

Phytoplankton assemblages of deep and surface water layers in a Mediterranean frontal zone

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SUMMARY: A consistent hydrographical feature of the Catalan Balearic Sea is the presence of a doming of the isopycnals, approximately mid-way between the Catalan coast and the Balearic Islands. The Catalan and Balearic boundaries of this feature are marked by two fronts. In July 1983, high chlorophyll concentrations were found near the coast and in a deep chlorophyll maximum which extended across the frontal zones. The phytoplankton distribution was basically determined by the vertical stratification patterns of the water column. The distribution of oxygen and nutrients across the Catalan front, and the presence of relatively high diatom concentrations in the deep chlorophyll maximum of the frontal zone suggested the existence of intermittent fertilization events.

Key words: fronts, phytoplankton, Catalan Sea, NW Mediterranean hydrography.

INTRODUCTION

Recent studies on the Catalan Sea (Northwestern Mediterranean) revealed the presence of two permanent frontal systems (FONT *et al.*, 1988; ESTRADA & MARGALEF, 1988). One of the fronts (the Catalan front) is located on the peninsular side, following the continental slope, and presumably belongs to a continuous structure extending from the Ligurian Sea to the south of the Catalan Sea. This shelf/slope front (WANG *et al.*, 1989) shows a salinity gradient enhanced by the influence of river runoff; it penetrates down to approximately 400 m depth and is important in limiting the exchange between the coastal waters and the open sea. The other main front (the Balearic or North-Balearic front), on the Balearic side of the Catalan Sea, seems to be linked to the front present off the northern coast of Corsica. Its main marker is the temperature gradient, that is readily detectable in winter by satellite imagery. This front reaches only to about 100 m depth and seems to limit the excursion of Atlantic waters into the central part of the northern Mediterranean basins (SALAT & CRUZADO, 1981).

The central zone in between the Catalan and the Balearic fronts has lower vertical stability than the margins. Vertical density profiles in this area reveal a permanent doming of the isopycnals which has

been interpreted as a divergence, although this suggestion, derived mainly from geostrophic calculations (OVCHINNIKOV, 1966; FONT, 1986), is now being challenged (FONT, SALAT and TINTORÉ, pers. com.).

This central zone may be affected by instabilities of both fronts. The North-Balearic front often shows meanders apparently related to anticyclonic eddies migrating from the Algerian current (MILLOT, 1987). The Catalan front seems to follow a more stable path, probably linked to the bottom topography, but instabilities of the associated current may produce energetic filaments that introduce coastal waters into the central region (WANG *et al.*, 1989).

The ageostrophic cross-frontal circulation and the instabilities of the fronts may contribute substantially to the enrichment of the central zone. In particular, as suggested by FONT *et al.* (1989), the bottom topography could enhance the development of cyclonic eddies derived from meanders of the frontal systems. These circulation patterns would produce upward motions that could be the origin of localized fertilization events.

The fine structure of the Liguro-Provençal-Catalan front has been studied across the Nice-Calvi section and other areas of the Ligurian Sea. Based on this information, PRIEUR & TIBERTI (1985) have sug-

gested a long mixing period (10 days) between the central zone and the periphery. The water is exposed at the surface for periods of 1 to 5 days at about 5 km away from the front, and for less than 1 day at the front. These complex three-dimensional circulation patterns could contribute to the winter water formation and to the primary production in that area (BOUCHER *et al.*, 1987). In the Catalan region, different fertilization mechanisms associated with the central divergence and the coastal fronts have been discussed by ESTRADA & MARGALEF (1988) and FLOS & TINTORÉ (in press). These mechanisms could help to explain questions such as the "paradox of the Mediterranean" (SOURNIA, 1973) or why the Western Mediterranean appears to be more productive, in terms of fish extracted, than existing primary production estimates lead us to expect.

The effects of the frontal dynamics on the phytoplankton biomass and production across the Catalan Sea have been studied in a series of cruises carried out on board the R/V "García del Cid", at different times of the year. These studies were based on a transect from Barcelona to beyond the sill between Majorca and Minorca, which was repeated on all the surveys. During the stratification period, the most apparent feature was the presence of a well defined deep chlorophyll maximum (DCM) at depths ranging from 50 to 90 m. The DCM was shallower and contained higher chlorophyll concentrations in the central zone of the isopycnal doming; oxygen concentrations were also higher than in neighbouring areas, suggesting enhanced phytoplankton production (ESTRADA, 1985a,b; MARGALEF, 1985). An analysis of the phytoplankton population (by inverted microscopy) during the July 1982 cruise showed that the assemblages at the DCM differed from those of the upper layers, and also revealed differences between the assemblages of the central area and those of the peninsular and Balearic sides (ESTRADA, 1985a). A similar picture was observed in a study of the microplankton (algae and Tintinnid ciliates) during the July 1982, July 1983 and May 1984 cruises (MARGALEF & ESTRADA, 1987).

One of the main objectives of the PEP 1983 cruise (30 June - 17 July 1983) was to determine the possible relationships between the phytoplankton assemblages associated with the DCM and those of the chlorophyll-rich coastal zone (ESTRADA, 1982). To study this point, we complemented the standard transect between Barcelona and the Balearic Islands with samples taken within a rectangular area of 25 × 25 miles, overlying the Catalan front. This paper analyzes the composition of the phytoplankton communities during the PEP 83 survey and relates their distribution patterns to those of the accompanying physico-chemical parameters. A study of the fine structure of the hydrographical features during

the same survey and their possible biological implications is reported in FLOS & TINTORÉ (in press).

MATERIAL AND METHODS

The distribution of the stations considered in this paper is shown in figure 1. The stations of the grid (numbers 1 to 36) were visited between June 30 and July 3; the other stations were occupied during the following two days. At each station, temperature and salinity profiles were recorded by means of a CTD (Neil Brown Mark III) probe. Water samples were obtained with a Rosette sampler attached to the CTD system. At stations 1-36, nine sampling depths were selected according to the temperature profile, whereas at the remaining stations water was taken from 10 m intervals between the surface and 120 m depth, and from five additional depths between 150 and 400 m. Nitrite, nitrate, phosphate and silicate concentrations were determined automatically using the methods of STRICKLAND & PARSONS (1972). Oxygen was analyzed following the Winkler method. Chlorophyll *a* concentration was determined fluorometrically (YENTSCH & MENZEL, 1963).

