Supply of nutrients to the Mediterranean photic zone along a persistent front

Mediterranean
Fronts
Nutrients
Primary production
Phytoplankton

Méditerranée
Fronts
Sels nutritifs
Production primaire
Phytoplancton

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ABSTRACT

Available hydrographic data for the Catalano-Balearic sea indicate the presence of a ridge-shaped elevation of the isopycnals, forming a front parallel to the Catalan coast, approximately mid-way between the Iberian peninsula and the Balearic islands. This structure appears as a divergence between the southwest-flowing coastal current on the Catalan side and a flow to the northeast on the island side, and is associated with consistent regularities in the biological distributions. Repeated studies of the mesoscale distribution of phytoplankton organisms have shown patterns that may be interpreted in relationship with the presence of the front. The divergence of the Catalan sea together with similar structures in the Ligurian area, the Tyrrhenian and along the southeast of Spain, probably form a continuum, along which hydrographical instabilities may travel preferentially. Estimates of the input of nutrients (phosphorus) from different sources into the euphotic zone of the Catalano-Balearic sea suggest that the contribution of the Catalan front and similar structures is significant ; this may help to explain the apparent excess of primary production in relationship with the classically recognized fertilization events.

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RÉSUMÉ

Apport d'éléments nutritifs à la zone euphotique méditerranéenne le long d'un front persistant

Des données hydrologiques collectées en mer catalano-baléare montrent de manière persistante une élévation des isopycnes qui dessine une structure allongée formant un front parallèle à la côte catalane, à peu près à mi-chemin entre la péninsule ibérique et les îles Baléares. Cette structure peut être interprétée comme une divergence entre le courant côtier dirigé vers le Sud-Ouest du côté catalan, et un courant vers le Nord-Est du côté des îles. La distribution des organismes phytoplanctoniques et d'autres variables biologiques étudiées montrent des régularités associées à la présence du front. La divergence de la mer catalano-baléare et les structures similaires de la Mer Ligure forment probablement un continuum le long duquel des instabilités hydrologiques peuvent se déplacer préférentiellement. L'évaluation des apports en éléments nutritifs (phosphore), à partir de différentes sources dans la zone euphotique de la mer catalano-baléare, indique que la contribution du front catalan et des structures similaires de la Méditerranée occidentale peut être significative ; nos calculs suggèrent quelques explications au problème que pose l'excès de production primaire qui semble exister lorsqu'on prend en compte les seuls mécanismes de fertilisation habituellement reconnus.

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INTRODUCTION

Although relatively small in extension, the Mediterranean is an area of considerable hydrographical heterogeneity. The functional anatomy of a sea, in the terms used by one former author (LeBlond, 1983), is an expression of its aptitude to produce and support life. Primary production is certainly related to the input of external energy (Margalef, 1978 ; Margalef, Estrada, 1981), which is a good predictor of the dominant phytoplankton life-forms.

Different power spectra, from advection to viscosity, could characterize different sites of production. Because the inputs of external energy, and their variance, are related to the total system extension ("window size"), the Mediterranean lacks the powerful forcing systems of the upwelling areas associated with the oceanic Eastern currents. The strongest production mechanisms in the Mediterranean may be those associated with the Alboran gyres and the chimneys of vertical mixing in the Gulf of Lions.

Even the modest mechanisms whereby work is done and production enhanced in the Mediterranean have remained for too long unknown or unappreciated. Work on Mediterranean phytoplankton has been mainly based on coastal laboratories and typically included the description of an annual cycle, with some speculation directed to the linkage of biomass, production and specific phytoplankton composition with local factors such as nutrient supply or thermocline evolution. One of the authors of the present study (RM), after many years of work in the coast of NE Spain, arrived at the conclusion that primary production was relatively modest, but rather stable over the years, and might be geared to a combination of fertilizing events. Although the individual events were somewhat random, their cumulated effect, over each year, was far less variable (Margalef, 1968 ; Margalef, Herrera, 1963). One fertilizing event comprises the breakdown of the thermocline, which occurs in November and lasts for some two weeks. The next event is a moderate upwelling, due to the action of wind, that brings to the surface water present at the shelf break, relatively rich in nutrients as a result of winter mixing ; this takes place in February and lasts about ten days. Later, from about the third week of March until May, surface water of Atlantic origin spreads and often reaches the coast, bringing some nutrients on which characteristic populations of *Rhizosolenia* and *Nitzschia* develop ; this event may be effective throughout a period of perhaps at least 100 days. This model accepts that the mechanisms enhancing production are concentrated in a (productive) season, from November to May. During the summer months, with well-stratified water, continued recycling, with a progressive decrease of the available nutrients, might be suspected. But life, from dinoflagellates to fishes, is found to continue in a way that seems almost miraculous. Furthermore, computation of the phosphate made available as a result of the identified events produced values that were too low, even after a generous estimate of the average number of recyclings in the photic zone. Runoff from land was considered to be low, as most phosphate was insoluble and came rapidly to the sediment.

