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Decoupling of primary production and community respiration in the ocean: implications for regional carbon studies

Javier Arístegui[1,*], William G. Harrison[2]

[1]Universidad de Las Palmas de Gran Canaria, Facultad de Ciencias del Mar, Campus Universitario de Tafira, PO Box 550, 35017 Las Palmas de Gran Canaria (Canary Islands), Spain

[2]Biological Oceanography Section, Ocean Sciences Division, Bedford Institute of Oceanography, PO Box 1006, Dartmouth, Nova Scotia B2Y 4A2, Canada

ABSTRACT: Primary production (*P*) and community respiration (*R*) were measured *in vitro* along 2 transects of a trans-oceanic section crossing the oligotrophic North Atlantic waters, and during a drifter experiment in the eutrophic waters of the Northwest Africa upwelling system. Our results indicate that the scales of variability of *P* and *R* are different, *R* being less variable than *P* in the 2 studies. In the first transect of the oceanic study, the mean *P*:*R* ratio was <1 (0.8), while in the second transect it was >1 (1.1), the difference being statistically significant. The cause was a significant increase in *P* in the second transect, which was decoupled from changes in chlorophyll *a* (chl *a*) or *R*. In upwelling waters, however, *R* was always significantly lower than *P* (*P*:*R* > 1), and enhancements in *P* were paralleled by increases in chl *a* but not in *R*. The close correlation between the *P*:*R* ratio and *P* (and the lack of correlation between *P*:*R* and *R*) supports the view that changes in *P* but not in *R* control the transition of the system from net heterotrophy to net autotrophy (in our study at $P > 56$ mmol C m^{-2} d^{-1}). The observed decoupling between *P* and *R* at temporal scales of days to weeks, has strong implications for addressing metabolic balances from *in vitro* experiments carried out during limited field samplings. We conclude that unless the scales of variability are established for the 2 metabolic rates, and particularly for *P*, it will not be feasible to accurately establish regional metabolic balances at seasonal to annual scales.

KEY WORDS: *P*:*R* decoupling · Primary production · Community respiration · North Atlantic · NW Africa upwelling

INTRODUCTION

Oceanic ecosystems contribute roughly half of the primary production (*P*) to the biosphere (Field et al. 1998). However, their role as regional biological sources or sinks of CO_2 is controversial. Recent studies compiling historical *in vitro* data of *P* and microbial community respiration (*R*) suggest that *R* exceeds *P* in oligotrophic seas (del Giorgio et al. 1997, Duarte & Agustí 1998, Duarte et al. 1999, Serret et al. 2001, Hoppe et al. 2002). If this is true, these extensive regions would behave as biological sources of CO_2, which in turn would have great implications for global biogeochemical cycles (Geider 1997, Williams 1998, Williams & Bowers 1999). To account for this heterotrophic situation, oxidation of allochthonous organic matter must exceed local photosynthetic production at an annual scale.

Ocean margins are known to export significant amounts of dissolved and suspended particulate organic carbon to the open ocean; thus, playing a key role in the marine biogeochemical cycling of carbon (Walsh 1991, Bauer & Druffel 1998, Liu et al. 2000, Wollast & Chou 2000). This situation is particularly noticeable in some eastern boundary regions, like the subtropical Northeast Atlantic, where net hetero-

*E-mail: jaristegui@ccbb.ulpgc.es

trophy seems to be the dominant state for the upper pelagic community (Hernández-León et al. 1999, Bode et al. 2001, Duarte et al. 2001, Serret et al. 2001, Hoppe et al. 2002). However, whether these export fluxes account for the overall oceanic shortfall resulting from comparing *in vitro* measurements of *P* and *R* (Duarte & Agustí 1998, González et al. 2001, Serret et al. 2001) is unclear.

A complementary and non-excluding hypothesis to explain the *P*:*R* imbalances would be that *P* is significantly underestimated at regional scale by *in vitro* data, as a result of misinterpreting the short-term, time-space variability of the 2 metabolic processes during field sampling. Although this hypothesis has been suggested before, to our knowledge, there are no *in vitro* field studies that support it. In contrast, in a former lagrangian experiment designed specifically to address the coupling between gross oxygen production (*P*) and *R* in surface planktonic communities, Williams (2000) observed no evidence for a clear temporal separation between *P* and *R*. The latter study, however, was carried out during a spring phytoplankton bloom event in the temperate North Atlantic, a situation which is infrequent in tropical and subtropical waters. Here, we present data on *P* and *R* obtained by *in vitro* measurements from 2 studies (a trans-oceanic section and a drifter experiment), performed during a JGOFS (Joint Global Ocean Flux Study) cruise carried out in the subtropical North Atlantic. The studies allowed us to have a temporal resolution of days to weeks. As we show in this paper, the scales of variability of *P* and *R* are different, leading to a time and space decoupling (lack of correlation) of both rates, and therefore to changes in the *P*:*R* ratio. In the short term, *P* is more variable in time and space than *R*, and therefore more susceptible to be underestimated at seasonal to annual scales through limited oceanographic cruises.

