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Seasonal compensation of microbial production and respiration in a temperate sea

Pablo Serret[1,*], Emilio Fernández[2], Jorge A. Sostres[1], Ricardo Anadón[1]

[1]Universidad de Oviedo, Departamento de Biología de Organismos y Sistemas, c/Catedrático R Uría s/n, 33071 Oviedo, Spain
[2]Universidade de Vigo, Departamento de Ecoloxía e Bioloxía Animal, Campus Lagoas-Marcosende, 36200 Vigo, Spain

ABSTRACT: Gross oxygen production (GP), dark respiration (DR) and net community production (NCP) were studied for 16 mo in the euphotic layer of 3 stations through the coastal transitional zone of the southern Bay of Biscay, and related to hydrographic and nutrient conditions, phytoplankton biomass and C incorporation. Microbial O_2 fluxes exhibited seasonal patterns linked to the seasonal cycle of water column stratification and mixing, with positive NCP during the spring, negative throughout the summer and close to zero in winter. This pattern was altered at coastal regions, where productive periods were linked to coastal upwelling, whereas in winter persistent net heterotrophy was measured, presumably in relation to increases in organic matter discharge of continental origin. The comparison of NCP with O_2 anomaly and NO_3 concentration in the euphotic zone, the spatial and temporal scales studied and the prevalence of steady-state conditions offshore support the conclusion that the maintenance of summer heterotrophy in the region was based upon the consumption of the surplus of organic matter produced in spring. The uncoupling in the microbial auto- and heterotrophic metabolisms, based on the accumulation and delayed consumption of dissolved organic matter as a consequence of the processes controlling phytoplankton growth and microbial heterotrophic activity in temperate seas, would explain such a pattern. The close relationship observed between the seasonal variability in NCP and the magnitude of spring net production and predictions derived from the seasonal cycles of O_2 anomaly in middle latitudes and atmospheric O_2 led us to conclude that the seasonal compensation of production and respiration processes is a characteristic of the dynamics of the pelagic ecosystem, at least in coastal temperate seas. The implications of this conclusion are of great relevance for the interpretation of new production and the estimation of the trophic status of the ocean from direct measurements of plankton net production.

KEY WORDS: Production-respiration balance · Trophic dynamics · Phytoplankton · Bacteria · Oxygen anomaly · Atmospheric oxygen

INTRODUCTION

Oceanic biota exerts a strong influence on the natural carbon cycle. Phytoplankton photosynthesis fixes CO_2 in the upper euphotic zone of the oceans, which may be ultimately recycled within that layer or exported, in particulate or dissolved form, to greater depths. Sequestration of exported biogenic carbon at ocean depths (biological C pump) causes a decrease in surface seawater CO_2 concentration, and eventually in atmospheric CO_2 concentration. Although the importance of these processes in modifying global climate is well established over geological time scales (e.g. Holligan 1992), too many uncertainties exist over shorter (ecological) scales on the rates of relevant processes for the biological pump. Specifically, the paucity of respiration data has been suggested to be the reason why most marine carbon flux models fail to balance (Biddanda et al. 1994, Jahnke & Craven 1995).

Net community production (NCP), defined as the difference between gross primary production and

*Present address: Centre for Coastal and Marine Sciences, Plymouth Marine Laboratory, Prospect Place, West Hoe, Plymouth PL1 3DH, United Kingdom.
E-mail: sipa@wpo.nerc.ac.uk

total community respiration, reflects the whole ecosystem dynamics better than the activity of primary producers or heterotrophs. Measured over adequate spatial and temporal scales, NCP may be equated to 'new' production, which represents the maximum exportable biomass to preserve the long-term integrity of the system (Eppley 1989, Quiñones & Platt 1991), and allows calculation of the availability of a 'surplus' of primary production, and hence the determination of the potential fate of organic carbon produced in the euphotic zone.

Annual production/respiration (P/R) ratios reported in the literature for the euphotic zone of the ocean often result in net heterotrophic balances of pelagic biological activity, as predicted by some models (Smith & Mackenzie 1987). This balance has been considered a consequence of the succession from a net autotrophic period during spring-winter to heterotrophic conditions in summer-autumn (see e.g. Rowe et al. 1986, review by Pomeroy & Wiebe 1993, Griffith & Pomeroy 1995). But, as stated by Pomeroy & Wiebe (1993), 'a net heterotrophic water column is possible not only because of a temporary imbalance of photosynthesis and consumption but also because of organic inputs from rivers and atmospheric fallout'. The clarification of the relative contribution of these processes, and the scales over which they operate, to seasonal heterotrophy in temperate seas has been difficult to establish, mainly as a consequence of diverse limitations for interpreting the results of microbial production and respiration within this context. In some studies microbial respiration has not been directly measured, but estimated from bacterial growth through the use of diverse conversion rates (e.g. Rowe et al. 1986, Lignell et al. 1993, Krstulovic et al. 1995, Smith et al. 1995). However, the extrapolation from bacterial production to respiration is uncertain, making it difficult to determine the role of bacterial communities in carbon cycling (e.g. Jahnke & Craven 1995). In other cases, the existence of auto- and heterotrophic phases has been deduced from independent studies performed within the different phases, and not directly observed over a complete time series including them all. In this regard, Pomeroy & Wiebe (1993) highlighted that more than 2/3 of 23 articles reviewed presented P/R ratios <1, suggesting strong seasonal and regional shifts from auto- to heterotrophy, and a negative net balance for the ocean. Nevertheless, these authors noted that most of the reviewed data derived from short-term studies in non-steady-state systems, which can produce strong heterotrophic situations. Some studies on P/R succession have monitored organic matter production and consumption rates over time scales >1 yr (Blight et al. 1995, Smith & Kemp 1995, Satta et al. 1996), however, these have been carried out in areas very close to the shore, in eutrophic conditions, or under strong tidal influence within estuaries or fjords, situations well away from steady state. Finally, some of the studies are restricted to surface P/R measurements (e.g. Blight et al. 1995, Iriarte et al. 1996).

Besides the difficulties in determining the time scales for plankton trophic interactions, the recent detection of a seasonal cycle in the concentration of atmospheric oxygen (Keeling & Shertz 1992, Bender et al. 1996) provides strong support for the idea of a temporal offset in the processes of synthesis and oxidation of organic matter in the sea (see reviews by Pomeroy & Wiebe 1993 and Sherr & Sherr 1996). A similar conclusion emerges from seasonal studies of the dissolved oxygen anomaly (the excess over saturation) in middle and high latitudes (see review by Najjar & Keeling 1997). The lack of synchrony in the cycles of activity of heterotrophic and autotrophic microbes, suggested by ocean and atmospheric O_2 cycles, would then establish the minimum temporal scale for carbon budget studies and, specifically, for the determination of the balance between production and respiration in order to quantify the 'trophic status' of the ocean.

The main objective of this paper is the study of the spatial and temporal scales of the linkage between microbial production and respiration processes in a temperate sea and, subsequently, the quantification of the net trophic balance over biogeochemically significant scales. A study of the spatial and temporal variability of phytoplankton biomass and C incorporation, and microbial O_2 production and consumption was carried out in relation to hydrographic and chemical characteristics, throughout a temporal series of 16 mo in a coastal middle latitude region. To the best of our knowledge this is the first report of microbial NCP obtained from true-depth measured oxygen fluxes in the whole euphotic zone of both shelf and oceanic waters, over a temporal scale >1 yr.

