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Local production does not control the balance between plankton photosynthesis and respiration in the open Atlantic Ocean

Pablo Serret[a,*], Emilio Fernández[a], Carol Robinson[b], E. Malcolm S. Woodward[b], Valesca Pérez[a]

[a]*Departamento de Ecología y Biología animal, Universidad de Vigo, 36200 Vigo, Spain*
[b]*Plymouth Marine Laboratory, Prospect Place, West Hoe, Plymouth PL1 3DH, UK*

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Abstract

Recent experimental data from the subtropical NE Atlantic appear to support the prevalence of net heterotrophy in unproductive pelagic ecosystems. However, the proximity of these studies to the NW African upwelling does not exclude the possibility that remote areas of the oceanic gyres are in metabolic balance. Here we present measurements of plankton gross photosynthesis (GPP) and community respiration (CR) made during a latitudinal transect (Atlantic Meridional Transect (AMT) cruise 11, 49°N–33°S) that traversed five biogeochemical provinces of the Atlantic Ocean, including both the subtropical NE Atlantic and the central part of the South Atlantic subtropical gyre. In these oligotrophic provinces, the euphotic zone average chlorophyll *a* concentration (0.15 ± 0.01 and $0.16 \pm 0.02\,mg\,m^{-3}$, respectively), the relative contribution of picoplankton (%Chl$a < 2\,\mu m$ 75 ± 1 and $76 \pm 1\%$, respectively), and GPP (0.41 ± 0.12 and $0.47 \pm 0.09\,mmol\,O_2\,m^{-3}\,d^{-1}$, respectively) were almost identical. However, net heterotrophy prevailed in the euphotic zone of the tropical NE Atlantic ($-0.28 \pm 0.13\,mmol\,O_2\,m^{-3}\,d^{-1}$, $n = 3$), while the net metabolism of the plankton community in the central S Atlantic gyre was autotrophic ($0.20 \pm 0.02\,mmol\,O_2\,m^{-3}\,d^{-1}$, $n = 5$). These results therefore suggest the existence of more than one type of unproductive open-ocean situation, that may be characterised by differences in the relative importance of local vs. allochthonous sources of organic matter.

Keywords: Marine plankton; Photosynthesis; Respiration; Net ecosystem metabolism; Nitrate; Subtropical gyres

1. Introduction

Knowledge of the range, spatial and temporal variability and control mechanisms of plankton photosynthesis in the open ocean (e.g., Karl and Lukas, 1996; Michaels and Knap, 1996; Marañón et al., 2000; and references therein) provides a basis for defining ocean biomes and estimating global photosynthetic activity of the World Ocean (e.g., Longhurst et al., 1995; Behrenfeld et al., 2001). The temporal and geographic extent of the current dataset of primary production measurements (mainly ^{14}C-derived) contrasts with the paucity of respiration measurements (see Williams and del Giorgio, 2005). This inconsistency hinders the determination of the contribution of the marine

*Corresponding author. Tel.: +34 986 813773; fax: +34 986 812556.
E-mail address: pserret@uvigo.es (P. Serret).

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biota to the biogeochemical cycle of carbon, as this ultimately depends on the balance between gross photosynthesis (GPP) and community (i.e. auto- plus heterotrophic) respiration (CR).

The poor coverage of direct measurements of the GPP:CR balance (net community production, NCP) in the ocean is aggravated by the spatial, temporal and ecological biases in the current dataset, with the oligotrophic regions and seasons of the year being especially under sampled (Robinson and Williams, 2005). Yet the metabolic balance of these extensive regions is key to determining the role of the ocean in the global C cycle.

The subtropical NE Atlantic Ocean (NAST-E, Longhurst et al., 1995) is one of the few oligotrophic regions of the ocean where measurements of net community production have been made consistently. Duarte et al. (2001) compiled GPP and CR data from nine cruises conducted between 1991 and 2000, concluding that the planktonic communities of this unproductive area respire more organic carbon than they produce. These data showed the GPP/CR ratio to decrease with GPP, such that where GPP was lower than ca. 92 mmol $O_2\,m^{-2}\,d^{-1}$, the plankton community tended to be net heterotrophic. Similar results were reported for the NAST-E by Arístegui and Harrison (2002), González et al. (2002), Morán et al. (2004), Serret et al. (2001) and Robinson et al. (2002).

From their significant relationship between GPP/CR and GPP, Duarte et al. (2001) concluded that the degree of heterotrophy of pelagic ecosystems is controlled by primary production (see also del Giorgio et al., 1997; Williams, 1998; Duarte and Agustí, 1998; Agustí and Duarte, 2005), and calculated the metabolic (im)balance in the entire NAST from the mean regional value of primary production in the NAST-E (see also del Giorgio and Duarte, 2002).

Although local production certainly influences community metabolism, net heterotrophy implies the higher consumption of organic matter than that supplied by local production. Duarte et al. (2001) and Robinson et al. (2002) identified the supply of dissolved organic matter (DOM) by the NW African upwelling and atmospheric deposition of terrigenous materials as the more likely input mechanisms needed to explain the observations (and predictions) of net heterotrophy in the subtropical Atlantic. However, these are allochthonous inputs that cannot be controlled by, nor need to be related to, local GPP. Moreover, their proposed supply from the E margin of the NAST, and their necessary depletion indicated by net heterotrophy in the NAST-E, imply that CR should decrease relative to local GPP away from the African coast.

In apparent support of this hypothesis, Serret et al. (2002) again found, during the AMT-11 cruise, that depth-integrated NCP was negative in the margin of the NAST-E, but it was positive in the centre of the South Atlantic Gyre (SATL, Longhurst et al., 1995). They concluded that the heterotrophic component of planktonic food webs plays a relevant role in defining the metabolic balance of oceanic communities. The heterotrophic consumption of allochthonous organic matter, whose distribution cannot be uniform throughout the open ocean, would break the generalised control of net community metabolism by local production.

However, Arístegui and Harrison (2002) and González et al. (2002) also extended their observations further west into the NAST and SATL, respectively. Contrary to the results in Serret et al. (2002), they found that net heterotrophy prevailed through the euphotic zone of both the E and W Atlantic whenever GPP was low, and that the GPP:GPP/CR relationships obtained in remote areas of the gyres were consistent with those previously obtained in the NAST-E.

Arístegui and Harrison (2002) concluded that "changes in P but not in R control the transition from net heterotrophy to net autotrophy", and González et al. (2002) identified "the degree of nutrient limitation (on autotrophic production) as a critical factor in the control of the microbial community metabolism in the oligotrophic ocean". This conclusion is also consistent with data obtained from mesocosm experiments by Duarte et al. (2004) and Agustí and Duarte (2005), leading these authors to identify regional to global thresholds of GPP for planktonic metabolic balance. A similar explanation, based on the nutrient control of community metabolism and the temporal decoupling between GPP and CR was given by Karl et al. (2003) and Williams et al. (2004) for the seasonal-annual net heterotrophy observations made at the HOT station in the N Pacific Subtropical Gyre. In the Atlantic Ocean, González et al. (2002) identified the seasonal and geographical variations in the relative depths of the nitracline and pycnocline, or mesoscale processes driving episodic pulses of new nitrogen into the euphotic zone, as the key controls of the trophic dynamics and variability of plankton

NCP. González et al. (2002) extrapolated their results to estimate that the average negative NCP and the C deficit in the SATL would be ca. 3 and 12 times higher, respectively, than in the NAST-E.

According to this view, the unusual positive GPP:CR balances in the central SATL of Serret et al. (2002) only could result from an increase in GPP because of either the seasonal, or an episodic input of new N into the euphotic zone. On the other hand, if the spatial variability in allochthonous organic matter and CR also influences net community metabolism in the open ocean (Serret et al., 2002), then the negative GPP:CR balances in the central SATL (González et al., 2002) and the central NAST (Arístegui and Harrison, 2002) demand the existence of suitable sources of allochthonous organic matter that are not present in the area studied by Serret et al. (2002).

Understanding these contrasting datasets constitutes a real test for the respective hypotheses on the control of net plankton metabolism in the open ocean. However, such a comparative exercise is impeded by the exclusive use of depth-integrated NCP data and the absence of any accompanying information on the physical and chemical fields in Serret et al. (2002).

We therefore present the vertical and spatial variation of plankton GPP, CR and NCP, in relation to the hydrographic field, nutrient status, productivity and community structure along the AMT-11 cruise track (40°N–30°S). We will utilise the vertical and geographical resolution of this combined database to assess the credibility and representative nature of our net community metabolism measurements, and to explore the differences with other data sets. We will test the hypotheses that (1) the variability of net community production is more strongly related to GPP than CR in the open Atlantic Ocean, and (2) the degree of nutrient limitation in the euphotic zone is the main controlling factor of NCP in the oligotrophic ocean.