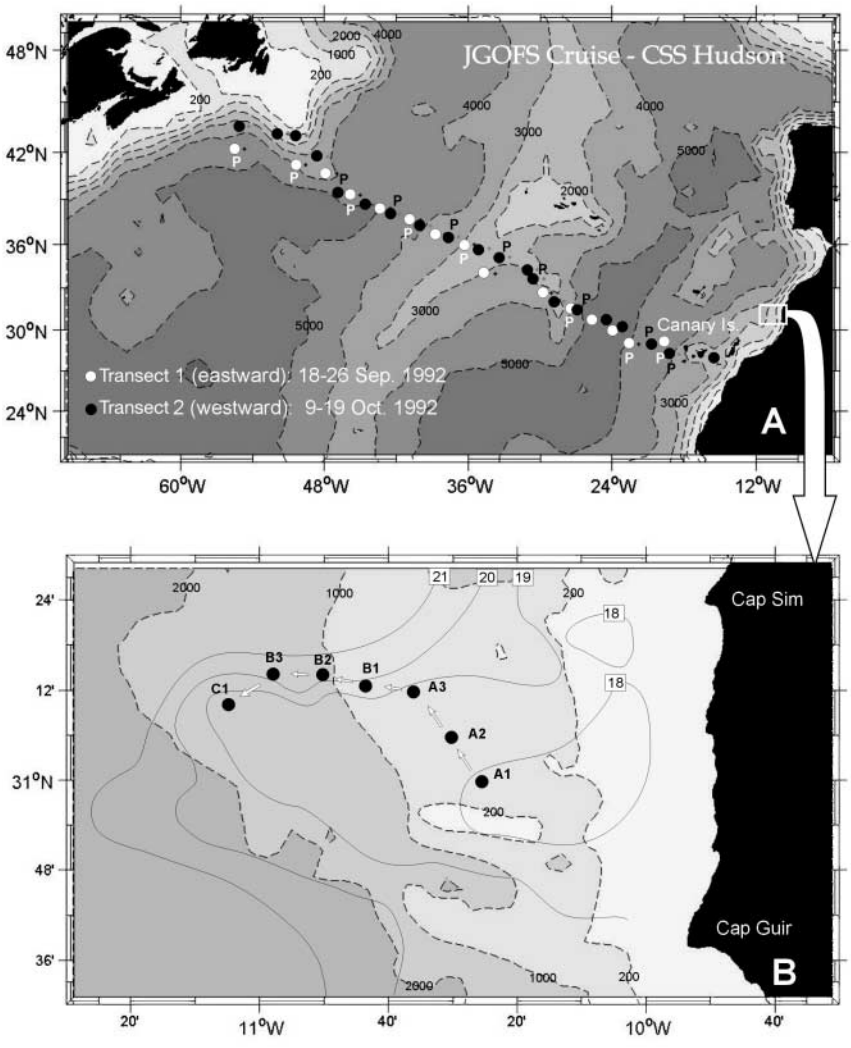

Fig. 1. Map of stations sampled during the oceanic section (A) and the drifter study in the Northwest Africa upwelling waters (B). *P*, in Transects 1 (white) and 2 (black) of the oceanic section, indicates stations where primary production measurements were performed. A1 to C1 in map B correspond to 7 stations where daily *in situ* incubations for metabolic rate processes were conducted. The stations were selected by following a free-floating drifter with sediment traps (the white arrows indicate the track of the drifter). Sea surface temperature is superimposed on the map (see Head et al. 1996 for details)

MATERIALS AND METHODS

Sampling and hydrographic measurements. Temperature, salinity, chlorophyll *a* (chl *a*), *P* and *R*, together with other parameters not reported in this work, were measured during 2 JGOFS studies conducted in the North Atlantic on board the CSS 'Hudson', during September and October 1992.

The first study corresponded to a trans-oceanic section extending from the coast of eastern Canada to the Canary Islands (Fig. 1). Two transects were studied with a time lag between them of 3 to 4 wk (W to E, 18 to 26 September; return E to W, 9 to 19 October). A total of 35 hydrographic stations were sampled along the 2 transects. The stations were occupied twice daily; once in the morning ~09:00 to 10:00 h and once in the evening ~20:00 to 21:00 h (local time). Based on this

routine sampling regimen, station spacing varied from ~100 n mile (between daytime stations) to ~130 n mile (between evening-next morning stations) (see details in Harrison et al. 2001).

The second study was carried out in the upwelling regime of Northwest Africa, at Cape Guir, during the course of time between the 2 oceanic transects. At this location, a giant upwelling filament is frequently observed in satellite images extending 100 km offshore (e.g. Van Camp et al. 1991). The filament is linked to a large cyclonic eddy, which was identified during the period of study, by means of a hydrological survey run by scientists at the University of Rostock, on board the RV 'A. von Humboldt'. Seven consecutive daily *in situ* incubations for rate processes were carried out following a free-floating sediment trap array. The trap was initially deployed in the eastern margin of the cyclonic eddy, at approximately 31° N, 10.5° W. Each day, the new incubation was deployed near the position of the trap. The trap drifted to the west and northwest following the periphery of the eddy, to approximately 31.3° N, 10.8° W after the 7 d experiment (Fig. 1) (see details in Head et al. 1996).

Water samples were collected with a rosette-style system equipped with 8 l Niskin-type bottles, with Teflon-coated internal springs, a CTD (Sea-Bird 911), fluorometer (Aquatracka) and 4π submersible light meter (Li-Cor; LI-193SA PAR sensor). Temperature, salinity and depth were logged at 1 m intervals from the CTD down trace. Additional samples for microplankton respiratory activity were collected down to 100 m along the oceanic section, using a submersible pumping system (Herman et al. 1984). Incident radiation was recorded continuously from a deck-mounted PAR sensor (Li-Cor, same as submersible sensor).

Chl *a* and carbon-determined *P*. Chl *a* samples were obtained from 18 depths in the upper 200 m along the oceanic section and from 6 depths in the upper 40 m during the upwelling study. Chl *a* was determined on acetone (90%) extracts of replicate (100 ml) samples concentrated on glass-fibre filters (Whatman GF/F). The fluorometric method of Holm-Hansen et al. (1965) was employed using a Turner Designs instrument.

Water from 7 depths was collected at 16 stations to measure the uptake rates of ^{13}C-bicarbonate (P_{C13}) in on-deck incubation experiments along the oceanic section (Harrison et al. 1993). The depths sampled for these experiments were chosen to correspond to the 60, 30, 12, 6, 3, 1 and 0.5% light penetration depths (down to 80 to 130 m), as determined by the rosette-mounted submersible light meter. After addition of isotope tracers ($H^{13}CO_3$: 0.2 µM) to 500 ml samples dispensed into clear polycarbonate bottles, samples were incubated for ~3 h in attenuated (perforated nickel screen) clear acrylic incubator tubes cooled with surface seawater under natural light conditions. Following incubation, particulates were concentrated on pre-combusted glass-fibre filters (Whatman GF/F) that were dried and later analysed for carbon content and isotope ratios by mass spectrometry using a Tracermass Stable Isotope Analyzer (Europa Scientific). Carbon uptake rates were calculated using equations described by Hama et al. (1983). Daily P_{C13} were approximated by multiplying measured hourly rates by 12.

