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VARIABILITY OF PHYTOPLANKTON BIOMASS AND PRIMARY PRODUCTIVITY IN THE SHELF WATERS OF THE UPWELLING AREA OF N-NW SPAIN

by

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SUMMARY

Chlorophyll-a and primary productivity on the euphotic zone of the N-NW Spanish shelf was studied in 125 stations between 1984 and 1992. Three geographic areas (Cantabrian Sea, Rias Altas and Rias Bajas), three batimetric ranges (20 to 60 m, 60 to 150 m and stations deeper than 200 m), and four seasonal periods (summer upwelling, spring and fall blooms, summer stratification and winter mixing) were considered.

One of the major sources of variability of chlorophyll and production data was seasonal, with equivalent mean and maximum values during bloom and summer upwelling periods. Average chlorophyll-a concentrations approximately doubled in every step of the increasing productivity sequence: winter mixing - summer stratification - high productivity (upwelling and bloom) periods. Primary production rates increased only 60% in the described sequence. Mean (±sd) values of chlorophyll-a and primary production rates during the high productivity periods 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 productivity resulted between geographic areas in most seasons. Only 27 stations showed effects of the summer upwelling that affected coastal areas in the Cantabrian Sea and Rias Bajas shelf, but also shelf-break stations in the Rias Altas area. The Rías Baixas area resulted with lower chlorophyll than both the Rías Altas and the Cantabrian Sea areas during blooms, but higher during upwelling events. On the contrary, primary production rates were higher in the Rías Baixas area during bloom periods. Mid-shelf areas showed the highest chlorophyll concentrations during high productivity seasons, probably due to the existence of various fronts in all geographic zones considered.

The estimated phytoplankton growth rates were comparable to those of other coastal upwelling systems, with average values lower than maximum potential growth rates. Doubling rates for upwelling and stratification periods in the northern and Rías Altas shelf were equivalent, despite larger biomass accumulations during upwelling events. Low turnover rates of the existing biomass in the Rías Bajas shelf during upwelling suggests that phytoplankton exported from the highly productive rías accumulates near shore, and that 'in situ' production is of less importance.

INTRODUCTION

The seasonal upwelling system of 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). Cold, nutrient-rich deep waters have been detected near surface in discrete observations through the period between March and October, especially in the north-western shelf (Fraga, 1981, Fraga et al., 1982, Rios et al., 1987, Varela and Costas, 1987, Varela et al., 1987a, b, 1988, 1991, Valdés et al., 1991). Observations of upwelling events for the northern shelf (Cantabrian Sea, Southern Bay of Biscay) are more scarce (Dickson and Hughes, 1981, Rios et al., 1987, Botas et al., 1990), and suggest that in this area the vertical advection of deep water is related to the intensity of the upwelling in the NW shelf, where lower surface temperatures ocurred.

During the thermal stratification period of the summer (May to September), this upwelling modifies the vertical structure of the water column, affecting distributions of phytoplankton in relation to the temperature and nutrient gradients (Varela et al., 1987a, b, 1991, Botas et al., 1990). In contrast, upwelling events during the spring and autumn are influenced by the local circulation patterns caused by poleward currents flowing parallel to the shelf-break (Frouin et al., 1990). These currents can have a great influence on the development of phytoplankton blooms that normally occur 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 contributions of exported nutrients and organic matter produced in the estuarine rías (Tenore et al., 1982, Lopez-Jamar et al., 1992). Biological productivity in the rías is enhanced by the combined effects of nutrient-rich water entering from the sea during upwelling events and local circulation (eg. Tenore et al., 1982, Blanton et al., 1984, Figueiras et al., 1985). Primary productivity of the rías was well studied, particularly in relation to intense mussel aquaculture (eg. Varela et al., 1984 and references therein). However, there are far less data on phytoplankton productivity and biomass in the open shelf areas (eg. Varela, 1992).

The objectives of this paper are:

1) To summarize the existing information on simultaneous measurements of primary productivity and biomass in the area affected by the coastal upwelling.

