Homage to Ramon Margalef; or, Why there is such pleasure in studying nature (J. D. Ros & N. Prat, eds.). 1991. *Oecologia aquatica*, 10: 157-185.

PHYTOPLANKTON ASSEMBLAGES ACROSS A NW MEDITERRANEAN FRONT: CHANGES FROM WINTER MIXING TO SPRING STRATIFICATION

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SUMMARY

A series of stations located along the transect between Barcelona and the Balearic Islands were sampled to study the composition of the phytoplankton community, during June 1984, March 1985, June 1985 and June 1986. In March, the concentration of phytoplankton cells presented a maximum in the upper part of the water column. The Catalan front, near the continental slope of the Catalan coast side, separated a diatom-dominated assemblage in the coastal zone from a flagellate-dominated assemblage offshore. In the spring cruises, the most characteristic feature of the phytoplankton distribution was the presence of a deep chlorophyll maximum (DCM) which corresponded to increased phytoplankton cell numbers. The influence of the front on the phytoplankton distribution was well marked in early June (1984), but in the cruises carried out later in the season, warm waters extended over the frontal zone. The distribution of the phytoplankton assemblages showed some regularities: during the spring cruises, diatom assemblages with *Chaetoceros* spp., *Nitzschia* spp. and *Thalassiosira* spp. formed patches in the DCM layer, while a flagellate and dinoflagellate assemblage occupied the upper part of the water column. In May 1984 and May 1986 a third assemblage with *Coscinodiscus radiatus*, *Dictyocha fibula* and *Oxytoxum margalefi* formed a background population in the DCM level. Thus, in spite of high environmental variability, persistent groupings of species could be recognized.

KEY WORDS: Phytoplankton, hydrographic front, NW Mediterranean

INTRODUCTION

Two major hydrographic features of the Catalano-balearic Sea are the Catalan and the Balearic frontal systems (ESTRADA & MARGALEF, 1988; ESTRADA & SALAT, 1989; LA VIOLETTE *et al.*, 1990, TINTORÉ *et al.*, 1990). The Catalan front follows the continental slope on the peninsular side, and its main marker is a salinity gradient between low salinity waters on the shelf and higher salinities offshore. The Balearic front, on the Balearic Islands side, appears to be connected to the front off the northern coast of Corsica; it is associated with temperature and salinity gradients, but during the summer months its surface signature does not correspond to the deeper structures, due to the extension, over the upper layers of the water column, of relatively warm and low salinity waters of Atlantic origin.

During the stratification period, which lasts approximately from April to November (MARGALEF & BALLESTER, 1967), the phytoplankton distribution typically presents a deep chlorophyll maximum (DCM) and the central zone between the Catalan and Balearic fronts shows a persistent doming of the isopycnals which is often associated with increased phytoplankton biomass in the DCM (ESTRADA, 1985a). This doming has been considered as a divergence (OVCHINNIKOV, 1966; FONT, 1986), although recent studies have challenged this interpretation. The central zone appears to have lower stability than the marginal sides and may be strongly affected by instabilities from both frontal regions (WANG *et al.*, 1990).

The distribution of oceanographic parameters across the main fronts of the Catalano-balearic Sea has been studied in a series of oceanographic cruises covering a transect from the Catalan coast to the channel between Majorca and Minorca. Information on nanoplankton composition and primary production during the first two cruises, carried out from 12 to 28 July 1982 and from 30 June to 17 July 1983, can be found in ESTRADA (1985a, b). The microplankton distribution during these cruises and the following one, carried out from 17 to 30 May 1984, was studied by MARGALEF (1985) and MARGALEF & ESTRADA (1987). These authors showed that the phytoplankton distribution during summer was strongly conditioned by the vertical stratification patterns of the water column. High phytoplankton and chlorophyll concentrations were found near the coast and in a deep chlorophyll maximum which extended across the frontal zones, at depths of 60-80 m in summer and 40-70 m in May. The present study is based on data from May 1984 and from the three following cruises, carried out in late winter and spring 1985 and in spring 1986 (Table I), and attempts to draw a generalized picture of the main changes in the distribution of the nanoplankton communities during the transition from the mixing to the stratification period. Details concerning winter 1985 and spring 1984 cruises have been given by ESTRADA & MARGALEF (1988). The basic data for all the cruises can be found in PEPS (1986) and MASÓ & PEPS (1988).

