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Phytoplankton size structure and water column metabolic balance in a coastal upwelling system: the Ría de Vigo, NW Iberia

B. Arbones*, C. G. Castro, F. Alonso-Pérez, F. G. Figueiras

CSIC, Instituto de Investigacións Mariñas, Eduardo Cabello 6, 36208 Vigo, Spain

ABSTRACT: The metabolic balance between gross primary production (GPP) and community respiration and its relationship with the plankton community structure was investigated in the Ría de Vigo, in the coastal upwelling system of the NW Iberian Peninsula. Measurements of *in situ* GPP, dark community respiration (DCR), size-fractionated biomass, size-fractionated primary production (^{14}C PP) and GPP from photosynthetic-irradiance incubations ($^{14}C\ PP_{P\text{-}I}$) were carried out in the Ría de Vigo between April 2004 and January 2005. Seasonal patterns of phytoplankton biomass and primary production were in phase with one another. The highest ^{14}C PP and biomass values, accounting mainly for the large-size phytoplankton (>20 µm), were observed under upwelling-favourable conditions (spring and summer). Minimum values of ^{14}C PP and phytoplankton biomass were registered in winter with a shift to small phytoplankton dominance (>80%). Integrated water column DCR varied between a summer maximum of 132 mmol O_2 m^{-2} d^{-1} and a winter minimum of 31 mmol O_2 m^{-2} d^{-1}. Community respiration was significantly related to primary production for the 2 upwelling cruises, pointing to a close coupling between these processes. However, no direct relationship was found for the other periods. Our results suggest that the water column metabolic balance inside the Ría de Vigo is dependent on phytoplankton size structure. The autotrophy degree of the system is high when the contribution of large-size phytoplankton is dominant, whereas it is almost in balance when the small phytoplankton fraction prevails.

KEY WORDS: Primary production · P/R balance · Microplankton size structure · Upwelling · Ría de Vigo

INTRODUCTION

Coastal regions, in spite of covering only 7% of the total ocean surface, play a major role in oceanic biogeochemical cycling, exchanging large amounts of matter with the open ocean. These biogeochemically active regions are characterised by high rates of primary production and respiration relative to open ocean waters (Duarte & Agustí 1998, Hopkinson & Smith 2005). About 14 to 20% of total global ocean production (Chen et al. 2003) and ca. 8 to 10% of total oceanic respiration (excluding benthic respiration) take place in coastal regions (del Giorgio & Williams 2005). Organic matter not respired in the water column may be transferred to higher trophic levels, transported offshore, exported vertically and mineralised, or buried in the sediment. In fact, shelves generate the biological production to support over 90% of global fish catches (Pauly et al. 2002). About 7% of the total primary production of the oceans is recycled in the coastal benthos, and the coastal regions are the burial site of 80% of the organic carbon derived from both oceanic processes and terrestrial sources (Wollast 1998, Chen et al. 2003).

The fate of allochthonous and autochthonous organic matter in a coastal region is defined by the net community production (NCP) of the system, the balance between gross primary production (GPP) and respiration (R) by all organisms. NCP is a useful index of the trophic status of the ecosystems (Odum 1956) and represents the amount of organic matter available for export to the benthos and adjacent ecosystems or for transfer to higher pelagic trophic levels. Autotrophic coastal systems receive large amounts of inorganic nutrients and organic carbon production is higher than

*Email: belen@iim.csic.es

respiration. In heterotrophic systems respiration exceeds production, receiving important inputs of allochthonous organic matter (Smith & Kemp 1995, Caffrey et al. 1998, Hopkinson & Smith 2005). Although there is often a general positive relationship between GPP and R in different systems (del Giorgio et al. 1997, Duarte & Agustí 1998) and at different spatial (Smith & Kemp 1995, Serret et al. 2001) and temporal scales (Blight et al. 1995), there is also a substantial unexplained variability between them. Several authors (Serret et al. 2001, Smith & Kemp 2001) have investigated the influence of phytoplankton size structure on the production/respiration (P/R) balance, observing that not only the overall magnitude of P but also the type of plankton community regulates the net balance of an ecosystem. Smith & Kemp (2001) found an important linkage between the size distribution of the primary producers and the overall balance of P and R in the plankton community, based on a strong inverse relationship between the P/R ratio of the total plankton community and the proportion of P attributable to the picoplankton fraction. Therefore, establishing the extent to which the P/R ratio is linked to phytoplankton size structure in highly productive coastal ecosystems is relevant to determine their export capability.

The coastal upwelling system of the Ría de Vigo (NW Iberian Peninsula) is characterised by predominant upwelling conditions from April to September and downwelling conditions the rest of the year, with dominant southerly winds (Wooster et al. 1976, Haynes & Barton 1990). During the upwelling period, the system is highly productive (Tilstone et al. 1999, Lorenzo et al. 2005), dominated by a large-sized phytoplankton community (Tilstone et al. 1999, Cermeño et al. 2006) that exhibits a net autotrophic metabolism (Moncoiffé et al. 2000). In contrast, during the downwelling season the ecosystem presents much lower primary production, and the pico- and nanoplankton-size fractions significantly increase their contribution to the primary production, dominating the winter community (Cermeño et al. 2006). In spite of the importance of the P/R balance on the fate of organic matter in the system, there is no previous work focused on studying the P/R balance in relation to phytoplankton size structure in the Rías Baixas. The aim of this study is to improve our understanding of the relationship between plankton community structure, production, and respiration in the coastal upwelling system of the Ría de Vigo. With this objective, *in situ* 24 h ^{14}C primary production (^{14}C PP) and oxygen incubations were conducted in the inner part of the Ría de Vigo over an annual cycle and at an additional station in the outer part of the Ría in July 2004. Concurrent ^{14}C photosynthesis-irradiance (^{14}C $PP_{P\text{-}I}$) relationships were also measured at the inner station, which together with the oxygen incubation measurements allowed us to estimate the photosynthetic quotients for the different seasonal periods.