It thus became necessary to look offshore. Patches with highly productive phytoplankton were identified in summer, and eventually associated with domes. The "dome" that lies regularly between Nice and Calvi (Corsica) has attracted special attention (Minas, Blanc, 1970 ; Coste, Minas, 1977 ; Belluau *et al.*, 1982 ; Prieur, 1979 ; 1981 ; Boucher, 1984). In fact, the separate domes resemble to be the coils of a great sea serpent, a continuous ridge that extends at least from Corsica to Eivissa (Ibiza). For simplicity, we shall use the term "front" to refer to this ridge although, from the hydrographical point of view, it may be appropriate to distinguish two associated fronts, one on the Catalan and the other on the Balearic side. Such structures may be a general feature of the Mediterranean. Comparable domes and fronts were recognized in the Tyrrhenean (Margalef *et al.*, 1966) ; in a transect from Corsica to Barcelona (Margalef, 1971) in March 1970, the front was clear, marked by high salinity, rich nannoplankton and high density of copepods, bounding diatom-rich coastal water. Front-building may also be obvious in the Adriatic (Zore-Armanda *et al.*, 1983). Our fronts seem to be appreciably different from fronts associated with tides, with important currents and with upwelling systems elsewhere, on which more attention has been centered. Another approach came through the study of the deep chlorophyll maximum (Estrada, 1982 ; 1985 *a* ; *b*). In the stratified summer water, the amount of chlorophyll is high, and production not too low, in a thin layer around 60 to 90 m depth. A dynamic unstable equilibrium between light and nutrients may be at its origin, but there is probably also some lateral supply of nutrients, as such maxima may be clearly rooted laterally on the fronts. At all events, the deep chlorophyll maxima may help to explain the persistence of biological activity throughout the year.

We soon became convinced of the continuity and importance of a front running more or less parallel to the Catalan coast, midway between the continent and the Balearic islands and probably extending from the north of Eivissa to the north of Corsica, although it seems to continue south of Eivissa. Once recognized, it proved impossible to find any appropriately sited hydrographic section in which it did not appear. Specifically, the presence and situation of the front has been confirmed in the months of February, March, April, May, June, July, October and November (Fig. 1 A, C). It is rooted on maximal depths (2 000 m) and shows up well in maps of dynamic topography of 500 above 1 000 db (Ovchinnikov, 1966). This indicates that a great deal of kinetic energy is associated with the front, which in turn explains its persistence. On the Catalan coast side, water flows to the southwest ; on the Balearic islands side, there is a slower current flowing to the northeast. The ridge of nutrient-rich water in the middle can be interpreted as a divergence, with upwelling of deep water, but there are other possibilities. The relatively high instability of the water column in the zone between the two currents can favour the progression

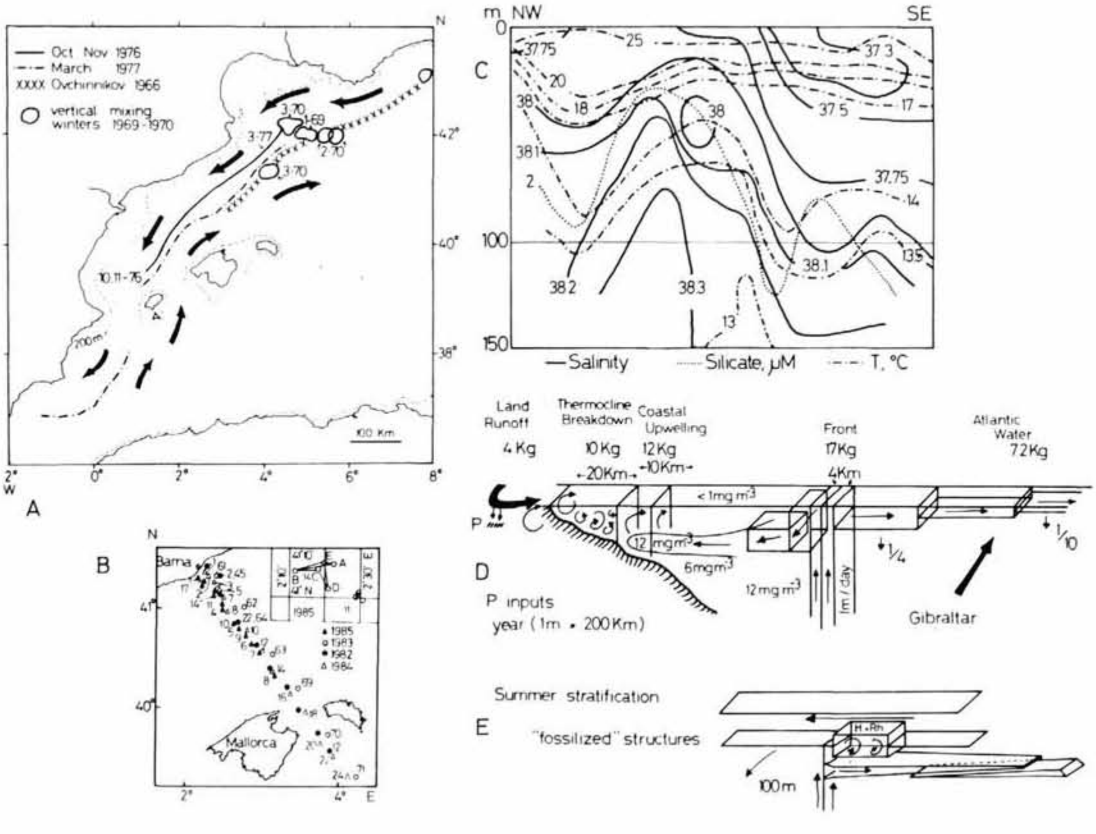

Figure 1

A) *Location of the front, according to different surveys and studies.* B) *Positions of the transects and stations referred to in the text (cruises* PEP-82, PEP-83, PEP-84 *and Fronts-3-85).* C) *Schema of the vertical distribution of several physico-chemical variables during the* PEP-82 *cruise. The section corresponds to the transect from stations* 1 *to* 12 *(July* 1982*) in Figure* 1 B. D) *Estimates of phosphorus inputs for a slice of water down to the bottom,* 1 m *wide and extending at least* 200 km *from the coast to the centre of the basin.* See *text for details.* E) *Part of the offshore structures in summer. H stands for* Hemiaulus *and Rh for* Rhizosolenia. See *text for details.*

