

The metabolic balance of the planktonic community in the North Atlantic Subtropical Gyre: The role of mesoscale instabilities

Abstract—We have studied the net community production (NCP) balance in the Eastern region of the Subtropical North Atlantic during two cruises, in August 1998 and April 1999. In August, heterotrophic bacteria were more abundant than picophytoplankton, which resulted in net heterotrophy (NCP = $-129 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1} \pm 18$; mean \pm SE), whereas these differences in plankton components were not apparent in April 1999, when the community was in metabolic balance (NCP = $-13 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1} \pm 19$). In April, the metabolic balance of microplankton communities was net heterotrophic outside (NCP = $-57 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1} \pm 26$) and lower than inside (NCP = $19 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1} \pm 19$) the mesoscale structures present in the area (subtropical front, cyclonic eddy Leticia, and the Great Meteor Tablemount). Positive NCP inside the cyclonic eddy (NCP = $20 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1} \pm 17$) was due to lower respiration rather than to higher gross primary production rates. Gross extrapolation suggests that the regional organic carbon deficit within the Eastern Subtropical Gyre ($0.98\text{--}1.88 \text{ Gt C yr}^{-1}$) should increase by $\sim 14\%$ and 52% in the absence of mesoscale structures.

The balance between microbial production and respiration determines the net community production (NCP) of the microbial community. When production exceeds respiratory losses, a net synthesis of organic carbon occurs, whereas a negative balance represents a net demand for an allochthonous supply of organic carbon or for the endogenous dissolved organic carbon reservoir. Recent studies have reported a tendency for respiration to exceed photosynthesis in oligotrophic regions of the ocean, resulting in a deficit of organic carbon (e.g., del Giorgio et al. 1997; Duarte and Agustí 1998; Duarte et al. 1999). However, other studies have argued that the open ocean as a whole is not substantially out of organic carbon balance (e.g., Williams 1998). Thus the issue, still unresolved, is important, since open ocean regions may contribute up to 80% of the global carbon export from the euphotic zone (Karl et al. 1996).

The controversy on the community metabolism of oligotrophic oceanic waters depends critically on the possibility of the existence of episodic pulses of enhanced net primary production, which can sustain extended periods of net heterotrophy (e.g., del Giorgio et al. 1997). Such pulses may be fuelled by nutrient injections associated with mesoscale features such as eddies (e.g., Oschlies and Garçon 1998; McNeil et al. 1999), seamounts (e.g., Odate and Furuya 1998), and fronts (e.g., Pereira-Brandini et al. 2000). Because of their sporadic biological response and/or occurrence in space and time, the possible role of these mesoscale instabilities in providing transient pulses of NCP remains hypothetical.

Two oceanographic cruises were conducted in the Eastern North Atlantic Subtropical area to study the temporal and spatial variability in the functioning of an oligotrophic eco-

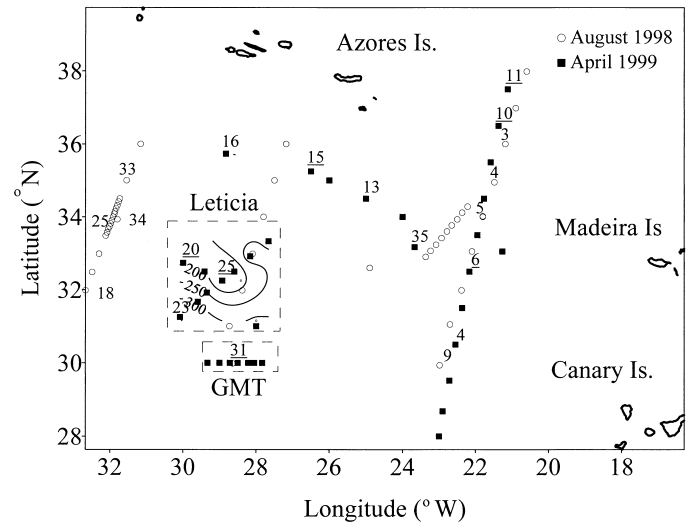


Fig. 1. Cruise tracks of BIO *Hespérides* showing CTD stations sampled in August 1998 and April 1999. Station number indicates that there are metabolic balance measurements and those underlined are within mesoscale features. A contour plot of the depth (m) of the 16°C isotherm is included to show the location of Leticia.