2) To study seasonal and spatial variability in chlorophyll-biomass and phytoplankton carbon production in relation to specific questions: ¿ Is the southern part of the area is more productive because the additional enrichment of the rías outflow ? ¿ How different are the values obtained during the high production seasons in the low-intensity upwelling area of the Cantabrian Sea and those obtained in the western shelf ?

3) To compare primary production and phytoplankton growth rates from high production periods in diverse areas of the N-NW Spanish shelf and other coastal upwelling areas.

METHODS

Figure 1 shows the positions of the stations in which phytoplankton biomass and primary production were studied between 1984 and 1992. Details of sampling 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 batimetric ranges were considered: 'Coastal' (20 to 60 m depth), 'Mid-shelf' (60 to 150 m) and 'Off-shelf' (stations deeper than 200 m).

Temperature and salinity were measured with CTD probes (cruises in the western shelf) or an induction salinometer (cruises in the Cantabrian Sea). Dissolved nutrient concentrations (nitrate and phosphate) 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 C-14 additions were 4 µCi ^{14}C in the western shelf cruises and 2 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 at the sampling depths. Incubations were made around noon and lasted from 2 to 4 h. Filters employed for chloropyll and productivity determinations were listed in Table 1. Corrections for dark uptake of C were made only in the western shelf cruises. All chlorophyll and production values were integrated in the euphotic zone.

Hydrographic and chlorophyll data were used to classify samples in definite seasonal oceanographic periods, following the information available in the area (Fraga et al., 1982, Ríos et al., 1987, Botas et al., 1988, Valdés et al., 1991, Varela, 1992). 'Bloom' samples correspond to stations studied during the spring and autumn that showed mean chlorophyll-a concentrations higher than 1 $\mu g\ l^{-1}$ in most of the euphotic zone and weak vertical water density gradients. 'Upwelling' samples are summer cases that showed cold (<14°C) and nutrient-rich (>5 $\mu M\ N\text{-}NO_3^-\ l^{-1}$, >0.4 $\mu M\ P\text{-}PO_4^{3-}$). All samples from the summer that did not show any characteristic of upwelling were classified in the group named 'Stratification'. Finally, stations that showed a thoroughly mixed water column, including some samples of spring and autumn with low chlorophyll concentrations, were classified as 'Winter'.

Carbon primary production to biomass ratios were estimated for the main periods and areas using average chlorophyll and primary production values. Chlorophyll-a was converted to carbon using a mean factor of 100 µC $(\mu g\ Chl\text{-}a)^{-1}$. Minimum and maximum range values were computed considering ratios of 50 and 200 µg C $(\mu g\ Chl\text{-}a)^{-1}$, respectively. These conversions are likely to produce conservative estimates of phytoplankton growth rates in upwelling areas (Brown et al., 1991), given the large variations in the carbon to chlorophyll ratios of natural phytoplankton (eg. Banse, 1977). The measured hourly carbon fixation rates were extrapolated to daily rates by assuming an effective daylenght of 10 h in summer 'Upwelling' and 'Stratification' periods, 8 h during spring and autumn 'Bloom' periods, and 6 h in the 'Winter' period.

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

RESULTS AND DISCUSSION

Temporal variations

Seasonal variations are a major component of variability in chlorophyll-a and primary production rates through the area. Figure 2 displays mean values calculated for the selected periods, indicating that the 'a priori' classification of samples was appropiate (F = 28.94, $p<0.0001$). Multiple comparisons between means revealed that differences in both chlorophyll and production between 'Bloom' and 'Upwelling' periods were not significantly different (Student-Neuman-Keuls test, $p>0.05$), but there were clear differences in all other groups. Average chlorophyll concentrations of the 'Stratification' period was approximately twice the value of the 'Winter' period, and half of the mean value of the high productivity periods ('Bloom' and 'Upwelling'). Mean (±sd) values of chlorophyll–a and primary production rates during the high productivity periods were 59.7 ± 39.5 mg Chl–a m^{-2} and 86.9 ± 44.0 mg C m^{-2} h^{-1}, respectively. These values are within the range obtained in other upwelling areas, like Benguela (40 – 340 µg C m^{-2} h^{-1}, Shannon and Field, 1975, Estrada and Marrase, 1987, Brown et al., 1991), but lower than those cited in other systems (eg. up to 1000 µg C m^{-2} h^{-1} in the Peru upwelling, Ryther et al., 1971).