Subsamples of 120 ml of water for phytoplankton counts were taken at stations 13, 14, 16, 18 and 25 to 30 of the grid, and at all the stations of the main transect; they were fixed with concentrated Lugol's solution (MARGALEF, 1972) and stored in Pyrex bot-

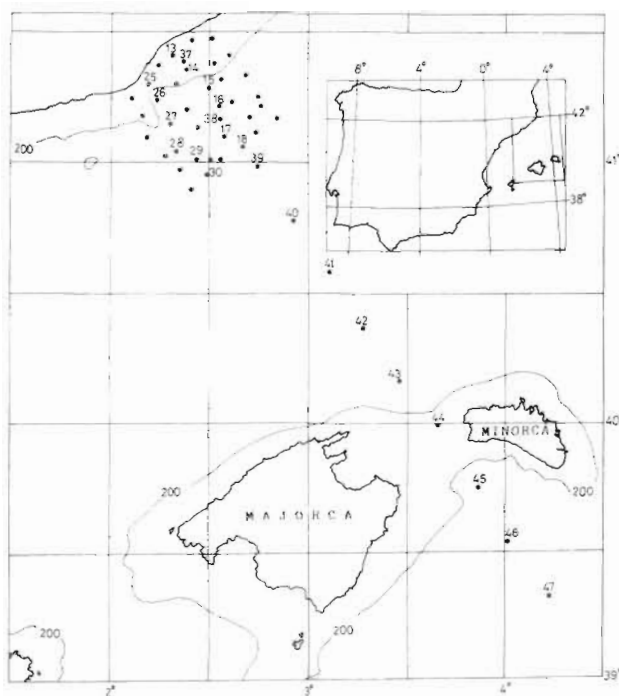


FIG. 1. — Positions of the transects and stations referred to in the text.

tles. The counts were performed using the inverted microscope technique, after allowing 100 ml of water to settle for 48 hours in a composite chamber. Transects of the chamber were scanned at 500 X to count the smaller and more frequent organisms. The entire chamber bottom was examined at 125 X to enumerate the large forms. Many of the observed phytoplankters could not be classified to the level of genus or species, and were placed in categories such as "flagellates" or "small dinoflagellates". Another limitation is the unsuitability of the inverted microscope technique for organisms in the picoplankton size group.

The information contained in the phytoplankton lists was summarized using principal component analysis (PCA; LEGENDRE & LEGENDRE, 1983). The whole data set consisted of 114 samples from the grid and 101 from the main transect. In total, 180 spe-

cies or groups were identified. From these, the 50 most frequent taxa were selected for the PCA. The calculations were performed on the correlation matrix among log-transformed phytoplankton abundance data. Different analyses were made with the entire data set and with the grid and transect samples separately. The results were similar, so that only those of the whole data set will be commented on here. The computer programs used were based on the Scientific Subroutine Package of IBM (1969).

RESULTS

Physico-chemical variables

Along the main transect, doming of the isotherms and the isohalines, reflected by water with temperature < 13 °C and salinity > 38.2 at depths shallower than 60 m, was observed midway between the coast of Barcelona and the sill between Majorca and Minorca (Fig. 2). The distribution of sigma-t was similar to that of temperature; the surface mixed lay-

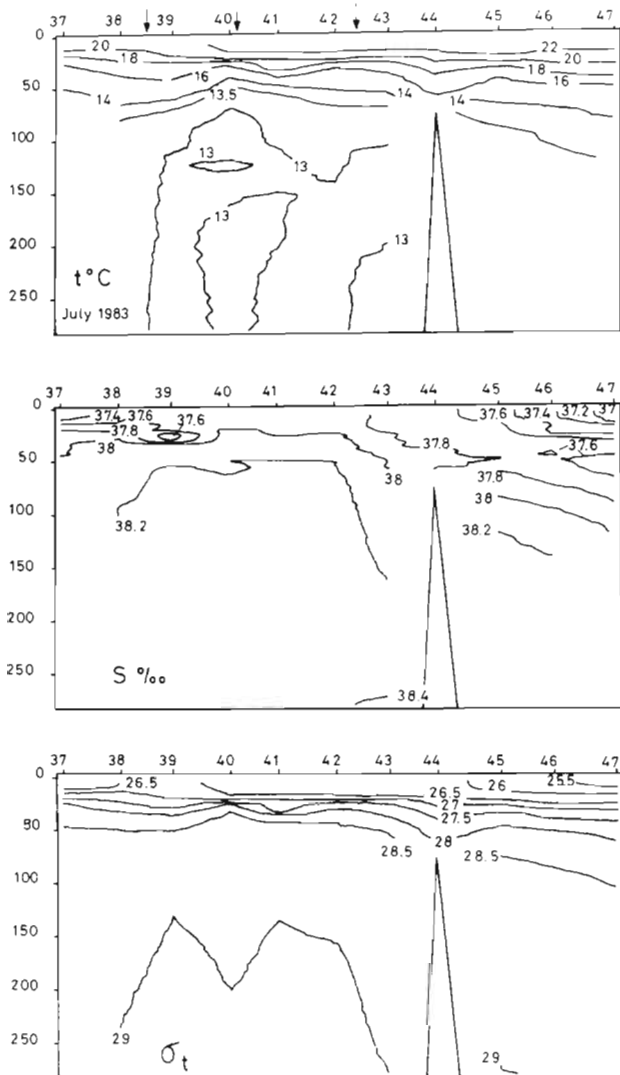


FIG. 2. — Distribution of temperature (T °C), salinity (S ‰) and sigma-t (σ_t) along the main transect (based on the CTD data). The arrows indicate the position of the main hydrographical features.

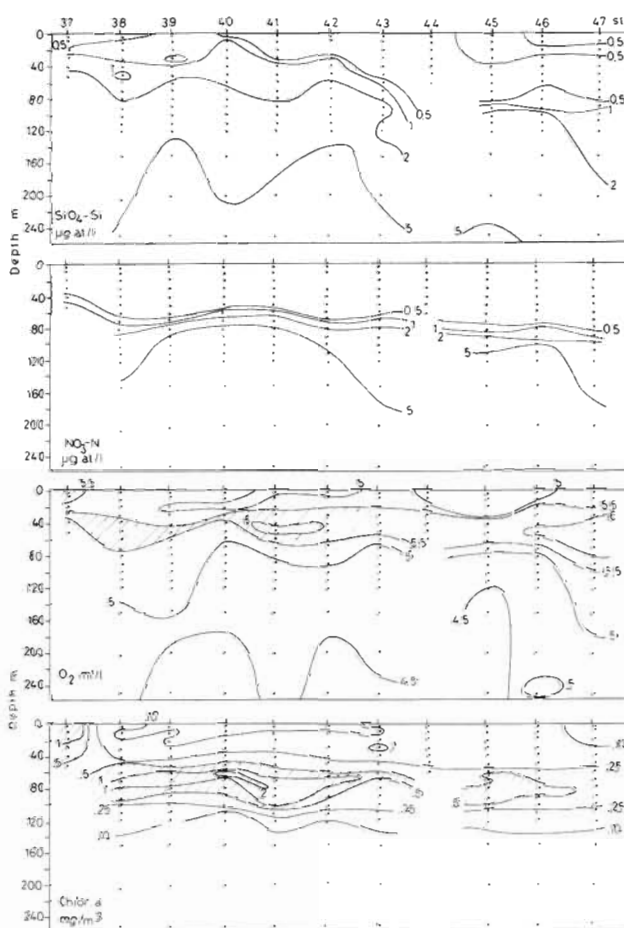


FIG. 3. — Distribution of silicate-Si ($\text{SiO}_2\text{-Si}$, $\mu\text{g-at l}^{-1}$), nitrate-N ($\text{NO}_3\text{-N}$, $\mu\text{g-at l}^{-1}$), oxygen (O_2 , ml l^{-1}) and chlorophyll a (Chlor. a, mg m^{-3}) along the main transect.

er was very thin, and a strong thermocline extended from approximately 10 to 60 m depth. The wide spacing of the stations did not allow us to identify the precise position of the Catalan front. Coastal influence was only apparent in a tongue of low salinity water in the upper 10 m.