system. Here we report an analysis of the microbial plankton metabolism to test whether oligotrophic ecosystems are in metabolic balance and to evaluate the possible contribution of mesoscale instabilities, such as the subtropical front (STF), a cyclonic eddy (Leticia), and the thermocline excursions induced by the presence of the GMT (30.0°N, 28.5°W). At each station, seawater was collected with a GO Rosette equipped with 24 \times 12 liter Niskin bottles and a conductivity, temperature, depth probe (CTD) (Neil Brown Mark III). Inorganic nutrients were measured colorimetrically by Continuous Flow Analysis, by use of a six-channel Technicon-Bran Luebbe AA II AutoAnalyzer. Nanomolar concentrations of nitrate were measured as described by Oudot and Montel (1988). After preliminary test CTD casts, incubators were set at the in situ temperature and irradiance found at four discrete depths: surface, thermocline, deep chlorophyll *a* maximum, and the depth receiving 1% of the surface irradiance (Table 1). Incubators were in-

Methods—Two cruises (August 1998 and April 1999) on board the Spanish BIO *Hespérides* were carried out in the Eastern region of the subtropical North Atlantic, following the tracks indicated in Fig. 1. During April 1999, we sampled several mesoscale features, the STF ($\sim 34^\circ\text{N}$), the cyclonic eddy Leticia (centered at $\sim 32.4^\circ\text{N}$, 28.7°W), and the thermocline excursions induced by the presence of the GMT (30.0°N, 28.5°W). At each station, seawater was collected with a GO Rosette equipped with 24 \times 12 liter Niskin bottles and a conductivity, temperature, depth probe (CTD) (Neil Brown Mark III). Inorganic nutrients were measured colorimetrically by Continuous Flow Analysis, by use of a six-channel Technicon-Bran Luebbe AA II AutoAnalyzer. Nanomolar concentrations of nitrate were measured as described by Oudot and Montel (1988). After preliminary test CTD casts, incubators were set at the in situ temperature and irradiance found at four discrete depths: surface, thermocline, deep chlorophyll *a* maximum, and the depth receiving 1% of the surface irradiance (Table 1). Incubators were in-

Table 1. Average (\pm SE) and range of selected variables within the euphotic zone in August 1998 and April 1999.

Variable	August	April
Thermocline depth (m)	48 \pm 6 (30–85)	45 \pm 4 (20–75)
DCM depth (m)	82 \pm 6 (50–110)	79 \pm 4 (40–97)
1% light depth (m)	105 \pm 8 (65–130)	112 \pm 3 (100–125)
Temperature ($^{\circ}$ C)	20	18
H. bacteria* bio-mass (mg C m $^{-2}$)	939 \pm 36	521 \pm 32
<i>Synechococcus</i> bio-mass (mg C m $^{-2}$)	60 \pm 6	168 \pm 36
<i>Prochlorococcus</i> bio-mass (mg C m $^{-2}$)	499 \pm 51	327 \pm 34
Picoeukariotes bio-mass (mg C m $^{-2}$)	155 \pm 23	138 \pm 25
Picoautotrophs bio-mass (mg C m $^{-2}$)	714 \pm 50	632 \pm 65

* HDNA.

sulated with expanded polystyrene and placed inside a controlled temperature cooler set at the in situ temperatures for each depth. In situ irradiance was simulated, according to the vertical photosynthetically available radiation (PAR) distribution measured prior to the incubation, by use of a set of blue plastic filters placed on the top of the incubators. To estimate the rates of net production and dark community respiration, seawater samples were transferred into calibrated borosilicate glass bottles with a nominal volume of 130 cm 3 . For each station and depth, six bottles were immediately fixed (zero bottles), six additional bottles were placed into opaque plastic boxes at the bottom of the incubators (dark bottles), and six more were placed at the top of the incubators and received the simulated irradiance (light bottles). Incubations lasted for 24 h. Measurements of dissolved oxygen were made with an automatic Winkler titration on the basis of a photometric end-point detector, as described in Williams and Jenkinson (1982). Respiration rate ($[O_2]_{zero\ bottle} - [O_2]_{dark\ bottle}$), NCP ($[O_2]_{light\ bottle} - [O_2]_{zero\ bottle}$), and gross primary production (NCP + community respiration) were then calculated as μ mol O $_2$ L $^{-1}$ d $^{-1}$. We obtained a pooled coefficient of variation of 0.12% \pm 0.005% (mean \pm SE). The concentration of Chl *a* was determined with a SAFAS flux spectrofluorometer calibrated with a pure Chl *a* extract obtained by high-performance liquid chromatography, after extraction with acetone 90% overnight at 4 $^{\circ}$ C. Bacterial activity was determined by measuring the uptake of radiolabeled leucine, following the method of Smith and Azam (1992). Rates of 3 H-leucine incorporation were corrected to bacterial carbon production values with the conversion factor of 3.1 kg C produced mol $^{-1}$ leucine incorporated. Samples were incubated in the dark and at the in situ temperature (as indicated above). Bacterial and picoalgae abundance were quantified by flow cytometry, following the method described by Gasol et al. (1999) and with use of a bench machine (FACScalibur; Becton & Dickinson) with a laser emitting at 488 nm. To convert cell abundance to carbon biomass, we used the following conversion factors: 20 fg C cell $^{-1}$ for heterotrophic bacteria and 2,100 fg C cell $^{-1}$ for

