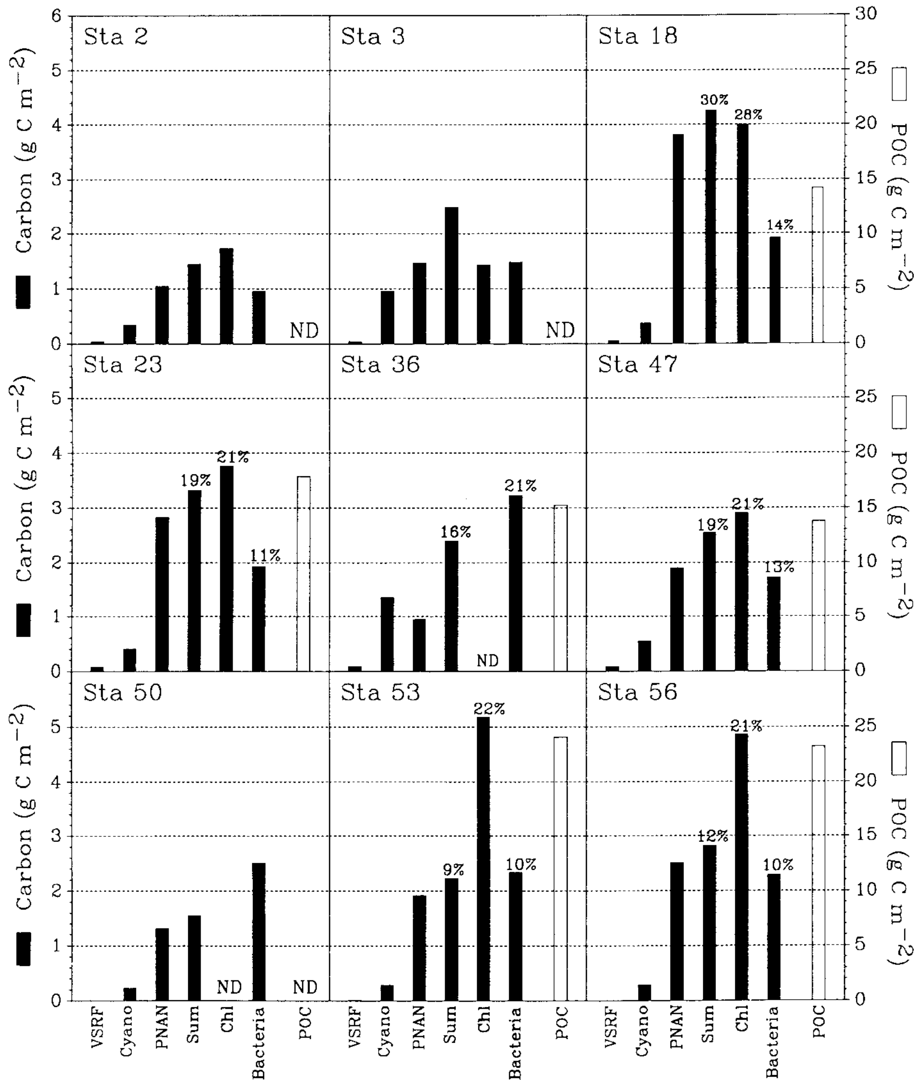

Fig. 4. Water-column integrated values of POC (□) and carbon biomass (■) of VSRF cells, cyanobacteria, PNAN, the sum of these three ("Sum"), Chl *a* and bacteria. Numerical percentages associated with "Sum", Chl *a* and bacteria indicate respective contributions to POC. ND indicates no data.

40°N, the factor was 1.0×10^{18} cells mol^{-1} for Tdr and 5.5×10^{16} cells mol^{-1} for Leu; at 45°N, the factor was 2.3×10^{18} cells mol^{-1} for Tdr and 1.7×10^{17} cells mol^{-1} for Leu.

Productivities and growth rates

Specific growth rates (μ, day^{-1}), carbon biomass (B, mgC m^{-3}) and rates of production (P, mgC m^{-3} day^{-1}) are related as follows (Li and Goldman, 1986):