The distribution of oxygen, nitrate, silicate and chlorophyll (Fig. 3) along the main transect followed the hydrographical structure and was typical of the stratified conditions of the water column. There was a deep chlorophyll maximum at depths ranging from 60 to 80 m, with chlorophyll concentrations exceeding 2 mg m^{-3} in the central zone. The high surface chlorophyll area close to the coast was due to a rich phytoplankton tongue extending offshore from Barcelona. Nitrate was undetectable in the upper layers and there was a strong nitracline at approximately the level of the DCM. The general distribution of phosphate (not shown in the figure) was similar, but often with low but measurable values at surface. Sili-

cate concentration showed a clear increase in the upper layers of the frontal zone and its vertical gradient was in general less marked. There was a nitrite maximum (not shown) accompanying the DCM and the nitracline, and a shallower oxygen maximum between 30 and 60 m depth.

The data of the coastal grid provided a more detailed view of the structure of the frontal zone. The isotherms presented a well stratified pattern and, in the layers below 30 m, tended to rise offshore. The isohalines showed a core of low salinity water in the upper layers of the coastal half of the transect, and a complex interleaving of relatively low and high salinity layers in the outer half; this feature was clearly represented in the vertical sections (Fig. 4). According to TINTORÉ *et al.* (in press), the low salinity water body is part of an anticyclonic eddy.

The nutrient distribution in the grid (Fig. 5) showed clearly the silicate enrichment in the zone of interleaving salinity layers (stations 17, 28 and 29).

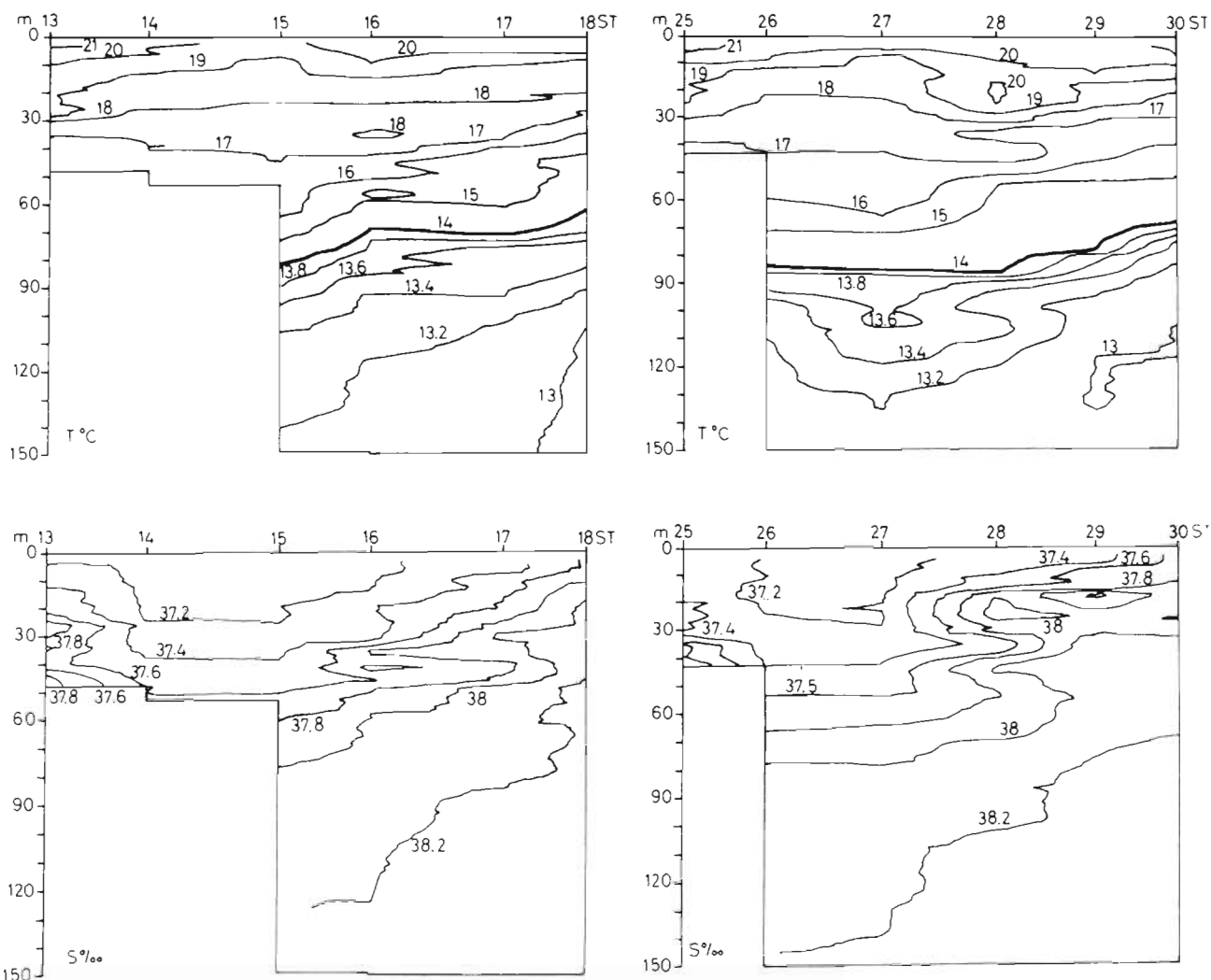


FIG. 4. — Distribution of temperature (T °C) and salinity (S ‰) in two sections of the coastal grid.

