

Primary production and phytoplankton in three Galician Rias Altas (NW Spain): seasonal and spatial variability*

ANTONIO BODE and MANUEL VARELA

Centro Oceanográfico de La Coruña. Instituto Español de Oceanografía. Apdo. 130. E-15080 La Coruña (Spain)

SUMMARY: Phytoplankton species composition, chlorophyll-a concentrations and primary production were studied in the Rias of Ares, Ferrol and the Bay of La Coruña (Galicia, NW Spain) in three oceanographic situations during 1993. The observations were representative of maxima and minima phytoplankton biomass and production values in this area during the seasonal cycle. A phytoplankton bloom studied in March, was characterized by a patchy distribution of chlorophyll and high primary production rates, especially near La Coruña and in the Ria de Ferrol. High phytoplankton biomass and production was also recorded in August, when an upwelling pulse allowed for enhanced growth. Diatoms were very abundant during these blooms but while *Chaetoceros socialis* was the dominant species in spring other species dominated in summer, when dinoflagellates and flagellates increased. In contrast, the phytoplankton observed in December had low abundances, and correspondingly low chlorophyll concentrations and primary production rates through the study area. Photosynthetic measurements at selected stations using P-I curves indicated that phytoplankton populations were well adapted to the existing light regime. The main source of variation in photosynthetic parameters was seasonal, and no significant differences resulted between rias. Using these parameters and the measured vertical profiles of chlorophyll and irradiance, areal estimations of primary production rates were made for the entire area studied. The resulting values were scaled to the rates measured using parallel simulated *in situ* incubations of phytoplankton. Maximum primary production values during blooms exceeded $2400 \text{ mg C m}^{-2} \text{ d}^{-1}$, whereas values estimated for the winter cruise were lower than $20 \text{ mg C m}^{-2} \text{ d}^{-1}$. These values are equivalent to those available for the nearby Rias Baixas, but because of the larger size of the latter the annual values of the studied Rias Altas were less than 10% of the reported primary production in the most productive Galician ria (Ria de Arousa). This study provides the first estimates of up-to-date primary production values for the Rias Altas, and points out the differential role of upwelling in the nearby shelf compared to its effects on the Rias Baixas region. Upwelling events occur in localized areas outside the Rias Altas, and their associated water dynamics may cause a large export of the produced organic matter to outer shelf areas. In contrast, upwelling has been detected well inside most Rias Baixas, inducing high accumulations of recently produced organic matter, that are exported to nearby coastal areas.

Keywords: Primary production, biomass, phytoplankton, upwelling, seasonality, Rias Altas, Galicia.

INTRODUCTION

The coasts of Galicia (NW Spain) seasonally receive the influence of wind-driven upwelling pulses that allow high yields of exploitable marine biological resources. The upwelling causes the fertil-

ization of coastal and shelf areas with deep water nutrients, in discrete events that can occur between March and October (Fraga, 1981; Blanton *et al.*, 1984). The seasonality of surface winds, along with coastal morphology and the presence of several coastal embayments or rias favours biological production processes (Fraga and Margalef, 1979; Tenore *et al.*, 1982). The resulting catches of fish and shellfish amount to about $1.6 \times 10^{11} \text{ g y}^{-1}$ over

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the shelf, and an equivalent figure of raft-cultivated blue mussels inside the rias (Xunta de Galicia, 1992).

The rias are unique systems because of their morphology and orientation with respect to the main coastline and, with their freshwater inputs, greatly influence the fate of the nutrients released by the upwelling (Blanton *et al.*, 1984; Fraga, 1996). The Rias Baixas, located to the south of Cape Fisterra, are oriented in a NE-SW direction, which favours the net influx of upwelled water and high levels of primary production (Fraga and Margalef, 1979; Tenore *et al.*, 1982). River runoff can be seasonally important in most Rias Baixas, contributing significantly to water dynamics and biogeochemistry (eg. Alvarez-Salgado *et al.*, 1996). In contrast, the Rias Altas, located to the north of Cape Fisterra display a variety of orientations and receive smaller inputs of freshwater. The Rias Altas support a significant number of mussel rafts and local fisheries, although their total yield is lower than that of the Rias Baixas (Xunta de Galicia, 1992). Because of the economical importance of the Rias Baixas and their resources, there are several studies dealing with their primary production (see Varela *et al.*, 1984 for a review). However, there are very few published data on this subject for the Rias Altas. (Bode *et al.*, 1994a; Casas, 1995; Bode *et al.*, 1996; Varela *et al.*, 1996).

In this paper we describe the main features of phytoplankton biomass, species composition and areal estimates of primary production in characteristic stages of the seasonal cycle in the Rias of Ferrol, Ares and the Bay of La Coruña. These results are compared with those available for the Rias Baixas and the continental shelf of Galicia. A description of general hydrographic characteristics, dissolved nutrients and plankton observed during this study can be found in Varela *et al.* (1996).

METHODS

Daily irradiance was measured at our laboratory in La Coruña using a LiCOR 2 π sensor. Large scale oceanographic conditions were estimated by the upwelling index values, calculated using the procedure described in Blanton *et al.* (1984) and wind data provided by the Centro Zonal de La Coruña (Instituto Español de Meteorología). Water samples and observations were collected during COPLA-393 (11-29 March 1993), COPLA-893 (3-10 August 1993) and COPLA-1293 (15-20 December 1993) cruises, as part of a large scale study on the continental shelf off La Coruña (Varela *et al.*, 1996). In the present study we include results from the stations located inside the Bay of La Coruña, the Rías of Ferrol and Ares, and the adjacent coastal areas