MATERIALS AND METHODS

Sampling. A transect of 3 stations across the shelf off the northern Iberian coast (southern Bay of Biscay) was sampled monthly from January 1994 to June 1995 (Fig. 1). Sampling usually started at 10:00 h and ended by 17:00 h. At every station vertical profiles of conductivity and temperature were performed with a SBE25-03 CTD. Photosynthetically available radiation (PAR) was measured with a submersible LiCOR spherical quantum sensor. Water samples for the determination of dissolved oxygen, inorganic nutrients and chl *a* concentrations were collected with 5 l Niskin bottles from 2, 10, 20, 30, 40 and 50 m at Stn 1, plus 75 and 100 m at Stn 2, and 150 and 200 m at Stn 3. Carbon incorpora-

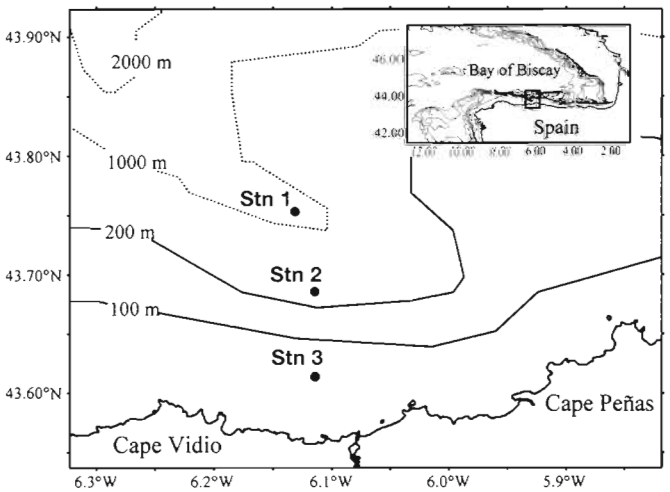

Fig. 1. Map of the region of study in the coastal transitional zone of the southern Bay of Biscay, showing the position of sampling stations

tion rates by phytoplankton were measured at 6 depths within the euphotic zone (corresponding to 100, 50, 20, 10, 5 and 1% of surface irradiance, I_0). Rates of microbial O_2 gross and net production and dark respiration (DR) were measured at 100, 20 and 1% I_0. Seawater for C incorporation and O_2 fluxes was immediately transferred into acid-washed polyethylene 5 l carboys and transported to the laboratory, where it was kept at *in situ* (±1°C) temperature and in darkness until dawn, when incubations started.

Dissolved oxygen. A 125 cm^3, gravimetrically calibrated, borosilicate bottle was carefully filled from every Niskin bottle by means of a silicone tube. Fixing and storage procedures, reagents and standardisation followed the recommendations of Grasshoff et al. (1983). Dissolved oxygen concentration was measured by automated precision Winkler titration performed with a Metrohm 716 DMS Titrino, utilising a potentiometric end point (Oudot et al. 1988, Pomeroy et al. 1994, Pakulski et al. 1995). Aliquots of fixed samples were delivered by a 50 cm^3 overflow pipette in order to improve the reproducibility of deliveries, as recommended by Pomeroy et al. (1994) for a stable platform.

Dissolved inorganic nutrients. Samples were collected in polystyrene tubes, frozen immediately after collection and stored at −20°C until analysis. Concentrations of nitrate, nitrite, ammonia, phosphate and silicate were measured according to the methods described in Grasshoff et al. (1983).

Chl *a*. Dark, 250 cm^3 polyethylene bottles were filled and transported at 4°C to the laboratory. Subsamples (100 cm^3) were filtered onto 25 mm Whatman GF/F filters, which were frozen immediately. Chl *a* concentration was determined using a Turner Designs 10 fluorometer after extraction in 90% acetone for 24 h at 4°C (Strickland & Parsons 1972).

Microplankton cell counts. At depths corresponding to 100, 20 and 1%, I_0 seawater samples were collected in 125 cm^3 glass bottles containing ca 1 cm^3 of Lugol's solution. Enumeration of organisms was carried out with an inverted microscope as described in Fernández et al. (1991).

Photosynthetic C incorporation. Seawater for the determination of C uptake by phytoplankton was collected at photic depths of ca 100, 50, 30, 20, 10, 1% I_0, and transferred to acid-washed 5 l carboys. Three 70 ml polycarbonate bottles were filled from each depth, inoculated with 370 Kbq (10 µCi) of $NaH^{14}CO_3$, and placed in outdoor water-cooled incubators. Once the incubation had finished, samples were filtered through Whatman GF/F filters under low vacuum pressure (<100 mm Hg). Filters were immediately frozen and stored at −20°C until later analysis. Samples were processed for determination of C incorporation into macromolecules (proteins, carbohydrates, lipids and low molecular weight metabolites), following the method described in Marañón et al. (1995). Total primary production was calculated as the sum of C incorporated into each fraction. The sum of ^{14}C activity in the 4 obtained metabolic fractions accounts for 90 to 104% of total activity as measured in parallel non-fractionated samples (Marañón et al. 1995). Samples were counted in a liquid scintillation Packard counter, after addition of Optiphase HI-safe scintillation liquid. Quenching was corrected by internal standard.

Oxygen production and consumption. O_2 production and consumption rates were determined by light- and dark-bottle incubations. Seawater was transferred from every 5 dm^3 carboy (corresponding to photic depths of 100, 20 and 1% I_0) to 4 light and 8 dark acid-cleaned, individually calibrated, 125 cm^3 nominal volume borosilicate glass bottles. Bottles were filled using silicone tubing, overflowing >250 cm^3. An initial set of 4 dark bottles was fixed immediately for initial oxygen concentration, the remainder being placed in the same incubator as C uptake bottles. O_2 and ^{14}C incubations always ran simultaneously. Incubation temperature was within ±1°C *in situ* temperature. The remaining 4 dark bottles were placed in dense black plastic bags, while every set of 4 light bottles was placed in neutral density mesh bags simulating the light intensity at the sampled depth. Incubations started at dawn and lasted 24 ± 0.5 h over a diel cycle with natural light. NCP and DR were estimated as the change in oxygen concentration in the light and dark bottles, respectively, after incubation. Gross oxygen production (GP) was estimated as the result of NCP minus DR. Dissolved oxygen concentration was determined following the method described above.

RESULTS

Physical and chemical characteristics

The vertical distribution of temperature and sigma-t through the period of study at the 3 sampling stations is shown in Fig. 2. A marked seasonal pattern driven by spring surface heating and winter mixing is evident. This general pattern, characteristic of temperate seas, was modified by several episodic hydrodynamic events, mainly slope currents and wind-driven coastal upwellings, a complete description of which is given elsewhere (Botas et al. 1990, Fernández et al. 1993). Fig. 2 also presents the spatio-temporal variation in nutrient concentration and oxygen saturation at the 3 sampling stations. Given the high correlation found between nitrate and phosphate ($r = 0.61$ (Stn 1), 0.82 (Stn 2) and 0.75 (Stn 3), $p < 0.005$) and nitrate and silicate concentrations ($r = 0.70$ (Stn 1), 0.85 (Stn 2) and 0.92 (Stn 3); $p < 0.005$), only nitrate data are shown. Nutrient concentration and oxygen saturation were inversely related ($r = -0.44$, -0.65 and -0.73 in Stn 1, Stn 2 and Stn 3, respectively; $p < 0.01$) and both followed seasonal trends strongly related to the temporal evolution of water-column stability.

In March and April 1994, although the thermal field was typical of winter (<13°C throughout the water column), sigma-t distributions show transient stratifications, after the intrusion of high salinity water onto the shelf, which resulted in the concurrence of high-salinity water (>35.60) at intermediate depths, together with low-salinity surface water. These intrusions, which generate clear thermohaline fronts separating coastal from oceanic waters (Fernández et al. 1993), are a consequence of warm, high-salinity slope currents flowing along the Atlantic and northern Iberian coast with decreasing thickness (e.g. Pingree & Le Cann 1990). The situations of transient vertical stability they generate are related to the development of spring phytoplankton blooms prior to the settlement of thermal stratification, as could be observed offshore in April 1994 when the signature of a bloom is clear in the marked decrease in NO_3 concentration and the concurrent increase in O_2 saturation at Stn 2 and Stn 3.