MATERIALS AND METHODS

Between April 2004 and January 2005, 16 oceanographic cruises were carried out at the inner part of the Ría de Vigo (Fig. 1, IR) within the framework of the Spanish project 'Acoplamiento de los flujos verticales y bentónicos en la Ría de Vigo' (FLUVBE). Sampling was conducted during 4 periods: spring (April), summer (July), autumn (October) and winter (January). Stn IR was visited twice a week for 2 wk during each period. An additional station at the outside area of the Ría de Vigo (Fig. 1, OU) was visited 4 times between July 19 and 29 in the framework of the EU 'Managing Benthic Ecosystems in Relation to Physical Forcing and Environmental Constraints' (MABENE) project. The sampling at Stn OU was carried out just after the FLUVBE July cruise.

Water samples for the analysis of nitrate, chlorophyll, oxygen and primary production were taken with 10 l PVC Niskin bottles mounted on a rosette, with a CTD (SBE 911 CTD). Salinity was calculated from conductivity measurements using the IAPSO (1985) equation. Photosynthetically active radiation was also continuously recorded with a profiler (Biospherical

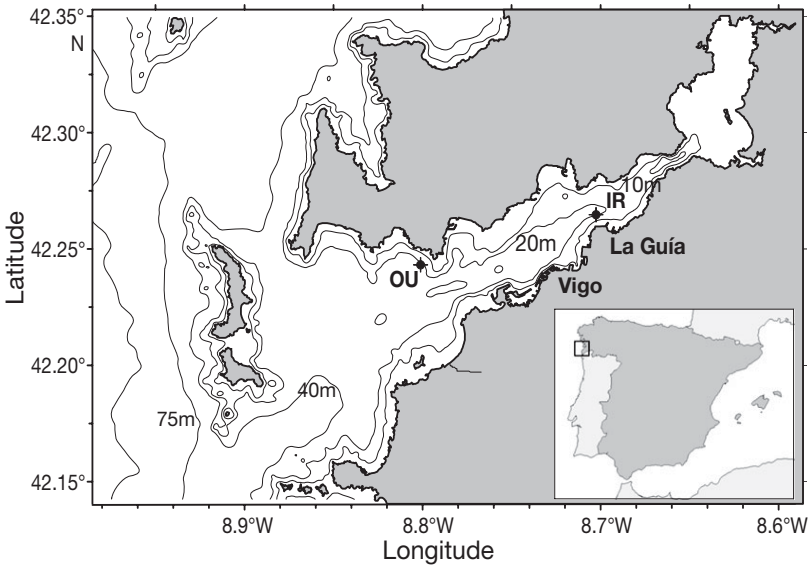


Fig. 1. Study area sampling station locations (IR: Inner Ría; OU: outside station)

QSP200PD) attached to the CTD. Nitrate levels were determined by segmented flow analysis with Alpkem autoanalyzers (Hansen & Grasshoff 1983). The analytical error was ±0.05 µM.

Size-fractionated chlorophyll *a* (chl *a*) concentration was determined by sequentially filtering 250 ml through 20 µm (microplankton), 2 µm (nanoplankton) and 0.22 µm (picoplankton) pore size polycarbonate filters. Sea water samples of 100 to 250 ml were also filtered through 25 mm Whatman GF/F filters for total chl *a*. After filtration, samples were frozen (–20 °C) until pigment extraction in 90% acetone over 24 h in the dark at 4°C. Chl *a* was determined by fluorescence of the pigment extracts using a Turner Designs fluorometer calibrated with pure chl *a* (Sigma).

Primary production was measured with the ^{14}C technique by means of 24 h *in situ* incubations at 4 depths in the photic layer with 3 light flasks and 2 dark flasks at each depth inoculated with 3.7×10^5 Bq (10 µCi) of $NaH^{14}CO_3$. After the incubation, samples were filtered sequentially through polycarbonate filters (20, 2 and 0.22 µm pore size), which were then exposed to HCl fumes to eliminate unincorporated inorganic ^{14}C. Disintegration per minute (DPM) values were determined with a liquid scintillator using the external standard method to correct for quenching.

Additionally, photosynthesis-irradiance (P-I) curves were obtained at the same 4 depths. Incubations were carried out at simulated *in situ* temperature under 14 irradiance levels in the lab. After 1 to 1.5 h of incubation time, samples were GF/F filtered. Photosynthetic parameters were determined using the equation of Platt et al. (1980). Integrated primary production was estimated according to Lorenzo et al. (2005), considering the photosynthetic parameters, daily and vertical spectra irradiance (determined with a Licor Li-1800UW spectro-radiometer) and phytoplankton absorption spectra measured following Arbones et al. (1996).

In spite of the existing controversy about what the P-I curve indicates, we consider P-I to be a measurement of GPP. A comparison between short-time 2 h *in situ* incubations with ^{14}C, ^{14}C $PP_{P\text{-}I}$ and 24 h *in situ* ^{14}C PP gave production values of 1.40, 1.41 and 1.13 µmol C kg^{-1} h^{-1}, respectively. These results indicate that primary production obtained from P-I curves was closer to GPP than net primary production.

Measurements of plankton community GPP, NCP, and dark community respiration (DCR) were determined by 24 h *in situ* light-dark bottle oxygen incubations at 5 depths. At each of the 4 photic depths, 4 light and 4 dark bottles were placed in a specially constructed plexiglass holder. For the aphotic depth, we only incubated 4 dark samples. A further set of 4 replicates at each depth was fixed at time 0. Dissolved oxygen was determined by an automated Winkler titration system. Net *in vitro* changes in the light and dark bottles gave NCP and DCR, respectively. Production and respiration rates were calculated as follows: NCP = ΔO_2 in light bottles in relation with the initial oxygen concentration; DCR = ΔO_2 in dark bottles in relation with the initial oxygen concentration; GPP = NCP + DCR.

