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The spatial and temporal structure of hydrographic and phytoplankton biomass heterogeneity along the Catalan coast (NW Mediterranean)

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ABSTRACT

The horizontal and temporal distribution of hydrographic properties and phytoplankton biomass along the Catalan coast were analyzed to determine their variance structure (i.e., variance partition between temporal, alongshore, and across-shore components), and the relationship between hydrographic heterogeneity and variability in phytoplankton biomass.

Temporal chlorophyll variability was highly seasonal, but horizontal biomass variability was related to hydrographic variability, as evidenced by significant correlations to temperature and salinity. The strength of chlorophyll-salinity correlations changed according to the extent of riverine influences within the area, but significant correlations were always negative, indicating enhanced phytoplankton growth due to river runoff. Temperature-chlorophyll correlations changed seasonally, from highly positive in early summer to negative by late summer. In addition, horizontal biomass patterns were dominated by an onshore-offshore decrease, which were altered by modifications of water circulation associated to topographic features such as canyons and shelf concavities.

1. Introduction

The coastal zone bears great environmental complexity which results from the interaction of multiple factors such as river discharge, coastal upwelling, topographic influences on coastal circulation and the interaction between coastal and oceanic water masses (Denman and Powell, 1984; Legendre and Demers, 1984).

Because phytoplankton growth depends on *in situ* conditions, the high spatial and temporal heterogeneity of coastal phytoplankton (e.g., Barale and Fay, 1986; Pan *et al.*, 1988) may derive from the environmental heterogeneity inherent to the coastal zone.

The notion that (mesoscale) variability in coastal phytoplankton biomass reflects the hydrographic variability inherent to the coastal zone has often been suggested in the past (e.g., Estrada, 1972; 1979; Prieur, 1979; Thomas and Emery, 1986; Townsend and Spinrad, 1986; Savidge and Lennon, 1987; Pan *et al.*, 1988), but has rarely been subject to explicit, quantitative test (e.g., McClain *et al.*, 1988; Michaelsen *et al.*, 1988; Smith *et al.*, 1988).

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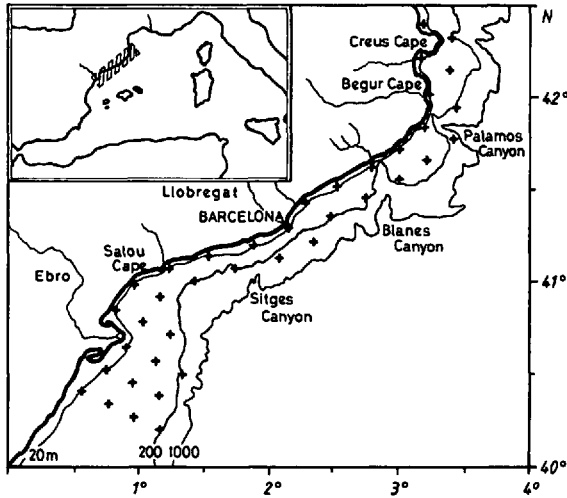


Figure 1. Map of the Catalan coast showing the major topographic and bathymetric features, and the location of the sampling stations.

Here we evaluate the association between phytoplankton heterogeneity and hydrographic variability along the Catalan coast (NW Mediterranean, Figure 1). To pursue this objective we will analyze data from 11 oceanographic cruises along the Catalan coast (ARECES program; April, 1983 to June, 1985) to (1) partition the variability in hydrographic properties (T-S) and phytoplankton biomass (as chlorophyll *a* concentrations) observed into its temporal and spatial components; (2) to describe their dominant spatial and temporal distributions (i.e., average values) as well as their variability (as variance); and (3) to quantify the relationship between hydrographic and phytoplankton variability (as the correlation coefficients).

The cruises encompass a period when primary production is particularly important because it corresponds to the spawning period for most of the fish species in the area (Palomera and Rubies, 1979). Because of the sampling design, the patterns described here apply only to mesoscale (>10 km) spatial patterns and to seasonal temporal patterns.

2. Methods

To obtain an adequate description of the variability in hydrographic conditions and phytoplankton biomass along the Catalan coast, we established a fixed grid comprised of 17 transects running offshore regularly distributed along the coast (Fig. 1), with sampling stations located at regular intervals (c. 10 miles) from c. 5 miles offshore to the margin of the shelf (c. 200 m deep) along each transect (2–4 sampling stations per transect; total 39 stations, Fig. 1). These stations were sampled aboard the R/V *Garcia de Cid* for a total of 11 cruises occurring between April and October, 1983 to 1985

Table 1. Cruise dates and methods used to measure salinity and temperature for the cruises analyzed. CTD stands for the use of a Neil-Brown CTD; and Niskin stands for the use of 5 l Niskin bottle at standard depths, fitted with a thermometer, and an induction salinometer for salinity measurements.

