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Phytoplankton size-structure, particulate and dissolved organic carbon production and oxygen fluxes through microbial communities in the NW Iberian coastal transition zone

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ABSTRACT: Contrasting hydrographic regimes were studied in the NW Iberian coastal transition zone in order to gain understanding of the relationship between planktonic community structure, production and loss rates, by concurrently measuring size-fractionated phytoplankton biomass and carbon incorporation as well as dissolved organic carbon production and dark respiration by microbial communities. Sampling was carried out in August 1998 and October 1999 at a series of stations representing vertical stratification and coastal upwelling conditions in summer, and vertical mixing and shelf-break poleward flow situations during the autumn. A close relationship was found between size-fractionated phytoplankton biomass and production, the relative allocation of total photosynthesis to dissolved and particulate organic carbon fractions, and the balance between production and respiration. Picoplankton-dominated communities showed net heterotrophic metabolism and were associated with relatively high rates of DOC production with respect to total carbon incorporation (>15%). In contrast, in coastal upwelling stations, where >2 µm cells dominated, less than 10% of total fixed carbon flowed to DOC, and the net metabolism of the microbial plankton community was autotrophic.

KEY WORDS: Phytoplankton size-structure · Primary production · DOC production · Respiration · NW Iberian coastal transition zone

INTRODUCTION

Shifts in planktonic community structure are expected to take place on decadal or centennial time scales due to altered physical forcing as a result of climate change (Doney 1999). In this scenario, unravelling the functional relationships between water column hydrodynamics, community structure and the circulation of energy and matter through the pelagic ecosystem is one of the major challenges of biological oceanography in the present decade.

It has been well established that hydrodynamics plays a crucial role in the allometric distribution of planktonic primary producers (e.g. Margalef 1978, Legendre & Le Fèvre 1989, Tremblay et al. 1997, Goericke 1998), mainly through their effect on the differential competitive abilities of phytoplankton species to take up inorganic nutrients and/or to remain in the euphotic layer (see e.g. Kiørboe 1993). Observational evidence (e.g. Legendre et al. 1993, Nielsen & Hansen 1995, Pesant et al. 1998, Tamigneaux et al. 1999) and conceptual models (e.g. Legendre & Le Févre 1989, Tremblay & Legendre 1994, Legendre & Rassoulzadegan 1995, Kiørboe 1996, Legendre & Michaud 1998) have pointed to phytoplankton size as the principal mechanism controlling the trophic organisation of planktonic communities and, consequently, the cycling of carbon through the pelagic ecosystem. According to these studies, in highly pro-

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ductive systems characterised by low vertical stability, such as upwelling areas, large-sized phytoplankton dominate, a herbivorous food web becomes established, and the photosynthetically produced particulate organic matter flows mainly through mesozooplankton and is finally transferred to higher trophic levels or exported to subsurface oceanic layers. In contrast, in stratified, oligotrophic systems, small primary producers form the bulk of the phytoplankton biomass, the microbial trophic pathway dominates, and a significant fraction of photosynthesised carbon is recycled *in situ*, thus limiting the export of organic matter to the deep ocean.

Empirical evidence has frequently failed to validate model predictions (e.g. Rivkin et al. 1996). One reason is likely to be the assumption of biogenic carbon (BC) export as the key variable summarising carbon fluxes through the pelagic ecosystem, since BC export may occur at spatio-temporal scales that do not necessarily match those at which processes such as organic matter production and consumption take place. Therefore, we have measured dissolved organic carbon (DOC) production rate as a flux potentially controlled by planktonic trophic organisation, which is presumed to play a key role in the determination of the scales of linkage between production and respiration of organic matter in upper ocean microbial populations (Pomeroy & Wiebe 1993, Sherr & Sherr 1996).

Another frequent limitation of such studies is that they are usually restricted to a limited spectrum of communities, and therefore extrapolation of their results to longer temporal or larger spatial scales is uncertain. In order to cover a wide range of planktonic community organisations, we examined contrasting hydrodynamic scenarios in the NW Iberian coastal transition zone during 2 seasons. The NW Iberian coastal transition zone is characterised by open ocean vertical stratification and coastal upwelling during summer (e.g. Wooster et al. 1976, Fraga 1981, Castro et al. 1994), and by coastal vertical mixing and a shelf-break poleward flow during autumn and winter (Frouin 1990, Haynes & Barton 1990, Castro et al. 1997).

This study aimed at gaining an understanding of the functional links between phytoplankton community structure and net planktonic metabolism by concurrently measuring size-fractionated phytoplankton biomass and photosynthetic carbon incorporation, as well as DOC production and community respiration by microbial communities.

MATERIALS AND METHODS

Sampling. Two oceanographic cruises were carried out in the NW Iberian upwelling region in summer 1998 (Omex-0898: 1 to 11 August) and autumn 1999 (Omex-1099: 14 to 20 October) on board RV 'Professor Shtockman' and RV 'Thalassa' respectively. Nineteen stations located along 3 transects perpendicular to the coastline were visited on each cruise (Fig. 1). Although Stns 13

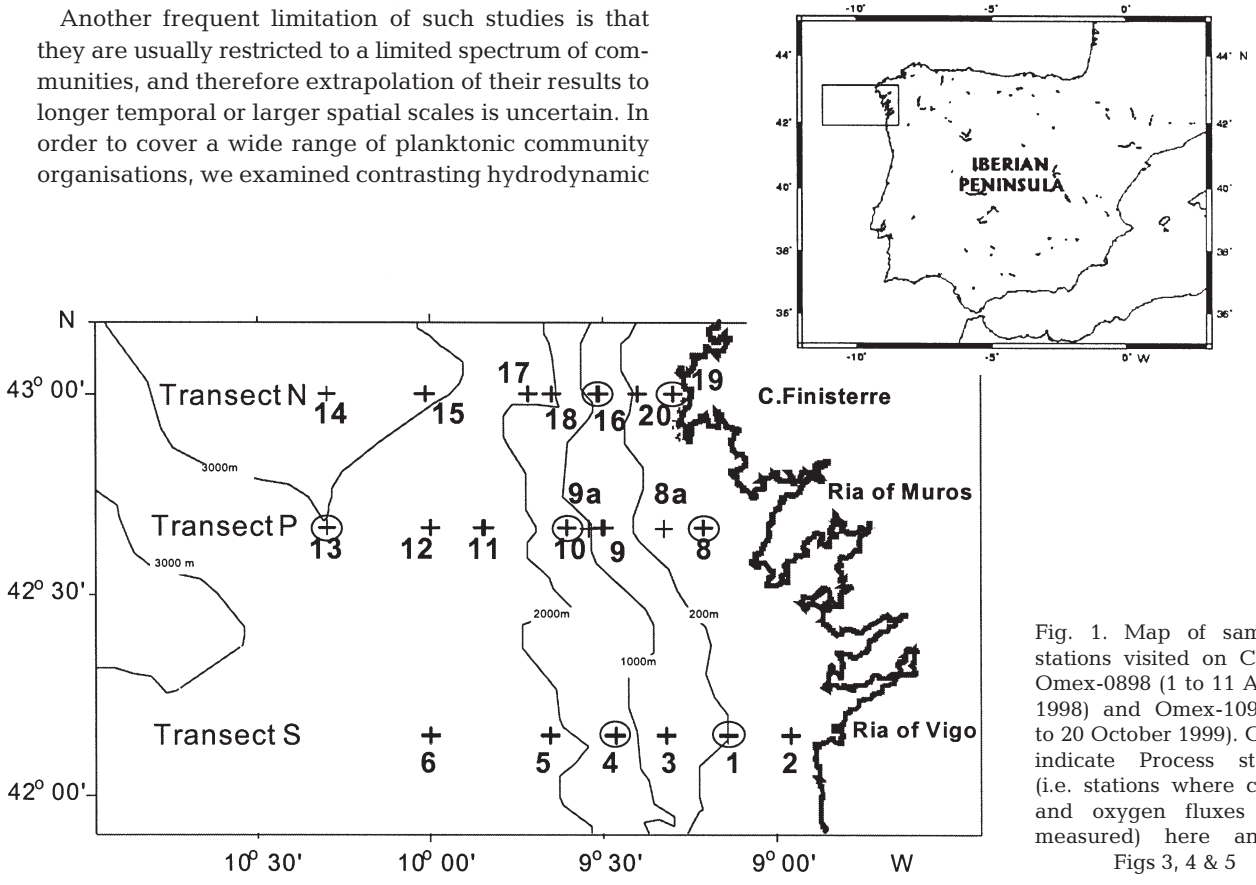

Fig. 1. Map of sampling stations visited on Cruises Omex-0898 (1 to 11 August 1998) and Omex-1099 (14 to 20 October 1999). Circles indicate Process stations (i.e. stations where carbon and oxygen fluxes were measured) here and in Figs 3, 4 & 5

and 14 were not sampled in October 1999 due to severe weather conditions, 2 additional stations (8a and 9a) were sampled during this cruise. Vertical profiles of temperature and salinity were conducted along the 3 longitudinal sections with a Neil Brown Mark III CTD attached to a rosette sampler equipped with 10 l Niskin bottles. The CTD conductivity sensor was calibrated using salinity determinations performed with an Autosal salinometer on water samples drawn from selected depths. CTD fluorescence was converted to chlorophyll *a* concentration by using the corresponding linear regressions obtained for Omex-0898 ($r^2 = 0.89$, $p < 0.005$, $n = 83$) and Omex-1099 ($r^2 = 0.69$, $p < 0.005$, $n = 77$) cruises. Additional irradiance and fluorescence vertical profiles were also obtained at the 12 process stations, where carbon and oxygen fluxes were measured using a Seabird SBE-25 CTD. Cross-calibration of CTD probes was made by deploying both CTDs in parallel at Stn 8 during Omex-0898 cruise.

Total and size-fractionated chlorophyll *a*. Total chlorophyll *a* concentration was determined fluorometrically after concentration of suspended matter by filtering 150 to 250 ml of seawater through Millipore APFF glass-fibre filters (operational pore-size equivalent to GF/F) that were immediately placed in 5 ml 90% acetone and kept in darkness at 5°C overnight. Seawater samples of 150 to 250 ml were filtered sequentially through 5 µm and 2 µm polycarbonate filters and Millipore APFF glass-fibre filters for size-fractionated determinations. Filters were frozen (–20°C) immediately, and fluorescence due to chlorophyll *a* was measured ashore with a Safas flx spectrofluorometer after extraction in 90% acetone at 4°C overnight. Concentrations were calculated after calibration with pure chlorophyll *a* extracts obtained by HPLC. Phytoplankton carbon biomass was estimated assuming a conservative carbon to chlorophyll *a* ratio of 50 (e.g. Longhurst 1995, Barlow et al. 1998).