Upwelling events are known to be very dynamic features, changing water–column properties and plankton communities during short time scales (Blasco et al., 1981). This is indicated by the fact that, despite most of the cruises employed in this study were made during the upwelling season, only a small fraction of samples (27 of 125) showed clear upwelling characteristics. Productivity and biomass is generally low during phases of intense water–mixing, when nutrient concentrations are high, and increases in phases or areas of moderate turbulence (Margalef and Estrada, 1981). We studied variations within the 'Upwelling' samples by means of a distinction of two phases: 'Initial', with high nutrient and low chlorophyll concentrations, and 'Final', with the converse conditions. Mean (±sd) values of chlorophyll–a for 'Initial' and 'Final' periods were 50.99 ± 28.46 µg Chl–a l^{-1} (n=10) and 69.95 ± 43.85 µg Chl–a l^{-1} (n=17), respectively. Primary production rates were 90.79 ± 44.57 µg C l^{-1} h^{-1} during the 'Initial' phases and 82.21 ± 42.41 µg C l^{-1} h^{-1} during 'Final' upwelling phases. However, no significant differences between two phases resulted for either chlorophyll–a nor primary production because of high variances (Mann–Whitney test, p>0.05). The relatively low number of upwelling cases used in this study difficults any attemp to study patterns of internal variation. There are some evidences of day–to–day variations in planktonic biomass and productivity associated to upwelling and downwelling phenomena in this area (Varela et al., 1991). 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 on 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.

Spatial variations

The geographical location of sampling was an important contribution to added variance in both chlorophyll and primary production values. Figure 3 shows the variance partition of both variables in seasonal ('Period') and geographic ('Area') components using a nested anova, with the 'Area' component as the nested factor. Samples for the winter period were excluded because there was no data for the Rías Baixas area. Seasonality was the main source of variation in chlorophyll–a values while geographic location was responsible for near 90 % of the variations in primary production rates. The mean values of Table 2 show that the Rías Baixas area resulted with higher production rates in the Rías Baixas area during 'Bloom' periods but also with the lowest rates during the 'Stratification' period. The Rías Altas area had intermediate production rates in all seasons, but mean chlorophyll–a concentrations resulted higher than in the other areas during 'Bloom' and 'Stratification' periods.

Another major source of variability in chlorophyll and primary production values was the depth of the studied stations and their position relative to the coast. Apart from the evident seasonal variability, there was a significant component of added variance due to the 'Zone' component when data form all geographic areas were combined (Table 3). Table 4 displays mean values for all combinations of pariods and zones, indicating higher chlorophyll concentrations in the mid–shelf zone during high production periods ('Bloom' and 'Upwelling'). 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 resulted more variable, with higher rates near the coast during 'Bloom' periods and in the mid-shelf zone in all other seasons.

Mid-shelf areas are a place where a variety of fronts can be expected (eg. Holligan, 1981), and the characteristics and biological implications of some of them in the Cantabrian Sea had been already described (Botas et al., 1988, Bode et al., 1990, Fernández et al., 1991, 1993). Large, and possibly permanent frontal systems, had been reported for the boundaries between the three geographic areas considered. Fraga et al. (1982) and Rios et al. (1992) recognized a distinct off-shore surface circulation and a permanent subsurface front off Cape Finisterre, between the Rías Altas and the Rías Baixas areas. Similarly, there are evidences of similar fronts off Cape Ortegal, between the Rías Atltas area and the Cantabrian Sea (Diaz del Rio et al., 1992). These fronts can determine the input of surface waters from the Central Atlantic into the southern Bay of Biscay (Pingree and Le Cann, 1990, Pingree, 1993). However, the biological implications of such fronts in the NW coast of Spain have been scarcely studied (eg. Varela et al., 1991).