picoeukariotes, both reported by Campbell et al. (1994), 103 fg C cell $^{-1}$ for *Synechococcus* and 32 fg C cell $^{-1}$ for *Prochlorococcus*, both reported by Zubkov et al. (1998). We differentiated bacteria with apparent high DNA content and bacteria with apparent low DNA, following the method described by Gasol et al. (1999).

We then used the measured metabolic rates to calculate the depth-integrated rates of respiration and gross primary production through the euphotic layer for August and April. The depth-integrated rates provide an accurate representation of the balance between autotrophic and heterotrophic processes in the ocean (Williams 1998).

Results and discussion—The northern boundary of the North Atlantic subtropical gyre is defined by a permanent thermohaline front, the STF, generally located at 34–35 $^{\circ}$ N, which is associated to a branch of the Gulf Stream flowing westward, the Azores Current (AC) (e.g., Gould 1985). A clear biological signature, as indicated by enhanced Chl *a* levels and primary production rates, which in April was centered at about Sta. 10 in transect A and at Sta. 14–15 in transect B (Fig 2). The 16 $^{\circ}$ C isotherm at 200 m marks the STF front, separating warmer and more saline Subtropical water, from colder and fresher northern waters (Gould 1985). We found nitrate concentrations <0.1 μ M in surface waters along the transects (Fig. 2). Variations in the nitrate isopleths followed those of the thermoclines. Higher Chl *a* concentrations were measured associated to the frontal structure (>0.25 mg m $^{-3}$; Fig 2). A marked outcropping of the isotherms and nitrate isopleths were found at Sta. 6 (transect A), possibly reflecting the signature of a mesoscale feature linked to the AC. Associated with this physical structure, a clear increase of Chl *a* was observed at the subsurface Chl *a* maximum (>0.3 mg m $^{-3}$). The meandering eastward flow of the AC can occasionally break off and seed rings in the subtropical water, thus exchanging properties across the AC-STF system (Gould 1985; Pingree et al. 1996; Pingree and Sinha 1998). In this study a cyclonic eddy, named Leticia, detached from the AC was surveyed. The internal temperature structure of Leticia showed an upward displacement of isolines of >100 m over horizontal scales of \sim 100 km (Fig. 2), extending from near surface (\sim 100 dbar) to \sim 1,500 dbar. The horizontal temperature anomaly was >1 $^{\circ}$ C, and the body of water was spinning cyclonically with maximum geostrophic velocities >25 cm s $^{-1}$ in the upper 200 m. Nitrate concentration was <0.5 μ M in the upper 100 m, except at the center of the eddy, where nitrate concentration was >1 μ M at this depth. Associated with the presence of Leticia, the subsurface chlorophyll maximum was located shallower (\sim 50 m), compared with stations outside the eddy (Sta. 17). Previous studies have provided evidence that interactions of oceanic seamounts with ocean currents develop local modification of physical and biological variables (see review in Rogers 1994). In this study, the GMT was surveyed during April 1999. Upward displacement of isotherms was observed over the seamount slope, with development of stratification in the upper 50 m of the water column. We found low (<0.1 μ M) levels of nitrate in surface waters over the seamount; however, vertical extent of the nitrate-depleted water was higher outside (100 m) than over the seamount

