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Biomass of bacteria, cyanobacteria, prochlorophytes and photosynthetic eukaryotes in the Sargasso Sea

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Abstract—Bacteria, cyanobacteria, prochlorophytes and photosynthetic eukaryotes were enumerated in depth profiles at a station in the northern Sargasso Sea occupied for 9 days during September 1988. Carbon biomass of each group was inferred from cell abundance using conversion factors taken from the literature. Over the upper 200 m in the water column, carbon biomass occurred in the approximate proportion of 1:2:4:8 for cyanobacteria: prochlorophytes: photosynthetic eukaryotes: bacteria. Taken together, the three phytoplankton groups represented about the same amount of carbon biomass as the bacteria. This conclusion was validated by the independent measure of bulk chlorophyll *a* (Chl *a*) if the carbon: Chl *a* ratio was assumed to be about 44 in the nitrate-depleted layer and about 15 in the nitrate-rich layer. In reporting the biomass co-dominance of bacteria and phytoplankton, we do not deny that bacteria may dominate phytoplankton at other times and places in the oligotrophic ocean. Biomass co-dominance between these two trophic groups admits the possibility that oligotrophic bacterial assemblages may have high growth rates.

INTRODUCTION

RECENT reports indicate that in the euphotic zone of the oligotrophic open ocean the carbon biomass of bacteria is commonly more than 2–3 times that of phytoplankton (FUHRMAN *et al.*, 1989; CHO and AZAM, 1990). An earlier report had indicated a factor of about 1.7 (LAWS *et al.*, 1984). A related observation is that the chlorophyll *a*: protein ratio of particulate matter, which is a relative index of phytoplankton to total biomass, is also low in oligotrophic areas (DORTCH and PACKARD, 1989). A corollary of these observations is that bacterial carbon comprises a substantial portion (*ca* 40%) of particulate organic carbon (CHO and AZAM, 1988, 1990). This apparent inversion of the normal biomass pyramid into one in which the heterotrophic biomass substantially exceeds the photoautotrophic biomass has important ecological and biogeochemical implications. Although inverted biomass pyramids have been recognized in plankton communities for some time (ODUM, 1971), the case here calls for special attention because most of the heterotrophic and autotrophic biomass is in the form of small unicells (i.e. bacteria and ultraphytoplankton) that may obey the same size–metabolic rate relationship. For steady state to be

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sustained, the turnover of the relatively low phytoplankton biomass must be at a sufficiently high rate to meet the carbon demands of the relatively large bacterial biomass. Models that assume a large ratio of microheterotroph (bacteria and protozoans) to phytoplankton biomass appear to simulate the principal features of *in vitro* ^{14}C dynamics in oligotrophic oceans (Smith *et al.*, 1984).

In this paper, we examine the generality of these recent assertions using calculations that explicitly take into account the occurrence of prochlorophyte picoplankters (Chisholm *et al.*, 1988; Li and Wood, 1988; Neveux *et al.*, 1989; Olson *et al.*, 1990a; Vaulot *et al.*, 1990; Veldhuis and Kraay, 1990). In oligotrophic marine waters, these organisms are likely the most abundant photoautotrophs. Like Fuhrman *et al.* (1989), we calculate bacterial and phytoplankton carbon from cell counts using cellular carbon conversion factors. We conclude that in September 1988 in the northern Sargasso Sea, the column-integrated (≤ 200 m) carbon biomass of ultraphytoplankters (i.e. prochlorophytes, cyanobacteria and photosynthetic eukaryotes) was essentially the same as that of bacteria, each representing about 10% of the particulate organic carbon.

METHODS

Sample collection

The main series of measurements was conducted during a 9-day occupation (10–18 September 1988) of Sta. NFLUX in the northern Sargasso Sea (36°N, 65°W, Fig. 1) aboard

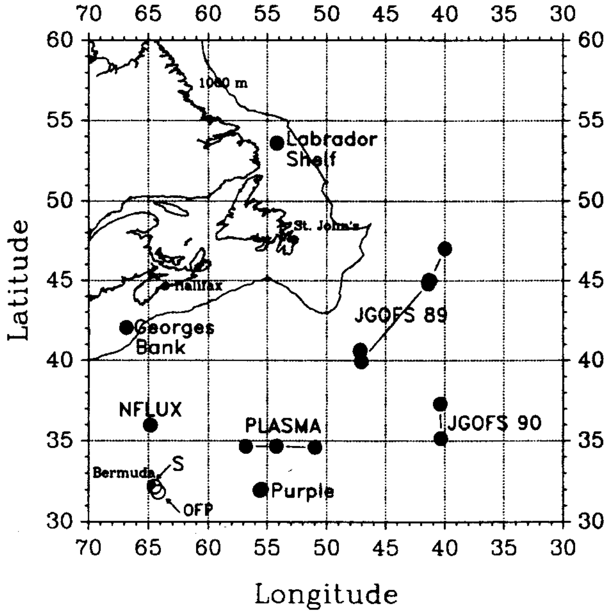

Fig. 1. Location of stations at which samples were collected for measurements of bacterial abundance and Chl *a* (●)—see Fig. 9. Station S (○) was sampled by Fuhrman *et al.* (1989); Sta. OFP (○) was sampled by Olson *et al.* (1990a).

C.S.S. *Hudson* (cruise 88-026). Longhurst *et al.* (1989) described NFLUX as a quiet region south of the Gulf Stream about 95 km from the nearest cold-core eddy. The station was defined by a drifting sediment trap array, which moved steadily (*ca* 20 cm s^{-1}) westward in the gyral current south of the main Gulf Stream, starting at 36°00.20'N, 64°01.25'W and ending at 36°06.35'N, 65°41.83'W.

An inspection of the bacterial abundance vs chlorophyll *a* (Chl *a*) relationship in various water masses was made using a database in which we have compiled measurements from other North Atlantic cruises (Fig. 1). These include data from the PLASMA cruise to the New England and Corner seamount chains (June 1987), Labrador Sea (May 1988), Georges Bank (August 1988), waters in the central North Atlantic during the spring bloom (Canadian Joint Global Ocean Flux Study: April–May 1989; April 1990), and Sta. Purple in the Sargasso Sea east of Burmuda at 31°57.1'N, 55°36.2'W (July 1987 and April 1989).

Seawater was collected using a rosette of Niskin bottles or a pump sampler system (Herman *et al.*, 1984). Water column characteristics (temperature, salinity, σ_t, *in vivo* Chl *a* fluorescence, light transmission and nitrate concentration) were profiled each time samples were collected (Li and Wood, 1988; Longhurst *et al.*, 1989).

Sample analyses

Details of cell counting procedures have been given elsewhere (Li and Wood, 1988; Li, 1989). Briefly, a shipboard arc-lamp flow cytometer was used to enumerate cyanobacteria, prochlorophytes and photosynthetic eukaryotes. Assignment of cells to these three groups was based on the so-called "ataxonomic–allometric" scheme (Phinney and Cucci, 1989) used earlier (Li and Wood, 1988; Li, 1989, 1990). Hence, small (<2 μm) cells that emitted fluorescence in the phycoerythrin waveband were deemed to be cyanobacteria; very small red-fluorescing bodies ("VSRF bodies" of Li and Wood, 1988) were deemed to be prochlorophytes; all other red-fluorescing cells were deemed to be photosynthetic eukaryotes (PEUK). An assessment of the errors in our flow cytometric counts indicated that the coefficient of variation likely ranged between 0.30 and 23% (Li, 1990). Flow cytometric data were recorded in relative units on a scale of 256 channels representing three logarithmic decades. Particle volumes were calibrated against plastic microspheres and expressed in μm^3 as equivalent spherical volume (Li, 1990). Fluorescence intensity was converted into linear units by cross-calibrating the logarithmic and linear scales with microspheres (Horan *et al.*, 1990). Epifluorescence microscopy was used to complement flow cytometry in counting cyanobacteria (Li and Wood, 1988). Bacteria were preserved in 2% formalin, filtered onto triplicate 0.2 μm Nuclepore® membranes, stained with DAPI (Porter and Feig, 1980) and counted by epifluorescence microscopy as detailed earlier (Li and Dickie, 1984).

Particulate matter collected on Whatman GF/F filters were analysed for Chl *a* by fluorometry and for particulate organic carbon (POC) by dry combustion. Filters for POC analyses were precombusted before use. Methodological details and results for analyses of Chl *a* and POC appear in a data report (Irwin *et al.*, 1990).

High resolution depth profiles (5 m interval) were not available for all measurements. Where required, a five-parameter curve-fit for the vertical distribution of cells (Li and Wood, 1988) was used to interpolate data so that comparison of the various measurements could be made at 5 m intervals.

