Hydrobiologia **341**: 225–234, 1996.

Phytoplankton biomass and production in shelf waters off NW Spain: spatial and seasonal variability in relation to upwelling

Antonio Bode[1], Benita Casas[1], Emilio Fernández[2], Emilio Marañón[3], Pablo Serret[3] & Manuel Varela[1]
[1]*Instituto Español de Oceanografía, Apdo 130, E15080, la Coruña, Spain*
[2]*Facultad de Ciencias del Mar, Universidad de Vigo, Spain*
[3]*Unidad de Ecologia, Departamento de Biologia de Organismos y Sistemas, Universidad de Oviedo, Spain*

Received 16 February 1996; in revised form 5 November 1996; accepted 12 December 1996

Key words: Phytoplankton, biomass, upwelling, seasonal pattern, N-NW Spain

Summary

Chlorophyll-*a* and primary production on the euphotic zone of the N-NW Spanish shelf were studied at 125 stations between 1984 and 1992. Three geographic areas (Cantabrian Sea, Rías Altas and Rías Baixas), three bathymetric ranges (20 to 60 m, 60 to 150 m and stations deeper than 200 m), and four oceanographic stages (spring and autumn blooms, summer upwelling, summer stratification and winter mixing) were considered. One of the major sources of variability of chlorophyll and production data was season. Bloom and summer upwelling stages have equivalent mean and maximum values. Average chlorophyll-*a* concentrations approximately doubled in every step of the increasing productivity sequence: winter mixing – summer stratification – high productivity (upwelling and bloom) stages. Average primary production rates increased only 60% in the described sequence. Mean ($\pm$ sd) values of chlorophyll-*a* and primary production rates during the high productivity stages were 59.7 ± 39.5 mg Chl-*a* m^{-2} and 86.9 ± 44.0 mg C m^{-2} h^{-1}, respectively. Significant differences in both chlorophyll and primary production resulted between geographic areas in most stages. Only 27 stations showed the effects of the summer upwelling that affected coastal areas in the Cantabrian Sea and Rías Baixas shelf, but also shelf-break stations in the Rías Altas area. The Rías Baixas area had lower chlorophyll than both the Rías Altas and the Cantabrian Sea areas during spring and autumn blooms, but higher during summer upwelling events. On the contrary, primary production rates were higher in the Rías Baixas area during blooms in spring and autumn. Mid-shelf areas showed the highest chlorophyll concentrations during high productivity stages, probably due to the existence of frontal zones in all geographic areas considered. The estimated phytoplankton growth rates were comparable to those of other coastal upwelling systems, with average values lower than the maximum potential growth rates. Doubling rates for upwelling and stratification stages in the northern and Rías Altas shelf areas were equivalent, despite larger biomass accumulations during upwelling events. Low turnover rates of the existing biomass in the Rías Baixas shelf in upwelling stages suggests that the accumulation of phytoplankton was due mainly to the export from the highly productive rías, while the contribution of *in situ* production to these accumulations was relatively lower.

Introduction

The seasonal upwelling system off the N and NW Spanish shelf is considered an important source of inorganic nutrients for primary production in that area (Blanton et al., 1984; Varela, 1992; Tenore et al., 1995). Cold, nutrient-rich deep waters have been detected near the surface in discrete observations throughout the period between March and November, especially in the north-western shelf (Fraga, 1981; Fraga et al., 1982; Rios et al., 1987; Varela & Costas, 1987; Varela et al., 1987a, b, 1988, 1991; Valdés et al., 1991; Alvarez-Salgado et al., 1993; Castro et al., 1994; Tenore et al., 1995). Observations of upwelling events for the northern shelf (Cantabrian Sea, Southern Bay of Biscay) are more scarce (Dickson & Hughes, 1981; Botas et al., 1990), and suggest that in this region the vertical advection of deep water is somehow related to the intensity of the upwelling in the NW shelf, where lower surface temperatures occurred.

During the thermal stratification period (May to September), upwelling modifies the vertical structure of the water column, affecting phytoplankton distributions in relation to the gradients of temperature and nutrients (Varela et al., 1987a, b, 1991; Botas et al., 1990). In contrast, upwelling events during spring and autumn are influenced by local circulation patterns caused by poleward currents flowing parallel to the shelf-break (Frouin et al., 1990). These currents can have a major influence on the development of phytoplankton blooms normally occurring in temperate coastal seas, as reported for the Cantabrian coast (Botas et al., 1988; Bode et al., 1990; Fernández et al., 1991, 1993).

Coastal waters of NW Spain receive important inputs of exported nutrients and organic matter produced in the rías (Tenore et al., 1982, 1995; Lopez-Jamar et al., 1992). Biological productivity in the rías is enhanced by the combined effect of nutrient-rich water entering from the sea during upwelling events and local circulation (Tenore et al., 1982; Blanton et al., 1984; Figueiras et al., 1985). There are some references to the high primary productivity levels inside the rías, particularly in relation to the intense mussel aquaculture (e.g. Varela et al., 1984 and references therein). However, there are far less data on phytoplankton productivity and biomass in open shelf areas (Varela, 1992; Bode et al., 1994a; Casas, 1995).

The objectives of this paper are three. First, to summarize the existing information on simultaneous measurements of primary productivity and biomass in the area affected by the coastal upwelling. Second, to study the patterns of seasonal and spatial variability in chlorophyll-biomass and phytoplankton carbon production in relation to upwelling in different areas of the shelf. Finally, we will compare the observed primary production and estimated phytoplankton growth rates from high production stages in diverse areas of the N-NW Spanish shelf with other coastal upwelling areas.