In both shelf and oceanic waters a thermocline developed from May 1994, separating a surface nutrient-depleted layer (<1 µmol NO_3 kg^{-1}, <0.2 µmol PO_4 kg^{-1}, <1.5 µmol Si kg^{-1}) from bottom, nutrient-rich waters. A coastal upwelling of cold, nutrient-rich and oxygen-impoverished deep water took place in June 1994, when summer vertical stratification prevailed offshore. During the summer, stratification was more intense and the surface mixed layer deepened offshore and, accordingly, nutrient depletion was more severe

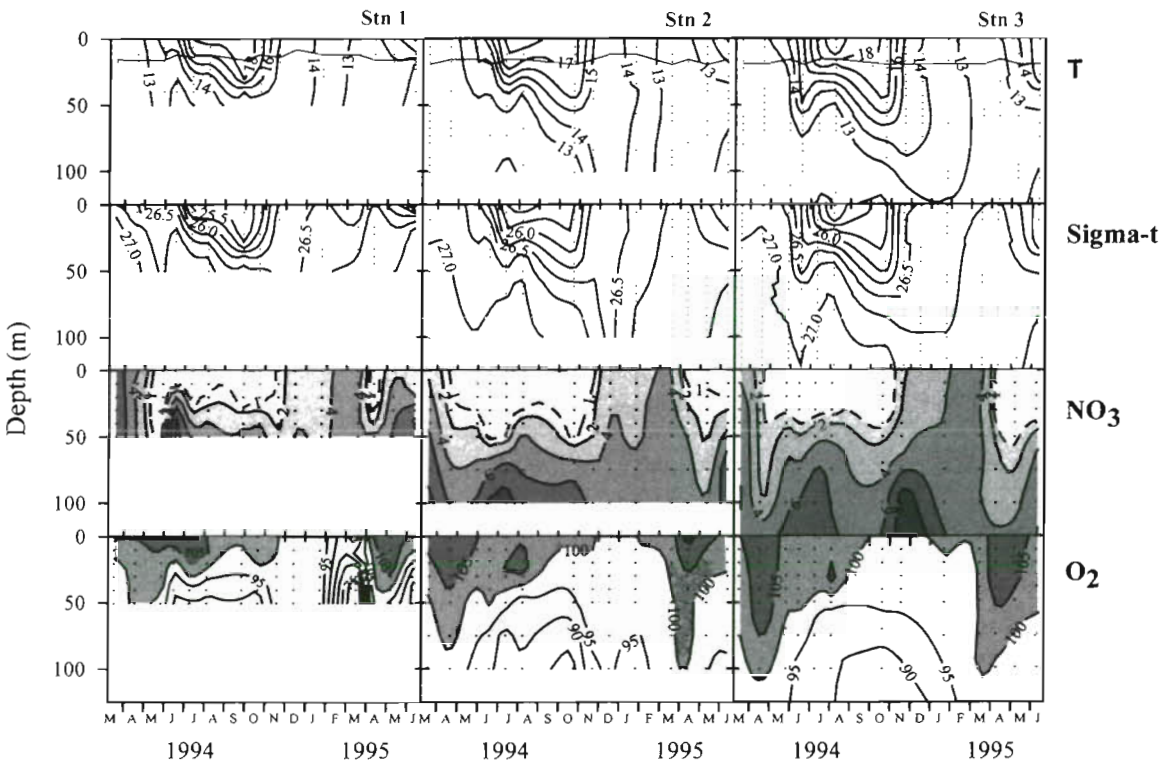

Fig. 2. Spatio-temporal distribution of temperature (T, °C), sigma-t, nitrate concentration (µmol kg^{-1}) and percentage of oxygen saturation at the 3 sampled stations. The depth of the euphotic layer (1% I_0) is superimposed on the temperature contours

in oceanic than in coastal waters. The thickness of the surface oxygen-saturated layer progressively decreased during the summer, while below the relatively mixed surface layer low values of oxygen saturation were observed. From June onwards, subsurface (25 to 30 m depth) maxima of dissolved oxygen concentration developed at Stn 2 and Stn 3, coinciding with the deepest part of the nutrient-depleted layer.

The summer pycnocline deepened between September and October and finally vanished in October–November. Consequently the euphotic zone nutrient content increased after mixing with deeper water. After November, thorough mixing reset winter conditions. The water column cooled to <14°C, and a completely mixed water column was found in coastal waters, while in oceanic waters the surface mixed layer extended to ca 100 m depth. The concentration of dissolved inorganic nutrients in the surface mixed layer was high, and typical values of >3 µmol NO_3 kg^{-1}, >0.3 µmol PO_4 kg^{-1} and >2 µmol SiO_4 kg^{-1} were measured throughout the water column, both at shelf and oceanic stations. Oxygen concentration was slightly below saturation, especially in coastal waters.

In April 1995 a new coastal upwelling pulse took place, in this case under mixed conditions. Although an increase in deep nitrate concentration was observed towards the coast, very low concentration of NO_3 was measured in surface coastal waters (<0.2 mmol NO_3 kg^{-1}). Nevertheless, a marked coastal increase in silicate and phosphate concentrations (>1.2 µmol kg^{-1}) (data not shown), as well as oxygen saturation levels, traced the advective process, suggesting that active phytoplankton growth occurred prior to sampling in surface coastal waters. Moreover, the offshore increase of surface O_2 saturation, and the deepening of both nutrient exhaustion and O_2 supersaturation show the movement of surface coastal water (O_2-enriched and NO_3-depleted) and its convergence at the shelf-break front.

In March 1995, after several storms which occurred in February, very low salinity (<35.00) was measured in surface water at Stn 1, thus provoking a strong haline stratification. No effect on NO_3 concentration was observed, but very low O_2 saturation (<85%) prevailed at all depths.

Phytoplankton biomass and photosynthetic carbon incorporation

Spatio-temporal distributions of chl *a* concentration and C incorporation (Fig. 3) showed a similar trend to that of oxygen saturation.

In April 1994 a marked increase in phytoplankton biomass paralleled sharp changes in nutrient content and O_2 saturation, all suggesting that a spring phytoplankton bloom had developed offshore (Stns 2 and 3) between March and April 1994. The sinking at the outermost station of elevated phytoplankton biomass is clear from the deep chl *a* maximum and the high chl *a* concentration (>1 mg m^{-3}) measured down to 100 m depth.

After the spring bloom, when surface nitrate content had been markedly reduced, phytoplankton biomass decreased and deep chl *a* maxima (DCM) developed. This feature was already evident in May 1994, when a vertical gradient >1°C developed in the upper 50 m. The upwelling in June 1994 altered the development of the summer DCM at the coastal station. In the relatively mixed and nutrient-enriched waters a marked increase in phytoplankton biomass was observed. Chl *a* concentration >7 mg m^{-3} was measured in the upper 20 m, and the euphotic zone integrated concentration amounted to >240 mg m^{-2}. Diatoms accounted for ca 70% of phytoplankton abundance. After the upwelling, thermal stratification returned and <0.5 mg chl *a* m^{-3} was measured in the nutrient-depleted surface layer during summer, while at depths between 20 and 40 m chl *a* concentration was >1.5 mg chl *a* m^{-3}.

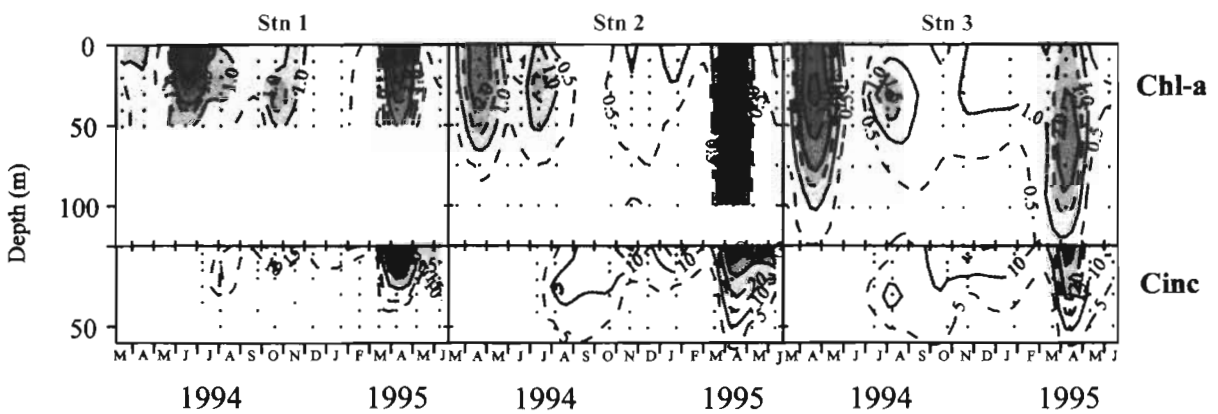

Fig. 3. Spatio-temporal distribution of chl *a* concentration (mg m^{-3}) and phytoplankton carbon incorporation (Cinc) (mg C m^{-3} d^{-1}) at the 3 sampled stations

C incorporation was low in the surface layer, especially offshore, increasing in the DCM (>10 mg C m^{-3} d^{-1} at 10% I_0). Ciliates were relatively abundant in the DCM, while diatoms and dinoflagellate densities were low.

The DCM disappeared when wind mixing deepened the surface mixed layer (September 1994 Stn 1; October 1994 Stn 2 and Stn 3). Vertically homogeneous concentrations of ca 0.7 mg chl *a* m^{-3} were observed in the upper 30 m of the water column. Coinciding with the autumn increase in NO_3 content after the vanishing of the pycnocline (October 1994 Stn 1; November 1994 Stn 2 and Stn 3), chl *a* concentration and C incorporation increased at all the stations.