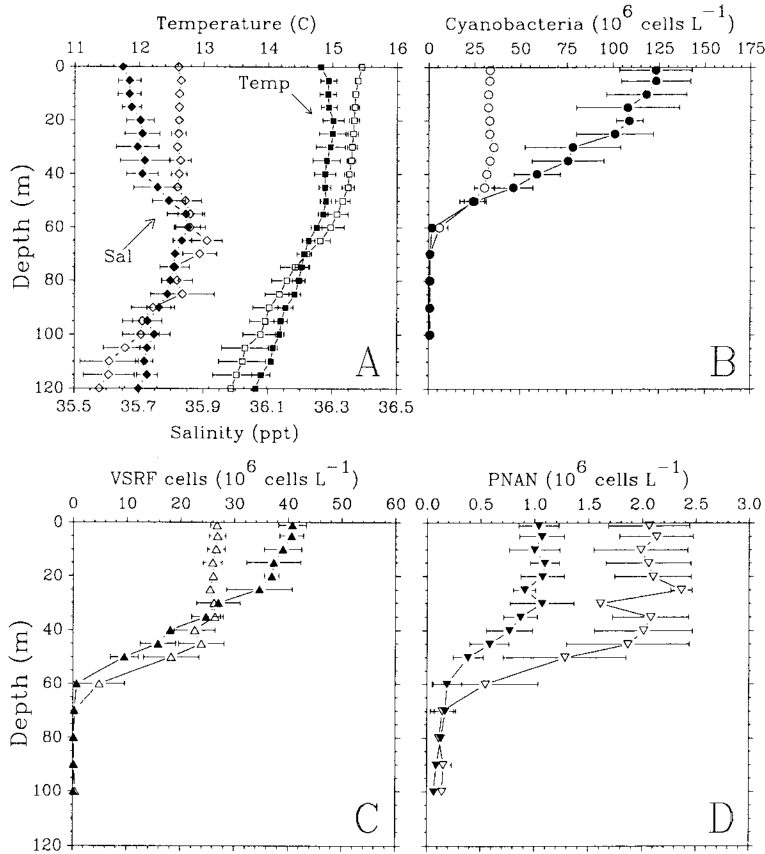

Fig. 5. Change in water mass at 40°N. (A) Temperature (upper X-axis) and salinity (lower X-axis). (B) Cyanobacteria. (C) VSRF cells. (D) PNAN. In all panels, hollow symbols are the means (n=4) of profiles sampled at 0730, 1011 and 1252 h on 1 May and 0827 h on 2 May. Solid symbols are the means (n=5) of profiles sampled at 1100, 1403, 1727 and 2300 h on 2 May and 0836 h on 3 May. Error bars indicate standard deviations amongst profiles within each of the two time-groups.

$$\mu = \frac{1}{\Delta t} \times \ln\left(\frac{B + P \times \Delta t}{B}\right). \tag{1}$$

Depth profiles of B, P and μ are shown for bacteria (Fig. 7) and phytoplankton (Fig. 8). At both 40 and 45°N, B_{bac} (Fig. 7A,D), P_{Tdr} (Fig. 7B,E) and P_{Leu} (Fig. 7B,E) all appeared to covary with depth so that neither μ_{Tdr} nor μ_{Leu} (Fig. 7C,F) indicated much systematic variation with depth. At 40°N, both μ_{Tdr} and μ_{Leu} were 0.08±0.02 day^{-1} (mean±S.D.); at 45°N, μ_{Tdr} was 0.25±0.04 day^{-1} and μ_{Leu} was 0.49±0.12 day^{-1}.

Integrating over the euphotic zone at 40°N, P_{Tdr} (80 mgC m^{-2} day^{-1}) was very similar to P_{Leu} (88 mgC m^{-2} day^{-1}); bacterial production represented 8% of phytoplankton production (Table 2) which was 1063 mgC m^{-2} day^{-1}. Integrating over the euphotic zone at 45°N, P_{Tdr} (207 mgC m^{-2} day^{-1}) was much lower than P_{Leu} (539 mgC m^{-2} day^{-1}); bacterial production represented 18 or 47% of phytoplankton production (Table 2) which was 1140 mgC m^{-2} day^{-1}.

Since bacterial productivity was not insignificant below the euphotic zone (Fig. 7B,E),