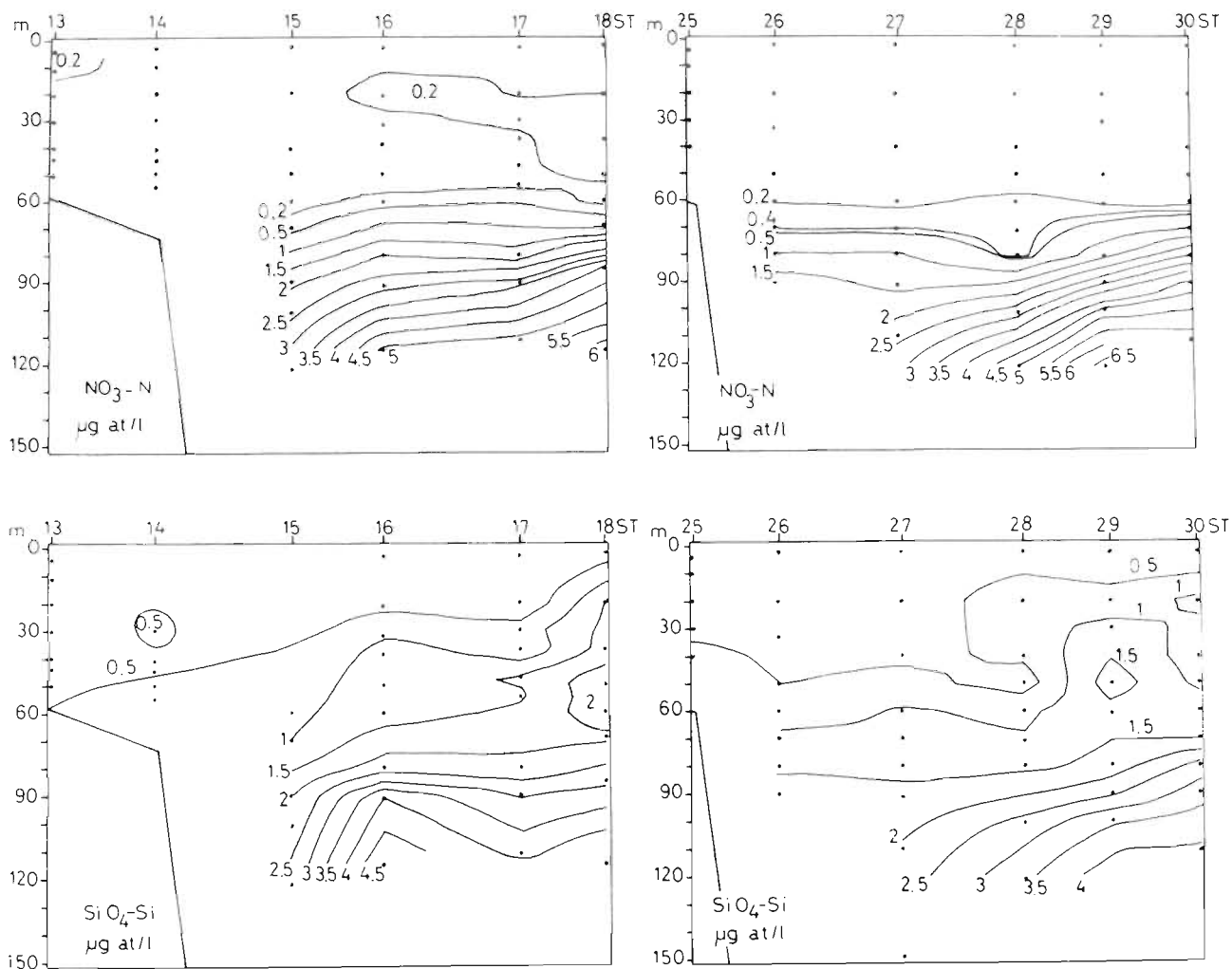


FIG. 5. — Distribution of nitrate-N ($\text{NO}_3\text{-N}$, $\mu\text{g-at l}^{-1}$) and silicate-Si ($\text{SiO}_4\text{-Si}$, $\mu\text{g-at l}^{-1}$) in two sections of the coastal grid.

The coastal tongue of high chlorophyll concentrations was apparent in one of the sections (Figs. 6 and 7), and a DCM was present at depths between 50 and 80 m. The distribution of oxygen (Fig. 7) was very patchy, especially at stations 17, 28 and 29.

Phytoplankton

Along the main transect, the highest phytoplankton cell numbers (Fig. 8) were found at the surface, in the coastal zone, and in a deep layer over the central divergence, at about the same depth as the DCM. Major phytoplankton groups such as diatoms and dinoflagellates (Fig. 8) showed a similar overall distribution, but while the deep diatom maximum was very patchy and coincided approximately with the DCM, the offshore dinoflagellate maximum was wider, more homogeneous and occupied shallower layers of the water column. Among the diatoms, the most abundant taxa were *Chaetoceros* spp., *Nitzschia* spp. and *Thalassiosira* spp. The dinoflagellate popu-

lations were dominated by small unidentified forms. Most of the difference between total phytoplankton and diatoms + dinoflagellates cell numbers was accounted for by unidentified flagellates whose distribution was relatively homogeneous throughout the euphotic zone. In the stations located to the southeast of the Majorca-Minorca sill, genera such as

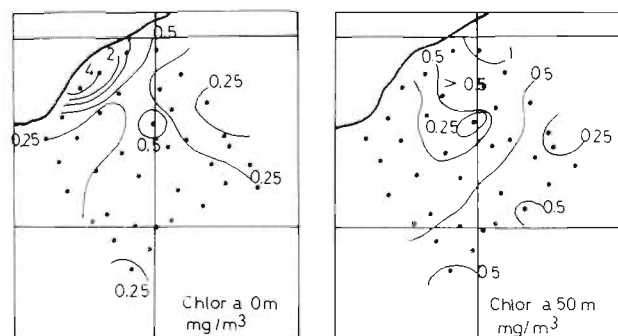


FIG. 6. — Distribution of chlorophyll *a* (Chlor. *a*, mg m^{-3}) at 0 and 50 m depth, in the coastal grid.