Phytoplankton growth rates

Doubling rates of the existing biomass may allow for comparison between different upwelling systems (eg. Brown et al., 1991). The values calculated with our data indicated that the areas of higher phytoplankton growth vary seasonally (Table 5). The highest rates were found in the Rías Baixas area during the 'Bloom' period, but high values were found in the Cantabrian Sea and Rías Altas area during 'Upwelling' and 'Stratification' periods, when phytoplankton growth in the Rías Baixas area was relatively slow. Values for the Cantabrian Sea resulted in general higher than those of the western part of the area, but 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 (in press) have shown that dark bottle substraction may severely underestimate primary production rates during periods of slow growth, like the 'Winter' period.

Average growth rates calculated for our mean doubling rates during the 'Upwelling' period resulted lower than the expected maximum growth rates calculated with the equation of Eppley (1972):

$$\log_{10} \underline{d} = 0.0275\ T - 0.070$$

where $\underline{d}$ is the doubling time (inverse of growth rate) expressed as days necessary to double the existing biomass, and T is the ambient (water) temperature. The temperature of surface waters in the studied area ranged between 13 and 20 °C and the corresponding maximum phytoplankton growth rates will be 0.51 and 0.33 doublings day^{-1}, respectively. With a mean temperature of surface water of 15 °C during upwelling events, the expected growth rate will be 0.45 day^{-1}, ie. phytoplankton biomass will double every 2.2 days. The estimated rates during upwelling events in our study area range from 0.47 day^{-1} (biomass double every 2.11 days) in the Cantabrian Sea, to 0.05 day^{-1} (biomass double every 19.2 days) in the Rías Baixas area. Low biomass turnover rates in the Rías Baixas area during upwelling events in the summer are in agreement with the hytpothesis that coastal areas in this region receive important inputs of phytoplankton and particulate organic matter from the nearby rías (Estrada, 1984). The high primary production rates 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 additional nutrients regenerated inside the rías than can be released with the outflow (Tenore et al., 1982, Lopez-Jamar et al., 1992) and 'in situ' regeneration (Mouriño 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. Despite hourly production rates for 'Bloom' and 'Upwelling' periods were comparable, the extrapolation to daily rates, which takes into account the effective daylenght, indicates that upwelling episodes produced during summer will produce higher biomasses. The fact that chlorophyll concentrations resulted similar for 'Bloom' and 'Upwelling' periods may be explained by a close-coupling between primary producers and consumers or, alternatively, by hidrographic mechanisms favouring sedimentation of recently produced organic material during summer upwelling events. Relatively high mesozooplankton biomasses have been reported in the area during periods of weak upwelling (Valdés et al., 1991, Varela et al., 1991). In addition, microbial-loop consumers are capable to remove a large fraction of the daily primary production in an upwelling event of the Rías Altas area (Bode and Varela, in press), and there are examples of rapid phytoplankton degradation through bacteria in other bloom areas (eg. Newell and Linley, 1984). On the other hand, there are reports of downwelling occurring shortly after the maximum productivity period 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) to large areas of the bottom (Lopez-Jamar et al., 1992). Probably both mechanisms occurred simultaneously.

Another interesting feature of the estimations displayed in Table 5 is that growth rates computed for the 'Stratification' period resulted sometimes comparable or higher than those of 'Upwelling' and 'Bloom' periods. Production maxima and chlorophyll accumulation in subsurface layers is one of the major characteristics of stratified water columns in most seas (Cullen, 1982, Estrada, 1985, Dortch, 1987, Fernández and Bode, 1991). Physiological indicators and 'in situ' measures of phytoplankton production indicate that in the Cantabrian Sea these subsurface chlorophyll maxima are produced by active growth (Fernández and Bode, 1991). Since sedimentation of particles below the euphotic zone in these periods is expected to be reduced, because of the large water density gradient near the picnocline, 'in situ' decomposition of organic matter by microplankton appears as a likely explanation of the low phytoplankton biomass. There are evidences that, at least in subsurface chlorophyll maxima inside the rías, close coupling of microheterotrophs and phytoplankton may occur during summer (Figueiras and Pazos, 1991).