In winter, during the phases of vertical homogeneity of the water column, low chl *a* concentration (<1 mg m^{-3}) and C incorporation rates were registered, both exhibiting weak surface maxima. Relatively high abundances of flagellates (70 cells ml^{-1}) and ciliates (>8 cells ml^{-1}) were observed at Stn 1. During slope current intrusions (March and April 1994, January 1995) increases of phytoplankton biomass and C incorporation were found at the surface of areas with relative vertical stability.

As in 1994 (see above), the 1995 spring phytoplankton bloom was not related to thermal stratification but to coastal upwelling. Very high chl *a* concentration and primary production were measured in the surface, NO_3-impoverished and O_2-enriched waters of the coastal region, while offshore sinking of biomass and a decrease in primary production were evident.

Oxygen fluxes

Figs. 4 to 6 show the temporal evolution of dark respiration (DR), and gross (GP) and net community (NCP) production of oxygen at the 3 sampled depths within the euphotic layer of the 3 stations. The seasonal trend of GP almost perfectly matched that of C incorporation ($r = 0.98$, 0.90 and 0.81 for every depth of Stn 1, Stn 2 and Stn 3, respectively; $p < 0.005$ in all cases). Although DR was not directly related to chl *a* concentration or C incorporation rates, both DR and NCP exhibited marked seasonal patterns coupled to the variation in biomass and activity of phytoplankton described above. As with C incorporation, the greatest seasonal variation in oxygen fluxes was observed in coastal waters, especially at the surface.

In April 1994, relatively high rates of GP were measured at Stn 2 and Stn 3 in samples from 100 and 20% I_0. These were related to the observed increase in phytoplankton biomass more than to an increase in activity, since GP rates normalised to chl *a* concentration were very low (ca 2 mmol O_2 mg^{-1} chl *a* d^{-1} at Stn 2; 0.8 mmol O_2 mg^{-1} chl *a* d^{-1} at Stn 3). Despite the large increase of phytoplankton biomass, low DR rates were measured at Stn 2. Hence at this station very high NCP rates were registered both at the surface and at 20% I_0 (ca 4 mmol O_2 m^{-3} d^{-1}), and even samples from 1% I_0 presented positive values of NCP. At Stn 3, where sinking of phytoplankton biomass occurred, DR was higher, and hence lower NCP rates were measured. At 1% I_0 depth, coinciding with the highest chl *a* concentration, negative NCP rates were found.

After the spring bloom, during the formation of the DCM (May 1994 at Stn 2 and Stn 3), high GP and NCP rates were recorded in the upper limit of the DCM, at 20% I_0. Relatively high values were also recorded from surface samples, while below the DCM, at the depth of 1% I_0, both GP and DR were very low, and NCP was nearly zero. A large increase in GP was recorded in June 1994 in the upwelled waters of the coastal station (Stn 1), mainly at the surface (ca 20 mmol O_2 m^{-3} d^{-1}). Concurrently, a marked decrease of DR occurred at all depths, despite the elevated phytoplankton biomass and activity. Consequently, NCP was very high throughout the euphotic zone of the coastal region. Offshore lower GP rates and higher DR rates were measured, especially in surface waters where NCP was negligible. Positive NCP was only measured off-

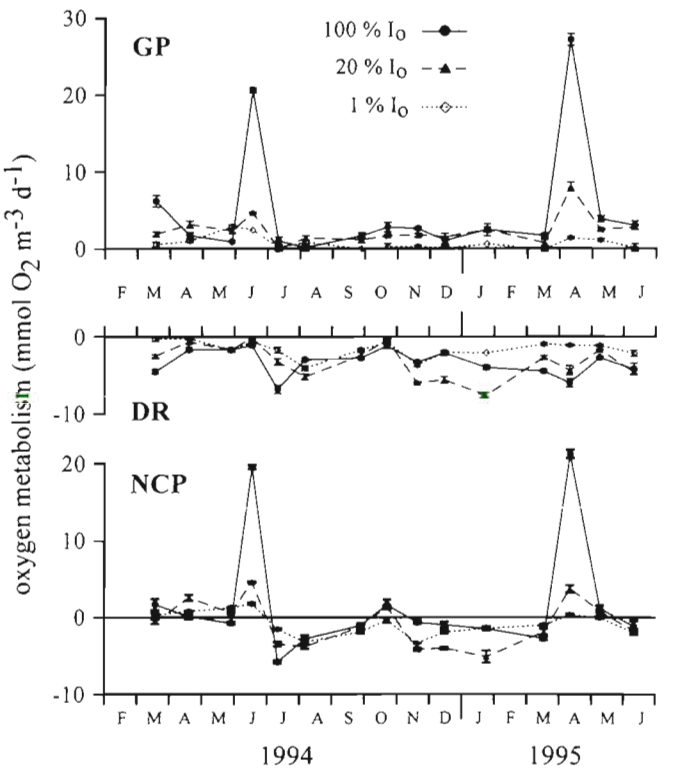

Fig. 4. Temporal variation in gross production (GP), dark respiration (DR) and net community production (NCP) rates at the 3 sampled depths (100, 20 and 1% I_0) at Stn 1. The average ± 1 SE of 4 replicates are shown

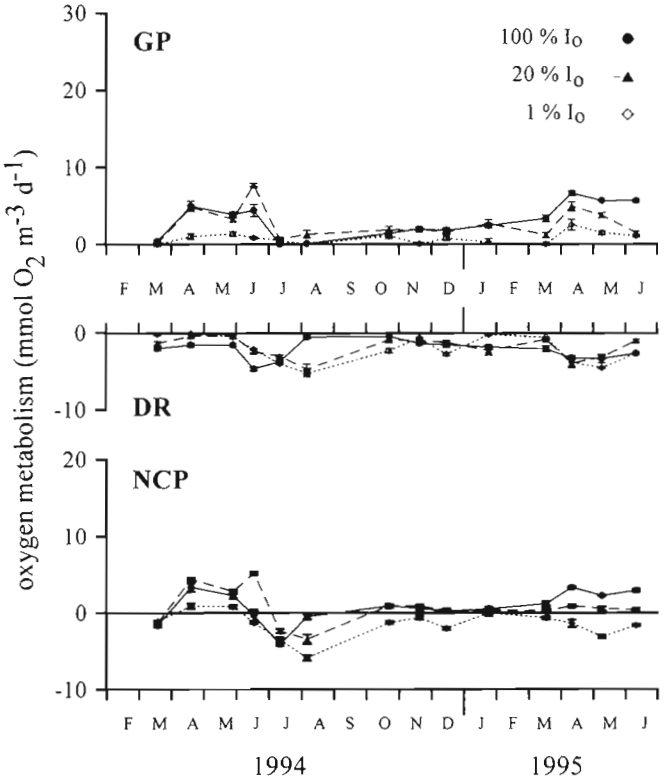

Fig. 5. Temporal variation in gross production (GP), dark respiration (DR) and net community production (NCP) rates at the 3 sampled depths (100, 20 and 1% I_0) at Stn 2. The average ± 1 SE of 4 replicates are shown

shore at 20% I_0 depth. After the upwelling, GP decreased and DR increased throughout the study area. When the summer DCM was well established (July 1994 at Stns 2 and 3; August 1994 at Stns 1, 2 and 3) very low GP rates were recorded at all depths. Surface GP was negligible and only ca 1 mmol O_2 m^{-3} d^{-1} was measured at 20% I_0, in the upper layer of the DCM. DR was always very high and hence negative NCP was recorded throughout the summer, even at the DCM.

In October–November 1994, coinciding with the deepening of the pycnocline, phytoplankton blooms developed (see Figs. 2 & 3) and relative increases of GP rates were observed at the surface and 20% I_0 depth at every station. Nevertheless, the marked decrease found at all depths in DR rates (reaching minima annual values), both in coastal and offshore waters, resulted in an increase of NCP to positive values at 100 and 20% I_0 depths.