RESULTS

Hydrographic conditions

The seasonal variability of the upwelling index, temperature, nitrate and chl *a* during the 5 study periods are shown in Fig. 2. The spring cruise corresponded to a transition from downwelling (April 19 and 22) to upwelling conditions, as we observed in the nitrate and temperature time series. At the beginning of this period, nitrate levels were low, increasing to >1 µM for the last 2 d when the highest chl *a* values were recorded. During the summer period, we observed a series of upwelling-relaxation cycles. The first 2 wk of July were mainly characterised by upwelling conditions, which favoured the development of a high phytoplankton standing stock with chl *a* as high as 14 mg chl *a* m^{-3}. However, the water column was mainly dominated by stratification during the last 2 wk of July. This situation was accompanied with a decrease in chl *a* and the sinking of the chl *a* maximum. The situation in October was the opposite that in April. The first week was mainly characterised by strong upwelling conditions with cold water and high nitrate concentrations at the bottom. The highest chl *a* concentration was observed at the beginning of the period, with low values at the surface and high values at the bottom. After October 11, there was a shift to southerly winds, and much lower nitrate and chl *a* concentrations were evenly distributed in the water column. The water column was homogenously distributed for the winter period with low temperatures (<13°C), high nitrate (>7 µmol kg^{-1}) concentrations and low chl *a* concentrations (<1 mg chl *a* m^{-3}).

Integrated size-fractionated chlorophyll and primary production

Water column integrated, size-fractionated chl *a* and primary production values showed similar seasonal patterns with high values in the spring and summer upwelling and low values in winter (Fig. 3). During April the chl *a* value was 92.3 mg chl *a* m^{-2} and the

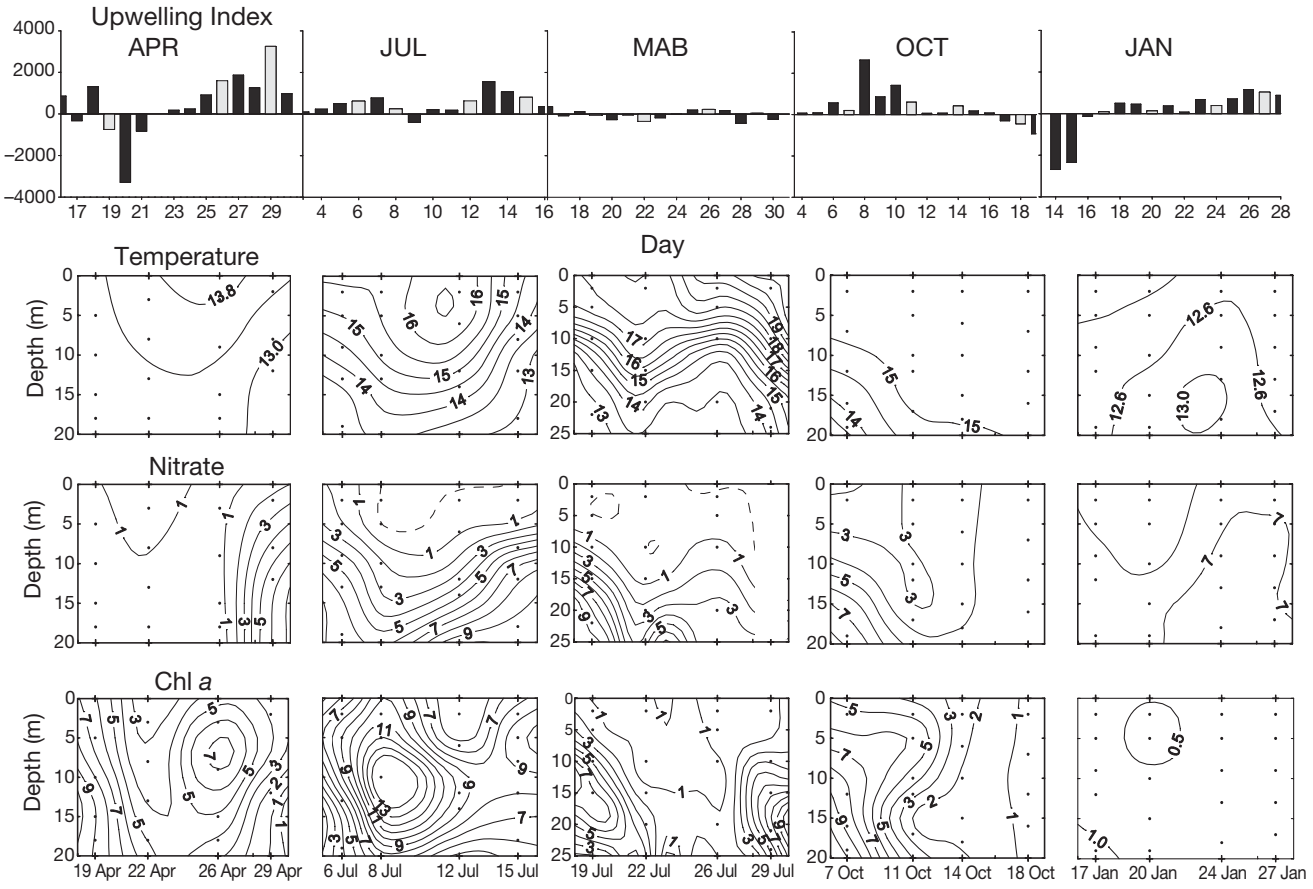
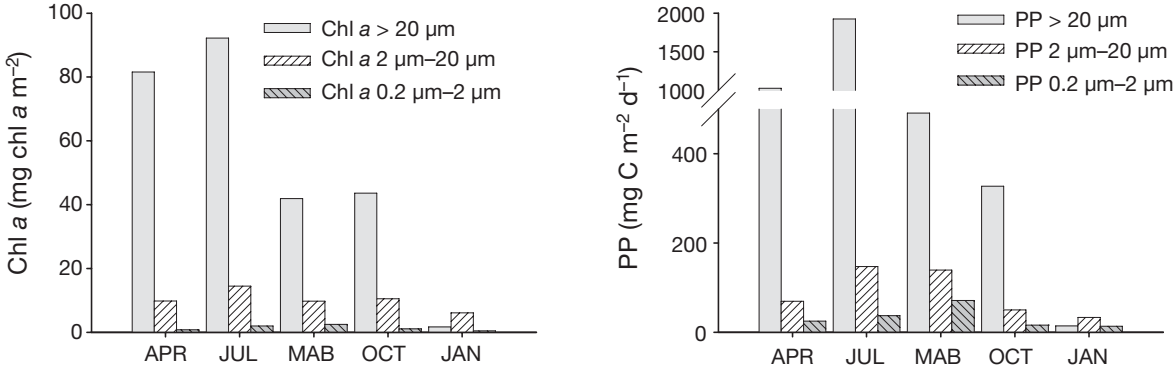