2. Methods

Sampling—A latitudinal (49°N–33°S) transect of 46 stations across the Atlantic Ocean (Atlantic Meridional Transect (AMT)-11 cruise—see Aiken et al., 2000) was conducted on RRS James Clark Ross between Grimsby, UK and Montevideo, Uruguay, between 14 September and 9 October 2000. Five biogeochemical provinces of the Atlantic Ocean were traversed: the mesotrophic North Atlantic Drift (NADR), Eastern (Canary) Coastal Province (CNRY) and Eastern Tropical Atlantic (ETRA), and the oligotrophic Eastern margin of the NAST (NAST-E) and central part of the SATL (Longhurst et al., 1995) (Fig. 1). Each day, two stations were sampled at between 04:00 and 05:00 a.m., and between 10:00 and 11:00 a.m. Vertical profiles of temperature and conductivity were performed at every station using a Seabird 911+ CTD fitted to a rosette of 12×10-dm^3 Niskin type sampling bottles. Except for chlorophyll *a* concentration, which was sampled at every station, all chemical and microbiological measurements presented here were derived from water collected during the early morning stations, which were spaced at approximately 350-km intervals. Vertical profiles of photosynthetically active irradiance (PAR, 400–700 nm) were calculated at the late morning stations by integrating the measurements of downwelling irradiance at seven SeaWiFS

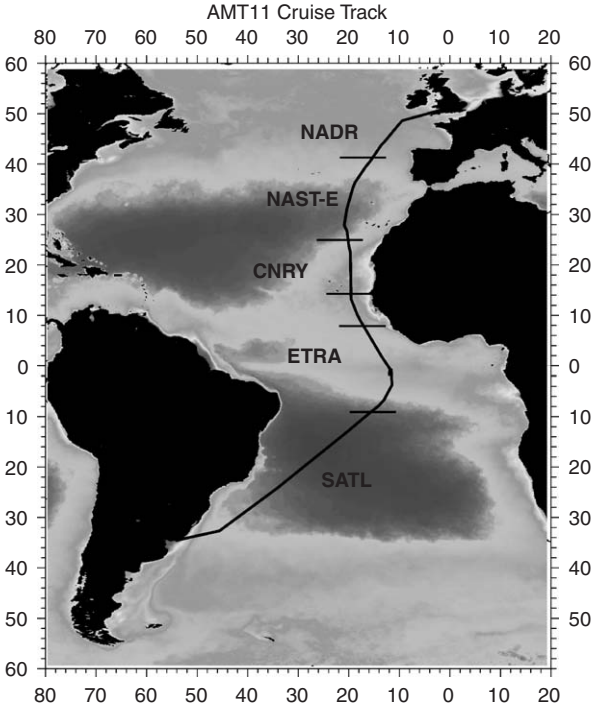

Fig. 1. AMT11 cruise track overlaid over SeaWiFS chlorophyll *a* September 1997–August 2000 composite image. Image provided by the SeaWiFS Project, NASA/Goddard Space Flight Center and ORBIMAGE. The approximate boundaries of the: North Atlantic Drift (NADR), North Atlantic Subtropical Gyral (NAST-E), Canary Coastal (CNRY), Eastern Tropical Atlantic (ETRA), and South Atlantic Gyral Province (SATL) biogeochemical provinces (Longhurst, 1998) are shown.

wavelength bands derived from casts of an optical profiler (SeaOPS) (Aiken et al., 2000).

Nitrate concentration—Micromolar nitrate concentrations were determined using a Technicon segmented flow colorimetric autoanalyser and methodology based on Brewer and Riley (1965). Clean sampling and handling techniques were employed and all samples were analysed within 90 min of sampling from the CTD-Rosette system.

Dissolved oxygen—Dissolved oxygen concentration was measured at 9 to 10 depths in the upper 250 m of each early morning station. A 120-cm^3 gravimetrically calibrated, borosilicate glass bottle was carefully filled from each Niskin bottle using silicon tubing, overflowing the volume of the bottle by ca. 1.5 times. Fixing reagents $-1\,cm^3$ of 3 M manganese chloride solution and $1\,cm^3$ of (8 M KOH + 4 M KI)—were added separately with an automatic multipipette. Fixing, storage and standardisation procedures followed the recommendations by Grasshoff et al. (1983). Measurements of dissolved oxygen were made with an automated Winkler titration system using a Metrohm 716 DMS Titrino and a potentiometric end point (Oudot et al., 1988; Pomeroy et al., 1994). Aliquots of fixed samples were delivered with a 50-cm^3 overflow pipette. Oxygen saturation was calculated using the equations for the solubility of oxygen in seawater of Benson and Krause (1984).

Size-fractionated chlorophyll a concentration—At every station, samples were collected from five to seven depths in the upper 200 m. 200 to 300-cm^3 water samples were sequentially filtered through 20-, 2- and 0.2-μm pore size polycarbonate filters. Chlorophyll *a* (chl *a*) was extracted from the filters in 90% acetone at $-20\,^{\circ}C$ for ca. 24 h. Measurements were made using a Turner 10-AU fluorometer calibrated against chlorophyll *a* standards, following JGOFS protocols (Knap et al., 1996).

Particulate organic carbon production ($PO^{14}CP$) rates—During the early morning station, seawater samples were collected from five to seven depths that were determined from the vertical distribution of temperature and fluorescence, together with the record of the vertical PAR profiles at the previous late morning station. These depths were chosen to correspond to optical depths ranging from 97 to 1% of surface irradiance. The reliability of these light depths was estimated to be ca. ±7%, after comparison with those depths determined from the next late morning PAR profile. Water from each depth was distributed into four 75-cm^3 acid-cleaned polypropylene bottles (3 transparent and 1 dark). Each bottle was inoculated with 370–740 KBq (10–20 μCi) $NaH^{14}CO_3$ and then incubated for 24 h in an on-deck incubator that simulated the irradiance at the original sampling depths using various combinations of neutral density and blue plastic filters. Incubations started before dawn. After the incubation period, samples were filtered at very low vacuum (<50 mm Hg) through 20-, 2- and 0.2-μm polycarbonate filters. To remove unfixed inorganic ^{14}C, filters were then fumed with concentrated HCl for 12 h. Radioactivity was measured with a Beckman LS6000 SC scintillation counter. Quenching was corrected using an external standard. Total primary production was determined by summing the size fractionated rates.

Gross primary production, net community production and dark community respiration—At the early morning stations, gross primary production (GPP), net community production (NCP) and dark community respiration (CR) were determined at five depths from in vitro changes in dissolved oxygen after light and dark bottle incubations. Sampling and incubation were carried out at the same depths, simultaneously and under the same conditions as for C incorporation experiments. Twelve 120-cm^3, gravimetrically calibrated, borosilicate glass bottles were carefully filled from each Niskin bottle using silicon tubing, overflowing by $>250\,cm^3$. From each depth, four replicate 'zero-time' bottles were fixed immediately with Winkler reagents, four bottles were kept in darkness, and four bottles were incubated under irradiance conditions simulating those of the original sampling depth as described above. After the 24-h incubation period, dissolved oxygen concentration was determined following the method described above. Production and respiration rates were calculated from the difference between the means of the replicate light and dark incubated bottles and zero time analyses: NCP = measured ΔO_2 in light bottles (mean of $[O_2]$ in 24-h light/dark − mean zero time $[O_2]$); CR = measured ΔO_2 in dark bottles (mean zero time $[O_2]$ − mean $[O_2]$ in 24-h dark); GPP = NCP + CR. The average coefficient of variation of the O_2 concentration measurements in the zero, dark and light bottles was 0.07%, and the mean of the standard errors of the NCP and CR rate measurements were 0.13 ($n = 92$) and 0.13 ($n = 99$) $mmol\,O_2\,m^{-3}\,d^{-1}$, respectively. Euphotic zone integrated values were obtained by trapezoidal integration of the volumetric data down to the depth

of 1% surface incident irradiance. Following Miller and Miller (1988), we calculated the standard deviation of integrated GPP, CR and NCP through propagation of the random error in the volumetric measurements as $\sigma_{\text{integral}} = \frac{1}{2}\sqrt{[\Sigma(z_{i+1} - z_i)^2(\sigma_{i+1}^2 + \sigma_i^2)]}$, where σ is the standard deviation, z is the sampled depth and i is the depth level.