During winter mixing periods (Dec 1994 Stns 1 and 2; March 1995 Stns 2 and 3), when phytoplankton biomass and C uptake were low, relatively low rates of GP were recorded throughout the region of study (ca 2 mmol O_2 m^{-3} d^{-1} at surface and 20% I_0 samples; negligible values at depths corresponding to 1% I_0). DR, however, exhibited marked differences between coastal and offshore waters. At Stn 2 and Stn 3 rates of DR were low and balanced GP both at the surface and 20% I_0; negative values of NCP were only found in samples from 1% I_0. At the coastal station, in contrast, high DR rates produced large negative values of NCP in the euphotic zone during the winter, even at the surface. As occurred with chl *a* concentration and C incorporation rates, slope current intrusions were related during this period to increases in GP and especially DR in the vertically stratified waters (see Stn 1 in March 1994, and Stn 3 in January 1995).

The upwelling during April 1995 gave rise to a marked increase in GP rates at Stn 1, especially at the surface, as during the June 1994 upwelling event. In contrast to June 1994, in April 1995 a clear increase of DR was observed both in coastal and offshore waters, the spatial distribution of DR matching that of chl *a* concentration (see Fig. 4). This general increase of DR rates following the offshore sinking of phytoplankton biomass and oxygen enriched waters, together with nitrate depletion in coastal surface waters, suggests that the situation observed in April 1995 corresponded to an aged upwelling. Moreover, DR spatial distribution in April 1995 was very similar to that observed in July 1994, 1 mo after the upwelling of June 1994.

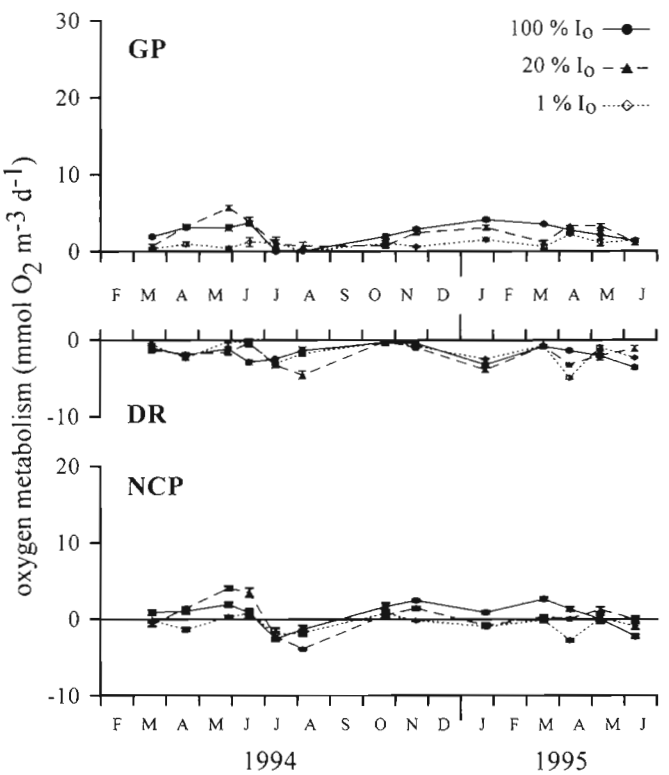

Fig. 6. Temporal variation in gross production (GP), dark respiration (DR) and net community production (NCP) rates at the 3 sampled depths (100, 20 and 1% I_0) at Stn 3. The average ± 1 SE of 4 replicates are shown

Euphotic zone integrated oxygen fluxes

When GP, DR and NCP rates were integrated throughout the euphotic zone (GPeu, DReu and NCPeu, Fig. 7) at every station, a very similar pattern emerged for the first 9 mo of sampling, characterised by positive NCPeu during spring, followed by a net heterotrophic balance throughout the summer, until autumn phytoplankton blooms. During winter, however, marked differences were found between coastal and offshore waters. While near zero net balances were observed at Stn 2 and Stn 3, very high DR rates were measured at Stn 1, resulting in negative values of NCPeu.

In April 1994, similar values of GPeu were obtained at both offshore stations where the spring phytoplankton bloom occurred. However, while very low DReu rates at Stn 2 (–22 mmol O_2 m^{-2} d^{-1}) gave rise to very high positive NCPeu, at the outermost station (Stn 3), where the sinking of elevated phytoplankton biomass was evident, higher DReu rates (–102 mmol O_2 m^{-2} d^{-1}) compensated the elevated GPeu. Positive NCPeu persisted, especially offshore, until the end of the spring.

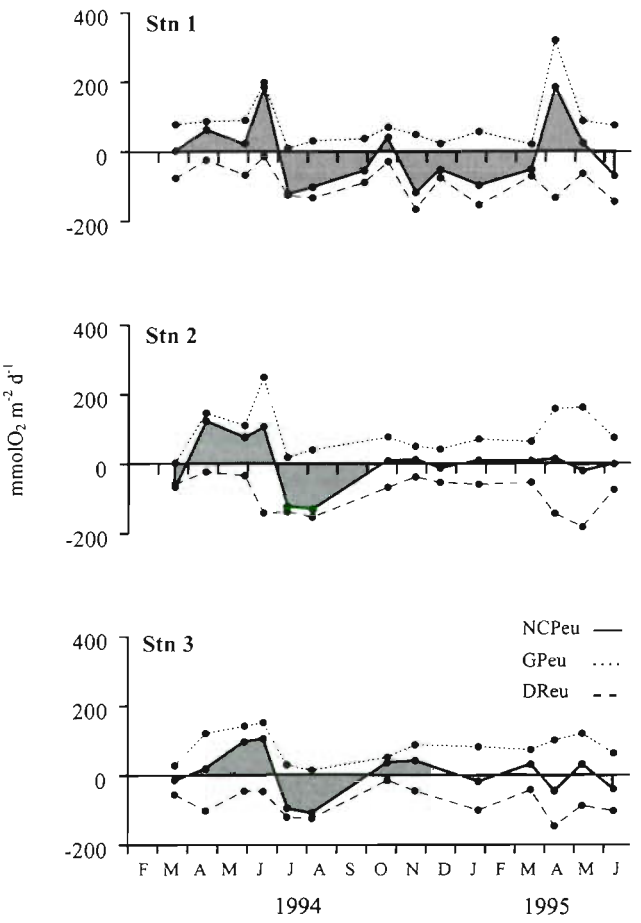

Fig. 7. Temporal variation in euphotic zone integrated rates of net community production (NCPeu), gross production (GPeu) and dark respiration (DReu) at the 3 sampled stations

Elevated GPeu and low DReu prevailed offshore while the DCM developed (May 1994). During the coastal upwelling in June 1995 a marked increase in GPeu and a sharp decrease in DReu (reaching the minimum value of the whole period of study) gave rise to a very high value of NCPeu at Stn 1. Although DReu increased offshore, high positive NCPeu was also measured at Stn 2 and Stn 3. During summer very low GPeu rates were recorded at the 3 sampled stations; however, despite the low phytoplankton biomass and primary production, very high DReu rates were found. Hence elevated heterotrophic balances in the euphotic zone (ca –100 mmol O_2 m^{-2} d^{-1}) of the region of study prevailed throughout the summer. This was the only period of sustained intense net heterotrophy at offshore waters, while similar negative NCPeu was obtained at coastal waters during the winter.

Autumn blooms (October–November 1994) were characterised by marked decreases in DReu and relative increases in GPeu, thus giving rise to positive balances in the euphotic zone of all the stations during this period.

During winter mixing periods, relatively low GPeu and DReu were measured offshore, giving rise to a NCPeu near zero. At the coastal region, although GPeu was also low, high DReu rates produced large negative values of NCPeu.

A marked increase in GPeu was observed, especially towards the coast, during the phytoplankton bloom associated with an upwelling pulse in April 1995. Contrary to the sharp decrease in DR rates observed in June 1994, a clear increase occurred in April 1995. During the latter event, and paralleling the offshore sinking of phytoplankton biomass, high DReu was also measured offshore, and negative NCPeu occurred at the outermost station.

Annual fluxes of oxygen

Fig. 8 presents the annual integration of production and consumption of oxygen in the euphotic zone of the 3 sampled stations. Given that more than 1 complete year was sampled, every (5) possible integral of 12 mo has been calculated. Taking into account the possibility of net heterotrophic periods being sustained by the excess production of previous autotrophic phases, those integrals in which a complete seasonal series including the spring productive phase followed by the subsequent heterotrophic phases (i.e. only the first 2 periods of 12 mo of our cycle) are highlighted.