Fig. 2. Time series of upwelling index ($m^3 s^{-1} km^{-1}$), temperature (°C), nitrate (µmol kg^{-1}), total chl *a* concentration (mg chl *a* m^{-3}) for the 5 study periods. MAB (MABENE project) corresponds to the July 19 to 29 period. Grey bars in upwelling index plot: sampling days



% Chl *a*	Apr	Jul	MAB	Oct	Jan
> 20 µm	88	85	77	79	20
2 – 20 µm	11	13	18	19	74
2 – 20 µm	1	2	5	2	6

% PP	Apr	Jul	MAB	Oct	Jan
> 20 µm	92	91	70	83	23
2 – 20 µm	6	7	20	13	55
2 – 20 µm	2	2	10	4	22

Fig. 3. Integrated size-fractionated chl *a* and primary production (PP). Tables under the graphs give the percent of the variable magnitude for the corresponding period. MAB corresponds to the July 19 to 29 period

daily integrated primary production was 1120 mg C m^2 d^{-1}. In the summer upwelling, the mean integrated chl *a* value was 108 mg chl *a* m^{-2} and the daily integrated PP was 2108 mg C m^{-2} d^{-1}. During the July stratification period and in autumn, chl *a* and primary production decreased in 1 and 2 orders of magnitude, respectively. In winter this reduction was 2 and 3 orders of magnitude, respectively, with an integrated chl *a* value of 8.25 mg chl *a* m^{-2} and mean seasonal primary production of 60 mg C m^{-2} d^{-1}.

In relative terms, the microplankton size fraction dominated for the entire year, except winter, when nanoplankton was the dominant fraction. The microplankton size fraction reached a contribution of >85% in biomass for the spring and summer upwelling; however, its contribution dropped to 77% during the July stratification and to 20% in winter. In ^{14}C PP terms, its contribution dropped from >91% for the spring and summer upwelling to 23% in winter. Although the contribution of the nanoplankton fraction was dominant for the winter period (74% and 55% in chl *a* and primary production, respectively), in absolute terms, these values were lower than its contributions during the other study periods.

Seasonal and vertical variability of ^{14}C PP, GPP, NCP and DCR

Rates of ^{14}C PP, GPP, NCP and DCR were highly variable, both seasonally and vertically (Fig. 4). During April, the highest values of ^{14}C PP were observed at sea surface with maximum values on April 26 (27 µmol C kg^{-1} d^{-1}). GPP and DCR for this period showed a similar structure to ^{14}C PP, with a surface maximum on April 26. Due to the high surface value of DCR on April 26, we did not observe such a striking maximum in the NCP time series for this date; however, the highest values were reached on the last 2 days. At the beginning of July, the upwelling-relaxation cycle favoured the development of high PP levels, reaching the maximum (47 µmol C kg^{-1} d^{-1}) on July 15. GPP time series also presented the highest values in the upper 5 m, and the maximum rates of DCR were observed just below the ^{14}C PP maxima. Consequently, NCP reached the highest values at the surface, becoming negative at a depths of 10 m, except for July 6. During the subsequent July stratification period (Fig. 4, MAB column), ^{14}C PP and GPP levels were lower than during the previous summer upwelling cruise. However, DCR levels