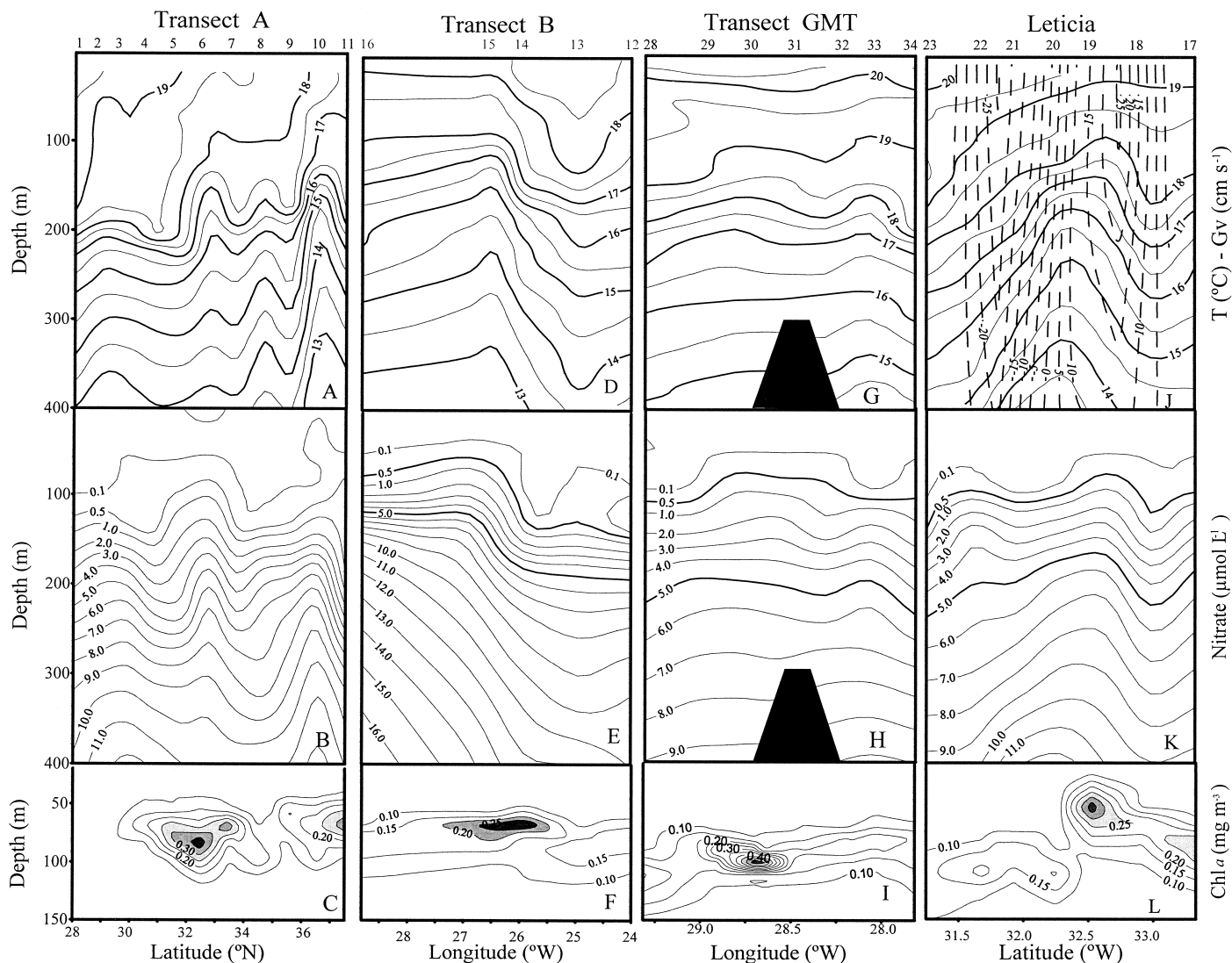


Fig. 2. Vertical distribution of temperature ($^{\circ}\text{C}$, upper panels, continuous line), nitrate ($\mu\text{mol L}^{-1}$, middle panels), Chl *a* (mg m^{-3} , low panels) and geostrophic velocity (cm s^{-1} , upper panel, only for Leticia, discontinuous line), across transect A, transect B, GMT, and across Leticia.

(50 m). Maximum Chl *a* ($>0.3 \text{ mg m}^{-3}$) observed at 100-m depth was associated with a shallower thermocline over the seamount slope (Fig. 2).

Gross primary production was always $<3 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ during both cruises. This is considered extreme oligotrophy and is at the lower end of the distribution of the observations reported in Williams (1998). The following reduced axis major (r.m.a) regression model of gross primary production (GPP) to community respiration (R) ratio as a function of GPP explained 65% of the variance in the ratio and tended to increase as the GPP of the system increased (GPP: $R = 0.977 \text{ GPP}^{1.14}$, $r^2 = 0.65$, $P < 0.0001$, $n = 65$, Fig. 3). The GPP required for open sea communities to become net autotrophic averaged $1 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ ($0.032 \text{ g O}_2 \text{ m}^{-3} \text{ d}^{-1}$; Fig. 3), similar to that derived from comparative analyses of oceanic ecosystems ($0.035 \text{ g O}_2 \text{ m}^{-3} \text{ d}^{-1}$) by Duarte and Agustí (1998). Our results showed that 63% (i.e., 12 of

19) of the depth-integrated profiles were heterotrophic ($R > \text{GPP}$).