Despite the different contribution to annual GPeu of the diverse productive processes observed in coastal

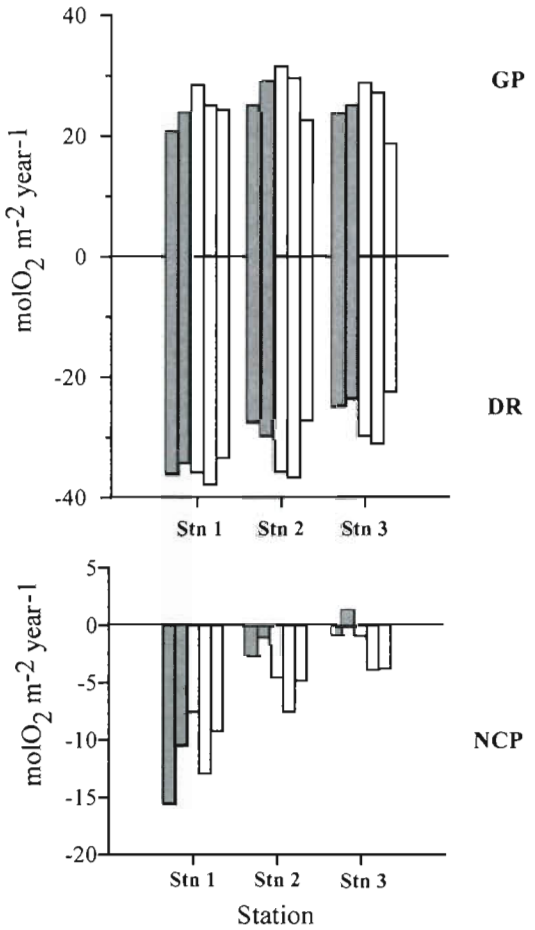

Fig. 8. Annually integrated rates of gross production (GP), dark respiration (DR) and net community production (NCP) in the euphotic zone at the 3 sampled stations. Values corresponding to the 5 successive periods of 12 mo are shown. Filled bars: first 2 integrals, which are the only ones starting in spring (see text for details)

and oceanic waters (phytoplankton blooms associated with coastal upwellings, spring and autumn blooms), annual GPeu was very similar at the 3 studied stations. Conversely, annual DReu increased towards the coast as a result of the marked differences found between coastal and oceanic waters in the winter DR rates (see Fig. 7). Consequently, these differences in DReu are the cause of the spatial pattern in annual NCPeu observed. This variable was negative at the coastal station, while an offshore trend towards P/R equilibrium was observed.

Trophic significance of oxygen P/R balances

Although the seasonal evolution of P and R rates in relation to hydrographic conditions, nutrient levels and phytoplankton biomass and activity, can be easily interpreted from an ecological perspective, the significance of temporal variability of depth-integrated rates is not so clear, especially in a biogeochemical context. This uncertainty arises from differences between the scales of the measured variables (daily rates of P and R) and the time span over which the inferred trophic status may apply. The observed annual cycle of P and R is by no means continuous, but a result of a series of relatively independent processes (e.g. upwellings, thermal or haline vertical stratifications, etc.), and it is not easy to ensure that every significant event has been sampled. The seasonal P/R cycles shown in Figs. 4 to 6 suggest that the time scales of variability in community metabolism may be shorter than the period of sampling. Hence, although auto-heterotrophy transitions are frequently observed between 2 consecutive samples, there is a lack of information on how these transitions developed. In addition, advection may modify the interpretation of P/R balances, since changes in P/R may be due to the departure from steady-state conditions rather than microbial physiology. Hence, before undertaking the interpretation of seasonal and annual P/R balances, it should be confirmed that the measured oxygen fluxes are an adequate representation of the annual cycle of microbial production and consumption of organic matter.

Under steady-state conditions, oxygen saturation in seawater is directly dependent upon the balance between photosynthesis and total respiration, i.e. NCP. Thus a comparison of O_2 saturation and NCP may indicate the extent to which steady-state conditions prevailed. Moreover, oxygen saturation summarises the recent history of water column net metabolism, and the comparison of NCPeu cycles and oxygen saturation will provide insight into the accuracy of using monthly measured NCP to estimate the annual cycle of P and R processes. Although over short time scales nutrient content in the euphotic zone is more dependent on photosynthesis than on respiration, its trend also portrays the metabolic history of the community and reflects the degree of steady-state conditions. Fig. 9 presents the concurrent variation of euphotic zone integrated values of oxygen saturation, nitrate concentration and NCPeu. Both O_2 saturation and nitrate concentration in the euphotic zone showed very similar annual trends, although sometimes slightly delayed (especially O_2) with respect to NCPeu. As expected, these variables reflected the history of community metabolism better than NCP, as seen in April 1994 (aged spring bloom offshore) or during upwellings. In June 1994 the recent coastal upwelling of deep water generated a sharp increase in nitrate concentration and NCP, but no change in oxygen saturation was observed until 1 mo later, when a marked decrease of nitrate content was also evident. On the contrary, dur-

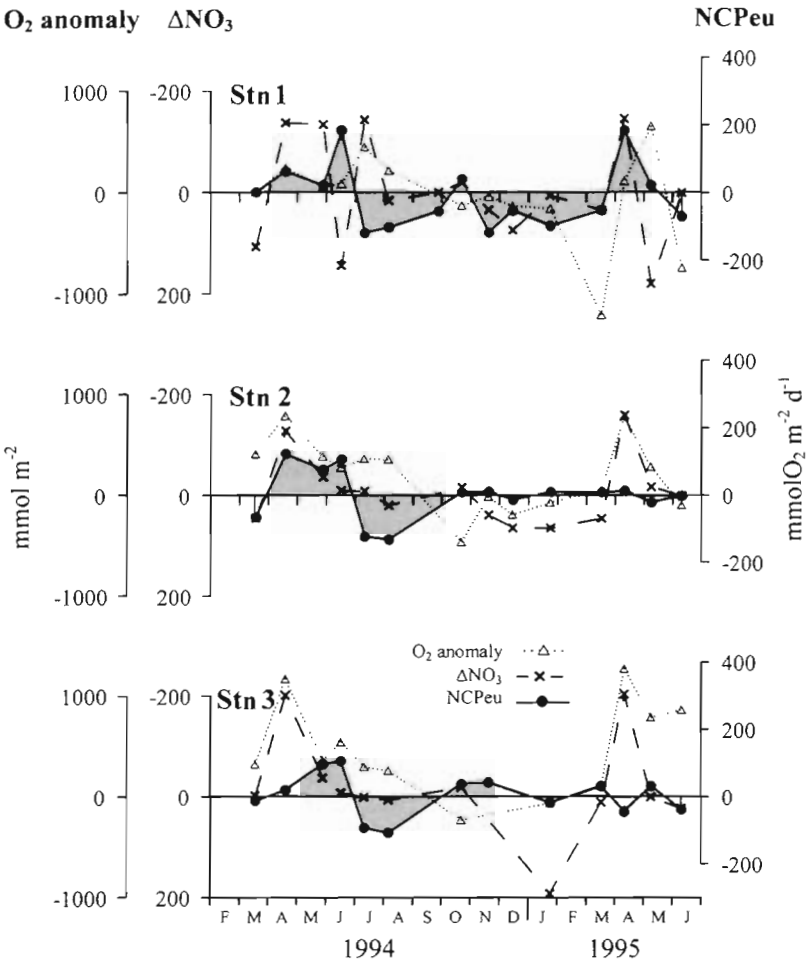

Fig. 9. Temporal variation in oxygen anomaly (mmol O_2 m^{-2} of difference with respect to the concentration of saturation) and monthly increase in NO_3 content (ΔNO_3) in the euphotic zone at the 3 sampled stations. Temporal variation in NCPeu is shown superimposed for comparison

ing the aged upwelling in April 1995, O_2 increase and nitrate decrease were not only concurrent to NCP increase, but also traced the offshore extension of the upwelling plume. This delay in the signal validates the use of the comparison between NCP and O_2 saturation and nitrate content in the euphotic zone in order to detect non-sampled hydrographic and/or microbiological events. It is worth noting that throughout the summer, while DR greatly exceeded GP, O_2 concentration remained oversaturated at the 3 sampled stations, but no trace of significant upwelling could be found.

