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Phytoplankton carbon incorporation patterns and biochemical composition of particulate matter in the eastern North Atlantic subtropical region

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Abstract. Photosynthetic carbon metabolism and the biochemical composition of late-winter phytoplankton assemblages in the eastern North Atlantic Ocean were studied during an oceanographic cruise carried out in March 1992. Enhanced levels of phytoplankton biomass and primary production were linked to the subtropical front–Azores Current (STF/AC) region. High values of the relative incorporation of carbon into proteins indicated that the phytoplankton was growing at a rate close to the maximum growth rate. A very high percentage of carbon was incorporated into the lipid fraction at southern latitudes, whereas incorporation into polysaccharides peaked at the AC. In general, the biochemical composition of particulate matter reflected the observed patterns of photosynthate partitioning. Latitudinal changes in phytoplankton species composition accounted for the geographical variability in ^{14}C labelling patterns. Turnover times of particulate matter estimated for the STF/AC region were relatively low (3–5 days) and suggested balanced growth of the microplankton community over daily time scales.

Introduction

The study of the patterns of allocation of photosynthate to the major intracellular macromolecules is a useful tool for understanding the metabolic behaviour of naturally occurring phytoplankton, as it provides information on the physiological state of the populations [see the review in Morris (1981)], and at the same time has the advantage of minimizing the interference caused by heterotrophic and/or detrital materials. This methodological approach also allows inferences to be drawn on phytoplankton growth and it is now well established that the rate of protein synthesis is better correlated with cell division than classical primary production measurements (Morris, 1981; Di Tullio and Laws, 1983).

Photosynthetic carbon metabolism is known to be affected by various environmental factors, such as irradiance, spectral quality, temperature and nutrients, both in cultured and natural phytoplankton populations (e.g. Morris, 1981; Harding *et al.*, 1985; Taguchi and Laws, 1987; and references therein), and also by the interaction among these variables (Rivkin, 1989; Hawes, 1990). Several studies have also pointed out that differences in species composition are of great relevance in determining the distribution patterns of carbon incorporation into organic compounds (Rivkin, 1985; Rivkin and Voytek, 1987; Madariaga, 1992). Little attention has, however, been devoted to the study of

the geographical variations in the synthesis of end-products of photosynthesis by open-ocean phytoplankton assemblages, and also to the relationship between these patterns and large-scale hydrographic structures such as fronts, eddies, convergences, etc. (Morris *et al.*, 1981; Li and Platt, 1982; Hama, 1988, 1992).

The present survey is centred in the eastern North Atlantic subtropical region. This region is characterized by the presence of a sharp thermohaline front approximately along 34–35°N (Kase and Siedler, 1982; Gould, 1985; Tokmakian and Challenor, 1993). Temperature and salinity variations in the frontal area are not completely density compensating, thus giving rise to strong geostrophic shears. In this regard the existence has been reported of an eastward, upper layer flow, quoted as the Azores Current (AC), closely associated with the subtropical frontal boundary (Kase and Siedler, 1982).

In a companion paper, Fernández *et al.* (1994a) reported for the first time the existence of a strong correlation between the subtropical front (SFT)–Azores Current and the distribution and abundance of phytoplankton during late winter. In the present paper, we focus instead on the physiological condition of phytoplankton in this region. The specific goals of this study were (i) to determine the patterns of carbon incorporation into photosynthetic end-products of the different phytoplankton assemblages in order to ascertain their physiological state and relative growth rates in a pre-spring bloom situation, and (ii) to estimate production rates for the major biochemical constituents (proteins and polysaccharides) in order to determine the relationship between the STF and a potential enhancing of the rates of carbon turnover in the microplankton community.

Method

An oceanographic cruise (CD66; leg I) was conducted on board R/V 'Charles Darwin' from 4 to 21 March 1992 in the subtropical North Atlantic region southeast of the Azores (Figure 1). Temperature, salinity and chlorophyll *a* fluorescence were measured continuously underway with a thermosalinograph system and an Aquatracka fluorimeter, both mounted on deck and fed with water from the ship's non-toxic water supply. An RDI 153 kHz acoustic doppler current profiler (ADCP) was also used to derive the current vectors in the upper 200 m of the water column. Calibrations and operational procedures of the underway measurements are detailed in Fernández *et al.* (1994a).

Intensive sampling of biological variables was concentrated on eight stations located approximately along the 26°W meridian between 30 and 35.5°N (Figure 1). At these stations, vertical profiles of temperature, salinity and chlorophyll *a* fluorescence were made with a Neil Brown mark III CTD attached to a rosette sampler equipped with 10 l Niskin bottles. In addition, 36 XBTs were launched along this section to obtain a more accurate view of the thermal structure of the subtropical front. On each CTD cast, water samples were drawn for the determination of nitrate, chlorophyll *a*, total particulate carbon and nitrogen (TPC and TPN) and particulate inorganic carbon (PIC), particulate proteins, carbohydrates and lipids, phytoplankton counting and ^{14}C uptake experiments.