MATERIAL AND METHODS

The distribution of the stations referred to in this paper is given in figure 1. Other details concerning the cruises are given in Table I. In general, the transects were completed in less than three days, except for the PEP 86 cruise and for the second transect of the FRONTS 3-85 cruise. In these cases, the stations were mainly devoted to biological experimentation work and each one was occupied for 24 hours; therefore, the resulting distributions should be interpreted with caution. Previous surveys had shown that the small-scale details of the phytoplankton biomass distribution presented great heterogeneity (ESTRADA, 1985a). However, the emphasis of the present work is on global patterns, and these tended to be persistent within the duration of each cruise.

Water samples were obtained by means of a Rosette sampler attached to a CTD system, during the first part of the FRONTS 85 cruise, and using 5-litre Niskin oceanographic bottles in the remaining cruises. Water was taken from nine depths at 10-20 m intervals between surface and 100 m depth in FRONTS 85 and at 10 m intervals between the surface and 110 m depth in the other cruises. Additional samples were taken at greater intervals down to 200 m (phytoplankton analyses) or 400 m (physico-chemical determinations). Information on the physico-chemical methodology is given in PEPS (1986) and MASÓ & PEPS (1988). Chlorophyll *a* concentration was determined fluoro- metrically (YENTSCH & MENZEL, 1963).

Subsamples of 120 ml of water for phytoplankton counts were fixed with concentrated Lugol's solution without acetic acid (MARGALEF, 1972) and stored in hermetically capped Pyrex bottles. 100 ml of water were sedimented in a composite chamber and examined using the inverted microscope technique. One transect of the chamber (approximately 1 ml of sample) was observed at 500 X to enumerate the smaller and more frequent organisms. An additional transect was examined at 125 X to count cells of intermediate size and the entire chamber bottom was scanned at 125 X to count the larger forms. Many organisms could not be classified at the level of genus or species and had to be lumped in categories such as "flagellates" (which also included small forms in which flagella could not be seen) and "unidentified dinoflagellates" (mainly