Material and methods

Figure 1 shows the position of the stations in which phytoplankton biomass and primary production were studied between 1984 and 1992. Details of sampling

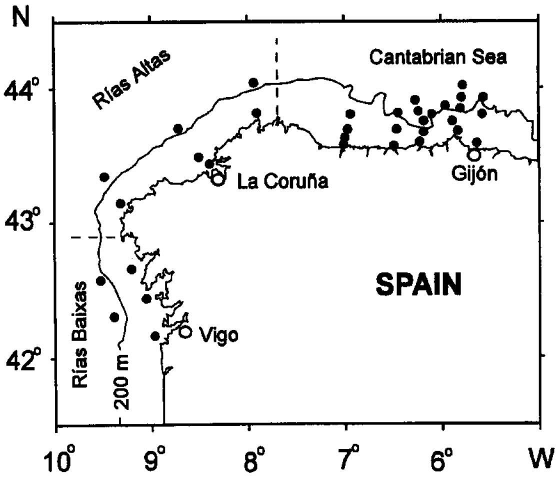

Figure 1. Location of stations studied.

and hydrographic data sources are listed in Table 1. Samples were grouped according to their geographical procedence: Cantabrian Sea, Rías Altas and Rías Baixas, and the depth of the station. Three bathymetric ranges were considered: coastal (20 to 60 m depth), mid-shelf (60 to 150 m) and outer-shelf (stations deeper than 200 m).

Temperature and salinity were measured with CTD probes (cruises on the western shelf) or an induction salinometer calibrated with Standard Seawater (cruises in the Cantabrian Sea). Dissolved nutrient concentrations were determined with an autoanalyser (Grasshoff et al., 1983). Photosynthetically available radiation (PAR) was measured with a submersible quantum sensor. Chlorophyll-*a* concentrations were measured fluorometrically on 90% acetone extracts of particulate material (Parsons et al., 1984). Primary production rates were determined at 5 to 7 selected depths, using *in situ* or *in situ* simulated conditions (Table 1) on duplicate 100 to 250 ml samples inoculated with $NaH^{14}CO_3$. Average ^{14}C additions were 4 μCi ^{14}C in the western shelf cruises and 4 to 10 μCi ^{14}C in the Cantabrian Sea cruises. Simulated *in situ* incubations were carried out using neutral density screens to simulate 5 to 7 light levels, corresponding to those received by the cells at the sampling depths. Incubations were made around noon and lasted from 2 to 4 h. Filters employed for chlorophyll and primary production determinations were listed in Table 1. Corrections for dark uptake of carbon were made only in the western shelf cruises. This correction can reduce primary production values by 30% during low productivity periods (Fernández &

Table 1. Source and methodological characteristics of data used in this study.

Cruise	Dates	Area*	Filter** Chl-*a*	Filter** Prod	Incubation type	Reference
BREOGAN-684	Jun 1984	RA, RB	M0.8	M0.8	'in situ'	Varela et al. 1987a; 1988
BREOGAN-984	Sep 1984	RA, RB	M0.8	M0.8	'in situ'	Varela et al. 1987b
BREOGAN-785	Jul 1985	RA, RB	M0.8	M0.8	'in situ'	Varela et al. 1991
BREOGAN-486	Mar–Apr 1986	RA, RB	M0.8	M0.8	'in situ'	unpubl. data
COCACE	Jan–Dec 1987	CA	GF/C	M0.8	'in situ'	Fernandez & Bode, 1991
ASFLOR-I	Aug 1989	CA	GF/F	GF/F	'in situ' simul.	Anadon et al. 1991
ASFLOR-II	Jul 1990	CA	GF/F	GF/F	'in situ' simul.	unpubl. data
La Coruña transect	Jan 1991– Dec 1992	RA	M0.8	M0.8	'in situ' simul.	Casas, 1995
Asturias transect	Aug 1991	CA	GF/F	GF/F	'in situ' simul.	unpubl. data

* CA: Cantabrian Sea; RA: Rias Altas; RB: Rias Baixas.
* M0.8: Millipore cellulose -membrane filter 0.8 μm pore-size; GF/C: Whatman GF/C glass-fiber filters; GF/F: Whatman GF/F glass-fiber filters.

Bode, 1993). All chlorophyll and production values were integrated in the euphotic zone for each station.

Primary production to biomass ratios were estimated for the main stages and areas using average chlorophyll and carbon incorporation values. Chlorophyll-*a* was converted to carbon using a mean factor of 50 g C (g Chl-*a*)$^{-1}$. Minimum and maximum range values were computed considering ratios of 40 and 75 g C (g Chl-*a*)$^{-1}$, respectively. The measured hourly carbon fixation rates were extrapolated to daily rates by assuming an effective daylength of 14 h in summer, 12 h during spring and autumn, and 9 h in winter. These values for daylength were average values measured at the Observatorio Meteorológico de Oviedo (Instituto Español de Meteorología). Maximum expected growth rates were calculated with the equation of Eppley (1972):

$$\log_{10} d = 0.0275t - 0.070,$$

where d is the doubling time (inverse of growth rate), and t is the ambient (water) temperature.

Significance of the differences between spatial and temporal classifications were tested using analysis of variance (anova) methods (Sokal & Rohlf, 1981), using logarithmic transformations of chlorophyll and production values. Due to the lack of data in certain combinations of oceanographic stages and areas a full nested anova design to obtain a complete partition of variance into seasonal, geographical and bathymetric zone components was not possible. We used single classification anova to test for seasonal differences, and nested anovas of spatial groups within oceanographic stages in the study of spatial components of variance.