Carbon : cell conversions

Bacterial counts (cells l^{-1}) were converted to carbon (μg C l^{-1}) using the factor 20 fg C per bacterium (**Lee** and **Fuhrman**, 1987; **Fuhrman** *et al.*, 1989; **Cho** and **Azam**, 1988, 1990). For cyanobacteria, we assumed 250 fg C per cell (**Kana** and **Glibert**, 1987). For prochlorophytes, we assumed an equivalent spherical cell diameter of 0.8 μm (**Chisholm** *et al.*, 1988; **Vaulot** *et al.*, 1990) and followed **Booth** (1988) in using 220 fg C μm^3 for small phytoplankton (<4 μm) to yield a factor of 59 fg C per prochlorophyte. For PEUK, carbon per cell was based on **Strathmann**'s (1967) carbon : volume conversion for phytoplankton excluding diatoms using the FACS™-measured Coulter volume spectra.

RESULTS

Depth profiles

As noted earlier (**Longhurst** *et al.*, 1989), there was relatively little variance among nine daily profiles at NFLUX. Accordingly, only mean profiles are presented. Stratification was strongly developed with temperatures of nearly 27°C in the upper 40 m and depletion of nitrate in the upper 90 m (Fig. 2).

Chlorophyll *a* was uniformly low (0.15 μg l^{-1}) in the upper 40 m and increased to a maximum of 0.62 μg l^{-1} at the top of the nitracline (Fig. 3). Numbers of bacteria varied between 3 and 4 × 10^8 cells l^{-1} (6 and 8 μg C l^{-1}) in the upper 90 m, then declined to between 1 and 2 × 10^8 cells l^{-1} (2 and 4 μg C l^{-1}) at depths below 100 m (Fig. 3). Measured

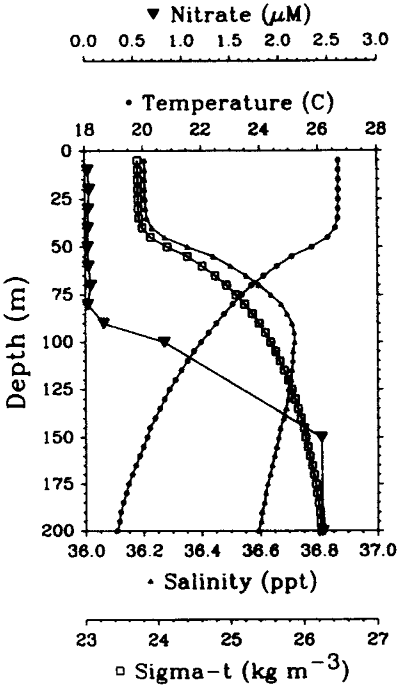

Fig. 2. Water column characteristics at Sta. NFLUX: temperature (●); salinity (▲); σ_t (□); nitrate (▼).

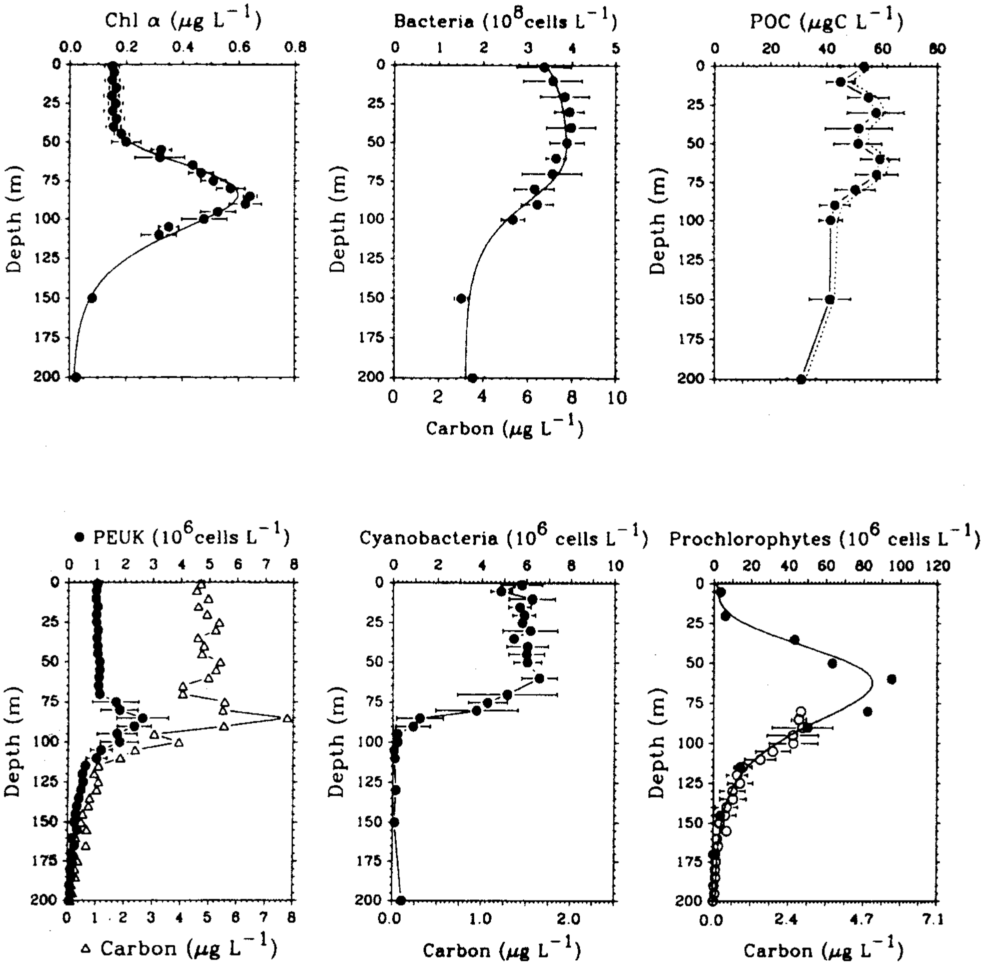

Fig. 3. Biological depth profiles at Sta. NFLUX: Chl *a* (μg l^{-1}); bacteria (10^8 cells l^{-1}, 20 fg C bacterium^{-1}); POC (μg C l^{-1}, dotted profile indicates values corrected for 47% of bacteria passing through GF/F filters); PEUK (10^6 cells l^{-1}, carbon estimated from Strathmann conversion of mean cell volume—see Fig. 4); cyanobacteria (10^6 cells l^{-1}, 250 fg C cyanobacterium^{-1}); prochlorophytes (10^6 cells l^{-1}, 59 fg C prochlorophyte^{-1}); ○ = measured by FACS™ at NFLUX, ● = measured at OFP by EPICS™ (Olson *et al.*, 1990a).

values of POC varied between 40 and 60 μg l^{-1}; a correction (cf. Cho and Azam, 1988) for 47% of bacteria passing through GF/F filters (Lee and Fuhrman, 1987) resulted in values that were only about 6% higher than measured POC (Fig. 3).

Cyanobacteria were relatively invariant at about 6 × 10^6 cells l^{-1} (1.5 μg C l^{-1}) in the upper 60 m and then declined sharply by about 2 orders of magnitude over the next 40 m (Fig. 3). Prochlorophytes were measurable only below 75 m; above this depth, fluorescence was below the detection limit of the FACS™ Analyser (Li and Wood, 1988). Recently, Olson *et al.* (1990a) were able to detect prochlorophytes throughout the water column in the Sargasso Sea using a laser-based flow cytometer modified to achieve 30-fold increased sensitivity. To extend our prochlorophyte distribution at Sta. NFLUX up to the sea surface, we used the cell abundance data published by Olson *et al.* (1990a) for Sta. OFP off Bermuda (31°50′N, 64°10′W) on 14 July 1989. Comparisons of the depth profiles for temperature, Chl *a*, cyanobacteria and eukaryotic phytoplankton indicate a general similarity between NFLUX and OFP. At NFLUX, the depth at which nitrate was first detected in significant amounts (90 m, Fig. 2) was about 15 m shallower than at OFP on 14 July 1989 (Olson *et al.*, 1990a). An excellent match of the two data sets was achieved by subtracting an offset of 15 m to the profile published by Olson *et al.* (1990a). The vertical distribution of prochlorophytes was distinguished by a single subsurface maximum at about 60 m, reaching a cell density of about 1×10^8 cells l^{-1} ($6\,\mu g\ C\ l^{-1}$) (Fig. 3).

Photosynthetic eukaryotes were distributed uniformly in the upper 70 m at about 1×10^6 cells l^{-1}; a peak in abundance (2.6×10^6 cells l^{-1}) occurred at 85 m (Fig. 3). Mean cell volume of PEUK was uniformly large ($21\,\mu m^3 \equiv 3.4\,\mu m$ ESD) in the upper mixed layer of constant σ_t, uniformly small ($8\,\mu m^3 \equiv 2.5\,\mu m$ ESD) in the deep nitrate-rich layer, and intermediate in the transitional depths marked by the pycnocline (Fig. 4). The depth profile of PEUK carbon biomass was inferred from the cell density profile and the mean cell volume profile (after conversion to cell carbon using the Strathmann equation). PEUK carbon biomass was about $5\,\mu g\ C\ l^{-1}$ in the upper 70 m, peaked at about $8\,\mu g\ C\ l^{-1}$ at 85 m, and then declined exponentially at greater depths (Fig. 3).