CONCLUSIONS

1. Seasonality resulted a major factor of variation of chlorophyll concentrations and primary production rates of the shelf area of NW Spain. Shorter time scales are likely to be very important during high production periods, but more data are needed to demonstrate patterns in both parameters during upwelling events.

2. There was a significant interaction between seasonal and spatial variability in chlorophyll and production values. The Rías Baixas area resulted with lower chlorophyll than both the Rías Altas and the Cantabrian Sea areas during blooms, but higher during upwelling events. On the contrary, primary production rates were higher in the Rías Baixas area during bloom periods. Mid-shelf areas showed the highest chlorophyll concentrations during high productivity seasons, probably due to the existence of various fronts in all geographic zones considered.

3. The estimated phytoplankton growth rates were comparable to those of other coastal upwelling systems, with average values lower than maximum potential growth rates. Doubling rates for upwelling and stratification periods in the northern and Rías Altas shelf were equivalent, despite larger biomass accumulations during upwelling events. Low turnover rates of the existing biomass in the Rías Bajas shelf during upwelling suggests that phytoplankton exported

from the highly productive rías accumulates near shore, and that 'in situ' production is of less importance.

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Table 1

Cruises and methodological characteristics of data used in this study.

Cruise	Dates	Area*	Filter** Chl-a	Filter** Prod.	Incubation type	References
BREOGAN-684	Jun 1984	RA, RB	MO.8	MO.8	"in situ"	Varela et al. 1987b,1988
BREOGAN-984	Sept 1984	RA,RB	MO.8	MO.8	"in situ"	Varela et al. 1987a
BREOGAN-785	Jul 1985	RA,RB	MO.8	MO.8	"in situ"	Varela et al. 1991
BREOGAN-486	Mar-Apr 1986	RA,RB	MO.8	MO.8	"in situ"	unpubl. data
COCACE	Jan-Dec 1987	CA	GF/C	MO.8	"in situ"	Botas et al. 1989
ASFLOR-I	Aug 1989	CA	GF/F	GF/F	"in situ simul."	Anadón 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	MO.8	MO.8	"in situ simul."	Valdés et al. 1991 and unpubl. data
Asturias transect	Aug 1991	CA	GF/F	GF/F	"in situ simul."	unpubl. data

*CA: Cantabrian Sea area
RA: Rías Altas area
RB: Rías Baixas area

**MO.8= Millipore cellulosa-acetate membrane filters 0,8 µm pore size.
GF/C= Whatman GF/C glass fiber filters.
GF/F= Whatman GF/F glass fiber filters.

Table 2

Mean (± sd) chlorophyll-a (Chl-a, mg m^{-2}) and production (Prod, mg m^{-2} h^{-1}) values for the different areas and oceanographic periods. Number of data points appear in brackets.

		Chl-a		
Area	Bloom	Upwelling	Stratification	Winter
Cantabrian	49.33±19.29 (7)	40.72±14.32 (4)	25.33±10.85 (27)	15.64±7.52 (9)
Rías Altas	67.68±49.49 (13)	57.84±41.86 (16)	37.55±24.44 (15)	15.64±3.80 (11)
Rías Baixas	32.84±10.50 (4)	87.11±34.04 (7)	35.53±20.45 (12)	–
		Production		
Cantabrian	93.11±50.66 (7)	96.13±45.84 (4)	57.54±30.31 (27)	38.07±25.07 (9)
Rías Altas	77.43±43.80 (13)	80.17±46.86 (16)	56.00±34.47 (15)	17.29±11.87 (11)
Rías Baixas	110.75±43.65 (4)	91.18±33.54 (7)	41.48±25.57 (12)	–

Table 3

Summary of anova results for the effects of three batimetric zones ('Coastal', 'Mid-shelf' and 'Off-shelf') within sampling periods ('Bloom', 'Upwelling', 'Stratification' and 'Winter mixing') on water column integrated chlorophyll-a (Chl-a) and production (Prod). <u>SS</u>: sum of squares, <u>DF</u>: degrees of freedom, <u>MS</u>: Mean squares, <u>F</u>: MS-ratio, <u>p</u>: probability of <u>F</u> values. The error terms correspond to within cell variability. <u>SS</u> for the effects were computed sequentially as they are listed below.