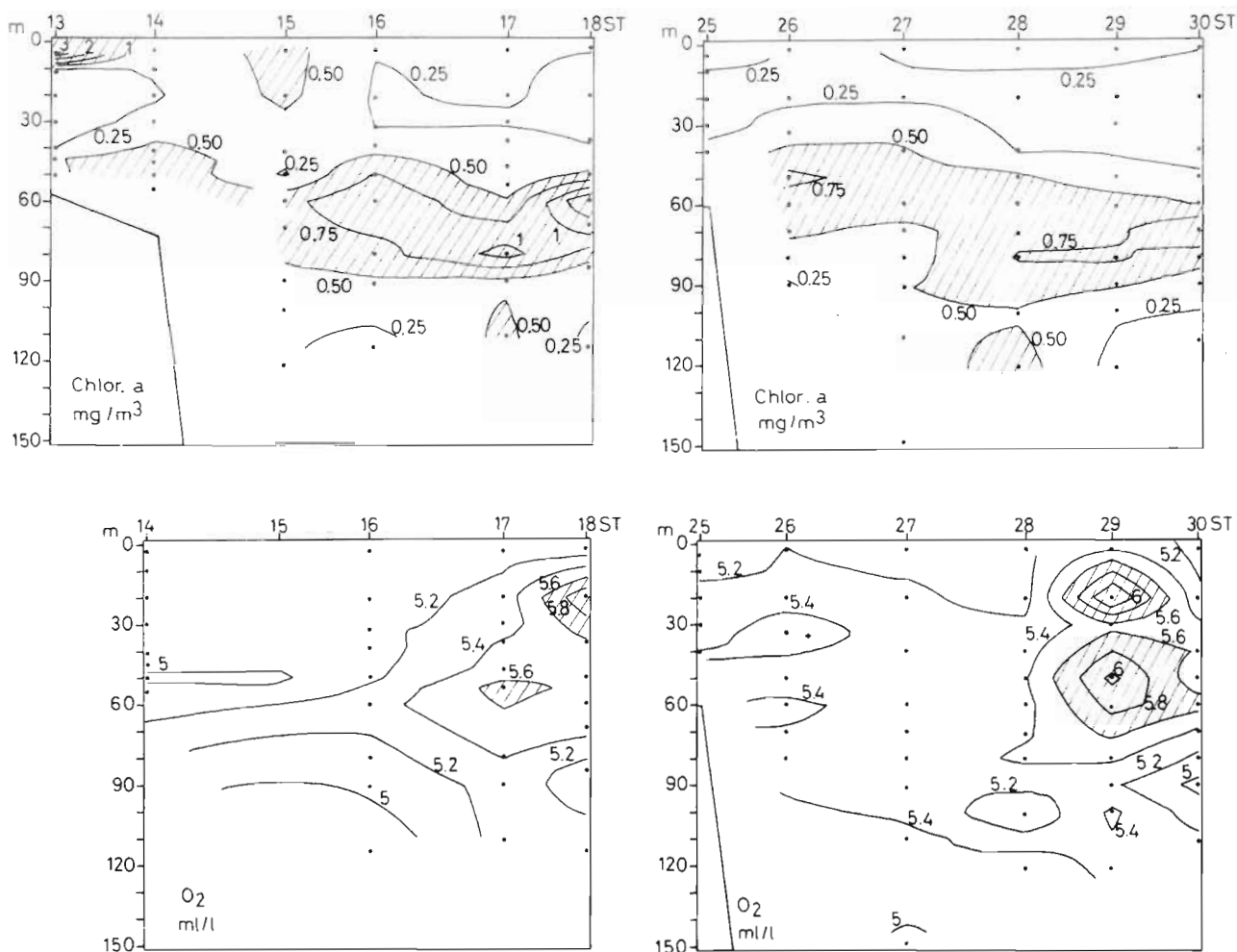


FIG. 7. — Distribution of chlorophyll *a* (Chlor. *a*, mg m⁻³) and oxygen (O₂, ml l⁻¹) in two sections of the coastal grid.

Brachydinium, *Ceratocoris* and *Histioneis*, typical of oligotrophic oceanic areas, were often recorded.

The phytoplankton distribution in the grid sections (Fig. 9) was dominated by the presence of the coastal upper layer maximum and only diatoms showed a concentration increase coinciding in part with the DCM.

The first three axes of the PCA explained, respectively, 15.6, 7.2 and 5.4 of the total variance. The first component was positively correlated with most of the taxa; none of the negative correlation coefficients was significant. The taxa showing the highest (> 0.6) correlations with this component were dinoflagellates of relatively large size: *Ceratium furca*, *Protoperidinium brochi*, *Prorocentrum micans*, *C. fusus*, *Pyrophacus cf. horologicum*, *Gymnodinium* sp. 1, *Protoperidinium* spp., *Dinophysis rotundata* and *C. tripos*.

The distribution of the component (Figs. 11 and 12) reflected the presence of all these dinoflagellate taxa in the high phytoplankton biomass tongue extending from the coast.

The second component (Fig. 10) presented the highest correlations, on the positive side, with the flagellates, with several species or groups of dinoflagellates ("Small dinoflagellates", *Cochlodinium* spp., *Gymnodinium* sp. 2 and "Unidentified *Scrippsiella*-like dinoflagellate") and with diatoms such as *Dactyliosolen mediterraneus* and *Nitzschia* spp.; its higher positive scores along the transect (Fig. 11) were found in a band following approximately the distribution of the DCM. In the coastal grid (Fig. 12), the distribution of this component showed also a deep positive maximum, but it tended to be located above the DCM.

The third component (Fig. 10) expressed a contrast between the diatom taxa, on the positive side, and flagellate and dinoflagellate taxa on the negative side; the distribution of this component (Figs. 11 and 12) showed positive scores in the zone of the coastal tongue but, basically, marked a gradient between a diatom assemblage in the deeper layers of the DCM, and a flagellate and dinoflagellate dominated assemblage at shallower levels.

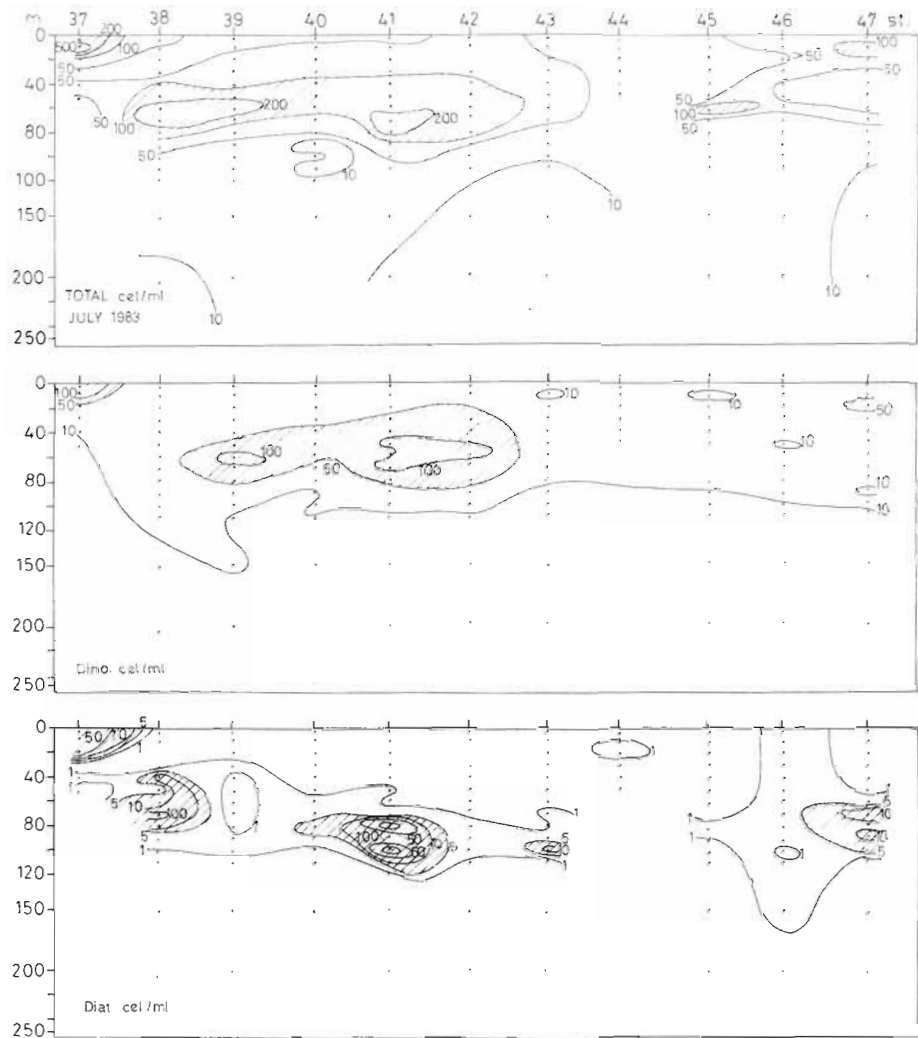


FIG. 8. — Distribution of total phytoplankton cells (Total. cells ml^{-1}), dinoflagellates (Dino., cells ml^{-1}) and diatoms (Diat., cells ml^{-1}) along the main transect.