Therefore evidence suggests that the sampled annual cycle of NCP reasonably represents the community metabolism throughout the period of study at the 3 stations. Furthermore, with the exception of some situations (e.g. upwellings), it is not necessary to consider advection in order to explain the chemical conditions found in the euphotic zone; these are better explained by biological activity within that layer, i.e. steady-state conditions prevailed during the period of study. In fact, the sum of monthly changes of nitrate content in the euphotic layer from March 1994 to March 1995 was only −48, +40 and −60 mmol m^{-2} yr^{-1} at Stn 1, Stn 2 and Stn 3, respectively.

DISCUSSION

If the seasonal cycle of atmospheric O_2 is caused by the temporal uncoupling in organic matter production and consumption in the sea (Keeling & Shertz 1992, Pomeroy & Wiebe 1993, Bender et al. 1996, Sherr & Sherr 1996), the seasonal evolution of NCP must echo its trend. The seasonal and spatial distributions (vertical and horizontal) of production and respiration rates (together with those of nutrient and oxygen concentrations, and phytoplankton biomass) determined in this study clearly show the linkage in P and R through the exchange of local surpluses of organic matter, as well as the importance of terrigenous influence. Although the vertical scale was not sufficient to study the final fate of organic matter produced during several net autotrophic periods (e.g coastal upwelling), the horizontal scale considered was enough to provide a fair representation of trophic shifts and, hence, to study the time scales of interaction between auto- and heterotrophic processes. Moreover, the verification of the prevalence of steady-state conditions, when the whole period and region of study are considered, will allow the interpretation of NCP data within a biogeochemical context.

Seasonal variation of P/R balance

In this study a strong seasonal pattern was observed for both O_2 production and consumption rates. A similar pattern of primary production rates, coupled to vertical stability transitions in the water column, has been described before in this region (e.g. Fernández & Bode 1991). The highest temporal and vertical variability in P rates was found at the coastal station, where more than 60% of total GP measured during 16 mo occurred at the surface layer, and was directly related to

episodic coastal upwelling (38% of total coastal euphotic zone GP). However, offshore productive periods were more related to the seasonal cycle of stratification and mixing, lasted longer, and were not dominated by surface processes. This highlights the importance of measuring P and R rates in subsurface layers in order to properly estimate the trophic balance of the community.

The range of DR rates was similar at the 3 stations studied. Also the seasonal trends, characterised by post-bloom and summer maxima, were similar except in winter, when high DR rates were only measured at the coastal station. Low phytoplankton biomass and activity, together with strong vertical mixing, suggest that high winter DR rates might be related to the consumption of allochthonous organic matter. Several processes may produce a winter increase of organic matter discharge to the coastal zone, e.g. the increase in flow and organic matter content of rivers (typically, lower salinity was found during the winter near the coast, ca 35.48, than offshore, ca 35.54), the seasonal breakage of macroalgae or the resuspension of settled material from the sediment.

Except during the winter at Stn 1, the pattern of P/R balance was relatively uniform in the region, being characterised by a spring to summer transition from auto- to heterotrophy, which agrees with the results reported in previous studies (e.g. Rowe et al. 1986, Pomeroy & Wiebe 1993, Blight et al. 1995, Griffith & Pomeroy 1995). Diverse processes have been postulated as causing this pattern, mainly depending on the observed degree of coupling between auto- and heterotrophic metabolism of the community, i.e. depending on the periodicity and length of the different phases. In our study, the coincidence of the highest rates of primary production with phases of low total respiration, and the absence of a relationship between chl *a* concentration and DR rate, point to a low phytoplanktonic contribution to DR rates. Assuming phytoplankton respiration to be 10 to 15% of gross production (Setchell & Packard 1979), the contribution of non-phytoplanktonic respiration to total measured respiration rate, over an annual scale, would be 87 ± 2.1%, 83 ± 3.6% and 81 ± 2.9% for Stn 1, Stn 2 and Stn 3, respectively.

At coastal waters off North Wales, Blight et al. (1995) found a short (ca 3 wk) heterotrophic phase immediately after a *Phaeocystis* sp. bloom. The observed lag of about 2 wk between GP and DR maxima, as well as the lack of a relationship between total respiration and temperature (as is the case in the present study) led these authors to explain the auto-heterotrophy transition in terms of delayed consumption of high molecular weight dissolved organic matter (DOM), which had accumulated after *Phaeocystis* sp. growth. This conclusion is consistent with the results obtained in other studies, showing a strong relationship, sometimes slightly delayed, between microbial heterotrophic activities and primary production (Simon & Tilzer 1987, Kirchman et al. 1991, 1994). This explanation would subscribe, as a special case given the slow processing of some high molecular weight DOM constituents, models of the regulation of bacterial activity by substrate availability (e.g. Cole et al. 1988, Wright 1988, Kirchman 1990).

Other authors (Pomeroy et al. 1991, Kirchman et al. 1993, Pomeroy & Wiebe 1993, Sampou & Kemp 1994, Shiah & Ducklow 1994, Smith & Kemp 1995) have attributed the seasonal variation in microbial respiration to the combined effect of temperature and substrate availability on heterotrophic bacterial metabolism. Experiments carried out with bacteria growing under a matrix of temperatures and substrate concentrations (Pomeroy et al. 1991, Wiebe et al. 1992, 1993) have shown a non-linear response of growth rate, with high Q_{10} values (>10) near the combination of minima temperature and substrate concentration. Temperature, then, appears to produce a marked effect on bacterial activity at the low substrate concentrations usually found in the ocean, while at high concentrations such an effect is considerably reduced. Pomeroy & Wiebe (1993) attributed the observed shift from winter-spring autotrophy to summer-autumn heterotrophy to the delay in the consumption of organic matter produced during the spring phytoplankton bloom until phytoplankton cell lysis or zooplankton excretion, defecation and sloppy feeding produced areas of high DOM concentration. In any case, a high bacterial contribution to total respiration has been frequently documented (see e.g. reviews by Williams 1981, Fuhrman 1992 and Sherr & Sherr 1996), emphasizing the important role played by the regulation of bacterial activity on the seasonality of P/R balances (Pomeroy & Wiebe 1993, Sherr & Sherr 1996).

In this study, the summer heterotrophic phase (2 to 3 mo) was considerably longer than previously reported in the literature. It has already been mentioned that steady-state prevailed during this study, at least in the oceanic region. Nevertheless, there still exists the possibility that the observed long heterotrophic phase could be the result of the coincidence of summer samplings with short heterotrophic periods following non-sampled phases of high productivity. The comparison between NCPeu and O_2 saturation and nutrient content in the euphotic zone allows the tracing of significant upwelling events. The observed trends of these variables (see Fig. 9) suggest that a significant event did not take place during the summer (apart from that in June 1994), and in any case suggest that the measured high DR rates did not derive from

the consumption of recently synthesised organic matter. This could only happen in the auto-heterotrophy transition observed between June and July 1994. However, considering the euphotic zone of the 3 stations, the negative NCP value registered in July would correspond to 90% of the positive value of June, which seems too high to result from direct consumption. An alternative explanation for the high DR measured during summer at every station could be the import of organic matter from adjacent marine regions or land. This is difficult to sustain, as a similar heterotrophic balance was observed at the 3 stations and during 2 to 3 consecutive months; moreover, the strong water column vertical stability, and the presumably low organic matter discharge from land during the summer, all point to a reduced allochthonous influence. Once the suggestion of rapid consumption of imported or recently synthesised organic matter has been discredited, the only possible explanation for the heterotrophic balance throughout the summer is a delayed consumption of organic matter previously synthesised in the region.

Accumulation of DOM during the final phases of phytoplankton blooms has been frequently reported (e.g. Brockman et al. 1983, Norrman et al. 1995, Smith et al. 1995). Several investigations have also shown active bacterial consumption of the recently produced DOM (Lignell 1990, Kirchman et al. 1991, Smith et al. 1995). In our study, low DR rates measured in shelf waters in April 1994, when high phytoplankton biomass and active algal growth were registered (Figs. 3 & 7), would be related to the delay in DOM accumulation, a necessary condition for activating bacterial growth at the relatively low temperature of spring water (Pomeroy & Wiebe 1993). Meanwhile, in oceanic waters, where bloom decay was presumed, the observed increase of DR rates (Fig. 7) would reflect the rapid consumption of accumulated labile DOM. Hence, the observed enhancement in DR rates would correspond to the short heterotrophic phase often described after spring blooms (e.g. Blight et al. 1995), although the uncoupling between P and R could be a simple result of low temperature, and not necessarily of the semi-refractory nature of produced DOM. A similar process may explain the very low DR rates in recent upwellings and their offshore increase following the export and sinking of biomass, especially in late phases (compare April 1994, recent upwelling, with June 1995, aged upwelling, in Fig. 7. See also Fig. 3).

