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Evidence for a heterotrophic subtropical northeast Atlantic

Abstract—The mean (±SE) depth-integrated gross production (P) of 2,600 ± 271 mg O_2 m^{-2} d^{-1} derived from a compilation of data from nine cruises conducted between 1991–2000 in the subtropical NE Atlantic was found to be significantly lower (*t*-test, $P = 0.005$, $N = 33$) than the mean (±SE) community respiration (R) of 3,821 ± 276 mg O_2 m^{-2} d^{-1}. Two-thirds of the stations investigated were heterotrophic, and the P/R ratio of the communities tended to increase as P increased, such that communities where P < 3,000 mg O_2 m^{-2} d^{-1} tended to be heterotrophic. The tendency for R to exceed P (P/R < 1.0) was statistically significant (Wilcoxon ranked sign test, $P < 0.05$) in the upper and deep layers of the photic zone, with an overall balance between P and R at intermediate depths. These results provide evidence that the subtropical NE Atlantic is a heterotrophic ecosystem, where planktonic communities respire more organic carbon than they produce, thereby acting as net sources of CO_2.

The present debate on the role of planktonic communities in the oligotrophic ocean as carbon sources (i.e., heterotrophic, del Giorgio et al. 1997; Duarte and Agustí 1998; Duarte et al. 1999) or sinks (i.e., autotrophic, Williams 1998; Williams and Bower 1999) is flawed by the limited observational set available for any one oligotrophic oceanic province (Duarte et al. 1999; Williams and Bower 1999). Hence, heterotrophy could be a transient phenomenon rather than the dominant state of oligotrophic oceanic ecosystems (del Giorgio et al. 1997; Williams 1998). We have compiled estimates derived from studies in nine cruises conducted between 1991 and 2000 (Table 1) of planktonic gross production (P) and community respiration (R) that provide compelling evidence for heterotrophy (R > P) in the photic layer of the subtropical NE Atlantic.

Net community production (NCP), community respiration (R), and gross production (P) were determined by oxygen evolution (Strickland 1960) at two to seven depths, depending on cruises, from surface to below the 1% surface irradiance (40 m in upwelling waters, 75 to 100 m in open ocean waters). At each station, seawater samples were collected with a conductivity–temperature–depth (CTD) rosette system equipped with 24-L Niskin bottles. Samples were carefully siphoned using a silicone tube from Niskin bottles into four to eight replicate time-zero, dark, and light 125-ml BOD bottles. Light bottles were incubated in situ or in temperature-controlled incubators simulating the in situ irradiance from dawn to dusk. Dark bottles were kept in temperature-controlled water baths (±0.1°C) at in situ temperature for 24 h. Dissolved oxygen was measured by the Winkler technique, following the recommendations of Carrit and Carpenter (1966), Bryan et al. (1976), and Grasshoff et al. (1983). The entire contents of the bottle were titrated in about 3 min. The titration was controlled by an automated system, with colorimetric endpoint detection (Williams and Jenkinson 1982) or redox endpoint detection (Oudot et al. 1988). The average precision achieved in replicates samples ranged from 0.05 to 0.12 among cruises. R was estimated from the difference in oxygen concentration between the time-zero and dark bottles. Net community production on a daily basis was estimated as the difference between the light and time-zero bottles, corrected for respiration during the night. Gross production was calculated as the sum of net community production and respiration. We tested the effect of the long 24-h incubations conducted over the estimates of P and R by testing for differences between P estimates derived from 12- versus 24-h estimates and by examining R at intervals of 4, 8, 12, and 24 h. Results from these experiments provided no evidence of altered rates in the 24-hr incubations used here, which was consistent with previous results for P in the area (Marañón et al. 2000). The data set contained estimates of depth-integrated community metabolism for 33 stations (≥4 depths) and an additional 147 estimates of volumetric community metabolism in surface and deep chlorophyll *a* maximum waters (Table 1).