of eddies, derived, for example, from meanders of the limiting currents. Potential vorticity arguments predict (Font *et al.*, 1988) that only cyclonic eddies will develop and enhance their cyclonic motion, producing discontinuous upward transport of deep water. The position 41° N, 3° E is a readily remembered reference for the front. Eventual shifts are small, although in March it may move a little closer to the coast. The expansion of blue water of Atlantic influence that advances towards the coast around the feast of Saint Joseph (19 March) is commemorated in local fishing traditions ; this water spreads as a thin layer over the front (Margalef, Herrera, 1963). In consequence, satellite imagery is not always reliable to pinpoint the position of the principal hydrographic structure. Minor shifts in the position of the front may show in series of data from studied stations nearby (Margalef, Castellví, 1967). One of the most exciting properties of the front is that the well-known chimneys of strong vertical mixing identified in winter in the Gulf of Lions (Nival *et al.*, 1972 ; Voorhis, Webb, 1970), are exactly superposed on it, probably move along it, more or less cut or deformed, and may be present as patches of instability further south. The appropriateness of the front to receive energy through cyclonic vorticity calls to mind an apparently amusing, but actually serious, short paper by Isaacs *et al.* (1975), published in *Nature* some years ago. Progression of eddies or other irregularities might have the regular form of waves. Internal wave activity observed in the Balearic side (Salat, unpublished data) disappeared at the front ; at all events, internal waves observed at the Catalan coast side were unrelated to those in the Balearic side. Any model to explain long term fluctuations through interaction between the atmosphere and the water, in which the sea acts as accumulator of heat, could lead to different spectra inside or outside the front. Many possibilities and suggestions can result from the comparison of this front with shelf-break fronts or fronts associated with westerly currents in the different oceanic regions. It could provide another example of many-celled structures along an *x-y* plane ; the study of differences along *y*, more or less parallel to the coast, commends itself as a future and valuable research project.

The aim of this paper is to estimate the contribution of the front to nutrient input in the euphotic zone and to show that it may be significant in the context of Mediterranean production. Partly because of the outstanding position of the front, more or less independent of the small-scale hydrographic structures all around, partly because physical oceanographers will provide better and more complete information, we shall not deal here with physical and chemical characteristics of water at the front. In general, salinity is above 38.3 in the front, and nutrient concentration is relatively higher than elsewhere. Silicate is a very reliable indicator. It is to be hoped that the physical oceanographers will be able to provide estimates of the upward water motion at the front and the amount of nutrients injected into the euphotic zone.

It may also be recalled that land- and coast-originated pollution may be confined in the coastal compartment, where it is driven towards the southwest, whereas blue and cleaner waters are still found in the centre of the main anticyclonic gyre, under a more generous supply of Atlantic water. In this context, differences in metal concentrations between both sides of the front could be expected.

PLANKTON AND THE FRONT

Surveys and basic data

Some evidence existed already in relation to the front in the area of the Catalano-Balearic sea. Since 1982, a number of cruises have been carried out with more precise objectives, centering around a transect running from Barcelona to a point beyond the channel between Mallorca and Menorca (Fig. 1 B). These were :

PEP-82, 12-28 July 1982 (Estrada, 1985 *a* ; Margalef 1985) ;
PEP-83, 30 June-17 July 1983 (Estrada, 1985 *b*) ;
PEP-84, 21-27 May 1984 ;
Fronts-3-85, 15-26 March 1985 ;
Fronts-6-85, 1-6 June 1985.

In addition, information is available from recent cruises with other objectives but covering the same general area.

The incentive for the PEP (Producció Estival Profunda : Deep summer production) cruises was the analysis of production at the deep chlorophyll maximum (DCM). In July, the DCM was duly identified (Estrada, 1985 *a*), generally below 60 m, with concentrations at some points of more than 2 mg/m^3. The topography of the DCM layer clearly reflected the presence of the front and was duplicated up to a certain point by the topography of the layer of maximum nitrite. The significance of such a layer has long been a major preoccupation with us (Margalef *et al.*, 1966 ; Blasco, 1971). One further impression gathered from the examination of the transects, checked against partial data on vertical profiles of temperature and salinity, was that the DCM could be made up of layers or "pancakes" of water, with particular populations trapped in them (Margalef, 1985), and limited by a reduced diffusion layer along the boundaries of the "pancakes". Taken together, such pancakes could be considered as a structure, frozen or "fossilized" (Fig. 1 E) below the seasonal thermocline. As the DCM could become thinner with distance from the front, we found it reasonable to suspect that the DCM was "nourished" laterally, at least in part, from the front itself. As evidence of instabilities is frequent in the front, we believe that boluses of mixed water could expand easily along the corresponding isopycnals. Above the DCM, at the level of the stronger gradient of the thermocline, the boundaries were not so clear, but blooms with *Hemiaulus* and *Rhizosolenia* were repeatedly (Margalef, 1985) observed in the proximity of the front. Distributions of chlorophyll and phytoplankton in the coastal water, between the front and the coast, were much more irregular, suggesting some convergence or irregular mixing motion.