During August, the water temperature was significantly higher than during April ($F_{1,77} = 11$; $P < 0.005$, $n = 79$, Table 1). Differences in biomass between picoalgae and heterotrophic bacteria were significant in August ($F_{1,24} = 14.02$, $P < 0.005$, $n = 26$) but not in April ($P > 0.5$, Table 1). *Prochlorococcus* dominated picoalgae biomass and seems to vary inversely with *Synechococcus* abundance. *Prochlorococcus* and *Synechococcus* were more abundant in August ($F_{1,24} = 10.21$, $P < 0.005$, $n = 26$) and in April ($F_{1,24} = 7.68$, $P < 0.05$, $n = 26$), respectively (Table 1), whereas differences in the abundance of picoeukaryotes between both months were not significant ($P > 0.05$). NCP in April was significantly higher than in August ($F_{1,17} = 16.8$, $P < 0.001$, $n = 19$, Fig. 4). R was significantly higher than GPP during August ($F_{1,13} = 60$, $P < 0.0001$, $n = 15$) but not during

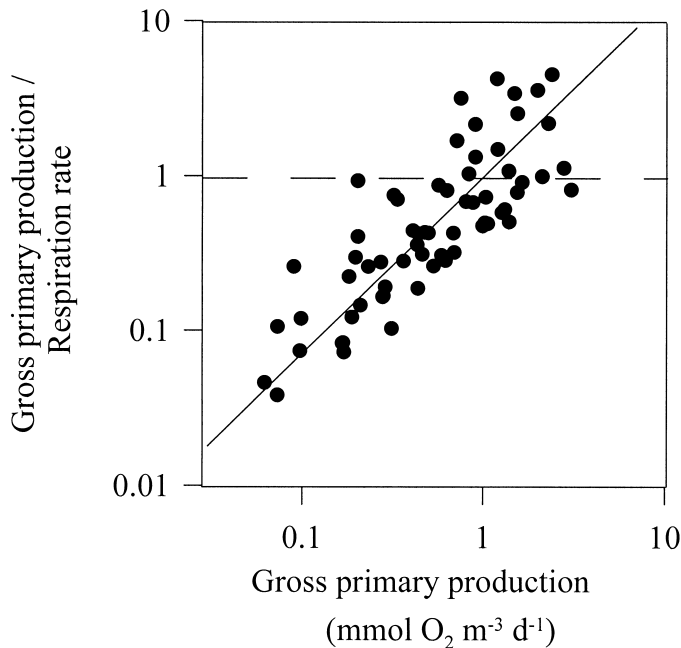


Fig. 3. Parameters of linear regression model, of the form $y = a (\log x) + b$, relating GPP:R and GPP ($\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$). The fitted line is the r.m.a regression. x (GPP), y (GPP:R), a (1.14 ± 0.16), b (-0.005 ± 0.085), $r^2 = 0.65$, $n = 65$, $P < 0.0001$, August 1998 and April 1999.

April ($P > 0.05$). Contrary to the finding by some authors (e.g., Longhurst 1995), we observed a marked temporal variability in microbial metabolism and abundance distribution within this oligotrophic area. In summary, August was a warmer period of net heterotrophy where heterotrophic bacteria biomass outweighed picoalgae biomass within the photic layer, whereas, during the colder month of April, there was metabolic balance ($\text{GPP} = \text{R}$) at which the biomass of the heterotrophic bacteria became equivalent to the picophytoplankton biomass.

Using the average depth-integrated data from April, we observed high spatial variability in the biological activity. We compared stations influenced by the mesoscale features (STE, GMT, and Leticia; Fig. 1) with stations not affected by these hydrodynamic singularities.