Variable	Effect	<u>SS</u>	<u>DF</u>	<u>MS</u>	<u>F</u>	<u>p</u>
Chl-a	Error	5.96	113	0.05		
	Period	41.34	3	13.78	261.39	0.000
	Zone within period	55.42	8	6.93	131.40	0.000
Prod.	Error	9.48	113	0.08		
	Period	55.54	3	18.51	220.72	0.000
	Zone within period	70.14	8	8.77	140.53	0.000

Table 4

Mean (± sd) chlorophyll-a (Chl-a, mg m^{-2}) and production (Prod, mg m^{-2} h^{-1}) values for three batimetric zones ('Coastal', 'Mid-shelf' and 'Off-shelf') and oceanographic periods ('Bloom', 'Upwelling', 'Stratification' and 'Winter mixing'). Number of data points appear in brackets.

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

Table 5

Estimates of phytoplankton growth rates for the studied area and periods using average water column integrated values of chlorophyll-a and production. Values are in doublings day^{-1} (see methods section for details of calculations). Maximum and minimum estimates appear in brackets.

Area	Bloom	Upwelling	Stratification	Winter
Cantabrian	0.151 (0.075-0.302)	0.236 (0.118-0.472)	0.229 (0.114-0.457)	0.170 (0.085-0.341)
Rías Altas	0.092 (0.046-0.183)	0.139 (0.069-0.277)	0.149 (0.075-0.298)	0.07 (0.039-0.155)
Rías Baixas	0.269 (0.134-0.540)	0.105 (0.052-0.209)	0.117 (0.058-0.257)	_