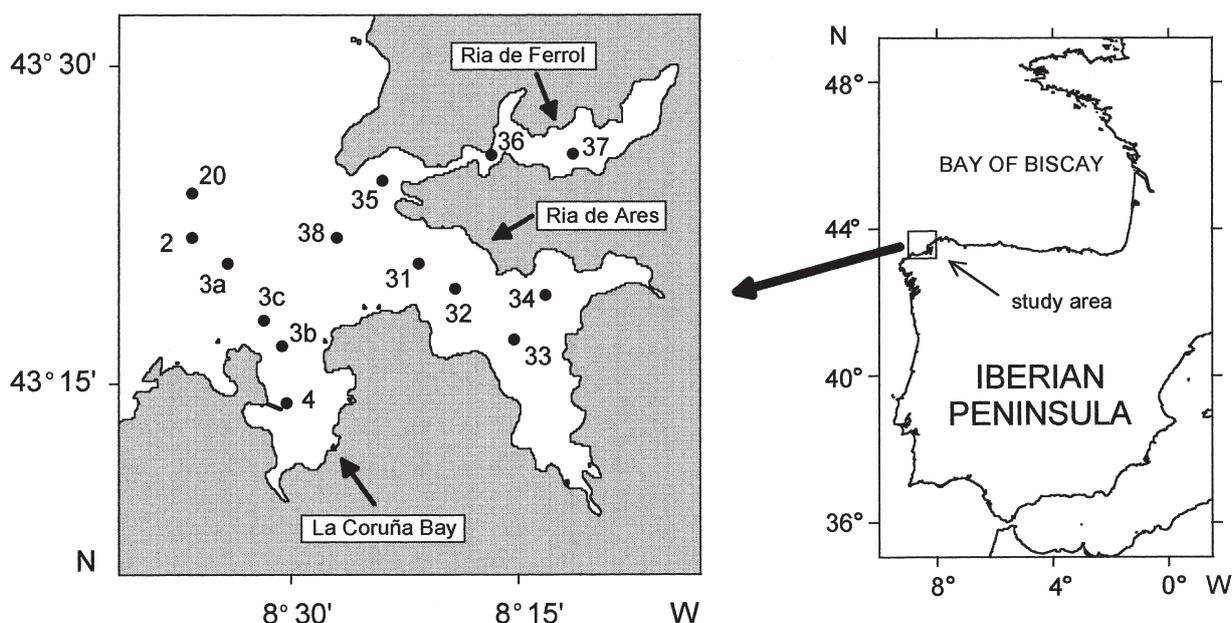


Fig. 1. – Map of the study area with the position of the sampling stations.

(Fig. 1). Temperature, salinity, and irradiance profiles were obtained at each station with a CTD Seabird SBE-25 equipped with a LiCOR spheric sensor. Water and phytoplankton samples were collected using Niskin bottles at the depths of 100, 50, 25, 10 and 1 % of the incident irradiance (I_0). Additional samples were taken at depths below the euphotic zone where bathymetry permitted. Chlorophyll-a concentrations were determined fluorometrically in samples from the euphotic zone in all stations. These samples were filtered through Whatman GF/F filters, and pigments were extracted in 90% acetone and analysed using the procedure described by Yentsch and Menzel (1963). Phytoplankton composition was determined in Lugol preserved samples from the euphotic zone in selected stations (Table 1).

TABLE 1. – Stations where simulated *in situ* production incubations (SIS), phytoplankton species composition (PSC) or P-I curves were measured during the different cruises.

Month	Cruise	Station number	
		SIS & PSC	P-I
March	COPLA-393	14, 32, 37	2, 4, 20, 32, 37
August	COPLA-893	20, 32, 36	2, 4, 20, 32, 36
December	COPLA-1293	2, 33, 36	2, 4, 31, 35, 37

Primary production was measured by two procedures in stations visited before noon (Table 1). The results from a nearby station (Sta. 14, 43° 20.74' N, 8° 34.38' W, 65 m depth) were included to complete the production values for the March cruise. Aliquots from each light intensity level within the euphotic zone were inoculated with 4 μCi (148 kBq) of $^{14}\text{CO}_3\text{Na}$ and were incubated on board for at least 2 h around noon in simulated *in situ* (SIS) conditions. The incubator was refrigerated by running surface seawater and illuminated by sunlight. Light levels were simulated using neutral density screens. In addition, photosynthesis - irradiance (P-I) curves were determined in 60 ml aliquots from water collected at the surface (100 % I_0) and at the base of the euphotic zone (1 % I_0), inoculated with 2 μCi (74 kBq) of $^{14}\text{CO}_3\text{Na}$ and incubated for up to 2 h in a linear incubator. These aliquots were illuminated with halogen lamps of 2 mmol quanta $\text{m}^{-2} \text{s}^{-1}$ of initial irradiance. The incubator was refrigerated with surface seawater. All incubations were terminated by filtration onto Whatman GF/F filters, that were acidified with two drops of 5 % HCl overnight and counted on a LKB Wallac 1409 liquid scintillation

counter using Instagel, as the scintillation medium. The P-I curves were adjusted using the functions described by Platt and Jassby (1976), in the case of no photoinhibition, and Platt *et al.* (1980) in cases of apparent photoinhibition. The chlorophyll-a normalized photosynthetic parameters α^B (production efficiency, $\text{mg C mg Chl-a}^{-1} \text{h}^{-1} \mu\text{mol quanta}^{-1} \text{m}^2 \text{s}$), P^B_S (light-saturated production rate, $\text{mg C mg Chl-a}^{-1} \text{h}^{-1}$), P^B_M (maximum production rate, $\text{mg C mg Chl-a}^{-1} \text{h}^{-1}$), β^B (photoinhibition, $\text{mg C mg Chl-a}^{-1} \text{h}^{-1}$), and saturation irradiance ($I_k \mu\text{mol quanta m}^{-2} \text{s}^{-1}$) were used to describe the photosynthetic properties of the phytoplankton in each station and to compute areal estimates of primary production.

Primary production estimations in the whole study area were made using the procedure of Sathyendranath and Platt (1993). First, primary production rates at each sampling depth were computed using the photosynthetic parameters α^B and P^B_M and the irradiance received at that depth. The resulting chlorophyll-normalized production values were then converted into carbon units using the chlorophyll concentration measured at the same depth. Water column rates were obtained by integration to the depth of the euphotic zone. The integral was com-