Results

Oceanographic stages

The observations were classified in distinct oceanographic stages taking into account the vertical structure of the water column, chlorophyll and nutrient concentrations and the composition of phytoplankton. A more detailed description of these stages can be found in Casas (1995) and Casas et al. (in press). The main characteristics of the water column during these stages are illustrated in Figure 2, using data from a coastal station near La Coruña. The bloom stage corresponds to stations studied during spring and autumn showing mean chlorophyll-*a* concentrations higher than 1 mg m^{-3} in most of the euphotic zone and weak vertical water density gradients. Nutrient concentrations are usually low in the upper layer. The samples classified as upwelling are summer cases that showed cold (<15 °C) and nutrient-rich water (>5 mmol NO_3^- m^{-3}) near the surface. In these cases, chlorophyll maxima are usually higher than 2 mg m^{-3} and are located closer to the surface than in other situations. The water column may display some degree of thermohaline stratification at the surface, as the case illustrated in Figure 2, but the position of the thermocline and nitracline indicated the recent ascent of cold and nutrient rich water. All summer samples that did not show upwelling characteristics and with chlorophyll concentrations lower than 2 mg m^{-3} were classified in the stage named stratification. Surface temperatures were generally higher than 16 °C and decreased to about 13 °C in the subsurface layer. However, the shape of

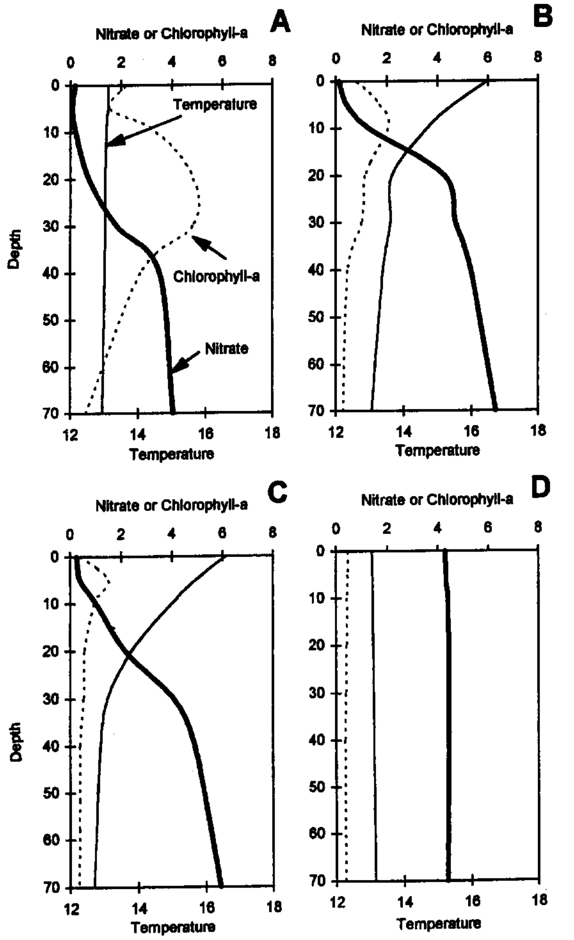

Figure 2. Vertical profiles of temperature (°C), chlorophyll-*a* (mg m^{-3}) and nitrate (mmol m^{-3}) measured at a coastal station near La Coruña on selected dates representative of each oceanographic stage considered. Depth is expressed in meters. A: 18 March 1992, spring bloom. B: 13 July 1992, summer upwelling. C: 29 August 1991, stratification. D: 22 January 1992, winter.

the vertical profiles of temperature and nitrate indicated that mixing between the upper and subsurface layers occurs frequently. Finally, stations showing a completely mixed water column, including some samples of spring and autumn with low chlorophyll concentrations, were grouped in the winter stage.

The phytoplankton composition of these stages indicates the importance of moderate mixing in the upper water layers during the year because most of the dominant species, excluding microflagellates and small dinoflagellates, are diatoms (Table 2). Chain-forming species are characteristic of the bloom stage, that may be dominated by large numbers of *Chaetoceros socialis* and generally shows a higher species

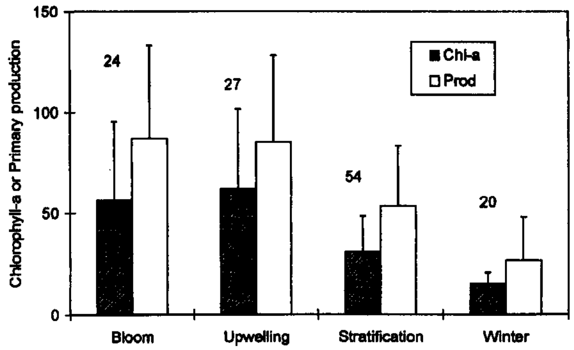

Figure 3. Mean (± sd) euphotic-zone integrated chlorophyll-*a* (mg Chl-*a* m^{-2}) and primary production (mg C m^{-2} h^{-1}) in selected oceanographic stages. Number of cases appear above each bar.

richness that summer upwelling blooms (Casas, 1995, Casas et al., in press). In the latter cases, diatom species with small cells dominated but other groups, like the Chrysophycean *Phaeocystis pouchetii*, may reach significant abundances. Even when they are reduced by comparison to the upwelling stage, the dominance of diatoms extends to the stratification stage, where they overcome dinoflagellates and large flagellates. The winter stage is characterised by mostly perennial species with low abundances.

Temporal variation

Seasonal variations are a major component of variability in chlorophyll-*a* and primary production rates off the NW coast of Spain. The mean values calculated for the selected stages (Figure 3) were significantly different, indicating that the *a priori* classification of samples was appropriate ($F = 28.94$, $p < 0.0001$). Multiple comparisons between means revealed that differences in both chlorophyll and production between bloom and upwelling stages were not statistically significant (Student-Neuman-Keuls test, $p > 0.05$), but there were clear differences between these and the remaining stages. Average chlorophyll concentrations during the stratification stage were approximately twice the values of the winter stage, and half of the mean value of the high productivity stages (bloom and upwelling). Mean (± sd) values of chlorophyll-*a* and primary production rates during the high productivity stages were 59.7 ± 39.5 mg Chl-*a* m^{-2} and 86.9 ± 44.0 mg C m^{-2} h^{-1} respectively, while values for the low productivity stages (stratification and winter) were 22.94 ± 18.56 mg Chl-*a* m^{-2} and 40.00 ± 36.99 mg C m^{-2} h^{-1}.