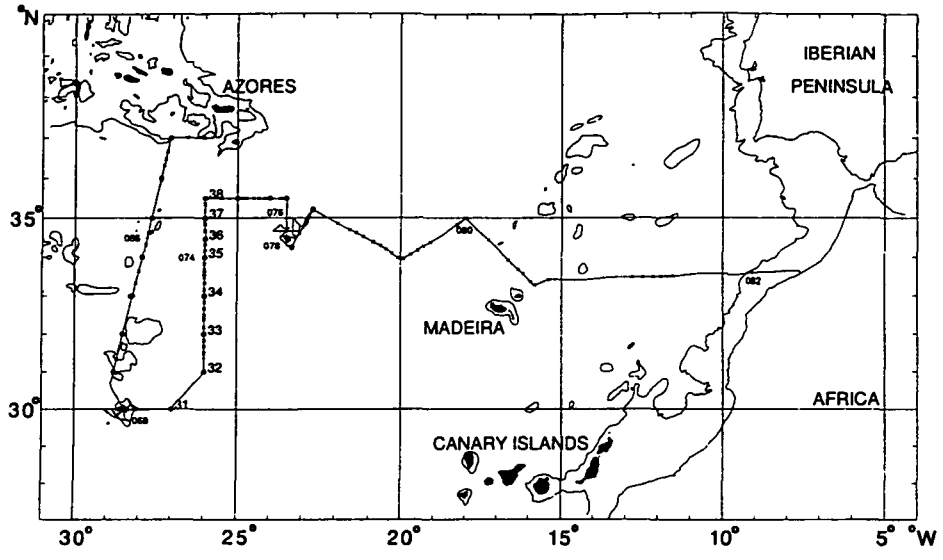

Fig. 1. CD66 cruise track (first leg) in the North-East Atlantic Ocean from 4 March (Day 64) to 22 March (Day 82). Open circles represent CTD stations. The CTD number is indicated to the right part of the track for those stations on the main section, approximately along the 26°W meridian. XBTs are shown by small crosses. Smaller numbers to the left or underneath the track line denote the year-day at 2 day intervals.

Vertical extinction coefficients for downwelling irradiance were estimated from the reading of the Secchi disk depth.

Concentrations of nitrate, chlorophyll *a* and TPC, TPN and PIC were determined following the methods described in Fernández *et al.* (1993). Particulate proteins, carbohydrates and lipids were measured as in Fernández *et al.* (1992) using bovine serum albumin, glucose and cholesterol as standards. The carbon content of each biochemical pool was assumed to be 53% of total weight for proteins, based on the average amino acid composition of microalgae (Laws, 1991), and 40 and 84% for carbohydrates and lipids, respectively, as calculated from the carbon composition of the standards employed. Microplankton samples were preserved both in Lugol's iodine solution and formaldehyde. On each sample, microplankton cells were identified, enumerated and the biomass estimated as in Holligan *et al.* (1984).

Rates of carbon incorporation into photosynthetic end-products were determined by filling triplicate 70 ml acid-cleaned polycarbonate bottles with water collected from 5–6 depths within the upper mixed layer. Bottles were inoculated with 486 kBq (13.15 μCi) $NaH^{14}CO_3$ and immediately placed in an on-deck incubator which simulated a range of irradiances (~100%, 50%, 30%, 20%, 10% and 5% of surface irradiance values) by means of neutral-density plastic screens and cooled by circulating surface water. The irradiance levels in the incubators were similar to the irradiance experienced by the cells at the sampling depth. In the case of those stations visited between mid-day and dawn (31°N, 34°N, 35°N and 35.30°N), water samples were stored in 2 l polycarbonate bottles

and placed inside the on-deck incubators in darkness until next morning when they were transferred to the incubation bottles and inoculated with radioactive label. Mean irradiance values during the incubations varied from 420 to 773 μE m^{-2} s^{-1}. Incubations lasted 24 h. After this period, samples were filtered onto GF/F glass fibre filters which were rinsed twice with 0.2 μm filtered seawater and kept frozen (−20°C) inside plastic vials until further fractionation (ashore) of the organic material retained on the filters.

Incorporation of ^{14}C into different cellular constituents was determined following a serial fractionation procedure modified from Li *et al.* (1980) and Lohrenz and Taylor (1987). This procedure separates cell material into four fractions: methanol/water-soluble compounds (low-molecular-weight metabolites, LMWM), chloroform-soluble compounds (lipids), hot trichloroacetic acid (TCA)-soluble compounds (polysaccharides and nucleic acids) and hot TCA-insoluble compounds (proteins). The analytical routine first involved vortex mixing of the filter with a mixture of chloroform and methanol/acetic acid (95:5, v/v). The filter was kept at 4°C for 10 min and the resulting suspension transferred to a graduated tube. After repeating this step again, 1 ml of distilled water was added to the suspension and then vortexed vigorously, centrifuged, and 1 ml aliquots taken from each phase. The aliquots were immediately transferred to a 6 ml scintillation vial, in the case of the upper phase containing LMWM, or allowed to dry, in the case of the chloroform phase, before scintillation cocktail (Optiphase Hi-Safe) was added. The filter was transferred to a glass tissue homogenizer and ground in 5% TCA. After rinsing with 5% TCA, the suspension was heated at 95°C for 20 min and subsequently centrifuged. The supernatant was transferred to a new tube, and the pellet resuspended with 5% TCA and extracted again at 95°C for 10 min. After centrifugation, the supernatant was transferred to the previous tube and the residual pellet sequentially rinsed with 0.1 N NaOH, distilled water and 1.0 M Tris (pH 7.0). Finally, a 1 ml aliquot from each fraction was transferred to 20 ml scintillation vials and 10 ml of scintillation cocktail added. Radioactivity was subsequently determined by liquid scintillation counting (LKB counter) ashore. Quenching was corrected by the channels ratio method. Preliminary experiments caried out with natural populations incubated for 24 h indicated that ^{14}C recovery values were between 93 and 100%, as compared to independently measured total carbon fixation (t-test $P > 0.25$, $n = 24$).