Carbon biomass comparisons

A summary of the carbon biomass profiles is presented in Fig. 5 showing the magnitude of the phytoplankton contribution (i.e. the sum of cyanobacteria, prochlorophytes and PEUK) in relation to that of the bacteria. Integrating over the upper 200 m, carbon standing stocks were 126, 317, 550 and 1103 mg C m^{-2} for cyanobacteria, prochlorophytes, PEUK and bacteria, respectively. The biomass ratio, in the same order, was approximately 1:2:4:8.

The percentage that each cell group contributed to "total" (i.e. phytoplankton + bacterial) biomass is indicated in Fig. 6. We enclose "total" in inverted commas because other groups, especially the heterotrophic nanoplankton, have been neglected in our study. When values were integrated over the 200 m water-column, the percentage of "total" biomass represented by cyanobacteria, prochlorophytes and PEUK was 6, 15 and 26%, respectively. The sum of the three preceding cell types (i.e. the total phytoplankton biomass) represented 47% of the "total" biomass, roughly equal to the percentage (53%) represented by bacteria (Fig. 6).

The percentage of column-integrated POC represented by phytoplankton was 10%, and by bacteria was 11%. If we restricted the column-integration to include only depths from the sea-surface to the 1% light penetration depth (110 m), phytoplankton would be 53% of the "total" biomass and bacteria would be 47%. The conclusion that phytoplankton and bacteria contributed about equally to carbon biomass was indicated whether integration was performed over the euphotic zone (110 m) or over all measured depths where phytoplankton were found (200 m).

The ratio of bacterial carbon to phytoplankton carbon as a function of Chl *a* is shown in depth sequence in Fig. 7. From the sea surface to 110 m, the mean ratio was 0.93 (range from 0.60 to 1.3); below 110 m, the ratio ranged from 1.7 to 14.1 (Fig. 7). The bacterial C:phytoplankton C ratio based on an integration of carbon values over 200 m was 1.1.

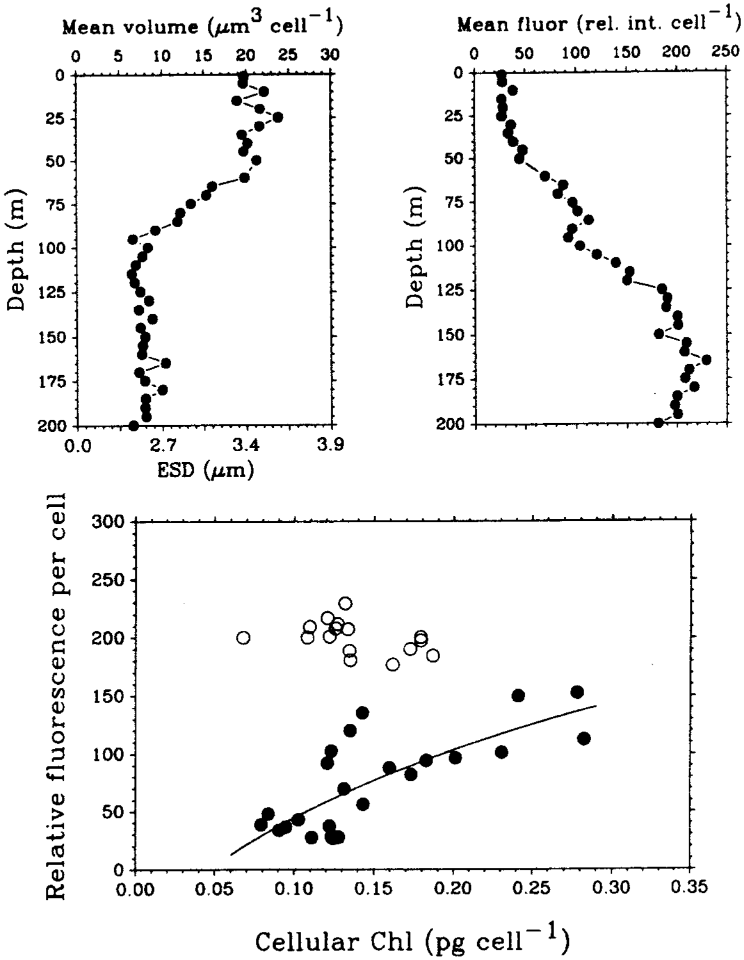

Fig. 4. Characteristics of PEUK at Sta. NFLUX. Mean cell volume is equivalent spherical volume (μm^3 cell^{-1}); mean cell fluorescence is in relative linear units on a scale of 1 to 1000. Relationship between mean fluorescence per cell and Chl *a* per cell (pg cell^{-1}): solid circles indicate samples ≤120 m, open circles indicate samples >120 m.

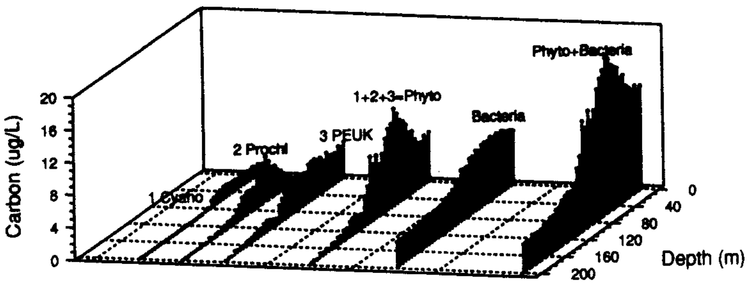

Fig. 5. Depth profiles of carbon biomass (μg C l^{-1}) at Sta. NFLUX. "Phyto" is the sum of cyanobacteria, prochlorophytes and PEUKs.

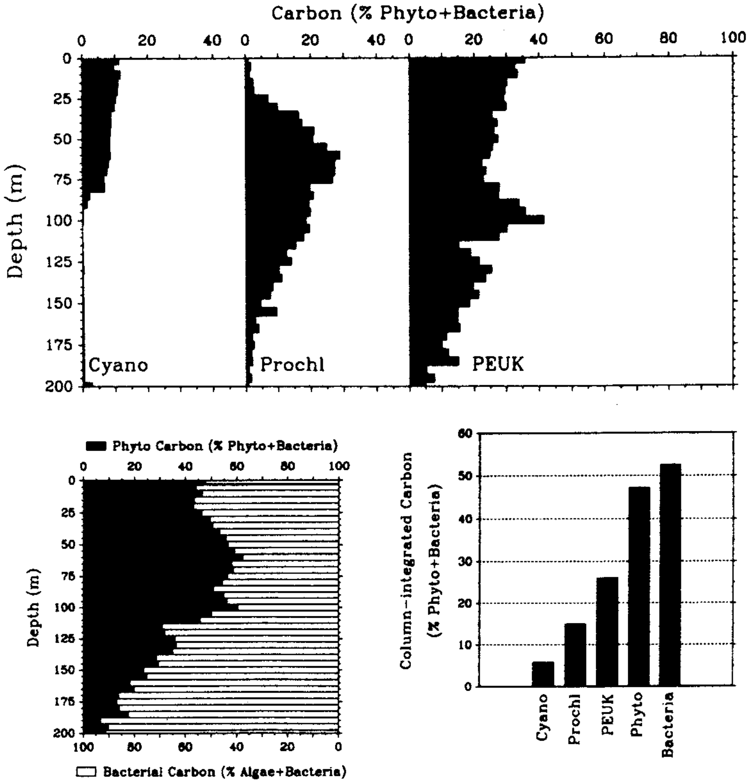

Fig. 6. Percentage contribution to "total" (= phytoplankton + bacteria) carbon biomass from cyanobacteria, prochlorophytes, PEUKs (upper three panels), phytoplankton and bacteria (lower left panel), and values based on 200 m column integration (lower right panel).

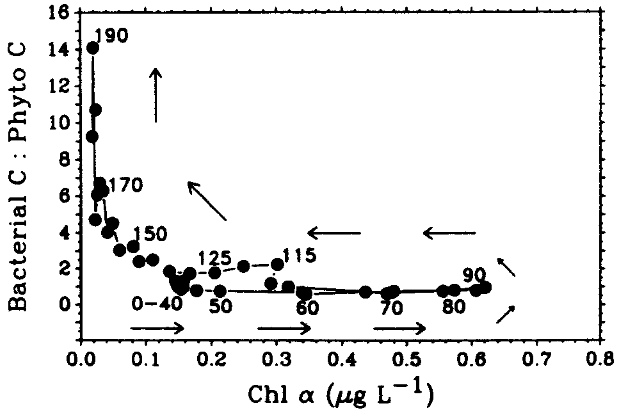

Fig. 7. The ratio of bacterial carbon to phytoplankton carbon as a function of Chl *a* concentration at Sta. NFLUX. Numbers adjacent to data points indicate sample depth; arrows indicate progression from sea surface to 200 m.