Phytoplankton and production

Detailed data on nutrients and primary production concerning the July 1982 and 1983 cruises have been published in Estrada (1985 *a* ; *b*). Accounts of the methodology are also given in these papers. Chlorophyll was determined by fluorimetric analysis of acetonic extracts. Primary production experiments using the ^{14}C method were carried out using simulated *in situ* incubators on deck of the ship. Concentration of chlorophyll close to the surface could be 1.5 to 2 times higher in the front than elsewhere. Chlorophyll concentration was also elevated in the deep maximum, and could reach much higher values than in the shallower levels. As an example, Figures 2-3 show the distribution of several hydrographic and biological parameters during the PEP-84 cruise.

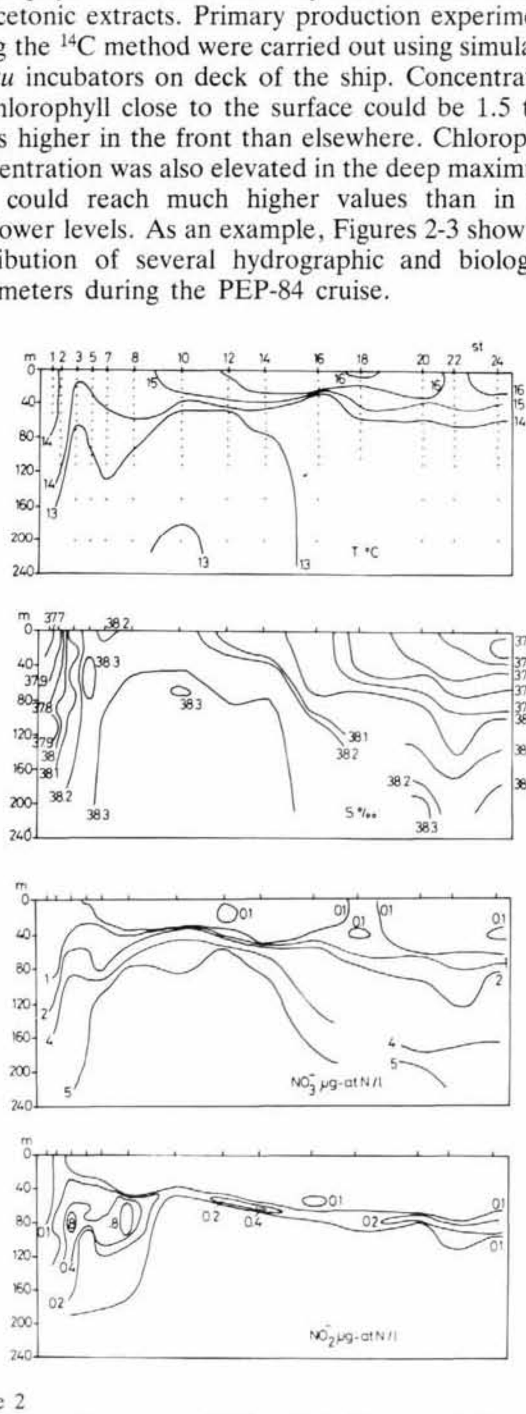

Figure 2
Distribution of temperature (T °C), salinity (S), nitrate (NO_3^-, µg-at N/l) *and nitrite* (NO_2^-, µg-at N/l) *along the first transect of* PEP-84 *(see position of the stations in Figure* 1 B*).*

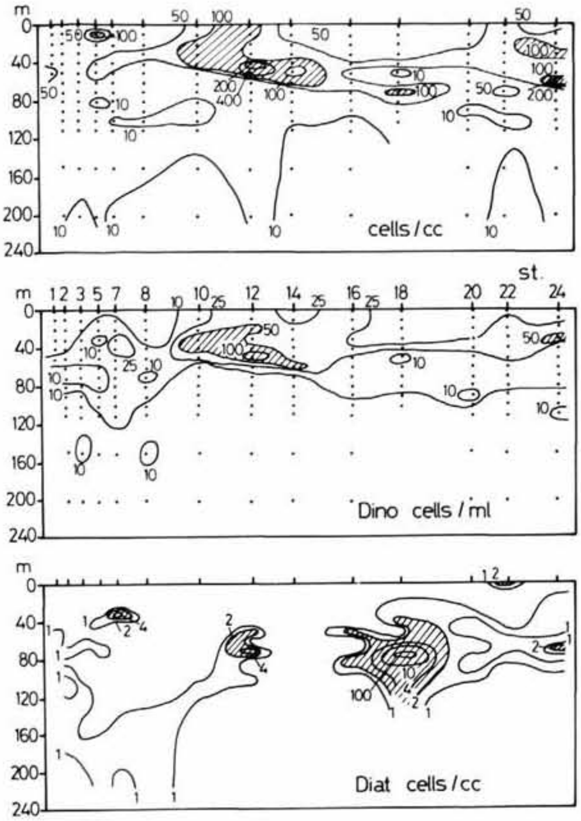

Figure 3
Distribution of oxygen (O_2, ml/l), chlorophyll (chlor. a, *mg/m^3), concentration of phytoplankton cells (cells/ml) and of diatoms (Diat. cells/ml) along the first transect of* PEP-84 *(see position of the stations in Figure* 1 B*).*