Size-fractionated primary production rates. At each station, four 75 ml acid-cleaned polypropylene bottles (3 transparent bottles and 1 dark bottle) were filled with seawater from 5 depths corresponding to optical depths ranging from 100 to 1% of surface irradiance levels. Each bottle was inoculated with 370 kBq (10 µCi) of $NaH^{14}CO_3$ and then incubated for 6 to 7 h in an on-deck incubator which simulated irradiance experienced by the cells at the original sampling depths. Previous studies did not show statistically significant differences between primary production estimates derived from these on-deck and *in situ* incubation procedures (Joint et al. 1993). The bottles were kept cool by pumping surface seawater into the incubator. After incubation, samples were filtered at very low vacuum pressure (<50 mm Hg) through the same type of filters described above for size-fractionated chlorophyll *a* determinations. In order to remove the dissolved inorganic ^{14}C, filters were exposed to fumes of concentrated HCl for 12 h; 3.5 ml of scintillation cocktail were then added to each filter and the radioactivity was measured ashore with an LKB β-scintillation counter. Quenching corrections were made using an external standard.

Daily rates of particulate organic carbon production (POC-pr) were calculated from hourly rates utilising the equation of Straskraba & Gnauck (1985), which rendered average daylight lengths of 14 and 11 h during the summer and autumn cruises, respectively. Total POC-pr rates were calculated as the sum of the rates in the different size fractions.

DOC production rates. Four 30 ml seawater samples were collected from selected depths, inoculated with 740 to 1295 kBq (20 to 35 µCi) of $NaH^{14}CO_3$, and kept in the on-deck incubator for 2 h in order to minimise concurrent bacterial consumption of recently released DOC during the incubation period (see review by Fogg 1983). Two 7 ml subsamples were drawn from each bottle and filtered through Millipore APFF glass-fibre filters. Labelled dissolved inorganic carbon was removed by acidifying the filtrates with 40 µl of 50% HCl and bubbling with CO_2-free air for 12 h. Filters were decontaminated as described above. Scintillation cocktail was then added to both filters and filtrates. Duplicate blank tests were run in parallel by inoculating and immediately processing 0.2 µm filtered seawater as described above.

Two recent papers have explicitly questioned the adequacy of using glass fibre filters for the measurement of POC and DOC production (Karl et al. 1998, Morán et al. 1999) because of ^{14}C-DOC adsorption onto these type of filters; consequently, the DOC production rates reported here should be considered as conservative estimations. Other types of filters (e.g. membrane filters) have not proved capable of rendering more accurate estimations of POC and DOC production rates (Karl et al. 1998, Morán et al. 1999).

The high capacity of glass fibre filters to retain picoeukaryotes has frequently been reported (e. g. Gasol & Morán 1999). Accordingly, we are confident that our dissolved fraction included only bacteria, virus and colloidal particles.

O_2 production and respiration rates. Oxygen production and consumption rates were determined by light- and dark-bottle incubations at 4 selected depths. Four light and 8 dark, 125 ml, gravimetrically calibrated, borosilicate bottles were carefully filled with water from each depth, using silicone tubing, overflowing at >250 ml. An initial set of 4 dark bottles was fixed immediately for initial oxygen concentration, the remainder being kept under a light-dark diel cycle in the same on-deck incubator as that used for ^{14}C incubations. Fix-

ing and storage procedures, reagents and standardisation followed the recommendations of Grasshoff et al. (1983). Dissolved oxygen concentration was measured through automated precision Winkler titration performed with a Metrohm 716 (Omex-0898 cruise) or Metrohm 721 (Omex-1099 cruise) DMS Titrino, using a potentiometric end-point detector as described by Serret et al. (1999). Net community production (NCP) and dark community respiration (DCR) 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 sum of NCP plus DCR.

Photic-zone integration. Photic-zone-integrated values of size-fractionated chlorophyll *a* and primary production, DOC production, NCP, DCR and GP were obtained by trapezoidal integration of the volumetric data down to the depth of 1% surface irradiance. Photic zone depth ranged from 30 m at nearshore stations to 60 m at off-shelf waters.

RESULTS

Thermohaline structure

Weekly composite sea-surface temperature (SST) satellite images corresponding to Omex-0898 and Omex-1099 cruises showed the typical thermal structures (summer upwelling and poleward flow during autumn-winter) for the NW Iberian region (Fig. 2). During the summer cruise, cold sea-surface waters, indicative of coastal upwelling, were found near the coast. Long tongues or filaments of cold water extending from the coastal zone to the open ocean were observed along the coastal transition zone. Warm surface water flowing northwards over the continental margin of the Atlantic coast of the Iberian peninsula was observed during the autumn cruise, decreasing in thickness along the north Spanish slope.

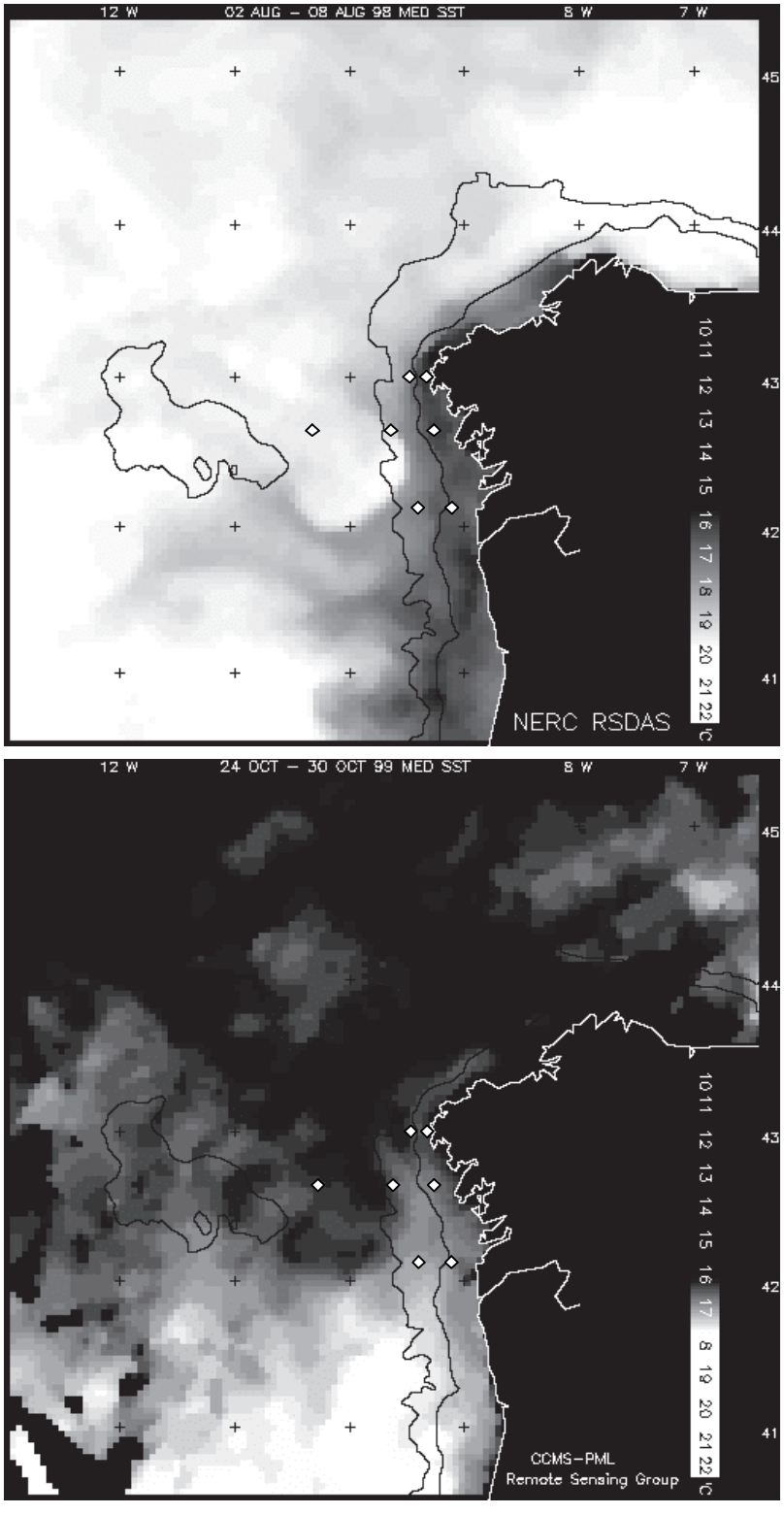

Fig. 2. Weekly composite sea-surface temperature (SST) satellite images for the NW Iberian coastal transition zone during August 1998 and October 1999. Note that temperature scales are slightly different in order to emphasise thermal structures. Images provided by the Remote Sensing Group, Plymouth Marine Laboratory, UK

The vertical distribution of temperature and salinity during August 1998 (Figs 3 & 4) reflected the typical thermohaline structure associated with upwelling conditions off the NW Iberian coast (e.g. Álvarez-Salgado et al. 1993, Castro et al. 1994, 1997). The upper water column was cooler at on-shelf than at oceanic stations, and isotherms rose in the water column towards the coast (Fig. 3). The 14°C isotherm, located at 90 m in