Cruise	Date	Method
Areces I	13-26/4/83	CTD
Areces II	14-20/5/83	CTD
Areces III	7-12/6/83	CTD
Areces IV	18-25/7/83	Niskin
Areces V	7-14/9/83	Niskin
Areces VI	3-10/10/83	Niskin
Areces VII	27/4-4/5/84	Niskin
Areces VIII	16-21/6/84	Niskin
Areces IX	17-22/8/84	CTD
Areces X	28/9-4/10/9/84	CTD
Areces XI	12-20/6/85	Niskin

(Table 1), each spanning about 7 days. Because surface and subsurface conditions may differ (e.g., river runoff) we sampled surface and subsurface (i.e., 20 m) waters.

Our analyses, therefore, ignore winter conditions and bear the spatial and temporal limitations inherent to ship surveys (e.g., Denman and Abbott, 1988). In particular, the persistence of mesoscale spatial distributions of phytoplankton biomass appears to be short (ca. 10 days; e.g., Denman and Freeland, 1985; Denman and Abbott, 1988), such that the spatial variance presented here incorporates short term (<7 days, the time lapse necessary to sample the area) temporal variability. This problem seems to be smaller for the more conservative temperature and salinity (e.g., Denman and Freeland, 1985). The reliability of the data obtained to estimate the "true" phytoplankton and hydrographic variability of the Catalan coast is, accordingly, uncertain, although we feel that the number of cruises and stations occupied is sufficient as to justify a reasonable expectation of a good correspondence between the observed patterns and the "true" patterns.

Hydrographic properties were characterized by salinity and temperature measurements, and phytoplankton biomass was approximated as chlorophyll *a* concentrations. Sampling methods for the hydrographic properties are outlined in Table 1. Water samples for chlorophyll *a* determinations were collected with a 5 l Niskin bottle. Chlorophyll *a* concentration was estimated after sample concentration on a Whatman GF/C filter, followed by grinding, acetone extraction, and fluorometrical determination (Yenstch and Menzel, 1963). Because of technical malfunctions, there were missing data values for some stations, such that the sample size for different variables differs slightly. However, bootstrap error analysis showed that estimates of average temperature, salinity, and chlorophyll *a* concentrations and their associated variances are stable for a sample size >10 stations. Since the data available for the different parameters in each cruise were always greater, increasing the number of stations

sampled here is unlikely to yield average and variance values different from those reported here.

The structure of the variability in the characteristics studied will be quantified by first partitioning their global heterogeneity (i.e., variance) between a temporal and spatial component. The horizontal variance will be partitioned between an alongshore (i.e., between transects) and an across-shore (i.e., within transects) component. Variance component analyses were performed using a nested ANOVA model for unbalanced designs (Sokal and Rohlf, 1969), that estimate the proportional contribution of the different components (temporal, alongshore, and across-shore) to the global variance observed.

The spatial distribution of chlorophyll *a* was, as observed in previous studies (e.g., Smith and Baker, 1982; Denman and Abbott, 1988), approximately lognormal. Therefore, we transformed the chlorophyll values logarithmically prior to nested ANOVA analysis (Sokal and Rohlf, 1969), and used geometric means to represent the central tendency in chlorophyll concentrations for the different cruises. However, since chlorophyll values for individual stations were approximately normally distributed, we used average values to describe the central tendency of the chlorophyll of individual stations. Because chlorophyll variance was dependent on the mean values, we used the coefficient of variation to compare the variability in chlorophyll values between cruises and between stations (Sokal and Rohlf, 1969).

The dominant spatial distribution of the variables studied was summarized by mapping the average values observed for each station (e.g., Smith *et al.*, 1988), and the temporal variability associated to these average values was summarized by mapping the variance in the values observed for each station (e.g., Smith *et al.*, 1988). The dominant temporal distribution of the variables studied was described by the temporal sequences of the (across-station) average values (median for chlorophyll) for the different cruises, and the temporal evolution of the spatial variability was represented by the temporal sequence of the within-cruise variance.