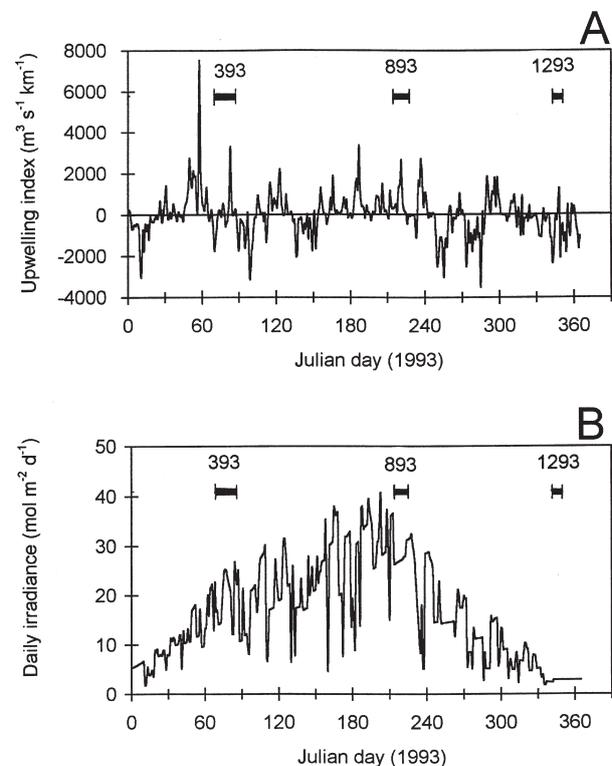


FIG. 2. – Daily values of the upwelling index (A, $\text{m}^3 \text{s}^{-1} \text{km}^{-1}$) and incident irradiance (B, $\text{mol quanta m}^{-2} \text{d}^{-1}$) measured at La Coruña during 1993.

puted by numerical integration of 1 m intervals, estimating values located between the discrete sampling depths by exponential smoothing. For comparative purposes we used the average daily irradiance value measured during each cruise and the depth attenuation coefficient measured at each station to estimate the irradiance received at each depth. The daily primary production rates obtained from this method were compared to estimations obtained by the SIS method.

RESULTS

Oceanographic conditions

The cruises were representative of significant oceanographic situations related to the annual cycles

of upwelling and solar irradiance (Fig. 2). The COPLA-393 cruise was made after the first marked upwelling pulse of the year, with positive values of the upwelling index for several days before the cruise and average irradiance values of ca. 20 mol quanta $m^{-2} d^{-1}$. The summer cruise COPLA-893 was also made in favourable upwelling conditions, but in this case the irradiance values were near the annual maximum. In contrast, mostly downwelling conditions and very low irradiances occurred during the COPLA-1293 cruise.

Surface temperature and salinity values indicated that the stations located inside the rias received little influence from freshwater discharges during the March cruise (Fig. 3 A). Most of the area had surface temperatures between 12.4 and 13°C, that were close to the annual minimum in this region (Casas *et al.*, 1997). Chlorophyll concentrations were high

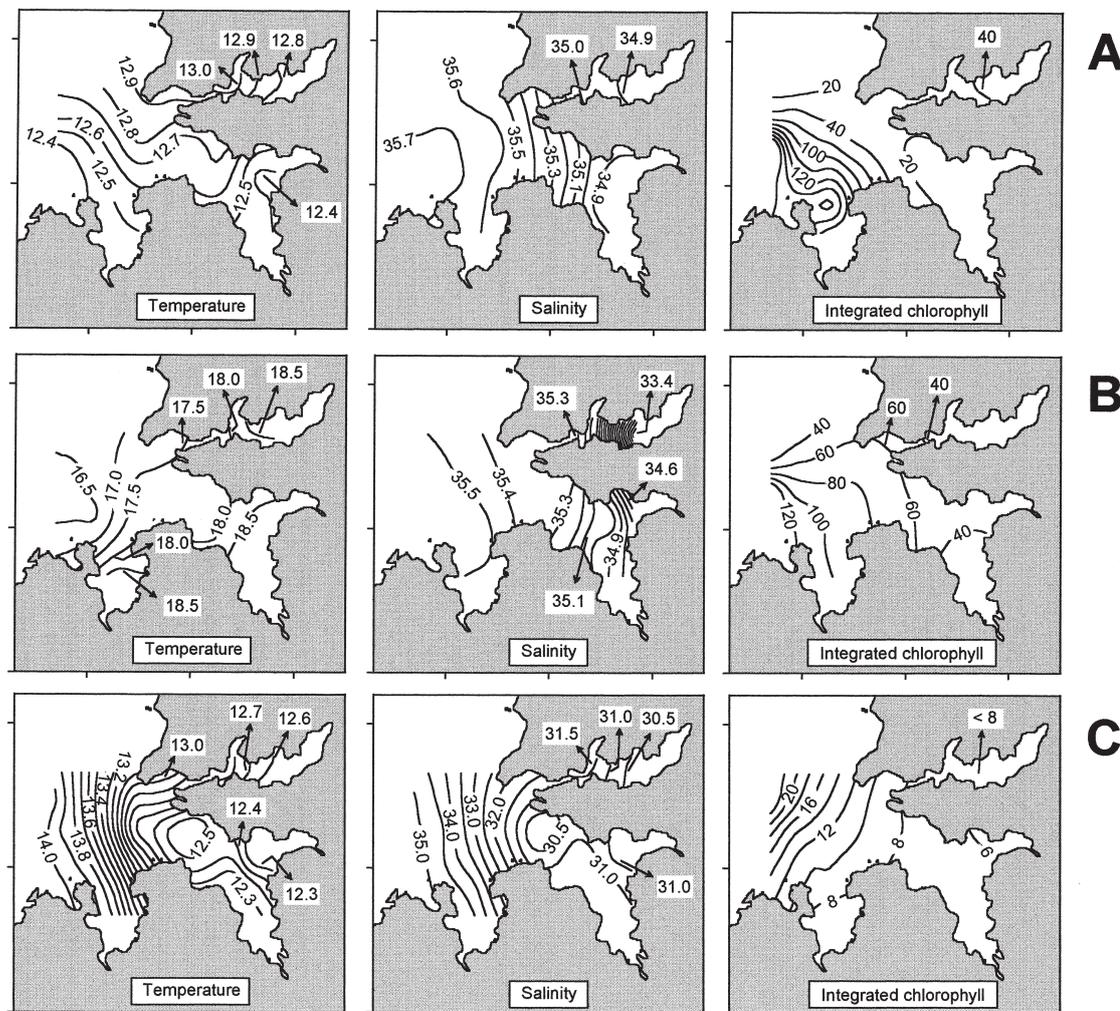


FIG. 3. – Surface distributions of temperature ($^{\circ}C$), salinity (psu), and water-column integrated chlorophyll ($mg m^{-2}$) from the cruises COPLA-393 (A), COPLA-893 (B) and COPLA-1293 (C).