Table 2. Mean, upper (hi) and lower (lo) 95% confidence limits of abundance (cells ml^{-1}) of the dominant phytoplankton species in the considered oceacenographic stages (see text). *n*: number of samples. Data are from a coastal station near La Coruña. Microflagellates and small dinoflagellates (< 30 μm) were excluded.

Stage	Species	Mean	hi	lo	*n*
Bloom	*Chaetoceros socialis*	70.0	105.4	35.6	64
	Lauderia borealis	6.3	22.6	0.0	64
	Nitzschia pungens	6.0	16.1	0.0	64
	Rhizosolenia delicatula	5.1	15.0	0.0	64
	Schoeredella delicatula	3.8	15.3	0.0	64
Upwelling	*Nitzschia pungens*	18.5	35.1	2.8	68
	Leptocylindrus danicus	8.1	25.2	0.0	68
	Rhizosolenia delicatula	7.8	24.4	0.0	68
	Chaetoceros socialis	6.4	33.8	0.0	68
	Phaeocystis pouchetii	5.8	18.7	0.0	68
Stratification	*Leptocylindrus danicus*	7.7	23.4	0.0	46
	Chaetoceros spp.	4.3	15.1	0.0	46
	Chaetoceros didymus	4.2	17.1	0.0	46
	Massartia spp.	4.1	14.4	0.0	46
	Phaeocystis pouchetii	4.1	18.1	0.0	46
Winter	*Nitzschia pungens*	2.9	11.2	0.0	180
	Nitzschia longissima	2.9	8.8	0.0	180
	Skeletonema costatum	2.9	10.8	0.0	180
	Chaetoceros socialis	2.5	10.4	0.0	180
	Rhizosolenia delicatula	2.4	9.0	0.0	180

Although most of the cruises considered in this study were made during the upwelling season, only a small fraction of samples (27 of 125) showed clear upwelling characteristics. We studied variations within the upwelling stage samples by means of a distinction of two additional stages: the initial stage, with high nutrients and lower surface temperature, and the final stage, with the opposite conditions. Mean ($\pm$ sd) values of chlorophyll-*a* for the initial and final upwelling stages were 50.99 ± 28.46 mg Chl-*a* m^{-3} ($n = 10$) and 69.95 ± 43.85 mg Chl-*a* m^{-3} ($n = 17$), respectively. Primary production rates were 90.79 ± 44.57 mg C m^{-3} h^{-1} during the initial stage and 82.21 ± 42.41 mg C m^{-3} h^{-1} during the final stage. However, no significant differences between the two stages resulted for either chlorophyll-*a* nor primary production because of their high variances (Mann-Whitney test, $p > 0.05$).

Spatial variation

The geographical location of sampling was an important contribution to added variance in both chlorophyll and primary production values (Table 3). Figure 4 shows the variance partition of both variables in seasonal (stage) and geographic (area) components using a nested anova, with the area component as the nested factor. Samples corresponding to the winter stage were excluded because there was no data for the Rías Baixas area. In this case, seasonality made a relatively low contribution to variation in chlorophyll-a values and primary production rates, while geographic location was responsible for near 90% of the variance. The mean values of Table 3 show that the Rías Baixas area had higher production rates during the bloom stage but also had the lowest rates during the stratification stage. The Rías Altas area had intermediate production rates in all stages, but mean chlorophyll-*a* concentrations were higher than in the other areas during bloom and stratification stages. However, the inclusion of winter samples may enhance the contribution of seasonality to total variance because of the low values expected in this stage (Figure 3).

Another major source of variability in chlorophyll and primary production values was the depth of the stations sampled and their position relative to the coast. Apart from the evident seasonal variability, there was

Table 3. Mean (± sd) chlorophyll-*a* (Chl-*a*, mg m^{-2}) and primary production (Prod, mg m^{-2} h^{-1}) values for the different areas and oceanographic stages. Number of cases appear in brackets.

Area	Bloom	Upwelling	Stratification	Winter
Chlorophyll-*a*				
Cantabrian	49.33 ± 19.29	40.72 ± 14.32	25.33 ± 10.85	15.64 ± 7.52
	(7)	(4)	(27)	(9)
Rias Altas	67.68 ± 49.49	57.84 ± 41.86	37.55 ± 24.44	15.64 ± 3.80
	(13)	(16)	(15)	(11)
Rias Baixas	32,8,4 ± 10.50	87.11 ± 34.04	35.53 ± 20.45	–
	(4)	(7)	(12)	
Primary production				
Cantabrian	93.11 ± 50.66	96.13 ± 45.84	57.54 ± 30.31	38.07 ± 25.07
	(7)	(4)	(27)	(9)
Rias Altas	77.43 ± 43.80	80.17 ± 46.86	56.00 ± 34.47	17.29 ± 11.87
	(13)	(16)	(15)	(11)
Rias Baixas	110.75 ± 43.65	91.18 ± 33.54	41.48 ± 25.57	–
	(4)	(7)	(12)	

Table 4. Mean (± sd) euphotic-zone integrated chlorophyll-*a* (Chl-*a*, mg m^{-2}) and primary production (Prod, mg m^{-2} h^{-1}) values for three bathymetric zones (Coastal, Mid-shelf and Outer-shelf) and oceanographic stages (Bloom, Upwelling, Stratification and Winter). Number of cases appear in brackets.