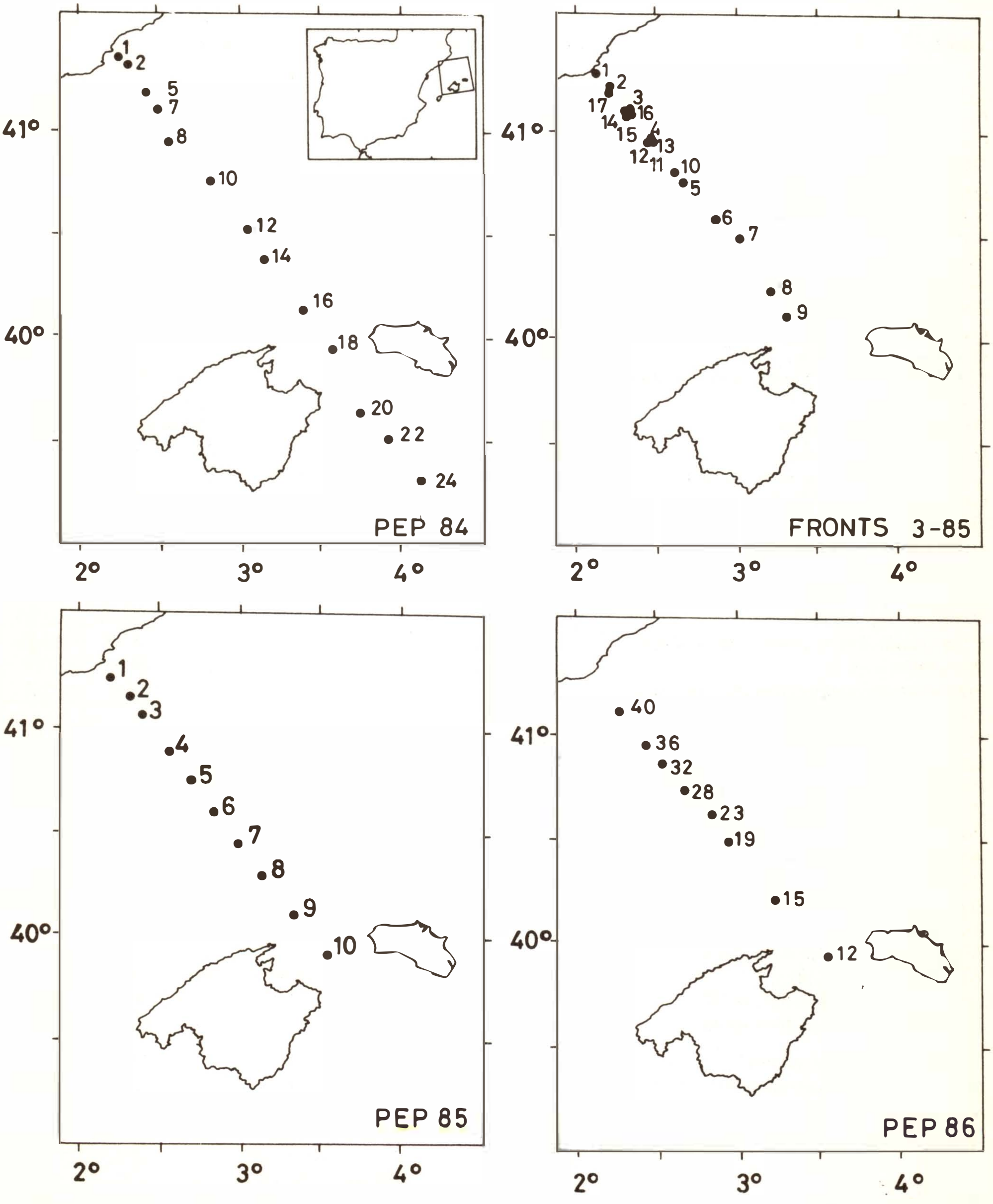


FIGURE 1. Position of the stations referred to in the text.

TABLE I. Sampling period and statistical data of the taxa used in the multivariate analyses corresponding to each cruise: m, mean number in cells ml^{-1}; s, standard deviation, computed for the number of occurrences (N. obs.). Code gives the key for the names used in figure 12.

CRUISE		FRONTS 3-85	PEP 84
Transect (first-last station)	1-9	10-17	1-24
Sampling period	15-16/3/85	24-26/3/85	16-19/5/84
Number of samples		131	200
Number of taxa selected		34	49

TAXA	CODE	N. obs.	m	s	N. obs.	m	s
Ceratium furca (Ehrenb.) Clap. and Lacm.	C. fur.				11	2.9	5.8
Ceratium fusus (Ehrenb.) Dujardin	C. fus.				8	1.2	0.4
Cochlodinium spp.	Cochlo.	11	4.68	7.81	62	13.7	36.1
Dinophysis cf. *ovum* Schütt	Din. ov.						
Dinophysis acuta Ehrenb.	Din. acu.						
Dinophysis rotundata Clap. and Lachm.	Din. rot.						
Dinophysis (*Phalachroma*) spp.	Dinop.1				7	1.3	0.7
Dinophysis spp.	Dinop. 2				8	1.1	0.3
Dissodium (*Diplopsalis*) spp.	Dis.						
Goniodoma polyedricum (Pouchet) Jörg.	Gon. pol.						
Goniodoma sphaericum Murray and Whitting	Gon. sph.						
Gonyaulax polygramma Stein	Gony. pol.						
Gonyaulax turbynei Murray and Whitting	Gony. tur.						
Gonyaulax spp.	Gony.				22	1.4	0.7
Gyrodinium spp. (large)	Gony. l						
Gyrodinium spp. (small)	Gony. s	18	18.45	35.42	85	16.0	25.4
Mesoporos perforatus Gran (Lillick)	Mes. perf	19	18.29	25.98	23	10.6	23.9
Oxytoxum margalefi Rampi	Ox. mar.				7	20.9	40.4
Oxytoxum scolopax Stein	Ox. sco.				9	3.5	6.4
Oxytoxum variabile Schiller	Ox. var.	7	101.94	41.27	10	97.7	64.3
Oxytoxum sp. D	Ox. sp. D				9	3.44	6.22
Oxytoxum spp. (large)	Ox. spp. l						
Oxytoxum spp. (small)	Ox. spp. s				13	50.88	53.96
Palaeophalachroma unicinctum Schiller ?	Pal. uni.				11	8.78	13.29
Pronoctiluca sp.	Pronoc.				10	9.05	9.86
Prorocentrum compressum (Bailey) Abe	Pr. comp.				27	3.0	5.2
Prorocentrum maximum (Gourret) Schiller	Pr. max.						
Prorocentrum micans Ehrenb.	Pr. mic.				7	3.89	7.07
Prorocentrum (*Exuviaella*) spp. (small)	Pr. spp.	29	10.91	22.53	63	46.8	63.6
Protoperidinium bipes (Paulsen) Balech	P. bip.				8	34.8	47.7
Protoperidinium crassipes (Kofoid) Balech	P. cras.						
Protoperidinium steini (Jörg.) Balech	P. ste.						
Protoperidinium spp. (large)	P. spp. l						
Protoperidinium spp. (small)	P. spp. s	26	14.75	31.28	61	12.9	28.4
Scrippsiella trochoidea (Stein) Loeblich	S. troc.	7	11.04	14.6	10	18.82	34.27
Protoperidinium spp. A	P. spp. A						
Torodinium robustum Kofoid and Swezy	Toro. rob.				25	4.8	7.3
Torodinium sp. (small)	Toro. s	47	24.97	48.84	100	45.8	77.5
Unidentified dinoflagellate sp. B	Dino B	68	846.4	643.23	62	413.5	309.6
Unidentified dinoflagellate sp. D	Dino D				14	4.2	5.5
Unidentified dinoflagellates	Dinos.	130	1640.99	1348.58	195	1309.9	1371.7
Emiliania huxleyi Lohmann Hay and Mohler	E. hux.	22	196.02	134.83	13	223.45	309.58
Syracosphaera cf. *pulchra* Lohmann	Syr. pul.						
Unidentified coccolithophorids	Cocol.	10	155.75	71.06	8	175.24	210.12
Chaetoceros sp. A	Chaet. A						
Chaetoceros spp. B	Chaet. B	15	101.31	100.14			
Chaetoceros spp. C	Chaet. C	13	355.5	545.59	19	946.8	2545.1
Coscinodiscus radiatus Ehrenb.	Cosc. rad.	23	2.01	4.14	13	1.3	0.6
Coscinodiscus spp.	Cosc. spp	15	2.75	5			