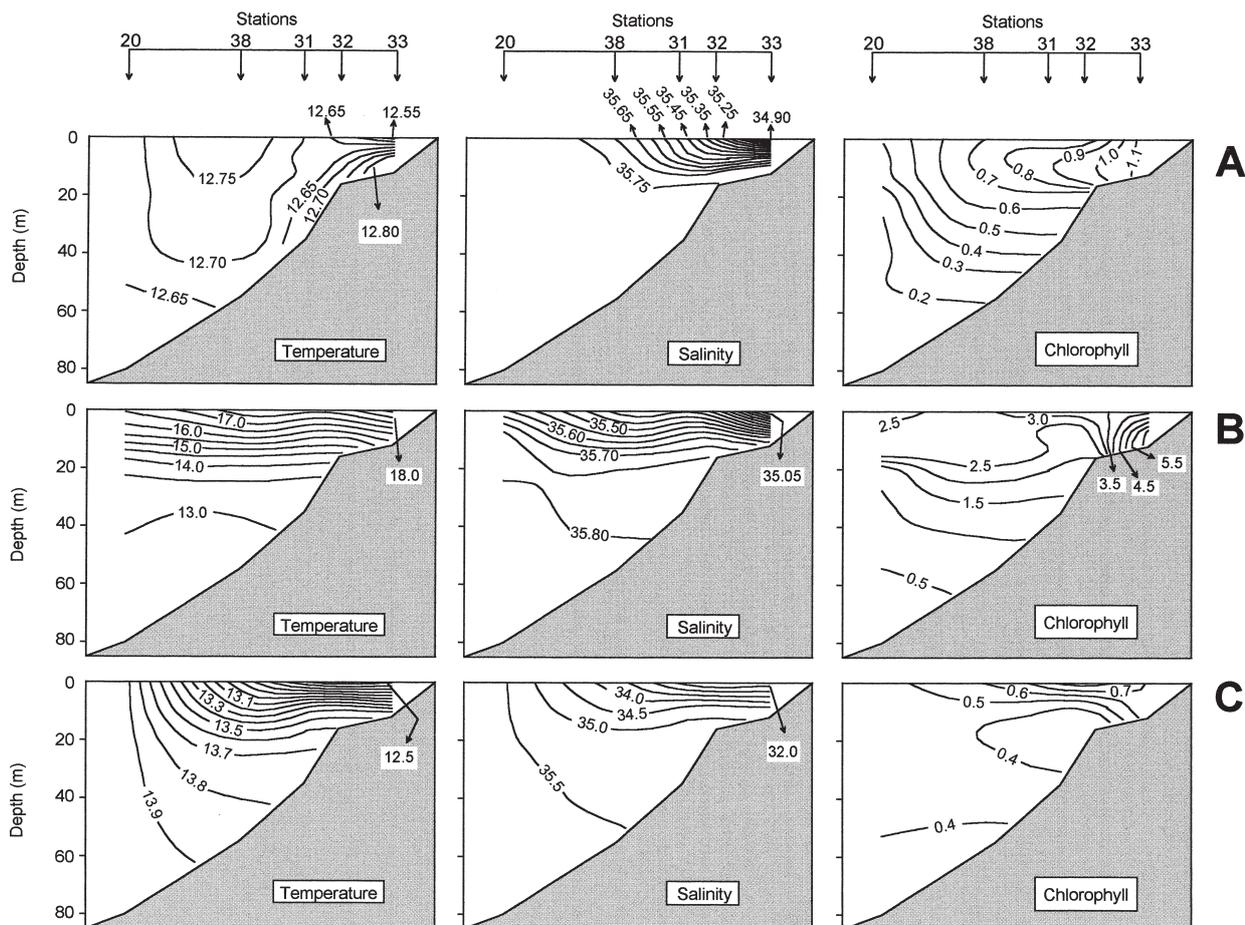


Fig. 4. – Spatial distribution of temperature ($^{\circ}\text{C}$), salinity (psu) and chlorophyll concentration (mg m^{-3}) in a transect from the inner part of the Ria de Ares to the open shelf during the cruises COPLA-393 (A), COPLA-893 (B) and COPLA-1293 (C).

near La Coruña (ca. $150 \text{ mg Chl-a m}^{-2}$), but reached very low values in the Ria de Ares and in the open shelf stations. In contrast, the Ria de Ferrol had relatively high chlorophyll concentrations (up to ca. 50 mg m^{-2}).

Higher temperature variations were found during the August cruise, when salinity values inside the rias, but also at the shelf, were lower than in March (Fig. 3 B). As a result, strong salinity gradients occurred from the inner to the outer stations in the rias. The prevailing upwelling conditions during this cruise were not clearly reflected in the surface, but the relatively low surface temperatures and high chlorophyll concentrations in the stations near La Coruña suggested that shelf stations in the western part of the study area were affected by the upwelling. In December surface temperatures showed minima values near the coast and inside the rias (Fig. 3 C). Surface salinity reached maximum values during this period, and chlorophyll concen-

trations were in general low, reaching values higher than 20 mg m^{-2} at open shelf stations.

Vertical distribution

The vertical distribution of these variables in a transect from the Ria de Ares to the open shelf, shows the existence of a body of relatively warm water that extends from the surface to ca. 40 m depth near the mouth of the ria in the March cruise (Fig. 4 A). The freshwater influence was restricted to the ria and caused marked stratification in the upper 20 m of the water column. In contrast, shelf waters were more homogeneous, with salinity values between 35.75 and 35.80 psu. Chlorophyll concentrations in this transect were higher inside the ria, but these values were low when compared with those of Ria de Ferrol or the stations near La Coruña.

During the August cruise, the stratification of the upper layer of the water column was well defined in

the whole transect (Fig. 4 B). The influence of the upwelling was not apparent except in the subsurface layer of the deepest station that had water with salinity values higher than 35.80 psu. Chlorophyll concentrations were generally high in the upper 20 m and inside the ria, where values higher than 5 mg m^{-3} were found near the bottom. The stratification of temperature and salinity values found during the December cruise affected only to the coastal stations, while the outermost station displayed a vertically mixed water column (Fig. 4 C). Chlorophyll concentrations were very low at all stations but a surface maximum of ca. 0.8 mg m^{-3} was measured near the mouth of the ria.