The estimates of gross production yield a significantly lower (*t*-test, $P = 0.005$, $N = 33$) mean (±SE) areal P of 2,600 ± 271 mg O_2 m^{-2} d^{-1} compared to the mean (±SE) R of 3,821 ± 276 mg O_2 m^{-2} d^{-1} within the photic layer of the subtropical NE Atlantic (P/R ratio = 0.68), which also holds for the data collected in each of the individual years comprised in the data set. Two-thirds of the stations investigated were heterotrophic (Fig. 1), with a tendency for the P/R ratio of the communities to increase as P increased, as described by the fitted regression equation

$$\log \mathrm{P/R} = -3.9 + 1.12(\pm 0.12)\log \mathrm{P}\ (\mathrm{mg\ O_2\ m^{-2}\ d^{-1}})$$

$$(R^2 = 0.72,\ P < 0.00001,\ N = 33).$$

Communities where P < 3,000 mg O_2 m^{-2} d^{-1} tended to be heterotrophic (i.e., P/R < 1, Fig. 2). The analysis of a larger ($N = 147$) data set on volumetric community metabolism confirmed the general tendency for R to exceed P (89% of the estimates) at different depths in the water column (Fig. 3). The tendency for R to exceed P (P/R < 1.0) was statistically significant (Wilcoxon ranked sign test, $P < 0.005$) in the upper and deep layers of the photic zone, with an overall balance between P and R at intermediate depths (Fig. 3).

The results presented portray the subtropical NE Atlantic as a heterotrophic ecosystem, where planktonic communities respire more organic carbon than they produce, thereby acting as net sources of CO_2. This conclusion is consistent with previous indications, derived from limited data sets, of an excess organic carbon demand relative to consumption in this area (Hernández-León et al. 1999; Agustí et al. in press). The values reported here do not represent, however, a time series, so the metabolic balance at the annual time scale remains unresolved. The seasonality of primary production in the area is, however, relatively well known and is characterized by a winter (late January–February) bloom (De León

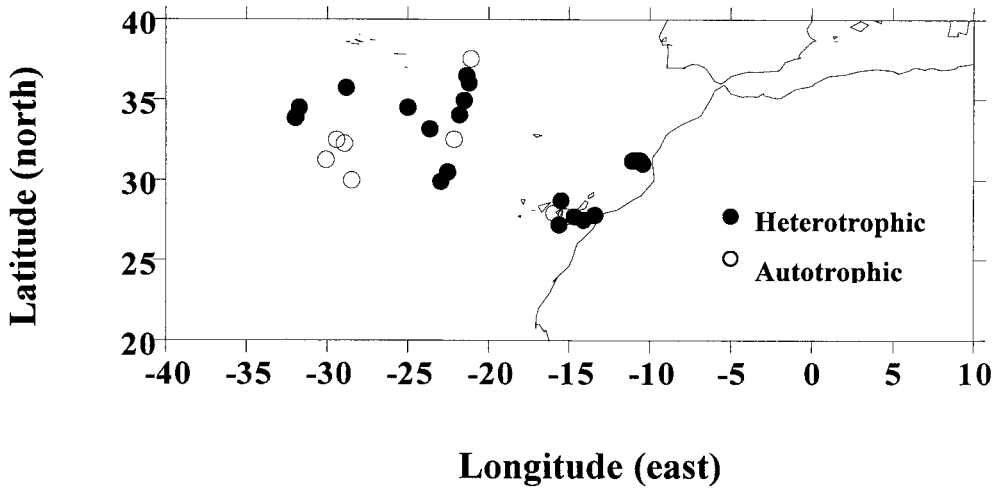

Fig. 1. The distribution of heterotrophic and autotrophic depth-integrated planktonic metabolism in stations studied in 1991, 1992, 1995, 1998, 1999, and 2000 in the subtropical NE Atlantic.

and Braun 1973; Davenport et al. 1999; Pacheco and Hernández-Guerra 1999; Arístegui et al. in press). The cruises conducted did not include this time of the year, so that it is possible that the annual metabolic balance of the region is more balanced than indicated by our results (cf. Sherr and Sherr 1996). A time series of community metabolism on the Canary coast has, however, indicated that the phytoplankton bloom, although associated with a period of net autotrophic metabolism, does not suffice to compensate the organic carbon deficit during the rest of the year (Arístegui et al. in press), so that the metabolic balance of the planktonic community remains heterotrophic at the annual time scale. This conclusion is further supported by the consideration that the climatological area-weighted mean P for the subtropical NE Atlantic (≈600 mg C m^{-2} d^{-1} for a composite of the Northeast Atlantic Subtropical Gyre and the Canary Coastal Current provinces in Longhurst et al. [1995]), somewhat lower than the mean P, calculated assuming a photosynthetic quotient (PQ) of 1, in our data set (975 mg C m^{-2} d^{-1}), is well below the threshold of P (≤1,125 mg C m^{-2} d^{-1}) where the communities sampled were found to be heterotrophic. Yet, the problem of integrating from the daily time scales conforming the empirical base for this study to longer time scales should be best addressed by the use of alternative approaches, such as oxygen and carbon mass balances, which would—if in agreement with our results—strengthen the conclusions reached here. The use of alternative approaches to the use of in vitro oxygen fluxes to test the findings reported here is necessary because of possible changes in the rates during the incubations, although not detected here, which may lead to an overestimation of P (e.g., Bender et al. 1999).