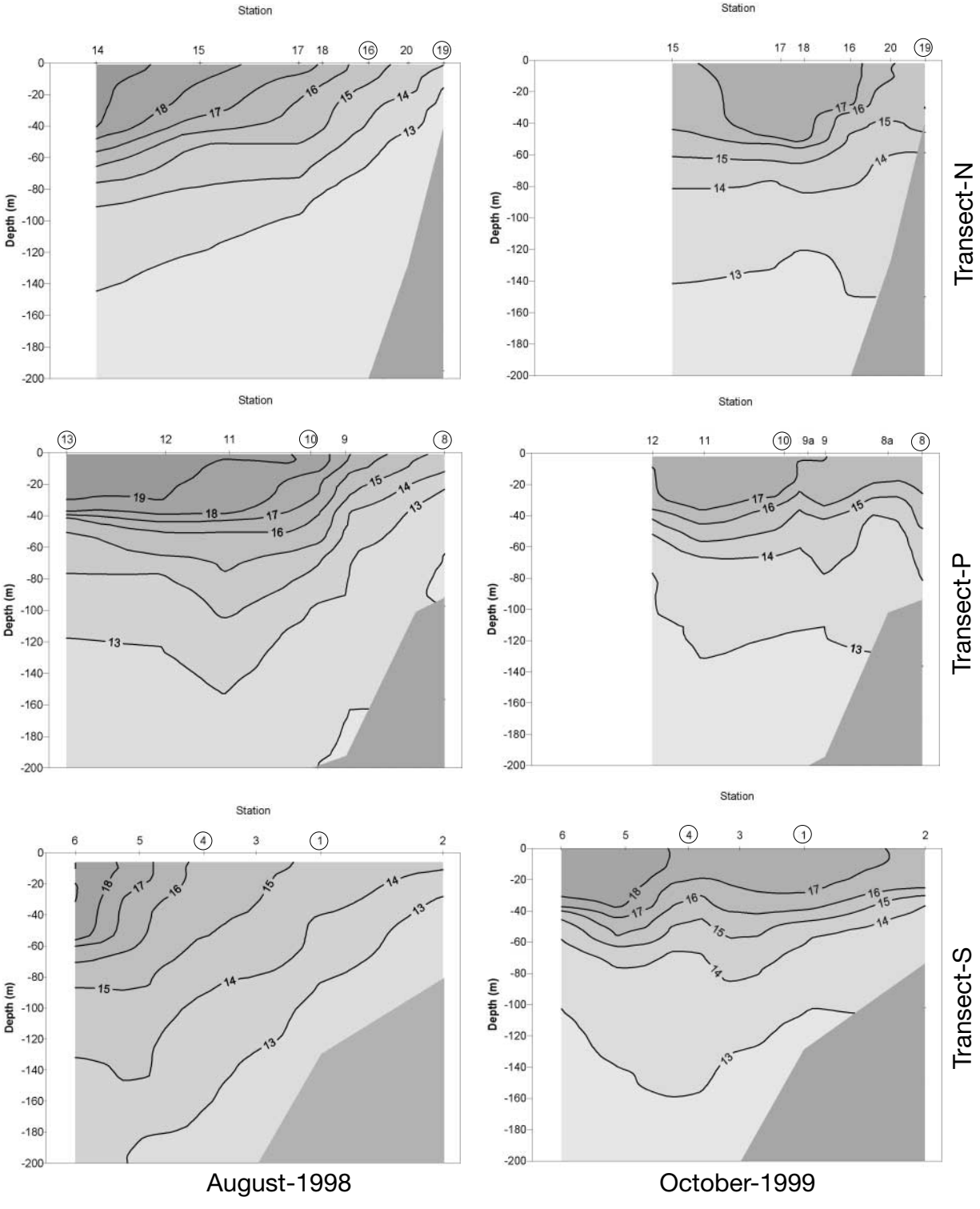

Fig. 3. Vertical distribution of temperature (°C) along Transects N, P and S in August 1998 (Omex-0898 cruise) and October 1999 (Omex-1099 cruise)

oceanic waters, reached the surface in the vicinity of Cape Finisterre (Stn 19), generating a surface temperature gradient of >0.05°C km^{-1}. Coastal waters were slightly fresher than off-shelf waters, especially on Transect P, where nearshore salinity values lower than 35.6 psu were measured (Fig. 4). The distribution of

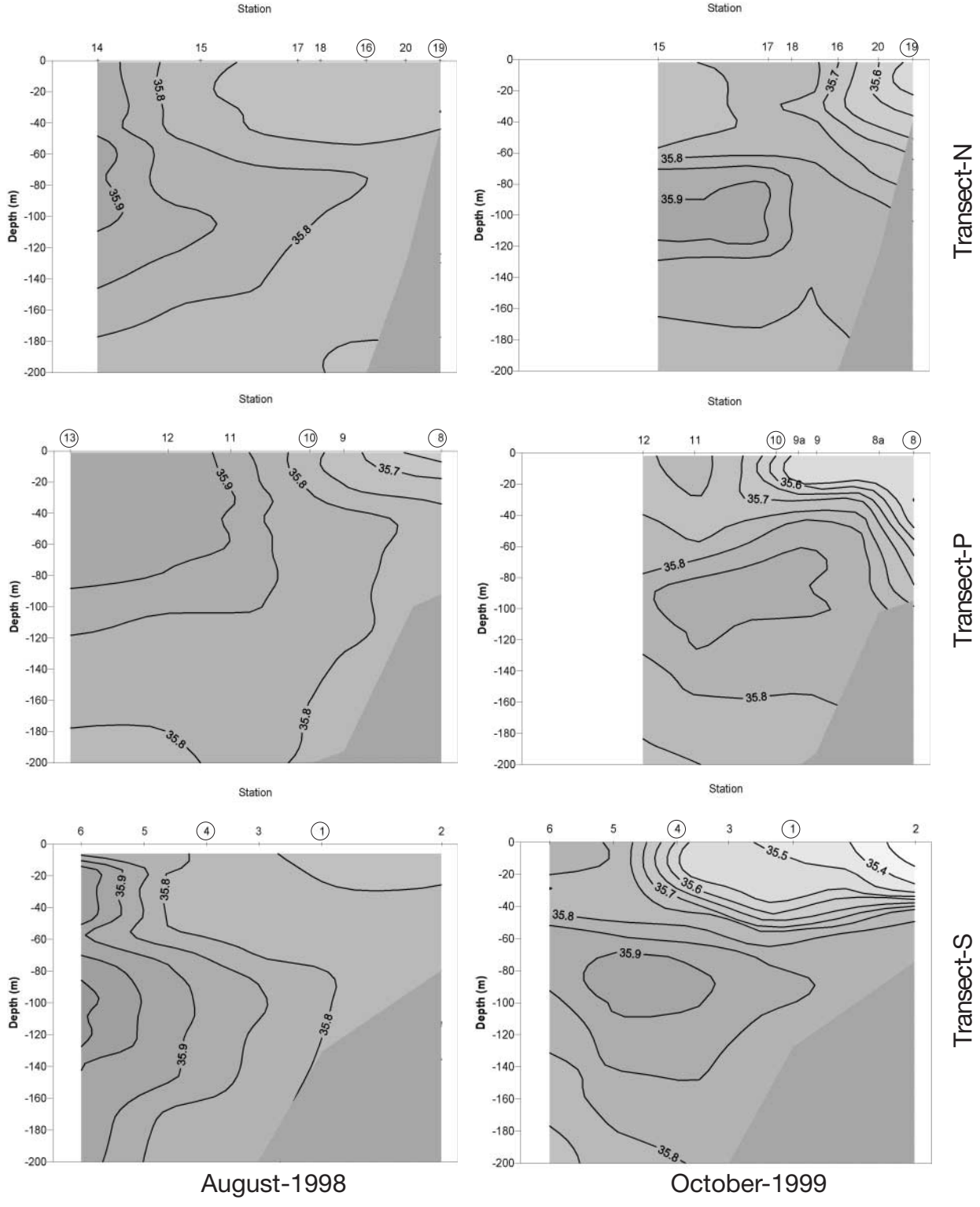

Fig. 4. Vertical distribution of salinity (psu) along Transects N, P and S in August 1998 (Omex-0898 cruise) and October 1999 (Omex-1099 cruise)

sigma-*t* was similar to that of isotherms (not shown), indicating advection of subsurface waters to the surface at coastal stations. The upwelling front, defined in this study by an outcrop of the 26.2 isopycnal to the surface (corresponding approximately with the appearance at the surface of the 16°C isotherm) separates coastal colder waters from stratified oceanic waters. On Transect P, and to a lesser extent on Transect S, deepening of isotherms at the shelf-break suggests the existence of frontal downwelling zones.

In autumn 1999 (Omex-1099 cruise), southerly winds prevailed and the thermohaline structure in the NW Iberian coastal transition zone was mainly characterised by a poleward flow of warm and saline water over the upper slope (Figs 2 to 4). The presence of the poleward slope current flowing along the NW Iberian Peninsula is typical of the autumn-winter period in the region (Frouin 1990, Haynes & Barton 1990, Pingree & Le Cann 1990, Castro et al. 1997). The poleward surface current was apparent throughout the study area, being characterised by a core of water of relatively high salinity (>35.85) between 50 and 150 m on Transect S which became fresher (maximum salinity decreased from 35.95 on Transect S to 35.91 on Transect N) and narrower northwards (Figs 2 to 4). This latitudinal trend could be related to lateral and vertical mixing with the surrounding North Atlantic Central Water (NACW), as pointed out by Haynes & Barton (1990). The influence of continental freshwater inputs was markedly higher than in summer 1998, and became more intense southwards. On northern transects, especially Transect P, freshwater inputs affected the entire water column, as shown by the depression of isohalines nearshore. In contrast, on Transect S, low salinity water only affected the upper 50 m of the water column and, as a consequence, a well-developed halocline was present even at on-shelf stations. The interaction between coastal water and the poleward slope flow retained low salinity water on-shelf, resulting in a marked haline stratification (saline front) at the shelf/shelf-break stations, and thus preventing the outflow of upper-layer water from the Rías Baixas (Castro et al. 1997). A nucleus of relatively warm (>17°C) water was found in the upper 40 to 50 m of the water column (Fig. 3). This core, detectable by infrared satellite imagery (Fig. 2), was located over the high salinity core of the poleward slope current (Fig. 4). A similar distribution pattern was observed for sigma-*t* (not shown).

Size-fractionated chlorophyll *a* and primary production

During upwelling conditions, total phytoplankton biomass, estimated from chlorophyll *a* (chl *a*) concentrations, was significantly higher at coastal stations, where concentrations exceeding 2 mg m^{-3} were measured in the upper 20 m (Fig. 5). Although the most intense upwelling conditions were observed near Cape Finisterre (Transect N), the highest concentration of chlorophyll *a* (>7 mg m^{-3}) was detected at Stn 8, off the Ría de Muros. A subsurface (50 to 80 m) chlorophyll *a* maximum (>0.5 mg m^{-3}) was found at open ocean stations. In October 1999, chlorophyll *a* concentration was lower than during upwelling conditions, with maximum values of 0.7 mg m^{-3} at a nearshore station off the Ría de Vigo (Stn 2: Fig. 5). The poleward flow favoured the accumulation of phytoplankton biomass in the upper 60 m of shelf and shelf-break stations. A subsurface (40 to 50 m) chlorophyll *a* maximum was present at oceanic stations. Small unidentified flagellates, dinoflagellates and Criptophyceans dominated the phytoplankton community during autumn, whereas during upwelling conditions large diatoms (e.g. *Pseudonitzschia* cf. *pungens*, *Leptocylindrus danicus*) formed the bulk of phytoplankton biomass (M. Varela pers. comm.).