The study area was divided in four zones corresponding to La Coruña Bay (Sta. 3b, 3c and 4), Ría de Ares (Sta. 31, 32, 33 and 34), Ría de Ferrol (Sta. 35, 36 and 37) and the open shelf (Sta. 2, 3a, 20 and 38). The profiles of chlorophyll were quite homogeneous in all zones during March and December, but subsurface maxima were clearly defined in August, particularly in the open shelf (Fig. 5). Most of these subsurface maxima were near 5 m depth in the rias and near 10 m depth in the open shelf. SIS primary production profiles showed the maximum values close to the surface in December, but in a subsurface layer in all other cruises. These subsurface maxima were generally above the chlorophyll maxima, but

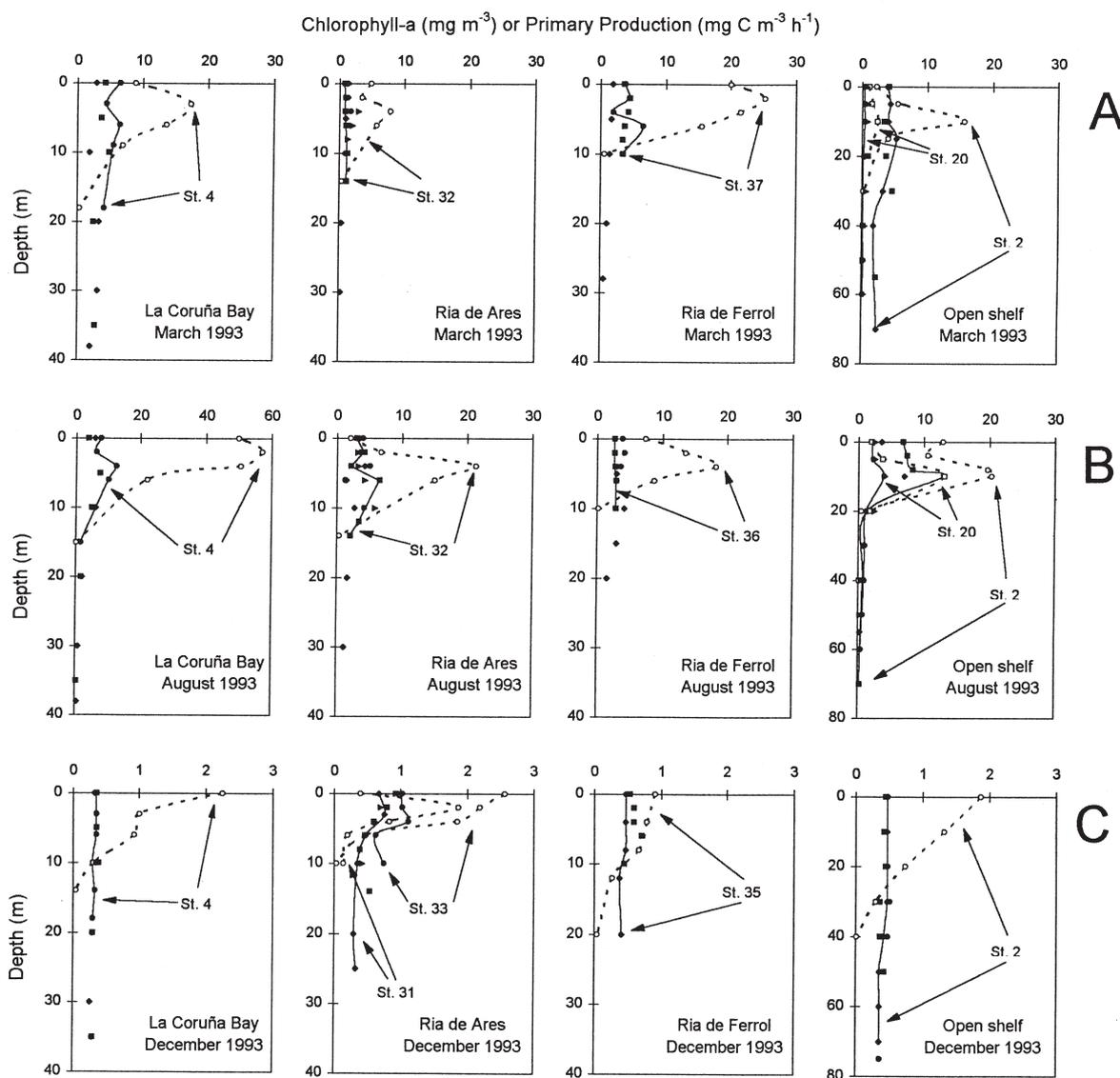


FIG. 5. – Vertical profiles of chlorophyll concentration (closed symbols and continuous lines, mg m^{-3}) and SIS primary production rates (open symbols and dashed lines, $\text{mg C m}^{-2} \text{ h}^{-1}$) in four zones during the cruises COPLA-393 (A), COPLA-893 (B) and COPLA-1293 (C). The station number is indicated by arrows.

in the open shelf stations during the August cruise both maxima occurred at the same depth (Fig. 5 B). The largest differences in chlorophyll and production profiles between cruises were in the absolute values reached, where values from the December cruise were ca. 10 times lower than those of March. The maximum production values measured were those of St. 4 in La Coruña Bay during August (ca. 50 mg C m⁻³ h⁻¹).

Phytoplankton species composition

Flagellates dominated phytoplankton abundance distributions in nearly all cruises (Table 2). However, the diatom *Chaetoceros socialis* Lauder reached high abundances in March, while *Leptocylindrus danicus* Cleve and *Skeletonema costatum* (Greville) Cleve were dominant in August. Small dinoflagellates were always present, but species of this group had higher abundances in summer when red-tide

forming organisms, like *Alexandrium lusitanicum* Balech and *Prorocentrum micans* Ehrenbergh, exceeded on average 90 cells ml⁻¹. Abundance values of phytoplankton were low during the December cruise (< 30 cells ml⁻¹, Table 2). There were some differences in the composition of phytoplankton in the three rias, particularly in the March cruise, when the Ria de Ferrol and the stations near La Coruña had the highest abundances of *Chaetoceros socialis* and the Ria de Ares and the outer shelf zone were dominated by flagellates.