The control of heterotrophic activity by the interaction between substrate availability and temperature may also produce a decrease of DR rates before the complete exhaustion of DOM, allowing the permanence in the euphotic zone of a surplus of non-consumed DOM (e.g. Pomeroy & Wiebe 1993, Sherr & Sherr 1996). Indeed, 1 mo after the spring bloom, although elevated GP remained in the euphotic zone, DR rates decreased to winter levels (see Fig. 7). The summer increase in water temperature would permit the bacterial heterotrophic activity to increase at relatively low substrate concentrations, allowing the consumption of DOM not utilised during spring, and producing the observed increase in DR rates.

Seasonal compensation of production and respiration processes is a characteristic of the dynamics of pelagic ecosystem in temperate seas

The seasonal cycle of microbial net metabolism observed in the present study has greater amplitude and significance than usually reported in the literature; this derives from the spatial and temporal scales considered. First, the importance of measuring P and R rates within the whole euphotic zone, in order to adequately describe the trophic status of the system, has been shown (see also Williams 1998). Second, the length of the heterotrophic phase is greater than the delay of 2 to 3 wk for the consumption of organic matter produced during spring blooms (e.g. Blight et al. 1995). Third, the observed coast-ocean patterns of seasonal variability suggest that the significance of the summer heterotrophic phase goes beyond the consumption of recently synthesised or allochthonous organic matter (e.g. Satta et al. 1996). The results presented in this paper strongly support the existence of a seasonal uncoupling in the processes of production and consumption of organic matter in the euphotic zone, emerging from the trophic dynamics of the pelagic ecosystem (e.g. Pomeroy & Wiebe 1993, Griffith & Pomeroy 1995, Sherr & Sherr 1996). Specifically, it would ultimately derive from the physical control of planktonic primary production, which results in the coincidence of high primary production rates with relative low water temperatures, and from the regulation of heterotrophic bacterial activity by the interaction between temperature and substrate availability.

The explanation given above for the seasonality in P/R balances implies the existence of an heterotrophic succession (see also reviews by Pomeroy & Wiebe 1993 and Sherr & Sherr 1996) in which, after rapid consumption of labile DOM (Riemann & Søndergaard 1984, Chen & Wangersky 1996), accumulated after the spring bloom (Kirchmann et al. 1991, Norrman et al. 1995, Smith et al. 1995), a decrease of bacterial activity would be caused by low water temperature (Pomeroy et al. 1991, Wiebe et al. 1992, 1993, Shiah & Ducklow 1994), thus allowing the permanence in the water column of a certain amount of DOM (both labile and

refractory, both accumulated during the winter and produced after the spring bloom) (Carlson et al. 1994). This DOM would be progressively consumed when the increase in water temperature allowed the utilisation of both low concentrations of substrate and semi-refractory compounds, giving rise to low bacterial growth efficiency (Kroer 1993) and, consequently, to elevated DR rates (Hopkinson et al. 1989). The preference for consumption of labile and/or N-rich DOM (Kirchmann 1990, Chen & Wangersky 1996) would generate a progressive increase in the proportion of semi-refractory and high C/N ratio compounds in the DOM. Hence, as high DR rates and a net heterotrophic balance remain until the end of the summer, a bacterial (specific or metabolic) succession from bacteria rapidly consuming labile DOM to the exoenzymatic degradation of semi-refractory and high C/N ratio DOM (see e.g. Azam et al. 1994) would be expected.

The described amplitude of the seasonal offset of P/R balances alone can explain the observed cycles of oxygen saturation and nutrient content in the euphotic zone (see Fig. 9), as well as the seasonal cycle of oxygen anomaly in middle and low latitudes (Najjar & Keeling 1997), and, of greater significance, the atmospheric oxygen cycle described by Keeling & Shertz (1992) and Bender et al. (1996). The air-sea O_2 fluxes associated with the seasonal cycle in atmospheric O_2 'are linked to the rate at which organic material is produced and exported from the euphotic zone' (Keeling & Shertz 1992). In the northern hemisphere these data show a winter minimum and a late summer maximum which are consistent with the cycles of net production and upper ocean ventilation and with the idea of a temporal offset in organic matter production and consumption in the sea (Pomeroy & Wiebe 1993, Sherr & Sherr 1996). As stressed by Six & Maier-Reimer (1996), 'atmospheric oxygen data provide an independent test for marine biota models. It is a unique quantity that gives information about net carbon production in the plankton community'. From the seasonal variation in atmospheric O_2, Keeling & Shertz (1992) estimated a spring ocean net production of organic carbon of ca 48 g C m^{-2}. Similarly, Bender et al. (1996) calculated a seasonal net production of 60 g C m^{-2} for the southern hemisphere. Independently, Sambrotto et al. (1993) estimated, from the seasonal dissolved inorganic carbon deficit in the euphotic zone, a seasonal net production in the North Atlantic of 48 g C m^{-2} If a photosynthetic quotient of 1.3 (Laws 1991) is applied to the results of seasonal oxygen P/R balance in the present study, NCPeu during the spring autotrophic phase would range from 46 g C m^{-2} at Stn 1 to 72 g C m^{-2} at Stn 2. This coincidence, both in the trends and absolute values, constitutes exceptional and independent confirmation of the idea that the long-term compensation of the seasonal P/R imbalances is an intrinsic process of the pelagic ecosystem, at least in temperate seas.

The consideration of such a process as a constituent of system dynamics has profound implications for the interpretation of trophic organisation and the calculation of new production from nitrate uptake. For instance, if summer heterotrophy is sustained by the excess production of the spring, then the processes of recycling during the summer would not only represent a loop of local production, but also, to some extent, a source of new nutrients at the scales usually considered for estimating new production. On the other hand the quantification of the maximum removable biomass for system integrity will only be possible at temporal and spatial scales comprising the connection between auto- and heterotrophic subsystems.

Annual net P/R balances

If the maintenance of the system during heterotrophic phases relies upon the consumption of the surplus of organic matter produced during preceeding autotrophic phases, then the annual net balance of the processes of production and consumption of organic matter must approach zero when steady-state conditions prevail, conditions that, in this study, tended to predominate towards the ocean.

Both the calculated values of annual P/R balance and, of greater significance, the coast-ocean trend of that balance, indicate that no surplus of produced organic matter, available to export, exists in the euphotic zone over an annual scale. That is, the fate of organic matter synthesised on the shelf seems to be oxidation *in situ* rather than export to ocean depths. This coincides with the results of several studies which stress the importance of microbial consumption of organic matter (e.g. Rowe et al. 1986, Biscaye et al. 1994), and seems to be a result of the seasonal compensation of P and R derived from the processes controlling phytoplankton growth and microbial heterotrophic activity in temperate seas (Griffith & Pomeroy 1995). Only certain processes (e.g. upwelling) which separate the system from steady-state, allow the export of a significant amount of organic carbon.

The recognition of the time and space scales relevant for the linkage between production and respiration processes in the sea is germane in order to ascertain the trophic status of the ocean. As pointed out by Smith & Hollibaugh (1997) the definition of the 'trophic status' of an ecosystem from NCP 'carries with it a condition (usually not explicitly stated and often ignored) of the time span over which the inferred trophic status applies'. The present debate about the trophic status of the ocean (e.g. del Giorgio et al. 1997, Geider 1997,

Duarte & Agustí 1998, Williams 1998) is based on the accumulation of local measurements of either a net heterotrophic or a net autotrophic balance. This assumes the prevalence of steady-state conditions during sampling, i.e. that a temporal or spatial linkage between P and R is not significant, beyond 'a very limited separation in time (5 to 10 d or less) between the 2 phases—with no protracted period of high heterotrophy following the autotrophic bloom' (Williams 1998). Although both del Giorgio et al. (1997) and Duarte & Agustí (1998) explained the net heterotrophy of unproductive regions as a result of temporal or spatial organic matter import, the data sets they used to derive their conclusion are biased, as no consideration is made of the scales over which the measured trophic statuses apply. The results of the present study indicate that an appreciation of the spatial and temporal scales at which the trophic dynamics of the pelagic ecosystem function is a priority, as only then may the determination of the balance between production and respiration help to elucidate the trophic status of the ocean.

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