The productivity index (gC fixed/g Chlorophyll *a*/hour) was strongly dependent on light (and presumably nutrients) with values up to 3 or more in the upper layers and as low as 0.3 in the level of 1 % of available surface light (approximately the depth of the DCM in July). In consequence, production associated with the DCM does not seem as high as might be expected, perhaps no more than 0.5 mg C/m^3/h or about 50 mg/m^2/day.

Estimates of primary production in 1982-1984 (PEP cruises) and March 1985 are given in Table 1. Although the number of experiments is too low, some remarks may be permitted. During the stratification period, production near the front is increased over production in the central area, between the front and the Balearic islands, especially when the differences in the depth of the euphotic zone (which may be large, as in May 1984) are taken into account. Comparison with production in the coastal waters is more difficult because other fertilization mechanisms may be operating there, and mixing tends to be more intense over the shelf than further offshore. The role of the front in enhancing primary production may be much more effective during the mixing period. The results of the cruise Fronts-3-85 may provide some clues, although bad weather prevented a more complete sampling. During this cruise, the front was located closer to the coast than in the previous ones. Chlorophyll concentration in the upper water layers near the front exceeded 1 mg/m^3 and reached in some locations 2 mg/m^3, a remarkably high value for the open Mediterranean. The complexity of the isolines of the physico-chemical parameters suggested a high dynamism of the hydrographic structures. Repeated casts at the same nominal positions (stations 11 and 14, Fig. 1 B) showed the presence of strong hydrographical gradients within small distances (Fig. 4). Profiles of chlorophyll and primary production corresponding to different times of the day are given in Figure 5. The vertical distribution of the physico-chemical variables at the beginning of station 14 (Fig. 4) showed nutrient-rich water at shallower depths than at station 11. However, the upper 50 m of station 14 were covered by low-salinity water of presumably coastal origin, and the biological properties, at the beginning of this station, were in sharp contrast with those of station 11, where there was strong mixing typical of the frontal situation. The highest midday values of carbon

Table 1
Estimates of primary production per unit surface and averaged for the integration depth (approximately down to the 1 % irradiance level) for stations occupied over or outside the front during a series of cruises. The number of the station is given in parentheses. Calculations are based on ^{14}C fixation by samples from 6-7 depths in simulated in situ *incubators.*

	Catalan coast side		Front		Between the front and the islands	SE of the Balearic islands	
PEP-82 July 1982							
mg C/m^2/day	149 (45)		116 (22),	274 (63)			
mg C/m^3/day (Average)	1.9		1.5	3.2			
PEP-83 July 1983							
mg C/m^2/day	211 (61)	227 (62)	263 (63)		236 (69)	267 (70)	311 (71)
mg C/m^3/day (Average)	2.8	2.7	3.5		3.1	3.1	4.1
PEP-84 * May 1984							
mg C/m^2/day	360/520 (28) **		412 (29),	357 (30)	372 (31)	279 (32)	262 (33)
mg C/m^3/day (Average)	6/8.7		6.9	6.0	4.1	3.1	2.9
Fronts-3-85 March 1985							
mg C/m^2/day	360/470 (14) **		862 (11)				
mg C/m^3/day (Average)	9/11.7		21.5				

* The positions of the PEP-84 stations (not shown in figure 1 B) are : 28, 41°9.9′ N, 2°26′ E ; 29, 40°36.3′ N, 2°48.7′ E ; 30, 40°22.5′ N, 3°9.3′ E ; 31, 39°56.9′ N, 3°33.8′ E ; 32, 39°35.7′ N, 3°43.0′ E ; 33, 39°21′ N, 4°5′ E.
** The two figures are estimates obtained using two different methods.

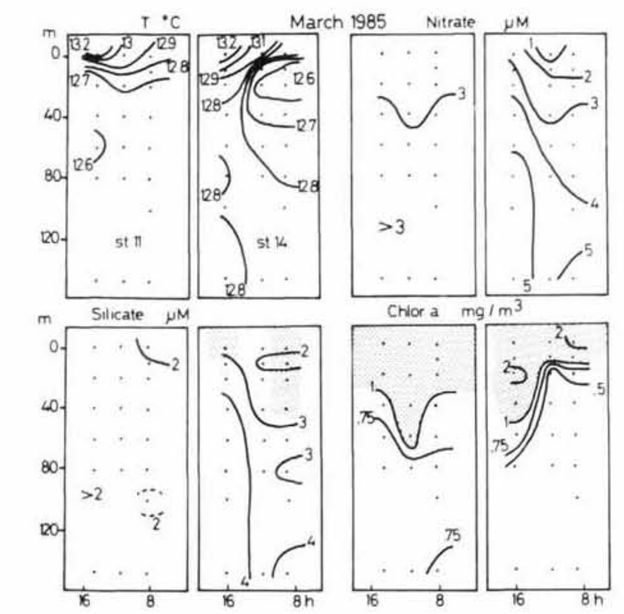

Figure 4

Variation of temperature (T °C), nitrate (μM), *silicate* (μM) *and chlorophyll (chlor.* a, mg/m³) *for repeated hydrographical casts at station* 11 *(left of each group) and* 14 *(right) of cruise Fronts*-3-85 (see *position of the stations in Figure* 1 B, *inset). The numbers in the abscissa give the time* (GMT) *of the day. Salinity was measured only for the first cast of station* 11 *and the first and third of station* 14. *The shaded areas in the silicate sections indicate salinities lower than* 38.