Photosynthetic characteristics and areal production

The photosynthetic parameters α^B and P_M^B were significantly different between cruises (ANOVA Kruskal Wallis test, n = 18, p < 0.001) and there were also statistically significant differences in I_k (p < 0.05). However there were no significant differ-

TABLE 2. – Abundance (cells ml⁻¹) of the dominant phytoplankton species in each sampling period. sd: standard deviation, n: number of samples.

species	mean	sd	March min	max	n
Flagellates 3-5 μ m	1508	791	215	3064	27
<i>Chaetoceros socialis</i> Lauder	1106	1941	0	7770	27
Flagellates 5-8 μ m	373	270	43	1021	27
Flagellates 8-10 μ m	158	106	14	400	27
<i>Cryptomonas</i> spp.	96	83	2	327	27
<i>Chaetoceros gracilis</i> Schütt	42	38	0	118	17
<i>Schroederella delicatula</i> (Peragallo) Pavillard	40	50	0	132	27
Dinoflagellates < 30 μ m	29	21	4	67	27
<i>Thalassiosira rotula</i> Meunier	18	23	0	97	27
<i>Chaetoceros didymus</i> Ehrenbergh	13	15	0	49	26
August					
<i>Leptocylindrus danicus</i> Cleve	4045	5917	21	29997	27
<i>Skeletonema costatum</i> (Greville) Cleve	3396	12305	0	64084	27
Flagellates 3-5 μ m	3105	2235	113	7491	27
Flagellates 5-8 μ m	606	591	1	2497	27
Flagellates 8-10 μ m	234	172	1	563	27
<i>Alexandrium lusitanicum</i> Balech	193	146	27	355	4
Dinoflagellates < 30 μ m	103	120	7	542	27
<i>Cryptomonas</i> spp.	103	119	4	527	27
<i>Prorocentrum micans</i> Ehrenbergh	92	219	0	1021	21
<i>Olisthodiscus</i> spp.	85	132	0	364	15
December					
Flagellates 3-5 μ m	708	338	172	1505	30
Flagellates 5-8 μ m	100	73	1	344	30
<i>Cryptomonas</i> spp.	63	41	0	168	30
Flagellates 8-10 μ m	33	28	5	129	30
Dinoflagellates < 30 μ m	30	18	3	84	30
<i>Lyngbya</i> sp.	11	55	0	300	30
<i>Cachonina hallii</i> Freudentahl & Lee	7	10	0	31	30
<i>Skeletonema costatum</i> (Greville) Cleve	4	6	0	27	30
<i>Paralia sulcata</i> (Ehrenbergh) Kützing	2	3	0	16	30
<i>Nitzschia longissima</i> (Brébisson) Grunow	2	0	0	5	30

TABLE 3. – Photosynthetic parameters obtained from P-I curves averaged by sampling periods (mean and standard deviation, sd) of P-I curves obtained for each cruise. Parameter units and symbols as described in the methods section.

Month	% I_0		α^B	P^B_s	β^B	P^B_M	I_k
March	100%	mean	0.0589	8.1288		8.1288	139
		sd	0.0060	0.9927		0.9927	25
	1%	mean	0.0612	5.5848	0.0018	4.9608	78
		sd	0.0180	2.6042	0.0014	2.6128	18
August	100%	mean	0.0170	7.2542	0.0025	4.5413	252
		sd	0.0122	5.1595	0.0025	3.5800	92
	1%	mean	0.0240	8.0802	0.0029	5.3549	221
		sd	0.0060	5.0245	0.0027	2.5570	87
December	100%	mean	0.0140	2.3267	0.0014	1.7187	135
		sd	0.0040	0.6593	0.0009	0.6117	70
	1%	mean	0.0184	2.6976	0.0020	1.8590	107
		sd	0.0121	1.3098	0.0018	0.9680	16

ences in these parameters between the different zones ($p > 0.05$). Therefore, photosynthetic parameters of each cruise were averaged in order to compute primary production in all stations (Table 3). Phytoplankton in March was well adapted to the increasing radiation received during the spring, as evidenced by high P^B_M values in surface waters. However it was also well adapted to relatively low irradiance values because of the high values of α^B and average values of I_k lower than $150 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$. The differences between P-I curves from the surface and the bottom of the euphotic zone, particularly in the apparent photoinhibition response of samples from the latter, indicated the presence of a vertical stratification within the euphotic zone. The adaptation to high irradiances was more evident in the samples from the August cruise, with characteristic low α^B and high P^B_M values. Saturation irradiances exceeded $200 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ and the values of the photoinhibition parameter β^B reached maximum values measured during this study. In summer there were no clear differences in the values of photosynthetic parameters between the upper and lower limits of the euphotic zone (Table 3). This can be explained by the frequent occurrence of upwelling pulses through the summer, that cause the movement of phytoplankton from deep layers to high irradiances near the surface. In December the phytoplankton was still adapted to relatively high irradiances, indicated by low values of α^B and I_k values similar to those of March. However, the low P^B_M values and the low degree of variation between surface and deep samples indicated that mixing events were frequent in the water column and that the production was probably light limited.

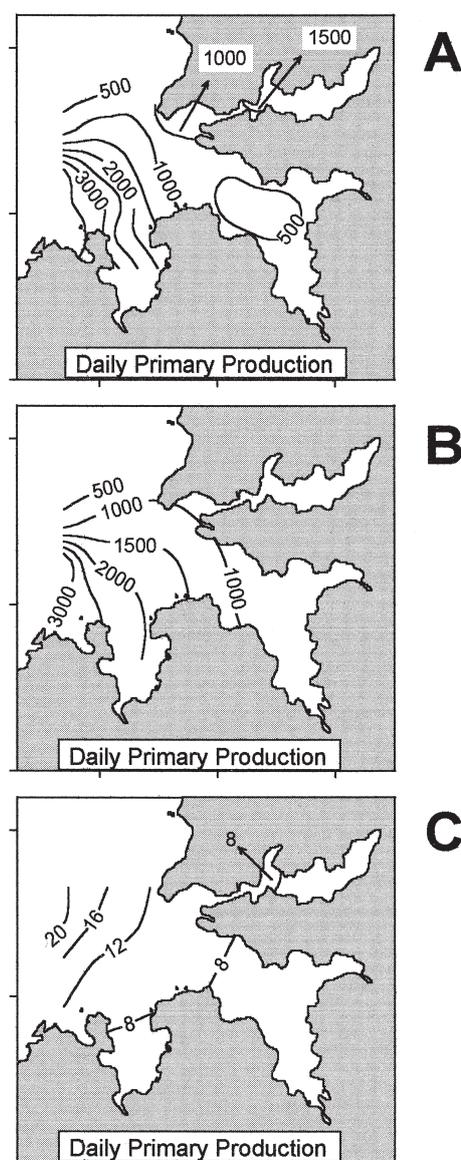


FIG. 6. – Spatial distribution of values of water-column integrated primary production ($\text{mg C m}^{-2} \text{d}^{-1}$) in the study area during the cruises COPLA-393 (A), COPLA-893 (B) and COPLA-1293 (C).