3. Results

3.1. Water column thermal structure and nitrate concentration

The spatial distribution of temperature (Fig. 2A) reflects the hydrographic characteristics of the different provinces traversed during the cruise: NADR, NAST-E, CNRY, ETRA and SATL (Longhurst, 1998). Fig. 2B shows the spatial variability of nitrate concentration. The depth of the euphotic zone (1% incident irradiance) is also presented in Figs. 2A and B (dotted line)

In the northernmost part of the transect (at ca. 48°N), a shallow thermocline was found in the nutrient rich waters of the European shelf. In the NADR province, the thermocline and nitracline were located at ca. 50 m depth. A broad frontal zone at ca. 39–35.5°N marked the transition from the NADR to the warmer, more saline (data not shown) waters of the NAST-E, where a broader thermocline and deeper, nutrient-depleted surface mixed layer were observed. To the south of the NAST-E, the cruise track approached the NW African coast

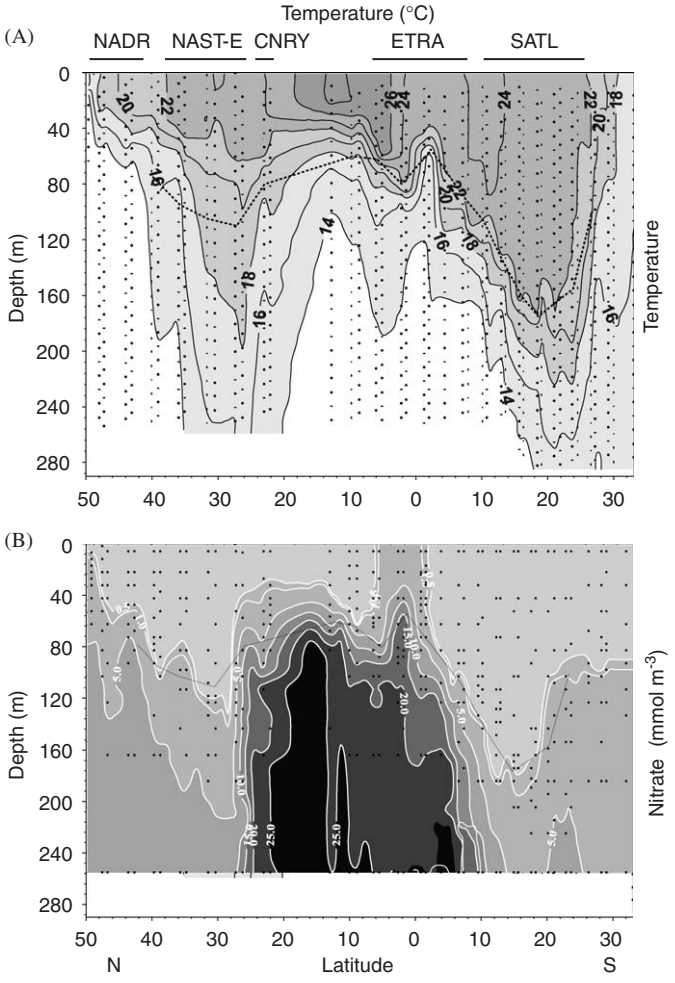

Fig. 2. Latitudinal distributions of (A) temperature (°C) and (B) the concentration of nitrate along the AMT11 transect. Dotted line, euphotic depth (1% surface PAR).

(Fig. 1), entering the CNRY province (ca. 23–15°N) (Longhurst, 1998), influenced by coastal upwelling. However, at the only station sampled within the CNRY province, surface waters were warmer than at the closest NAST station, and, apart from a minor tilting in deeper isotherms, no evidence for upwelling was found in either the temperature or nitrate distributions. South of the Guinea dome, (centred at ca. 13°N), and entering the ETRA province (ca. 7°N–8°S), the northern tropical convergence lying between the North Equatorial Counter Current (Guinea Current) and the South Equatorial Current can be seen in the deepening of the isotherms at ca. 6°N. Within the ETRA, the equatorial divergence is clearly seen in the sloping of the thermocline centred at ca. 2°S. Relatively high nitrate concentrations were found throughout the surface waters of the ETRA, reaching $>1\,\mathrm{mmol\,m^{-3}}$ at the equatorial divergence. The upper thermocline (marked by the 22 °C isotherm) shoaled to ca. 50 m at the equatorial divergence from ca. 75 and 95 m, north and south, respectively. Southwest from ca. 8°S, a progressive deepening of the thermocline indicates the transition from the ETRA to the SATL province, where the nutrient-depleted upper mixed layer reached the maximum depth on the transect (ca. 160 m). A marked frontal zone south of ca. 24°S marked the transition from

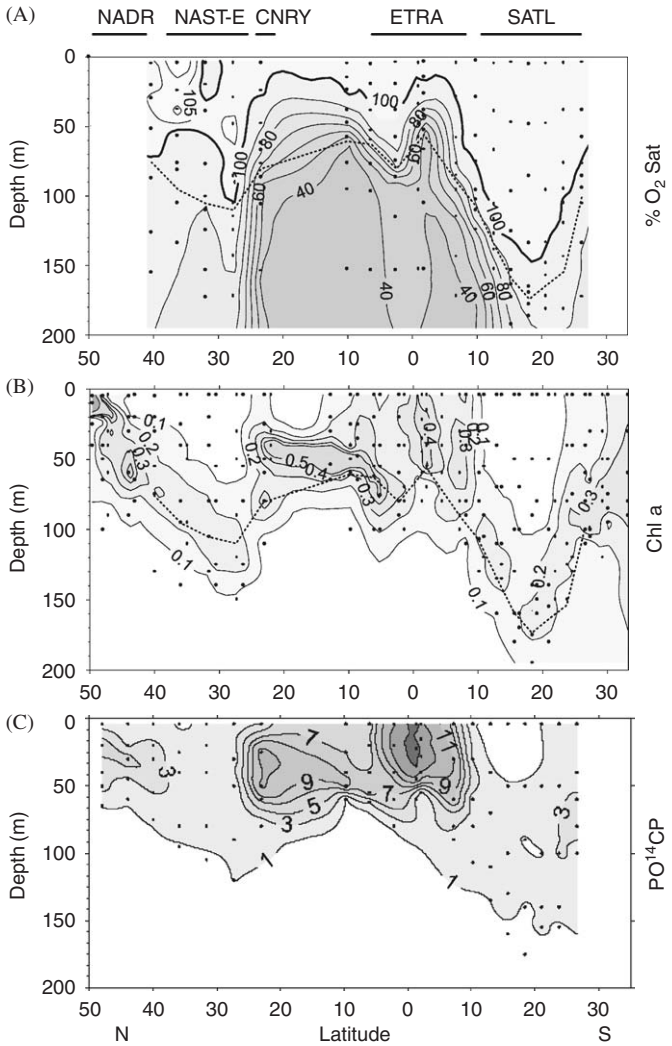

Fig. 3. Latitudinal distributions of (A) the percentage of oxygen saturation (% O_2 sat), (B) chlorophyll *a* (chl *a*) concentration ($\mathrm{mg\,m^{-3}}$) and (C) ^{14}C primary production ($PO^{14}CP$) ($\mathrm{mg\,C\,m^{-3}\,d^{-1}}$) along the AMT11 transect. Dotted line in A and B, euphotic depth (1% surface PAR).

the SATL to the cooler and vertically more homogeneous waters of the South American shelf. However, there was little or no change in nitrate concentrations in the upper 70 m.

3.2. Oxygen saturation and chlorophyll a concentration

Figs. 3A and B show the spatial variability of the percentage of oxygen saturation (% O_2 sat) and chl *a* concentration, respectively, along the AMT11 transect. The % O_2 sat in the upper ocean provides a summary of the recent history of biological activity (e.g., Najjar and Keeling, 1997; Chapman and Shannon, 1985). O_2 concentrations higher than the level of saturation were found in the surface mixed layer of the vertically stratified waters of the NAST-E, ETRA and SATL. The tilting of isotherms at the Guinea Dome, the coastal upwelling in the CNRY and the equatorial upwelling in the ETRA are associated with a shoaling of undersaturated deep waters. These strong vertical oxygen gradients are characteristic of upwelling systems (e.g. Chapman and Shannon, 1985). The highest level of oxygen saturation ($>115\%$ in the surface, $>105\%$ through the upper 50 m) was found in the northern area of the NAST-E, while O_2 undersaturation was only found in the upper 25 m at one station in the NAST-E. This higher variability in the oxygen field in the NAST-E indicates higher variability in the physical-chemical or/and biological fields in the upper mixed layer of the NAST-E relative to that of the central SATL.