The distribution of size-fractionated chlorophyll *a* was highly variable both spatially and seasonally. During upwelling conditions, >2 µm phytoplankton cells dominated at coastal stations, accounting for more than 80% of total chlorophyll *a*. The contribution of >2 µm cells was also significant (more than 50%) at the subsurface chlorophyll *a* maximum at shelf/shelf-break stations on Transect N. In contrast, at open ocean stations, the subsurface chlorophyll *a* maximum, located at 80 m, was formed largely by small-sized particles containing chlorophyll *a*. In autumn, the relative contribution of >2 µm phytoplankton to total chlorophyll *a* was generally <70% in the upper 40 m and never exceeded 80%. In general, the proportion of large cells increased progressively with increasing depth. Picoplankton dominated in the upper layer of on-shelf stations in Transect S (>60%), coinciding with the body of low salinity water derived from freshwater inputs (Fig. 4).

Vertical profiles of total particulate organic carbon production (POC-pr) rates and total chlorophyll *a* concentrations during August 1998 and October 1999 are shown in Figs 6 & 7, respectively. During summer (Fig. 6), near surface rates of POC-pr ranged from >20 mg C m^{-3} h^{-1} in coastal upwelling conditions (Stn 8) to <0.5 mg C m^{-3} h^{-1} at oceanic stations. In contrast, while subsurface rates decreased sharply with increasing depth in coastal upwelled waters, subsurface maxima developed offshore. Relatively low rates of POC-pr were found at coastal stations in Transect S, where upwelling conditions were less intense. The vertical distribution of POC-pr rates largely paralleled the concentration of chlorophyll *a* during the upwelling

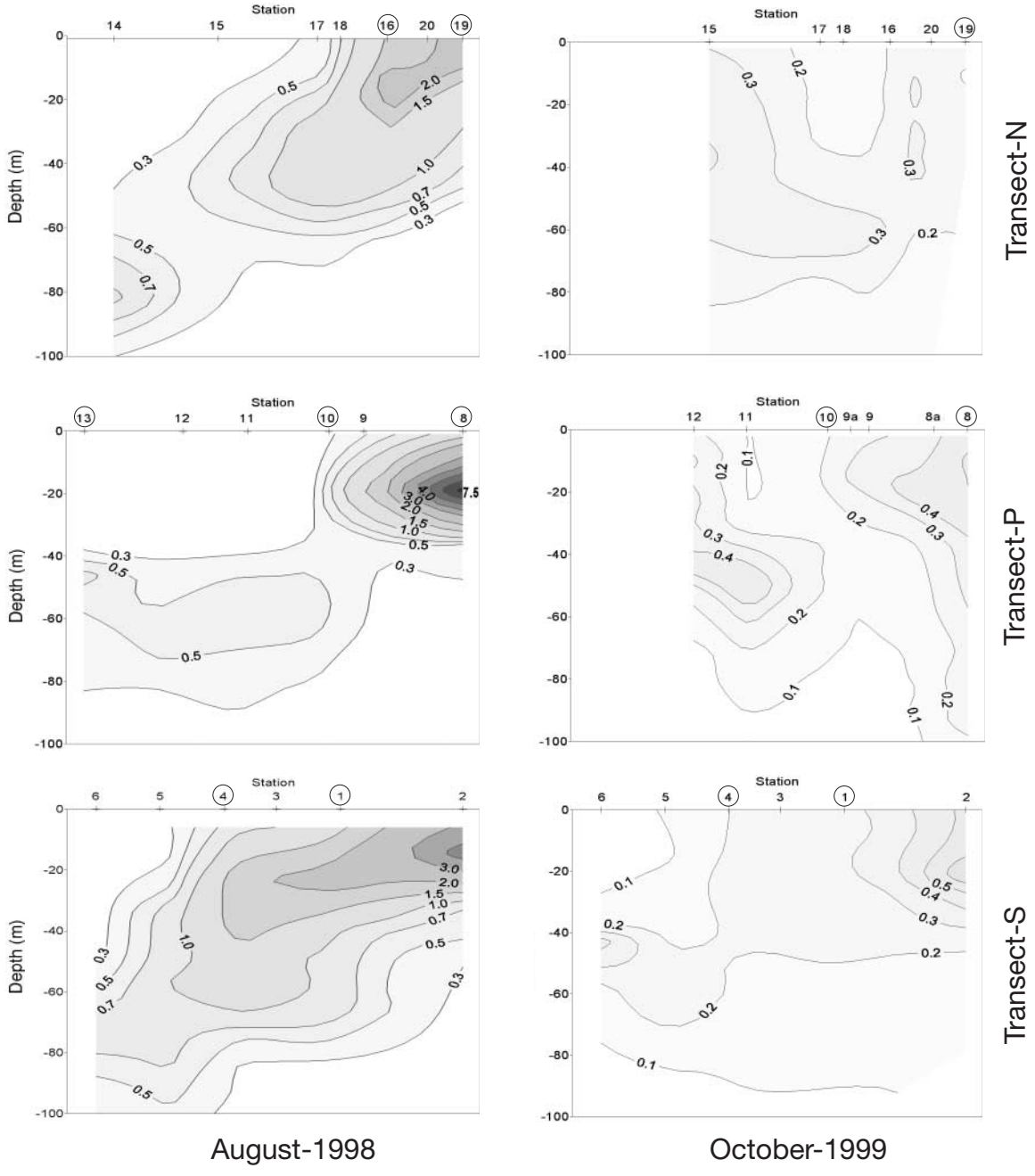

Fig. 5. Vertical distribution of total chlorophyll *a* (mg chlorophyll *a* m^{-3}) along Transects N, P and S in August 1998 (Omex-0898 cruise) and October 1999 (Omex-1099 cruise)

event. Photic zone-integrated POC-pr rates ranged from 3220 to 7413 mg C m^{-2} d^{-1}, with a mean value of 4292 ± 797 mg C m^{-2} d^{-1}. These rates were higher than those reported by Bode et al. (1994) for the Rías Baixas during upwelling conditions (ca 1000 mg C m^{-2} d^{-1}: average value for 1984 to 1992), and very close to those reported by Tilstone et al. (1999) during an upwelling event in the Ría de Vigo in summer 1993 (2780 to 3690 mg C m^{-2} d^{-1}). POC-pr rates measured in stratified waters (486 ± 18 mg C m^{-2} d^{-1}) agreed well with the average value reported by Bode et al. (ca 490 mg C m^{-2} d^{-1}).

In general, rates of total POC-pr in autumn (Fig. 7) were of the same magnitude as those measured at offshelf stations in summer 1998. The maximum rate (4.4 ± 0.1 mg C m^{-3} h^{-1}) was measured at Coastal Station 8, where relatively high chlorophyll *a* concentration was found associated with the accumulation of low

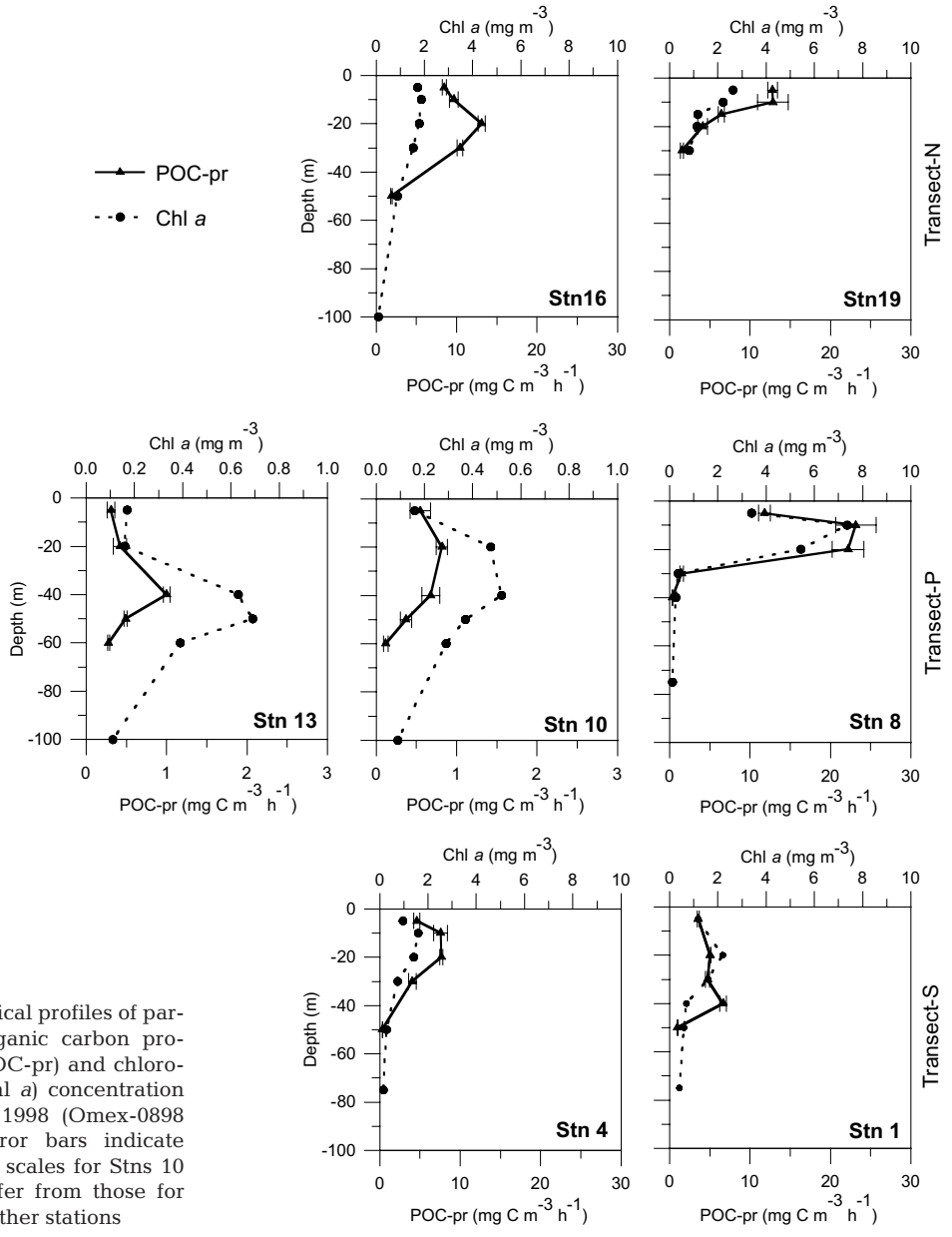

Fig. 6. Vertical profiles of particulate organic carbon production (POC-pr) and chlorophyll *a* (Chl *a*) concentration in August 1998 (Omex-0898 cruise). Error bars indicate ± SE. Note scales for Stns 10 and 13 differ from those for the other stations

salinity coastal water (Figs 4 & 5). The highest rates of carbon fixation were always measured near the surface, irrespective of the vertical distribution of phytoplankton biomass.