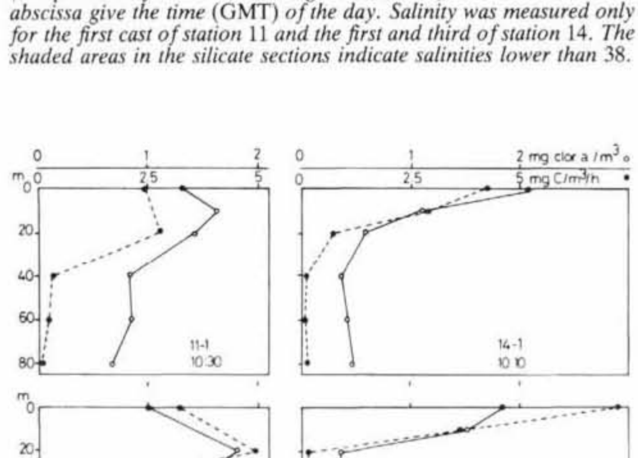

Figure 5

Vertical profiles of primary production for different casts of stations 11 *and* 14 *of cruise Fronts*-3-85. *Central times of incubation* (GMT) *are given in each graph.*

fixation corresponded to the surface samples of station 14, but primary production and chlorophyll concentration per m² were higher at station 11 (Tab. 1). From Table 1, we can estimate that the proximity of the front may enhance primary production by 50-200 mg/C/m²/day above other areas ; this may be related to a direct supply of nutrients as compared with the recycling that occurs everywhere. Assuming a concentration of 12 mg P/m³ in deep, nutrient-rich water, and a relation in weight C : P of 40 : 1, a difference of 100-200 mg C/m²/day could be associated with an upward transport of water, at the front, of 0.2-0.5 m/day.

The distribution of phytoplankton during the July 1982 cruise has been described in Margalef (1985) and Estrada (1985 *a*). Cell concentrations in the DCM reached 500/ml over the front, with diatoms as the dominant group. Small flagellates and dinoflagellates were abundant throughout the euphotic zone. Coccolithophorids were present only in the proximity of the front and in the coastal area. Cyanobacteria *(Synechococcus ?)* were only sporadically abundant and we are not inclined to attribute a major role to them (concentrations of phycobilins measured in a June 1986 survey have confirmed this view). The general features of the phytoplankton distribution in the July 1983 cruise appeared to be comparable, but the data are still being processed. Earlier in the year, as the PEP-84 data showed, there may be a well formed DCM offshore, and mixing near the coast (Fig. 2). In May 1984, the DCM was located at depths of about 40 m (approximately 3 % of surface irradiance) over the front and at 60 m further offshore. Chlorophyll concentrations and phytoplankton population densities reached the highest values near or over the front. Small flagellates and dinoflagellates were the dominant group almost everywhere (Fig. 3) ; diatoms were only abundant in the DCM layers of the front and also at depth in the stations close to the channel between Mallorca and Menorca.

During the cruise Fronts-3-85, 20 l water samples, which were filtered through a net of 40 μm mesh size, were obtained at station 11, at the front, and station 14, about 7 miles away in the direction of the coast (Fig. 1 B). Four casts were made at each station, at approximately 6-hour intervals. Whole water samples were also taken for study with the inverted microscope.

The drift of the ship during the stations allowed a dissection of the structures in such a way that the general gradient could be visualized. The pattern observed was typical of situations in which stratified water contacts an active front, with mixing at the boundary. The following characteristics were noted :

1) Nannoplankton was dominant in the front ; the concentration of chlorophyll was high, but the number of organisms retained in a 40 μm-mesh net was low.

2) Large cells *(Coscinodiscus, Halosphaera)* that presumably tend to sink, were common and dispersed everywhere.

3) Foraminifera were common in the front, and more heavily calcified than specimens found at a few miles distant from it.

4) Away from the front, stratification increased. The responses of the species were different, and the small scale structure very rich. *Thalassiosira* multiplied close to the front, and its cells sank quickly. As stratification increased and layers differentiated, *Dic-*

tyocha and *Ceratium* were common in top layers ; *Rhizosolenia, Nitzschia* and *Hemiaulus* were close to the top layers (in other cruises the same vertical distribution was observed in the eastern or central side of the front) ; *Ditylum* and *Chaetoceros* were at intermediate depths ; and *Planktoniella sol* and *Ceratium platycorne* were in deeper water. *Bacteriastrum* was distributed like *Chaetoceros,* but suggesting an earlier development.