The use of average values permits a synoptic description of the data at the expense of loss of detail on particular processes (by smoothing extreme situations). We attempt to compensate for this limitation by providing representations of the extreme spatial patterns observed for each variable examined, and by appraising statistical differences in the behavior of pairs of locations (e.g., onshore-offshore, surface-20 m) using nonparametric methods (Wilcoxon ranked sign test) that rely on the comparison of all data pairs instead of using average values alone (Sokal and Rohlf, 1969).

3. Studied area

The studied area extends along the continental shelf of the Catalan coast (NW Mediterranean, Fig. 1). The width of the continental shelf changes considerably along the coast, with a narrow shelf interrupted by numerous submarine canyons in the northern part and a wider shelf toward the southern zone (Fig. 1). The coastal profile is

modified in the northern zone by the Creus Cape and Begur Cape that confine the Roses Gulf, the cape formed by the Llobregat Delta in the center, and the Salou Cape and the Tortosa Cape (formed by the Ebro Delta) that confine the St. Jordi Gulf in the southern portion (Fig. 1).

The Ebro River is the only important river discharging within the studied area, although smaller rivers may be locally important after intense storms (e.g., Estrada, 1979). The Rhone River, that discharges into the Gulf of Lyon (c. 200 km northeast of the studied area), is the most important source of continental water to the Catalan coast.

Shelf and deep oceanic waters are separated by a permanent, albeit instable (Wang *et al.*, 1988; Tintore *et al.*, 1989), density front (cf., Font *et al.*, 1988), largely defined by a salinity difference between river-influenced shelf waters and more saline oceanic ones. This front influences significantly surface circulation, inducing a southward geostrophic flow (15–30 cm sg^{-1}), along the continental slope (Font *et al.*, 1988). The southward flow is enhanced by the strong buoyancy input of the Rhone River in the northern part, the horizontal density gradients induced being greater in spring and early summer.

Topographic features appear to influence local water circulation significantly. Masó *et al.* (1989) showed evidence of surface flow modification by the submarine canyons in the northern part of the Catalan coast. The canyons act as barriers deflecting the southward current and inducing an offshore flow along their southern sides. Further, even modest topographic features can induce important circulation changes. Slope waters penetrate onto the shelf along a concavity on the eastward projection of the continental margin off the Ebro Delta the coast, causing a permanent upwelling northeast of the delta (Font *et al.*, 1989).

The period of vertical mixing spans from October to April with the onset of the summer thermocline sometime between late May and mid June. The summer thermocline starts up as a very shallow (10–20 m) structure and deepens progressively to attain a depth of c. 50 m by mid summer. Vertical stability is further enhanced in spring by river discharge.

4. Results

a. Variance structure of hydrographic properties and phytoplankton biomass

Insight into the variance structure of hydrographic properties and phytoplankton biomass along the Catalan coast, and thus insight into the dynamics and interrelation between these variables, can be gained by examining the relative contribution of temporal and spatial components to their global variance. This procedure demonstrated the (predictable) seasonal nature of temperature variations, because >85% of the temperature variance was attributable to temporal variations (Fig. 2a). Salinity variance, in turn, had a more balanced partition between temporal and spatial domains

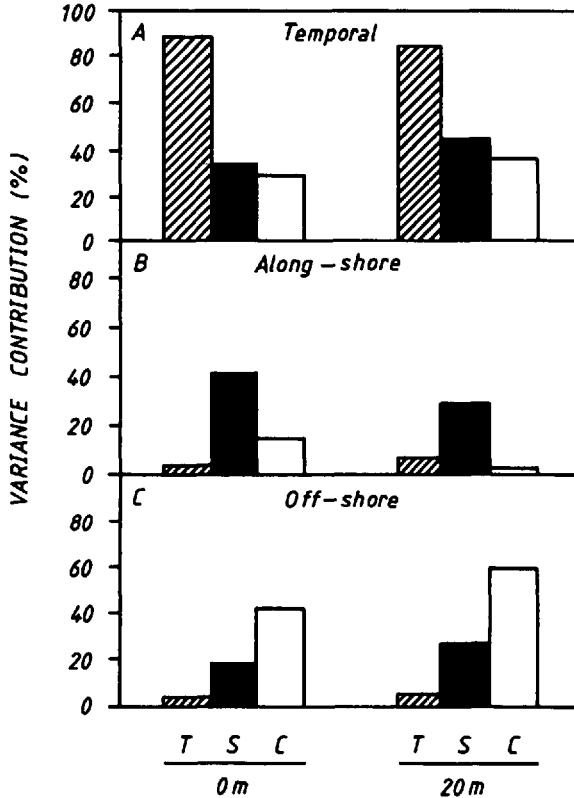


Figure 2. Variance component analysis showing the percentile contribution of the temporal (a), alongshore (b), and offshore (c) components to the total variance in temperature (T), salinity (S), and chlorophyll *a* concentration (C) at surface and 20 m waters.