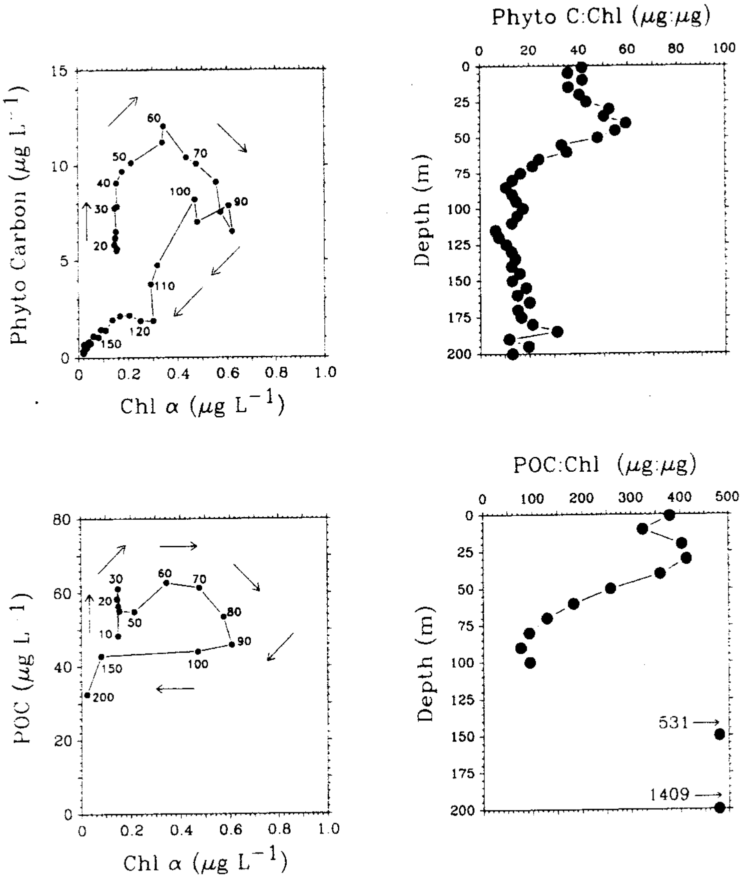

Fig. 8. Relationship between phytoplankton carbon to Chl *a* (upper panels) and POC to Chl *a* (lower panels). Plots of carbon vs Chl *a* (left panels) show sample depths indicated by numbers and progression from sea surface to 200 m indicated by arrows. Right panels indicate depth profiles of phytoplankton carbon : Chl *a* (θ) and POC : Chl *a*.

Carbon : *Chl* a *ratio*

Plots of phytoplankton carbon and corrected POC vs Chl *a* are indicated in depth sequence in Fig. 8. It is evident that the ratios of both phytoplankton carbon : Chl *a* (θ) and POC : Chl a were dependent on depth. In the upper mixed layer, θ was about 44 and POC : Chl *a* was about 375; in the deep nitrate-rich layer, θ was about 15 and POC : Chl *a* exceeded 500 (Fig. 8).

Fluorescence : *Chl* a *relationship for PEUK*

For PEUK, we were able to infer the relationship between FACS™-measured fluorescence per cell (relative linear units from 1 to 1000) and Chl *a* content (pg cell^{-1}). Mean fluorescence per cell increased with depth (Fig. 4). The Chl *a* content of PEUK was calculated from mean carbon per cell (converted from mean volume per cell using the Strathmann equation) and assuming the phytoplankton carbon : Chl *a* ratio derived in the previous section (Fig. 8). There was a positive, slightly curvilinear relationship between fluorescence per PEUK and Chl *a* per PEUK in the upper 120 m; below this depth, there was no significant relationship between the two variables (Fig. 4).

Bacteria : *Chl* a *relationship*

To place the NFLUX data in the context of literature values and other of our own North Atlantic data, we plotted bacterial abundance (cells l^{-1}) versus Chl *a* concentration ($\mu g\ l^{-1}$) in Fig. 9.

For a given Chl *a* concentration in the Sargasso Sea, the NFLUX bacterial data were generally slightly higher than those collected at Sta. Purple (Fig. 1) in April 1989, but lower than those at Purple in July 1987. The geometric mean Model II regression (RICKER, 1973; LAWS and ARCHIE, 1981) of all our Sargasso Sea data yielded a relationship that was

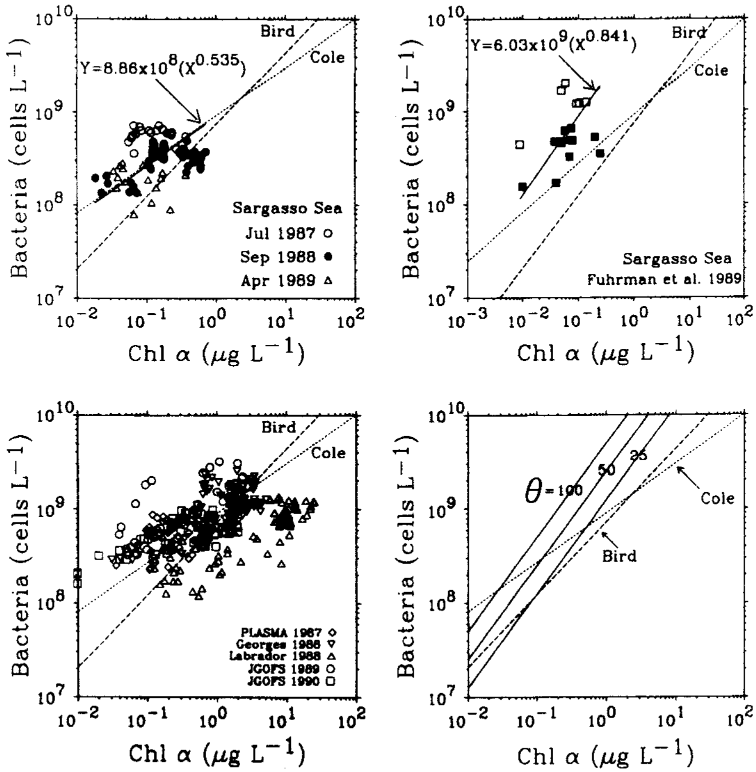

Fig. 9. Relationship between bacterial abundance (cells l^{-1}) and Chl *a* concentration ($\mu g\ l^{-1}$). Sargasso Sea data from Bedford Institute cruises (upper left panel): NFLUX (●), Purple 1987 (○), Purple 1989 (△); geometric mean Model II regression for all data gives $Y = 8.86 \times 10^8\ (X^{0.535})$. Sargasso Sea data from FUHRMAN *et al.* (1989) (upper right panel): Sta. S 1987 (■), Sta. S 1988 (□); geometric mean Model II regression for all data gives $Y = 6.03 \times 10^9\ (X^{0.841})$. Other North Atlantic data from Bedford Institute cruises (lower left panel): PLASMA (◇), Georges Bank (▽), Labrador shelf (△), JGOFS 1989 (○), JGOFS 1990 (□). Lines indicating carbon biomass co-dominance by phytoplankton and bacteria (lower right panels): for $\theta = 25$, 50 and 100. For reference, all panels indicate the regressions of BIRD and KALFF (1984) and COLE *et al.* (1988).

indistinguishable from that of Cole *et al.* (1988) which was based on a comprehensive literature survey. We found that $Y = 8.86 \times 10^8$ ($X^{0.535}$) where Y = bacteria l^{-1} and X = μg Chl l^{-1} (Fig. 9). In contrast, the data of Fuhrman *et al.* (1989) (their Table 3 and 20 fg C per bacterium) for Sta. S in the Sargasso Sea (Fig. 1) yielded a significantly different relationship: $Y = 6.03 \times 10^9$ ($X^{0.841}$) (Fig. 9).

A consideration of other data sets from our previous cruises show a large degree of scatter in the bacteria : Chl *a* relationship (Fig. 9). In particular, in the cold Labrador Sea (−1 to 0°C), bacterial abundance was consistently lower than indicated by the Cole *et al.* relationship; and during the North Atlantic spring bloom (JGOFS 1989), there were instances where bacterial abundance was very much higher than indicated by the overall trend (Fig. 9).

DISCUSSION

Our data from the northern Sargasso Sea indicate that over the upper 200 m, the biomasses of bacteria and phytoplankton were essentially equivalent. It was only at depths below the 1% light level that this ratio assumed significantly larger values (Fig. 7). Our conclusion differs from those of Fuhrman *et al.* (1989) and Cho and Azam (1990) because of lower bacterial biomass and higher phytoplankton biomass. We recognise the pitfalls of relying on cellular conversion factors to estimate biomass from cell counts (Li, 1986; Psenner, 1990) but reiterate that we used the same ones that both Fuhrman *et al.* (1989) and Cho and Azam (1990) did. Importantly, our conclusions about Sta. NFLUX differ from studies at the other sites because of differences in bacterial abundance, phytoplankton abundance and Chl *a* concentration rather than because of uncertainty in the proper selection of conversion factors.