DISCUSSION

The main feature of the distribution of the phytoplankton — related parameters in the main transect was the presence of a DCM associated with cell number and diatom maxima. The general situation was similar to that found in July 1982 (ESTRADA, 1985a). Although drawing of the isolines involves many subjective decisions, examination of the grid sections (Figs. 7 and 9) suggests that the deep maxima of chlorophyll and diatoms reached the coast without intermixing with other features of the upper layers. The surface zone of high chlorophyll extending off Barcelona was probably due to local enrichment by coastal runoff, and presented a very mature (in the sense of MARGALEF, 1958) phytoplankton community with an important contribution of large dinoflagellates, typical of stratified situations with adequate nutrient supply. While in the main transect the DCM corresponded closely to a cell number maximum, this was not the case in the coastal grid, where the DCM

was well developed, but the highest cell concentrations were always at surface. This is due in part to a high contribution of flagellates and small dinoflagellates in the upper layers of the coastal zone, where chlorophyll concentrations generally exceeded 0.25 mg m^{-3} . Given the small size of these forms, it is likely that the contribution of an increased chlorophyll concentration per cell in the DCM overrode the contribution to the total chlorophyll concentration of the higher cell numbers in the upper layers.

The position of the shelf/slope front in the grid sections was observed mainly in the salinity field, which presented a complex structure of interleaving layers. Due to the strong thermocline, there was no corresponding feature in the temperature and sigma-t profiles, which presented a more typical pattern of vertical stratification with only a discrete offshore upwards tilt of the deeper isolines. Silicate and oxygen showed clearly the presence of the front, while the nitrate sections presented almost no evidence of it.

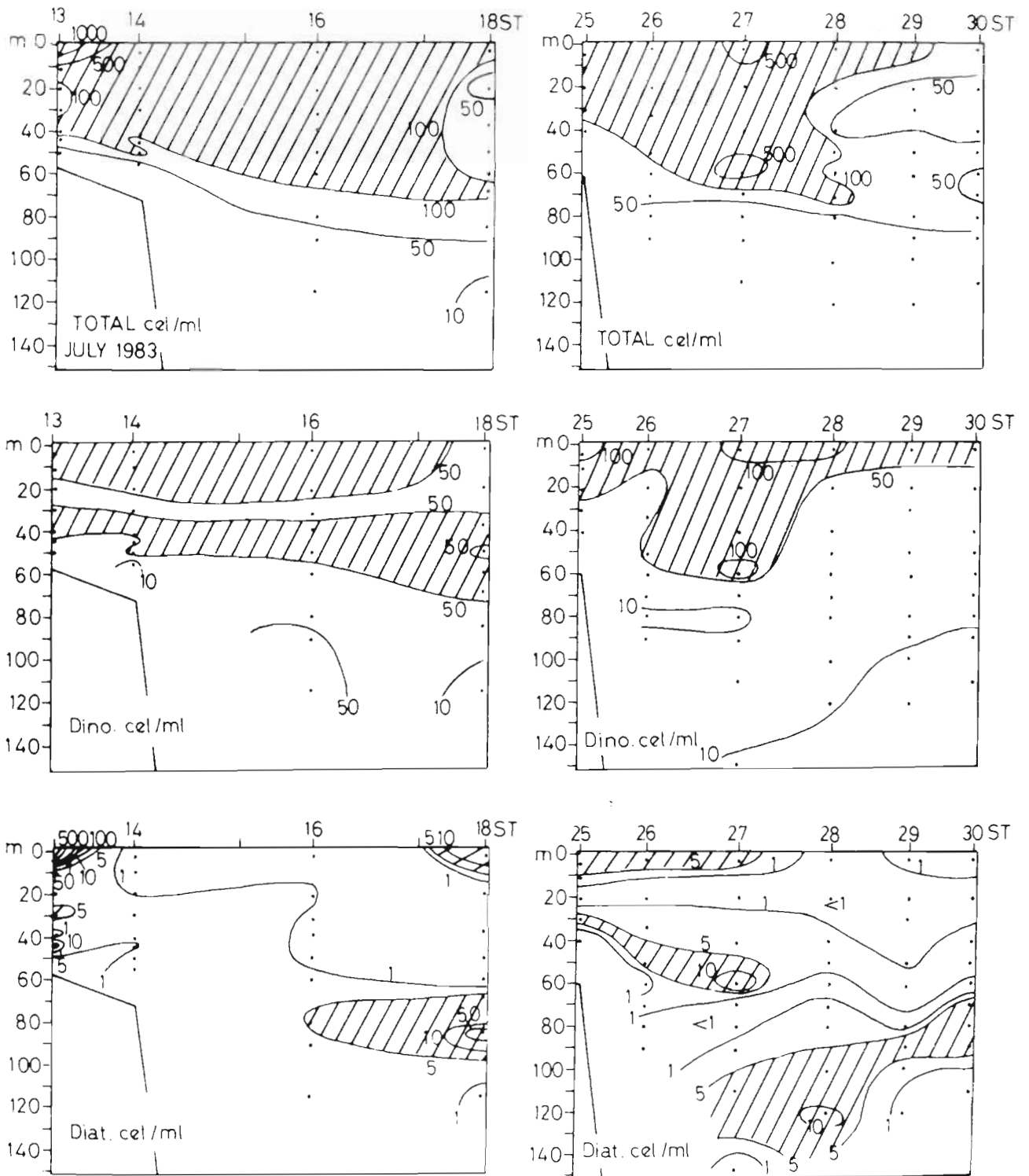


FIG. 9. — Distribution of total phytoplankton cells (Total, cell ml⁻¹), dinoflagellates (Dino., cell ml⁻¹) and diatoms (Diat., cell ml⁻¹) in two sections of the coastal grid.