Carbon incorporation values were converted into daily specific production rates for proteins and carbohydrates according to the equation:

$$SPR = \log_e[(C_p + \Delta C_p)/C_p]$$

where ΔC_p is the amount of carbon incorporated into the given biochemical compound after 24 h incubation and C_p is the carbon content of the biochemical pool. Lipid SPRs were calculated, but as the number of samples where carbon incorporation rates and lipid concentration were determined simultaneously was very small in the upper 40 m, a description of the main patterns of variability was not performed.

Results

Physical structure and chlorophyll a distribution

The most relevant physical feature observed during this cruise was a meandering thermohaline front located about 34–35°N, extending from 15 to 28°W (Figure 2A and B). Surface temperature varied from 18.4°C at the southern part of the cruise track (30°N) to <16.8°C at the northernmost region. The thermal gradient at the front was sharp, with temperature variations of ~1°C over spatial scales of <100 km. The subtropical front was characterized by relatively high levels of chlorophyll *a* (Figure 2C). Surface pigment concentrations were, however, generally <0.15 mg m^{-3}, with the exception of the frontal boundary where concentrations reached up to 0.4 mg m^{-3}.

The vertical physical structure of the STF can be visualized from a latitudinal

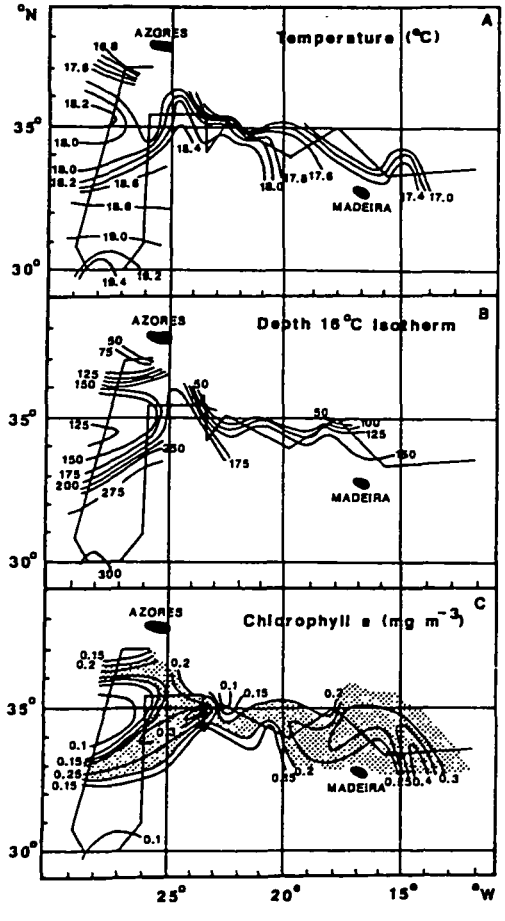

Fig. 2. Surface distribution of (A) temperature (°C), (B) depth of the 16°C isotherm (m) and (C) chlorophyll *a* (mg C m^{-3}) along the cruise track. The stippled area in (C) corresponds to chlorophyll *a* concentrations >0.2 mg m^{-3}.

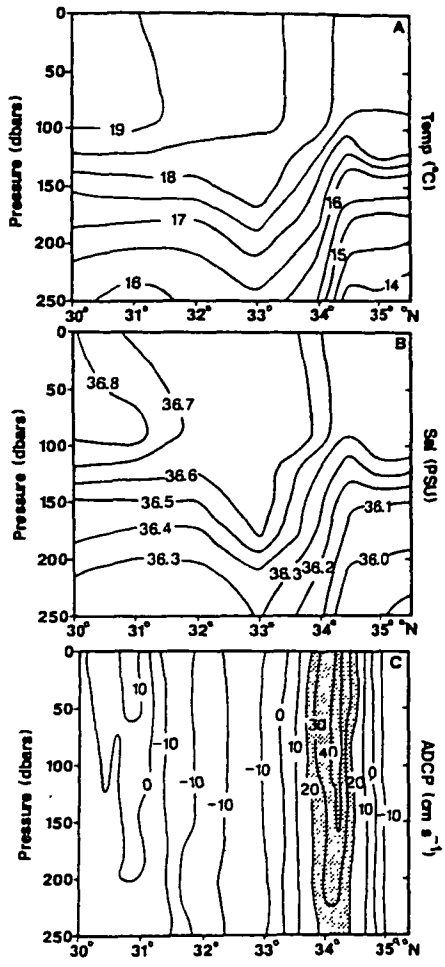

Fig. 3. Section (against latitude) of (A) temperature (°C), (B) salinity (p.s.u.) and (C) east component of ADCP velocity (cm s^{-1}) along the 26°W meridian. The stippled area in (C) corresponds to eastward current speeds >20 cm s^{-1}.

section running approximately along the 26°W meridian (Figure 3). Both isotherms and isohalines outcropped at ~34°N, giving rise to a front separating warmer, more saline Western Atlantic Water (WAW) to the south from colder and fresher Eastern Atlantic Water (EAW) to the north (Gould, 1985) (Figure 3A and B). There was a close relationship between the thermohaline front and the strong, eastward-flowing, AC, with easterly current speeds >0.40 m s^{-1} at the core of the current and extending down to at least 250 m. Water at both sides of the front moved towards the west at ~0.10 m s^{-1}. Mixed-layer depths were rather constant along the section (Table I), ranging from 100 m in the AC area to 125 m on the northern side of the front. In this layer, nitrate was homogeneously distributed at a concentration >5 mmol m^{-3} (Table I). The

