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Variability of chlorophyll and primary production in the Eastern North Atlantic Subtropical Gyre: potential factors affecting phytoplankton activity

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Abstract

Size-fractionated chlorophyll-*a* and carbon incorporation rates were determined on a series of 13 cruises carried out from 1992 to 2001with the aim of investigating the patterns and causes of variability in phytoplankton chlorophyll and production in the Eastern North Atlantic Subtropical Gyral Province (NASE). Averaged ($\pm$SE) integrated chlorophyll-*a* concentration and primary production rate were $17 \pm 1\,mg\,m^{-2}$ and $253 \pm 22\,mg\,C\,m^{-2}\,d^{-1}$. Small-sized cells ($<2\,\mu m$) formed the bulk of phytoplankton biomass (71%) and accounted for 54% of total primary production. A clear latitudinal gradient in these variables was not detected. By contrast, large seasonal variability was detected in terms of primary production, although integrated phytoplankton biomass, as estimated from chlorophyll-*a* concentration, remained rather constant and did not display significant changes with time. Variability in primary production (PP) was related mainly to variability in surface temperature and surface chlorophyll-*a* concentration. The control exerted by surface temperature was related to nutrient availability. By contrary, euphotic-zone depth, depth of maximum concentration of chlorophyll-*a* and integrated chlorophyll-*a* did not contribute significantly to the high variability in primary production observed in this oligotrophic region.

Keywords: Phytoplankton; Chlorophyll-*a*; Primary production; Latitudinal and seasonal variability; Eastern North Atlantic Subtropical Gyre

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1. Introduction

Determination of time-varying plankton productivity in the world ocean has been one of the main goals of biological oceanography from its beginning in the mid-19th century (Barber and Hilting, 2002). The oligotrophic gyres of the three major oceans account for about a quarter of global primary production (Longhurst, 1995) and contribute up to 50% of global carbon export (Emerson et al., 1997). However, after more than 50 years of measurements, the magnitude of primary production in the oligotrophic ocean gyres is still a matter of controversy. A major problem lies in the low number of observations and the poor coverage of both temporal and spatial scales. Most investigations of phytoplankton variability in tropical and subtropical seas have covered either the temporal or the spatial scale (e.g. Menzel and Ryther, 1960; Bienfang et al., 1984; Frazel and Berberian, 1990; Malone et al., 1993; Karl et al., 1996; Michaels and Knap, 1996; Goerike and Welschmeyer, 1998; among others). However, both spatial and temporal variability must be addressed concurrently in order to gain an adequate understanding of plankton distribution and activity, and of the functioning of pelagic ecosystems.

Because of the stability of the physical environment, tropical and subtropical regions have been traditionally regarded as the least variable oceanic regions in terms of biological activity (Bienfang et al., 1984) as well as the least productive. Accordingly, phytoplankton biomass and primary production would remain nearly constant over both spatial and temporal scales. By contrast, a more dynamic vision of the phytoplankton physiological state at the Subtropical Gyres has emerged over the past two decades (Platt and Harrison, 1985; Goldman, 1988, 1993), and as a consequence the investigations in these oligotrophic regions have received a considerable impulse. Several works have shown a certain degree of spatial or temporal variability in primary productivity (e.g. Bienfang et al., 1984; Marañón and Holligan, 1999; Harrison et al., 2001; Marañón et al., 2000, 2003) and, to a lesser extent, chlorophyll-*a* concentration (e.g. Goerike and Welschmeyer, 1998). However, the patterns and mechanisms of variability characteristic of these regions still remain poorly understood. Time-series stations in the Sargasso Sea off Bermuda (BATS) and in the subtropical NE-Pacific Ocean (HOTS) have allowed a good description of the temporal variability over both seasonal and interannual scales (Karl and Lukas, 1996; Michaels and Knap, 1996). By contrast, the characterisation of temporal variability in the subtropical NE-Atlantic Ocean and in southern regions of both the Pacific and Atlantic Oceans has been rather limited. Large-scale surveys, aiming at the adequate description of spatial variability are scarce. Some ocean basin-scale studies have revealed a considerable meridional and zonal variability in the N central Pacific Subtropical Gyre (Hayward, 1987) and in the North and South Atlantic (e.g. Frazel and Berberian, 1990; Strass and Woods, 1991; Buck et al., 1996; Vinogradov et al., 1999; Agustí et al., 2001; Harrison et al., 2001; Marañón et al., 2003). In addition to the rather limited number of observations in subtropical regions, some recent studies confirm that traditional sampling strategies tend to underestimate episodic increments of primary production associated with hydrodynamical singularities occurring at relatively short temporal or spatial scales (McGillicuddy et al., 1998; Oschlies and Garçon, 1998; Garçon et al., 2001) or with the atmospheric deposition of iron and nitrogen (Paerl, 1985; Young et al., 1991; Baker et al., 2003). Karl et al. (2003) suggested that under-sampled episodic events of higher primary production would have a profound effect on the estimation of the metabolic balance of the sea, which demands a very careful interpretation of the available information and also, in the near future, an intensive data collection effort (Lewis, 2002).

During the past 12 years intensive investigations carried out by our group have enabled the collection of a valuable database of phytoplankton chlorophyll-*a* and production in the Eastern North Atlantic Subtropical Gyral province (NASE) across different seasons of the year. This province represents the poleward part of the North Atlantic anticyclonic gyre, which lies under the influence of the westerly winds which are usually weaker than

in the provinces further to the north (Sathyendranath et al., 1995; Longhurst, 1998). Considering the large impact that oligotrophic gyral provinces have on the global cycles, our main objective in this work was to investigate the patterns and causes of both latitudinal and seasonal variability in phytoplankton chlorophyll-*a* and productivity in the NASE province.

2. Methods

We sampled 82 oligotrophic sites in the eastern North Atlantic Subtropical Gyral (NASE) biogeochemical province (25–44°N) during 13 cruises (CD66, CD83, AMT-1, 2, 3, 4, 5, 6 and 11, Azores-1, Azores-2, Pos273 and Circana-1) carried out from 1992 to 2001 (see Fig. 1 for station locations). The cruises CD66 and CD83 were conducted on board RRS Charles Darwin during March 1992 and December 1993, respectively. AMT cruises were carried out on board RRS James Clark Ross between September 1995 and October 2000. Azores-1 and Azores-2 cruises, on board BIO Hespérides, were carried out during July–August 1998 and April 1999, respectively.

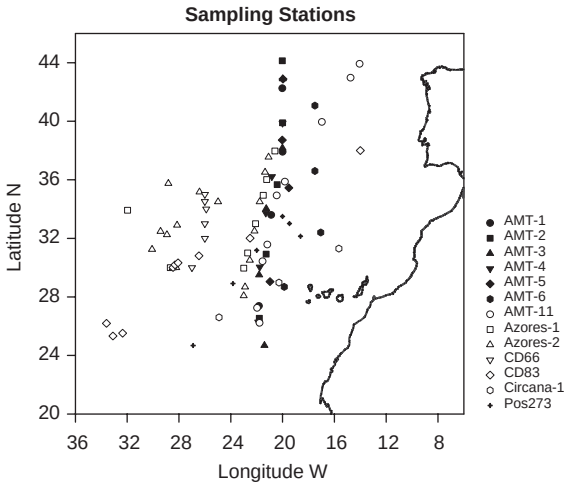

Fig. 1. Locations of sampling stations included in this study grouped by cruises. AMT-2, AMT-4, AMT-6, Azores-2 and Pos273 were conducted during spring; Azores-1, during summer; AMT-1, AMT-3, AMT-5, AMT-11 and Circana-1 during autumn; CD-66 and CD83 during winter.

Pos273 was conducted during April 2001 on board RV Poseidon, and, finally, Circana-1 was carried out on board BIO Hespérides, during October–November 2001.

Vertical profiles of temperature and salinity were conducted at each station with a CTD probe attached to a rosette sampler equipped with Niskin bottles. CTD temperature and salinity sensors were calibrated with digital reversing thermometers and water samples drawn for salinity determinations. Water sampling and handling techniques followed JGOFS protocols (http://www.uib.no/jgofs/Publications/Report_Series/).