Area	Bloom	Upwelling	Stratification	Winter
Chlorophyll-*a*				
Coastal	43.13 ± 21.23	62.36 ± 36.40	33.21 ± 21.26	15.33 ± 8.79
	(9)	(17)	(16)	(5)
Mid-shelf	82.70 ± 52.23	65.09 ± 55.29	32.25 ± 19.39	15.17 ± 4.19
	(9)	(7)	(14)	(12)
Outer-shelf	37.35 ± 12.33	60.76 ± 19.30	28.66 ± 16.04	18.03 ± 6.10
	(6)	(3)	(24)	(3)
Primary production				
Coastal	97.83 ± 53.13	83.88 ± 43.05	59.78 ± 34.74	21.42 ± 13.94
	(9)	(17)	(16)	(5)
Mid-shelf	90.25 ± 44.16	95.88 ± 44.80	65.44 ± 30.73	29.38 ± 25.25
	(9)	(7)	(14)	(12)
Outer-shelf	68.11 ± 34.67	69.43 ± 43.85	42.67 ± 24.85	24.38 ± 16.46
	(6)	(3)	(24)	(3)

a significant component of added variance due to the zone component when data form all geographic areas were combined (anova, $p<0.001$). Table 4 displays mean values for all combinations of stages and zones, indicating higher chlorophyll concentrations in the mid-shelf zone during high production stages. Chlorophyll concentrations in the outer-shelf zone were generally lower than in stations close to the coast. However, the pattern exhibited by primary production rates was more variable, with higher rates near the coast during the bloom stage and in the mid-shelf zone in all other stages.

Phytoplankton growth rates

Doubling rates of the existing biomass may allow for comparison between different upwelling systems (e.g. Brown et al., 1991). The values calculated with our

Table 5. Estimations of phytoplankton carbon doubling rates for the studied area and stages using average water column integrated values of chlorophyll-*a* and primary production. Values are in days. Maximum and minimum values appear in brackets.

Area	Bloom	Upwelling	Stratification	Winter
Cantabrian	2.41	1.51	1.57	2.29
	(1.93–3.61)	(1.21–2.27)	(1.26–2.36)	(1.83–3.42)
Rias Altas	3.97	2.58	2.40	5.03
	(3.18–5.96)	(2.06–3.87)	(1.92–3.59)	(4.02–7.54)
Rias Baixas	1.35	3.41	3.06	–
	(1.08–2.02)	(2.73–5.12)	(2.45–4.59)	–

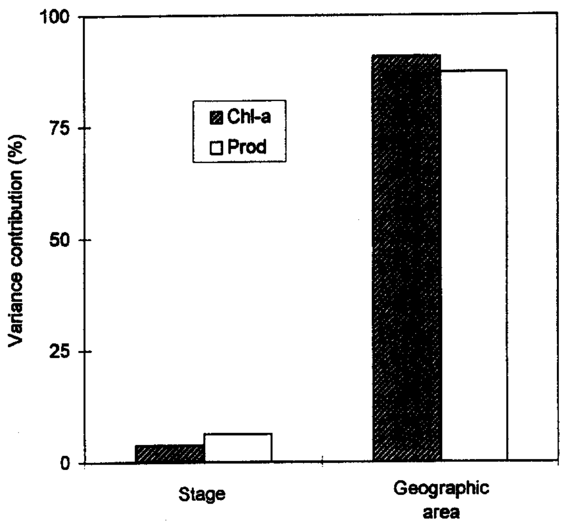

Figure 4. Relative contribution of temporal (Stage) and spatial (Geographic area) factors to total variance in water-column integrated chlorophyll-*a* (Chl-*a*) and primary production (Prod).

data indicated that the areas of higher phytoplankton growth vary seasonally (Table 5). The lowest doubling rates were found in the Rías Baixas area during the bloom stage, but low values were found also in the Cantabrian Sea and Rías Altas area during upwelling and stratification stages, when phytoplankton growth in the Rías Baixas area was relatively slow.

The average growth rates calculated for the upwelling stage resulted lower than the expected maximum growth rates. The temperature of surface waters in the studied area ranged between 13 and 20 °C and the corresponding maximum phytoplankton doubling rates between 1.94 and 3.03 days, respectively. With a mean temperature of surface water of 15 °C during upwelling events, the expected growth rate is 2.22 days. The estimated rates during upwelling events in our study area range from 1.21 days in the Cantabrian Sea to 5.11 days in the Rías Baixas area. Another interesting feature of the estimations displayed in Table 5 is that doubling rates computed for the stratification stage resulted sometimes comparable or higher than those of upwelling and bloom stages.

Discussion

Upwelling areas have an extraordinary biological importance because they allow for primary production rates that exceed those of stratified, low-nutrient waters. In recent years, they have received special attention as they have been suggested as potential sinks or sources of CO_2 (Siegenthaler, 1990). The primary production rates observed in our study are within the range obtained in other upwelling areas, like Benguela (40–340 mg C m^{-2} h^{-1}, Shannon & Field, 1985; Estrada & Marrasé, 1987; Brown et al., 1991), but lower than those cited in other systems (e.g. up to 1000 mg C m^{-2} h^{-1} in the Peru upwelling; Ryther et al., 1971). However, comparison of mean values or ranges can be misleading. Upwelling events are known to be very dynamic features, modifying water-column properties and plankton communities during short time scales (Blasco et al., 1981). Productivity and biomass is generally low during stages of intense water-mixing, when nutrient concentrations are high, and increases in stages or areas of moderate turbulence (Margalef & Estrada, 1981). There are some evidences of day-to-day variations in planktonic biomass and productivity associated with upwelling and downwelling phenomena in the studied area (Varela et al., 1991; Tenore et al., 1995). This feature deserves much larger attention in future studies, because variations in both physical and biological characteristics in short time and space scales may have important implications for the fate of the phytoplanktonic biomass produced by upwelling events. One major question in relation to this subject is the determination of the capability of this upwelling to export organic matter out of the euphotic zone, and its variations in the different geographic areas. Using estimates based on biomass of planktonic organisms in this area, Bode & Varela (1994) have estimated that up to 50% of the nitrogen required daily for primary production after an upwelling event in the Rías Altas area may be provided by heterotrophic processes in the water column.