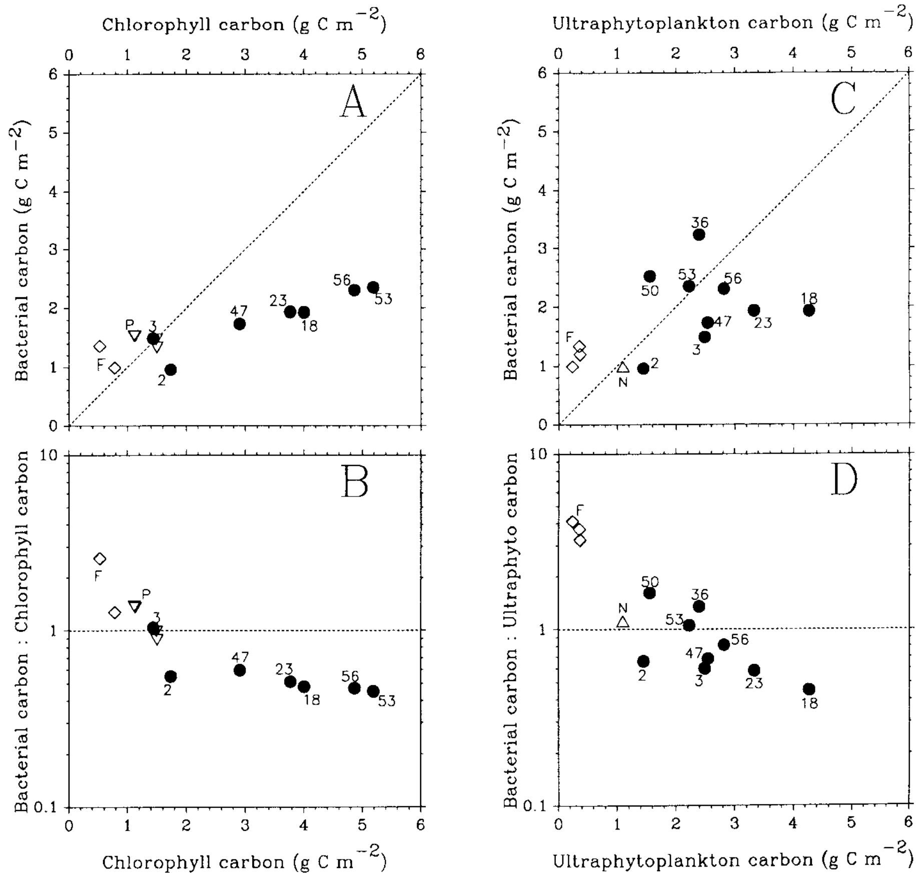

Fig. 6. Comparison of (A, B) bacterial carbon to Chl *a* carbon and (C, D) bacterial carbon to ultraphytoplankton carbon. Solid symbols refer to current JGOFS data set with numbers indicating stations listed in Table 1. Hollow symbols refer to other data sets: NFLUX ("N", △) from Li *et al.* (1992); PLASMA stations Purple, Indigo, Nashville and Yakutat ("P", ▽) from Li and Wood (1988); Sargasso Sea Sta. S ("F", ◊) from Fuhrman *et al.* (1989); (data from their Table 2 was used in panels A and B; data of 17 Aug. and 11 Nov. 1987 from their Table 3 was used in panels C and D).

the ratio of bacterial to primary production was clearly influenced by depth. Thus at 40°N, bacterial productivity was about 4% of primary productivity at the sea surface, 8% over the euphotic zone, and 12% over the upper 100 m which extended below the euphotic zone (Table 2).

DISCUSSION

Theoretical considerations (Parsons, 1975), observations in neritic waters (Gillen *et al.*, 1990) and a modelling exercise of the oceanic Sargasso Sea (Fasham *et al.*, 1990) all indicate that in spring, bacteria as well as phytoplankton undergo a bloom sequence, but the peak in bacterial abundance lags behind that of the phytoplankton. Accordingly, the ratio of bacterial production to primary production depends on the stage of the phytoplankton bloom. Prior to the bloom when biomass of both bacteria and phytoplankton are low, bacterial production may be about 10% of primary production (Nielsen and