An inspection of the bacterial abundance vs Chl *a* relationship in the Sargasso Sea (Fig. 9) indicates that for a given level of chlorophyll, the variability of bacterial abundance is sufficient to render differing conclusions regarding the dominance, or lack thereof of bacterial biomass in oligotrophic oceans. We therefore conclude that in oligotrophic oceans, bacterial biomass may sometimes dominate phytoplankton biomass, but not always. The conditions under which one or the other dominate in the Sargasso Sea are not clear. In Lake Ontario, which undergoes a marked seasonal temperature variation, Pick and Caron (1987) present results that appear (by visual inspection) to indicate a shift in biovolume dominance from phototrophic pico- and nanoplankton to heterotrophic pico- and nanoplankton depending on the time of year. With greater recognition of the importance of spatial heterogeneity and temporal intermittency for the dynamics of biological properties in the Sargasso Sea (Platt *et al.*, 1989), it would be tenable to speculate that the biomass ratio of bacteria to phytoplankton varies as a consequence of differential evolution, in space or time, of the processes linking these trophic groups together. Fuhrman *et al.* (1989) also hinted that phytoplankton may dominate following intermittent mixing or upwelling events.

The conclusion that bacterial biomass was lower at NFLUX than in the central North Pacific gyre (Cho and Azam, 1990) is based solely on lower bacterial counts because the same value was used to convert cell counts to carbon, namely 20 fg C per bacterium. Are the numbers of bacteria we counted at NFLUX (*ca* 3 to 4 × 10^8 cells l^{-1} in the upper mixed layer) typical of the Sargasso Sea? At Sta. Purple, we counted higher numbers (3 to 7 × 10^8 cells l^{-1}) in July 1987 (Li and Wood, 1988) but lower numbers (1 to 3 × 10^8 cells l^{-1}) in

April 1989 (Fig. 9). At Sta. S, FUHRMAN *et al.* counted $4.3 \pm 1.5 \times 10^8$ cells l^{-1} in 1987 and $1.3 \pm 0.5 \times 10^9$ cells l^{-1} in 1988. Other mixed-layer values in the Sargasso Sea are 2 to 3×10^8 cells l^{-1} (GLOVER *et al.*, 1988); 2 to 6×10^8 cells l^{-1} (BURNEY *et al.*, 1981; WATERBURY *et al.*, 1986); 4 to 8×10^8 cells l^{-1} (DAVIS *et al.*, 1985). Early in the life of warm-core Gulf Stream rings which entrain Sargasso Sea water, bacterial abundances measured in the upper mixed-layer of the ring centre are about 3 to 4×10^8 cells l^{-1} (DUCKLOW, 1983, 1984, 1986). Based on these literature values and the apparent conformity of NFLUX data to the COLE *et al.* (1988) relationship (Fig. 9), we judge that our NFLUX bacterial counts are not atypical of the Sargasso Sea. Further, we suggest that the following generalizations may apply in the Sargasso Sea: the minimum bacterial abundance is about 3×10^8 cells l^{-1} in the upper mixed layer, about 2×10^8 cells l^{-1} at the bottom of the euphotic zone (1% light penetration depth), and about 1×10^8 cells l^{-1} at 200 m where some phytoplankton can still be found.

We next consider the inventory of phytoplankton carbon. It is recognized that phytoplankton larger than the nanoplankton have a potentially significant contribution to carbon biomass (GOLDMAN, 1988). However, it is almost certain that rare large phytoplankton would have escaped our attention due to the detection limits of our counting techniques. At NFLUX, occasional measurements indicated that Chl *a* collected on 3 μm Nuclepore membranes comprised only about 15% of the total Chl *a*, a percentage slightly smaller than the mean value in the equatorial Atlantic Ocean (HERBLAND *et al.*, 1985). Furthermore, FUHRMAN *et al.* (1989) indicated that at Sta. S, only 6% of Chl *a* was retained on 10 μm mesh. It is therefore unlikely that our conclusion regarding the co-dominance of phytoplankton and bacteria would be altered by rare large phytoplankton. If large phytoplankton entered into our accounting, they would further reduce the relative contribution of bacteria to microbial carbon biomass.

A comparison of data from NFLUX (Fig. 5) and from Sta. S in 1987 (FUHRMAN *et al.*, 1989) shows that bacterial carbon biomass was the same: 1103 mg C m^{-2} (NFLUX) vs 990–1340 mg C m^{-2} (Sta. S). On the other hand, phytoplankton carbon biomass was substantially higher at NFLUX. We report 550 mg C m^{-2} for PEUK but FUHRMAN *et al.* (1989) found only 120–200 mg C m^{-2} for photosynthetic nanoplankton. We report 443 mg C m^{-2} for the sum of cyanobacteria and prochlorophytes while FUHRMAN *et al.* (1989) found only 120–200 mg C m^{-2}. Thus the inventory for phytoplankton carbon at NFLUX was 993 mg C m^{-2} whereas that at Sta. S was only 240–370 mg C m^{-2}. Significantly, Chl *a* concentrations were also higher at NFLUX (Fig. 2) than at Sta. S (FUHRMAN *et al.*, 1989). For comparison, phytoplankton carbon biomass in North Pacific central water has recently been estimated at about 1600 mg C m^{-2} (FURUYA, 1990). If we had chosen the conversion factor 124 fg C per prochlorophyte used by VELDHUIS and KRAAY (1990), phytoplankton carbon biomas at NFLUX would have been higher at 1342 mg C m^{-2}.

At NFLUX, the subsurface Chl *a* maximum was not the overall maximum for phytoplankton carbon; rather, it was a local carbon maximum, largely comprising PEUK and prochlorophytes. The major phytoplankton carbon maximum lay *ca* 25 m above the Chl *a* maximum and all three types of phytoplankton made a significant contribution. The depth-integrated biomass ratio of 1:2:4 for cyanobacteria:prochlorophytes:PEUK is intriguing but likely fortuitous since there is temporal and geographic variation in the abundance of all three groups (MURPHY and HAUGEN, 1985; ITURRIAGA and MARRA, 1988; OLSON *et al.*, 1990a,b). Prochlorophytes were extremely abundant but because of their small size, they did not dominate the phytoplankton carbon pool. Nevertheless, exclusion of these cells would have yielded a bacterial C:phytoplankton C ratio of 1.6, a value similar to that in the study of LAWS *et al.* (1984) which did not consider prochlorophytes. In spite of the numerical dominance of picophytoplankton (cyanobacteria and prochlorophytes), it was the nanophytoplankton (PEUK) which dominated the phytoplankton carbon pool. The same has been found in the western Pacific Ocean (FURUYA, 1990).

We estimated phytoplankton carbon by counting cells; an alternative approach would be to infer phytoplankton carbon from measurements of Chl *a* (cf. CHO and AZAM, 1990). The merit of the Chl approach is that all phytoplankton in the sample, regardless of size or taxon, are included. This is especially pertinent here because in our cell counting approach, we had to assume that the prochlorophytes at NFLUX and OFP (OLSON *et al.*, 1990a) were similarly distributed. The weakness of the Chl approach lies in the uncertainty in choosing an appropriate phytoplankton C:Chl *a* ratio, θ (BANSE, 1977; CULLEN, 1982). In a stratified water column, photoadaptive regulation of cellular Chl *a* content is undeniably important (CULLEN and LEWIS, 1988) and probably explains the obvious depth-related increase in fluorescence per cell observed in our data (Fig. 4). Thus, the usual practice of regressing carbon onto Chl to estimate θ, reliable under certain circumstances (TAGUCHI and LAWS, 1989), is questionable in an extremely stable water column (Fig. 8). GEIDER (1987) provided an empirical relationship to calculate θ from photon flux density and temperature; however, the relationship is valid only for exponentially-growing nutrient-sufficient phytoplankton. For nutrient-limited cells, values of θ range from 10 to 500 or 600 (CAPERON and MEYER, 1972; THOMAS and DODSON, 1972; EPPLEY and RENGER, 1974; LAWS and WONG, 1978; LAWS and BANNISTER, 1980; LAWS *et al.*, 1983) and are negatively associated with relative growth rate (GOLDMAN, 1980).

It is obvious that the choice of θ is very important. To illustrate using NFLUX data, consider the following three cases. First, we let $\theta = 47$ for all depths: this was the method of CHO and AZAM (1990). In this case, the bacterial C:phytoplankton C ratio based on column-integrated carbon values is 0.53. Second, we let $\theta = 100$ for shallow samples and $\theta = 40$ for deep samples: this was one method used by FUHRMAN *et al.* (1989) and the values are similar to those obtained by FURUYA (1990) in the western Pacific Ocean. In this case, the bacterial C:phytoplankton C ratio is 0.35. Third, we let $\theta = 35$ for samples above the pcynocline and $\theta = 17$ for those below: this was the situation for equatorial Pacific phytoplankton ($>5\,\mu$m) examined by VEDERNIKOV *et al.* (1977) at their Sta. 1458 (139°27′W at the equator) (see LONGHURST and HARRISON, 1989). In this case, the bacterial C:phytoplankton C is 1.2. Of the three results based on different choices of θ, only the last one (VEDERNIKOV) is similar to the ratio we inferred earlier (1.1) using flow cytometric cell counts. The similarity is a reflection of the comparable θ values at all depths (Fig. 8).