There was a significant linear correlation between water column estimates of daily primary production using the average values of a^B and P_M^B and the values measured in some stations with the SIS method ($r = 0.819$, $n = 16$, $p < 0.001$). The slope of the regression line between these variables was not significantly different from 1 (1.343 ± 0.251 , s.e.) and the intercept was not significantly different from 0 (-22.269 ± 280.851), as determined by Student-t tests ($p < 0.05$). Consequently, the primary production values estimated from P-I parameters and chlorophyll profiles are statistically equivalent to those measured by the SIS method, more frequent in other studies of primary production made in Galician waters (e.g. Bode *et al.*, 1996).

Primary production rates were higher in the western stations of the study area during March and August, both with equivalent maximum values exceeding $3000 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Fig. 6 A, B). The spatial pattern of primary production was also similar in both seasons, excepting the lower production rates of the Ria de Ares in March. In contrast, primary production values estimated for the December cruise were ca. 1 % of those measured during previous cruises. In this case, only one station located near the mouth of the Ria de Ares reached more than $20 \text{ mg C m}^{-2} \text{ d}^{-1}$, while maximum values in the open shelf stations were ca. $14 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Fig. 6 C). The mean values measured during the cruises (Fig. 7) were statistically significant (ANOVA, $p < 0.001$), but the values of the March and August cruises were equivalent and significantly higher than the mean production measured in December ('*a posteriori*' Student-Newman-Keuls test, $p < 0.05$). However, due to the large variations found in each zone described, there were no significant differences in daily production estimates between zones (ANOVA, $p > 0.05$).

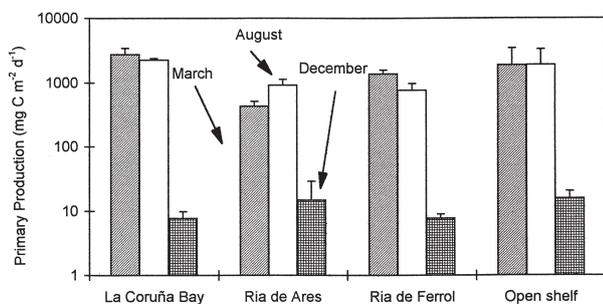


FIG. 7. – Mean (+ sd) values of water column integrated primary production ($\text{mg C m}^{-2} \text{ d}^{-1}$) in four zones during March, August and December 1993.

DISCUSSION

The described variations in biomass and species composition are consistent with the annual cycle and the oceanographic stages related to the phytoplankton described for the coast of La Coruña (Valdés *et al.*, 1991; Bode *et al.*, 1994a; Casas, 1995; Bode *et al.*, 1996; Casas *et al.*, 1997). However, maximum abundance and chlorophyll concentration values found during this study were lower than those reported previously (Casas, 1995). This can be attributed to the occurrence of the main upwelling peaks before the cruise (as in the case of March) or at the end of the cruise (as in August) and a delay in the response of phytoplankton to the upwelling forcing of up to 13 days (Casas, 1995). There is also a correspondence between our findings and the seasonal succession of phytoplankton in other Galician rias (eg. Margalef *et al.*, 1955; Mariño *et al.*, 1985; Figueiras and Niell, 1987). Therefore, our study provides results characteristic of phytoplankton blooms (spring and summer cruises) and of low phytoplankton abundance, biomass and production (winter cruise).

Phytoplankton blooms are caused in the study area by two main phenomena. On one hand, blooms produced during the spring can be originated by small density gradients near the surface of the water column, as those found in the Ria de Ferrol in this study. The first occurrence of these blooms is generally in March (Casas, 1995; Casas *et al.*, 1997), when the mean daily irradiance at the sea surface is greater than $20 \text{ mol quanta m}^{-2} \text{ s}^{-1}$. The density gradients can be caused by freshwater runoff, as in the rias, or by the upwelling. In the latter case, the upwelling cause the movement of water from the ocean to the shelf, where water was generally well mixed at this time of the year (Fraga, 1981; Casas *et al.*, 1997). In some cases, water with a salinity higher than the shelf water can be found near the shelf break, as part of the poleward current that flows seasonally in the Eastern North Atlantic (Frouin *et al.*, 1990). This water may reach inner shelf and coastal areas causing density gradients in the water column (Varela *et al.*, 1996; Casas *et al.*, 1997), and can be detected in our March cruise as the shelf water with a salinity higher than 35.75 psu (Fig. 4 A). A similar phenomenon was described by Castro *et al.* (1994) in the same area. The role of upwelling pulses during these blooms would be more related to the creation and maintenance of the stratification by forcing the penetration of a dense watermass into the

shelf than to the fertilization with new nutrients, because nutrient concentrations in shelf water are already high at this time of the year (Valdés *et al.*, 1991; Varela *et al.*, 1996; Casas *et al.*, 1997).

In contrast, blooms produced in late spring or in summer, as in our August cruise, would be more dependent on the nutrient enrichment caused by the upwelling. Even when surface nutrients are rarely depleted in this coast, their concentrations in the surface during summer generally do not exceed 0.5 mmol m^{-3} in the case of nitrate (Valdés *et al.*, 1991; Casas *et al.*, 1997). Upwelling events can introduce a significant amount of new nutrients into the euphotic zone (Bode and Varela, 1994), allowing for discrete phytoplankton blooms that can be traced through most of the spring and summer (Casas *et al.*, 1997). During the August cruise surface nutrient concentrations were low, but shelf stations located to the north of the Ria de Ferrol had more than $2 \text{ mmol nitrate m}^{-3}$ and temperatures lower than 14.5°C at 10 m depth, indicating a recent upwelling (Varela *et al.*, 1996). There was also a difference in the composition of phytoplankton populations between spring and summer blooms. Spring blooms were typically dominated by *Chaetoceros socialis* (as in our March cruise) and other species of the same genus, while the composition of phytoplankton during summer blooms was often more diverse (Casas, 1995). In our study, the phytoplankton of the summer cruise was dominated by two species of diatoms, but several flagellates and dinoflagellates reached significant abundances. The high abundance of flagellates in all cruises may indicate a high potential for the oxidation of organic matter in the water column. Varela *et al.* (1996), based on counts of flagellates with and without autofluorescence, reported that only during the March cruise was there an equivalent number of autotrophic and heterotrophic cells, while during the August and December cruises more than 80% of cells were heterotrophic. This result supports the hypothesis that a large fraction of the organic matter produced by phytoplankton after an upwelling pulse in summer is consumed in the water column by the existing microbial populations (Bode and Varela, 1994).