The highest concentration of chl *a* ($2.44\,mg\,m^{-3}$), and the only surface maximum, was observed in waters of the European shelf. Further south, through the NADR, surface chl *a* concentration decreased and a deep chl *a* maximum (DCM) followed the deepening of the thermocline. In both subtropical gyres (NAST-E and SATL), very low chl *a* concentrations ($<0.1\,mg\,m^{-3}$) were measured in the O_2-saturated, nutrient-depleted surface mixed layer. In these areas, a DCM of $>0.2\,mg\,chl\,a\,m^{-3}$ was observed at ca. the level of 1% of surface irradiance, in accordance with previous observations at low latitudes in the Atlantic Ocean (Marañón et al., 2000, and references therein).

In the NAST-E, no relationship was found between the distributions of O_2 saturation, nitrate or chl *a*, in agreement with previous results in both the NAST-E and ETRA in May 1998 (Serret et al., 2001). In the NAST-E, most of the DCM (where chl *a* concentration was $>0.2\,mg\,m^{-3}$) was in waters undersaturated in O_2. On the contrary, in the SATL, the transition from O_2 super- to subsaturation occurred within the DCM. At the stations sampled in the CNRY province and the Guinea Dome area, chl *a* concentration increased in both the surface ($>0.1\,mg\,m^{-3}$) and the DCM ($>0.5\,mg\,m^{-3}$), which was shallower (ca. 50 m depth) than in the neighbouring NAST-E (see Oudot, 1989). In accordance with the weak upwelling conditions found in the CNRY province, no surface chl *a* maxima were found, and the integrated concentration was relatively low ($27\,mg\,Chl\,a\,m^{-2}$). Within the ETRA, the chl *a* concentration was relatively high throughout the euphotic zone ($>0.2\,mg\,m^{-3}$), with the highest values ($>0.4\,mg\,Chl\,a\,m^{-3}$) found within the area of the equatorial upwelling (ca. 2°S). South of the SATL, surface chl *a* concentration increased and the DCM shoaled and became broader.

3.3. Primary production and community respiration

The spatial variations in particulate organic carbon production ($PO^{14}CP$) (Fig. 3C) and O_2 GPP (Fig. 4A) were very similar and related to the distribution of chl *a* (Fig. 3B). The relationship between the rates of O_2 GPP and $PO^{14}CP$ is described by the equations GPP ($mmol\,O_2\,m^{-3}\,d^{-1}$) $= 1.94$ $PO^{14}CP$ ($mmol\,C\,m^{-3}\,d^{-1}$) $+ 0.32$, $n = 89$, $r^2 = 0.69$, $p < 0.01$ (volumetric), and GPP ($mmol\,O_2\,m^{-2}\,d^{-1}$) $= 1.94$ $PO^{14}CP$ ($mmol\,C\,m^{-2}\,d^{-1}$) $+ 29.33$, $n = 19$, $r^2 = 0.78$, $p < 0.01$ (euphotic zone integrated). This agrees with the results in Bender et al. (1999) who found 24-h $PO^{14}CP$ rates to represent ca. 45% of O_2 GPP in the equatorial Pacific. The relationship between NCP and $PO^{14}CP$ is described by the equation NCP ($mmol\,O_2\,m^{-3}\,d^{-1}$) $= 1.52$ $PO^{14}CP + 0.13$, $n = 92$, $r^2 = 0.55$, $p < 0.01$; excluding the negative NCP data, such a relationship is given by the equation NCP ($mmol\,O_2\,m^{-3}\,d^{-1}$) $= 1.46$ $PO^{14}CP + 0.14$, $n = 64$, $r^2 = 0.72$, $p < 0.01$. The average molar ratio of NCP in the euphotic zone to $PO^{14}CP$ was 1.54 ± 0.14, which is close to the theoretical molar ratio of net community O_2 production in the photic zone to new production, in terms of CO_2 uptake of 1.5 ± 0.1 (Laws, 1991). Although these comparisons lend credibility to our data, further interpretation is not possible as we lack detailed information on ecosystem properties (e.g., nutrient status and utilisation, metabolic pathways and rates, organisms, dissolved

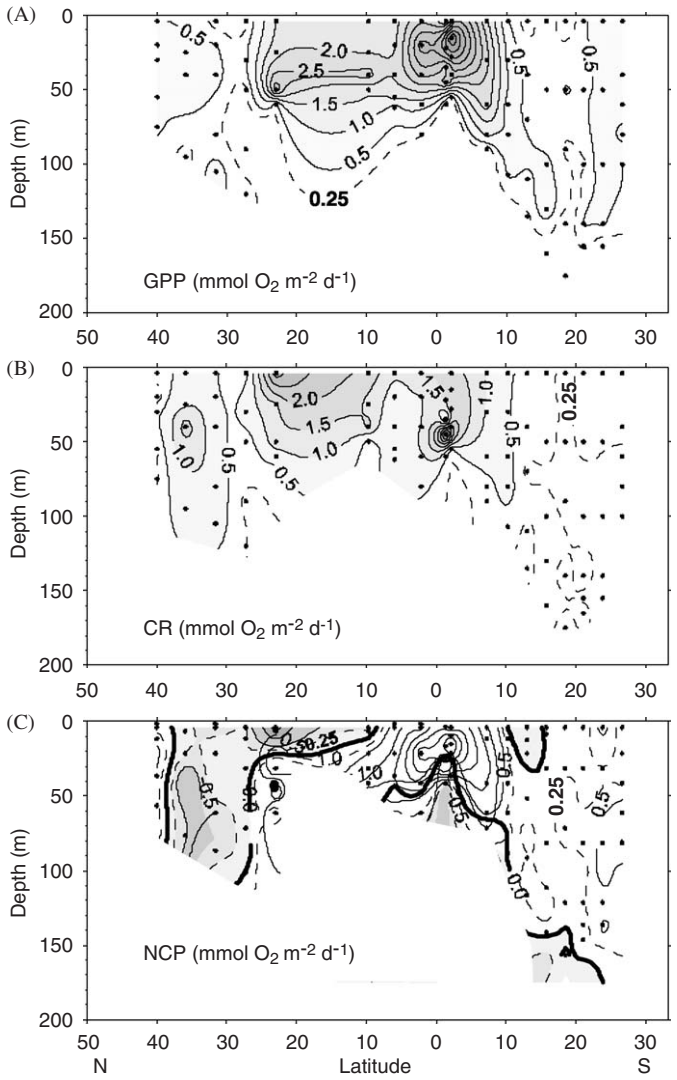

Fig. 4. Latitudinal distributions of (A) gross primary production (GPP), (B) dark community respiration (CR) and (C) net community production (NCP) along the AMT11 transect. Regions where CR > GPP i.e. NCP is negative are shaded grey in 4C.

organic carbon (DOC) production and trophic coupling), which contribute to the O_2:$PO^{14}CP$ ratio.

Throughout the transect, the variation of GPP was relatively low, consistent with the relatively low variability in chl *a* concentration. The highest GPP rates were measured in the Equatorial upwelling, within the ETRA (Fig. 4A). In this area, where chl *a* concentration was vertically homogeneous throughout the euphotic zone, strong vertical gradients of GPP were observed, with maximum rates near the surface ($>5\,\mathrm{mmol\,O_2\,m^{-3}\,d^{-1}}$ at ca. 12–25 m depth) and values $<0.5\,\mathrm{mmol\,O_2\,m^{-3}\,d^{-1}}$ at the 1% light level depths (below ca. 55 m). The vertical distribution of GPP in the CNRY and Guinea Dome areas followed that of chl *a*, with high rates of GPP ($>2\,\mathrm{mmol\,O_2\,m^{-3}\,d^{-1}}$) measured at the depths of the DCM. The lowest values of GPP (maximum of $0.5\,\mathrm{mmol\,O_2\,m^{-3}\,d^{-1}}$) were measured in the two subtropical gyral provinces (NAST-E and SATL). As with the percentage of O_2 saturation, the weak vertical variation of GPP was related to the position of the DCM and the nitracline in the SATL, but not in the NAST-E. South of the SATL and north of the NAST-E, higher and more homogeneous GPP rates ($>0.5\,\mathrm{mmol\,O_2\,m^{-3}\,d^{-1}}$) were measured throughout the euphotic layer. These increases in GPP were, however, lower than those observed in the chl *a* concentration (see Fig. 3B).