The relative contribution of the >2 µm phytoplankton size-fraction to total POC production is shown in Fig. 8. During summer, nano- and net-phytoplankton constituted 70 to 98% of total primary production, except at the most oceanic station, 13. This contribution markedly decreased with increasing depth at Stn 13, reaching a minimum value of 16% at 60 m. The contribution of non-picoplankton primary producers to total carbon fixation during autumn was significantly lower than in the upwelling season, with values <60%, except in the upper 20 m of Stn 19. The lowest value was found at Stn 1, where the relative contribution of >2 µm phytoplankton to total POC-pr was <20% within the euphotic zone.

Rates of DOC production by the microbial community

Rates of DOC production (DOC-pr) by microbial populations ranged from 0.10 to 2.81 mg C m^{-3} h^{-1} during the upwelling season (Fig. 9). The highest rates (>1.5 mg C m^{-3} h^{-1}) were found at the coastal upwelled stations, 8 and 19, where the vertical distribution of DOC-pr matched those of chlorophyll *a* and

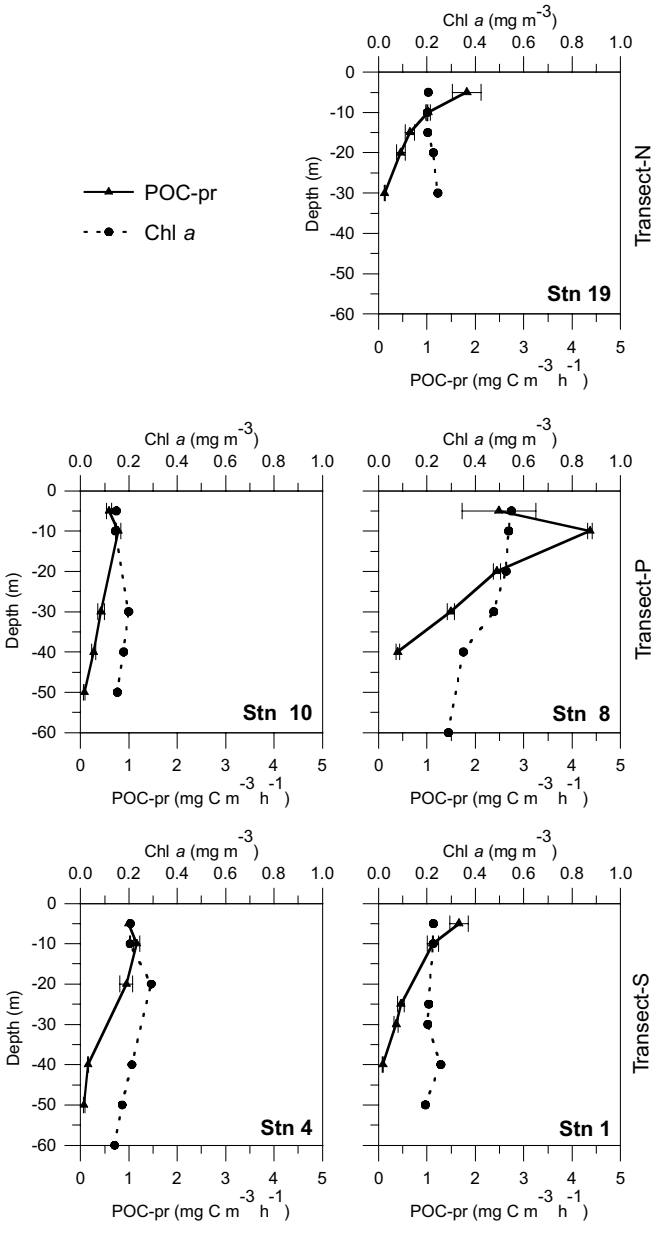

Fig. 7. Vertical profiles of particulate organic carbon production (POC-pr) and chlorophyll *a* (Chl *a*) concentration in October 1999 (Omex-1099 cruise). Error bars indicate ± SE

POC-pr (Fig. 6). The average rate of DOC-pr calculated for the autumn cruise (0.7 ± 0.2 mg C m^{-3} h^{-1}) was not significantly different ($p = 0.27$) from the mean value estimated for the autumn cruise (0.4 ± 0.1 mg C m^{-3} h^{-1}), although in the summer cruise the measured rates were less variable, ranging from 0.13 to 1.02 mg C m^{-3} h^{-1}. In contrast, statistically significant differences were found in the relative contribution of DOC production to total carbon incorporation ($p < 0.002$) between the 2 seasons. In summer, the percentage of DOC released by microbial populations ranged from 3 to 46%, and averaged 11 ± 3%, whereas in autumn 28 ± 4% of the recently incorporated carbon flowed to the DOC pool, with values ranging from 10 to 60%. In general, the relative contribution of DOC to total carbon fixation increased systematically with depth during both sampling periods. Unfortunately, we failed to measure DOC-pr rates at open ocean stations during the summer and at Stn 19 in autumn.

A statistically significant log-log linear relationship was found between volumetric POC and DOC production rates (Fig. 10). The log transformation was performed in order to attain normality and homoscedasticity. We performed the same slope analysis carried out by Baines & Pace (1991) in their study of the relationship between rates of extracellular release and particulate primary production. Following the recommendations given by Sokal & Rohlf (1995), the ordinary least-squares (OLS) linear regression model was used instead of the major axis regression method, despite the fact that both the POC and DOC production rates are subject to measurement errors, since our objective was to obtain an expression for the prediction of DOC-pr rates from POC-pr rates (see also Legendre & Michaud 1999). DOC-pr increased as a function of increasing particulate production; however, the deviation of the observed relationship from the line of Slope 1 indicates that the DOC-pr rate was not a constant fraction of the total amount of carbon incorporated by primary producers. The linear regression corresponding to the whole data set was calculated (log [DOC-pr] = 0.37 log [POC-pr] – 0.54, $r^2 = 0.51$, $p < 0.0001$, $n = 31$) because of its potential usefulness for the estimation of DOC-pr rates in the region on annual scales. It is worth noting that different relationships were obtained from the data sets corresponding to the different cruises: log [DOC-pr] = 0.43 log [POC-pr] – 0.45 ($r^2 = 0.51$, $p = 0.003$, $n = 15$) for autumn, and log [DOC-pr] = 0.52 log [POC-pr] – 0.74 ($r^2 = 0.68$, $p < 0.0001$, $n = 16$) for summer. Although the slopes of both regression lines were not significantly different (ANCOVA *F*-test, $p = 0.57$), statistically significant differences were found between the intercepts (ANCOVA *F*-test, $p = 0.024$); i.e. the DOC-pr rate for a given rate of POC-pr was consistently higher in autumn. The equations were used for the estimation of DOC-pr rates at those stations where only POC-pr was determined. The higher scatter of POC and DOC production rates during autumn could have resulted from the predominance of trophic (grazing, lysis) versus physiological (exudation) processes implied in the release of dissolved organic materials, which would be expected from the dominance of picoplankton (>40%).

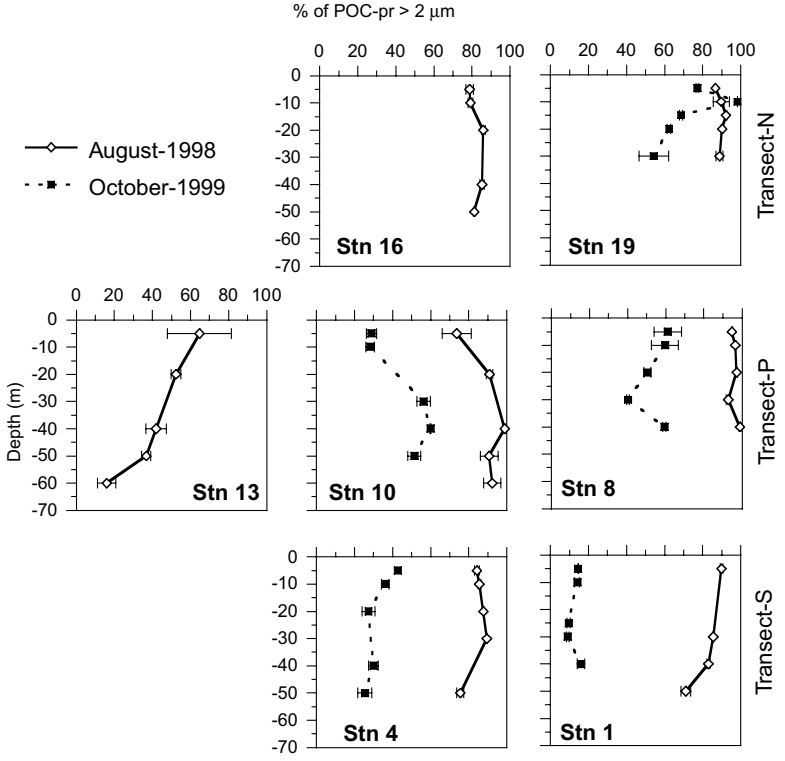

Fig. 8. Vertical distribution of the relative contribution of the >2 µm phytoplankton size fraction to total particulate organic carbon production (%) in August 1998 (Omex-0898 cruise) and October 1999 (Omex-1099 cruise). Error bars indicate ± SE

Net community production by microbial populations

Vertical profiles of GP, DCR and NCP rates during August 1998 and October 1999 are represented in Fig. 11. A statistically significant linear relationship was found between GP (mmol O_2 m^{-3} d^{-1}) and total POC-pr (mmol C m^{-3} d^{-1}) rates; GP = 0.92 POC-pr + 0.38 (r^2 = 0.82, $p < 0.000001$, n = 32). In general, DCR decreased with increasing depth. Absolute rates of DCR were generally higher in August, and were significantly correlated with phytoplankton biomass during the upwelling season (r = 0.73, p = 0.001). Photic-depth-integrated rates of DCR ranged from 21 to 145 mmol O_2 m^{-2} d^{-1}, and integrated rates of NCP ranged from –41 to 372 mmol O_2 m^{-2} d^{-1} (Table 1). Coastal upwelling stations sampled in summer 1998 exhibited a net autotrophic microbial metabolism, as shown by the positive rates of NCP production measured in the entire photic zone (Fig. 12). The same situation was found at the coastal Stn 8 in autumn. In contrast, off-shelf stations where characterised by negative NCP rates. In autumn, heterotrophic metabolism of the microbial community was observed both in oceanic and in coastal stations.