It is worthwhile noting that the mean value of $\theta = 44$ inferred from the flow cytometric counts for cells in the upper mixed-layer at NFLUX (Fig. 8) was essentially the same as that used by CHO and AZAM (1990), which was measured by the ^{14}C-Chl labelling technique of REDALJE and LAWS (1981). This rather low value of θ for cells in the nitrate-depleted zone implies a high relative growth rate ($\mu:\mu_{max}$) (GOLDMAN, 1980), consistent with recent reports for oligotrophic phytoplankton (LAWS *et al.*, 1984, 1987; TAGUCHI *et al.*, 1988). In the nitrate-rich deep layer, the mean value of $\theta = 15$ (Fig. 8) was slightly lower than predicted by GEIDER (1987) but within the range of previously reported values (WELSCHMEYER and LORENZEN, 1984). We further note that over the upper 200 m at NFLUX, the mean θ was 25 ± 15 which is not very different from the mean value of 30 reported by Booth *et al.* (1988) for subarctic Pacific phytoplankton. We conclude that our suggestion of biomass co-dominance by phytoplankton and bacteria at NFLUX is supported by both the cell count method and the Chl method. Furthermore, it appears that this suggestion is conservative: Chl methods that assume $\theta > ca\ 50$ for shallow samples and $> ca\ 20$ for deep samples indicate dominance by phytoplankton biomass.

A simple graphical method can be used to indicate domains of phytoplankton or bacterial dominance. If we assume 20 fg C per bacterium and simply select various values of θ, say 25, 50 and 100, lines can be drawn on the bacterial abundance (cells l^{-1}) vs Chl *a* ($\mu g\ l^{-1}$) plot that indicate co-dominance at the respective θ values (Fig. 9). Over the Chl *a* range from 0.01 to $10\ \mu g\ l^{-1}$, the Bird–Kalff line (Bird and Kalff, 1984) lies completely below the $\theta = 50$ line, indicating the dominance of phytoplankton biomass throughout this range. On the other hand, the Cole *et al.* (1988) line crosses the $\theta = 50$ line at $0.12\ \mu g$ Chl *a* l^{-1}: below this Chl *a* value, bacteria are dominant; above this value, phytoplankton are dominant.

One of the promising features of flow cytometric analysis is the potential for estimating cellular Chl *a* content from fluorescence intensity per cell. Although a positive relationship exists between these two variables (Phinney and Cucci, 1989), it appears that interspecific differences cannot be ignored (Sosik *et al.*, 1989). For PEUKs in the euphotic zone at NFLUX, fluorescence per cell bore the same general positive relation to Chl *a* per cell (Fig. 4) as shown by *Thalassiosira weissflogii*, *Hymenomonas carterae* and *Amphidinium carteri*, in spite of the much larger sizes of the laboratory cultured cells (Sosik *et al.*, 1989). However, before this relationship can be used in a predictive manner, many more measurements of a similar kind will have to be made for natural oligotrophic phytoplankton. No relationship between the variables was apparent for cells below the euphotic zone (1% I_0) where average photon flux densities (PFD) were less than the lowest used in the culture studies of either Phinney and Cucci (1989) or Sosik *et al.* (1989). These deep PEUK cells were subject to the combined effects of an exponentially decreasing PFD and a steep vertical gradient in nitrate concentration. It is known that fluorescence yield per chlorophyll bears a negative relationship to both increasing light and nutrient concentration (Kiefer, 1973; Cullen, 1982): it remains to be verified in the laboratory if these trends, which oppose each other as depth increases, can account for the observations made for deep NFLUX cells (Fig. 4).

An important implication of biomass co-dominance by phytoplankton and bacteria is to admit the possibility of higher bacterial growth rates. The following line of reasoning makes this clear. Equations (1)–(3) are by definition: (1) consumption of carbon (from phytoplankton by bacteria (C_b, mg C m^{-2} day^{-1}) is bacterial production (P_b, mg C m^{-2} day^{-1}) divided by the gross growth efficiency (E_b, unitless) which we take to be 0.5; (2) P_b is the product of bacterial biomass (B_b, mg C m^{-2}) and specific bacterial turnover (growth) rate (μ_b, day^{-1}); (3) μ_b is the inverse of the time to double (T_b, days per doubling) multiplied by the natural logarithm of 2:

$$C_b = \frac{P_b}{E_b} \qquad (1)$$

$$P_b = B_b \mu_b \qquad (2)$$

$$\mu_b = \frac{\ln 2}{T_b}. \qquad (3)$$

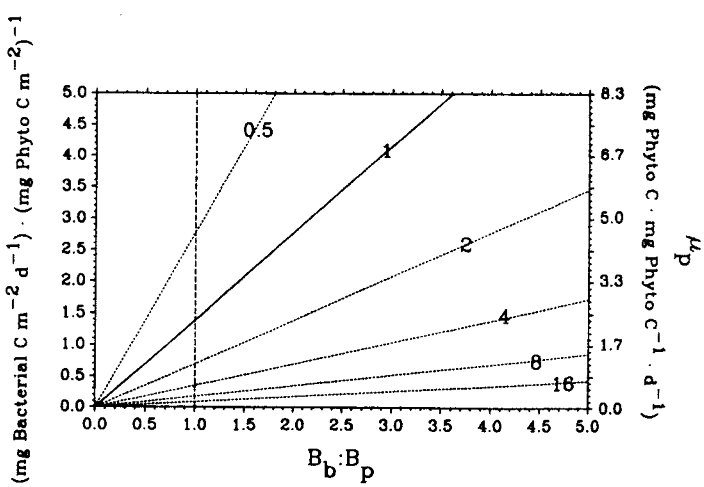

Fig. 10. Relationship between specific carbon consumption rate (i.e. multiples of phytoplankton carbon standing stock consumed by bacteria per day) vs the ratio of bacterial carbon : phytoplankton carbon, assuming gross growth efficiency of 50% (left ordinate). Relationship between specific phytoplankton growth rate vs bacterial carbon : phytoplankton carbon ratio, assuming bacterial production : net primary production = 0.3 (right ordinate). Numbers on the sloping lines indicate bacterial doubling times in days.

Substitution of (2) and (3) into (1) and division by phytoplankton biomass (B_p, mg C m^{-2}) gives equation 4, the specific rate for bacterial consumption of phytoplankton carbon (C_b/B_p, [mg bacterial C m^{-2} day^{-1}] [mg phytoplankton C m^{-2}]$^{-1}$): in other words, the multiples of phytoplankton carbon standing stock consumed per day by bacteria. Equation (4) expresses C_b/B_p as a function of bacterial C:phytoplankton C ratio (B_b/B_p) and is plotted in Fig. 10 for various values of T_b using the left ordinate axis:

$$\frac{C_b}{B_p} = \left(\frac{\ln 2}{E_b T_b}\right)\left(\frac{B_b}{B_p}\right). \tag{4}$$

Note also that C_b/B_p can also be expressed by defining numerator and denominator terms:

$$\frac{C_b}{B_p} = \left(\frac{P_b}{E_b}\right)\left(\frac{P_p}{\mu_p}\right)^{-1}. \tag{5}$$

Equating (4) to (5) and rearranging gives the expression for specific phytoplankton turnover (growth) rate (μ_p, day^{-1}) as a function of B_b/B_p. We take the ratio of bacterial production : phytoplankton production ($P_b:P_p$, depth-integrated areal basis) to be 0.3 (Cole *et al.*, 1988). This expression (equation 6) is plotted in Fig. 10 for various values of T_b using the right ordinate axis:

$$\mu_p = \left(\frac{P_b}{P_p}\right)^{-1}\left(\frac{\ln 2}{T_b}\right)\left(\frac{B_b}{B_p}\right). \tag{6}$$

For illustration, take $\mu_p = 2$ day^{-1} (2.9 doublings day^{-1}). Under steady state condition, and given that $P_b:P_p = 0.3$ and $E_b = 0.5$, a value of $C_b/B_p = 1.2$ is implied (equation 5). To sustain $C_b/B_p = 1.2$, bacteria would only have to double over $T_b = 3.5$ days if

$B_b:B_p = 3$ (equation 4); on the other hand, it is possible to admit a shorter doubling time (faster growth), say $T_b = 1.1$ day, if $B_b:B_p = 1$. We can phrase this another way. If phytoplankton grow at 2 day^{-1} and bacteria grow at 0.7 day^{-1} (i.e. 1 doubling day^{-1}), then $B_b:B_p = 3$ implies $C_b/B_p = 4.2$ whereas $B_b:B_p = 1$ implies $C_b/B_p = 1.4$. (Fuhrman *et al.* (1989) stated that $C_b/B_p = 7$ for their 1987 data which was $B_b:B_p = 3.64$ as calculated from entries in their Table 2; $C_b/B_p = 7$ would be correct only for $\mu_b = 1$ day^{-1} ($T_b = 0.7$ days) and not for $\mu_b = 0.7$ day^{-1} ($T_b = 1$ day), the latter of which was used by the authors.) In many ways, a lower rate of bacterial consumption of phytoplankton carbon is more easily reconciled with considerations of how carbon is thought to flow from phytoplankton to bacteria within the euphotic zone (e.g. phytoplankton excretion, "sloppy feeding" by zooplankton, etc.).