Table I. Mixed-layer averaged and integrated values of selected variables in representative locations along the 26°W meridian

Variable	Latitude (°N)					
	30	32	33	34	34°30′	35
Mixed-layer depth (m)	110	105	110	100	105	125
Averaged mixed-layer temperature (°C)	19.2	18.7	18.6	18.3	17.6	17.6
Averaged mixed-layer nitrate (mmol m^{-3})	5.6	5.6	5.7	5.7	5.2	5.1
Integrated chlorophyll *a* 0–80 m (mg m^{-2})	8.5	12.1	16.8	17.4	9.7	11.0
Integrated particulate organic carbon 0–80 m (g m^{-2})	3.3	3.6	3.1	4.2	3.6	5.6
Phytoplankton-C/particulate organic carbon (0–80 m)	0.16	0.15	0.39	0.12	0.13	0.17
% Diatom biomass (0–80 m)	0.2	22.2	28.1	1.0	23.2	32.5
% Coccolithophorid biomass (0–80 m)	12.6	17.5	10.7	13.5	19.5	14.6
% Flagellate biomass (0–80 m)	86.2	58.1	60.5	84.3	54.2	50.7
Integrated primary production 0–80 m (mg C m^{-2} h^{-1})	29	69	78	85	67	44

vertical extinction coefficient for downwelling irradiance showed little variation along the section ranging from 0.040 to 0.045 m^{-1}, corresponding to 1% light depths of ~102–115 m.

Distribution and composition of particulate matter

Particulate organic carbon (POC) values were close to 40 mg C m^{-3} in most of the section (Figure 4A). An apparent maximum was detected in the northern side of the STF, with values up to 70 mg C m^{-3} in subsurface layers at 35°N. The concentration of PIC followed a gradually decreasing trend towards the north (Figure 4B). PIC values >4 mg C m^{-3} were measured south of 31°N. The contribution of PIC to total particulate carbon was always low, never exceeding 15%. The C/N ratio was close to the Redfield ratio in the region, with the exception of the northern frontal boundary (34–35°N) and the southernmost region, where this ratio yielded values >7. Accumulation of detritus and phytoplankton debris are the most likely explanations for the observed POC concentrations at 35°N (Fernández *et al.*, 1994a). As previously shown (Figure 2C), chlorophyll *a* peaked at the front (Figure 4D). Values >0.2 mg m^{-3} were measured in the STF–AC region down to 100 m depth. Size-fractionated chlorophyll *a* analyses carried out at some selected stations revealed that most of the phytoplankton (65–75%) was in the <2 μm size fraction. The contribution

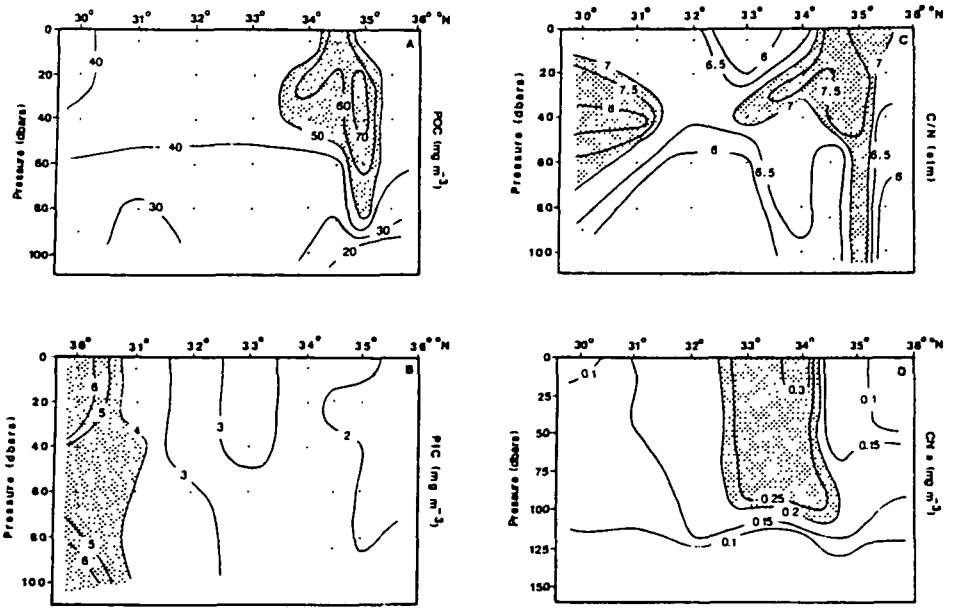

Fig. 4. Section (against latitude) of (A) particulate organic carbon (POC; mg C m^{-3}), (B) particulate inorganic carbon (PIC; mg C m^{-3}), (C) particulate carbon/nitrogen ratio (atoms; C/N) and (D) chlorophyll *a* (Chl *a*; mg m^{-3}) along the 26°W meridan. Stippled areas indicate POC, PIC, C/N and Chl *a* values >50 mg C m^{-3}, 4 mg C m^{-3}, 7 and 0.2 mg Chl *a* m^{-3}, respectively. Note the different vertical scale for chlorophyll *a*.

of the smallest size fraction to the total chlorophyll *a* concentration was maximum at the AC station (34°N), where it reached values >90%.

Clear differences in the composition of particulate matter were observed along the 26°W section (Figure 5). The protein-C concentration ranged from <8 mg C m^{-3} at 33°N to >14 mg C m^{-3} at the AC region (Figure 5A).