Apart from the rías, most of the upwelling cases recorded in the NW Spanish shelf were close to the coast (Varela & Costas, 1987; Varela et al., 1987a, b, 1988; Valdés et al., 1991; Castro et al., 1994; Tenore et al., 1995; Casas, 1995). However, in some instances the upwelling was observed in mid- and outer shelf-areas (Varela et al., 1991; Bode et al., 1994b). A large variety of fronts can be expected in these areas (e.g. Holligan, 1981), and the characteristics and biological implications of some of them in the Cantabrian Sea have been already described (Botas et al., 1988; Bode et al., 1990, Fernández et al., 1991, 1993). Large, and possibly permanent frontal systems, have been reported for the boundaries between the three geographic areas considered. Fraga et al. (1982) and Ríos et al. (1992) recognized a distinct off-shore surface circulation pattern and a permanent subsurface front off Cape Finisterre, between the Rías Altas and the Rías Baixas areas. Castro et al. (1994) found a convergent front in the mid-shelf after an upwelling event close to this coast. Similarly, there are evidences of similar fronts off Cape Ortegal, between the Rías Altas area and the Cantabrian Sea (Díaz del Rio et al., 1992). The extent of these fronts can determine the input of surface waters from the Central Atlantic into the southern Bay of Biscay (Pingree & Le Cann, 1990; Pingree, 1993). However, the biological implications of such fronts in the NW coast of Spain have been scarcely studied (e.g. Varela et al., 1991; Bode et al., 1994b).

The estimated doubling rates of phytoplankton biomass for the Cantabrian Sea resulted in general higher than those for the western part of the region. Methodological differences may account for part of this discrepancy, since no substraction of dark bottle counts have been applied to the Cantabrian Sea data. Fernández and Bode (1993) have shown that dark bottle substraction may underestimate primary production rates during phases of slow growth, like the winter stage. On the other hand, underestimation of biomass or primary production values due to the use of glass-fiber GF/C filters or membrane filters of 0.8 μm pore-size filters was less likely because the phytoplankton cells and colonies of this area are predominantly larger than 12 μm (Bode et al., 1994a).

Low biomass turnover rates in the Rías Baixas area during upwelling events in summer are in agreement with the hypothesis that coastal areas in this region receive important inputs of phytoplankton and particulate organic matter from the nearby rías (Fraga, 1981; Alvarez-Salgado et al., 1993; Perez et al., 1993). The high amounts of phytoplankton biomass produced inside these shallow, protected environments (Varela et al., 1984) is effectively exported to coastal areas, where local circulation patterns may determine its accumulation near the coast or further export to other shelf areas (Lopez-Jamar et al., 1992). Our data suggest that *in situ* production in coastal areas near the Rías Baixas is low compared to production in other shelf areas, despite of the presence of additional nutrients regenerated inside the rías than can be released with the outflow (Tenore et al., 1982; Alvarez-Salgado et al., 1993) and *in situ* regeneration (Mourino et al., 1984; Iglesias et al., 1984).

The comparison of phytoplankton productivity values computed for different time-scales reveals that these calculations may have an important effect in the estimation of the impact of the high productivity events in the pelagic ecosystem. Although hourly production rates for bloom and upwelling stages were comparable, the extrapolation to daily rates, which takes into account the effective daylength, indicates that upwelling episodes produced during summer produce higher biomasses. The fact that chlorophyll concentrations were similar for bloom and upwelling stages may be explained by a close coupling between primary producers and consumers or, alternatively, by hydrographic mechanisms favouring sedimentation of recently produced organic material during summer upwelling events. Relatively high mesozooplankton biomasses have been reported in the area during stages of weak upwelling (Valdés et al., 1991; Varela et al., 1991). In addition, microbial-loop consumers can potentially remove a large fraction of the daily primary production after an upwelling event in the Rías Altas area (Bode & Varela, 1994). On the other hand, there are reports of downwelling occurring shortly after the maximum productivity phase during upwelling events (Blanton et al., 1984; Varela et al., 1991). The rapid sinking of surface water may enhance the effective sedimentation of the produced material out of the euphotic zone (Varela et al., 1991). Probably both mechanisms occurred in this area, but they may operate over different time and space scales. Biological regeneration of nutrients might be expected when stable, stratified water column conditions are maintained for several days to weeks, after an upwelling pulse.

Acknowledgments

We are indebted to the various scientists, technicians and ship-crews that collaborated in the measurements taken at sea and in laboratory analysis during all these years. We thank the Observatorio Meteorológico de Oviedo (Instituto Español de Meteorologia) for the data of effective daylenght. R. Carballo and A. Botas, provided hydrographic and chemical data, and J. Lorenzo assisted with sampling and graph drawing. BREOGAN cruises were funded by the Joint Spanish-USA Program FOG CCA83/023 and the Instituto Español de Oceanografia (IEO). COCACE cruises were funded by Hidroeléctrica del Cantábrico S.A. and the Universidad de Oviedo. ASFLOR cruises were supported by CICYT grant MAR88-0408 to the Universidad de Oviedo. The continued sampling at La Coruña and Asturias transects is supported by IEO Program 1007. This paper was prepared in part with funds of the project CICYT AMB93/0014. B.C., E.M. and P.S. received PFPI fellowships from the Ministerio de Educación y Ciencia (Spain).

References

Alvarez-Salgado, X. A., G. Rosón, F. F. Pérez & Y. Pazos, 1993. Hydrographic variability off the Rías Baixas (NW Spain) during the upwelling season. J. Geophys. Res., 98 (C8): 14447–14455.

Anadón, R., E. Fernández, A. Botas, A. Bode, P. Serret, J. L. Acuña, J. Cabal, J. Sostres & F. Alvarez-Marqués, 1991. Datos básicos de la campaña 'ASFLOR I'. Biobas. Revta. Biol. Univ. Oviedo (Suppl.) 5: 1–36.

Blanton, J. O., L. P. Atkinson, F. Fernández de Castillejo & A. Lavin Montero, 1984. Coastal upwelling off the Rías Bajas, Galicia, Northwest Spain. I. Hydrographic studies. Rapp. P-V. Reun. Cons. int. Explor. Mer 183: 79–90.