(Fig. 2). This is probably a consequence of the sporadic and localized nature of the sources of salinity variance. Most of the variance in surface salinity, however, was due to differences among transects (i.e., alongshore component, Fig. 2b), but salinity variance at 20 m was largely temporal (Fig. 2a). This reflects the occurrence of strong, surficial salinity gradients along the coast both in the northern zone and around the Ebro Delta (see below).

Chlorophyll *a* concentrations showed little (<20%) alongshore variability, and had most of its variance associated to the offshore and temporal components (Fig. 2a,c).

b. Spatial and temporal structure

i. Temperature. The dominant pattern in surface temperature was the occurrence of warmer waters north of the Creus Cape and around the Ebro Delta, and a colder water mass around the Blanes Canyon (Fig. 3a). Temporal temperature variability was greatest in the southern zone and around the Blanes Canyon, whereas the northern

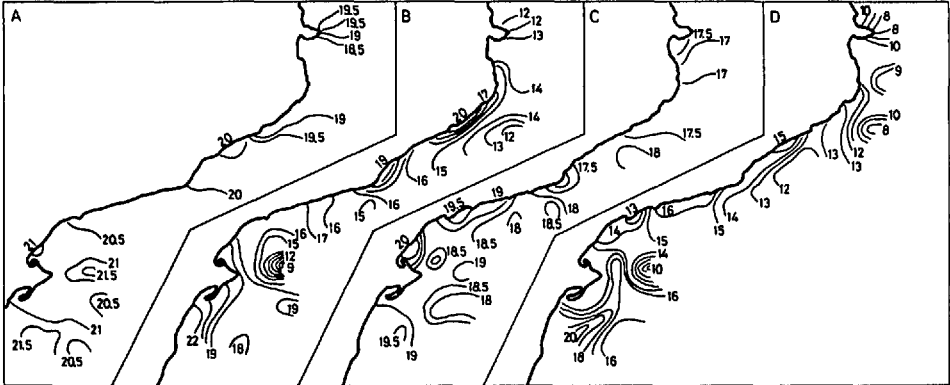


Figure 3. Spatial distribution of the isopleths of average temperature and the associated variability at surface (a,b, respectively) and subsurface (20 m) waters (c,d respectively).

zone showed little temperature variability (Fig. 3b). The thermal cycle was apparent in the time course of the average water temperatures for the different cruises (Fig. 4). Warmer surface temperatures in late spring and early summer compared to subsurface ones (Fig. 4) reflect the occurrence of shallow (<20 m) thermoclines, which are transient features of thermocline structure. Spatial heterogeneity in water temperature (Fig. 4), was small in early spring (period of vertical mixing, Fig. 5a), increased as summer progressed (stratified period, Fig. 5b), and decreased in the fall (thermocline erosion, Fig. 5c).

ii. Salinity. Dominant surface salinity patterns consisted of two regions of low salinity waters in the north and south of the Catalan coast (Fig. 6a), attributable to the influence of low salinity waters from the Rhone and Ebro rivers, respectively. Subsurface waters only showed the influence of the continental waters from the Rhone River (Fig. 6c). High temporal salinity variance was associated to sporadic occurrence and the extent of inputs from the Rhone River (Fig. 6b,d), whereas the smaller variability in the southern zone reflects a more permanent presence of waters from the Ebro River (Fig. 6b,d). Minimum average salinities in late spring (Fig. 4) reflect the intrusion of water from the Rhone River (Fig. 7a), which, in turn, contribute to increased salinity heterogeneity within the area (Fig. 4). Salinities remained high during the summer (Fig. 4), the reduced riverine influence leading to small horizontal salinity variability (Fig. 4), except for permanent gradients associated with the Ebro River (Fig. 7b).

iii. Phytoplankton biomass. The most salient spatial pattern in chlorophyll *a* concentrations (Figs. 8a,c) was the marked tendency toward biomass decrease offshore (Wilcoxon ranked sign test, $P < 0.001$) that reflects an ubiquitous tendency (e.g., McClain *et al.*, 1988; Smith *et al.*, 1988) toward reduced chlorophyll concentration at deeper stations ($r_{20\text{ m}} = -0.40$, $r_{0\text{ m}} = -0.45$; $P < 0.001$). The spatial structure of