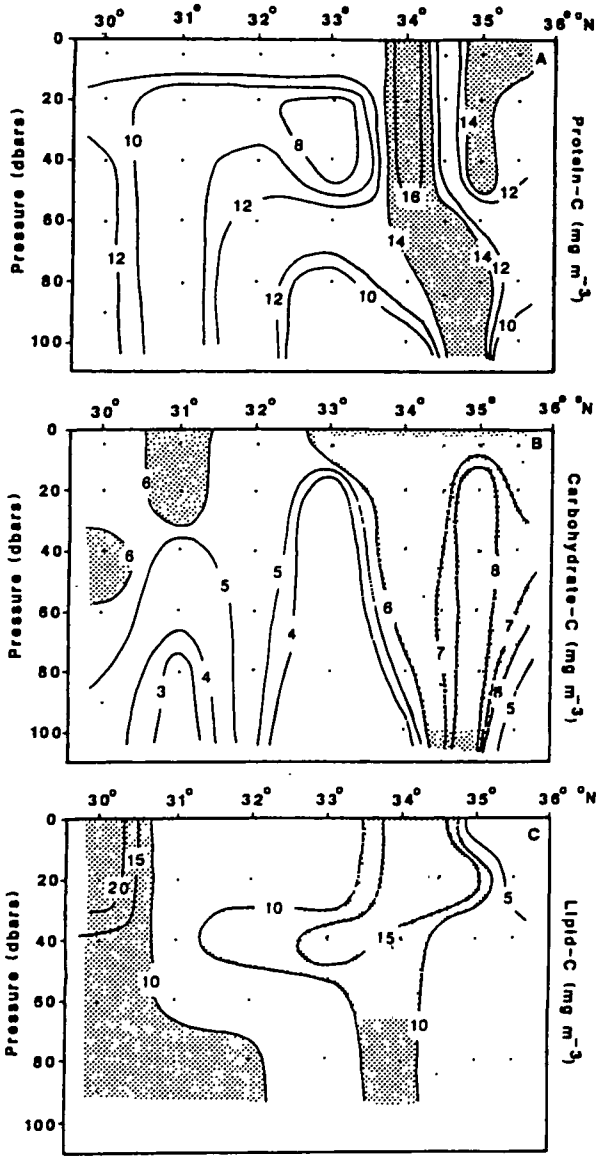

Fig. 5. Section (against latitude) of (A) particulate protein carbon (protein-C; mg C m^{-3}), (B) particulate carbohydrate carbon (carbohydrate-C; mg m^{-3}) and (C) particulate lipid carbon (lipid-C; mg C m^{-3}) concentration along the 26°W meridian. Stippled areas indicate protein-C, carbohydrate-C and lipid-C concentrations >14, 6 and 10 mg C m^{-3}, respectively.

Carbohydrate-C was higher in the northern part of the section, with values >8 mg C m^{-3} at 35°N (Figure 5B). On the contrary, the concentration of lipids was maximum at the surface near 30°N, also being high at the frontal region (Figure 5C). The total amount of carbon calculated from the sum of protein-C, carbohydrate-C and lipid-C agreed well with the amount of POC determined independently (Figure 4A), with the exception of the maximum of POC measured at 35°N. Larger errors associated with the measurement of high absolute values of the variables are likely to account for this disagreement.

Distribution of major phytoplankton groups

Phytoplankton carbon biomass, as estimated from cell volumes, showed two distinct maxima located at the southern (33°N) and northern (35°N) side of the subtropical front (Figure 6A). Surprisingly, the chlorophyll *a* maximum associated with the AC (see Figure 4) was not reflected at all in terms of phytoplankton-C. Moreover, the relatively high biomass of phytoplankton at 35°N was not reflected in high concentrations of chlorophyll *a*. The predominance of very small cells at the AC and 'unhealthy' (pale) populations of diatoms at 35°N are likely to explain the observed mismatch.

Diatoms (Figure 6B) and/or flagellates, the latter mainly prymnesiophytes (Figure 6D), accounted for a large porportion of the total biomass of phytoplankton, although diatoms were virtually non-existent at 30°N and also at