CR rates were high in the most productive, chl *a* rich, waters of the CNRY and ETRA (Fig. 4B). The highest rates were measured in the subsurface waters (ca. 40–50 m depth) of the equatorial upwelling, below the maximum of GPP but where chl *a* concentration was still high (>0.4 mg chl *a* m^{-3}). Consequently, in this area, the vertical distribution of the balance between GPP and CR (net community production, NCP. Fig. 4C) exhibited an intense gradient with high positive values in the upper mixed layer and negative NCP below ca. 40 m depth, coinciding with the thermocline and the level of ca. 5% of incident irradiance (I_0). At the other stations in the ETRA ($n = 4$), lower CR rates were found, and the vertical distributions were more homogeneous or showed weaker surface maxima. The distribution of NCP in the ETRA was therefore similar to that of GPP and, as in the equatorial upwelling, the upper thermocline coincided with a transition from positive to negative NCP, at ca. the depth of 5% I_0.

In the Guinea Dome and especially in the CNRY, high CR rates (>1.5 mmol $O_2\,m^{-3}\,d^{-1}$) were measured in the upper mixed layer, where chl *a* concentration and GPP were low. CR rates decreased with depth and showed no clear relationship with the DCM or the GPP maximum. Consequently, vertical gradients of NCP were strong, but were the inverse of those observed in the ETRA. Negative NCP was measured in the upper 10–20 m where chl *a* concentration and GPP were low and O_2 concentration was higher than the level of saturation. Conversely, in subsurface O_2 undersaturated waters, and following the distribution of chl *a* and GPP, positive NCP was measured, with maxima >1 mmol $O_2\,m^{-3}\,d^{-1}$ at ca. 50 m depth (ca. 20% I_0). Such an inverse relationship between the instantaneous NCP measurements and % O_2 saturation reveals the highly dynamic nature of these systems.

Both subtropical gyral provinces (NAST-E and SATL) were characterised by similarly low chl *a* concentrations (20.5 ± 1.4 and 19.7 ± 0.6 mg Chl*a* m^{-2}, respectively) and low GPP rates throughout the euphotic zone (0.38 ± 0.07 and 0.42 ± 0.05 mmol $O_2\,m^{-3}\,d^{-1}$, respectively), but differed in their respective CR ranges. High CR rates (0.6 ± 0.1 mmol $O_2\,m^{-3}\,d^{-1}$) were measured throughout the euphotic zone of the NAST-E. However in the SATL, very low rates (0.2 ± 0.03 mmol $O_2\,m^{-3}\,d^{-1}$) were found. The vertical distributions of CR and chl *a* concentration were not related in either of these oligotrophic provinces. Since these provinces both exhibited low GPP rates, these differences in CR are reflected in the NCP rates. Net heterotrophy ($NCP<0$) was found throughout the euphotic zone of the three stations sampled in the NAST-E, with no apparent relationship with the % O_2 sat, chl *a* concentration or GPP distributions. In the SATL, by contrast, positive NCP was measured throughout the upper mixed layer (ca. 150 m depth), except at one station where the surface rate was -0.27 ± 0.06 mmol $O_2\,m^{-3}\,d^{-1}$. Net heterotrophy was found from the thermocline downwards, and the transition from net auto- to net heterotrophy occurred within the DCM and matched the transition from oxygen over- to undersaturation (see Fig. 3A). The SATL was the only province where the instantaneous trophic balance (NCP) was coherent with the distribution of O_2 saturation. North of the NAST-E and south of the SATL, where the chl *a* concentration was relatively high and GPP low, very low CR rates were measured. Hence low positive NCP was found throughout the euphotic zone.

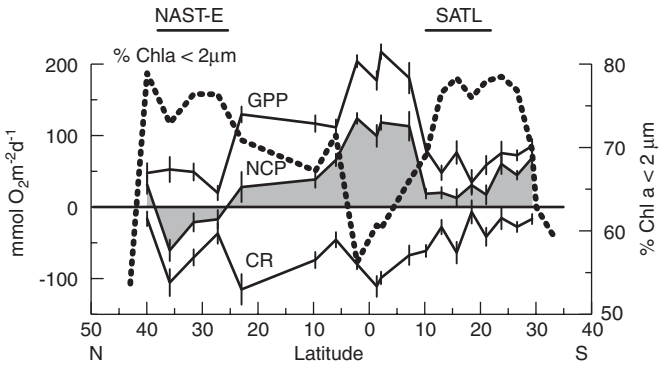

Fig. 5. (Modified from Serret et al., 2002). Latitudinal distributions of euphotic zone integrated percentage of chlorophyll *a* in cells <2 µm (% Chl $a<2$ µm) (dotted line), GPP, CR (solid lines) and NCP (shadowed trend) along the AMT11 transect.

3.4. Integrated oxygen fluxes and percentage of chl a in cells $<2\,\mu m$

Fig. 5 presents the latitudinal variability of plankton metabolism and the percentage of total chl *a* in cells $<2\,\mu m$, integrated to the depth of the 1% I_0 (euphotic depth). Cells $<2\,\mu m$ represented the dominant phytoplankton size class throughout the transect, except at the station sampled in waters of the European shelf (ca. 50°N), where the highest chl *a* concentration was measured near the surface (see Fig. 3B), and cells $>2\,\mu m$ represented ca. 70% of the total phytoplanktonic biomass (data not shown). At those latitudes where O_2 fluxes were measured (ca. 40°N to ca. 30°S), the percentage of euphotic zone integrated chl *a* concentration attributable to cells $<2\,\mu m$ showed a significant inverse relationship with integrated GPP (Figs. 5 and 6A), and varied from $>75\%$ in both unproductive subtropical gyres, to $<60\%$ in the most productive Equatorial upwelling area.

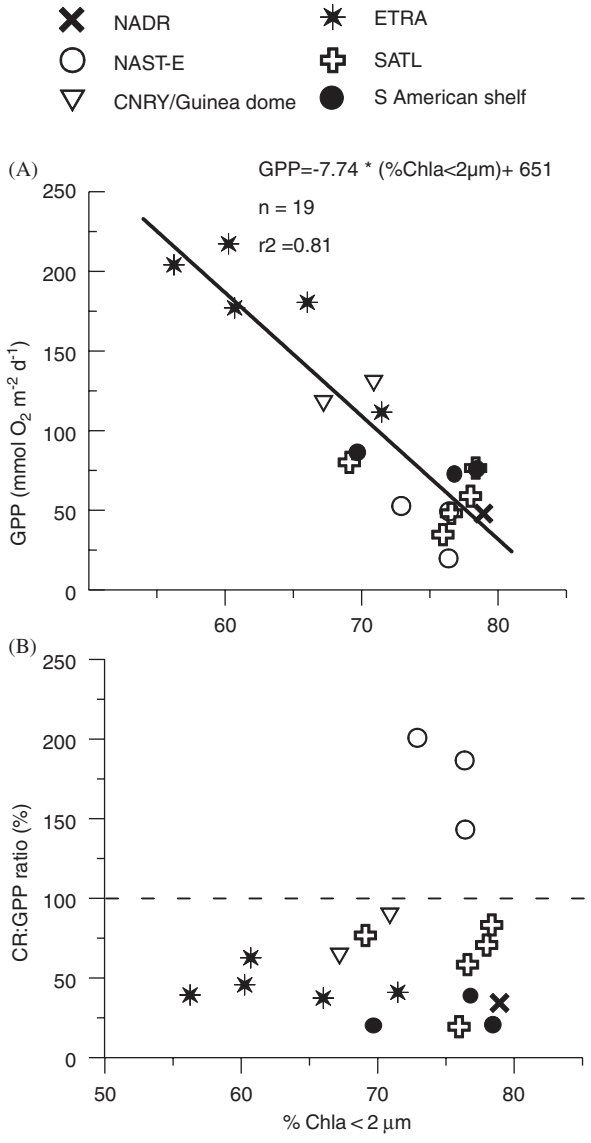

Fig. 6. (A) Relationship between the integrated percentage of chlorophyll *a* in cells $<2\,\mu m$ (% Chl $a<2\,\mu m$) and gross production (GPP). The solid line is the best fit equation (GPP $= -7.74$ (% Chl $a<2\,\mu m)+651$, $n=19$, $r^2=0.81$, $p<0.0001$). (B) Relationship between integrated % Chl $a<2\,\mu m$ and integrated % of GPP attributable to CR (%CR). The dashed line is where GPP = CR.

The range of latitudinal variation of euphotic zone integrated CR was ca. half that of GPP (Fig. 5) and, contrary to GPP, the CR:GPP ratio did not exhibit a significant relationship ($p>0.1$) with either total or $<2\,\mu m$ phytoplankton biomass (Fig. 6B). Although integrated CR seems to co-vary with integrated GPP within provinces (see Fig. 5), similar values of CR were found in different provinces with different integrated GPP rates (e.g., NAST-E and ETRA. Fig. 5). Also, lower CR rates were found, despite the similar GPP rates, in the SATL than in the NAST-E ($0.27\pm0.07\,mmol\,O_2\,m^{-3}\,d^{-1}$ vs. $0.72\pm0.22\,mmol\,O_2\,m^{-3}\,d^{-1}$, respectively) (see Fig. 5).