During Azores-2 and AMT-11 cruises, dissolved inorganic nitrogen was determined with a Technicon segmented flow colorimetric auto-analyzer as described in Tréguer and Le Corre (1975)(Azores-2) and in Woodward (1994) (AMT-11).

Samples were collected for the determination of size-fractionated chlorophyll-*a* and primary production rates from 5 to 10 depths in the upper 200 m. In CD66 and AMT-1 only total determinations of chlorophyll-*a* and primary production rates were performed.

Total chlorophyll-*a* (chl-*a*) was measured fluorometrically after concentration of particulate matter by filtering 100–250 ml of seawater through glass fibre filters (Millipore APFF or Whatman GFF), which were immediately kept in 5–10 ml 90% acetone at −20 °C overnight. Size-fractionated chl-*a* was determined in the same way, but after filtering subsequently through 20, 2 and 0.2 μm polycarbonate filters. Actual chl-*a* concentration values, obtained fluorometrically on filtered samples, were used to calibrate the signal from the fluorometer attached to the CTD probe.

For the determination of primary production, four 75 ml acid-cleaned polycarbonate or Corning bottles (3 transparent and 1 dark bottle) were filled with seawater from each of five to seven depths corresponding to optical depths ranging from 100 to 0.1% of surface irradiance. Bottles were inoculated with 360–540 KBq (10–15 μCi) $NaH^{14}CO_3$ and then incubated for 6–24 h in an on-deck incubator covered with blue filters simulating the light field experienced by the cells at the original sampling depths. The bottles were placed in a flow-through incubator and maintained at sea-surface

temperature (SST) with sea surface water from the ship's continuous water supply. After the incubation period, samples were filtered at very low vacuum pressure (< 50 mm Hg) through the same type of filters described for chl-*a* determinations. Unincorporated dissolved inorganic carbon remaining on the filters was removed by exposure to fumes of concentrated HCl for 12 h. Radioactivity was determined by liquid scintillation counting either ashore (CD66, CD83, Azores-1 and Pos273) or on board (AMT cruises, Azores-2 and Circana-1). Quenching corrections were made with an external standard. Daily production rates were calculated from hourly rates taking into account the daylight period and assuming that dark respiratory losses amount to 20% of the carbon incorporation during the light period (Geider, 1992). Integrated total chl-*a* values (expressed as $mg\,m^{-2}$) were calculated down to the depth of 0.1% of the surface irradiance (photic zone). Primary production was always integrated down to 150 m and expressed as mg $C\,m^{-2}\,d^{-1}$. The relative contribution of picophytoplankton (phytoplankton $<2\,\mu m$) to total phytoplankton biomass and photosynthesis was expressed as percentages.

The Kruskal–Wallis (K–W) test was used in order to test for differences between 3 or more groups for a given variable. A non-parametric test was applied because of the non-normal distribution of most of the variables considered. The K–W test is a non-parametric equivalent to a one-way analysis of variance by ranks. It tests the null hypothesis that 3 or more groups all come from the same distribution. It uses the ranks of data and is therefore resistant to outliers. The Mann–Whitney significance test was applied *a posteriori* to analyse the differences between every pair of groups.

3. Results

3.1. Latitudinal and seasonal variability of thermohaline properties

The vertical distribution of temperature and salinity along a latitudinal section, centred around 20 °W, from ~20°N to ~44°N (corresponding to sections carried out during AMT cruises) is shown in Fig. 2. Because of the interannual variability observed in the thermohaline conditions along this section (see, e.g. Marañón et al., 2000), we have chosen two representative sections for the spring period and two for autumn conditions.

Upper layer temperature progressively decreased northwards with variations of about 5 °C along the section both in autumn (from 25 to 20 °C) and spring (from 22 to 17 °C). The northward sloping of the 16 to 18 °C isotherms and the 36.2 to 36.4 isohalines is related to the subtropical front (STF) boundary, which separates more saline Subtropical Water (STW) to the south and colder and fresher Eastern North Atlantic Central Water (ENACW) to the north. Specifically the location where the 16.2 isotherm and the 36.2 isohaline reach 150 m has been used as an indicator of the STFs position (Pérez et al., 2003).

The water column of the section was always stratified at the time the observations were conducted although vertical thermal and haline gradients varied seasonally. Higher surface temperatures and more intense water column stratification corresponded with the autumn period as a result of summer warming.

During the spring period some stratification can be observed as a consequence of the weak winter mixing characteristic of this province. The upper layer (about 40 m) was well mixed along all the sections. During spring 1998, upwelling of colder waters can be observed at the southern part of the section, associated with the Mauritania upwelling system. A similar, although less intense, situation was detected in spring 1997.

3.2. Latitudinal and seasonal variability in vertical distributions of phytoplankton chlorophyll and production

In order to analyse seasonal variability of phytoplankton biomass and primary production rates, the 82 stations sampled were grouped into four sampling periods: spring, summer, autumn and winter. In addition, because of the large spatial extent of the frontal signature in the Azores Current system, all the observations included in

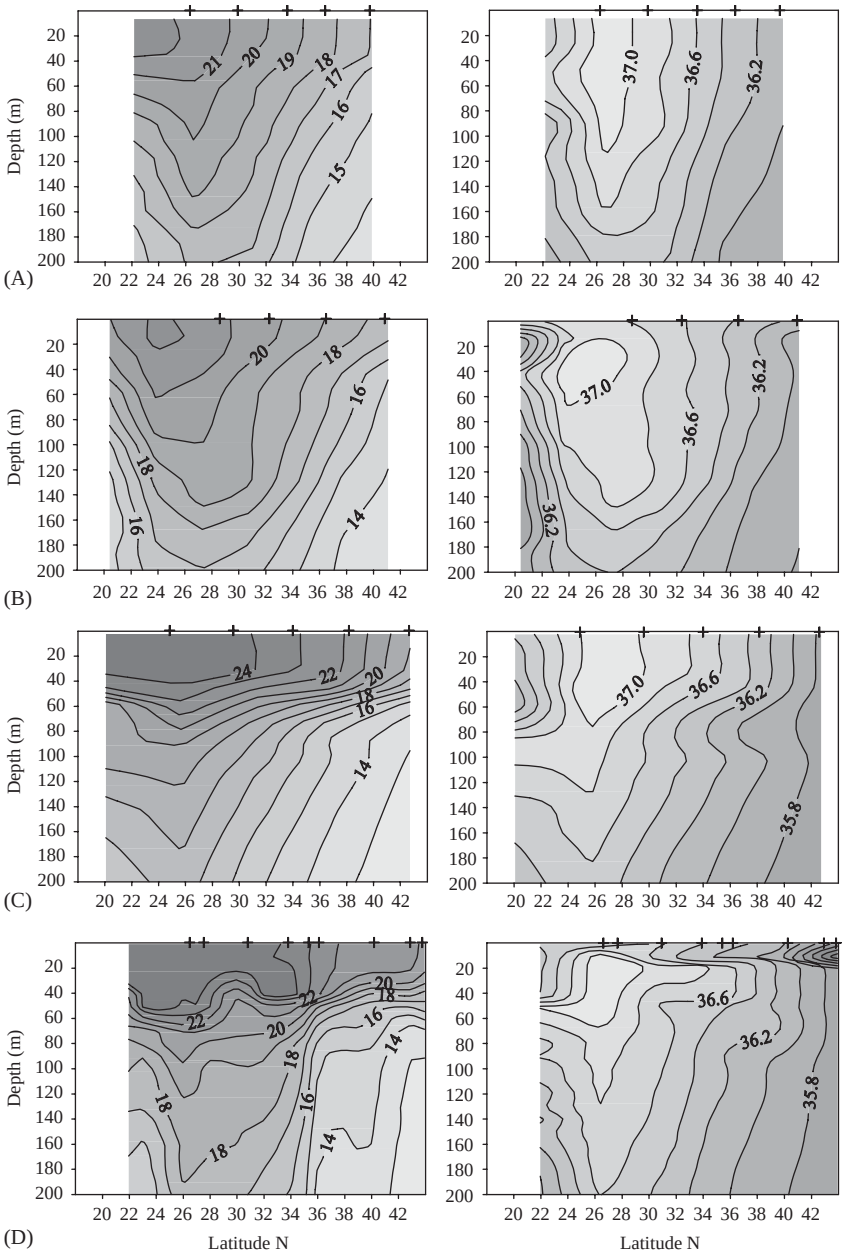

Fig. 2. Latitudinal distributions of temperature ((°C, left panels) and salinity (right panels) along transects centred at 20° W during: (A) spring 1997, AMT-4; (B) Spring 1998, AMT-6; (C) autumn 1996, AMT-3; and (D) autumn 2000, AMT-11. Positions of the stations sampled within the North Atlantic Subtropical Gyral province (NASE) are marked on the upper axis.

the present investigation were grouped into three zones determined by their position in relation to the STF: temperate, transition and subtropical zones. The transition zone was defined as the region between 32°N and 36°N, on the basis of the location of the front (Fernández and Pingree, 1996; Pérez et al., 2003; Mouriño et al., 2004). The temperate region lies to the north of the front,

whereas the subtropical region is located to the south. The defined transition zone would be characterised by maxima in eddy kinetic energy, as compared with the temperate and subtropical zones (Garçon et al., 2001; Mouriño et al., 2003).