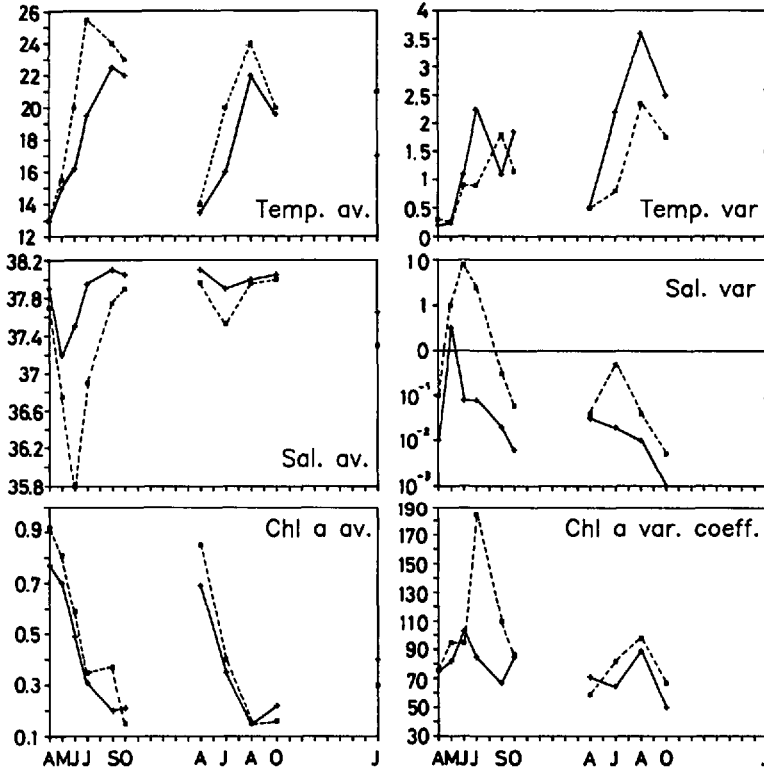


Figure 4. Temporal sequence of the average temperature salinity and chlorophyll a concentration, and their associated variabilities for surface and 20 m waters.

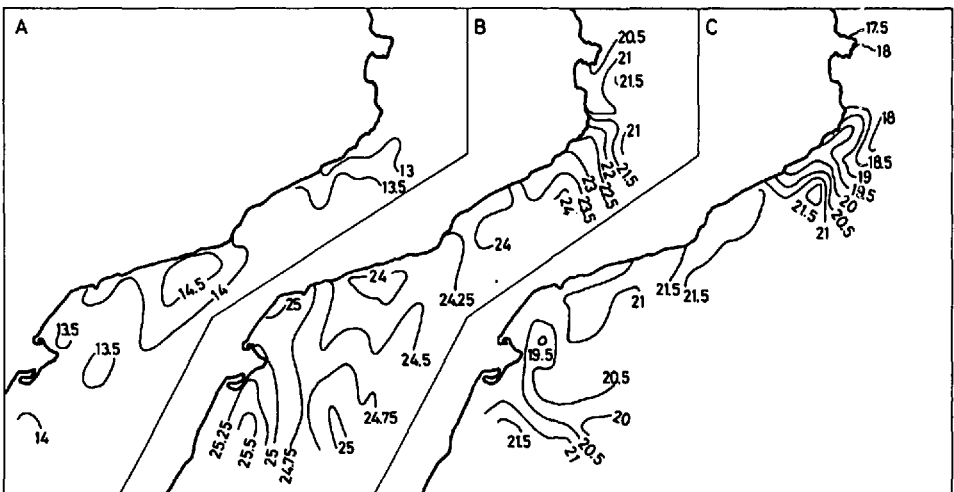


Figure 5. The surficial temperature distribution observed in April 1983 (a), August 1984 (b), and October 1984 (c).

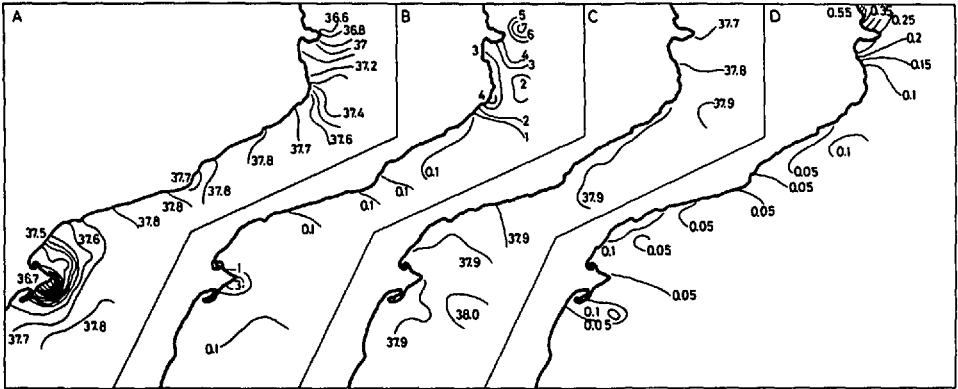


Figure 6. Spatial distribution of the isopleths of average salinity and the associated variability at surface (a,b, respectively) and subsurface (20 m) waters (c,d, respectively).