4. Discussion

The metabolic balance in the open ocean remains an important unresolved issue in current biological oceanography (del Giorgio and Williams, 2005). Net heterotrophy usually prevails in snapshot measurements derived from incubated samples (see Robinson and Williams, 2005 and references therein), but not, or only marginally, in many regional or global mass-balance calculations (e.g., Hansell et al., 1995; Robinson and Williams, 2005). These discrepancies have raised concerns as to the credibility, representative nature and general applicability of bottle measurements. However, any direct comparison of results derived from methods that differ so markedly in their spatial and temporal scales is uncertain. A significant scaling-up of snapshots of community metabolism should rely on a conceptual framework that includes the trophic functioning of the foodweb, and hence considers the relevant long and large scales of the connection between the production and respiration of organic matter in the sea (Serret et al., 1999, 2001; Arístegui and Harrison, 2002) including the dynamics of dissolved organic matter. This approach is impeded

by the paucity and bias of rate measurements (Robinson and Williams, 2005). The lack of such a functional framework implies that spatial and temporal integrations of GPP and CR data based simply on their concurrency do not necessarily estimate the *trophic status* of any pelagic ecosystem (i.e. the GPP:CR balance at the scale of ecosystem functioning; see Smith and Hollibaugh (1997), Serret et al. (2002), and references therein). Consequently, the extrapolation of any set of individual GPP and CR measurements to longer periods of time or larger areas of ocean, where results may be compared to biogeochemical estimations, must be viewed with caution (e.g., Williams et al., 2004; Karl et al., 2003).

The same arguments also apply to the comparison of distinct measurements of NCP. In this regard, understanding the differences between our results and those obtained by other authors in remote areas of the Atlantic requires a knowledge of the ecological background to these snapshot measurements.

4.1. Are our data credible?

Several biogeographic provinces were sampled during the AMT11 cruise, however the stations sampled north of the NAST-E and south of the SATL corresponded to the transitional zones between the NAST-E and NADR and the Brazil Current Coastal Province (BRAZ) and SATL, respectively. Also, the only station sampled in the CNRY province is not representative of this highly dynamic upwelling system, and the station sampled at the Guinea dome is in the transition zone between the CNRY and the ETRA. On the other hand, the stations sampled in the NAST-E, ETRA and SATL appear to be characteristic of the respective provinces, although the direct comparison with independent GPP and CR measurements in these regions is limited by the poor database of open ocean respiration measurements. Measurements of net community production in the ETRA made during a previous meridional transect (AMT6 cruise) (Serret et al., 2001, Robinson et al., 2002) did not include the equatorial upwelling. The AMT6 measurements were made ca. 250–1000 km east of those made during AMT11, i.e. closer to the African coast, and during May rather than September, hence coinciding with the low primary production season in the region (Longhurst, 1998), instead of the typically high productive summer-autumn. Correspondingly, the average integrated GPP in the ETRA during AMT6 (Serret et al., 2001) was more than 4 times lower than the rates measured during AMT11, while integrated CR rates in May (Serret et al., 2001) were ca. twice those presented here. Rates of GPP and CR measured during this study in the equatorial E Atlantic (ca. 2°N–2°S. See Fig. 4) agree well with those reported by Bender et al. (1999) from the Equatorial Pacific (see Pérez et al., 2005 for a thorough analysis).

The only province sampled where a sensible quantitative comparison with independent data is possible is the NAST-E (see Table 1). The GPP and CR data set compiled by Duarte et al. (2001) comprises measurements made in the NAST-E during nine cruises conducted between 1991 and 2000. Data from the coastal upwelling system of CNRY are included in this compilation, and no discrimination is made between data collected during different seasons; hence this work can only be used as a context for our observations. GPP varied from ca. 20 to 220 mmol O_2 m^{-2} d^{-1}, while CR ranged from ca. 50 to 230 mmol O_2 m^{-2} d^{-1} (Duarte et al., 2001). The rates of GPP presented here for the NAST-E, measured in September 2000, averaged 41 ± 10 mmol O_2 m^{-2} d^{-1} ($n = 3$), and rates of CR were 71 ± 19 mmol O_2 m^{-2} d^{-1} ($n = 3$) (see Fig. 5), both within the range reported by Duarte et al. (2001). The integrated GPP data in September are similar to those measured in June 1998 (Serret et al., 2001), as both sampling periods lie within the low production season in the NAST-E (Longhurst, 1998). However, integrated CR (71 ± 19 mmol O_2 m^{-2} d^{-1}) was low in comparison with both the rates measured in June 1998 (150 ± 26 mmol O_2 m^{-2} d^{-1}) and those predicted from GPP using the GPP:GPP/CR relationship of Duarte et al. (2001) (ca. 158 mmol O_2 m^{-2} d^{-1}). Such low CR rates in relation to the post productive season would be consistent with the progressive consumption of organic matter seasonally imported from the neighbouring coastal upwelling that peaks in spring-summer (Longhurst, 1998), or organic matter accumulated in the area during the preceding local productive season (March to May), a trend consistently found in seasonal temperate ecosystems (e.g. Serret et al., 1999 and references therein, Arístegui and Harrison, 2002).

Interestingly, González et al. (2002) measured NCP rates in April–May 1997 averaging ca. 163 ± 146 mmol O_2 m^{-2} d^{-1}, while negative values were found by these authors in September–October (see

Table 1
Measurements of gross primary production (GPP), community respiration (CR) and net community production (NCP) in the open Atlantic Ocean

Reference	Province	No. of stations	Date	GPP ($mmol\,O_2\,m^{-2}\,d^{-1}$)	CR ($mmol\,O_2\,m^{-2}\,d^{-1}$)	NCP ($mmol\,O_2\,m^{-2}\,d^{-1}$)
Duarte et al., 2001	NAST-E	33	Several	81 ± 8	119 ± 9	
Serret et al., 2001	NAST-E	3	June	42 ± 22	150 ± 26	-111 ± 17
González et al., 2002	NAST-E	3	Spring	280 ± 195	117 ± 54	163 ± 146
		3	Autumn	35 ± 9	300 ± 214	-265 ± 218
This work	NAST-E	3	September	41 ± 10	71 ± 19	-33 ± 14
Arístegui and Harrison, 2002	NAST	8	September	(P_{C13}) 44 ± 4	(R_{ETS}) 62 ± 2	
	(E and W)	8	October	(P_{C13}) 63 ± 7	(R_{ETS}) 63 ± 4	
Gonzalez et al., 2001	SATL	2	Spring	85 ± 15	200 ± 150	-50 ± 130
		2	Autumn	110 ± 10	160 ± 120	-115 ± 135
This work	SATL	5	September	60 ± 8	40 ± 10	20 ± 3

All data based on in vitro changes in dissolved O_2 concentration, except Arístegui and Harrison (2002), where primary production was estimated from ^{13}C incorporation and CR from ETS activity. Means $\pm$ s.e. of euphotic zone integrated values are given for each study.

also Arístegui and Harrison, 2002; Morán et al., 2004). In the Azores Front region, Doval et al. (2001) have measured rates of DOC accumulation in the upper 100 m during August 1998 of $0.47\,mmol\,C\,m^{-3}\,d^{-1}$, i.e., ca. 50% of the negative NCP rates in the NAST-E in May (Serret et al., 2001), and 170% of those measured in September (present study). The consumption of previously accumulated DOC also has been proposed as the mechanism explaining rates of DOC mineralisation, which exceed concurrent primary production rates in the Sargasso Sea (NAST-W) (Hansell et al., 1995; see also Hansell and Carlson, 1998). Although González et al. (2002) attributed the seasonality of NCP exclusively to changes in GPP, the results presented here indicate that the seasonality in CR, and not only in GPP, may play an important role in the long-term metabolic balance in this oceanic province.