In Fig. 3 we represented the vertical profiles of temperature, chl-*a*, contribution of picophytoplankton (phytoplankton $<2\,\mu m$) to total chl-*a*, primary production and contribution of picophytoplankton to total primary production grouped into the four seasons and the three zones previously mentioned. With the aim of synthesising and providing a better interpretation of the available information, we calculated averaged seasonal profiles for each zone.

The variability in the vertical distribution of temperature reflected the seasonal pattern. The stability of the water column increases from spring to summer, when the mixed layer is shallowest (10–30 m). From autumn to winter, mixed layer depth deepens, favouring the entrainment of deep cold waters into the photic zone. As expected, the vertical profiles of temperature showed clear differences between the three zones (Fig. 3a). During spring the SST in the subtropical zone never fell below 19 °C, whereas in the temperate zone, temperatures $<17\,^{\circ}C$ were measured in the upper layer.

The vertical distribution of phytoplankton biomass, estimated from chlorophyll-*a* (chl-*a*) concentration , showed relatively low values over the whole region and was always <0.4 mg chl-$a\,m^{-3}$ (Fig. 3b). During spring, summer and autumn, the vertical profiles of chl-*a* clearly show the typical deep chl-*a* maximum (DCM) located between 80 and 120 m in the case of the subtropical and the transition zones, and slightly shallower (between 50 and 80 m) in the temperate zone. The maximum concentration of chl-*a* was found at the deepest level during summer (100–120 m), being shallowest during winter (20–40 m). Seasonal deepening of the DCM could be observed from winter to summer. Although the highest surface concentration of chl-*a* was found in the temperate zone, the concentration of chl-*a* at the DCM remained rather constant (between 0.2 and 0.3 mg chl-$a\,m^{-3}$). Seasonal variability in chl-*a* vertical distribution, although always relatively small, was more apparent in the temperate zone.

The vertical profiles of the contribution of picophytoplankton to total chl-*a* concentration, expressed as the percentage of chl-*a* in the size range 0.2–2 μm, were both seasonally (except in the temperate zone) and spatially variable, mainly in surface waters (Fig. 3c). Picophytoplankton contributed more than 60% to total chl-*a* at the DCM. This contribution ranged from $<40\%$ in the surface of the subtropical and transition zones during summer, to $>80\%$ throughout the water column in the subtropical zone during winter.

The vertical distribution of primary production rates presented a considerable seasonal variability (Fig. 3d). Rates of carbon incorporation were higher during spring and winter in the three zones, coinciding with deeper mixed layer depths (Fig. 3a). The lowest rates were measured during summer, when stratification of the water column was highest. The highest rates were measured during winter in the subtropical and transition zone, with values $>0.5\,mg\,C\,m^{-3}\,h^{-1}$ in the upper 60 m of the water column.

The contribution of picophytoplankton to total primary production generally increased with depth, and percentages of about 20% were found in the surface during the summer (Fig. 3e). In contrast, the vertical profiles of the contribution of small cells to total chl-*a* did not show this clear increasing trend with depth, except in the subtropical and transition zones during the summer (Fig. 3c). A relatively high degree of seasonal variability could be observed in the three zones. In the subtropical zone, picophytoplankton contributed more than 75% of total PP and total biomass during winter throughout the water column. It is worth pointing out that the contribution of picophytoplankton to total chl-*a* was more important (about 70%) than the contribution of this size class to total carbon incorporation by phytoplankton (about 50%). This mismatch between the contribution of small phytoplankton to biomass or to PP was more evident in surface waters (0–50 m) during summer and in the temperate zone.

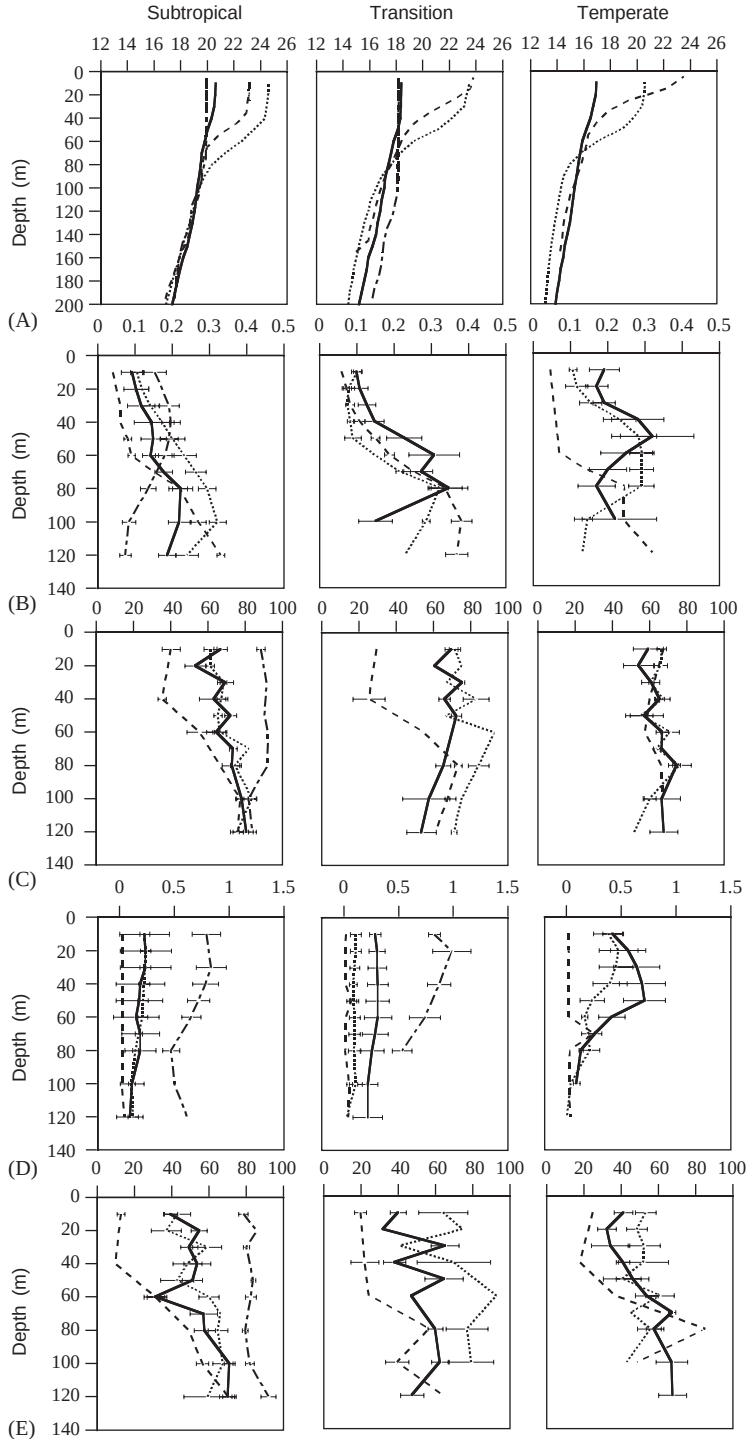

Fig. 3. Averaged (± SE) vertical profiles of (A) Temperature, °C; (B) chlorophyll-*a* concentration, mg chl-*a* m^{-3}; (C) contribution of <2 μm phytoplankton to total chl-*a*, %; (D) rates of primary production, mg C m^{-3} h^{-1}; and (E) contribution of <2 μm phytoplankton to total primary production, %. Solid line, spring; dashed line, summer; dotted line, autumn; and dash-dotted line, winter.