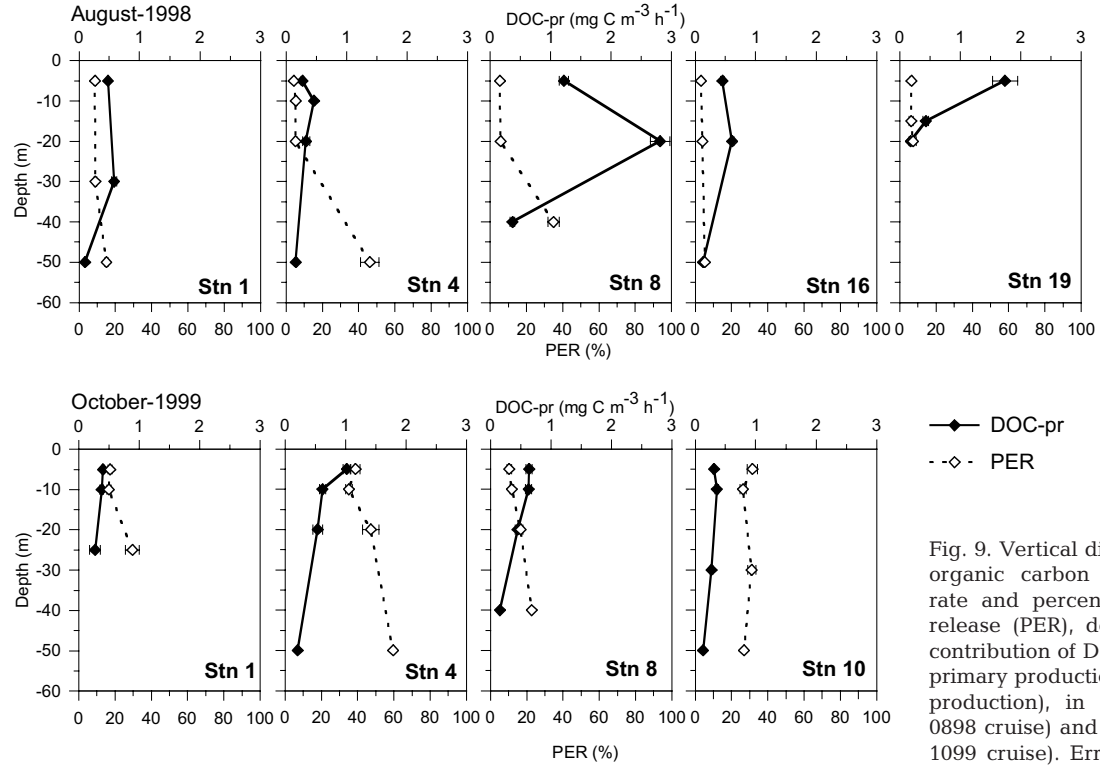

Fig. 9. Vertical distribution of dissolved organic carbon production (DOC-pr) rate and percentages of extracellular release (PER), defined as the relative contribution of DOC production to total primary production (TPP = POC + DOC production), in August 1998 (Omex-0898 cruise) and October 1999 (Omex-1099 cruise). Error bars indicate ± SE

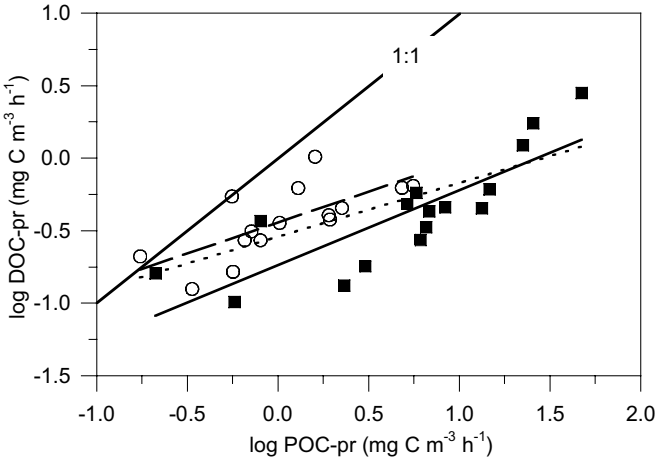

Fig. 10. Log-log relationship between POC and DOC production rates. Black and open symbols correspond to Omex-0898 (August 1998) and Omex-1099 (October 1999) cruises, respectively. Regression lines calculated for each season (continuous and dashed lines correspond to Omex-0898 and Omex-1099, respectively) and for whole data set (dotted line). Regression equations given in 'Results'

Biogenic carbon fluxes through the microbial communities

The results presented so far allowed us to build up carbon budgets for 3 contrasting scenarios defined in the coastal transition zone off the NW Iberian peninsula (Fig. 12). Oxygen fluxes were expressed in carbon units by using a respiration quotient of RQ = 1 (Packard 1979, del Giorgio & Peters 1993). It was assumed that the relative contribution of different size classes to DOC-pr was equivalent to the relative contribution of the different size-classes to total POC-pr. During the summer upwelling, very high total organic carbon production (TOC-pr) rates were associated with a major contribution (>80%) of large cells (>2 µm) to both primary production and phytoplankton standing stock, low relative DOC-pr (<10%), and net autotrophic metabolism: <50% of TOC-pr was respired by the microbial community (Fig. 12). In stratified waters, both a relatively high contribution of DOC to TOC-pr (19%) and respiration equalling production rates were associated to a phytoplankton standing stock dominated by small cells and primary production equally shared by small and large cells. During autumn, shelf and shelf-break stations located within the poleward slope current were characterised by a high contribution of DOC (>30%), very high rates of community respiration (>130% of TOC-pr), low rates of total primary production (mainly due to small cells >70%), and a co-dominance of both small and large phytoplankton cells.

Relationship between phytoplankton size, DOC production and NCP

All the biological stations sampled during the 2 cruises were grouped according to the relationship between standing stock and production rates of large and small phytoplankton size fractions, as proposed by Tremblay & Legendre (1994) (Fig. 13a). Coastal upwelling stations sampled in August 1998 (Stns 1, 4, 8, 16 and 19) are closely grouped in the left lower corner of the production-biomass (PB) plot in Fig. 13a, indicating the dominance of large cells in terms of both biomass and primary production. The 2 stratified stations sampled in summer 1998 (Stns 10 and 13) differed widely. The phytoplankton standing stock was dominated by small cells in both cases. However, while at Stn 10, located close to the frontal upwelling zone, >2 µm phytoplankton accounted for ca 90% of total carbon fixation, this proportion was only 45% at Stn 13. This difference is likely to be related to an efficient removal of large cells by mesozooplankton grazing, as suggested by Legendre et al. (1993) and Tamigneaux et al. (1999).

The stations visited in autumn are located in the PB diagram (Fig. 13a) along a gradient from a situation where small cells dominated primary production and both large and small cells contributed similarly to phytoplankton standing stock (shelf/shelf-break Stns 1, 4 and 10) to a situation where large cells accounted for more than 50% of phytoplankton biomass and production (Stn 8). Stn 19 was not represented due to the lack of size-fractionated biomass data.

The close relationship found between size-fractionated phytoplankton biomass and production and the relative contribution of DOC-pr to total primary production and net community production allowed the characterisation of distinct modes of trophic organisation (Fig. 13). Picoplankton-dominated communities

Table 1. Photic zone-integrated net community production (NCP), dark community respiration (DCR) and gross oxygen production (GP) rates (mmol O_2 m^{-2} d^{-1}) during August 1998 and October 1999. nd: not detectable

Stn	Integration depth (m)	NCP	DCR	GP
August 1998				
1	50	92.9	145.2	238.1
13	50	–28.4	43.3	14.9
16	50	372.2	125.5	497.7
October 1999				
1	40	–22.6	66.2	43.6
4	50	–26.5	20.8	nd
8	40	57.9	48.0	115.9
10	50	–40.6	61.8	21.3
19	30	–2.7	24.4	21.7