In the upwelling study, *P* was estimated by ^{14}C-bicarbonate uptake experiments (P_{C14}) in water samples incubated *in situ* in polycarbonate bottles deployed in drifting arrays. Samples were collected at about 05:00 h at standards depths (1, 5, 10, 15, 20, 25, 30 and 40 m, the latter depth being well below the base of the euphotic zone) using Niskin bottles mounted on a hydro-wire, deployed at sunrise (07:00 h ± 30 min) and recovered at sunset (19:00 h ± 1 h). Comparisons of *P* measurements using ^{13}C and ^{14}C gave equivalent estimates, i.e. regression intercept 0, slope not statistically different from 1.0. Neither in the ^{13}C- nor in the ^{14}C-uptake experiments, was the dissolved organic production fraction estimated.

Gross and net *P* and *R* by oxygen changes. Gross primary production (P_g), net community production (P_n), and dark community respiration (R_d) were determined by oxygen evolution inside borosilicate bottles, at the same depths selected for ^{14}C-uptake experiments, in all the upwelling stations. Water samples were carefully siphoned using a silicone tube into 4 to 5 replicate 't_0', dark and light 125 ml BOD bottles. Light bottles were placed in the drifting arrays and incubated *in situ* as described above. Dark bottles were kept in temperature-controlled water baths (±0.1°C) at *in situ* temperature for 24 h. R_d was estimated from the difference in oxygen concentration between the t_0 and dark bottles. P_n on a daily basis was estimated as the difference between the light and t_0 bottles, corrected for 24 h respiration (i.e. after subtracting 12 h of dark respiration), by assuming that respiration in the dark and light were equal. P_g was calculated as the sum of P_n and R_d.

Dissolved oxygen was measured by the Winkler technique, following the recommendations of Carrit & Carpenter (1966), Bryan et al. (1976) and Grasshoff et al. (1983). The entire contents of the bottles were titrated within ~3 min by means of an automated precise titration system with colorimetric end-point detection (Williams & Jenkinson 1982). The precision achieved in replicates was %CV = ~0.05.

***R* derived from respiratory electron transport system activity.** The respiratory electron transport system (ETS) activity of microplankton communities was measured at 33 stations (17 day and 16 night) placed along the 2 oceanic transects. Water was collected at 11

depths from 1 to 100 m (plus an additional surface sample taken with a bucket), either by means of submersible pump or rosette sampler. No significant differences were observed in ETS activity of replicate samples collected both with the pump and the bottles. Water samples were pre-filtered through 200 µm mesh and poured into acid-cleaned plastic carboys, before being filtered for ETS measurements or used for oxygen consumption experiments. Five to 8 l of seawater were filtered through 47 mm Whatman GF/F filters, at a low vacuum pressure (<⅓ atm). The samples were immediately stored in liquid nitrogen until assayed in the laboratory (2 to 3 wk after the cruise). ETS determinations were carried out according to the Kenner & Ahmed (1975) modification of the tetrazolium reduction technique proposed by Packard (1971), as described in Arístegui & Montero (1995). A time and temperature kinetic study was performed before sample analysis. An incubation time of 20 min at 20°C was used. ETS activities measured at 20°C were converted to activities at *in situ* temperatures by using the Arrhenius equation.

R derived from ETS activity (R_{ETS}) was calculated by converting the ETS data to actual rates using the following regression equation obtained by Arístegui & Montero (1995) for oceanic waters: $\log R_d = 0.357 + 0.750 \times \log$ETS activity (units: mg O_2 m^{-3} d^{-1}; n = 197, $r^2 = 0.75$, $p < 0.0001$).

Fifty R_d data of the above equation were obtained during the present study. Samples for oxygen consumption experiments were collected at 2 to 5 depths from the upper 80 m of the water column and incubated at *in situ* temperatures for 24 h. Comparison of predicted R_{ETS} data using the regression equation generated with the whole data set (197 values) and with the subset (50 values) of R_d data of the present study yield similar results (intercept = 0, slope = 0.96, r^2 = 0.96). However, the general equation explains a higher percentage of variance, since the ranges of R_d and ETS values along the oceanic section were very narrow.

R_{ETS} was integrated in the upper 100 m and expressed in carbon units using a respiratory quotient of 0.8, i.e. the average value obtained by conventional stoichiometry of heterotrophic respiration (Robinson & Williams 1999, and references therein). R_d was integrated in the water column (0 to 80 m) only at the few stations where 4 to 5 depths were sampled in order to compare with derived R_{ETS}.

RESULTS

Oceanic section

Fig. 2 illustrates the vertical distribution of temperature, salinity, chl *a* and derived community respiration (R_{ETS}) along the repeated oceanic section. A sharp temperature and salinity front is evident along the westward transect, at approximately 47 to 49° W, indicating the transition between the cold and fresh Labrador Sea water, and the warm and salty open ocean water of the North Atlantic subtropical gyre. The front is less apparent along the eastward transect, since at that time the section intercepted a warm-core ring, as evidenced by the salinity and temperature signals. The chl *a* maximum deepened from west to east independently of the depth of the thermocline, but following the depth of the nitracline (see Harrison et al. 2001). The chl *a* maximum reached depths greater than 100 m west of the Canary Archipelago, at 20 to 25° W, coinciding with the deepest nitracline level. A high patch of chl *a* (with values > 4 mg m^{-3}) was observed along the second transect associated with the intrusion of Labrador Sea water at 50° W. Another patch of chl *a* (with values > 1 mg m^{-3}) was also found along the westward transects in the waters overlaying a seamount near the Atlantic Central Ridge, at 34° W.

R_{ETS} was rather constant between transects and did not show a significant relationship with chl *a*, suggesting that phytoplankton biomass contributed little to the microbial respiration. Relative R_{ETS} maxima (>0.8 mmol C m^{-3} d^{-1}) were however observed in the western sector of the section. For the first transect, the increase in respiratory activity was associated with the anticyclonic warm Ring. For the second transect, high R_{ETS} values were observed bounding the cold and rich-chl *a* Labrador Sea water. Particularly, high rates extended from the surface to 100 m at the sharp front between Labrador Sea water and Gulf Stream water.