3.3. Latitudinal and seasonal variability of depth-integrated phytoplankton biomass and production

For each of the 13 cruises conducted in the NASE region, we analysed the latitudinal (25–44°N) variability of the depth-integrated biological variables : chl-*a* concentration, primary production, and contribution of picophytoplankton to total chl-*a* concentration and total primary production (Fig. 4).

Depth-integrated total chl-*a* ranged from 7 to 31 mg m^{-2} and depth-integrated primary production from 14 to 800 mg C m^{-2} d^{-1}. The variation coefficients were 34% and 77%, respectively. These results illustrate the differential degree of variability of phytoplankton biomass and photosynthetically incorporated carbon found in our data set.

A clear latitudinal trend in depth-integrated chl-*a* and primary production (PP) values was not detected. High values of PP (>400 mg C m^{-2} d^{-1}) were measured in both the southern and northern edge of the province, as well as in the subtropical frontal boundary (32–36°N). The highest values (>650 mg C m^{-2} d^{-1}) were found at two stations sampled during late winter (CD66), located in the vicinity of the STF boundary and in temperate waters during spring (AMT-2). Enhanced depth-integrated primary production rates at stations located in the STF boundary were not evident except for CD66, conducted during winter, and Azores-1, during summer, although in Azores-1 the magnitude of such enhancement was lower than in CD66. A large degree of intercruise variability was observed, even when those cruises conducted during the same sampling period were

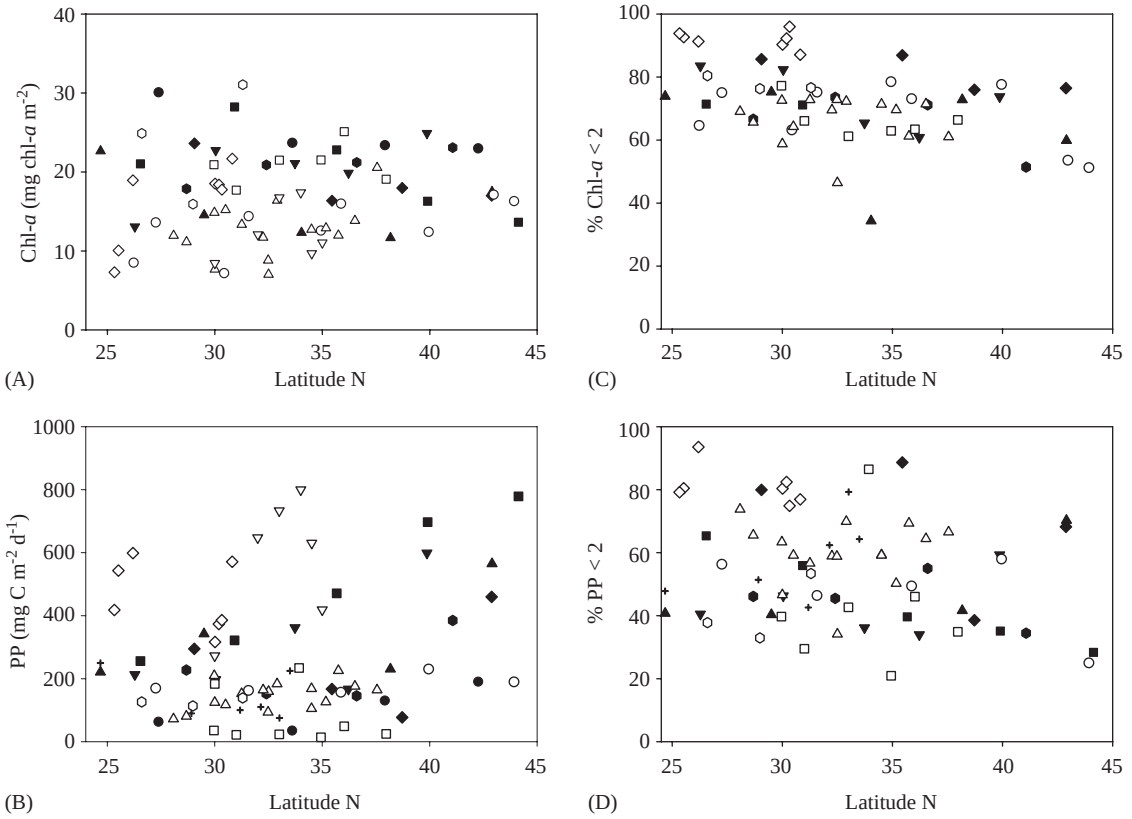

Fig. 4. Latitudinal distribution of depth-integrated (A) chlorophyll-*a* concentration, mg chl-*a* m^{-2}; (B) rates of primary production, mg C m^{-2} d^{-1}; (C) contribution of <2 μm phytoplankton to total integrated chl-*a*, %; and (D) contribution of <2 μm phytoplankton to total integrated primary production, %. Symbols as in Fig. 1.

considered (e.g. AMT-1, AMT-3, AMT-5, AMT-11; and AMT-2, AMT-4), a fact likely related to interannual variability. We cannot discard the possibility, however, that this large intercruise variability at least partially derives from the differential effect of mesoscale activity on phytoplankton biomas and production.

A slight decrease of the relative contribution of picoplankton to total phytoplankton biomass was observed northwards, from about 80% in the south to around 60% in the north (Fig. 4c). This trend is less evident in the case of the relative contribution of picoplankton to primary production, which showed a higher variability among cruises (Fig. 4d). As already observed in the vertical profiles (Fig. 3), the contribution of picophytoplankton to total integrated biomass was, on average, higher and less variable than its contribution to total integrated PP.

We further conducted a statistical analysis in order to assess the significance of the latitudinal/seasonal variability of the averaged values of the biological properties considered in this study grouped by season and zone (Table 1). All the variables analysed showed statistically significant seasonal variability, except depth-integrated chl-*a* (Table 2). Surface chl-*a* concentration, depth-integrated PP, and the contribution of picophytoplankton to both biomass and production showed significantly higher values in winter and lower values in summer (Tables 2 and 3). Despite the statistical significance, it is important to bear in mind that the number of observations conducted is not equal for all the categories, and specifically, that the observations for summer are all derived

Table 1
Averaged values (±SE) of surface chlorophyll-*a* (chl-*a*), mg m^{-3}; depth-integrated chl-*a*, mg m^{-2}; depth-integrated primary production, mg C m^{-2} d^{-1}; and contribution of picophytoplankton to both chl-*a* and PP, %, grouped into regions and seasons

Season	Property	Subtropical ($n=43$)	Transition ($n=21$)	Temperate ($n=18$)	NASE ($n=82$)
Spring ($n=36$)	Surface chl-*a*	0.05±0.01	0.06±0.02	0.16±0.04	*0.09±0.02*
	Integrated chl-*a*	15±1	14±3	19±1	*16±1*
	Integrated PP	164±15	220±52	389±88	*226±28*
	% chl-*a* <2 μm	70±2	65±2	65±3	*68±2*
	% PP <2 μm	55±2	57±6	47±5	*53±2*
Summer ($n=8$)	Surface chl-*a*	0.05±0.01	0.06±0.00	0.05	*0.05±0.00*
	Integrated chl-*a*	19±1	23±1	19	*21±1*
	Integrated PP	80±42	80±45	25	*73±28*
	% chl-*a* <2 μm	72±4	63±1	66	*66±2*
	% PP <2 μm	43±7	49±11	35	*43±7*
Autumn ($n=25$)	Surface chl-*a*	0.07±0.01	0.08±0.01	0.10±0.01	*0.08±0.01*
	Integrated chl-*a*	19±2	16±2	17±1	*18±1*
	Integrated PP	181±28	120±35	259±55	*203±28*
	% chl-*a* <2 μm	75±2	68±10	67±4	*71±3*
	% PP <2 μm	45±3	69±14	50±7	*50±4*
Winter ($n=13$)	Surface chl-*a*	0.16±0.02	—	—	*0.16±0.02*
	Integrated chl-*a*	15±2	13±2	—	*14±1*
	Integrated PP	459±40	616±90	—	*516±44*
	% chl-*a* <2 μm	92±1	—	—	*92±1*
	% PP <2 μm	81±2	—	—	*81±2*
Global ($n=82$)	Surface chl-*a*	*0.08±0.01*	0.07±*0.01*	0.13±*0.02*	0.09±*0.01*
	Integrated chl-*a*	16±*1*	16±*1*	18±*1*	17±*1*
	Integrated PP	227±*20*	264±*54*	306±*51*	253±*22*
	% chl-*a* <*2 μm*	76±*2*	65±*3*	66±*2*	71±*2*
	% PP <2 μm	56±*2*	57±*5*	48±*4*	54±*2*