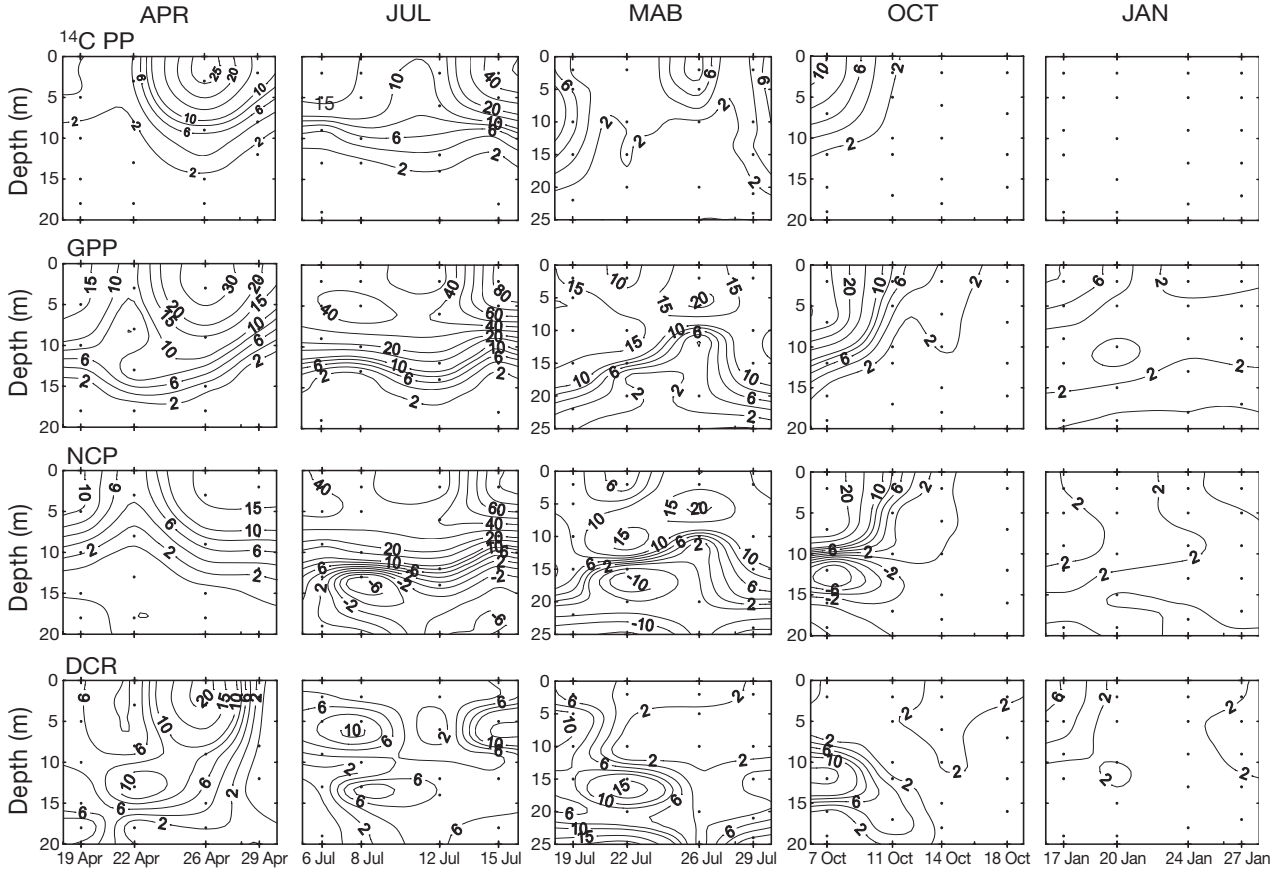


Fig. 4. Time series of ^{14}C primary production (^{14}C PP), gross primary production (GPP), net community production (NCP) and dark community respiration (DCR) for the 5 sampling periods. Units µmol kg^{-1} d^{-1}. MAB corresponds to the July 19 to 29 period

Table 1. Average values and SD (in brackets) of integrated photic water column chlorophyll a (chl *a*), respiration in the photic and aphotic layer (dark community respiration, DCR), gross primary production (GPP), ^{14}C primary production (^{14}C PP) and gross primary production from photosynthetic-irradiance incubation (^{14}C $PP_{P\text{-}I}$). MAB corresponds to the July 19 to 29 period (for which there is no data [nd] regarding ^{14}C $PP_{P\text{-}I}$)

Cruise	Chl *a* (mg chl *a* m^{-2})	DCR photic (mmol O_2 m^{-2} d^{-1})	DCR aphotic (mmol O_2 m^{-2} d^{-1})	GPP (mmol O_2 m^{-2} d^{-1})	^{14}C PP (mmol C m^{-2} d^{-1})	^{14}C $PP_{P\text{-}I}$ (mmol C m^{-2} d^{-1})
Apr 04	92.3 (51.5)	104.5 (72.2)	9.2 (7.5)	200.6 (83.8)	96.0 (73.9)	119.7 (65.7)
Jul 04	108.6 (27.6)	74.5 (27.3)	21.9 (16.0)	462.0 (116.9)	180.3 (85.9)	227.3 (115.1)
MAB 04	52.0 (35.4)	74.9 (59.8)	57.0 (51.4)	224.3 (61.2)	60.0 (24.5)	nd
Oct 04	55.2 (53.3)	50.1 (26.4)	1.5 (0.3)	96.4 (119.6)	34.1 (36.6)	55.1 (65.7)
Jan 04	8.25 (1.39)	30.2 (16.8)	0.4 (0.1)	52.5 (20.7)	5.2 (0.9)	6.4 (0.7)
All data	62.8 (48.9)	66.4 (53.3)	23.2 (35.5)	207.1 (167.7)	71.4 (72.6)	105.9 (113.8)

were relatively higher and the aphotic layer was more heterotrophic, as the NCP distribution suggests. The autumn cruise started with relatively high ^{14}C PP values at sea surface (10 µmol C kg^{-1} d^{-1}), associated with favourable upwelling conditions. After that, ^{14}C PP fell to <0.5 µmol C kg^{-1} d^{-1}, with a reversal to southerly winds. GPP and NCP showed a similar structure due to low DCR levels. Finally, the winter period was characterised by very low primary production with DCR at about the order of GPP. NCP was homogeneous throughout the entire water column due to the intense winter mixing. In summary, we emphasize the strong temporal and vertical variability in ^{14}C PP, GPP, DCR and NCP inside the Ría de Vigo for the entire year. The compensation depth, where NCP = 0, was variable over the annual cycle, reaching the sea surface in autumn and winter.

Photosynthetic community coefficients

Photosynthetic community quotients (PQ) were calculated by linear regression (Model II) between the quantity of oxygen released (GPP) measured by the light-dark method and the quantity of assimilated carbon measured by ^{14}C $PP_{P\text{-}I}$. We have estimated the PQs for each period except the summer stratification when we did not run the ^{14}C $PP_{P\text{-}I}$ measurements. The theoretical PQ defined as the molar amount of O_2 produced per CO_2 consumed can vary between 1, if the polysaccharide photosynthesis dominates, and 1.4, if the protein photosynthesis dominates (Laws 1991). We have obtained a high correlation between GPP and ^{14}C $PP_{P\text{-}I}$ with $r^2 = 0.88$ (Tables 1 & 2) and a slope of 1.73 ± 0.08 SD for the whole data set. Analysing the data by periods, we observed that during April and July the PQs were 1.56 ± 0.17 and 1.75 ± 0.21, respectively, (Table 2) with $r^2 \geq 0.85$. These values were not significantly different from the theoretical value, 1.4 ($p < 0.01$). In October, the GPP slope versus ^{14}C $PP_{P\text{-}I}$ was higher than for the previous periods. During winter we did not find any relationship between the 2 variables.