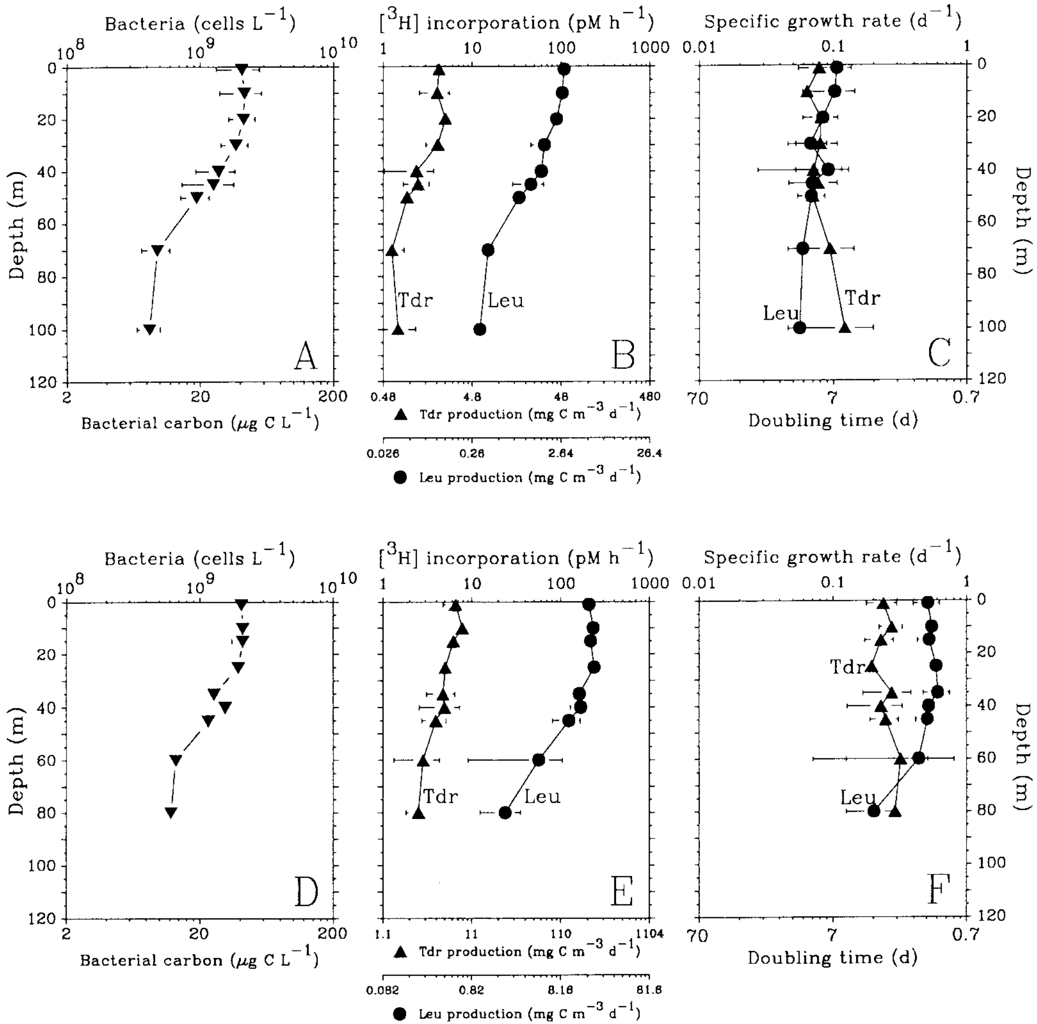

Fig. 7. Profiles of bacterial biomass, rates of production based on [^{3}H]Tdr and [^{3}H]Leu incorporation, and specific growth rates based on [^{3}H]Tdr and [^{3}H]Leu incorporation at 40°N (A,B,C) and at 45°N (D,E,F).

Richardson, 1989). Subsequently, during the early explosive growth phase of phytoplankton when primary production is high, this percentage may decrease to <10% (McManus and Peterson, 1988; Nielsen and Richardson, 1989). Throughout the duration of the bloom, this percentage extends from 5 to 25% which is also the range typifying marine plankton systems in general (Van Es and Meyer-Reil, 1982; Ducklow, 1983; Moriarty, 1986; Cole *et al.*, 1988.) In lakes, bacterial production is also about 20% of primary production during the bloom (Weisse *et al.*, 1990 and references therein). In the post-bloom phase, this percentage may increase to 50% (McManus and Peterson, 1988) or even close to 100% (Lucas *et al.*, 1986) with the inference that bacteria are supported by POC of detritus and DOC from cell death, lysis and zooplankton feeding.

In our study of the North Atlantic spring bloom, we were not able to conduct long time-