Such observations can be compared with others that reveal the contrast between mixed and productive spots and more stratified surrounding water [*cf.* for example the study of diversity and spectra of diversity of phytoplankton made in 1968 in Castelló (Margalef, 1969), observations at the margin of red tide patches and so on]. As the speed of change slows down around the more productive spots, the populations diversify and it would be of interest to describe the richness of the generated patterns. But this can be done only in more general terms, singling out simply the complication of structures evolved in an unpredictable manner over a field of low available energy.

RELATIVE CONTRIBUTIONS TO PRODUCTION, MODELS AND PERSPECTIVES

All effective research is constructed in support of or opposition to certain systems of beliefs or hypotheses, however inexact or even erroneous these may be. Provisory recognition of the importance of the front poses a number of new questions that could be better specified on the basis of preliminary and very tentative assumptions.

We shall suppose that phosphorus is the main limiting nutrient. Some early experiments suggested this (Margalef, 1963) and, in addition, budgets for phosphorus have better worked out than for other nutrients. In any case, the main conclusions should not change if the calculations could be repeated assuming limitation by another nutrient such as nitrogen (on this subject *see* Berland *et al.,* 1980).

As reference values for final concentrations of available phosphorus we take :

Deep water, below 200 m
0.4 μm or 12 mg P/m^3 (against 2.4 μM in major oceans).
Mid-deep, border of the shelf
6 mg P/m^3.
Atlantic inflow, at Gibraltar
2 mg P/m^3.
Surface of the Mediterranean much below
1 mg P/m^3.

It has been assumed that, in certain situations, turnover of phosphorus may proceed more rapidly than recycling of nitrogen or carbon. This is often suggested by leakage or excretion in protists and animals. But if very labile phosphorus compounds exist, others, like DNA, have a slower turnover. Recognizing this problem, at this stage we shall assume parallel and proportional exchanges of P, C, N.

According to Béthoux (1981), a little more than 2 g P/m^2/year is available, in the Western Mediterranean basin, on average. Of course, local values may depend on the intensity of small-scale processes. The total supply of phosphorus may be made up of 30 % from land runoff, 68 % in the form of vertical transfer from deeper layers, and 2 % as surface fluxes. Accepting a (weight) ratio C : P of 40 : 1, this could allow a potential fertility close to 90 g C/m^2/year, even without recycling (*see* also Sournia, 1973). Allowing for partial recycling in the photic zone, potential primary production may be much higher.

Against these data we can examine schematically the significance of the front. To this end, let us consider a slice of water, down to the bottom, 1 m wide (*y*-axis) and extended at least 200 km (Fig. 1 D), from the coast to the centre of the basin. As the slices converge in the centre, estimates could require correction, but this is unimportant at this stage. More important are the bottom and coastal irregularities, which are able to enhance mixing and to increase fertility in an irregular and poorly-known manner. In consequence, the average slice is a highly idealized unit of reference, as are the separation and characterization of the different mechanisms of fertilization.

The contribution of seasonal and regular fertilizing mechanisms operating over large areas could be summarized as follows :

1) Breakdown of the thermocline in November and local mixing that lasts for two or three weeks of strong production. Water with less than 1 mg P/m^3 passes to a concentration verging on 6 mg P/m^3. The importance of the event is hard to estimate with extant data, because we do not know what happens offshore. A conservative estimate would be 20 km × 100 m deep, or 100 × 20 000 × 5 (mg P/m^3) = 10 kg P contributed to the slice.

2) Coastal upwelling under the force of local winds that bring to the surface nutrient-rich water present close to the shelf break, 50-100 m depth ; the presence and amount of such water at the appropriate level is related to the strong mixing processes a few weeks earlier (December). This local upwelling may extend for one month, during February and March and usually in February, and may be effective over an area at least 10 km wide, parallel to the coast. The contribution of phosphorus may be 100 × 10 000 × 12 (mg P/m^3) = 12 kg P.

3) Inflow and expansion of water of Atlantic origin in March-May, beginning on about 20 March and affecting, at least on the Catalan side of the front, a very thin layer of water (less than 50 m). It is hard to provide estimates. If the inflow at Gibraltar is 45 000 km^3/year, with a content of 2 mg P/m^3 at the outset (2 t P/km^3), an even distribution over the Mediterranean could produce 45 000 × 2 ×10^9/2.5 × 10^{12} m^2 = 36 mg P/m^2. If the reference slice has 200 000 m^2, the total input may reach 7.2 kg P.

Other inputs can be linked to ergoclines (Legendre, Demers, 1985) of constant position, as the coast and the front.

4) The Mediterranean basin under consideration has several important rivers (Rhône, Ebro) and the total runoff from land may amount to nearly 100 km^3/year. Estimates of the terrestrial contribution through runoff may be exceedingly diverse. On the basis of the contribution from the human population in the basin, and accepting that this amount is supported by maximal concentrations measured in rivers, total contribution in phosphorus to the Western Mediterranean may exceed 25 000 t per year (Aubert, Aubert, 1985). More realistic estimates, based on actual average concentration of phosphate dissolved in rivers and on the consideration that particulated material sediments rapidly in the lower segments of the rivers and in the deltas, point to values of phosphate below 7 000 t per year, which distributed along more than 1 500 km of coast would give a quota per m of approximately 4 kg P/year.