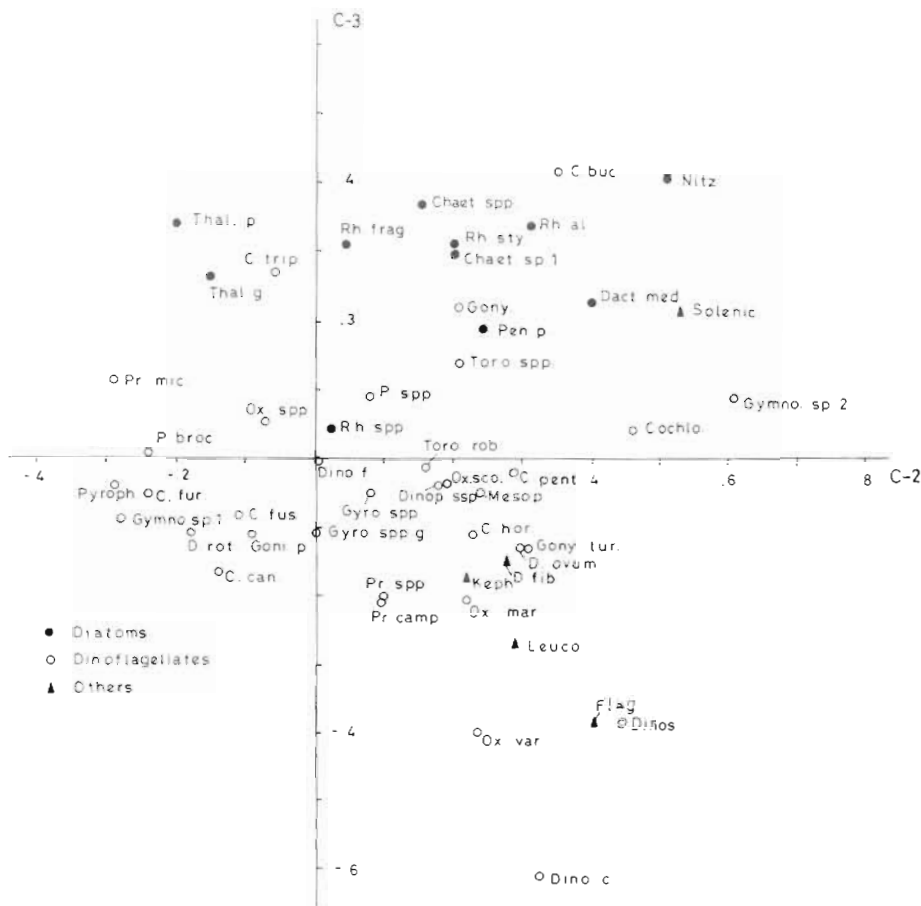


FIG. 10. — Position of the extremes of the 50 species-vectors in the space determined by the first and second principal components. Key: C. buc. = *Ceratium buceros*; C. can. = *C. candelabrum*; C. fur. = *C. furca*; C. fus. = *C. fusus*; C. hor. = *C. horridum*; C. pent. = *C. pentagonum*; C. trip. = *C. tripos.*; Cochlo. = *Cochlodinium* spp.; D. ovum. = *Dinophysis ovum*; D. rot. = *Dinophysis rotundata*; Dinop. spp. = *Dinophysis* spp.; Goni. p. = *Goniodoma polyedricum*; Gony. tur. = *Gonyaulax turbynei*; Gony. = *Gonyaulax* spp.; Gymno. sp. 1 = *Gymnodinium breve*-like; Gymno. sp. 2 = *Gymnodinium* spp. 2; Gyro. spp. g. = *Gyrodinium* spp. (large); Gyro. spp. = *Gyrodinium* spp. (small); Mesop. = *Mesoporos* spp.; Ox. mar. = *Oxytoxum margalefi*; Ox. sco. = *O. scolopax*; Ox. var. = *O. variabile*; Ox. spp. = *Oxytoxum* spp. (small); Pr. comp. = *Prorocentrum compressum*; Pr. mic. = *P. micans*; Pr. spp. = *Prorocentrum (Exuviaella)* spp. (small); P. broc. = *Protoperidinium brochi*; P. spp. = *Protoperidinium* spp.; Pyroph. = *Pyrophacus* sp.; Toro. rob. = *Torodinium robustum*; Toro. spp. = *Torodinium* spp.; Dino c. = Unidentified *Scrippsiella*-like dinoflagellate; Dino. f. = Unidentified spindle-shaped dinoflagellate; Dinos. = Unidentified dinoflagellates; Chaet. spp. = *Chaetoceros* spp.; Chaet. sp. 1 = *Chaetoceros* sp. 1; Dact. med. = *Dactyliosolen mediterraneus*; Nitz. = *Nitzschia* spp.; Rh. al. = *Rhizosolenia alata*; Rh. frag. = *R. fragilissima*; Rh. sty. = *R. styliformis*; Rh. spp. = *Rhizosolenia* spp.; Thal. p. = *Thalassiosira* spp. (small); Thal. g. = *Thalassiosira* spp. (medium-sized); Pen. p. = Unidentified pennate diatoms (small); D. fib. = *Dityocha fibula*; Caly. = *Calycomonas* spp.; Leuco. = *Leucocryptos*; Solenic. = *Solenicola setigera* (symbiont of *Dactyliosolen mediterraneus*).

and the same happened with chlorophyll. These hydrographical features suggest that the salinity inversions in the frontal zone were caused by lateral mixing of water bodies from comparable depths at different sides of the front, and with similar temperatures due to seasonal heating. The nutrient enrichment associated with vertical motions, mixing and seaward spreading of filaments of coastal water at the front (TINTORÉ *et al.*, in press), could be responsible for the proliferation of diatoms in the frontal zone (Figs. 8 and 9). The different patterns of the silicate and nitrate distributions suggest that the nitrate provided by the fertilization mechanisms had already been consumed. The oxygen maxima (Fig. 4) suggest also an increased primary production in the

front. However, diatom patches and oxygen maxima associated with the DCM may also be found in the central zone of isoline doming, as can be seen in figures 1, 3 and 8 (station 41). The presence of localized phytoplankton proliferations at the DCM has been pointed out on other occasions (ESTRADA 1985a; MARGALEF, 1985; ESTRADA & MARGALEF, 1987), and suggests that significant *in situ* growth must be occurring there, presumably related to intermittent mechanisms allowing increased nutrient inputs into the upper water layers.

The trends of variability expressed by the PCA of the PEP-1983 data were comparable to those found in the July 1982 analyses (ESTRADA, 1985a). It is interesting to note that both the first component of the