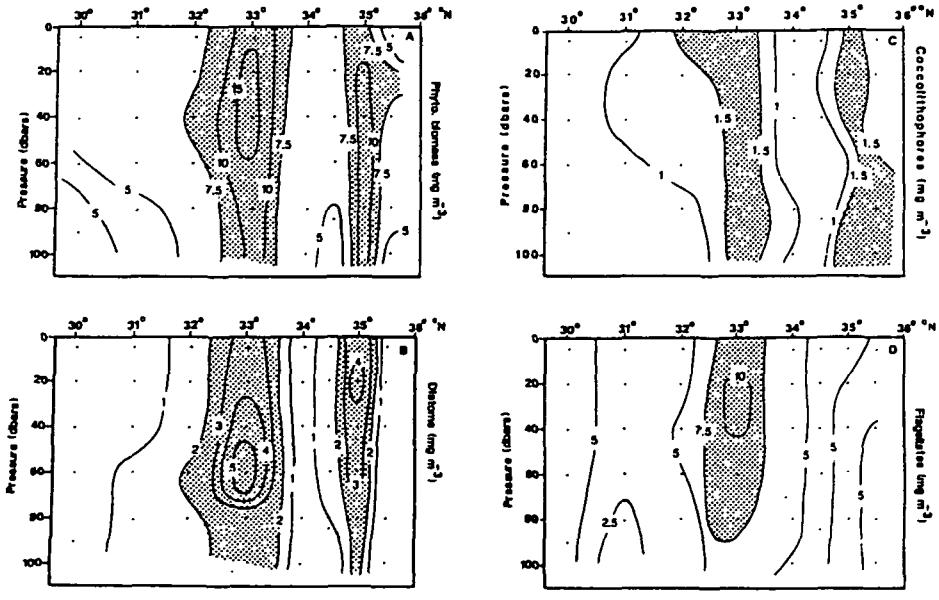

Fig. 6. Section (against latitude) of (A) estimated phytoplankton carbon biomass (mg C m^{-3}), (B) diatom carbon biomass (mg C m^{-3}), (C) coccolithophorid carbon biomass (mg C m^{-3}) and (D) flagellate carbon biomass (mg C m^{-3}) along the 26°W meridian. Stippled areas indicate total phytoplankton, diatom, coccolithophorid and flagellate carbon biomasses >7.5, 2, 1.5 and 7.5 mg C m^{-3}, respectively.

the AC (see Table I). The coccolithophorid distribution followed the same pattern as diatoms and flagellates, although the latitudinal abundance gradients were much less marked. Their relative contribution to total phytoplankton biomass was higher at 34°30′N and at the southern edge of the section, where they accounted for 15–20% of the total phytoplankton biomass (Table I). Phytoplankton represented on average ~12–16% of POC, except at 33°N where this value rose to 39% (Figures 4A and 6B, and Table I). Previous studies in the subtropical gyres indicate that phytoplankton biomass accounts for no more than 30% of the seston in oligotrophic surface waters (Sharp *et al.*, 1980).

Carbon incorporation patterns and turnover times

Rates of integrated primary production were highest at the STF–AC region coinciding with the highest concentrations of chlorophyll *a* (Figure 4, Table I), i.e. up to 85 mg C m^{-2} h^{-1} in the upper mixed layer at the AC. The lowest rates were measured in the southern part of the transect (30°N), where carbon incorporation rates did not exceed 30 mg C m^{-2} h^{-1}.

The percentages of ^{14}C incorporated into proteins, polysaccharides, lipids and LMWM are shown in Figure 7A, B, C and D, respectively. The relative amount of carbon incorporated into proteins ranged from 30–35% south of 32°N and in surface layers of the whole 26°W section to ~40–45% in subsurface layers over the rest of the transect. Incorporation into polysaccharides contributed to <14%

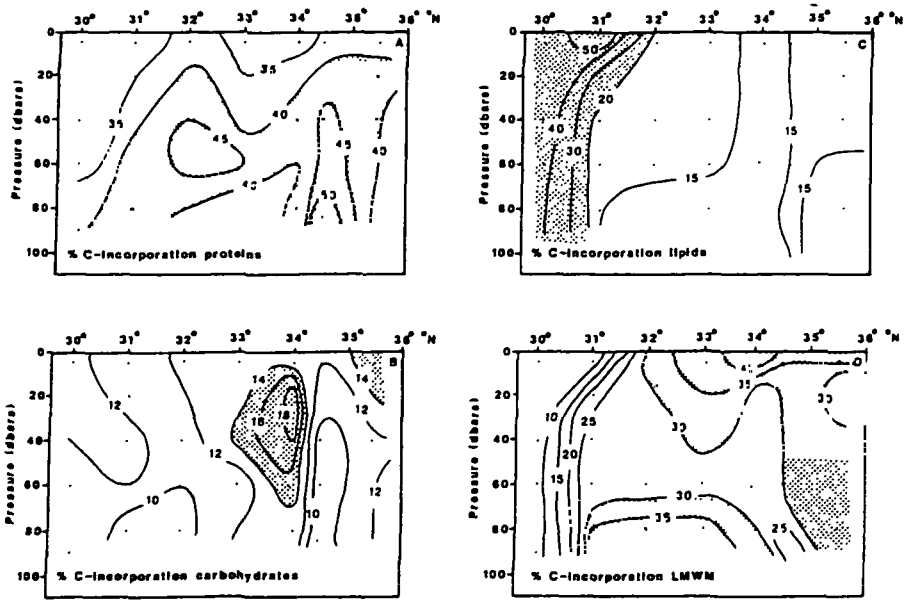

Fig. 7. Section (against latitude) of the percentage of carbon incorporated photosynthetically into (A) proteins, (B) polysaccharides, (C) lipids and (D) low-molecular-weight metabolites (LMWM) along the 26°W meridian. Stippled areas indicate relative incorporation rates into proteins, polysaccharides, lipids and LMWM >40, 14, 20 and 30% respectively.

in most of the samples. However, a relatively high carbon incorporation rate into this metabolic pool characterized the phytoplankton assemblages at the AC (34°N). Very high relative synthesis rates of lipids (>30–40% of the total carbon incorporation) were typical of the southern edge of the transect. Lower values, close to 17%, were measured at northern stations. In general, the distribution of the percentage of carbon incorporated into LMWM followed an opposite trend to that into lipids, with relative incorporation rates increasing towards the northern part of the transect.