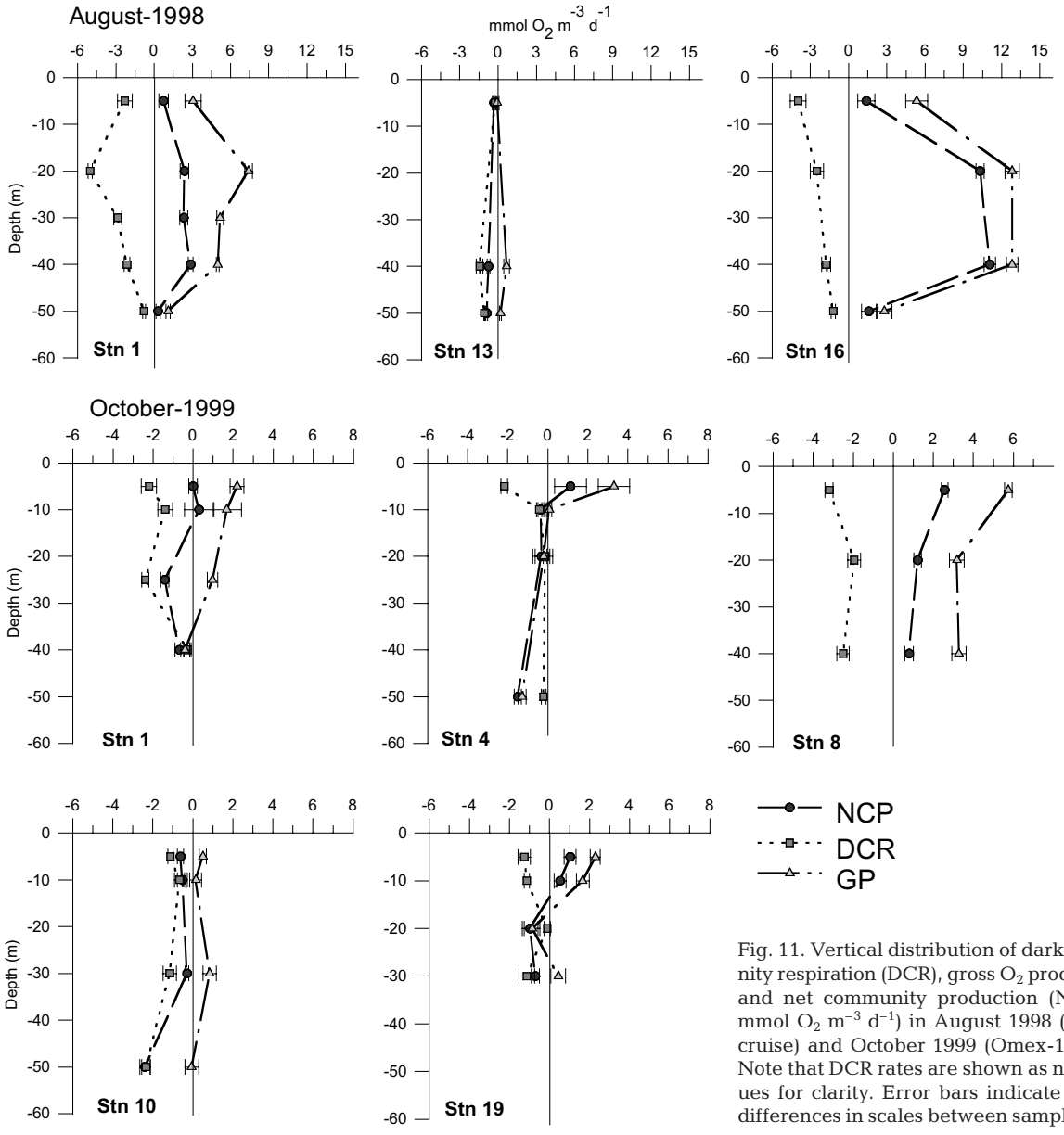

Fig. 11. Vertical distribution of dark O_2 community respiration (DCR), gross O_2 production (GP) and net community production (NCP) (all in mmol O_2 m^{-3} d^{-1}) in August 1998 (Omex-0898 cruise) and October 1999 (Omex-1099 cruise). Note that DCR rates are shown as negative values for clarity. Error bars indicate ± SE. Note differences in scales between sampling seasons

were associated with relatively high rates of DOC-pr compared to total carbon incorporation (>15%) and heterotrophic metabolism of the microbial communities. In contrast, in coastal upwelling stations, where >2 µm cells dominated, less than 10% of the total amount of carbon fixed flowed to DOC, and an autotrophic microbial metabolism prevailed. The net heterotrophic metabolism of the microbial community in this coastal-transition domain could result from allocthonous inputs of organic matter, including export from the coastal zone to the open ocean, and/or accumulation of biogenic carbon in the water column as a result of preceding high productivity episodes (e.g. Duarte & Agustí 1998, Williams 1998, Serret et al. 1999).

DISCUSSION

Phytoplankton size-structure and hydrodynamic conditions

The results in this paper clearly indicate that different planktonic community structures, as derived from differences in the size-structure of phytoplankton biomass and production, were characteristic of the 3 contrasting hydrodynamic scenarios defined in this study (Fig. 12): coastal upwelling and stratification in summer and weak stratification associated with a poleward flow on the shelf/shelf-break during autumn. Both summer upwelling and poleward flow conditions constitute thermohaline features characteristic of the

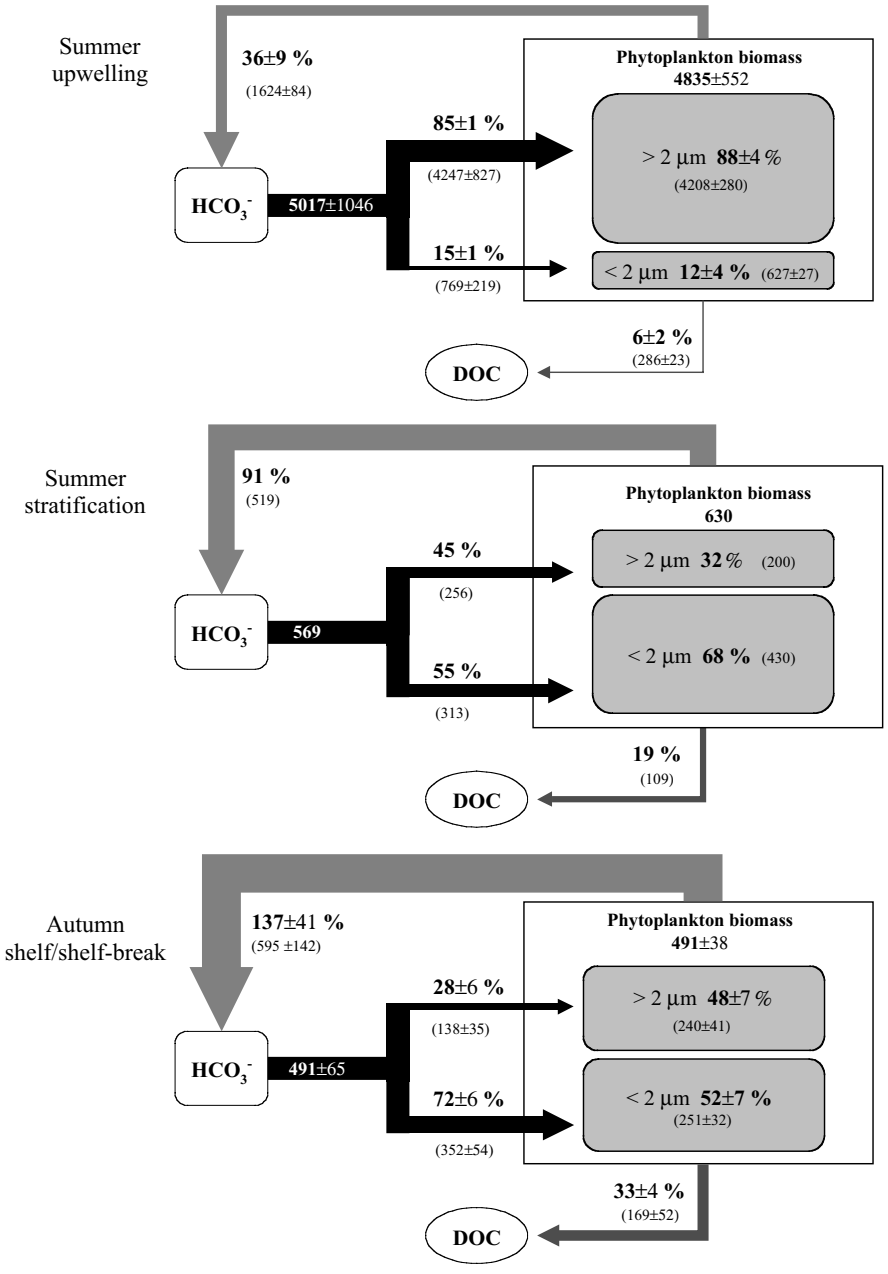

Fig. 12. Carbon budgets for the 3 contrasting environments sampled in the coastal-transition zone off NW Iberian peninsula. Phytoplankton biomass expressed in mg C m^{-2} (±SE). Fluxes expressed in mg C m^{-2} d^{-1} (±SE). Only stations where all the fluxes were concurrently measured were used: Stns 1 and 16 for summer upwelling, Stn 13 for summer stratification and Stns 1, 4 and 10 for autumn shelf/shelf-break. Calculations and conversion factors are explained in 'Results'. Boldfaced values represent the relative contribution of any given flux or phytoplankton size class with respect to total organic carbon production (TOC-pr) or total phytoplankton biomass, respectively. Numbers in parentheses are absolute values

annual cycle in the NW Iberian region (Wooster et al. 1976, Pingree & Le Cann 1990, Castro et al. 1997). The high spatio-temporal hydrodynamic variability in the coastal transition zone off the NW Iberian Peninsula allowed us to study a wide range of productivity and phytoplankton biomass levels as well as a wide spectra of phytoplankton size structures, characterised by a relative contribution of picoplankton (<2 µm cells) to total chlorophyll *a* of 3 to 68 %, and to total primary production of 8 to 87 % (Fig. 13a).

According to the typology of pelagic marine ecosystems proposed by Legendre & Le Fèvre (1991), the oceanic stratified station sampled during summer (Stn 13: Fig. 12) would be representative of Ecosystem Type 4, showing slight differences between the proportion of primary production and biomass accounted for by large phytoplankton; whereas primary production was dominated by both large and small cells, small cells contributed to a larger proportion of the phytoplankton standing stock. In this case, the model proposed by Tremblay & Legendre (1994) predicts higher export (by sinking, grazing or advection) of large cells than their contribution to primary production, and consequently an accumulation of small cells. Loss of large cells in stratified waters would simply reflect their incapacity to remain within the photic layer.