Blasco, D., M. Estrada & B. H. Jones, 1981. Short time variability of phytoplankton populations in upwelling regions. The example of northwest Africa. In: F. A. Richards (ed.), Coastal Upwelling. American Geophysical Union, Washington DC: 339–347.

Bode, A. & M. Varela, 1994. Planktonic carbon and nitrogen budgets for the N-NW Spanish shelf: The role of pelagic nutrient regeneration during upwelling events. Scient. Mar. 58: 131–141.

Bode, A., B. Casas & M. Varela, 1994a. Size-fractionated primary productivity and biomass in the Galician shelf (NW Spain): Netplankton versus nanoplankton dominance. Scient. Mar 58: 131–141.

Bode, A., E. Fernández, A. Botas & R. Anadón, 1990. Distribution and composition of suspended particulate matter related to a shelf-break saline intrusion in the Cantabrian Sea (Bay of Biscay). Oceanol. Acta 3: 219–228.

Bode, A., M. Varela, E. Fernández, B. Arbones, N. Gonzalez, R. Carballo, M. T. Alvarez-Ossorio, R. Anadón & S. Baquero. 1994b. Biological characteristics of the plankton associated to a shelf-break front off the Galician coast. Gaia 8: 9–18.

Botas, J. A., A. Bode, E. Fernández & R. Anadón, 1988. Descripción de una intrusión de agua de elevada salinidad en el Cantábrico Central: distribución de los nutrientes inorgánicos y su relación con el fitoplancton. Invest. Pesq. 52: 559–572.

Botas, J. A., E. Fernández, A. Bode & R. Anadón, 1990. A persistent upwelling off the Central Cantabrian Coast (Bay of Biscay). Estuar. Coast. Shelf Sci. 30: 185–199.

Brown, P. C., S. J. Painting & K. L. Cochrane, 1991. Estimates of phytoplankton and bacterial biomass and production in the northern and southern Benguela ecosystems. S. Afr. J. Mar. Sci. 11: 537–564.

Casas, B., 1995. Composición, biomasa y producción del fitoplancton en la costa de La Coruña: 1989–1992. Ph. D. Thesis. Universidad de Santiago de Compostela: 340 pp.

Casas, B., M. Varela, M. Canle, N. González & A. Bode, 1997. Seasonal variations of nutrients, seston and phytoplankton, and upwelling intensity off La Coruña (NW Spain). Estuar. Coast. Shelf. Sci.

Castro, C. G., F. F. Pérez, X. A. Alvarez-Salgado, G. Rosón & A. F. Ríos, 1994. Hydrographic conditions associated with the relaxation of an upwelling event off the Galician coast (NW Spain). J. Geophys. Res. 99 (C3): 5135–5147.

Diaz Del Rio, G., J. Alonso, M. J. García Fernández, J. M. Cabanas & J. Molinero, 1992. Estudio dinámico de la plataforma continental del norte de Galicia (Abril–Junio 1991). Inf. Téc. Inst. Esp. Oceanogr. 34: 1–23.

Dickson, R. R. & D. G. Hughes, 1981. Satellite evidences of mesoscale eddy activity over the Biscay abyssal plain. Oceanologica Acta 4: 43–46.

Eppley, R. W., 1972. Temperature and phytoplankton growth in the sea. Fishery Bull., Wash. 70: 1063–1085.

Estrada, M. & C. Marrasé, 1987. Phytoplankton biomass and productivity off the Namibian coast. S. Afr. J. Mar. Sci. 5: 347–356.

Fernández, E. & A. Bode, 1991. Seasonal patterns of primary production in the Central Cantabrian Sea (Bay of Biscay). Sci. Mar. 55: 629–636.

Fernández, E. & A. Bode, 1993. Seasonal patterns of dark carbon incorporation by natural phytoplankton in the Central Cantabrian Sea (Bay of Biscay). P.S.Z.N.I.: Mar. Ecol. 14: 175–183.

Fernández, E., A. Bode, A. Botas & R. Anadón, 1991. Microplankton assemblages associated with saline fronts during a spring bloom in the central Cantabrian Sea: differences in trophic structure between water bodies. J. Plankton Res. 13: 1239–1256.

Fernández, E., J. Cabal, J. L. Acuña, A. Bode, A. Botas & C. García-Soto, 1993. Plankton distribution across a slope-current induced front in the southern Bay of Biscay. J. Plankton Res. 15: 619–641.

Figueiras, F. G., F. X. Niell & M. Zapata, 1985. Hidrografia de la Ria de Pontevedra (NO de España) con mención especial al banco de Placeres. Invest. Pesq. 49: 451–472.

Fraga, F., 1981. Upwelling off the Galician Coast, Northwest Spain. In F. A. Richards (ed.), Coastal upwelling. American Geophysical Union, Washington, DC 176–182.

Fraga, F., C. Mouriño & M. Manriquez, 1982. Las masas de agua en la costa de Galicia: junio–octubre. Res. Exp. Cient. 10: 55–77.

Frouin, R., A. Fiuza, I. Ambar & T. J. Boyd, 1990. Observations of a poleward surface current off the coasts of Portugal and Spain during winter. J. Geophys. Res., 95 (C1): 679–691.

Grasshoff, K., M. Ehrhardt & K. Kremling, 1983. Methods of seawater analysis. 2nd edn. Verlag Chemie, Weinheim: 419 pp.

Holligan, P. M., 1981. Biological implications of fronts on the northwest European continental shelf. Phil. Trans. r. Soc. Lond. A302: 547–562.

Iglesias, M. L., N. Gonzalez, J. M. Cabanas & T. Nunes, 1984. Condiciones oceanográficas de las Rías Bajas gallegas y de la plataforma adyacente. Cuadernos da Area de Ciencias Mariñas. Seminario de Estudos Galegos 1: 107–118.