Comparison of our results in the SATL is limited by the paucity of independent data (see Robinson and Williams, 2005) (see Table 1). González et al. (2002) sampled seven stations in the SATL, but these NCP results are difficult to compare because only depth-integrated rates are given, with no indication of the individual statistical confidence from the replicated measurements. González et al. (2002) organised their NCP results in the SATL according to the season. However, both subsets include one station located at ca. 5°S as representative of the SATL, which according to the tilting of the isolines of temperature and nitrate is located within the influence of the equatorial upwelling. Actually, the range 5°S–32°N selected as representative of the subtropical oligotrophic gyre for community metabolism, does not coincide with the 10°S–32°N selected by the same authors as representative for temperature and nitrate (González et al., 2002). As the latter agrees well with the boundaries of the SATL province defined by Longhurst et al. (1995), and with the actual location of the gyre according to the vertical structure of the water column in both González et al. (2002) and this study, we will only consider NCP results within this latitudinal band (10°S–32°N) as belonging to the SATL. Still one of their NCP values in this band presents an integrated rate of CR that is >10 times higher than the mean of $116\pm8.5\,mmolO_2\,m^{-2}\,d^{-1}$ ($n=186$) reported for the open ocean in the global dataset compiled by Robinson and Williams (2005) (this dataset can be accessed at http://www.pml.ac.uk/amt/data/respiration.xls). Considering other aquatic ecosystems, the measured rate of ca. $1200\,mmol\,O_2\,m^{-2}\,d^{-1}$ is only similar to the mean areal respiration in freshwater peat bogs (Williams and del Giorgio, 2005). Excluding this result (which was deposited with the global CR database but not included in the analysis of Robinson and Williams, 2005) leaves the dataset in González et al. (2002) with only two data points in both the austral spring and autumn. In both cases, the integrated net metabolism was negative at one station and marginally positive at the other (ca. -180 and $80\,mmol\,O_2\,m^{-2}\,d^{-1}$ in spring and -250 and $20\,mmol\,O_2\,m^{-2}\,d^{-1}$ autumn). This contrasts with our five consecutive measurements of positive

NCP along the central SATL (range 13 ± 12 to 31 ± 10 mmol O_2 m^{-2} d^{-1}).

4.2. Are our data representative?

Comparison of ΔO_2 data of community metabolism with independent measurements or alternative instantaneous rates (e.g., rates of $PO^{14}CP$; see results) is useful in assessing the coherence of the measurements, but tells us nothing about whether those data adequately represent the trophic functioning of the sampled community. This issue is especially relevant for interpreting the differences between our community metabolism data in the SATL and those in González et al. (2002). González et al. (2002) concluded that the net metabolism of the oligotrophic SATL (actually the whole oligotrophic Atlantic) was characteristically net heterotrophic, but punctuated by net autotrophic episodes caused by increases of GPP in response to episodic pulses of new nitrogen into the euphotic zone (see also Gonzalez et al., 2001; Arístegui and Harrison, 2002; Duarte et al., 2004). Karl et al. (2003) and Williams et al. (2004) identified the undersampling of such productive events as the reason for the apparent prevalence of net heterotrophy in the oligotrophic North Pacific subtropical gyre. Our positive NCP data therefore would correspond to a transient episode of high productivity rather than being representative of the metabolism of the plankton community characterising the central SATL.

To explore the correspondence between our instantaneous NCP measurements based on bottle incubations and the rates sustained in situ by the natural community we compare the ΔO_2 NCP rates (24 h) with integrative chemical or ecological tracers of the community metabolism, e.g., O_2 saturation (ca. days to weeks), or biomass structure (ca. days to weeks).

The significant inverse relationship found in the euphotic zone between GPP and the percentage of total chl *a* attributable to cells $<2\,\mu m$ (Fig. 6A) agrees well with current conceptual models (Legendre and Lefevre, 1991; Moloney and Field, 1991; Kiørboe, 1993) and empirical observations (Legendre et al., 1993; Tamigneaux et al., 1999) of the hydrodynamic control of phytoplankton dynamics. This relationship thus suggests that our data are representative of functional plankton communities (see Serret et al., 2001, for a thorough discussion). However, the concurrent lack of a relationship between NCP and the %Chl $a<2\,\mu m$, indicates that CR variability does not conform with the steady-state models of the physical control of plankton productivity.

Assessing the biological activity from the O_2 saturation field is not possible in the ETRA because of the advection of deep O_2 undersaturated waters at the equatorial upwelling. At the Guinea Dome and CNRY stations, an inverse relationship was observed between the vertical distribution of instantaneous NCP, the % O_2 saturation and the chlorophyll *a* concentration. This reflects the highly dynamic nature of these systems, and suggests the uncoupling (in either time or space) of the processes of production and consumption of organic matter (see also Arístegui and Harrison, 2002). Similarly, in the NAST-E, where NCP was <0 throughout the euphotic zone of the three sampled stations, no apparent relationship was found between the spatial distributions of NCP and those of the % O_2 saturation, chl *a* concentration or GPP. A similar maintenance of O_2 supersaturation with net heterotrophy was observed in the euphotic zone of the stratified oligotrophic waters of the NAST-E and ETRA in May–June 1998 (Serret et al., 2001) and in the southern Bay of Biscay during the summer (Serret et al., 1999), which is consistent with a slow consumption of organic matter previously produced in the same water (although not necessarily in the same area).

Interestingly, the central SATL was the only province where the instantaneous trophic balance (NCP) was coherent with the distribution of O_2 saturation (see Results and Figs. 3A and 4C). Moreover such a pattern is in agreement with the spatial distribution of phytoplankton photosynthetic activity and biomass (Figs. 3C and B), and in relation to the vertical structure of the water column and the nitrate field (Figs. 2A and B), which suggests a system close to steady-state, with a tight and rapid recycling of any organic matter produced locally. No indication exists of a recent input of new nitrate or a mesoscale perturbation of the hydrographic field.

It is worth remembering that our stations in the SATL were the only ones located in the central part of a mid ocean gyre in the Atlantic Ocean (see Fig. 1), i.e. away from the proposed sources of organic matter sustaining the net heterotrophic metabolism in the NAST-E (Duarte et al., 2001). The phytoplankton community structure, total biomass and activity were all very similar in

both subtropical gyral provinces (see also Poulton et al., 2006), but CR differed (Figs. 4B and 5). If we express the respective values in the euphotic zone of the NAST-E and SATL as weighted means (i.e. integrated values divided by the euphotic depth), in order to account for differences in the depth of the 1% I_0 at different locations, then the chl *a* concentrations (0.15 ± 0.01 and $0.16 \pm 0.02\,mg\,m^{-3}$, respectively), GPP rates (0.41 ± 0.12 and $0.47 \pm 0.09\,mmol\,O_2\,m^{-3}\,d^{-1}$, respectively), as well as the $\% < 2\,\mu m$ chl *a* (75 ± 1 and $76 \pm 1\%$, respectively) were almost identical. However, rates of CR were 0.27 ± 0.07 in the SATL and $0.72 \pm 0.22\,mmol\,O_2\,m^{-3}\,d^{-1}$ in the NAST-E.

This observation is especially important because the main difference between our net autotrophy measurements in the SATL and the net heterotrophy data of González et al. (2002) is that the stations sampled during AMT cruises 4 and 5 by González et al. (2002) were not actually located in the central part of the ocean gyre, but at its western periphery, near South America, ca. 500–1000 km W from ours. Unfortunately, no O_2 saturation data are presented in González et al. (2002), which prevents us from investigating the idea that their negative NCP data in the SATL were related to the non-steady state of the peripheral communities (as in our data in the NAST-E). Similarly, the two oceanic transects from Canada (42°N) to the Canary Islands (27°N) where Arístegui and Harrison (2002) measured net heterotrophy, traversed through the northern periphery of the NAST.

4.3. Does GPP control NCP in the oligotrophic open ocean?

González et al. (2002), Arístegui and Harrison (2002), Duarte et al. (2004), and Agustí and Duarte (2005) attributed the control of net community metabolism in the open ocean to GPP and nutrient limitation, so that the more oligotrophic, less productive an open-ocean community, the more heterotrophic its net metabolism. However, our positive NCP measurements in the central SATL occurred alongside GPP rates and nutrient stress, which were similar and higher respectively than in the area of the NAST-E with negative NCP (Figs. 2B and 5). In addition, our positive NCP values in the central SATL occurred alongside similar nutrient conditions but with GPP rates 50% lower than those corresponding to the negative NCP in the SATL described by González et al. (2002). Hence net heterotrophy is not always associated with high nutrient stress, and NCP does not always co-vary positively with GPP.

Our results and the comparisons presented here conform with the hypothesis that "changes in P but not in R control the transition from net heterotrophy to net autotrophy" (Arístegui and Harrison, 2002), but only within productive ecosystems and peripheral areas of the gyres where the supply of allochthonous organic matter may sustain high rates and lower variability of CR compared to GPP (see GPP and CR results from 40°N to 10°S in Fig. 5). However, when the isolated central parts of the gyres are considered, changes in CR, possibly influenced by the supply of allochthonous organic matter relative to local GPP, become important in the transition from net autotrophy to net heterotrophy (Figs. 5 and 4).