Heterotrophic bacteria and picoalgae groups biomass did not change significantly ($P > 0.5$), although they tended to

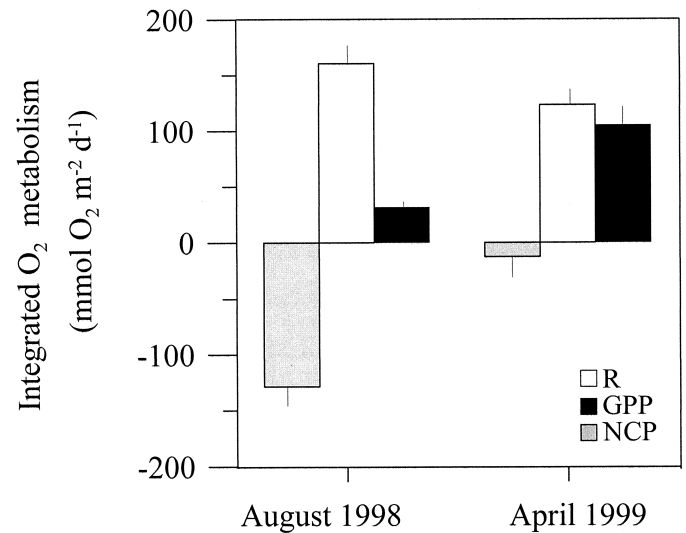


Fig. 4. Average mean \pm SE, depth-integrated rates of oxygen consumption (R), GPP, and NCP within the euphotic layer during August 1998 (8 stations) and April 1999 (12 stations).

be lower within the mesoscale features (Table 2). NCP was significantly higher inside the mesoscale features than outside ($F_{1,10} = 5.66$, $P < 0.05$, $n = 12$), and, particularly in Leticia, net autotrophy was caused by lower respiration rates than outside ($F_{1,5} = 4.21$, $P = 0.09$, $n = 7$) rather than by higher GPP ($F_{1,5} = 0.09$, $P = 0.76$, $n = 7$).

Harris et al. (1997) reported differences in Chl *a* concentration but not in primary production between a cyclonic eddy and adjacent waters. Boyd et al. (1997) observed little variation between rates of new production inside and outside of this eddy. By contrast, high differences between cyclonic eddies and surrounding waters have been observed in primary production rates and Chl *a* concentration (e.g., Falkowski et al. 1991; McNeil et al. 1999) and bacterial abundance (Lochte and Pfannkuche 1987). The TOPEX-POSEIDON altimetry data received indicated that Leticia was detected for ~ 400 d (24 May 1998–28 June 1999) but with a diminishing signal for ~ 3 months after the cruise (Mouriño et al. pers. comm.). The maximum geostrophic velocity within Leticia was about half of that measured within the cyclonic eddy Physalia, of similar characteristics to this ring (Pingree et al. 1996), suggesting that Leticia might be a less energetic water body. Therefore, the little variation encountered in GPP, Chl *a* con-

Table 2. Averaged depth-integrated values (\pm SE) of selected biological inside and outside the mesoscale features and within the cyclonic eddy Leticia (April 1999).

Variable	Outside	Inside	Leticia
Gross primary ($\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$)	85 ± 18	129 ± 21	95 ± 8
Respiration ($\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$)	142 ± 18	110 ± 18	75 ± 24
Net community production ($\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$)	-57 ± 26	19 ± 19	20 ± 17
Bacteria biomass (mg C m^{-2})	960 ± 77	854 ± 50	882 ± 25
Bacteria activity ($\text{mg C m}^{-2} \text{ d}^{-1}$)	30 ± 10	26 ± 5	24 ± 0.01
Total Chl <i>a</i> (mg m^{-2})	11 ± 1	13 ± 1	12 ± 2
<i>Synnechococcus</i> (mg C m^{-2})	228 ± 75	110 ± 20	71 ± 17
<i>Prochlorococcus</i> (mg C m^{-2})	357 ± 63	377 ± 32	366 ± 58
Picoeukariotes (mg C m^{-2})	149 ± 44	126 ± 36	99 ± 11