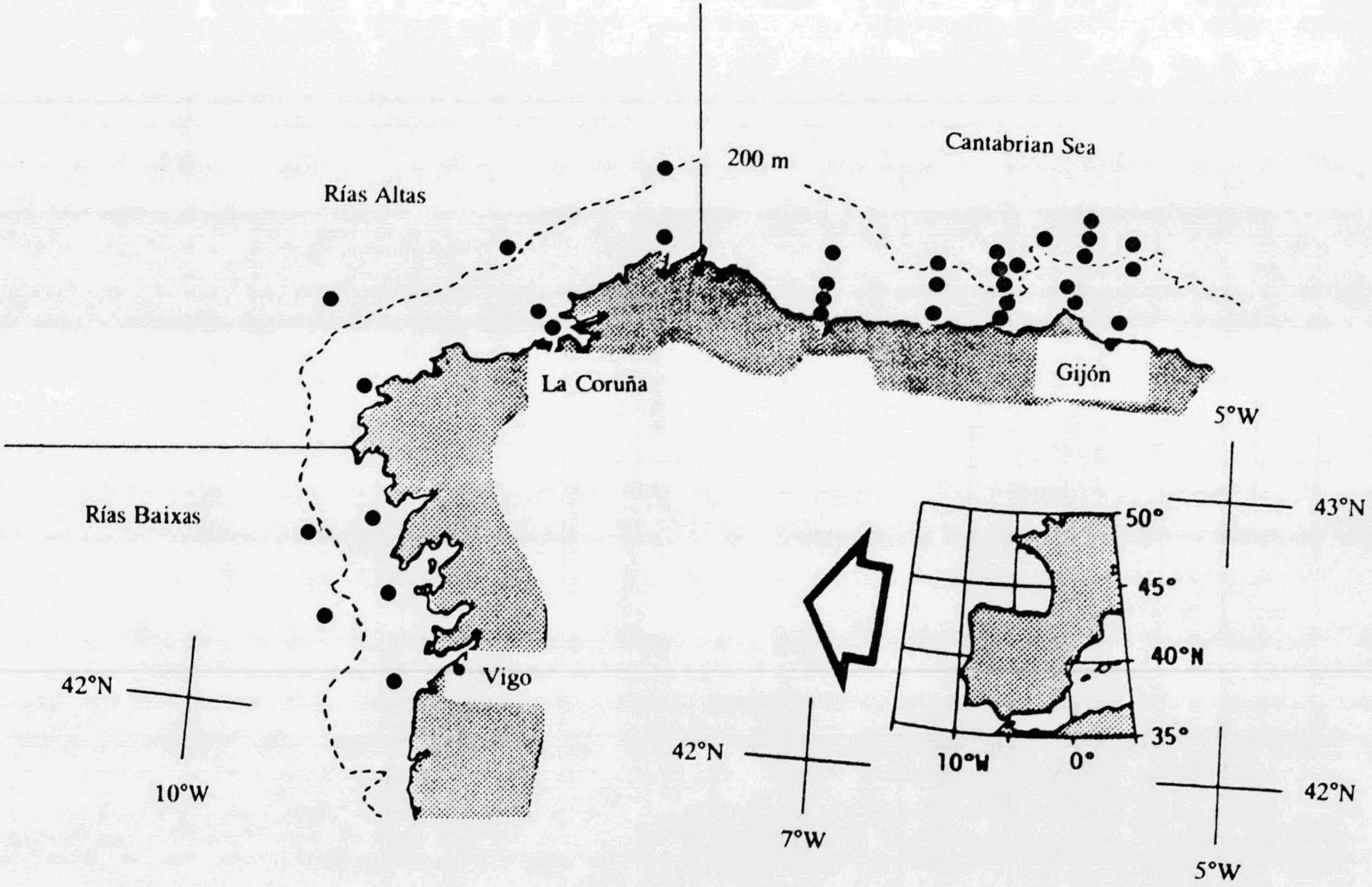

Figure 1.- Position of stations studied.