The integrated values of chl *a* (water column), ^{13}C-determined production (P_{C13}, euphotic zone), derived community respiration (R_{ETS}, from 0 to 100 m) and dark community respiration (R_d, from 0 to 80 m), as well as the P_{C13}:R_{ETS} and P_{C13}:R_d ratios, are represented in Fig. 3 for those stations where the 3 properties were measured. The plots do not include those stations where high chl *a* values were observed, since no productivity measurements were performed there. R_d was plotted only for a few stations along the first transect, where 4 or more measurements allowed integration in the upper 80 m. Comparison between integrated R_{ETS} and R_d (Fig. 3) show a good agreement in absolute values, although R_d is a bit lower as a result of the smaller integration depth, adding confidence to the derived respiration from ETS activity.

The along-transect and inter-transect variability was higher in P_{C13} than in R_{ETS} or chl *a* when considering only the common stations for the 3 properties (Table 1). The mean chl *a* and R_{ETS} values were not significantly different between transects (Table 2). Conversely, the

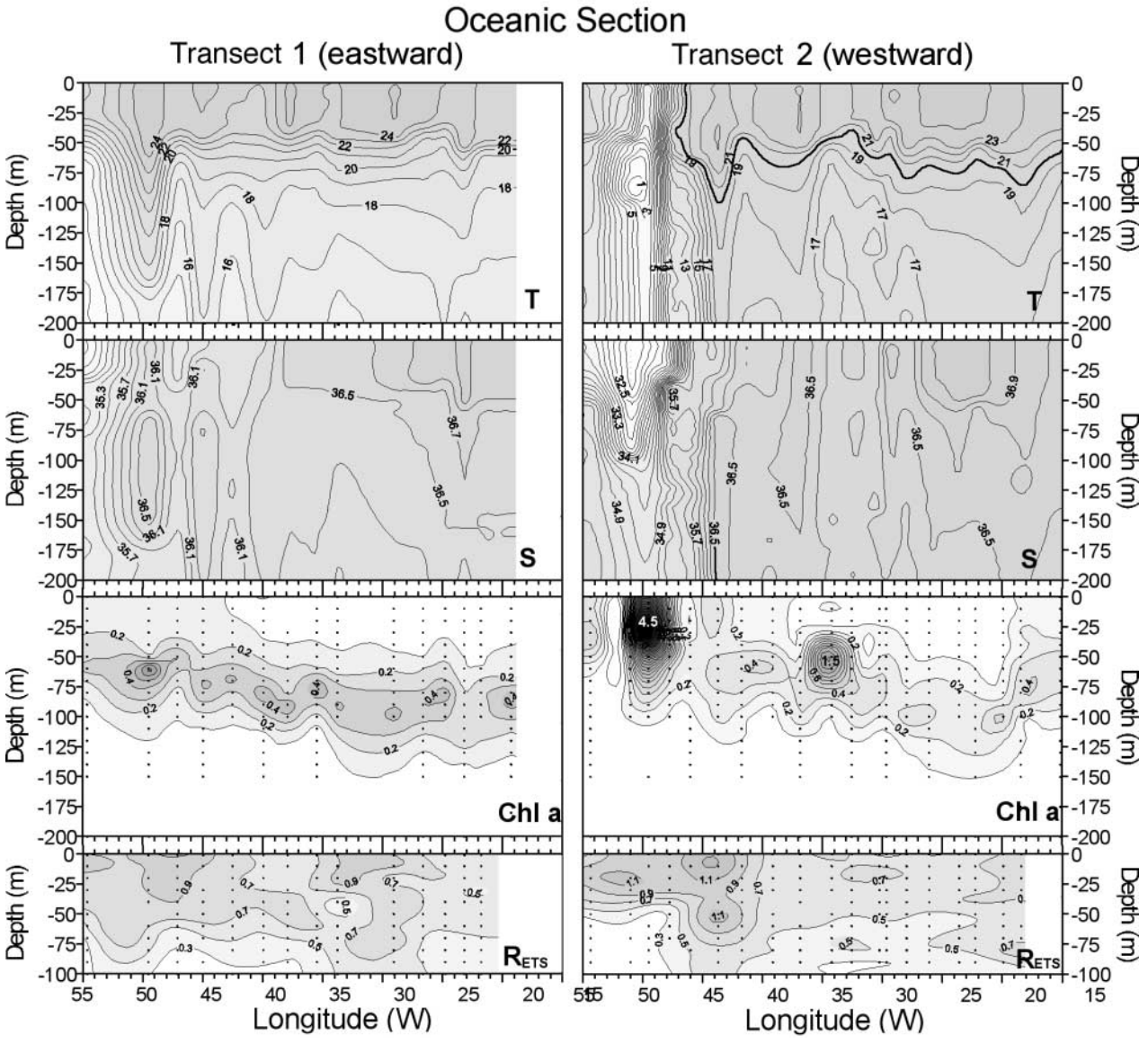

Fig. 2. Vertical sections of potential temperature (T, °C), salinity (S), chlorophyll *a* (Chl *a*, mg m^{-3}), and community respiration derived from respiratory ETS activity (R_{ETS}, mmol C m^{-3} d^{-1}), along the 2 transects of the oceanic section. Notice that the hydrographic front apparent at about 50° W along Transect 2 is obscured by a warm-core ring in Transect 1. See text for conversion details of ETS to respiration.

mean P_{C13} increased significantly along the second transect with respect to the first one. When comparing the mean values of P_{C13} and R_{ETS} for the same stations of the first transect alone, R_{ETS} (59.2 mmol C m^{-2} d^{-1}) is statistically higher than P_{C13} (44.5 mmol C m^{-2} d^{-1}). However, this does not apply to the second transect or the 2 transects together, where the differences in the mean values of the 2 rates are not statistically different (Table 2). The overall mean P_{C13}:R_{ETS} ratio was close to 1, but the mean ratio of the first transect (0.8) was significantly lower than the mean ratio of the second transect (1.1), as a consequence of the P_{C13} inter-transect variability (Table 2).

Upwelling study

The vertical profiles of chl *a*, P_g, P_{C14} and R_d for the 7 *in situ* stations are represented in Fig. 4. R_d and P_g were converted into carbon units using a respiratory quotient (RQ) of 0.8 (see above), and a photosynthetic quotient (PQ) of 1.2, obtained from the slope of the regression equation between P_g and P_{C14} (Fig. 5). The correlations between P_g or P_n and P_{C14} were highly significant (r^2 = 0.94 and 0.96, respectively). As expected, the P_{C14} values laid in the range between P_n and P_g, (Fig. 5), P_{C14} being closer to P_n at high production rates and to P_g at low rates.