Our measurements indicate that in all cruises phytoplankton cells were well adapted to the existing light regimes. Maximum production values (P_M^B) occurred near the surface and during summer, and maximum saturation irradiances were always close to incident irradiances at noon in each season. The largest differences in photosynthetic parameters

occurred between the seasons studied. This feature, common in coastal and temperate areas (eg. Schofield *et al.*, 1993), contrasts with the constancy of these parameters in oceanic environments (Platt *et al.*, 1992). The pattern described by our values of α^B differs with that of average seasonal values for coastal areas in the north Atlantic reported in Sathyendranath *et al.* (1995), because in our case the values of α^B and P_M^B observed in spring were comparable or even higher than those observed in summer. The later authors recognize that the coastal environments are heterogeneous and that the effect of local conditions in photosynthetic parameters may be of greater importance than seasonal changes. This emphasizes the value of experimental estimations of these parameters in local areas where major environmental changes occur, like the upwelling forcing in our case.

The fact that our results do not show a statistically significant depth dependence of either α^B and P_M^B support the hypothesis that mixing phenomena, involving most of the euphotic zone, are very frequent in the studied area even during summer, the season where thermal stratification is likely to occur. Several authors (eg. Lewis *et al.*, 1984 and Lizon *et al.*, 1995, among others) have shown that phytoplankton populations can be physiologically heterogeneous only in moderately mixed water columns. Upwelling pulses, that occur in this area with a periodicity of 4 to 22 days (Casas, 1995), would allow phytoplankton cells to be exposed to high irradiance levels as the pycnocline is moved upwards. In addition, there are other physical processes that can produce the same effect, like tides and internal waves. As a consequence, these cells are adapted to frequent oscillations in the light field, as in other upwelling areas (eg. González-Rodríguez, 1994). It is not surprising that diatoms are a significant fraction of phytoplankton in the study area because they can tolerate large variations in irradiance (Sakshaug *et al.*, 1987). However, other studies have shown that photosynthetic parameters at various depths within the mixed layer can be very different, following also circadian variations (Lizon *et al.*, 1995). Therefore, the values provided in the present study must be taken as preliminary, and more experimental data are required in future studies for a better understanding of light adaptations of phytoplankton in this area.

Average water-column integrated primary production values during either spring and summer cruises were comparable to those measured in the

TABLE 4. – Comparison of areal and annual estimates of primary production in the studied Rías Altas and two Rías Baixas. Annual production was computed in all cases by multiplying the mean daily production by 365. Area and volume data are from Fraga (1996).

Ría	Area (km ²)	Volume (km ³)	Annual production (g C m ⁻² y ⁻¹)	Reference	Total Production (Mg C y ⁻¹)
Rías Altas					
La Coruña	24	0.24	608	this study	14587
Ares	72	0.75	166	this study	11970
Ferrol	27	0.22	261	this study	7038
Rías Baixas					
Arousa	230	4.34	250	Varela <i>et al.</i> , 1984 (1)	57500
Arousa	230	4.34	537	Alvarez-Salgado <i>et al.</i> , 1996 (2)	123407
Vigo	176	3.12	260	Fraga, 1976 (1)	57760
Vigo	176	3.12	288	Prego, 1993 (3)	50749

(1) primary production determined either by 'in situ' or simulated 'in situ' incubations.

(2) primary production estimated from P-I curves.

(3) primary production calculated from carbon budgets.

Galician shelf (Bode *et al.*, 1994a; 1996). In contrast, values for the winter cruise were among the lowest recorded in this region. The highest values of chlorophyll and primary production were found in shelf stations near La Coruña. Primary productivity data collected over several years in the mid-shelf zone often exceeded values measured near the coast (Bode *et al.*, 1996). Also several studies have pointed out the existence of mid-shelf and shelf-break upwelling areas in spring and summer (Varela *et al.*, 1991; Tenore *et al.*, 1995; Bode *et al.*, 1994b; Prego and Bao, 1997). In our case study, the thermohaline front that divided the shelf in a north-south direction during the March cruise (Varela *et al.*, 1996) probably was caused by an intrusion of a saline wedge of the poleward current over the shelf, having associated high chlorophyll concentrations and primary production values.

Published data of daily primary production in the Rías Baixas are similar to our measurements (Table 4). Fraga (1976) report for the Ria de Vigo maximum and mean primary production rates of 2.82 and 0.71 g C m⁻² d⁻¹ respectively. González *et al.* (1982), in their study of the Ria de Pontevedra in winter, cite values between 0.05 and 0.46 g C m⁻² d⁻¹. Tenore *et al.* (1982) report values for the Ria de Arousa that range between 0.03 and 0.10 g C m⁻² d⁻¹ in winter and are higher than 1 g C m⁻² d⁻¹ during phytoplankton blooms in spring and autumn. Even when the resulting value of annual primary production for La Coruña (608 g C m⁻² y⁻¹) is somewhat higher than those measured by the SIS method at the same stations by Casas (1995), the small surface and volume of the Bay of La Coruña compared with the two Rías Baixas gives a total annual value that represents only from 10 to 25 % of primary production in the Ria de Arousa. At the

same time, this value is very similar to that of Ria de Ares, three times larger. The lower absolute value of total annual production corresponds to the Ria de Ferrol, because of its small size.

The results obtained in this study are consistent with the hypothesis of a differential effect of the upwelling in the Rías Altas when compared to the Rías Baixas. In the latter, the upwelling dynamics cause an export of the organic matter produced inside the rias to nearby shelf areas, that display sediments enriched in organic matter (López-Jamar *et al.*, 1992). In the Rías Altas, the irregular distribution of upwelling pulses over the shelf could be responsible for the low organic content (López-Jamar *et al.*, 1992) and the distribution of biogenic silica (Prego and Bao, 1997) of shelf sediments in this area. There is evidence of low sedimentation of particulate matter near the coast of La Coruña during active upwelling pulses (Bode *et al.*, 1998). Most of the produced organic matter could either be exported to offshore areas by the dominant surface circulation or remineralized in the water column (Bode and Varela, 1994).

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