We emphasize that the analysis portrayed in Fig. 10 does not purport to be a necessarily realistic depiction of an actual trophodynamic relationship. The analysis is meant foremost to indicate the possible qualitative implications of lower $B_b:B_p$ values given a set of restrictive, and possibly unrealistic simplifying assumptions. Our analysis is based only on algebraic formalism with no pretence at specifying the underlying ecological mechanisms. Thus, although it is important to understand how the individual terms (e.g. B_b, B_p, P_b, P_p) are controlled, a lack of knowledge at this level does not necessarily invalidate the inferences that arise in a scheme that depends on the ratios of these terms (e.g. $B_b:B_p$, $P_b:P_p$). In fact, the scheme might be used as a starting point to think about the consequences of various specific situations.

In conclusion, the results from our study in the northern Sargasso Sea indicate that cyanobacteria, prochlorophytes and photosynthetic eukaryotes were all important contributors to phytoplankton carbon biomass. Furthermore, they were also important contributors to microbial biomass, at the approximate ratio of $B_b:B_p = 1:1$. In reporting the co-dominance of bacteria and phytoplankton, we do not deny that bacteria may dominate phytoplankton at other times and places in the oligotrophic ocean; it is certain that even in the oligotrophic ocean, biological conditions are not always and everywhere the same (Platt *et al.*, 1989). The extension of $B_b:B_p$ to lower values admits the possibility that oligotrophic bacterial assemblages may have high growth rates.

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REFERENCES

Banse K. (1977) Determining the carbon-to-chlorophyll ratio of natural phytoplankton. *Marine Biology*, **41**, 199–212.

Bird D. F. and J. Kalff (1984) Empirical relationship between bacterial abundance and chlorophyll concentration in fresh and marine waters. *Canadian Journal of Fisheries and Aquatic Sciences*, **41**, 1015–1023.

Booth B. C. (1988) Size classes and major taxanomic groups of phytoplankton at two locations in the subarctic Pacific Ocean in May and August, 1984. *Marine Biology*, **97**, 275–286.

Booth B. C., J. Lewin and C. J. Lorenzen (1988) Spring and summer growth rates of subarctic Pacific phytoplankton assemblages determined from carbon uptake and cell volumes estimated using epifluorescence microscopy. *Marine Biology*, **98**, 287–298.

Burney C. M., P. G. Davis, K. M. Johnson and J. McN. Sieburth (1981) Dependence of dissolved carbohydrate concentrations upon small scale nanoplankton and bacterioplankton distributions in the western Sargasso Sea. *Marine Biology*, **65**, 289–296.

CAPERON J. and J. MEYER (1972) Nitrogen-limited growth of marine phytoplankton. I. Changes in population characteristics with steady-state growth rate. *Deep-Sea Research*, **19**, 601–618.

CHISHOLM S. W., R. J. OLSON, E. R. ZETTLER, R. GOERICKE, J. B. WATERBURY and N. A. WELSCHMEYER (1988) A novel free-living prochlorophyte abundant in the oceanic euphotic zone. *Nature*, **334**, 340–343.

CHO B. C. and F. AZAM (1988) Major role of bacteria in biogeochemical fluxes in the ocean's interior. *Nature*, **332**, 441–443.

CHO B. C. and F. AZAM (1990) Biogeochemical significance of bacterial biomass in the ocean's euphotic zone. *Marine Ecology Progress Series*, **63**, 253–259.

COLE J. J., S. FINDLAY and M. L. PACE (1988) Bacterial production in fresh and saltwater ecosystems: a cross-system overview. *Marine Ecology Progress Series*, **43**, 1–10.

CULLEN J. J. (1982) The deep chlorophyll maximum: comparing vertical profiles of chlorophyll *a*. *Canadian Journal of Fisheries and Aquatic Sciences*, **39**, 791–803.

CULLEN J. J. and M. R. LEWIS (1988) The kinetics of algal photoadaptation in the context of vertical mixing. *Journal of Plankton Research*, **10**, 1039–1063.

DAVIS P. G., D. A. CARON, P. W. JOHNSON and J. McN. SIEBURTH (1985) Phototrophic and apochlorotic components of picoplankton and nanoplankton in the north Atlantic: geographic, vertical, seasonal and diel distributions. *Marine Ecology Progress Series*, **21**, 15–26.

DORTCH Q. and T. T. PACKARD (1989) Differences in biomass structure between oligotrophic and eutrophic marine ecosystems. *Deep-Sea Research*, **36**, 223–240.

DUCKLOW H. W. (1983) Production and fate of bacteria in the oceans. *Bioscience*, **33**, 494–501.

DUCKLOW H. W. (1984) Geographical ecology of marine bacteria: physical and biological variability at the mesoscale. In: *Current perspectives in microbial ecology*, M. J. KLUG and C. A. REDDY, editors, American Society for Microbiology, Washington, D.C., pp. 22–31.

DUCKLOW H. W. (1986) Bacterial biomass in warm-core Gulf Stream ring 82-B: mesoscale distributions, temporal changes and production. *Deep-Sea Research*, **33**, 1789–1812.

EPPLEY R. W. and E. H. RENGER (1974) Nitrogen assimilation of an oceanic diatom in nitrogen-limited continuous culture. *Journal of Phycology*, **10**, 15–23.

FUHRMAN J. A., T. D. SLEETER, C. A. CARLSON and L. M. PROCTOR (1989) Dominance of bacterial biomass in the Sargasso Sea and its ecological implications. *Marine Ecology Progress Series*, **57**, 207–217.

FURUYA K. (1990) Subsurface chlorophyll maximum in the tropical and subtropical western Pacific Ocean: vertical profiles of phytoplankton biomass and its relationship with chlorophyll *a* and particulate organic carbon. *Marine Biology*, **107**, 529–539.

GEIDER R. J. (1987) Light and temperature dependence of the carbon to chlorophyll *a* ratio in microalgae and cyanobacteria: implications for physiology and growth of phytoplankton. *New Phytologist*, **106**, 1–34.

GLOVER H. E., B. B. PRÉZELIN, L. CAMPBELL and M. WYMAN (1988) Pico- and ultraplankton Sargasso Sea communities: variability and comparative distributions of *Synechococcus* spp. and algae. *Marine Ecology Progress Series*, **49**, 127–139.

GOLDMAN J. C. (1980) Physiological processes, nutrient availability; and the concept of relative growth rate in marine phytoplankton ecology. In: *Primary productivity in the sea*, P. G. FALKOWSKI, editor, Plenum Press, New York, pp. 179–194.

GOLDMAN J. C. (1988) Spatial and temporal discontinuities of biological processes in pelagic surface waters. In: *Toward a theory on biological–physical interactions in the world ocean*, B. J ROTHSCHILD, editor, Kluwer Academic, Deventer, The Netherlands, pp. 273–296.

HERBLAND A., A. LEBOUTEILLER and P. RAIMBAULT (1985) Size structure of phytoplankton biomass in the equatorial Atlantic Ocean. *Deep-Sea Research*, **32**, 819–836.

HERMAN A. W., M. R. MITCHELL and S. W. YOUNG (1984) A continuous pump sampler for profiling copepods and chlorophyll in the upper oceanic layers. *Deep-Sea Research*, **31**, 439–450.

HORAN P. K., K. A. MUIRHEAD and S. E. SLEZAK (1990) Standards and controls in flow cytometry. In: *Flow cytometry and sorting*, 2nd edition, M. R. MELAMED, T. LINDMO, M. L. MENDELSOHN, editors, Wiley-Liss, New York, pp. 397–414.

IRWIN B., J. ANNING, C. CAVERHILL, M. HODGSON, A. MACDONALD and T. PLATT (1990) Primary production in the northern Sargasso Sea in September 1988. *Canadian Data Report of Fisheries and Aquatic Sciences*, **798**, 1–93.

ITURRIAGA R. and J. MARRA (1988) Temporal and spatial variability of chroococcoid cyanobacteria *Synechococcus* spp. specific growth rates and their contribution to primary production in the Sargasso Sea. *Marine Ecology Progress Series*, **44**, 175–181.