centration, and picoplankton biomass could be due to surface heating and mixing processes (Harris et al. 1997) or the dynamic equilibrium with the surrounding waters (Ring Group 1981) when the eddy depicts a low-energy stage. High heterotrophic bacterial abundance has been observed both in mature (Harris et al. 1997) and in young eddies (Lochte and Pfannkuche 1987). The mean bacterial abundance within the photic layer observed by Campbell et al. (1997) in the oligotrophic subtropical central Pacific was 4.2×10^5 cell ml⁻¹, similar to the values measured in this study in the oligotrophic waters outside the mesoscale features (4.4×10^5 cell ml⁻¹). Although differences in depth-integrated heterotrophic bacteria biomass were not significant between inside eddy and the surrounding waters (see below, $P > 0.05$), differences in volumetric abundance of heterotrophic bacteria were significant ($F_{1,24} = 7.58$, $P < 0.05$, $n = 26$) between inside the eddy ($3.30 \pm 0.25 \times 10^5$ cell ml⁻¹) and outside the mesoscale features ($4.37 \pm 0.21 \times 10^5$ cell ml⁻¹). These differences arise from the distinct abundance of heterotrophic bacteria at the 1% irradiance level ($F_{1.6} = 5.91$, $P = 0.05$, $n = 8$) between inside the eddy ($2.61 \pm 0.08 \times 10^5$ cell ml⁻¹) and outside the mesoscale features ($3.96 \pm 0.30 \times 10^5$ cell ml⁻¹), because of advection of deep waters with lower bacterial densities to the upper layers. The mean bacterial abundance below the photic layer observed by Campbell et al. (1997) was $\sim 2.2 \times 10^5$ cell ml⁻¹, lower than the bacterial abundance within the eddy (3.30×10^5 cell ml⁻¹). However, the high levels of detrital carbon observed within eddies (Harris et al. 1997) or nutrient concentration in our study may be able to increase the low bacterial abundance to the concentrations reported here.

The reduced respiration rate within the mesoscale features, and particularly within Leticia, can be attributed to (1) lower temperature, (2) differences in bacterial numbers and activity, and (3) maximization of carbon use under oligotrophic conditions. The temperature dependence of the respiration is probably weak and should not influence the lower respiration inside Leticia. To quantify the response of oxygen consumption to the lower temperature within the mesoscale features, we considered a Q_{10} value of 2 for the temperature coefficient of plankton respiration (e.g., Robinson and Williams 1993). We compared one station at the center of Leticia (Sta. 20) with a subtropical station not affected by mesoscale features (Sta. 4). The predicted respiration rate inside Leticia was 7% lower than that observed outside, but it was still 1.6 times higher than the observed rate (expected rate, 83 mmol O₂ m⁻² d⁻¹; observed rate, 51 mmol O₂ m⁻² d⁻¹). Therefore, temperature alone cannot explain the lower respiration rate inside Leticia. The alternative explanation may be the lower bacterial abundance measured in the deeper waters of the water column. Bacterial respiration typically accounted for 50%–95% of the total microbial respiration (Jahnke and Craven 1995)—then changes in microbial respiration are partially explained by changes in bacterial numbers (Griffith and Pomeroy 1995). Another possible explanation may be the maintenance respiration, which in heterotrophic bacteria seems to be higher in oligotrophic systems (del Giorgio and Cole 1998). We estimated the bacterial respiration using the equation of del Giorgio and Cole (1998), $BR = 3.42 \times BP^{0.61}$, where BR is the bacterial respiration and BP is the bacterial

Table 3. Minimum and maximum area ($\times 10^{12}$ m²) and metabolic balance (g C m⁻² yr⁻¹) for the Storms, STF, and outside mesoscale features.

	Minimum		Maximum	
	Area	Metabolic balance*	Area	Metabolic balance*
Storm	0.42 (Leticia)	16	0.75† (Physalia)	162
STF	0.10‡	-102	0.22§	199
Outside	3.23	-511	3.68	-355

* Minimum and maximum metabolic balance, under the assumption of a PQ of 1 for the STF (48 ± 151 g C m⁻² yr⁻¹), inside the Storm (89 ± 73 g C m⁻² yr⁻¹, under the assumption of 1 yr of lifetime and outside mesoscale features (-432 ± 78), considering the average during August, and outside mesoscale features in April.

† Estimated from data in Pingree and Sinha (1998).

‡ Minimum front length of 1,800 km, if a simple linear shape between 20°W and 40°W and minimum front width of 55 km, calculated by a marked depression of isotherms (Fig. 2).

§ Maximum front length of $\sim 2,070$ km, if the actual meandering shape of the 16°C isotherm is 200 m for our study (figure not shown), and maximum front width of 104 km.

|| Total surface area of the Eastern Subtropical Gyre (4.2×10^{12} m²), minus minimum and maximum figures for mesoscale structures.

production, both in $\mu\text{g C L}^{-1} \text{ h}^{-1}$. The mean respiration per bacteria in August (0.24 ± 0.018 fmol O₂ cell⁻¹ h⁻¹) was comparable with the mean value (0.1–0.3 fmol O₂ cell⁻¹ h⁻¹) proposed by Biddanda et al. (1994), was higher than that in April (0.079 ± 0.008 fmol O₂ cell⁻¹ h⁻¹), and was higher outside the mesoscale instabilities (0.086 ± 0.011 fmol O₂ cell⁻¹ h⁻¹) than inside Leticia (0.062 ± 0.009 fmol O₂ cell⁻¹ h⁻¹).