phytoplankton biomass was, therefore, closely related with the shape and slope of the continental shelf (Fig. 1), and average chlorophyll isolines closely contoured the profile of the continental shelf (Figs. 1, 8a,c). However, the coastal zone around the Palamós and Blanes canyons was characterized by very low algal biomass (Fig. 8a,c), with a local maximum off the Blanes Canyon (Fig. 8a), and a focus of low algal biomass in the platform was observed off the Ebro Delta (Fig. 8a,c). Maximum chlorophyll concentra-

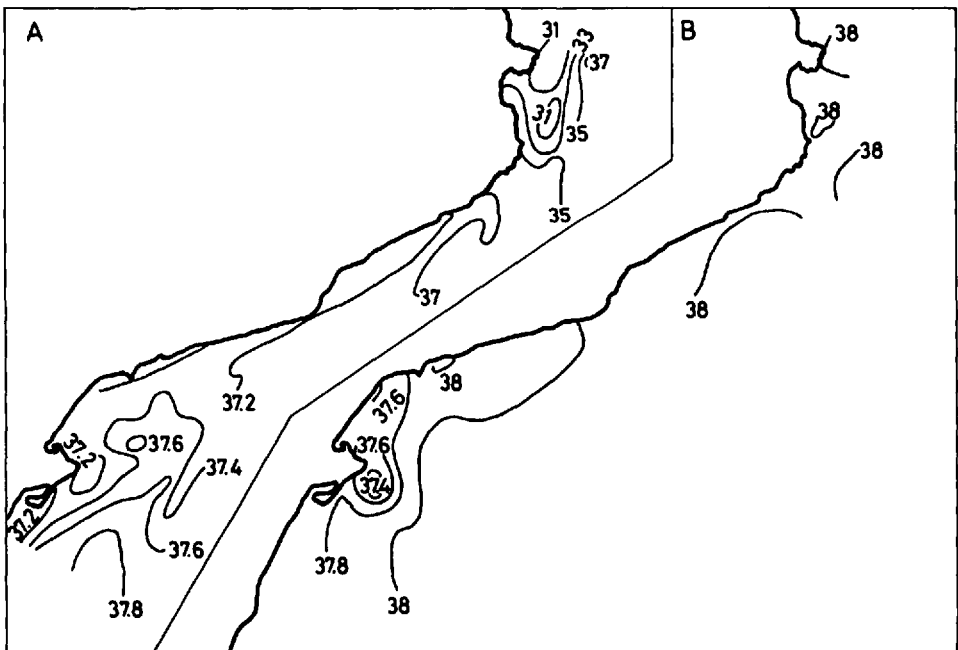


Figure 7. The surficial salinity distributions observed in June 1983 (a), and October 1983 (b).

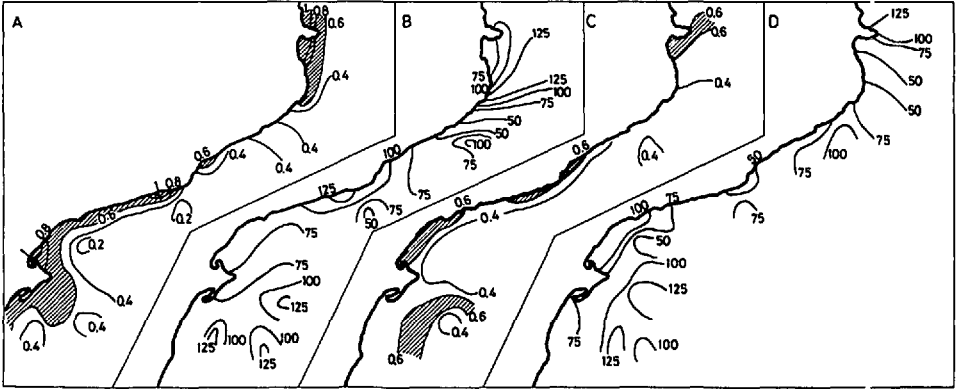


Figure 8. Spatial distribution of the isopleths of average chlorophyll concentration and the associated variability at surface (a,b, respectively) and subsurface (20 m) waters (c,d, respectively).

tions were observed off Barcelona, north of the Creus Cape, associated with low salinities due to Rhone River discharge, and near the coast north of the Ebro Delta (Fig. 8a,c), although high chlorophyll concentrations there were not associated to the lowest surface salinities (Fig. 6a).