Table 2. Photosynthetic community quotients, including slope, SE and r^2

Cruise	GPP/^{14}C $PP_{P\text{-}I}$		
	Slope	SD	r^2
Apr 04	1.56	0.17	0.88
Jul 04	1.75	0.21	0.85
MAB 04	nd	nd	nd
Oct 04	2.13	0.22	0.88
Jan 04	8.56	2.28	0.01
All data	1.73	0.08	0.88

Seasonal variability of depth integrated rates

Water column integrated ^{14}C PP, NCP and chl *a* show a similar pattern, with maximum values during the summer upwelling and minimum values in winter (Fig. 5, Table 1). Water column integrated DCR was higher during April and July than during October and January, associated with higher primary production values for the spring and summer periods. Water column integrated DCR ranged between a maximum of 132 and a minimum of 31 mmol O_2 m^{-2} d^{-1}, and integrated ^{14}C PP varied between a maximum of 180 mmol C m^{-2} d^{-1} for the summer upwelling period and minimum of 5 mmol C m^{-2} d^{-1} for winter. The aphotic zone integrated DCR was <10% of the total DCR for all the periods, except for the summer stratification period when it reached 30%. Integrated water column NCP showed that the pelagic system was mainly autotrophic. During the upwelling period the system was clearly autotrophic, while in winter NCP was practically 0. We did not find negative NCP values for the study year, except on October 18 when column integrated NCP was –28 mmol O_2 m^{-2} d^{-1}.

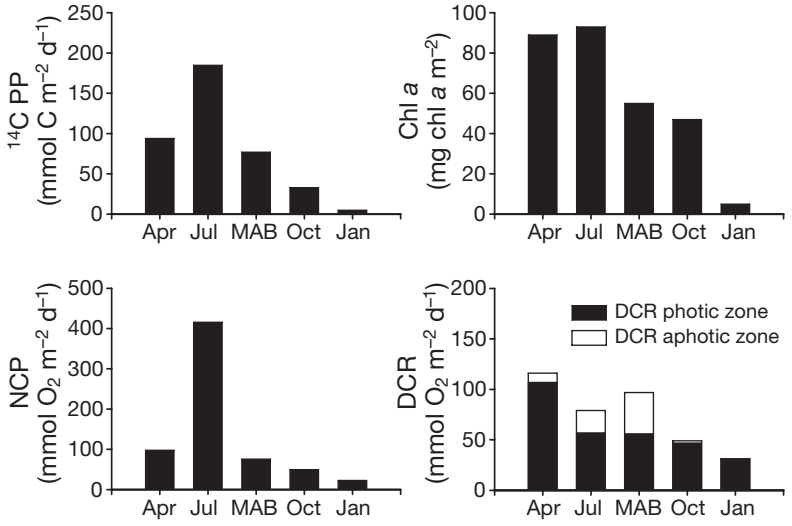


Fig. 5. Water column integrated ^{14}C primary production (^{14}C PP), net community production (NCP), dark community respiration (DCR), and chl *a* concentration for the 5 study periods. Units mmol m^{-2} d^{-1} for the rates and mg chl *a* m^{-2} for chl *a*. MAB corresponds to the July 19 to 29 period

Table 3. Linear correlation analyses between dark community respiration (DCR) (µmol O_2 kg^{-1} d^{-1}) and temperature (°C), chl *a* (mg chl *a* m^{-3}) and ^{14}C primary production (^{14}C PP; µmol kg^{-1} d^{-1}). Values in **bold**: $p \leq 0.05$. MAB corresponds to the July 19 to 29 period

	Temperature	Chl *a*	^{14}C PP
All data	0.17	**0.48**	**0.37**
Apr 04	**0.71**	0.46	**0.62**
Jul 04	−0.33	0.20	**0.79**
MAB 04	0.53	0.31	−0.02
Oct 04	**0.73**	**0.82**	0.00
Jan 04	−0.44	0.13	−0.23

Simple correlation analysis for the entire data set showed that DCR was significantly correlated with ^{14}C PP and chl *a* concentration but not with temperature (Table 3). When we closely analysed by periods, we observed that a strong correlation between DCR and ^{14}C PP existed only during the spring and summer upwelling cruises. During the April cruise, there was also a high correlation between DCR and temperature. Finally, during the October cruise, microplankton respiration was strongly correlated with temperature and chl *a* but not with the other variables.

DISCUSSION

Seasonal changes in the size structure of phytoplankton biomass and production

The temporal patterns of total size-fractionated phytoplankton biomass and primary production described here agreed with previous studies in the Rías Baixas, with maximum values for the summer upwelling period (avg. 109 ± 28 mg chl *a* m^{-2} and 2108 ± 1003 mg C m^{-2} d^{-1}) and minimum values during the winter season (avg. 8.3 ± 1.4 mg chl *a* m^{-2} and 60 ± 10 mg C m^{-2} d^{-1}). Seasonal patterns of phytoplankton biomass and production were in phase with one another, and the seasonal averages fell in the previously reported ranges for the Rías Baixas (1 to 3 g C m^{-2} d^{-1}; Tilstone et al. 1999, Varela et al. 2004, Cermeño et al. 2006), except for winter. The only study reporting phytoplankton and primary production values for the winter period (Cermeño et al. 2006) reported relatively higher values than our observations (from 10 to 27 mg chl *a* m^{-2} and from 224 to 975 mg C m^{-2} d^{-1}, respectively).