5) We come to the contribution of the front. Everything depends on the estimate of the deep water that is injected into the photic zone per unit of time in a 1 m wide slice normal to the front, bearing in mind that the intensity of the process may be highly variable in time. As a first guess, we shall assume a 4 km wide front with average upwards speed of 1 m/day, and 12 mg P/m^3 in ascending water. This gives $4\,000 \times 365 \times 12 = 17$ kg P/year.

Summing up the different contributions, referred always to a slice 1 m wide approximately perpendicular to the coast and to the front, and some 200 km in length, we should obtain :

	kg P	% of total
1) local mixing at breakdown of thermocline	10	20
2) upwelling at shelf break	12	24
3) surface influx from Atlantic	7.2	14
4) land runoff	4	8
5) contributed by front	17	34
Total	50.2	100 %

Initial enthusiasm may have led to an over-evaluation of the contribution of the front, but our considered opinion is that it cannot account for much less than 1/3 of the total. One difference with Béthoux's estimates concerns the contribution of land runoff, for the reasons explained : we cannot accept exceedingly high concentrations of phosphate in solution in river water, although we agree that further research on the transport of different forms of phosphorus is urgently called for.

The total amount of over 50 kg P per slice and year may represent a little more than 0.25 g P/m^2/year, obviously unevenly distributed. This is an external input allowing for "new" production, not much more than 10 g C/m^2/year. The figure seems low but is sufficient. Now, the question remains of obtaining some estimate of the amount of recycling and losses to deep water, and of what may be considered as new production. If 1/5 of the primary production is lost down to the deep sea, with no outside contribution, the primary production of the system would die down at a rate 0.8^n (where n is the number of cycles) ; a contribution of 0.2 would keep it even, at a production rate of 1. Then, under such assumptions, the computed input of P could support a primary production of the order measured over the Western Mediterranean basin.

Of course, the most simple, but probably even more incorrect approximation would have been to assume a single annual uniform mixing, as if the Mediterranean were a monomictic lake, able to introduce in the photic layers a column 100 m high with an extra 3 to 4 mg P/m^3, that is, 0.3 to 0.4 g P/m^2/year, giving another estimate of the same order as ours.

To a certain extent, the frontal systems might be compared to a chemostat or to a river, in which upwelled nutrients mix and recycle progressively, "spiralling", as some limnologists would say, downwater, going away from the front.

A very simplified model of production, proposed by one of us (Margalef, 1978), has the form :

Production = input (non renewable resources, new production) + external energy × [covariance in the distribution of the factors of production (renewable resources, cycling)].

We may safely assume that the fraction of new input decreases gradually with distance from the front, especially in the central part or on the Balearic islands side of it. On the coastal side, perturbations leading to confusing situations may arise, especially during the cold season. By choosing a large scale, or large dimension, the input from outside may be internalized, giving the expression.

(Production, P) =(external energy, A) × (covariance in the distribution, C), and after taking derivatives with respect to time

$$dP/dt = a\, dA/dt + b\, dC/dt\ .$$

A basic ecological assumption in population dynamics and in succession theories should lead to a linking of the deceleration of production with a decay of available energy and a more advanced segregation in the distribution of the factors of production (cells, light, nutrients, *etc.*). Comparison between stations close to the front and stations 50-100 km distant from it — especially in the central area, where gradients seem to be more regular — may be helpful for the understanding of the changes in plankton populations along the projection in space of what may be essentially a succession process. As a working hypothesis, based on observed trends and averages in the area, we submit a number of values and relations that could be tested in future surveys (Tab. 2). These data will have to be subjected to a great deal of critical attention before using them as reference hypotheses for actual observations and experiments. In particular, the degree of stratification, vertical migration and the contribution of animal life to the transport of materials and recycling should be taken into account.

It is often assumed that some 1/4 of primary production sinks out of the photic zone, and that in oligotrophic systems, the fraction lost may be as low as 1/10. Such estimates involve much guesswork and should probably be continuously reviewed and directly

Table 2
Estimated properties of plankton populations close to and 50-100 km to the east of the front.

	Close to the front	Far from the front
Chlorophyll, mg/m^3	0.6	0.06-0.1
Cells/ml	200-500	20-40
Chlorophyll per cell, pg	2	3
Phytoplankton biomass, mg C/m^3	24	6
Ratio C : chlorophyll *a*	40	100
Cell size, average, μm^3	1 000 (picoplankton not included)	3 000
Cell carbon content, pg	80	300
Primary production mg C/m^2/day	600	150
g C/m^2/year	200	50
mg C/m^3/hour	1.25	0.16
g C/g chlorophyll/hour	2	2.6
Mean turnover time for phytoplankton, days	2	3.5
Ratio primary producers : heterotrophs, C : C	1-4 : 1	1 : 2-3
Mean turnover time for total pelagic life, days	4	15
Accepted C : P ratio, weight	40	40
Phosphorus, concentration in water, mg/m^3	6-12	1-2
daily consumption, mg/m^3/day	0.3	0.04
in % available	2.5-5	2-4
in mg P/m^2/day	12	2.4
total biomass mg P/m^3	1.2	0.6
daily loss through sedimentation mg P/m^2/day	4	1.2
in % of production	30	50
in % of total biomass	8-9	3-8

tested as soon as possible. They must be supported by the observation of settling of material through the lower limits of the photic zone, where the sinking organic material supports heterotrophic growth and where metabolism could be estimated through oxygen depletion. The role of large animals, such as fishes cannot be minimized.

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