TABLE I (Cont.)

Diploneis sp.	Diplo.	7	6.81	9.19			
Ditylum brightwelli Grunow	Dit. bri.	7	1.29	0.7			
Hemidiscus cuneiformis Wallich	Hem. cun.	12	1.5	0.65	11	1.3	0.5
Leptocylindrus danicus Cleve	Lep. dan.				7	25.6	51.0
Nitzschia (*Pseudonitzschia*) spp. (small)	Nitz. s						
Nitzschia (*Pseudonitzschia*) spp. (large)	Nitz. spp	14	39.73	66.21	14	87.2	178.3
Pleurosigma spp.	Pleuro.	31	6.04	20.15	7	6.77	9.13
Rhizosolenia alata Cleve	Rh. al.				7	13.1	18.6
Rhizosolenia imbricata Brightwell	Rh. imb.	11	8.16	12.24			
Rhizosolenia spp.	Rh. spp.				15	3.8	7.0
Schröderella delicatula (Per.) Pavillard	Sch. del.				8	10.35	13.65
Thalassionema nitzschioides Grunow	Thaln. nit.						
Thalassiosira spp. (small)	Thal. s	53	347	517.8	17	111.99	90.08
Thalassiosira spp. (medium)	Thal. m	36	33.72	87.59	21	21.7	39.8
Thalassiosira spp. (large)	Thal. l						
Thalassiothrix frauenfeldii (Grunow) Cleve and Möller	Thalx. fr.						
Unidentified centric diatoms	Diats.						
Pennate diatoms (small)	Pen. s	38	98.71	122.51	9	76.86	75.14
Pennate diatoms (large)	Pen. l	17	10.56	15.44			
Unidentified pennate diatom sp. A	Pen. A	42	14.7	36.03	52	24.75	65.39
Dictyocha fibula Ehrenb.	Dic. fib.	97	55.65	81.72	68	39.4	50.1
Dictyocha speculum	Dic. spec.						
Flagellates	Flag.	131	6450.4	15981.02	193	1975.9	3096.1
Calycomonas spp.	Calyc.	25	127.21	37.74	44	196.8	132.8
Phaeocystis sp.	Phaeo.	9	288.94	490.21			
Cryptomonads	Cryptos.	58	595.91	1060.62	42	483.1	1103.3
Leucocryptos?	Leuco.	36	170.29	113.36	77	401.4	445.9
Solenicola setigera	Sol. set.				9	2127.4	4780.6
Mesodinium sp.	Mesod.				12	7.8	12.7
Ciliates	Cili.	101	130.29	135.87			

CRUISE	PEP 85	PEP 86
Transect (first-last station)	1-10	12-40
Sampling period	1-2/6/85	17-24/6/86
Number of samples	129	107
Number of taxa selected	47	50