Phytoplankton size structure was mainly dominated by >20 µm cells in terms of biomass (>75%) and carbon production (>70%) for all the study periods but winter. During the winter period, the community structure changed drastically. The >20 µm phytoplankton contribution dropped to 20%, with a concomitant increase of the small fraction (<20 µm), probably associated with a change in the hydrodynamic conditions of the water column, low daily average irradiance, strong mixing and high nutrient concentrations. A similar seasonal variation with a shift to small phytoplankton (<20 µm) prevalence during winter was described by Cermeño et al. (2006).

Seasonal variability of GPP, DCR and NCP

Plankton community production also presented seasonal variability in terms of GPP and NCP, with maxima during the summer upwelling (462 and 406 mmol O_2 m^{-2} d^{-1} for GPP and NCP, respectively) and minima during winter (52 and 22 mmol O_2 m^{-2} d^{-1} for GPP and NCP, respectively).

Integrated respiration rates for the euphotic zone were among the values reported in the literature for other coastal systems (Jensen et al. 1990, Smith & Kemp 1995, Caffrey et al. 1998, Eissler & Quiñones 1999, Hitchcock et al. 2000). It ranged from 10 to 195 mmol O_2 m^{-2} d^{-1} with an avg. value of 66 ± 53 mmol O_2 m^{-2} d^{-1}. However, the volumetric respiration rates were in general slightly lower than values reported by Moncoiffé et al. (2000) for the Ría de Vigo.

Like the plankton community production rates, integrated respiration rates varied seasonally, with maximum values during spring and summer and minimum

values during winter (Table 1). High and low pelagic respiration coincided with maximum and minimum values of primary production, suggesting a close relationship between these 2 metabolic processes. In fact, we obtained a significant correlation between integrated respiration and ^{14}C PP for the entire data set and no correlation between integrated respiration rate and temperature. This pattern is consistent with an ecosystem in which pelagic metabolism is based on phytoplankton production rather than allochthonous input of organic matter (Hopkinson 1985), like that of the Ría de Vigo. According to Prego (1993) the terrestrial and anthropogenic organic matter input in the Ría de Vigo is negligible compared with *in situ* phytoplankton production (<2%). The volumetric rates presented significant correlation coefficients between primary production and respiration for the spring and summer upwelling periods and no relationship for the rest of the cruises, including the summer stratification period (Table 3).

The strong correlation for spring and summer point to a phytoplankton-dependent respiration, due to an enhancement of community metabolism in the water column, or conversely, heterotrophic respiration can limit autotrophic productivity under nutrient-limited conditions, as suggested by Smith & Kemp (1995). In our case, there was no nutrient limitation during the spring and summer, and thus, the high respiration rates were probably associated with an increased production of organic matter that stimulated algal and/or bacterioplankton respiration with only a short time lag. In contrast, during the summer stratification period, the high respiration rates were not correlated with primary production or chl *a*, suggesting a longer time scale for the coupling between production and respiration processes, probably related to the presence of a complex mix of autotrophic and heterotrophic species for this period. For the autumn and winter periods, the lower respiration rates were associated with low primary production and chl *a* levels. In fact, the significant correlation between respiration and chl *a* during the autumn cruise suggested the use of autotrophic biomass as a substrate of heterotrophic respiration.

Thus, our observations suggest that pelagic respiration rates are higher during periods of high biomass due to autotrophic and/or heterotrophic respiration based on the coupling with primary production. During periods of low primary production, as on the autumn and winter cruises, respiration, besides being lower, seemed to be mainly controlled by heterotrophic processes.

Estimate of photosynthetic quotients

Results show that the correlation between GPP and ^{14}C $PP_{P\text{-}I}$ was maintained for all the periods but winter, when there was no relationship between the 2 variables. For the April and summer upwelling cruises, the PQs did not differ significantly from the theoretical upper limit of 1.4 at $p < 0.01$, following Laws (1991). However, for the autumn cruise the estimated PQ was significantly higher than 1.4, which suggests that there was oxygen production without an associated production of particulate organic carbon. Conversely, the P-I curves could be underestimating gross particulate organic ^{14}C assimilation. According to Grande et al. (1989), GPP derived from *in vitro* light/dark incubations of oxygen tend to underestimate gross production because light respiration exceeds dark respiration. Hence, we should expect that an underestimation of ^{14}C gross production from the P-I curves is the main cause for the high PQs obtained in autumn.

Another possible explanation of the gross ^{14}C production underestimation is an unaccounted production of dissolved organic carbon (DOC-pr). Several authors (Arístegui et al. 1996, Robinson et al. 1999) observed a substantial underestimation of gross production by the ^{14}C method in comparison with oxygen production and argued that unaccounted exudation of DOC during the ^{14}C uptake experiments could explain this discrepancy. Results of Teira et al. (2001) indicate that a progressively higher fraction of the photosynthesised organic carbon flows to the DOC pool as the contribution of small phytoplankton cells to both primary production and biomass increases. They estimated that this DOC-pr represented ca. 10% of the total primary production at large-phytoplankton dominated stations, while the percentage increased to 33% of total carbon incorporation at those stations with a predominance of small phytoplankton (<2 µm). If we applied these estimates to our data, PQ values would decrease 12% for the spring and summer upwelling and 14% for autumn. Applying this correction, the autumn PQ is still higher than the theoretical 1.4 upper limit.

An additional possible reason for this GPP underestimation is that the filters did not retain the smallest phytoplankton fractions, which would cause a significant underestimation of gross production, mainly during the periods when there is a predominance of these populations, autumn and winter. In fact, GPP data from P-I curves (GF/F filters) did not concur with size-fractionated primary production data from 2 h ^{14}C incubations (0.22 µm polycarbonate filters) for the surface waters during the October and January cruises. Our ^{14}C $PP_{P\text{-}I}$ resulted in values 19 to 38% lower than those from the 2 h incubations, pointing to a significant underestimation and consequently to an overestimation of PQ values. This additional factor explains the high PQ for the autumn cruise. However, our observations do not explain the PQ values obtained for the winter period.