In autumn 1999, the low rates of TOC-pr measured at weak stratified shelf/shelf-break stations were related to a high contribution of <2 µm cells (Fig. 12), whereas the phytoplankton standing stock was dominated by both small and large cells; this does not correspond to any ecosystem type defined by Legendre & Le Fèvre (1991). Following the model proposed by Tremblay & Legendre (1994), this situation would result from a lower export of large cells than their share of primary production. Legendre et al. (1993) interpreted a similar negative difference between the proportions of production and biomass accounted for by >5 µm cells as the result of low sedimentation of large phytoplankton relative to that of small phytoplankton. Accumulation of large phytoplankton in the production layer in our

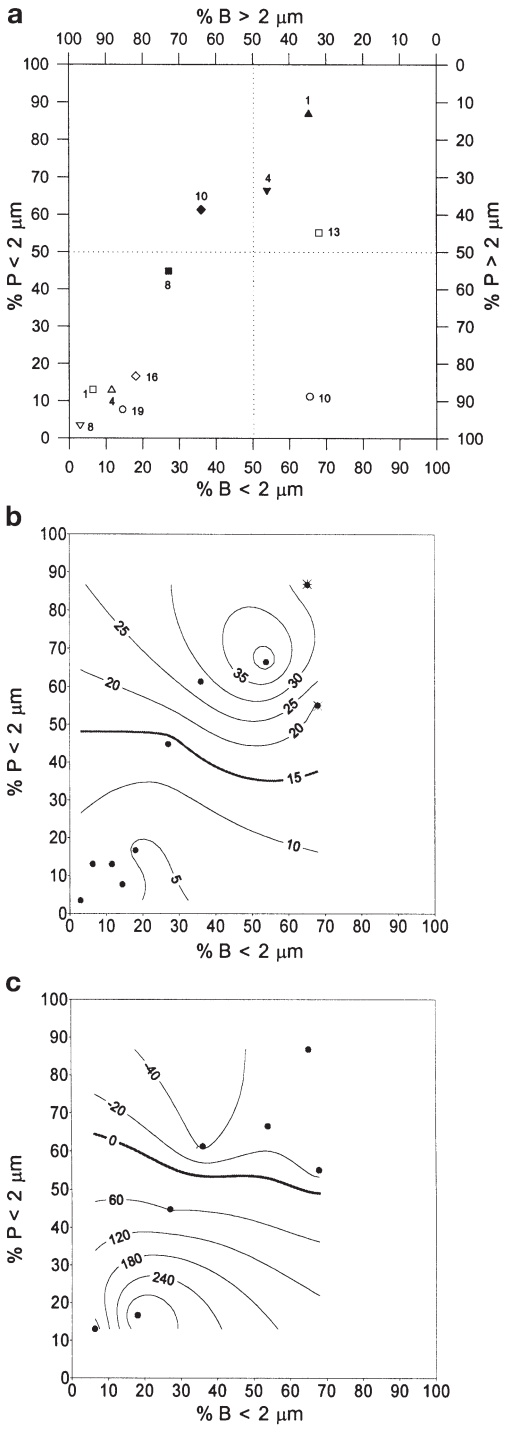

Fig. 13. (a) Plot of the biological stations in the space defined by the relative contribution of picoplankton to total photic zone-integrated chlorophyll *a* (% B <2 µm) and particulate primary production (% P <2 µm); (b) production-biomass (PB) plot of biological stations with superimposed isolines representing the relative contribution of photic zone-integrated DOC production to total primary production, i.e., PER (%); (c) PB-plot of biological stations with superimposed isolines representing photic zone-integrated net community production rates (mmol O_2 m^{-2} d^{-1})

study may have been associated with the presence of a well developed halocline at shelf/shelf-break waters (Fig. 4).

Finally, following Legendre & Le Fèvre (1991), summer coastal upwelling stations, characterised by both primary production and phytoplankton standing stocks dominated by large cells (Fig. 12), would correspond to Ecosystem Type 1 whereby, in accordance with the model proposed by Tremblay & Legendre (1994), large cells are exported in the same proportion as their contribution to primary production.

Although we did not directly measure biogenic carbon export (sinking, grazing, advection), our observations appear consistent with the classical conceptual models of the hydrodynamic control of the allometric distribution of primary producers. Therefore, it is possible to identify the main pathways of biogenic carbon circulation from measurements of size-fractionated phytoplankton biomass and primary production rates. Legendre & Rassoulzadegan (1996) reduced the flows of biogenic carbon to 5 broad pathways, ordered along a continuum of decreasing export relative to primary production and increasing contribution of small cells: sinking of ungrazed phytoplankton; herbivorous, multivorous, and microbial food webs; and the microbial loop. In each of these situations, the amount of biogenic carbon available for export would be ultimately determined by the balance between production and respiration processes; thus, the analysis of the production/respiration balance (P/R) of the microbial community in this study constitutes an alternative and complementary approach to that of biogenic carbon export models, since, on adequate scales, the former provides information on the trophic status of the ecosystem (Serret et al. 1999). We also measured DOC production by microbial populations as another loss rate potentially controlled by planktonic trophic organisation given its crucial role in the determination of the scales of linkage between production and respiration of organic matter in the upper ocean layers.

Phytoplankton size-structure, primary production and DOC release

A considerable degree of evidence has been presented on the existence of an inverse relationship between the rate of particulate organic carbon production and the relative contribution of DOC to total carbon fixation (e.g. Berman & Holm-Hansen 1974, Mague et al. 1980, Fogg 1983, Teira et al. 2001). In the present investigation, we found a significant relationship between POC-pr and DOC-pr volumetric rates (Fig. 10). The slope of the log-log linear re-

gression obtained using the whole data set (0.37) was significantly <1, reflecting an inverse relationship between POC-pr and the relative contribution of DOC-pr to total organic carbon production (see Figs 6, 7 & 9). The same inverse pattern results when photic-zone integrated values are used (Fig. 12); at coastal upwelling stations, characterised by the highest rates of integrated POC-pr, the percentage of carbon flowing to the DOC pool represented <10% of total primary production, whereas at shelf/shelf-break stations sampled during autumn, where the lowest integrated POC-pr values were measured, DOC production accounted on average for 33% of total carbon incorporation. Similar results have already been reported by Berman & Holm-Hansen (1974), who measured percentages of extracellular release (PER) ranging from 6 to 12% in eutrophic waters and from 17 to 27% in oligotrophic oceans. By taking into account the possible sources of error in the determination of DOC production rates, Fogg (1983) concluded that PER values of ca 5% of total carbon fixation in eutrophic waters and up to 40% in oligotrophic waters can be considered as reasonably correct; these values are in agreement with our measurements. Our data also show that for a similar range of POC-pr values, higher rates of DOC-pr were measured during autumn than in summer (Fig. 10). This pattern can be attributed to differences in plankton community structure, as discussed above. Hence, not only the magnitude of carbon incorporation rates but also phytoplankton community structure should be considered in order to predict the magnitude of DOC production by microbial populations at different spatio-temporal scales.

A significant positive relationship was observed in this study between PER and the contribution of picoplankton to total primary production, ranging from 6% at upwelling stations, where picoplankton accounted for only 15% of primary production, to 33% at shelf/shelf-break stations during autumn, where the contribution of picoplankton to total carbon fixation was 72% (Fig. 13). To our knowledge, this is the first empirical evidence that relates DOC production to phytoplankton size structure, although there are previous studies on the link between PER and phytoplankton size from a physiological perspective (e.g. Bjørnsen 1988, Kiørboe 1993). According to these 2 authors, the release of dissolved compounds from intact algae cells would simply result from passive diffusion across the permeable cell membrane, and a more intense release would be expected from small cells as a result of their higher surface to volume ratio. Kiørboe (1993) went deeply into the processes implied in the liberation of dissolved materials in the oceanic environment, and suggested that DOC produced during zooplankton grazing on phytoplankton would be the most important source of dissolved organic compounds in stable stratified oligotrophic waters, where the highest fluxes of DOC to bacteria and the highest relative importance of microbial processes would be expected to occur.

Phytoplankton size-structure and loss terms

As shown, the different phytoplankton communities initially defined from the size-fractionated production-biomass data set displayed distinct patterns in terms of loss rates (Fig. 13).

In stratified oligotrophic environments, microbial food webs, based on multiple trophic interactions and a rapid flow of matter through the biological compartments, are likely to suffer relatively important losses of organic matter as a result of processes such as phytoplankton cell lysis (Brussaard et al. 1995, Gobler et al. 1997, Agustí et al. 1998) or grazing by protozoans (Nagata & Kirchman 1992, Landry et al. 1997, Strom et al. 1997). In this regard, Agustí et al. (1998) reported high lysis rates in surface NW Mediterranean waters, representing on average 50% of the gross phytoplankton growth rate; the authors suggested that phytoplankton cell lysis can occur at rates high enough to influence food-web dynamics and biogeochemical cycles in oligotrophic environments. Agustí et al. (1998) also related the measured lysis rates with high heterotrophic activity in surface waters of the NW Mediterranean which, since cell lysis will ultimately result in the release of dissolved organic compounds, is consistent with the measurement of high heterotrophic activity related to high PER values found in the present study. Grazing by protozoans has recently been considered as the most important source of DOC production in the ocean (Nagata 2000), and field measurements have demonstrated that microzooplankton can consume >80% of daily primary production in many oceanic regions dominated by small phytoplankton, such as the central equatorial Pacific (Landry et al. 1997), the Eastern North Atlantic Subtropical gyre (Quevedo & Anadón 2001), or even the coastal waters off the Gironde estuary during spring (Sautour et al. 2000), thus keeping the phytoplankton biomass in a *quasi* steady-state condition. Although in this investigation we measured neither phytoplankton cell lysis rates nor grazing by microzooplankton, the high PER values measured in the picoplankton-dominated planktonic communities analysed suggest that grazing and lysis processes could be playing a significant role in these oligotrophic habitats. Unfortunately, the method for DOC production measurement does not allow us to distinguish between DOC released by these 2 processes

(lysis and grazing) and direct excretion from intact algae cells.

The significant amounts of recently produced DOC would ultimately fuel bacterial populations, which have been considered as the main factor responsible for heterotrophic respiration in the water column (Pomeroy & Wiebe 1993, Sherr & Sherr 1996; and references therein). The higher losses of photosynthesised materials to the dissolved organic matter (DOM) pool and tight complex trophic interactions imply that microbial food webs would constitute an almost balanced system (see Legendre & Rassoulzadegan 1995) wherein most of the autotrophic production would be respired in the photic layer (see Legendre & Le Fèvre 1995). Consequently, the influence of allochthonous organic matter input on the net metabolism of the system would increase in picoplankton-dominated communities, and could thus be related to the finding of bacterial respiration exceeding net primary production in unproductive aquatic systems (del Giorgio et al. 1997).

In upwelling conditions, the low PER values measured are likely to be simply the result of direct exudation from healthy phytoplankton cells. This is in good agreement with the conclusions of Sharp (1977). He first concluded that excretion during active growth of phytoplankton was not a relevant source of DOC production in the ocean, which is consistent with the low average PER value (about 6%) measured during the upwelling conditions in our study. Secondly, he proposed degradation of old and dying phytoplankton and losses during food web transfer as more important sources of organic matter in the sea, which is in accordance with the idea of cell lysis (both by natural death or viral infection), and grazing by protists as processes implied in the release of DOC.

Our observations provide empirical evidence indicating that, as the contribution of small phytoplankton cells to both primary production and biomass increases, a progressively higher fraction of the photosynthesised organic carbon flows to the DOC pool and the metabolism of the microbial community tends to be more prone to net heterotrophy. The close relationship between planktonic community structure and loss terms reported here is evidence for the influence of phytoplankton size distribution on carbon and oxygen fluxes through microbial communities in the upper ocean.

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