Lopez-Jamar, E., R. M. Cal, G. Gonzalez, R. B. Hanson, J. Rey, G. Santiago & K. R. Tenore, 1992. Upwelling and outwelling effects on the benthic regime of the continental shelf off Galicia, NW Spain. J. Mar. Res. 50: 465–488.

Margalef, R. & M. Estrada, 1981. On upwelling, eutrophic lakes, the primitive biosphere, and biological membranes. In F. A. Richards (ed.), Coastal Upwelling. American Geophysical Union, Washington DC: 522–529.

Mouriño, C., F. Fraga & F. Fernández, 1984. Hidrografia de la Ría de Vigo. 1979–1980. Cuadernos da Area de Ciencias Mariñas. Seminario de Estudos Galegos 1: 91–106.

Parsons, T. R., Y. Maita & C. M. Lalli, 1984. A manual of chemical and biological methods for seawater analyses. Pergamon Press, Oxford: 173 pp.

Pérez, F. F., C. Mouriño, F. Fraga & A. F. Ríos, 1993. Displacement of water masses and remineralization rates off the Iberian Peninsula by nutrient anomalies. J. Mar. Res. 51: 869–892.

Pingree, R. D., 1993. Flow of surface waters to the west of the British Isles and in the Bay of Biscay. Deep-Sea Res. 40: 369–388.

Pingree, R. D. & B. Le Cann, 1990. Structure, strenght and seasonality of the slope currents in the Bay of Biscay region. J. Mar. Biol. Ass. UK 70: 857–885.

Ríos, A., F. Fraga, F. G. Figueiras, R. Prego & F. F. Perez, 1987. Campañas oceanográficas 'Asturias I, II, III y IV'. Datos informativos Instituto Investigaciones Marinas, Vigo: 22: 1–140.

Ríos, A. F., F. F. Perez & F. Fraga, 1992. Water masses in the upper and middle North Atlantic Ocean east of the Azores. Deep-Sea Res. 39: 645–658.

Ryther, J. H., D. W. Menzel, E. M. Hurlbert, C. J. Lorenzen & N. Corwin, 1971. The production and utilization of organic matter in the Peru coastal current. Invest. Pesq. 35: 43–59.

Shannon, L. V. & J. G. Field, 1985. Are fish stocks food-limited in the southern Benguela pelagic ecosystem? Mar. Ecol. Progr. Ser. 22: 7–19.

Siegenthaler, U., 1990. El Niño and atmospheric CO_2. Nature 345: 295–296.

Sokal, R. R. & F. J. Rohlf, 1981. Biometry. 2nd edn. W. H. Freeman and Co., San Francisco: 858 pp.

Tenore, K. R., L. F. Boyer, R. M. Cal, J. Corral, C. García-Fernández, N. Gonzalez, E. Gonzalez-Gurriarán, R. B. Hanson, J. Iglesias, M. Krom, E. Lopez-Jamar, J. Mcclain, M. M. Pamatmat, A. Perez, D. C. Rhoads, G. Santiago, J. Tietjen, J. Westrich & H. L. Windom, 1982. Coastal upwelling in the Rías Bajas, NW Spain: Contrasting the benthic regimes of the Rías de Arosa and de Muros. J. Mar. Res. 40: 701–772.

Tenore, K. R., M. Alonso-Noval, M. Alvarez-Ossorio, L. P. Atkinson, J. M. Cabanas, R. M. Cal, H. J. Campos, F. Castillejo, E. J. Chesney, N. González, R. B. Hanson, C. R. McClain, A. Miranda, M. R. Roman, J. Sanchez, G. Santiago, L. Valdés, M. Varela & J. Yoder, 1995: Fisheries and oceanography off Galicia, NW Spain: Mesoscale spatial and temporal changes in physical processes and resultant patterns of biological productivity. J. Geophys. Res. 100 (C6): 10943–10966.

Valdés, L., M. T. Alvarez-Ossorio, A. Lavin, M. Varela & R. Carballo, 1991. Ciclo anual de párametros hidrográficos, nutrientes y plancton en la plataforma continental de La Coruña (NO España). Bol. Inst. Esp. Oceanogr. 7: 91–138.

Varela, M., 1992. Upwelling and phytoplankton ecology in Galician (NW Spain) rías and shelf waters. Bol. Inst. Esp. Oceanogr. 8: 57–74.

Varela, M. & E. Costas, 1987. Distribución del tamaño de las especies del fitoplancton en un área de afloramiento. Invest. Pesq. 51: 97–106.

Varela, M., M. T. Alvarez-Ossorio, L. Valdés, R. Cal, A. Miranda, G. Santiago & E. Costas, 1988. Partición de la materia orgánica particulada en el área de afloramiento de la plataforma de Galicia (NO España) durante la Campaña Breogán 684. Bol. Inst. Esp. Oceanogr. 5: 97–108.

Varela, M., J. M. Cabanas, M. J. Campos, E. Penas, J. Sanchez, A. Larrañaga, F. F. Castillejo & G. Diaz del Rio, 1987a. Composición y distribución del fitoplancton en la plataforma de Galicia durante la Campaña Breogán 684 (junio de 1984). Bol. Inst. Esp. Oceanogr. 4: 75–94.

Varela, M., M. J. Campos, J. M. Cabanas, F. F. Castillejo & G. Diaz del Rio, 1987b: Composición y distribución del fitoplancton en la plataforma de Galicia durante la Campaña Breogán 984 (septiembre 1984). Bol. Inst. Esp. Oceanogr. 4: 95–106.

Varela, M., G. Diaz del Rio, M. T. Alvarez-Ossorio & E. Costas, 1991. Factors controlling phytoplankton size class distribution in the upwelling area of the Galician continental shelf (NW Spain). Sci. Mar. 55: 505–518.

Varela, M., J. M. Fuentes, E. Penas & J. M. Cabanas, 1984. Producción primaria de las Rías Baixas de Galicia. Cuadernos da Area de Ciencias Mariñas. Seminario de Estudos Galegos 1: 173–182.