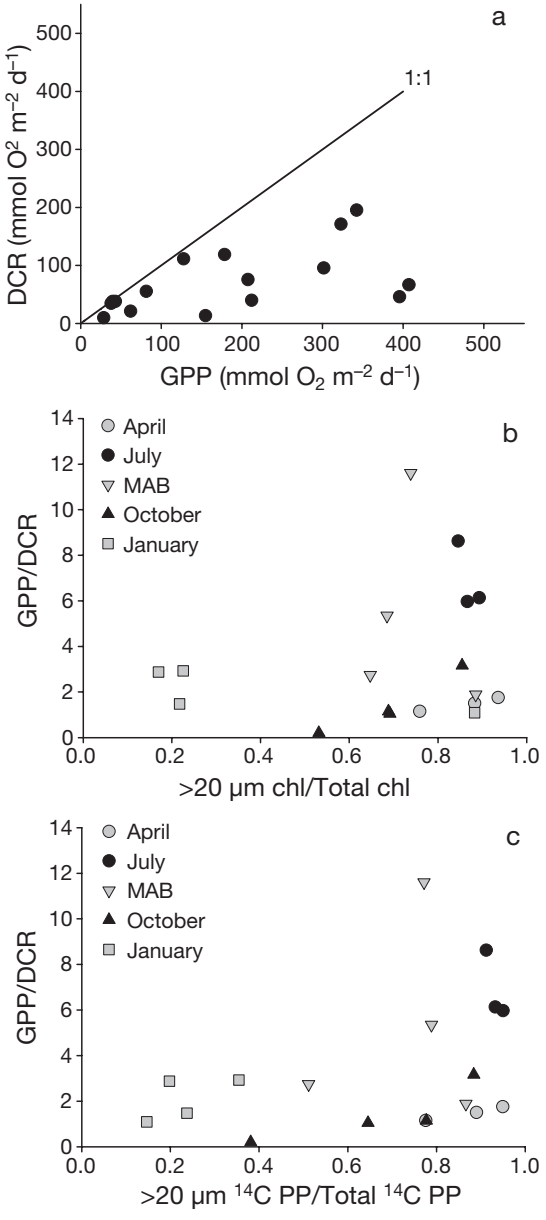


Fig. 6. Relationship between gross primary production (GPP) and dark community respiration (DCR) rates. (a) Water column integrated GPP vs. water column integrated DCR. Solid line corresponds to DCR = GPP. (b) GPP:DCR vs. contribution of microplankton chlorophyll (>20 µm chl) to total chlorophyll (chl_{total}). (c) GPP:DCR vs. contribution of microplankton primary production (>20 µm ^{14}C PP)/total primary production (^{14}C PP_{total}). MAB corresponds to the July 19 to 29 period

Water column metabolic balance

One of the main purposes of this study was to establish the trophic status of the system on a yearly base, taking into account not only the primary production of the system but also its phytoplankton size structure to determine if the trophic status is dependent on the size structure of the primary producers. The relationship between integrated GPP and integrated DCR (Fig. 6a), shown with a great deal of scatter, demonstrates that the study system was always autotrophic or in balance, based on the projections of the points onto the DCR = GPP line. Almost all the points are located in the right corner of the plot where GPP > DCR. Even during winter, when GPP decreased by 82% and DCR by 76% relative to the spring–summer average, the system did not reach heterotrophy and it was almost in balance (NCP winter avg. of 22.3 mmol O_2 m^{-2} d^{-1}). Only on October 18 did the system show net heterotrophy, with water column integrated NCP of –28 mmol O_2 m^{-2} d^{-1}. Thus, over the annual cycle, the water column in the Ría de Vigo was net autotrophic during the spring and summer seasons and autotrophic or almost in balance during the winter and autumn seasons, with an annual NCP avg. of 144 mmol O_2 m^{-2} d^{-1}.

This is consistent with conditions reported previously for other systems also characterised by large inorganic nutrient inputs, such as Narragansett Bay (Nixon & Pilson 1984) and Chesapeake Bay (Smith & Kemp 1995). It is important to keep in mind that our analysis only considers plankton metabolism and not the whole ecosystem, including benthic metabolism. It is possible that the trophic status changes if this compartment is included. For example, at a shallow location in San Francisco Bay, Caffrey et al. (1998) described how the system changed from a net autotrophy to a net heterotrophy status associated with an enhancement of benthic respiration, for which the contribution increased from 39 to 88% between spring and autumn. For the Ría de Vigo, further research should focus on estimating the benthic contribution to the net ecosystem metabolism.

As in previous studies (Duarte & Agustí 1998, Duarte et al. 2001, Arístegui & Harrison 2002), we obtained a significant correlation between integrated DCR and integrated GPP ($r^2 = 0.35$, $p < 0.05$ for the entire data set), suggesting that over the range of observed rates, the magnitude of GPP partly controls the trophic status of the system. However, a substantial variation in the P/R balance was not explained by GPP per se. We further explored a possible relationship between the autotrophy degree of the system, expressed as the ratio of GPP to DCR, and its phytoplankton community structure by grouping our observations, taking into account the contribution of the microplankton to the total chl *a* and primary production of the system. Fig. 6b,c shows a clear trend of the GPP/DCR ratio and the proportion of chl *a* and primary production attributable to the large phytoplankton fraction. The degree of autotrophy is greater with a higher contribution of the microplankton. On those days when the contribution of large phytoplankton fraction to primary produc-

tion was high (> 70%), the degree of autotrophy was also high. However, the observations during winter and autumn, characterised by low contribution of large phytoplankton (<20%), were in metabolic balance. When we included the contribution of the microplankton in the relationship between the GPP/DCR ratio and GPP, the percentage of explained variability increased from 50% to 60% and 65% in terms of primary production and chl *a* contribution, respectively. Thus, our results also point to an influence of the plankton community structure on the trophic status of the system.

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