Table 2
Kruskal–Wallis test for the variables in Table 1

Variable	Season	Region
Surface chl-*a*	$^{**}n = 65$	$^{**}n = 65$
Integrated chl-*a*	n.s. $n = 74$	n.s.$n = 74$
Integrated PP	$^{***}n = 77$	n.s.$n = 77$
% chl-*a* $<2\,\mu m$	$^{***}n = 66$	$^{**}n = 66$
% PP $<2\,\mu m$	$^{***}n = 70$	n.s.$n = 70$

Levels of significance: n.s., not significant; $^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$.

Table 3
Mann Whitney significance tests between seasons in terms of: PP, daily depth-integrated primary production; chl-*a*, surface chlorophyll-*a*; % PP, contribution of picophytoplankton to total integrated PP; and % chl-*a*, contribution of picophytoplankton to total depth-integrated chlorophyll-*a*

		Spring	Summer	Autumn	Winter
Spring	PP		**	n.s.	***
	chl-*a*		n.s.	n.s.	*
	% PP		n.s.	n.s.	***
	% chl-*a*		n.s.	*	***
Summer	PP	<		**	***
	chl-*a*	=		*	**
	% PP	=		n.s.	*
	% chl-*a*	=		n.s.	**
Autumn	PP	=	>		***
	chl-*a*	=	>		**
	% PP	=	=		***
	% chl-*a*	>	=		***
Winter	PP	>	>	>	
	chl-*a*	>	>	>	
	% PP	>	>	>	
	% chl-*a*	>	>	>	

Upper right symbols represent the level of significance: (n.s.), not significant; $^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$.
Lower left symbols compare seasons in first column with seasons in first row.

from the same cruise. Significant differences were not observed between autumn and spring, except in terms of the contribution of picophytoplankton to total integrated chlorophyll-*a*, which was higher during autumn. Only surface chlorophyll-*a* and picophytoplankton contribution to total integrated chl-*a* differed statistically by region (Table 2). Surface chlorophyll-*a* showed maximum values

Table 4
Mann–Whitney significance tests between regions in terms of: chl-*a*, surface chlorophyll-*a*; and % chl-*a*, contribution of picophytoplankton to total depth-integrated chlorophyll-*a*

		Subtropical	Transition	Temperate
Subtropical	chl-*a*		n.s.	**
	% chl-*a*		**	*
Transition	chl-*a*	=		**
	% chl-*a*	<		n.s.
Temperate	chl-*a*	>	>	
	% chl-*a*	<	=	

Upper right symbols represent the level of significance: (n.s.), not significant; $^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$.
Lower left symbols compare regions in first column with regions in first row.

in the temperate zone and minimum values in the subtropical and transition zones; by contrast, the contribution of small phytoplankton to total integrated chlorophyll-*a* was higher in the subtropical zone than in the temperate and in the transition zones (Table 4).

3.4. Relationship between physical and biological variables

To investigate which key factors drive the observed seasonal changes in PP we first analysed the relationship between physicochemical (surface temperature, stability, mixed layer depth, 1% irradiance depth, depth of nitracline, depth of DCM) and biological (surface chl-*a*, integrated chl-*a*, and contribution of picophytoplankton to total integrated chl-*a* and PP) variables and depth-integrated PP. The temperature gradient between 10 and 150 m was used as a proxy of the vertical stability of the water column. The mixed layer depth was estimated as the depth where the gradient of temperature was $>0.5\,^{\circ}C\,m^{-1}$. The depth of the nitracline is defined as the depth where the concentration of nitrate reaches $>0.5\,\mu M$. The correlation matrix between these variables and PP is shown in Tables 5 and 6. All the variables that did not comply the assumption of normality where log transformed before the statistical analysis. Depth-integrated PP was

Table 5
Correlation matrix for log PP (logarithm of daily depth-integrated PP), and physicochemical variables

Variable	Log PP	stability	ML	1% I	Nitracline	DCM	SST
log PP	1.000	−0.427	0.085	−0.323	−0.449	−0.461	−0.549
stability	**	1.000	−0.217	−0.104	−0.062	0.171	0.709
ML	n.s.	n.s.	1.000	0.015	−0.115	−0.168	−0.614
1% I	n.s.	n.s.	n.s.	1.000	0.446	0.489	0.295
Nitracline	**	n.s	n.s.	**	1.000	0.677	0.426
DCM	**	n.s	n.s.	**	***	1.000	0.632
SST	***	***	n.s.	n.s.	*	***	1.000

ML, depth of mixed layer; SST, sea surface temperature; 1% I, depth reached by 1% of surface irradiance; DCM, deep chlorophyll maximum depth.
Upper right values show correlation coefficients and the lower left symbols represent the level of significance: (n.s.), not significant; $^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$, $N=35$.

Table 6
Correlation matrix for log PP (logarithm of daily depth-integrated PP), and biological variables

Variable	log PP	log chl-*a*	int chl-*a*	log% chl-*a*	log% PP
log PP	1.000	0.424	−0.129	0.335	0.586
log chl-*a*	**	1.000	0.387	0.192	0.175
int chl-*a*	n.s.	**	1.000	−0.160	−0.257
log % chl-*a*	*	n.s.	n.s.	1.000	0.542
log % PP	***	n.s	n.s.	***	1.000

Chl-*a*, surface chlorophyll-*a*; int chl-*a*, depth-integrated chlorophyll-*a*; % chl-*a*, contribution of picophytoplankton to total chl-*a*; % PP, contribution of picophytoplankton to total PP.
Upper right values show correlation coefficients and the lower left symbols represent the level of significance: (n.s.), not significant; $^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$, $N=50$.

negatively correlated with stability, nitracline depth, surface temperature and depth of the DCM (Table 5). Surface temperature was positively correlated with water column stability, the depth of nitracline and the depth of DCM; but not with the mixed layer depth or the depth reached by 1% of surface irradiance. The depth of DCM was positively correlated with the depth of nitracline and the depth of 1% irradiance (Table 5). The limited available incident photosynthetically active radiation (PAR) data precluded its inclusion in the correlation matrix. However, we calculated the correlation coefficient between the available incident PAR data and integrated PP, and a significant positive correlation was found between the two variables ($r=0.546$, $p=0.0094$, $n=21$). The statistical analysis also revealed a significant positive correlation between depth-integrated PP and surface chl-*a* concentration (Table 6). There was no correlation between depth-integrated PP and depth-integrated chl-*a*. The size-structure of the phytoplanktonic community, expressed as the relative contribution of picoplankton cells to phytoplankton biomass or production showed a significant positive correlation with primary production.