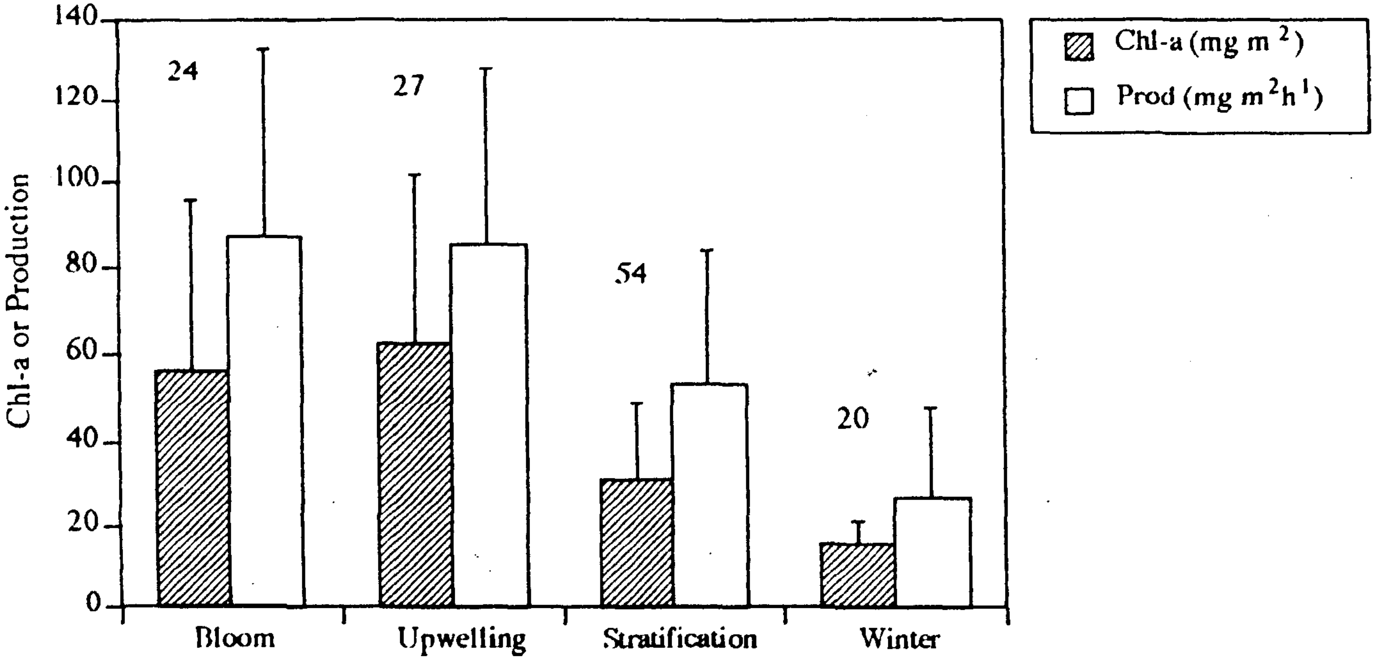

Figure 2.- Mean (±sd) integrated chlorphyll-a (mg Chl-a m^{-2}) and primary production (mg C m^{-2} h^{-1}) in selected oceanographic seasons.

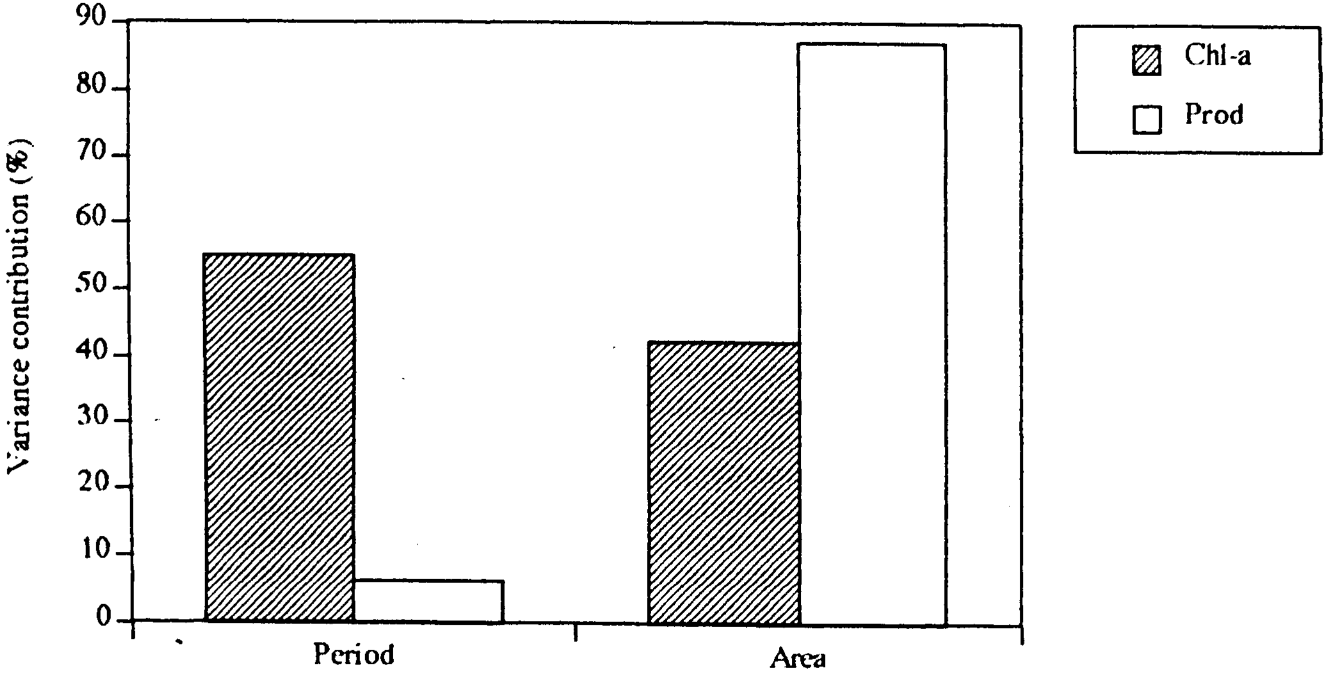

Figure 3.– Relative contribution (percent) of temporal (Period) and spatial (Area) factors to total variance in water–column integrated chlorophyll–a (Chl–a) and production (Prod) data.