Turnover times for proteins and carbohydrates were calculated for the whole 26°W section from the specific production rates (SPR) estimated for each pool, as derived from the ^{14}C labelling patterns and the measured chemical composition of the particulate matter (Figure 8). Turnover times for proteins and carbohydrates were comparable in magnitude and followed a similar distribution pattern. The lowest turnover times for both pools, between 3 and 5 days, were determined at the central part of the section, between 32 and 34°N, and related to the STF–AC physical structure. These maximum turnover times correspond to specific synthesis rates ranging from ~0.14 to 0.23 day^{-1}. Turnover times increased progressively towards the edges of the section and also

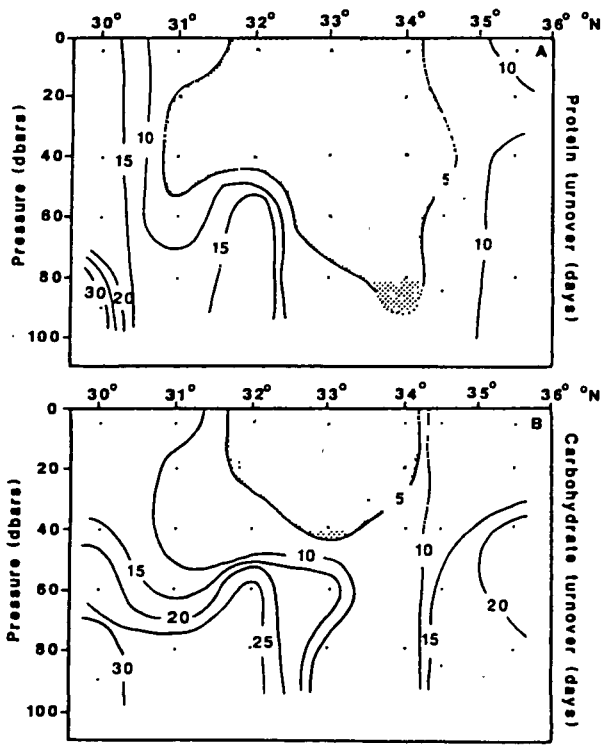

Fig. 8. Section (against latitude) of the turnover time (days) of (A) total particulate proteins and (B) total particulate carbohydrates, along the 26°W meridian. Stippled areas indicate protein and carbohydrate turnover times <5 days.

with depth. Values of up to 1 month were calculated for subsurface layers at 30°N.

Discussion

Physical structure and phytoplankton biomass

Several studies dealing with phytoplankton distribution (Kahru *et al.*, 1991), and/or primary production (Platt *et al.*, 1983; Fasham *et al.*, 1985; Jochem and Zeitzschel, 1993), have been carried out in the eastern North Atlantic subtropical region during spring–summer, when oligotrophic conditions prevailed in the upper mixed layer. These studies have shown the existence of a distinct subsurface chlorophyll maximum as the main biological feature (Fasham *et al.*, 1985), and concluded that small-sized cells are the main contributors to the primary production in this region (Platt *et al.*, 1983). Although differences in phytoplankton abundance (Kahru *et al.*, 1991) and photosynthetic efficiency (Fasham *et al.*, 1985) have been reported between water masses at either side of the STF, none of these studies have shown any enhancement of chlorophyll *a* in the STF/AC. In this connection, Fasham *et al.* (1985) stated that there is little evidence to suggest that chlorophyll *a* in the front was higher than in the adjacent water masses.

This survey was undertaken prior to the development of the spring diatom bloom, when inorganic nutrients were still abundant in the upper water column (Table I) and the deep chlorophyll *a* maximum was not yet developed. Concentrations of chlorophyll *a* were relatively high in the upper 100 m along the STF region (Figures 2, 4 and 6). Accumulation of phytoplankton cells at the STF has been interpreted in terms of increased residence time of these populations in the upper water column due to increased stability (Sverdrup, 1953) resulting from the surface outcrop of the front (Fernández *et al.*, 1994a). A further mechanism likely to be responsible for phytoplankton accumulation is the motility of flagellated cells, which are predominant at 33°N, and accumulate at frontal interfaces due to the interactive effect of swimming behaviour and vertical circulation (Franks, 1992).

Carbon incorporation patterns

The measurement of the rate of carbon incorporation into proteins is one of the few techniques available which enables phytoplankton growth rates to be estimated in those natural environments where the biomass of phytoplankton constitutes only a small fraction of the seston. In this regard, Di Tullio and Laws (1983) reported that cultures of phytoplankton growing at their maximum growth rates showed ratios of protein to total organic carbon in photosynthetic products of 39–55% with an average of 46%. Furthermore, Di Tullio and Laws (1986), studying five species of phytoplankton, found a linear relationship between the relative growth rate and the percentage of carbon incorporated into protein. If these conclusions are applied to our results, it can be concluded that the phytoplankton assemblages present in the subtropical North Atlantic during

winter–spring 1992 were growing close to their maximum rate. The same has been reported for oligotrophic communities in subtropical gyres (Laws, 1991). Similar results were also reported by Hama (1992) who, using an approach based on the incorporation of ^{13}C by phytoplankton, found a relative synthesis of protein of up to 58% in a warm-core ring associated with the Kuroshio current. The high amounts of carbon flowing into proteins detected in our study may also reflect the dominance of a small-sized phytoplankton community, as small phytoplankters are known to incorporate more carbon into proteins as compared to larger cells (Taguchi and Laws, 1987; Howard and Joint, 1989). This observation is consistent with the observed increase in maximum growth rate with decreasing cellular size (see Chisholm, 1992). The relative synthesis of proteins increased at mid depths (~60 m), largely at the expense of LMWM (Figure 7). The enhancing effect of low irradiance upon the relative incorporation of carbon into proteins has been reported both for cultures and natural phytoplankton populations (Morris and Skea, 1978; Morris *et al.*, 1981). The same pattern was observed in the chemical composition of the particulate matter (Figure 5).