To illustrate the relationship between temperature, nutrients, irradiance levels and DCM depth we represented depth profiles of temperature, nitrate concentration and fluorescence due to chl-*a* along two latitudinal transects, centred at 20°W, conducted in spring and in autumn (Azores-2 and AMT-11 cruise) (Fig. 5). The photic zone, defined as the depth reached by 1% of the surface irradiance, is also indicated in the plots. A close relationship was observed between the depth of the

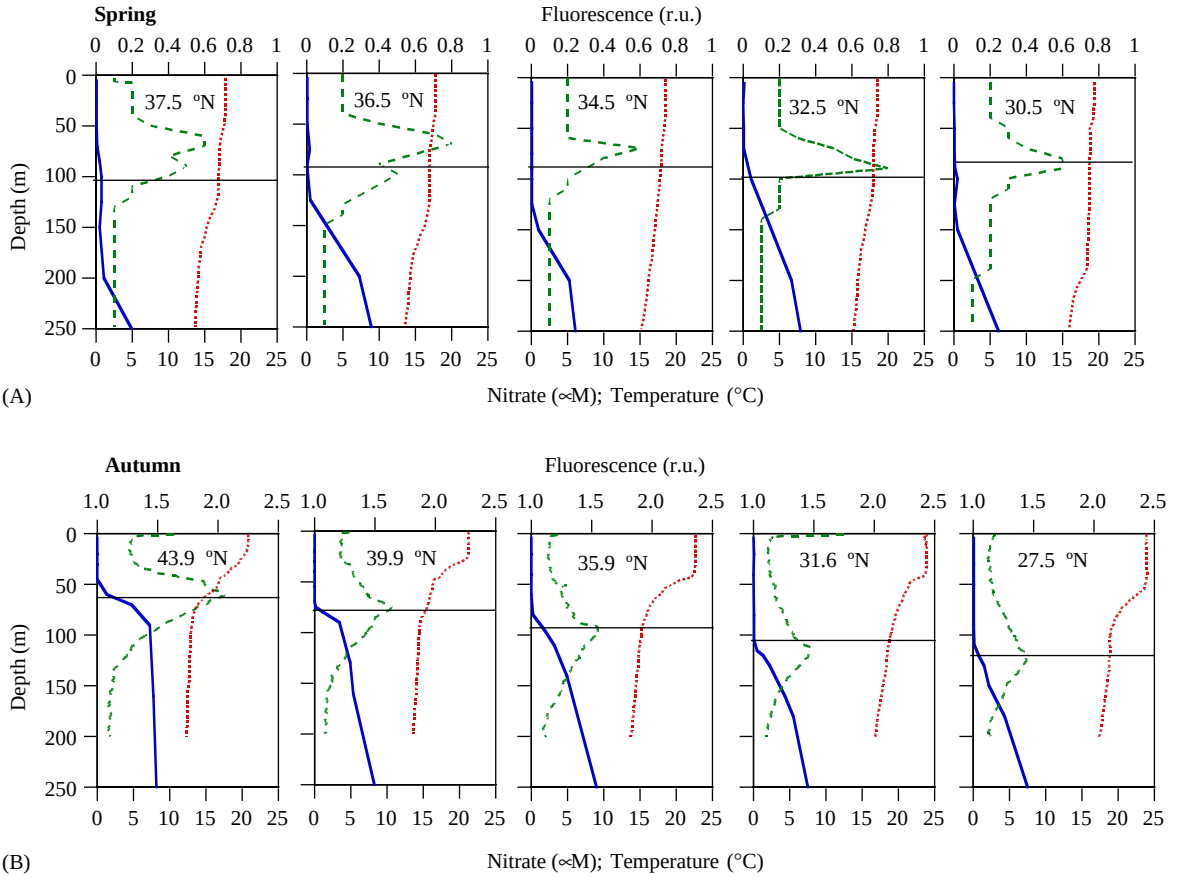

Fig. 5. Vertical profiles of nitrate concentration (solid line, μM), fluorescence due to chlorophyll-*a* (dashed line, r.u) and temperature (dotted line, °C) along two latitudinal sections centred at 20°W conducted during: (A) spring 1999, Azores-2; and (B) autumn 2000, AMT-11. The depth reached by 1% of surface irradiance is represented as a horizontal solid line.

DCM and the depth of the nitracline in autumn, whereas such a relationship weakens during spring. The DCM tended to be shallower northwards. During autumn, the DCM, the nitracline and the limit of the photic zone are well correlated, whereas during spring, the DCM developed mainly above the limit of the photic depth and did not show an upward trend northwards. The mixed layer showed also an upward trend northwards during autumn. The mixed layer depth remained rather constant during spring (ca. 55 m). An stepwise regression analysis was conducted in an attempt to model daily integrated primary production in NASE. We introduced as independent variables all those variables which showed a highly significant correlation with integrated PP (Tables 5 and 6): water column stability, depth of the nitracline, depth of the DCM, SST, and surface chl-*a*. The contribution of picophytoplankton to PP was not included as it is not an independent variable. The best model, using all the stations where all these variables were available, included only surface chl-*a* and SST. The corresponding multiple regression equation was: $\log \mathrm{PP} = 0.34 \log \text{chl-}a - 0.05\,\mathrm{SST} + 3.61$ ($r^2 = 0.42$, $p = 0.0002$, $n = 35$).

The multiple regression model using all the stations where both SST and surface chl-*a* were available was: $\log \mathrm{PP} = 0.43 \log \text{chl-}a - 0.07\,\mathrm{SST} + 4.16$ ($r^2 = 0.43$, $p < 0.0001$, $n = 57$).

4. Discussion

4.1. Variability patterns of chlorophyll-a concentration

We have shown that surface chl-*a* concentrations and the depth of the subsurface chl-*a* maximum are subjected to high latitudinal and seasonal variability (Fig. 3b). The magnitude of the DCM, which remained rather constant in the province (0.2–0.3 mg chl-*a* m^{-3}), was in good agreement with previous observations in the Subtropical N Atlantic (e.g Li and Harrison, 2001; Steinberg et al., 2001; Lefèvre et al., 2003). The existence of a DCM constitutes a widespread phenomenon in the open ocean. A DCM develops everywhere nitrate concentrations are reduced to limiting levels across this province (Longhurst, 1998). The analysis of our database showed that the depth of the DCM in the NASE province follows a downward trend from spring to summer, then rises again in autumn and reaches 20–40 m in winter, when the mixed layer deepens down to 80–100 m. The same pattern was observed in the western North Atlantic Subtropical Gyral province (Steinberg et al., 2001). There is also an upward trend of the DCM towards northern latitudes, due to cooler surface waters and shallower mixed layers. Agustí and Duarte (1999) found a similar trend in the central Atlantic Ocean, where a strong correlation existed between the DCM and the thermocline depth. This latitudinal trend of the DCM is nicely illustrated in Fig. 5. Except during winter, the DCM usually appears somewhat deeper than the productivity maximum, probably because of light limitation at the DCM. Marañón et al. (2000) found that in the Atlantic Ocean the DCM is not generally a biomass maximum but the result of a decrease of the carbon to chl-*a* (C/chl-*a*) ratio with depth. The same pattern was also found by Arin et al. (2002) in the Mediterranean Sea. The latter authors also found and increasing trend in the C/chl-*a* ratio from high to low nutrient conditions and with phytoplankton cell size. As a consequence of the uncoupling between the vertical distribution of chl-*a* and that of primary production, surface chl-*a* would be a better predictor of depth-integrated productivity than depth-integrated chl-*a* concentration. Surface chl-*a* concentration showed a clear seasonal cycle in the NASE province, which conformed very well to the model of Longhurst (1995) (Fig. 6a), particularly from June to December. Part of the represented seasonal variability could reflect spatial heterogeneity within the NASE (excluding the AMT-1 to AMT-5 cruises, all cruises covered different zones within NASE) or temporal variability, both interannual and at shorter scales (some of the monthly averages include data from 2 or more different cruises). The statistical analysis confirmed this seasonal pattern, with the highest values of surface chl-*a* occurring in winter and the lowest in summer (Tables 2 and 3). Surface chl-*a* was significantly higher in the temperate than in the subtropical and transition zone (Tables 2 and 4). This is due to the