During the 7 d experiments, R_d varied little (%CV = 14) compared to the variation in chl *a* (%CV = 54), P_g (%CV = 35.6) or P_n (%CV = 54) (Table 1). This is clearly illustrated in the representation of the integrated values of chl *a*, P_g and R_d at the 7 drifting stations (Fig. 6). Conversely to the oceanic section, R_d was always lower than P_g (i.e. net autotrophic situation), the P_g:R_d ratio ranging from between 1.3 and 2.5.

DISCUSSION

Our results from 2 different marine ecosystems (coastal upwelling and subtropical open ocean waters) show that, regardless of the trophic status of the system and the different approaches used to estimate the metabolic rates, *R* is less variable than *P*. In the oceanic study, this applies both for the along-section and between-transect variability (Table 1). The mean chl *a* per transit also remains constant between the 2 transects of the cruise (if we exclude the 2 particular patches in the westward transect, where no *P* data are available). This contrasts with the significant increase in the mean P_{C13} during the second transect with respect to the first one. Presumably, grazers kept pace with the phytoplankton production maintaining biomass at rather constant levels despite the apparent increase in phytoplankton specific growth rates (e.g. Banse 1992). The oceanic situation differs from the upwelling regime, where the increase in primary production is matched by an increase in chl *a* concentration, indicating a decoupling between phytoplankton growth rate and zooplankton grazing.

Along the oceanic section, R_{ETS}, although less variable than P_{C13}, show enhancements at sites where organic matter generally accumulates. This is the case, for example, of the warm-core ring, which presumably concentrated organic matter in its core as other anticyclonic eddies do (Olson & Backus 1985, Arístegui et al. 1997). Also, the sharp hydrological front between the Labrador Sea waters and the Gulf Stream waters shows a marked enhancement in *R*, which is not paralleled by an increase in chl *a*.

The lack of correlation between *R* and chl *a* supports the view that heterotrophic organisms are the major respirers of the sea (e.g. Williams 1981). Bacterial respiration has been traditionally reported to account for most of the microbial community respiration in the ocean (Williams 1981, Blight et al. 1995, Jahnke & Craven 1995). Thus, changes in bacterial biomass and activity would have to be reflected in the overall microbial respiration (Griffith & Pomeroy 1995). Nevertheless, in a complementary study, Harrison et al. (2001) did not find a significant correlation between microbial respiration and either bacterial biomass or activity for

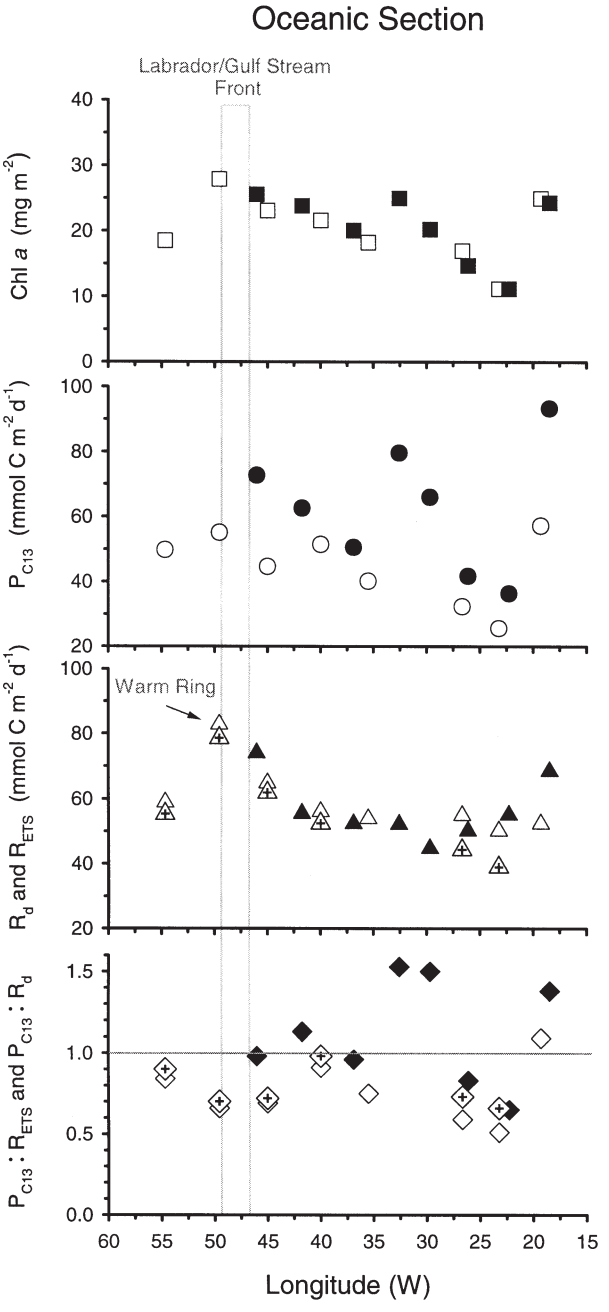

Fig. 3. Zonal variability in column-integrated values of chlorophyll *a* (Chl *a*, water column), ^{13}C-determined production (P_{C13}, euphotic zone), community respiration derived from respiratory ETS activity (R_{ETS}, upper 100 m), and the ratio P_{C13}:R_{ETS} along Transect 1 (open symbols) and Transect 2 (solid symbols). Only those stations where the 3 biological properties were measured are represented. Integrated dark respiration rates (R_d, upper 80 m; crossed triangles) and the ratio P_{C13}:R_d (crossed diamonds) are also plotted for those stations where 4 or 5 sampling depths allowed integration (see text for details). The approximated position of the front between the Labrador Sea waters and the Gulf Stream waters for Transect 2, and the respiration value at the warm-core ring station are indicated. Notice the higher variability in production with respect to respiration, which affects the *P*:*R* ratios.