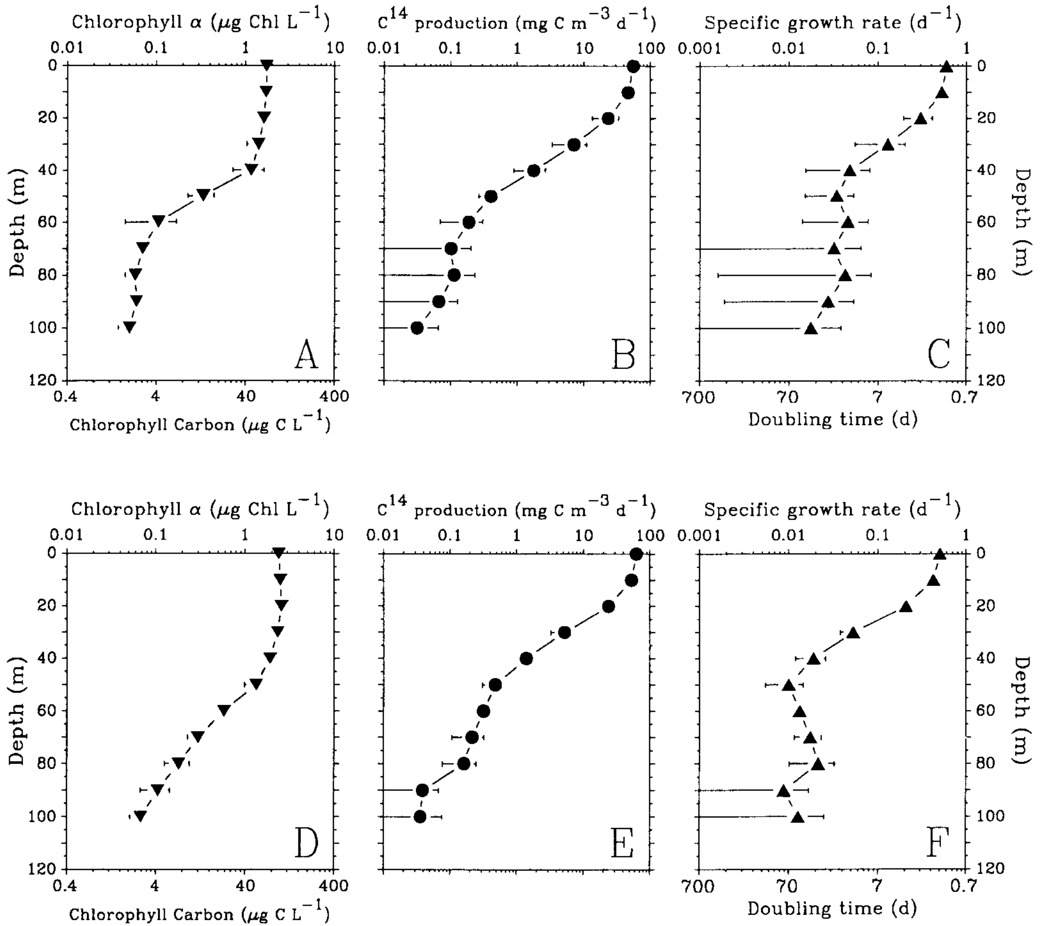

Fig. 8. Profiles of Chl *a* biomass, rates of primary production, and specific growth rates of phytoplankton at 40°N (A,B,C) and at 45°N (D,E,F).

Table 2. Bacterial productivity (P_{Tdr}, P_{Leu}) as a percentage of primary productivity (PP)

		P^*_{Tdr}	P^*_{Leu}	PP*	P_{Tdr}:PP (%)	P_{Leu}:PP (%)
Surface sample	40°N	2	3	55	4	5
	45°N	7	17	63	12	27
Σ→ 1% light level	40°N	80	88	1063	8	8
	45°N	207	539	1140	18	47
Σ→ 100 m	40°N	125	124	1070	12	12
	45°N	456	963	1160	39	83

*mgC m^{-3} day^{-1} for surface samples, mgC m^{-2} day^{-1} for depth integrated values.

series measurements covering the various phases of the bloom. Instead, our observations were made at two sites representing different water masses. On the basis of Chl *a* levels, primary production rates (Fig. 8) and nutrient concentrations (HARRISON *et al.*, 1993), it was clear that the phytoplankton bloom was well underway at both sites. At the time we sampled, bacteria were already very abundant (Fig. 7). By inference from production rates (based on the [^{3}H]Tdr method) and an assumed bacterial growth efficiency of 50% (COLE *et al.*, 1988), euphotic zone bacteria must have been demanding 16–36% of the primary production (Table 2). It is therefore apparent that phytoplankton spring blooms, whether oceanic or neritic, may support a significant level of bacterial activity. Recent evidence indicates that bacterial carbon growth efficiency may be much lower than 50% during some periods of the spring bloom (KIRCHMAN *et al.*, 1991), implying bacterial demand on primary production approaching or even exceeding 100%. DUCKLOW *et al.* (1993) discuss possible mechanisms by which the heavy bacterial carbon demand might be met via subsidies from the bulk POC and/or DOC pools.