4.4. The metabolic balance of the oligotrophic open ocean?

The current debate about the net metabolism of oligotrophic pelagic ecosystems has been based on deriving generalised thresholds of GPP for the metabolic balance of plankton communities (e.g., Williams, 1998; Duarte et al., 1999; Agustí and Duarte, 2005), predicting GPP:CR balances from GPP measurements and generalised empirical GPP:CR relationships (e.g., Duarte et al., 2001; del Giorgio and Duarte, 2002), or extrapolating a small number of measurements to entire biogeographic provinces or ocean basins (e.g., González et al., 2001, 2002). These regional to global extrapolations and generalisations derived from snapshots of community metabolism in different oceans assume that (1) *the oligotrophic open ocean* is a single ecosystem, or that the controls and trophic behaviour of the planktonic communities in the different oligotrophic ecosystems are the same, and (2) the magnitude of photosynthesis of any pelagic ecosystem provides sufficient information to predict its trophic balance, i.e. GPP controls NCP.

Our analysis indicates that the latter is not correct. The heterotrophic component of planktonic food webs in the open ocean, and not only GPP, also plays an important role in defining the community metabolic balance, and should play a role in defining and understanding geographical and temporal patterns of NCP. The supply of allochthonous DOM and the complexity of the food web (which may increase the proportion of respiration)

exert a greater influence on the CR than GPP (Serret et al., 2001, 2002 and references therein). This conclusion implies that plankton respiration is not only scaled to primary production, so that generalisations of local observations of net community metabolism or GPP:CR relationships to larger or longer scales may be confusing if only based on the variation of local GPP (Williams, 1998; Duarte and Agustí, 1998; del Giorgio and Duarte, 2002). The decoupling of GPP and CR (Arístegui and Harrison, 2002 and references therein) implies that at low primary production rates the effects on respiration of variations in inputs of allochthonous organic matter and in community structure (Serret et al., 2001, 2002) also need to be considered.

Even biogeographic extrapolations may be misleading whenever the provinces are exclusively based on the response of phytoplankton to nutrient limitation and physical forcing. For example, assuming that the GPP:CR relationships obtained with six and seven data points were valid throughout these provinces, González et al. (2002) calculated that the C deficit in the ca. $18 \times 10^6\,km^2$ of the SATL was ca. 12 times higher than in the ca. $4.5 \times 10^6\,km^2$ of the NAST. Although our data in the NAST-E are consistent with this prediction, a similar calculation from our data in the SATL would lead us to conclude that this is a net autotrophic province of the ocean. However, this would be a similarly spurious statement when based on a small number of data and a single GPP:CR relationship (see also Gonzalez et al., 2001).

The results presented here confirm the conclusion in Serret et al. (2002) that the existence of important differences in the long-term trophic dynamics of distinct regions within 'the unproductive open ocean' makes the universal scaling of CR or NCP to GPP (Williams, 1998; Duarte and Agustí, 1998; del Giorgio and Duarte, 2002) untenable. We suggest that the discussion on the metabolic balance of the open ocean should move on from arguing which is the right model, to looking for where and when each model is correct (Serret et al., 2002).

In this regard, we may ask ourselves whether *the oligotrophic open ocean* does actually exist from a trophic perspective. There are areas of the ocean and periods of the year when oligotrophic conditions prevail, i.e. when primary productivity is limited by the supply of inorganic nutrients to the euphotic zone. However, our results indicate that the nutrient status is not enough to characterise the structure and functioning of ocean ecosystems, as different trophic behaviour exists in similarly oligotrophic but geographically different areas of the open ocean. While any part of the ocean may be considered oligotrophic, ''the oligotrophic open ocean'' does not represent a functional ecological entity nor a specific type of ecosystem. For this reason, even a thorough integration of GPP and CR measurements in different oligotrophic habitats of the world ocean would be difficult to interpret in terms of metabolic balance, because plankton communities that share a low level of primary productivity are not necessarily functioning in a similar manner.

The difficulties in ascertaining the spatial and temporal connection between GPP and CR in the ocean (i.e. the ecosystem scale) may explain the disagreements between comparisons of GPP:CR balance estimations based on methods greatly differing in their scale of measurement or calculation, e.g., geochemical estimates of new or export production and microbiological NCP measurements (Emerson et al., 1995; Duarte et al., 2001; Robinson et al., 2002; Williams et al., 2004). The relationship between NCP and new or export production (see Quiñones and Platt, 1991) is complicated whenever allochthonous organic matter plays a role in the functioning of the ecosystem. The input of allochthonous organic matter to an ecosystem represents a source of energy (potentially affecting CR), and also a source of new organic nutrients (potentially affecting photosynthesis). Differences in the nature and timescale of recycling and remineralisation processes means that the long-term NCP does not necessarily equate to new production, nor constrains export production. For example, the new production of a pelagic ecosystem may be greater than expected from the inputs of inorganic nutrients if allochthonous organic nutrients are remineralised; however, given that the combined efficiencies of remineralisation, assimilation and biosynthesis cannot be 100%, the net metabolism of such an ecosystem, where new and export production may be significant, may be heterotrophic.

Interestingly, this scenario is consistent with the discrepancy observed in the subtropical ocean between the estimates of inorganic nutrient supply to the euphotic zone and measurements of new or export production (Poulton et al., 2006; Doney, 1999; Williams and Follows, 1998), and with differences between the latter and NCP estimates. Observations of net heterotrophy in oceanic systems (NAST-E; Duarte et al., 2001; Robinson et al., 2002) have been criticised because difficulties exist

in envisaging the physical mechanism required to transfer the external input of DOM (Williams and Bowers, 1999). However, the alternative, i.e. that the subtropical open ocean, where a marked thermocline permanently separates a nutrient-depleted surface layer from nutrient-rich deep waters, and where part of the organic matter formed in the upper layer sinks to the deep ocean (as new and export production estimates suggest), is net autotrophic throughout the annual cycle is similarly difficult to conceive if it has to also be regionally isolated. The difficulty here is identifying the mechanism(s) transporting the inorganic nutrients required to support the permanent excess primary production in the euphotic zone (Doney, 1999; Williams and Follows, 1998). We can then conclude that the euphotic zone of oligotrophic and regionally isolated oceanic regions cannot be reasonably expected to be either net heterotrophic or net autotrophic, which possibly indicates that the assumption of isolation is not always correct. All these uncertainties suggest that there is no a priori constraint on the C balance in oceanic regions because both the auto- and heterotrophic metabolism may partly depend on the balance and use of imported materials (nutrients, organic matter), whose relative importance may vary regionally within 'the oligotrophic open ocean'.

4.5. Towards a trophic-biogeographic partition of the world ocean

Biogeography aims to delineate areas of the world where the processes governing either the distribution and abundance, or the activity (e.g., primary production) of organisms are relatively uniform (Platt and Sathyendranath, 1999; Longhurst, 1998). Current biogeographic partitions of the world ocean (Platt and Sathyendranath, 1988, 1999; Longhurst et al., 1995; Longhurst, 1998) are based on knowledge of regional oceanography and the response of phytoplankton to seasonal physical forcing. Given the strong relationships between hydrodynamics, phytoplankton growth and community structure at both spatial and temporal scales (e.g., Kiørboe, 1993; Tremblay and Legendre, 1994), these partitions are considered tools for understanding the functional structure of the entire pelagic ecosystem (Longhurst, 1998; Platt and Sathyendranath, 1999). However the results presented here, which confirm the long/large-scale decoupling of GPP and CR (e.g., Serret et al., 1999; Arístegui and Harrison, 2002), indicate that the environmental forcing of algal growth is not enough to delineate provinces of the ocean characterised by similar trophic structure or rates of net community metabolism.

Moreover, the idea underlying biogeographic partitions is that interactions within provinces are functionally more significant than those between them. This may be correct for isolated areas of the ocean or where allochthonous inputs of organic matter are very small relative to GPP, e.g., the central part of the SATL. However for regionally subsidised, net heterotrophic oceanic provinces (e.g., NAST-E), trophic interactions between provinces also must be taken into consideration. In these situations the relative contribution of locally produced vs. imported organic matter will determine the organisation and net metabolism of the plankton communities (Cole et al., 2000; Jansson et al., 2000; Hanson et al., 2003). The systematic classification of these complexities into a trophic biogeography of the ocean appears necessary prior to addressing the global impact of the marine biota on the biogeochemical carbon cycle.

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