Our analysis, similar to previous studies (del Giorgio et al. 1997; Duarte and Agustí 1998; Williams 1998; Duarte et al. 1999; Williams and Bower 1999), does not include respiration by metazoans and plankton in the ocean's interior, suggesting that the extent of heterotrophy in the subtropical NE Atlantic should be even greater than indicated here.

Table 1. Summary of cruises and the stations occupied in the NE subtropical Atlantic.

Date	Stations occupied (No.)	Depths sampled (No.)
Mar 1991	2	4
Sep–Oct 1992	7	6
Mar 1995	35	2
Nov 1995	6	2
Aug 1998	7	4
Apr 1999	12	4
Aug 1999	4	6
Oct 1999	2	1
Mar 2000	4	1–4

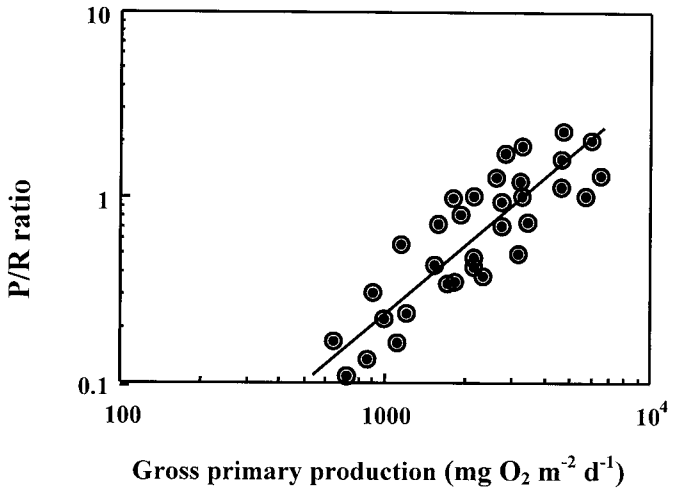

Fig. 2. The relationship between the ratio of depth-integrated plankton community respiration and production (P/R) and the depth-integrated gross production (P) in the subtropical NE Atlantic. The solid line represents the fitted regression equation.

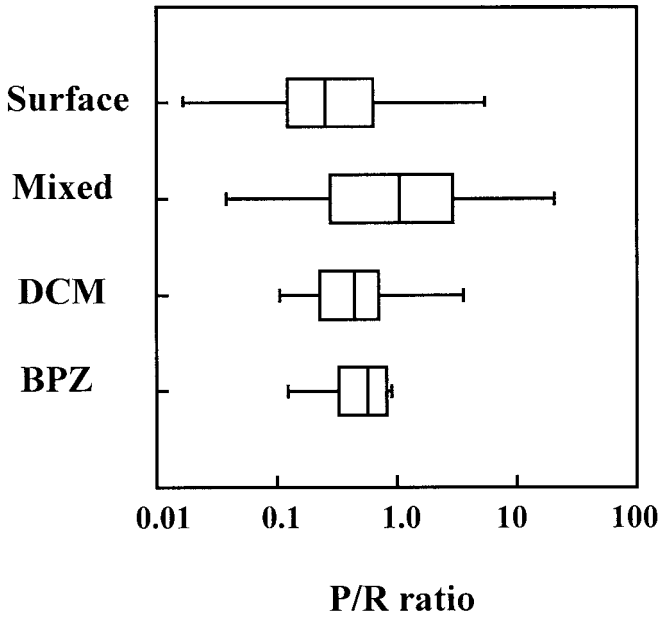

Fig. 3. The distribution of the P/R ratio at different depths in the subtropical NE Atlantic. Surface (~5 m), mixed (30–50 m), deep chlorophyll *a* maximum (DCM, 50–110 m), and bottom of photic layer (BEZ, the depth receiving 1% of the surface irradiance [60–130 m]). The boxes enclose the 25 and 75% percentiles of the data, the central line represents the median, and the bars encompass 95% of the data.