One of the most vexing problems in estimating carbon biomass is the uncertainty associated with converting measured variables (cell counts, Chl *a*) to carbon values using parameters (carbon content per cell, carbon to Chl *a* ratio) which may vary according to environmental conditions. We recognize the weaknesses of relying on fixed conversion factors to estimate biomass from cell counts (LI, 1986; PSENNER, 1990) but except in the case of PNAN for which we measured cell volume, we were obliged to accept literature values for these factors. Our choice of values for cellular carbon (fgC cell^{-1}) was based on the desire to compare present results with those of similar recent work (FUHRMAN *et al.*, 1989; CHO and AZAM, 1990; FURUYA, 1990; HERNDL, 1991; LI *et al.*, 1992) but we acknowledge that these values are not universally accepted (JOINT and POMROY, 1987).

The choice of our carbon to Chl ratio ($\theta = 40$) deserves some discussion. It is temptingly easy to estimate θ from a scatterplot of POC versus Chl using model II linear regression of the equation POC = (non-phytoplankton POC) + ($\theta \times$Chl *a*). However, the pitfalls of doing this are well known (BANSE, 1977). This method gave us values of θ that we judged too high for phytoplankton under bloom conditions, namely 88 at 40°N and 122 at 45°N. BANSE (1977) explained how θ can be overestimated when non-phytoplankton carbon does not vary independently of phytoplankton carbon: this indeed may have influenced our results because Chl *a* (Fig. 8), bacteria (Fig. 7) and heterotrophic nanoplankton (HARRISON *et al.*, 1993) all covaried with depth. Studies in which phytoplankton carbon has been estimated by cell counts (EPPLEY *et al.*, 1977; BOOTH *et al.*, 1988; FUHRMAN *et al.*, 1989; citations in LONGHURST and HARRISON, 1989; FURUYA, 1990; HEWES *et al.*, 1990; LI *et al.*, 1992) or the ^{14}C-Chl *a* labelling technique (REDALJE and LAWS, 1981; LAWS *et al.*, 1984; WELSCHMEYER and LORENZEN, 1984; TAGUCHI *et al.*, 1988; GIESKES and KRAAY, 1989) yield a wide range of θ values which may reflect different environmental conditions. Under phytoplankton bloom conditions, the value of θ appears to be about 40: RIEMANN *et al.* (1989) reported 36 and HEWES *et al.* (1990) reported 46. The value of 40 for phytoplankton growing under a light–dark cycle is supported by the work of GOLDMAN (1980), whose data are replotted here (Fig. 9) to indicate that a value of $\theta = 40$ allows enough latitude to encompass a range of relative growth rate as wide as 0.4–1.

Given our choices for biomass conversion factors, we conclude that at 40°N, essentially all the phytoplankton Chl-carbon could be accounted for by the sum of PNAN, cyanobacteria and VSRF cells (Fig. 4, Stas 18 and 23). In contrast, at 45°N, only about half of the phytoplankton Chl-carbon could be accounted for by the ultraphytoplankton (Fig. 4, Stas

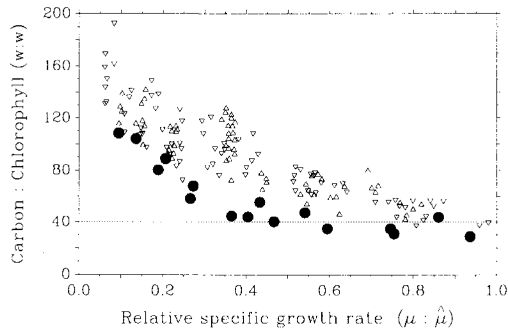

Fig. 9. Data of GOLDMAN (1980) on variation of cellular carbon to chlorophyll ratio with relative specific growth rate for marine phytoplankton grown in nitrogen-limited continuous cultures. Filled circles (●) symbolize cultures of *Thalassiosira pseudonana*, *Pavlova lutheri* and *Dunaliella tertiolecta* grown under 12 h light/12 h dark cycle. Hollow triangles symbolize growth of *Thalassiosira pseudonana* (▽) and *Dunaliella tertiolecta* (△) under continuous light.

53 and 56), implying a significant biomass of microphytoplankton. This interpretation is consistent with measurements of Chl *a* concentrations in size-fractions at the two sites which showed a greater contribution to phytoplankton biomass from large cells at 45°N than at 40°N (HARRISON *et al.*, 1993). Furthermore, at 45°N, it was observed by microscopy and indicated by HPLC pigment analysis that diatoms and dinoflagellates were common members of the microplankton (HARRISON *et al.*, 1993). By conventional comparison, the phytoplankton regimes at both sites were almost identical, each having surface Chl *a* levels of about 2 mg Chl *a* m^{-3} and column productivities of about 1 gC m^{-2} day^{-1}. However, these conceal the different nature of the bloom at the two sites: one being dominated by ultraphytoplankton, and the other co-dominated by ultra- and microphytoplankton. The prevalent notion that diatoms invariably dominate during spring blooms must be modified to acknowledge the possible role of pico- and nanoplankton.