In general, ^{14}C incorporation into polysaccharides in the subtropical region was low—10–20% of the total incorporation—as could be expected in a high-nutrient environment. It is notable that the highest relative incorporation rates into this pool were measured in the AC region, where a phytoplankton community of cells <2 μm accounted for the chlorophyll maximum observed in this water body. Although the species composition of this assemblage is unknown, it may be of relevance that similar values (18–20%) for the incorporation of ^{14}C into polysaccharides have been reported for cultures of cyanobacteria (Cuhel and Waterbury, 1984; Howard and Joint, 1989) and also in naturally occurring picoplankton (Howard and Joint, 1989).

One of the most unexpected results was the high percentages (>30–40%) of carbon incorporation into lipids in the southern part of the 26°W section (Figure 7). A corresponding pattern was observed for the fraction of lipid carbon to total organic carbon in the particulate matter (Figure 5), with values between 35 and 60% at 30°N. This is also reflected in the particulate C/N ratios, which show higher values at southern latitudes (Figure 4). Typical values of the percentage of carbon incorporated into lipids reported in the literature varied within the range 5–30%, with an average of 15–20% [see Wainman and Lean (1992) and references therein]. An exception to this general pattern was found in Antarctic phytoplankton, for which percentages may be as high as 35–80% in low light and temperature (Smith and Morris, 1980). Other authors, however, have failed to reproduce such high values, whether in the Arctic (Li and Platt, 1982) or the Antarctic (Palmisano *et al.*, 1988).

It has been assumed that increased lipid synthesis is associated with slow growth (Shifrin and Chisholm, 1981; Taguchi *et al.*, 1987). In our case, however, irradiance and nutrient concentrations were sufficient for rapid phytoplankton growth, and changes in the relative synthesis of lipids were not light dependent, as can be deduced from its homogeneous vertical distribution. In addition, the percentage of carbon incorporated into proteins suggested that phytoplankton

populations at 30°N were growing actively. The explanation for the high rates of lipid synthesis measured in this region might be sought in terms of differences in species composition between northern and southern latitudes along the 26°W section. Flagellates, most of them prymnesiophytes, and coccolithophorids, made up >98% of the phytoplankton biomass at 30°N, whereas diatoms contributed a significant proportion of the phytoplankton biomass at northern latitudes, with the exception of the AC (Figure 6, Table I). Madariaga (1992), studying the fate of recently incorporated carbon by six phytoplankton species belonging to different taxonomic classes, found high relative rates of lipid synthesis (up to 45%) during exponential and stationary phases of growth in the prymnesiophyte *Pavlova lutheri*. Similar values have recently been measured in cultured and naturally occurring blooms of the coccolithophorid *Emiliania huxleyi* (Fernández *et al.*, 1994b). These results illustrate how variations in intracellular photosynthetic carbon flows, derived from latitudinal changes in phytoplankton species composition, may account for the differences observed in the carbon to nitrogen ratio of particulate matter in the upper mixed layer.

Microplankton turnover times

The concomitant determination of both the incorporation of $^{14}HCO_3$ into the specific fractions under study and the concentration of the corresponding biochemical pools make it possible, on the basis of isotopic incorporation measurements, to estimate the net synthesis rate of the various types of compounds. The turnover times estimated in this study, however, refer to the standing stocks of each biochemical pool in the particulate fraction, and therefore are not restricted only to phytoplankton. The results presented above in fact indicate that a large proportion of the POC was not part of phytoplankton biomass. Thus, turnover times for phytoplankton alone may be seriously overestimated, so that these data must be interpreted in a wider microplankton ecological perspective rather than from a phytoplankton physiological viewpoint.

The few studies reporting SPRs of proteins and carbohydrates in natural assemblages of phytoplankton appear to lie inside a narrow band of values in general agreement with the maximum SPRs measured in the STF region by us (0.14–0.23 day^{-1}). This, for example, pertains to the data by Morris *et al.* (1981) for the tropical western Atlantic. Moreover, Hama (1992), using the ^{13}C incorporation technique, calculated protein SPR of ~0.12–0.24 day^{-1} in a warm-core ring and Hama *et al.* (1990) found values varying from <0.05 to ~0.2 day^{-1} during an annual cycle in a freshwater environment. A similar range of values has been reported by Hama *et al.* (1988) for diatom blooms occurring in experimental enclosures. Nevertheless, they estimated much higher rates (up to 0.063 h^{-1}) during the early exponential phase of these blooms under nutrient-rich, high-light conditions.

The similar turnover times estimated for both of the biochemical pools suggest balanced growth (*sensu* Shuter, 1979) of the microplankton community, at least as far as these cellular constituents are concerned, and over time scales of 24 h.

This is in agreement with previous observations from recently upwelled nutrient-rich waters, but not from aged or non-upwelled waters (Hama, 1988) or in nutrient-depleted waters off Japan (Hama, 1992). It must be remembered, however, that these turnover times represent both the photosynthetic and heterotrophic component of the microplanktonic system.

The following conclusions can be drawn from the results obtained in this study. (i) The phytoplankton populations characteristic of the subtropical North Atlantic prior to the spring diatom bloom were growing at a rate close to their maximum nutrient-saturated growth rate. (ii) Latitudinal changes in phytoplankton species composition may have accounted for most of the observed changes in ^{14}C labelling patterns and may also have been partially responsible for the geographical variation in the composition of the particulate organic matter. (iii) Turnover times for protein and carbohydrate were relatively low (<5 days) at the STF region, suggesting that microplankton growth was balanced over the time scales considered in this study.

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