KANA T. M. and P. M. GLIBERT (1987) Effect of irradiances up to 2000 μE m^{-2} s^{-1} on marine *Synechococcus* WH7803—I. Growth, pigmentation, and cell composition. *Deep-Sea Research*, **34**, 479–495.

KIEFER D. A. (1973) Chlorophyll *a* fluorescence in marine centric diatoms: responses of chloroplasts to light and nutrient stress. *Marine Biology*, **23**, 39–46.

LAWS E. A. and J. W. ARCHIE (1981) Appropriate use of regression analysis in marine biology. *Marine Biology*, **65**, 13–16.

LAWS E. A. and T. T. BANNISTER (1980) Nutrient- and light-limited growth of *Thalassiosira fluviatilis* in continuous culture, with implications for phytoplankton growth in the ocean. *Limnology and Oceanography*, **25**, 457–473.

LAWS E. A. and D. C. L. WONG (1978) Studies of carbon and nitrogen metabolism by three marine phytoplankton species in nitrate-limited continuous culture. *Journal of Phycology*, **14**, 406–416.

LAWS E. A., D. M. KARL, D. G. REDALJE, R. S. JURICK and C. D. WINN (1983) Variability in ratios of phytoplankton carbon and RNA to ATP and chlorophyll *a* in batch and continuous cultures. *Journal of Phycology*, **19**, 439–445.

LAWS E. A., D. G. REDALJE, L. W. HAAS, P. K. BIENFANG, R. W. EPPLEY, W. G. HARRISON, D. M. KARL and J. MARRA (1984) High phytoplankton growth and production rates in oligotrophic Hawaiian coastal waters. *Limnology and Oceanography*, **29**, 1161–1169.

LAWS E. A., G. R. DITULLIO and D. G. REDALJE (1987) High phytoplankton growth rate and production rates in the North Pacific subtropical gyre. *Limnology and Oceanography*, **32**, 905–918.

LEE S. and J. A. FUHRMAN (1987) Relationships between biovolume and biomass of naturally derived marine bacterioplankton. *Applied and Environmental Microbiology*, **53**, 1298–1303.

LI W. K. W. (1986) Experimental approaches to field measurements: methods and interpretation. In: *Photosynthetic picoplankton*, T. PLATT and W. K. W. LI, editors, Canadian Bulletin of Fisheries and Aquatic Sciences, **214**, 251–286.

LI W. K. W. (1989) Shipboard analytical flow cytometry of oceanic ultraphytoplankton. *Cytometry*, **10**, 564–579.

LI W. K. W. (1990) Particles in "particle-free" seawater: growth of ultraphytoplankton and implications for dilution experiments. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 1258–1268.

LI W. K. W. and P. M. DICKIE (1984) Rapid enhancement of heterotrophic but not photosynthetic activities in arctic microbial plankton at mesobiotic temperatures. *Polar Biology*, **3**, 217–226.

LI W. K. W. and A. M. WOOD (1988) Vertical distribution of North Atlantic ultraphytoplankton: analysis by flow cytometry and epifluorescence microscopy. *Deep-Sea Research*, **35**, 1615–1638.

LONGHURST A. R. and W. G. HARRISON (1989) The biological pump: profiles of plankton production and consumption in the upper ocean. *Progress in Oceanography*, **22**, 47–123.

LONGHURST A. R., A. BEDO, W. G. HARRISON, E. J. H. HEAD, E. P. HORNE, B. IRWIN and C. MORALES (1989) NFLUX: a test of vertical nitrogen flux by diel migrant biota. *Deep-Sea Research*, **36**, 1705–1719.

MURPHY L. S. and E. M. HAUGEN (1985) The distribution and abundance of phototrophic ultraplankton in the North Atlantic. *Limnology and Oceanography*, **30**, 47–58.

NEVEUX J., D. VAULOT, C. COURTIES and E. FUKAI (1989) Green photosynthetic bacteria associated with the deep chlorophyll maximum of the Sargasso Sea. *Comptes Rendus de l'Acadamie des Sciences Paris*, **308**, Serie III, 9–14.

ODUM E. P. (1971) *Fundamentals of ecology*. Third edition, W. B. Saunders, Philadelphia, 574 pp.

OLSON R. J., S. W. CHISHOLM, E. R. ZETTLER, M. A. ALTABET and J. A. DUSENBERRY (1990a) Spatial and temporal distributions of prochlorophyte picoplankton in the North Atlantic Ocean. *Deep-Sea Research*, **37**, 1033–1051.

OLSON R. J., S. W. CHISHOLM, E. R. ZETTLER and E. V. ARMBRUST (1990b) Pigments, size, and distribution of *Synechococcus* in the North Atlantic and Pacific Oceans. *Limnology and Oceanography*, **35**, 45–58.

PHINNEY D. A. and T. L. CUCCI (1989) Flow cytometry and phytoplankton. *Cytometry*, **10**, 511–521.

PICK F. R. and D. A. CARON (1987) Picoplankton and nanoplankton biomass in Lake Ontario: relative contribution of phototrophic and heterotrophic communities. *Canadian Journal of Fisheries and Aquatic Sciences*, **44**, 2164–2172.

PLATT T., W. G. HARRISON, M. R. LEWIS, W. K. W. LI, S. SATHYENDRANATH, R. E. SMITH and A. F. VEZINA (1989) Biological production of the oceans: the case for a consensus. *Marine Ecology Progress Series*, **52**, 77–88.

PORTER K. G. and Y. S. FEIG (1980) The use of DAPI for identifying and counting aquatic microflora. *Limnology and Oceanography*, **25**, 943–948.

PSENNER R. (1990) From image analysis to chemical analysis of bacteria: a long-term study? *Limnology and Oceanography*, **35**, 234–237.

REDALJE D. G. and E. A. LAWS (1981) A new method for estimating phytoplankton growth rates and carbon biomass. *Marine Biology*, **62**, 73–79.

RICKER W. E. (1973) Linear regressions in fishery research. *Journal of the Fisheries Research Board of Canada*, **30**, 409–434.

SMITH R. E. H., R. J. GEIDER and T. PLATT (1984) Microplankton productivity in the oligotrophic ocean. *Nature*, **311**, 252–254.

SOSIK H. M., S. W. CHISHOLM and R. J. OLSON (1989) Chlorophyll fluorescence from single cells: interpretation of flow cytometric signals. *Limnology and Oceanography*, **34**, 1749–1761.

STRATHMANN R. R. (1967) Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. *Limnology and Oceanography*, **12**, 411–418.

TAGUCHI S. and E. A. LAWS (1989) Biomass and compositional characteristics of Kaneohe Bay, Oahu, Hawaii, phytoplankton inferred from regression analysis. *Pacific Science*, **43**, 316–331.

TAGUCHI S., G. R. DITULLIO and E. A. LAWS (1988) Physiological characteristics and production of mixed layer and chlorophyll maximum phytoplankton populations in the Caribbean Sea and western Atlantic Ocean. *Deep-Sea Research*, **35**, 1363–1377.

THOMAS W. H. and A. N. DODSON (1972) On nitrogen deficiency in tropical Pacific oceanic phytoplankton. II. Photosynthetic and cellular characteristics of a chemostat-grown diatom. *Limnology and Oceanography*, **17**, 515–523.

VAULOT D., F. PARTENSKY, J. NEVEUX, R. F. C. MANTOURA and C. A. LLEWELLYN (1990) Wintertime presence of prochlorophytes in surface waters of the North-western Mediterranean Sea. *Limnology and Oceanography*, **35**, 1156–1164.

VEDERNIKOV V. I., O. J. KOBLENTZ-MISHKE, I. N. SUKHANOVA, G. S. KARABASHEV and J. K. FISHER (1977) A comparison of the vertical distribution of seston, chlorophyll phytoplankton and pigment luminescence in the equatorial and Peruvian regions of eastern Pacific Ocean. *Polskie Archiwum Hydrobiologii*, **24** (Suppl.), 215–226.

VELDHUIS M. J. W. and G. W. KRAAY (1990) Vertical distribution and pigment composition of a picoplanktonic prochlorophyte in the subtropical North Atlantic: a combined study of HPLC-analysis of pigments and flow cytometry. *Marine Ecology Progress Series*, **68**, 121–127.

WATERBURY J. B., S. W. WATSON, F. W. VALOIS and D. G. FRANKS (1986) Biological and ecological characterization of the marine unicellular cyanobacterium *Synechococcus*. In: *Photosynthetic picoplankton*, T. PLATT and W. K. W. LI, editors, Canadian Bulletin of Fisheries and Aquatic Sciences, **214**, 71–120.

WELSCHMEYER N. A. and C. J. LORENZEN (1984) Carbon-14 labeling of phytoplankton carbon and chlorophyll *a* carbon: determination of specific growth rates. *Limnology and Oceanography*, **29**, 135–145.