Furthermore, it appears as if even in situations where ultraphytoplankton is dominant, the relative importance of its components (i.e. cyanobacteria, VSRF cells, PNAN) may be quite different in adjacent water masses. This was indicated by our observations over a 49 h period from 1 to 3 May at 40°N (Fig. 5). During that time, extremely large differences in abundances of the three ultraphytoplankton components coincided with a change in water mass whilst the ship was on station. Initially, phytoplankton carbon was overwhelmingly represented by PNAN; subsequently, cyanobacteria became the dominant component.

The abundance of bacteria we found (1.5–2 × 10^9 cells l^{-1} at the surface) was rather high for oceanic waters. In most cases, slightly more bacteria were present, for a given level of Chl *a* than indicated by recent statistical summaries of literature values (BIRD and KALFF, 1984; COLE *et al.*, 1988). Oceanic values of ⩾2 × 10^9 cells l^{-1} have been reported previously but these were mainly from the frontal region of warm-core rings (DUCKLOW, 1986). Most pertinently, DUCKLOW *et al.* (1993) also report surface values of ⩾2 × 10^9 cells l^{-1} at the eastern North Atlantic JGOFS site (47°N, 20°W) during the 1989 NABE. Recent papers have called attention to the observation that bacterial biomass is often greater than phytoplankton biomass in oligotrophic waters but not in mesotrophic and eutrophic waters (DORTCH and PACKARD, 1989; FUHRMAN *et al.*, 1989; CHO and AZAM, 1990; HERNDL, 1991). However, LI *et al.* (1992) found that bacterial and phytoplankton biomass were about

equal at Sta. NFLUX which was a well-stratified water column in the Sargasso Sea in summer. The question arises: how oligotrophic must a system be for the bacteria to dominate the phytoplankton? In Fig. 6, we compared the column integrated values obtained on the JGOFS cruise with previously published data (Li and Wood, 1988; Fuhrman *et al.*, 1989, Li *et al.*, 1992). A trend of decreasing B_{bac}:B_{chl} with increasing B_{chl} (Fig. 6B) is evident. Although plots similar to Fig. 6 have been published (Cho and Azam, 1990; Herndl, 1991), they were based on estimates of biomass per unit volume of seawater. Since the vertical distributions of bacteria and phytoplankton do not match exactly everywhere (especially where there is a prominent and deep sub-surface Chl *a* layer), estimates of biomass based on unit area of water column allow comparisons to be made that integrate depth-related differences. The boundary below which a system can be considered oligotrophic enough for bacteria to dominate phytoplankton appears to be between 1 and 2 g phytoplankton-C m^{-2} (Fig. 6B), but there is much uncertainty in this value because of data scatter. Thus, even within the confines of the Sargasso Sea, bacteria may (Fuhrman *et al.*, 1989) or may not (Li *et al.*, 1992) be dominant depending on the actual phytoplankton biomass. However, there is a greater certainty (foreseen by Fuhrman *et al.*, 1989) that during the spring bloom, bacterial biomass, though large, does not dominate the phytoplankton, or even the ultraphytoplankton to any significant degree.

Bacterial carbon productivity is difficult to estimate, chiefly because there is no method that directly measures the production of bacterial carbon itself over time. The dark $^{14}CO_2$ assimilation method of Romanenko (1964) has been used with some success (e.g. Sorokin, 1990) but remains a method that, in principle, measures the rate of $^{14}CO_2$ incorporation in the dark by all microbial cells rather than production of new carbon by heterotrophic bacteria. As a substitute, we measure the synthesis of DNA using [^{3}H]Tdr and of protein using [^{3}H]Leu. When growth is balanced, the rates of synthesis of both macromolecules are the same; agreement between production rates derived from these independent methods lends confidence to the results. Such appears to have been the case at 40°N where P_{Tdr} and P_{Leu} were very similar (Fig. 7B,C; Table 2). At this site, the values of the empirically determined conversion factors (1.0×10^{18} cells mol^{-1} for Tdr and 5.5×10^{16} cells mol^{-1} for Leu) were virtually identical to the mean values of Kirchman and Hoch (1988). For Tdr, the value of about 1×10^{18} cells mol^{-1} is appropriate in many cases (Riemann *et al.*, 1987; Bell, 1990) and has a sound theoretical basis (Fuhrman and Azam 1980, 1982; Moriarty, 1988). For Leu, in principle, there is no useful theoretical range for the conversion factor because protein turnover (isotope incorporation but little or no net synthesis) would yield a very low factor, and isotope dilution (if extensive) would yield a very high factor. However, given certain assumptions, a probable range might be from 2.7×10^{16} to 1.1×10^{17} cells mol^{-1} (Kirchman *et al.*, 1986).