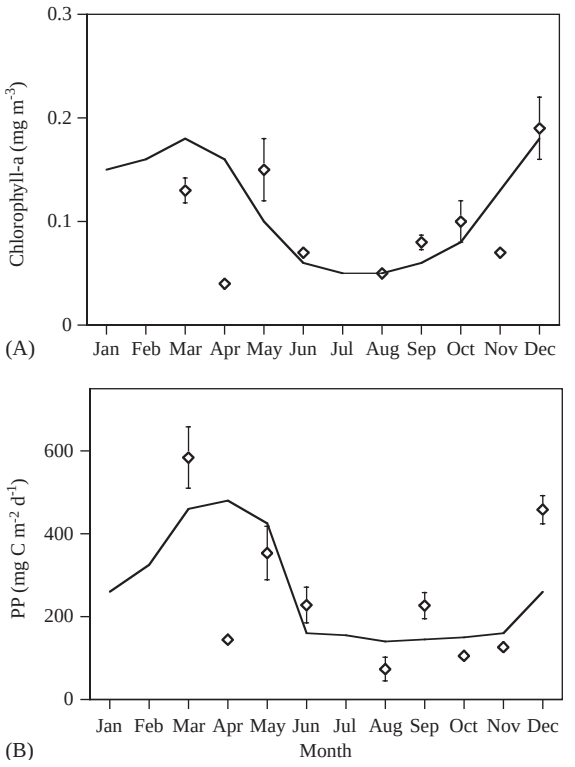

Fig. 6. Seasonal cycles of monthly averaged (±SE) surface chlorophyll-*a* (mg chl-*a* m^{-3}) and integrated primary production (mg C m^{-2} d^{-1}) in the NASE province (symbols with error bars) as compared with the model by Longhurst (1995) (solid line).

inclusion of stations affected by the spring bloom, which extends from 39 to 50°N (Longhurst, 1998). By contrast, depth-integrated chl-*a* concentration remained rather constant, averaging 17 mg chl-*a* m^{-2}. This mean value is in good agreement with previously reported measurements in the region (e.g. Li and Harrison, 2001; Harrison et al., 2001). The statistical analysis did not show any significant variability, either seasonal or latitudinal, in the depth-integrated chl-*a*. Other authors have found the same result for phytoplankton biomass in this region (Harrison et al., 2001). The lack of statistically significant latitudinal and seasonal variability in depth-integrated chl-*a*, regardless of the variability found in surface chl-*a* (Table 2), could be related to higher seasonal changes in the carbon to chl-*a* ratio in surface waters as compared with deeper waters (Lefevre et al., 2003). Such changes can occur by cell pigment reduction under conditions of high irradiance and restricted nutrient availability (Taylor et al., 1997).

4.2. Variability patterns of primary production

The variability in the vertical distribution of PP was mainly seasonal (Fig. 3d). The most striking feature was the very high rates of PP measured during winter in the subtropical and transition zones. During autumn and spring, the highest rates of PP were found in temperate waters. In spring, the high values in the temperate zone corresponded to stations affected by the North Atlantic spring bloom, which starts between March and April in the latitudinal band between 40 and 45°N (Follows and Dutkiewicz, 2002). Integrated PP rates ranged from 14 to 800 mg C m^{-2} d^{-1} and covered the range of previously published values for the same region (~210 mg C m^{-2} d^{-1}, Jochem and Zeitzschel, 1993; between 140 and 260 mg C m^{-2} d^{-1}, Frazel and Berberian, 1990; between ~300 and ~1000 mg C m^{-2} d^{-1}, Harrison et al., 2001). However, our database also includes lower values than those reported in the literature. These extreme values correspond with data collected in August, a month that was not covered in the reviewed studies.

Our observations partially conform to the model by Longhurst (1995) (Fig. 6), with higher rates of primary production occurring during winter and lower in summer, and thus reinforce the rejection of the traditional view of a constant environment in subtropical oceans. We recorded a higher degree of seasonal variability than predicted by his bio-optical model. Although statistically significant, this result relies on a relatively limited number of observations in summer and winter, as compared with spring and autumn. However, as we did not find chl-*a* and PP production data for this region during winter and summer in the reviewed literature, we could not compare these high and low values recorded during winter and summer, respectively. There is a clear need of increasing the sampling efforts in this region, in order to better describe the magnitude of the seasonal cycle. In addition, as stated before, the constructed seasonal cycle could include also spatial, interannual and short-term variability. Some recent works have stressed the relevance of interannual variability in the subtropical North Atlantic despite the rather low interannual variability in meteorological forcing (Steinberg et al., 2001; Follows and Dutkiewicz, 2002; Pätsch et al., 2002; Mouriño et al., 2003). Decadal changes in satellite-derived global ocean chlorophyll concentrations and in PP have also been detected between the periods 1979–1986 and 1997–2000 (Gregg and Conkright, 2002; Gregg et al., 2003). These authors found chlorophyll decreases of 10–15% during summer and global PP reductions of about 6% in the N Atlantic since the early 1980s. The statistical analysis showed that the spatial variability of PP is less important than seasonal variability (Table 2), with no clear patterns of latitudinal variability (Fig. 4). Such a finding contrasts with previous investigations that found clear latitudinal (Frazel and Berberian, 1990; Planas et al., 1999) and longitudinal (Li, 1995; Harrison et al., 1996; Waser et al., 2000) variability in biological properties in the subtropical North Atlantic Ocean. However, all these studies covered greater geographical ranges than the NASE. The lack of latitudinal variability both in depth-integrated chl-*a* and PP provide additional support to the established limits for the NASE province.

We also did not find a significant enhancement in PP in the transition zone related to the higher mesoscale activity associated with the STF. It is important to point out that the sampling resolution adopted in this study did not resolve the mesoscale. However, a recent study estimated that the increase of net PP associated with the STF would only be $<5\%$ over the annual net PP estimated for the whole NE Atlantic subtropical region (Mouriño et al., 2004).

Variability was considerably higher for rates of primary production than for surface chl-*a* concentration and depth-integrated chl-*a* concentration (Figs. 3 and 4 and Tables 1 and 2). Depth-integrated PP variability was one order of magnitude higher than that of depth-integrated chl-*a*, a pattern that was previously observed in this oligotrophic region (e.g. Harrison et al., 2001). If we assume that depth-integrated chl-*a* concentration is a good indicator of phytoplankton biomass, this would mean that there is a tight coupling between production and consumption that maintains the stock of primary producers at a rather constant level. It has been suggested that in oligotrophic regions grazing must play an important role in keeping phytoplankton biomass at low and relatively constant levels (Banse, 1995). In accordance with this hypothesis, Stelfox-Widdicombe et al. (2000) reported that microzooplankton grazed between 65% and 167% of the daily phytoplankton production in the subtropical NE Atlantic, and Quevedo and Anadón (2001) found that protists can consume between 79% and 109% of PP in this region. However, the later studies were conducted during the spring–summer period. Direct concurrent measurements of plankton photosynthesis and community respiration made in this area during different times of the year (Duarte et al., 2001; Robinson et al., 2002) are consistent with the idea that microheterotrophs play a role in plankton community dynamics. On the other hand, Marañón et al. (2003) showed a highly significant inverse relationship between PP and *Prochlorococcus* abundance. In this connection, Karl et al. (2001) also presented evidence of long-term changes in PP related to phytoplankton compositional changes. Unfortunately, the compositional studies of picophytoplankton in the Subtropical Gyres has so far been limited mainly to the estimation of the relative contribution of 3 majors groups: *Synechococcus* spp., *Prochlorococcus* spp. and picoeukaryotes (Campbell et al., 1997; Zubkov et al., 1998; Gin et al., 1999).

4.3. Variability patterns of phytoplankton size structure

A relevant aspect related to the functioning of any planktonic ecosystem is the size distribution of primary producers, which has been recognised to exert a great impact on trophodynamics in the photic layer (e.g. Legendre and Rassoulzadegan, 1996). Picophytoplankton (phytoplankton cells between 0.2 and 2 μm) has been widely reported as the dominant size fraction in the oligotrophic ocean. In the NASE province the size structure of the phytoplanktonic biota inhabiting the mixed layer during late spring differs from that of the North Atlantic Drift (NADR) province located to the north: large cells (>10 μm) represent only 4% of total phytoplankton biomass, whereas in the NADR, these cells contribute much more equally to the total phytoplankton biomass (Longhurst, 1998).