Table 1. Summary statistics (mean, SD and CV) of chlorophyll *a* (Chl *a*, mg m^{-2}), primary production (P_{C13}, P_{C14}, P_g, P_n; mmol C m^{-2} d^{-1}), community respiration (R_{ETS}, R_d; mmol C m^{-2} d^{-1}), and the *P*:*R* ratio (P_{C13}:R_{ETS}, P_g:R_d) for the oceanic section (Transects 1 and 2, T1 and T2) and the upwelling study (UW). Values in parentheses for T1 and T2 are calculated including only those stations where primary production was estimated. n: number of stations. See text for abbreviations

	Chl *a*			P_{C13}		P_{C14}	P_g	P_n	R_{ETS}		R_d	P_{C13}:R_{ETS}		P_g:R_d
	T1	T2	UW	T1	T2	UW	UW	UW	T1	T2	UW	T1	T2	UW
Mean	19.4 (20.3)	33.0 (21.0)	60.9	44.5	62.8	122.0	135.7	78.1	62.0 (59.2)	62.8 (56.6)	72.0	0.8	1.1	2.3
SD	4.0 (5.2)	41.5 (4.8)	33.0	11.2	19.3	42.3	48.3	42.2	9.2 (10.5)	17.3 (9.8)	10.2	0.2	0.3	0.6
CV (%)	20.8 (25.7)	125.6 (23.0)	54.2	25.1	30.8	34.6	35.6	54.0	14.9 (17.7)	27.6 (17.3)	14.1	24.7	28.8	26.7
n	14 (8)	19 (8)	7	8	8	7	7	7	14 (8)	19 (8)	7	8	8	7

the oceanic section. Recently, it has been suggested that protozoa play a key role in oligotrophic oceanic waters, not only as being the dominant source of dissolved organic carbon for bacteria, but also by being one of the main respirers in microbial food webs (e.g. Nagata 2000). Albeit, bacteria might contribute significantly to *R* in oligotrophic seas and the fact that the role of protozoa was not considered in this process, could have flawed the estimation of the relationship between *R* and bacteria biomass.

As observed in previous studies (Duarte & Agustí 1998, Duarte et al. 2001, González et al. 2001), a highly significant correlation exists between the *P*:*R* ratio and *P*. We show in our study that this stems for the fact that *P*, at short-term scales, is much more variable than *R*. Thus, the predictable close correlation between *P*:*R* and *P* (r^2 = 0.93, including all the data set; Fig. 7), and the lack of correlation between *P*:*R* and *R*, strongly suggest that changes in *P* but not in *R* control the trophic status of the system, and therefore, the transition of the ecosystem from net autotrophy to net heterotrophy and vice versa. This statement has been partly questioned by Serret et al. (2001), who concluded from a latitudinal study across the eastern Atlantic Ocean that not only the overall magnitude of P_g, but also the structure of the planktonic community, greatly influence the *P*:*R* balances. In our study, at *P* > 56 mmol C m^{-2} d^{-1} (~670 mg C m^{-2} d^{-1}), the system would tend to be net autotrophic. About 60% of the oceanic data presented *P*:*R* ratios <1, while the upwelling data presented *P*:*R* ratios always >1. These estimates rely, however, on several assumptions, which may slightly alter the final metabolic balance in oceanic waters, although not the overall conclusions of the work. First, it is not clear whether the ^{13}C and ^{14}C techniques measure P_g or P_n. It is widely accepted that at high production rates the ^{14}C technique approximates to P_n in 12 to 24 h experiments, while at low rates it would approximate more to P_g (e.g. Marra 2002; Fig. 5). In our case, incubations in the oceanic transects lasted only for 2 h and since production rates were low, our ^{13}C uptake measurements would approximate P_g. Unaccounted DOC production would, however, increase the final production lowering the *P*:*R* rates. Nevertheless, if we assume that 12% of carbon production is released directly by algal cells as dissolved organic carbon (see review in Nagata 2000), the *P*:*R* ratios would only vary from 0.8 ± 0.2 to 0.9 ± 0.2 in Transect 1 and from 1.1 ± 0.3 to 1.3 ± 0.4 in Transect 2, resulting in 50% of oceanic data with *P*:*R* < 1. Second, the photosynthetic (PQ) and respiratory (RQ) quotients used in our study represent average values, which in the latter case is obtained from the literature. The reported variability in the average RQ (0.7 to 1.0; e.g. Robinson & Williams 1999) is, in any case, small enough not to have modified substantially the meta-

Table 2. Probability of significance (*p < 0.05, **p < 0.001, ns: not significant) of the difference in the median values between paired comparisons of chlorophyll *a* (Chl *a*, mg m^{-2}), primary production (P_{C13}, mmol C m^{-2} d^{-1}), derived respiration (R_{ETS}, mmol C m^{-2} d^{-1}), and dark respiration (R_d, mmol C m^{-3} d^{-1}), from the oceanic Transects 1 and 2 (T1 and T2). Values in parentheses are calculated including only those stations where primary production was estimated. The analysis of R_d was performed comparing mean volumetric values (obtained from 2 to 5 depths) at 7 stations along T1 and 5 stations along T2. See text for abbreviations. MWRST: Mann-Whitney Rank Sum Test

Variable	p	Test
Chl *a*–T1 vs Chl *a*–T2	ns	MWRST
	(ns)	(*t*-test)
P_{C13}–T1 vs P_{C13}–T2	*	*t*-test
R_{ETS}–T1 vs R_{ETS}–T2	ns	*t*-test
	(ns)	(MWRST)
R_d–T1 vs R_d–T2	ns	*t*-test
P_{C13}: R_{ETS}–T1 vs P_{C13}: R_{ETS}–T2	*	*t*-test
P_{C13}–T1 vs R_{ETS}–T1	*	*t*-test
P_{C13}–T2 vs R_{ETS}–T2	ns	*t*-test