Bacterial production was higher at 45 than at 40°N because of higher rates of radioisotope incorporation (pmol l^{-1} h^{-1}) and also higher conversion factors (more than double the values at 40°N). Moreover, at 45°N, P_{Leu} was double P_{Tdr} (Fig. 7E,F; Table 2), implying a state of unbalanced growth. With protein being synthesized more rapidly than DNA, the bacteria appeared to be in a state of shift-up in growth. Unbalanced growth of marine bacteria in nature is not unusual (Hanson and Lowery, 1983; Hanson *et al.*, 1986; Chin-Leo and Kirchman, 1990) and a state of shift-up could be expected during that period of the spring bloom when phytoplankton production is at a rate sufficient to invoke the bacterial bloom. Taken at face value, the fact that cell numbers increased more slowly

than Tdr and Leu incorporation rates implicates unbalanced growth. Similar lack of correspondence between increases in cells and macromolecular synthesis has been previously reported (DUCKLOW and HILL, 1985; BJØRNSEN and KUPARINEN, 1991) and most pertinently also by DUCKLOW *et al.* (submitted) at the eastern North Atlantic JGOFS site during the 1989 NABE.

Earlier, DUCKLOW and HILL (1985) suggested that the ratio of the specific rate of increase in cell number to the specific rate of increase in substrate incorporation might be an indication of the fraction of active cells. More recently, DUCKLOW *et al.* (submitted) state that this cannot be the case because there is no ratio of growing to non-growing cells that can reproduce experimental observations when the increase rate if incorporation is held constant. DUCKLOW *et al.* (submitted) conclude that open ocean bacteria are often not in stable, balanced growth.

To place the magnitude of our bacterial production estimates in context, we refer again to the literature summary by COLE *et al.* (1988) who give bacterial production of about 242 mgC m^{-2} day^{-1} (90% confidence from about 97 to 575 mgC m^{-2} day^{-1}) when primary production is 1000 mgC m^{-2} day^{-1}. At this level of primary production (Table 2), P_{Tdr} and P_{Leu} at 40°N, integrated to 100 m, were lower than the COLE *et al.* value (but within 90% confidence); P_{Tdr} at 45°N was higher (within 90% confidence), but P_{Leu} at 45°N exceeded even the upper confidence limit set by COLE *et al.* As a check on P_{Leu} we recalculated this value using the considerations of SIMON and AZAM (1989) which do not rely on the growth conversion factor. Using values of 0.86 g bacterial carbon per g bacterial protein, 131.2 as the formula weight of Leu, 7.3 mol% of Leu in bacterial protein, and intracellular isotope dilution of 2 (SIMON and AZAM, 1989), we calculated P_{Leu} at 45°N to be 876 mgC m^{-2} day^{-1} which is similar to the high value of 963 mgC m^{-2} day^{-1} (Table 2) based on the empirical leucine conversion factor. Although apparently valid, the very high value of P_{Leu} at 45°N suggests that the true rate of bacterial production, as opposed to protein synthesis, must have been closer to the P_{Tdr} value which was 456 mgC m^{-2} day^{-1}.

To sum up our findings on bacterial biomass and productivity, we consider the derived parameter of specific growth rate based on [^{3}H]Tdr incorporation [equation (1)]. Values of 0.08 day^{-1} at 40°N and 0.25 day^{-1} at 45°N, though low in comparison with coastal values (MORIARTY, 1986), appear congruent with other oceanic values (FUHRMAN *et al.*, 1989; BØRSHEIM, 1990). As FASHAM *et al.* (1990) also noted, growth rates are low because the expected production rates are divided by high bacterial biomass.

In summary, we conclude that ultraphytoplankton and bacteria played significant roles in the 1989 North Atlantic spring bloom. Ultraphytoplankton, in particular the photosynthetic nanoplankton, represented a substantial part of the phytoplankton standing stock. Bacteria, although constituting only half the carbon biomass of phytoplankton, were present at high levels of abundance. Rates of bacterial production, when considered with an assumed growth efficiency of 50%, implied a demand for primary production on the order of 16–36% over the euphotic zone or 24–78% over the upper 100 m in the water column. It remains to be seen how robust these conclusions are as more refined techniques become available to estimate cell abundance, production rates and conversion factors.

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