We also found a great seasonal variability in the vertical distribution of the contribution of small phytoplankton to both biomass and PP (Fig. 3c and e). The contributions of picophytoplankton to chl-*a* and PP were $>50\%$ and $>35\%$, respectively, except in the upper 60 m of the subtropical and transition zones during the summer. Several studies (Agawin et al., 2000a, b; Marañón et al., 2001) have recently addressed the globally high contribution of small phytoplankton to biomass and PP in the ocean. From the averaged integrated values calculated in Table 1, and from the statistical analysis (Tables 2–4), it can be derived that the dominance of picophytoplankton is highest in winter ($>80\%$ both in biomass and activity), when PP rates are also highest, and lowest in summer ($<70\%$ in biomass, and $<45\%$ in activity), when very low rates of PP were measured. This pattern does not fit with the largely accepted negative relationship between the contribution of small phytoplankton to chl-*a* and PP (Malone, 1980; Kiørboe, 1993). This

positive correlation between picophytoplankton dominance and PP was statistically significant ($r = 0.586$, Table 6). A lack of relationship between the size structure of the phytoplankton community and integrated PP rates was found by Marañón et al. (2003) in oligotrophic waters of the Atlantic, when data from NASE and SATL biogeochemical provinces were included. However this work included only data from spring and autumn, and our results suggest that the main shift in the phytoplankton community structure could take place in winter. Unfortunately, limited data on phytoplankton size–structure are available for the winter period in this region. It could be that the commonly accepted negative relationship between PP and contribution of picophytoplankton to chl-*a* and PP would solely hold if data from very diverse environments, including coastal zones where large diatoms tend to dominate, are considered. The average contribution of picophytoplankton to chl-*a* and PP was 71% and 54%, respectively (Table 1), very similar to the mean values reported by other authors in oligotrophic waters (Li and Harrison, 2001). The potential causes for this unequal contribution of picophytoplankton to total biomass and productivity were specifically addressed by Fernández et al. (2003). They concluded that the observed disagreement between the relative contribution of large ($>2\,\mu m$) phytoplankton to total chl-*a* biomass (BL:BT ratio) and their contribution to PP (PL:PT ratio) could be related to a higher photosynthetic efficiency of larger phytoplankton. Our analysis, including seasonality and spatial heterogeneity showed that there is also a temporal variability in such discrepancy (Table 1, Fig. 7). In Fig. 7, we have represented the BL:BT vs. PL:PT relationships as in Fernández et al. (2003), using all the available data derived from integrated data, but grouping the data points into the 4 seasons. Our data show that the discrepancy is highest during summer and lowest in winter, i.e., the higher photosynthetic efficiency of larger phytoplankton hypothesised by Fernández et al. (2003) would occur mainly during periods of low nutrient availability and low productivity. In addition, as observed in Fig. 3, the differences are highest in the upper water column during summer, which

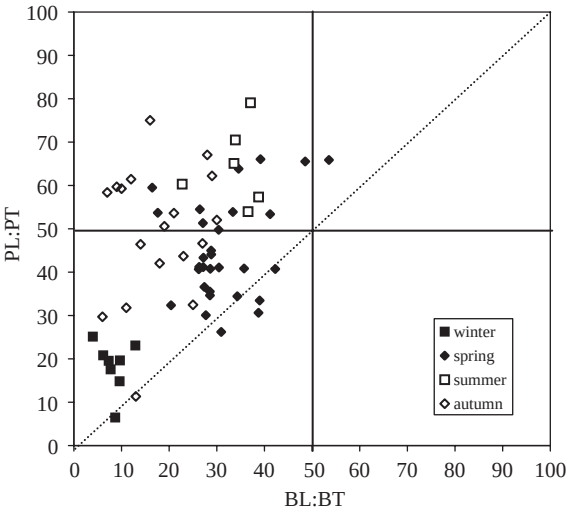

Fig. 7. Relationship between the ratios large phytoplankton biomass:total phytoplankton biomass (BL:BT) and large phytoplankton production:total phytoplankton production (PL:PT) for the NASE province, grouped into seasons. Ratios were calculated from depth-integrated values.

suggest that the lower contribution of small phytoplankton in terms of PP could be also related to high irradiance levels and stratification, which is higher during the summer period. Several studies have shown that ultraviolet (UV) radiation reduces photosynthesis and that the extent of damage is inversely related to cell size (e.g. Raven, 1991; Garcia-Pichel, 1994; Barbieri et al., 2002), although recent works also indicate that the taxonomic composition would be determinant for UV-sensitivity in phytoplankton communities (Laurion and Vincent, 1998; Barbieri et al., 2002). The UV flux in oligotrophic oceans at lower latitudes can be seasonally variable and an order of magnitude greater than at the poles (Whitehead et al., 2000). It could be hypothesised that, if some members of the picophytoplankton are highly sensitive to UV radiation or nutrient stress, a considerable fraction of the cells would be damaged, and as a consequence, the chl-*a* concentration and even carbon biomass would not necessarily indicate the biomass of viable cells, thus resulting in discrepancies between the contribution of small cells to total biomass or total PP.

4.4. Factors controlling PP variability

The correlation and multiple regression analysis allowed us to investigate the relative contribution of different physical, chemical and biological variables (phytoplankton community structure) to the observed PP variability in the NASE province. Although integrated PP was significantly correlated with surface temperature, water column stability, depth of nitracline, DCM, surface chl-*a* concentration and phytoplankton community structure, only surface temperature and surface chl-*a* concentration were included in the multiple regression model. The lack of correlation between PP and integrated chl-*a* and euphotic zone depth indicates that the vertical distribution of phytoplankton biomass and irradiance are not key factors driving changes in integrated PP within this oligotrophic region, and it is consequently of uncertain relevance for estimating ocean productivity from satellite-derived measurements. Our results confirm previous analyses that pointed out the limited capability of incident irradiance to explain changes in oceanic productivity within a constrained phytoplankton biomass range (Behrenfeld and Falkowski, 1997, Marañón et al., 2003).

As recently explained by Marañón et al. (2003), SST would not exert a direct control on PP variability. The inverse relationship observed between integrated PP and surface temperature can be explained from the correlation analyses. The highly significant positive correlation between SST and water column stability (Table 5) suggests that warmer surface waters would be associated with a higher water column stratification and, thus, limited nutrient availability in the euphotic zone. The positive correlation between SST and the depth of the nitracline confirms the hypothesis of nutrient supply, although the depth of the nitracline would explain only ~20% of the variability in PP. However, the lack of correlation between water column stability and the depth of the nitracline supports the existence of different mechanisms controlling the vertical extension of the nutrient depleted layer. The highly significant correlation between the depth of the nitracline and the DCM would indicate that the depth of the nitracline is controlled mainly by phytoplankton activity.

A recent work related decadal reductions in PP with accompanying increases in sea-surface temperature in the North Atlantic (Gregg et al., 2003). These authors also explained this relationship by increased stratification and reduced nutrient supply. The same explanation was given by Gruber et al. (2002) to explain the interannual variability in the North Atlantic ocean carbon cycle.

The moderate winter mixing in the NASE ensures that the mixed layer deepens for a limited time period, when new nutrients are injected within the photic zone, and, consequently, the rate of primary production increases through the winter, reaching a nutrient-limited peak in late spring (Longhurst, 1998). The relatively low proportion of PP variability within the NASE province explained by the multiple regression model (43%) could be related to stochastic nutrient loading processes other than wintertime convection when the upper water layer is nutrient-depleted (submesoscale features, allochthonous inputs of dissolved organic nitrogen from the NW African coastal upwelling, or atmospheric deposition). Indeed, the relationship between temperature, DCM, nitracline and photic zone illustrated in Fig. 5, was clear during autumn, but not during spring.

The results presented in this paper confirmed some of the general patterns already described for the region and revealed a series of new aspects about the dynamics of primary producers in this oligotrophic region. The reported variability in phytoplankton activity is higher than previously observed in the North Atlantic Subtropical Gyre, and the sampling strategy does not appear to adequately resolve the different variability scales. It becomes clear that sampling efforts need to be increased in order to obtain higher resolution, both at temporal and spatial scales, and to fully characterise the seasonal phytoplankton dynamics in this vast region of the ocean.

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