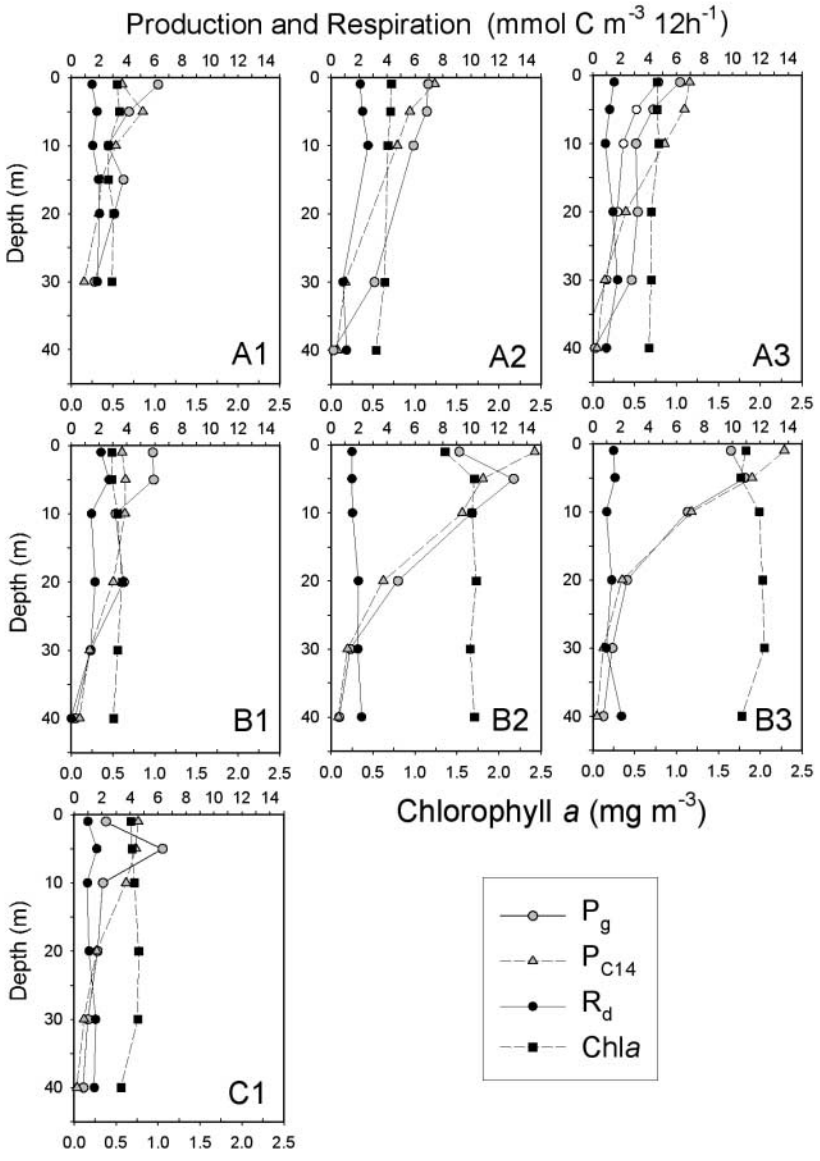

Fig. 4. Vertical profiles of chlorophyll *a* (Chl *a*), gross primary production (P_g), ^{14}C-determined production (P_{C14}), and dark community respiration (R_d) for the 7 stations sampled during the drifter experiment in upwelling waters at Cape Guir (NW Africa). Oxygen-based production (P_g) and respiration (R_d) were transformed to carbon units using, respectively, a photosynthetic quotient = 1.2 and a respiratory quotient = 0.8. See text for details

bolic balance of microbial communities. Third, the statistical analysis used to look for differences between *P* and *R* did not include the oceanic sites where respiration was enhanced, since no productivity measurements were performed there. Hence, although the general pattern of *R* show little spatial and temporal variation related to *P*, we must be aware that *R* can be more variable than *P* in certain specific scenarios. Indeed, hydrodynamical convergence features, like fronts or anticyclonic eddies, or nearshore regions with high loading of allochthonous organic matter, can be sites of strong heterotrophy (Smith & Mackenzie 1987). In these cases, changes in *R* can be greater than in *P*, as observed during the relaxation periods of the NW African upwelling system, when the coastally produced organic matter is spread offshore (J. Arístegui unpubl. data).

Some studies carried out in temperate coastal (Blight et al. 1995, Serret 1999) and oceanic (Williams 2000) waters have shown that *R* increases as a response of organic matter production during intense phytoplankton bloom events. Nevertheless, the time scale of separation of the autotrophic and heterotrophic processes differ among these studies, ranging from an almost perfect coupling of *P* and *R* observed during a lagrangian experiment in oceanic waters (Williams 2000), to a 1 or 2 wk delay of *R* in respect to *P* in coastal studies (Blight et al. 1995, Serret 1999). Blight et al. (1995) explained the metabolic delay on the basis of the nature of the organic matter, and the routes and passage of time of organic material between producers and consumers. Low molecular weight (LMW) compounds exudated by phytoplankton would be readily assimilated by bacteria, inducing a close coupling between autotrophic and heterotrophic processes. Conversely, if the available pool of organic material results from the slower decomposition of organic detritus by a complex microbial community, *P* and *R* would show a marked displacement. In this case, there would be a gradual increase in *R* with time, since microbial food webs (Azam et al. 1983, Sherr & Sherr 1988) with many recycling flows, will tend to homogenise the distribution of energy among their components (Higashi et al. 1993a,b, Nagata 2000). Thus, when the direct exudation of labile organic compounds by phytoplankton is small compared to the organic matter recycled from detritus by the microbial food web, a mismatch between the 2 metabolic processes may occur. This would explain why in temperate coastal ecosystems, smaller peaks in *P* after the larger spring phytoplankton bloom are not generally paralleled by increases in *R* (Blight et al. 1995, Serret 1999). The lack of correlation between *P* and *R* would be even larger when pelagic respiration is mainly based on allochthonous

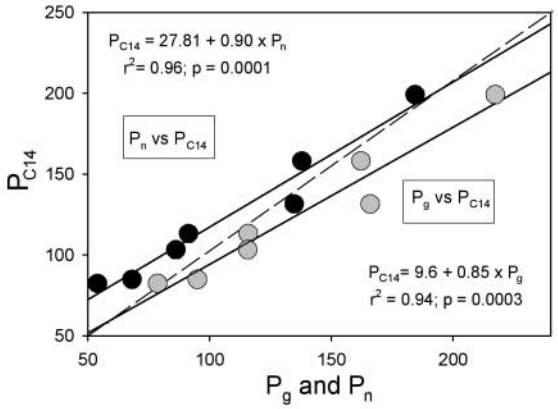

Fig. 5. Relationship between gross (P_g) and net (P_n) community production and the ^{14}C-determined production (P_{C14}) for data of the upwelling study. The dashed line represents the 1:1 distribution. All units are in mmol C m^{-2} 12 h^{-1}