Metazoan zooplankton, in particular, have been found to respire an equivalent to 7.4% of the primary production in the area studied (Hernández-León et al. 1999), which should enhance the heterotrophy of the system. Provided the mean vertically integrated P/R ratio in the data set and an annual primary production of 1.14 Pg C in the 5.26 10^6 km^2 covered by the subtropical NE Atlantic (Northeast Atlantic Subtropical Gyre and Canary Coastal Current provinces in Longhurst et al. [1995]), we calculate (assuming PQ = respiratory quotient = 1) a conservative annual CO_2 release of about 0.5 Pg C yr^{-1} by the planktonic community.

The organic carbon needed to support the net CO_2 production of planktonic communities in the subtropical NE Atlantic must be supplied by lateral inputs from the productive, upwelling areas in the NW African coast and atmospheric deposition. Robust evidence for the presence of significant lateral inputs of organic carbon to the subtropical NE Atlantic has been derived from the analysis of sediment trap arrays (Fisher et al. 1996). Upwelling filaments, stretching offshore from the productive NW African coast to the open ocean, have been shown to be effective mechanisms to transfer organic carbon laterally to the subtropical NE Atlantic (Arístegui and others 1997; Barton et al. 1998; Pacheco and Hernández-Guerra 1999). In addition, the subtropical NE Atlantic is known to be the province of the ocean with the highest atmospheric deposition (Barton et al. 1998), although the organic carbon delivered in this form remains to be quantified. This analysis provides evidence for a dominance of heterotrophy in the subtropical NE Atlantic and confirms the conclusion that the biota of oligotrophic oceanic systems affected by allochthonous inputs of organic matter act as CO_2 sources.

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The heterotrophic bacterial response during a mesoscale iron enrichment experiment (IronEx II) in the eastern equatorial Pacific Ocean

Abstract—The response of the heterotrophic bacterial community to iron addition was determined during the mesoscale iron-enrichment experiment conducted in the eastern equatorial Pacific during May–June 1995 (IronEx II). Bacterial abundance and ^{3}H-leucine incorporation rates were measured for samples collected from the middle of the mixed layer (15 m) over the course of the iron-induced phytoplankton bloom and its decline. Bacterial abundance and productivity increased 1.7- and threefold, respectively, compared to un-enriched waters. Specific growth rates of heterotrophic bacteria increased three- to fourfold. These results demonstrate that iron addition to this high-nitrate, low-chlorophyll region affects both autotrophic and heterotrophic microorganisms and that bacterial carbon demand can be potentially met by the fivefold increase in photosynthetic productivity in the mixed layer.

Over the last decade, considerable effort has been directed toward understanding the relationship between phytoplankton productivity and the availability of iron, particularly as the reason for the lack of significant autotrophic growth in high-nitrate, low-chlorophyll (HNLC) regions of the open ocean. The results of iron enrichment incubation experiments conducted in the subarctic North Pacific (e.g., Martin and Fitzwater 1988), equatorial Pacific Ocean (e.g., Martin et al. 1991) and the Southern Ocean (e.g., de Baar et al. 1990), as well as in situ Fe enrichment experiments conducted in the equatorial Pacific (e.g., Coale et al. 1996) and the Polar Front in the south of Australia (Boyd et al. 2000), strongly support the idea that phytoplankton growth in HNLC areas are limited, at least in part, by the availability of Fe. These studies have focused primarily on the phytoplankton response to an alleviation of Fe deficiency, presumably because of the crucial role of Fe in photosynthesis, chlorophyll synthesis, and nitrate assimilation. Heterotrophic bacteria have been less studied despite their numerical dominance in oligotrophic waters (e.g., Fukuda et al. 1998) and their importance in the cycling of carbon and nutrients, including iron (Tortell et al. 1996). The few studies examining iron limitation of heterotrophic bacterial communities have reached contradictory conclusions, and the relative importance of iron versus dissolved organic matter in controlling the rates of bacterial growth in HNLC regions is still unclear.

Previous incubation experiments in Fe-depleted regions have suggested that Fe enrichment may affect heterotrophic bacteria, either directly by the alleviation of Fe limitation or indirectly through the effects of enhanced phytoplankton growth and the increased supply of dissolved organic matter suitable for bacterial utilization. During experiments conducted in the coastal Southern Ocean (Gerlache Strait), Pakulski et al. (1996) found that Fe enrichment increased both heterotrophic bacteria abundance and cell-specific growth rates. These experiments, conducted in the dark and in the absence of phytoplankton and bacterivores, suggest a direct stimulation of heterotrophic bacterial growth by Fe enrich-