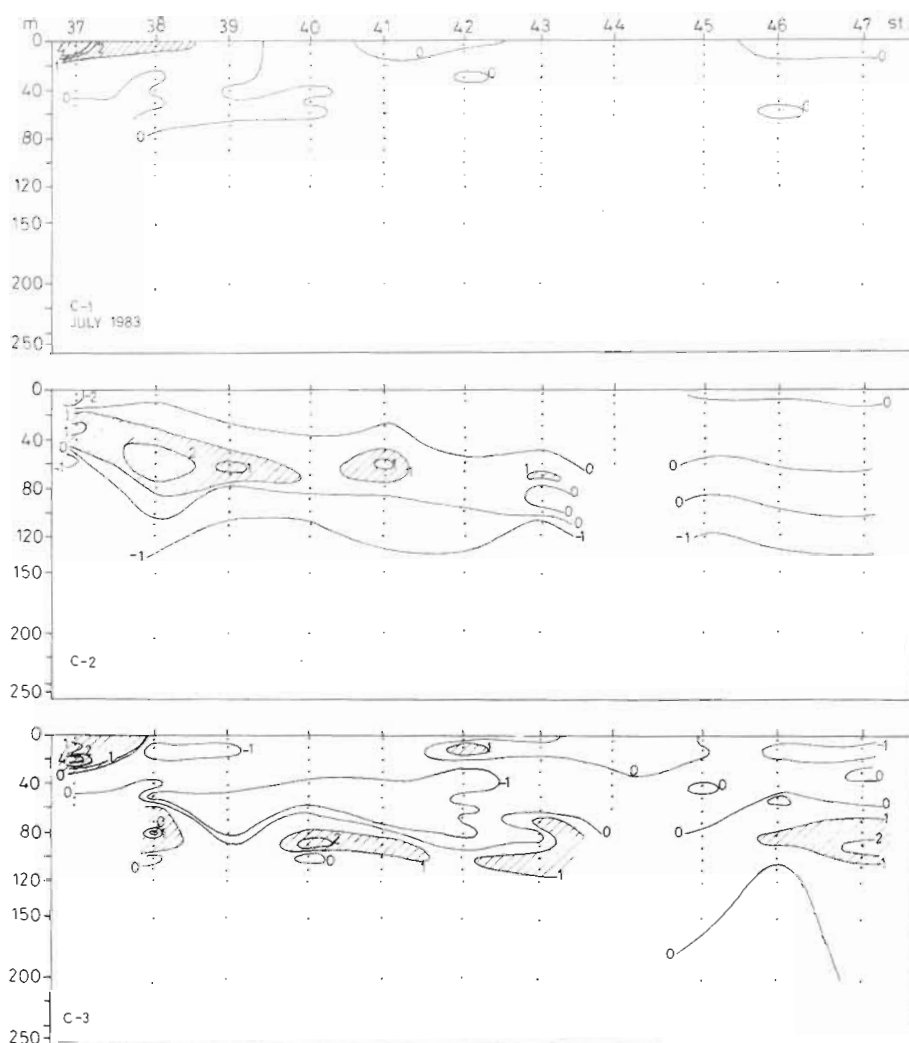


FIG. 11. — Distribution of the values of the first three principal components (C-1, C-2 and C-3) along the main transect.

PEP-83 analysis and the third component of the PEP-82 analysis reflected the presence at surface of large dinoflagellates such as *Ceratium furca*, *C. fusus* and *Protoperdinium brochi*, although the 1982 transects did not cross any tongue of high surface chlorophyll near the coast. Presumably these dinoflagellate forms are typical of summer conditions at the surface and coastal enrichment contributes to the increase in their population densities. The PEP-82 analysis showed the presence of a particular diatom assemblage near the Catalan coast, but the spacing of the stations did not allow us to establish its relationship with the Catalan front. In the PEP-83 transects, the distribution of total phytoplankton, dinoflagellates and the third principal component, with a sharp boundary between stations 27 and 29, reflected partially the structure of the salinity field, but otherwise the phytoplankton composition appeared to be comparable on both sides of the salinity front. This similarity may be partially an artifact due to the lumping together of different taxa, mainly of flagellates and small dinoflagellates, in the microscope

examinations, but it may be better explained as a seasonal feature. The effects of the front on the phytoplankton composition were obvious in sections carried out in May 1984, early in the stratification season (ESTRADA, in preparation; ESTRADA, & MARGALEF, 1988); later on, a warm water layer covers the frontal zone, the phytoplankton maximum deepens, and the vertical stratification patterns dominates the phytoplankton community structure on both sides of the front.

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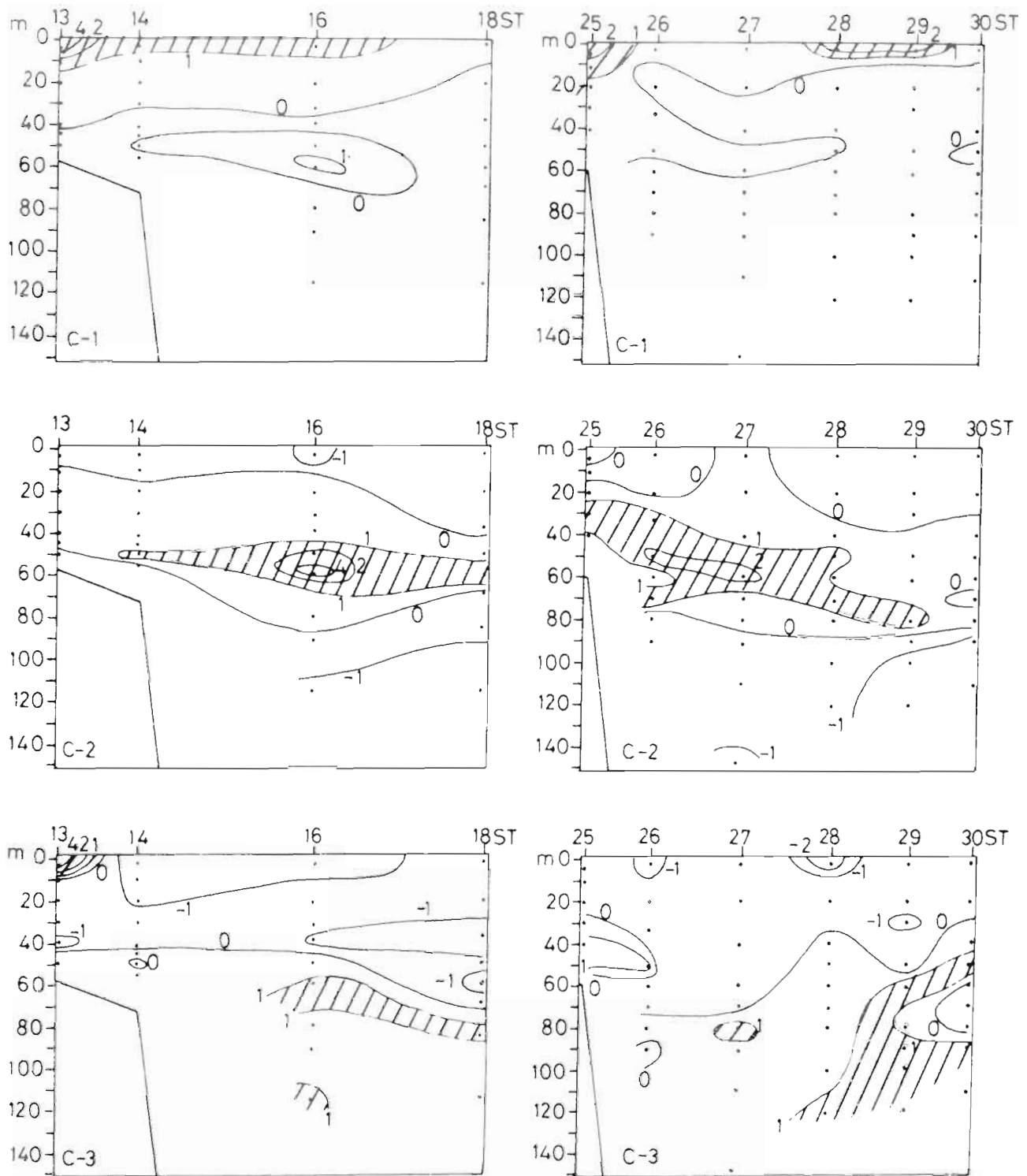


FIG. 12. — Distribution of the values of the first three principal components (C-1, C-2 and C-3) in two sections of the coastal grid.

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