The spatial distribution of temporal variance (as coefficients of variation) in phytoplankton biomass (Fig. 8b,d) resembled the spatial distribution of phytoplankton biomass (Fig. 8a,c), with variance reductions offshore and a tendency toward greater variability in areas with higher biomass.

Chlorophyll *a* concentrations remained low throughout the studied period (Fig. 4), and followed similar patterns in surface and 20 m waters ($r = 0.60$, $P < 0.01$), although surface biomass tended (Wilcoxon ranked sign test, $P < 0.001$) to be greater than that at 20 m. The temporal sequence of chlorophyll concentration showed a reproducible seasonal pattern (Fig. 4), inverse to that of temperature (Fig. 4), with a biomass peak in early spring (e.g., Fig. 9a), and decreasing values as summer progressed (e.g., Fig. 9b). Spatial variability in chlorophyll *a* concentrations was high for all cruises (coefficient of variation = 60–180%, Fig. 4), due to permanent variability, such as onshore-offshore differences (e.g., Fig. 9a,b), compounded with sporadic variability, such as that induced by intrusion of Rhone River waters (e.g., Fig. 9c).

c. The relationship between phytoplankton variability and hydrographic variability

The contribution of hydrographic variability to spatial phytoplankton variability was examined by calculating the correlation coefficients between phytoplankton biomass and hydrographic properties for each cruise (Fig. 10). Correlation coefficients between water temperature and chlorophyll concentrations declined from strong ($P < 0.01$), positive correlations in late spring and early summer to negative values in late summer (Fig. 10). This pattern, repeated for the two seasons studied, implies that

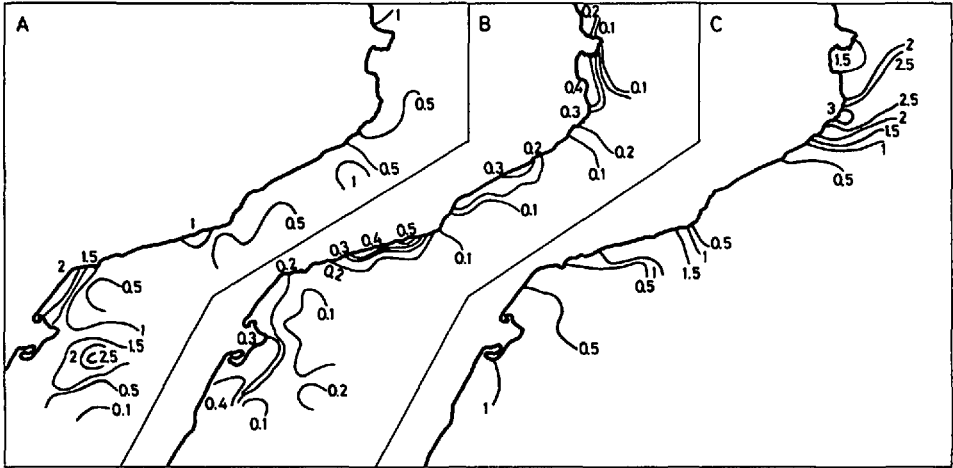


Figure 9. The surficial distribution of chlorophyll concentrations observed in April 1984 (a), October 1984 (b), and June 1983 (c).

locations with warmer waters support the highest biomass in early summer, the pattern reversing as summer proceeds. The temporal sequence in chlorophyll-temperature correlations (Fig. 10) was parallel to that of average chlorophyll (Fig. 4).

The incursion of riverine waters, with their associated nutrients, appears to enhance phytoplankton growth, because strong negative correlations between phytoplankton biomass and station salinity were observed (Fig. 10) for surface waters whenever low salinity waters occurred along the Catalan coast (Fig. 4). Further, these correlations show that riverine intrusions are important sources of spatial heterogeneity in phytoplankton biomass.