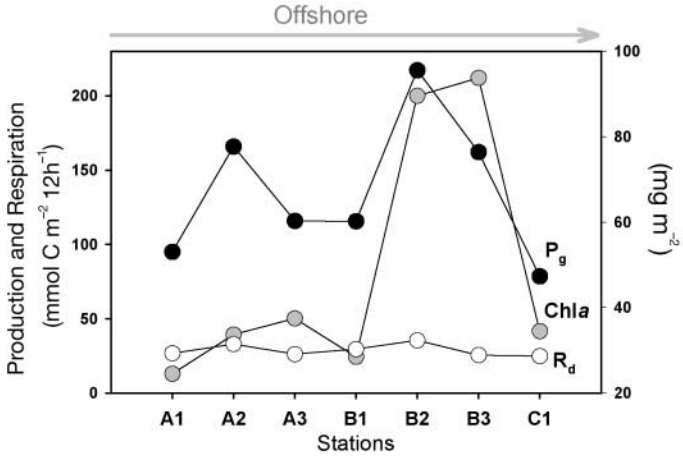

Fig. 6. Variability in column-integrated values of chlorophyll *a* (Chl *a*), gross primary production (P_g) and dark community respiration (R_d) among the 7 stations sampled during the drifter experiment in upwelling waters. Notice the increase in Chl *a* and P_g in B2 and B3, not paralleled by an increase in R_d

inputs of organic matter rather than on phytoplankton autochthonous production, a situation that may take place in transition regions between eutrophic and oligotrophic ecosystems, where surface advective transport prevails (e.g. Duarte et al. 2001).

High rates in *R* with low time/space variability compared to *P*, seems to be the general trend in subtropical waters, where pelagic food webs are dominated year round by small autotrophic and heterotrophic cells. Previous studies (del Giorgio et al. 1997, Duarte & Agustí 1998, Duarte et al. 1999, Serret et al. 2001, Hoppe et al. 2002) have shown that in most situations the balance between the 2 *in vitro* metabolic rates leads to moderate to strong heterotrophy, although it is not clear whether coastal export fluxes may account for the observed heterotrophy in oceanic waters in all instances (Williams 1998, Williams & Bowers 1999).

Our work, in spite of the limitations of the *in vitro* studies, has allowed us to demonstrate, by repeating a trans-oceanic section and by carrying a drifting experiment, that *P* is more variable than *R* at scales of days to weeks in subtropical waters. The variability in *P* would result mainly from mesoscale processes. Pulses of inorganic nutrients into the base of the oligotrophic ocean euphotic zone can be produced by variable-scale events, like internal waves (Venrick 1990, Hernández-León et al. 1999, Uz et al. 2001) or mesoscale eddies (Arístegui et al. 1997, Falkowski et al. 1991, McGillicudy et al. 1998, González et al. 2001). Recent work describing the temporal and spatial variability of organic carbon (Carlson et al. 1994), autotrophic and heterotrohic biomasses (Buck et al. 1996, Campbell et al. 1997) or *P* (Basterretxea & Arístegui 2000, Marañón et al. 2000) in oligotrophic seas, strongly support the growing consensus that the frequency of 'episodic pulses' of new nitrogen into the mixed layer of the oligotrophic ocean must be higher than formerly considered.

In vitro studies of oxygen metabolism in oceanic waters are generally constrained by the limited number of experiments that can be carried out during a regular oceanographic cruise. Hence, unless a huge effort is devoted to performing oxygen experiments and/or a combination of methods is used to estimate metabolic rates (as we did in this study), the probability of skipping small patches of high production in the ocean increases, leading to an underestimation of the *P*:*R* ratio, and therefore to an erroneous generalisation

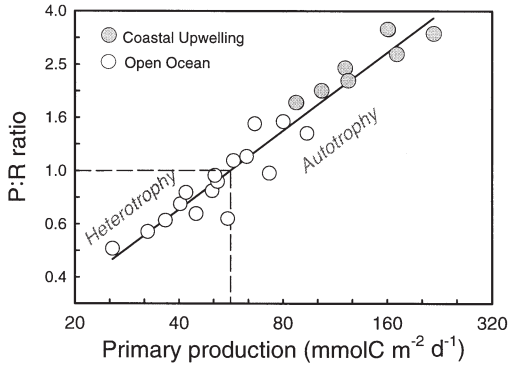

Fig. 7. Relationship between the ratio (*P*:*R*) of depth-integrated primary production (P_{C14} and P_g) and community respiration (R_{ETS} and R_d) and the depth-integrated production. Data correspond to both the oceanic section (P_{C13}:R_{ETS}) and the upwelling study (P_g:R_d). At $P > 56$ mmol C m^{-2} d^{-1} (~ 667 mg C m^{-2} d^{-1}) the system tends to be net autotrophic. Approximately 60% of oceanic stations were in a heterotrophic situation during the period of study (but see text for discussion)

of the trophic status of the system. The oxygen method is undoubtedly the more unambiguous *in vitro* approach to estimate *P*:*R* balances in surface waters. However, the limitations of the method, due to the lower sensitivity and longer required incubation times than other *in vitro* techniques, makes it necessary to combine it with other direct and indirect methodologies which provide a field sampling with a closer time/space resolution (e.g. Arístegui & Montero 1995). Only by improving this resolution would we be able to resolve the apparent match/mismatch of *P* and *R* observed in different oxygen metabolism studies in oceanic waters (Williams 2000, Serret et al. 2001). Moreover, it will also allow the comparison of *in vitro* metabolic rates with biogeochemical estimates of water-column metabolism. In turn, this would allow us to address the 3-dimensional variability in the external inputs of carbon to a given region and to understand the scales of variability of uncoupled processes like *P* and export of particulate organic carbon (Buesseler 1998), or the cycling of dissolved and particulate organic carbon (Druffel et al. 1992, Carlson et al. 1994).

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