These results suggest that, when bacteria are subjected to limited substrate or inorganic nutrients conditions (summer and outside mesoscale features), bacterial metabolism exhibits different degrees of uncoupling (del Giorgio and Cole 1998), for example increasing the respiration rates. In summary, metabolic balance and picoplankton biomass have an important degree of temporal (between cruises) and spatial (inside and outside the mesoscale features) variability within the subtropical northeastern Atlantic. This variability could potentially explain the net heterotrophic behavior reported for these remote areas (e.g., del Giorgio et al. 1997; Duarte and Agustí 1998; Duarte et al. 1999) by the use of the organic matter produced during earlier periods or inside structures where higher primary production rates were measured. By making a series of assumptions on the number of storm eddies in the area at any time (~ 6 according to Pingree and Sinha 1998), the surface area of the eddies, the STF, and the metabolic balance inside and outside the mesoscale structures (Table 3), it is possible to obtain a gross picture of the contribution of the mesoscale structures to the overall metabolic balance of the region. The organic carbon deficit within the surface area of the Eastern Subtropical Gyre amounts between 0.98 and 1.88 Gt C yr⁻¹ (Table 3). There is a controversy about whether the contribution of mesoscale structures could sustain the nutrient requirements in the oligotrophic oceans. We compiled data from studies in which the influence of the mesoscale eddies within the oligotrophic waters of the open oceans was calculated (see Table 4). We

Table 4. Net metabolic balance and eddy supply in the oligotrophic systems.

Reference	Metabolic balance	Method	Region
Duarte (1998)	P:R = 0.74	Review	Oligotrophic waters
del Giorgio (1998)	P:R < 1	Review	Oligotrophic waters
Williams (1998)	P:R = 1.36	O ₂	NE Atlantic
This study	P:R = 0.72	O ₂	Subtropical NE Atlantic
	Eddy supply (g Cm ⁻² yr ⁻¹)		
Ring group (1981)	2	Net living organic material (Plankton biomass)	Sargasso Sea
Jenkins (1988)	36	New production (³ He)	North Atlantic subtropical ocean
Falkowski et al. (1991)	239	Primary production (fluorescence)	Subtropical Pacific
McGillicuddy and Robinson (1997)	30 ± 9	New production (simulation)	BATS (Sargasso Sea)
McGillicuddy et al. (1988)	16 ± 9	New production (satellite-based)	BATS (Sargasso Sea)
Oschlies and Garçon (1998)	7	New production (simulation and satellite-based)	North Atlantic Ocean
McNeil (1999)	230	New production (moorings)	BATS (Sargasso Sea)
This study	89 ± 73	Net production (O ₂)	Subtropical NE Atlantic

observed that the organic carbon fueled by mesoscale eddies varied by over two orders of magnitude, which might be a consequence of the traditional sampling strategy that tends to undersample these episodic processes (McNeil et al. 1999). The gross extrapolation undertaken in this study suggests that between 12% and 23% of the region contains mesoscale features (not included the seamounts) and that the regional carbon deficit would be increased between 14% and 52% in the absence of mesoscale features (Table 3). Other sources of nutrients that contribute to the new production have been proposed to support the heterotrophic metabolism within oligotrophic gyres. The atmospheric dust deposition modeled by Prospero et al. (1996) fueled a new production of 0.3 g C m⁻² yr⁻¹ within the North Atlantic basin (20–40°N, 20–40°W). The lateral advection within the North Subtropical Gyre modeled by Williams and Follows (1998) provided a new production of between 4.7 and 9.5 g C m⁻² yr⁻¹. The N₂ fixation by *Trichodesmium* is considered another important input of nitrogen into the euphotic layer within the oligotrophic subtropical oceans providing a new production ranging between 0.008 and 2.11 g C m⁻² yr⁻¹ (Capone et al. 1997). Nutrient supplies (wintertime convection, diapycnal diffusion, Ekman flow, and eddy upwelling) described by McGillicuddy et al. (1998) provided a new production of 38 g C m⁻² yr⁻¹. In summary, our observations lead us to conclude that mesoscale features are important sources of organic carbon to the pelagic ecosystems in oligotrophic areas. However, they do not suffice the organic matter deficit measured in the eastern North Atlantic Subtropical Gyre; therefore, alternative sources should be considered, and more intensive study of these features and their seasonal variability are required.

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