5. Discussion

Our analyses demonstrate that even the relatively small coastal area studied here displays great physical and biological diversity. Temporal variability in hydrographic properties results from seasonal processes (reflected in temperature changes, Fig. 4), and sporadic riverine discharges (Fig. 4). The spatial structures observed appear to be partially a reflection of temporal events, for longshore asynchronicities in thermocline development along the Catalan coast result in horizontal temperature differences, and localized riverine inputs produce the observed horizontal salinity patterns.

The great heterogeneity observed in phytoplankton biomass involved temporal and spatial variability. Temporal variability was related to the thermal cycle (Fig. 4), and to sporadic (unpredictable) intrusions of low salinity waters. Spatial variability in chlorophyll concentration was related to hydrographic variability (Fig. 10), resulting from the localized nature of river discharge, and asynchronisms in the thermal development of the water column along the coast (e.g., Townsend and Spinrad, 1986).

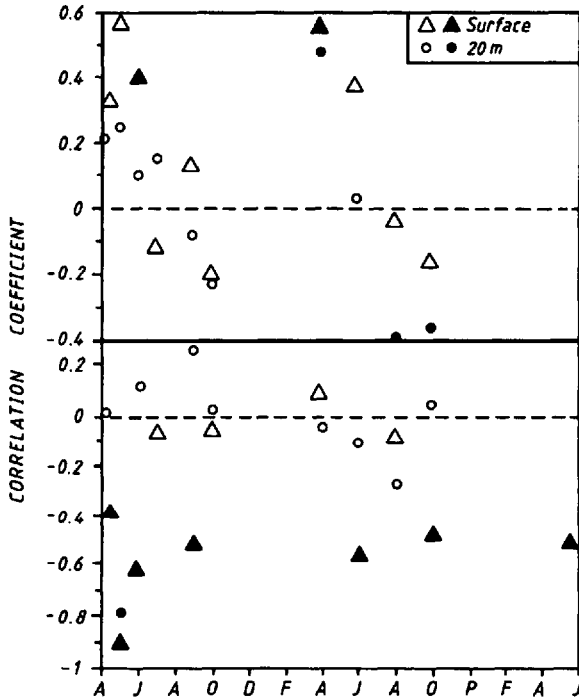


Figure 10. Temporal sequence of the correlation coefficient between chlorophyll *a* concentration and the temperature (above) and salinity (below) of surface and 20 m waters. Significant values ($P < 0.01$) are shown as full symbols.

Differences in the timing of the thermal cycle along the coast explain the shift from positive chlorophyll-temperature correlations in late spring to negative ones in late summer (Fig. 10). The highest biomass were observed in stations with warm waters in early summer, which presumably correspond to those showing earlier thermocline development; whereas high algal biomass in late summer were associated to stations with colder waters, which probably correspond to those experiencing advanced thermocline erosion. These observations support the strong relationship between the vertical dynamics of the water column (stratified or mixed) and the temporal development of phytoplankton populations (e.g., Margalef and Castellvi, 1967; Winter *et al.*, 1975; Pingree *et al.*, 1976).

Although phytoplankton biomass variability is related to hydrographic heterogeneity, both temporal and spatial (Figs. 4, 6), substantial heterogeneity in phytoplankton biomass persisted even when hydrographic heterogeneity was small (e.g., April 1983; Fig. 4). This may result if the environmental heterogeneity reflected by hydrographic variability did not yield an immediate response in phytoplankton biomass, as suggested by the existence of time lags in the response of phytoplankton communities to growth stimuli (Collos, 1986). On the other hand permanent phytoplankton biomass variabil-

ity is associated with the onshore-offshore differences that could be related to the permanent influence of bathymetric variability.

The horizontal distribution of phytoplankton biomass is also influenced by water circulation patterns. Anomalies to the onshore-offshore pattern around the Blanes Canyon (Fig. 8a,c) appear related to flow modifications associated to the canyons (Masó *et al.*, 1989), which may involve upwelling of deeper waters (Kinsella *et al.*, 1987; Freeland and Denman, 1982). A focus of low algal biomass over the shelf off the Ebro Delta (Fig. 8a,c) appears to result from the upwelling of slope water through a concavity of the shelf (Font *et al.*, 1989). This current modification may explain the high algal biomass downcurrent (*cf.*, Font *et al.*, 1989) from the upwelling focus (northern side of the Ebro Delta; Fig. 8a). Topographic features, therefore, provide the physical complexity necessary to support the great complexity in hydrographic conditions and water circulation that underlie the high biological variability characteristic of the coastal zone (*cf.*, Cannon and Lagerloef, 1983; Denman and Powell, 1984; Legendre and Demers, 1984; Barale and Fay, 1986; Traganza *et al.*, 1987).

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