TAXA	N. Obs.	m	s	N. obs.	m	s
Ceratium furca (Ehrenb.) Clap. and Lacm.	11	1.36	2	9	2.78	3.08
Ceratium fusus (Ehrenb.) Dujardin	12	2	1.6			
Cochlodinium spp.	54	25.7	55.29	73	21.96	57.57
Dinophysis cf. *ovum* Schütt	8	3.75	6.53			
Dinophysis acuta Ehrenb.				10	1.5	0.92
Dinophysis rotundata Clap. and Lachm.	12	5.12	7.38	32	1.5	0.83
Dinophysis (*Phalachroma*) spp.				12	2.8	5.68
Dinophysis spp.				16	1.5	1.06
Dissodium (*Diplopsalis*) spp.				8	1.75	1.98
Goniodoma polyedricum (Pouchet) Jörg.				8	1.75	1.98
Goniodoma sphaericum Murray & Whitting				22	1.23	0.6
Gonyaulax polygramma Stein				8	1.25	0.43
Gonyaulax turbynei Murray & Whitting				9	12.73	26
Gonyaulax spp.				8	18.01	37.58
Gyrodinium spp. (large)				19	1.37	0.67
Gyrodinium spp. (small)	54	21.82	46.79	59	8.58	21.69
Mesoporos perforatus Gran (Lillick)	18	10.59	11.82	44	13.55	37.74
Oxytoxum margalefi Rampi	8	25.74	37.12	27	33.93	55.42
Oxytoxum scolopax Stein				10	3.05	6.15
Oxytoxum variabile Schiller	10	118.78	45.61	8	130.71	91.36

TABLE I (Cont.)

Oxytoxum sp. D						
Oxytoxum spp. (large)	9	16.01	35.87			
Oxytoxum spp. (small)	17	57	69.82			
Palaeophalachroma unicinctum Schiller ?						
Pronoctiluca sp.						
Prorocentrum compressum (Bailey) Abe				46	2.7	2.29
Prorocentrum maximum (Gourret) Schiller				9	26.86	72.42
Prorocentrum micans Ehrenb.						
Prorocentrum (*Exuviaella*) spp. (small)	63	117.99	367.04	53	9.35	68.19
Protoperidinium bipes (Paulsen) Balech	8	94.2	74.55			
Protoperidinium crassipes (Kofoid) Balech				12	1	0
Protoperidinium steini (Jörg.) Balech				9	1.56	0.5
Protoperidinium spp. (large)	8	1.25	0.43	11	1.18	0.57
Protoperidinium spp. (small)	59	61.72	90.48	64	5.93	15.66
Scrippsiella trochoidea (Stein) Loeblich	8	81.25	74.14			
Protoperidinium spp. A	13	165.41	180.83			
Torodinium robustum Kofoid and Swezy	26	5	7.13	51	12.03	61.8
Torodinium sp. (small)	35	37.61	62.28	37	18.7	30.9
Unidentified dinoflagellate sp. B	30	251.96	225.38	62	325.75	229.9
Unidentified dinoflagellate sp. D	10	7.94	8.75	21	5.27	6.52
Unidentified dinoflagellate sp. F	18	21.85	35.15	31	14.91	9.56
Unidentified dinoflagellates	126	2862.57	2442.46	107	2513.13	1981.89
Emiliania huxleyi Lohmann Hay and Mohler						
Syracosphaera cf. *pulchra* Lohmann	8	79.59	78.35			
Unidentified coccolithophorids						
Chaetoceros sp. A	14	8008.9	9094.06			
Chaetoceros spp. B	7	106.37	111.77	10	744.07	1323.27
Chaetoceros spp. C	17	995.76	1611.15	8	1168.61	1546.39
Coscinodiscus radiatus Ehrenb.	9	1	0	29	2.17	1.42
Coscinodiscus spp.						
Diploneis sp.						
Ditylum brightwelli Grunow						
Hemidiscus cuneiformis Wallich				39	4.35	5.87
Leptocylindrus danicus Cleve				12	866.2	2338.27
Nitzschia (*Pseudonitzschia*) spp. (small)	15	103.46	157.96			
Nitzschia (*Pseudonitzschia*) spp. (large)	10	82.22	70.84	15	477.87	841.35
Pleurosigma spp.						
Rhizosolenia alata Cleve	8	16.2	38.71	28	49.27	92.79
Rhizosolenia imbricata Brightwell						
Rhizosolenia spp.	15	78.09	89.07	18	66.74	170.85
Schröderella delicatula (Per.) Pavillard						
Thalassionema nitzschioides Grunow				11	8.7	13.16
Thalassiosira spp. (small)	13	454.72	1071.33			
Thalassiosira spp. (medium)	8	50.18	115.04			
Thalassiosira spp. (large)	10	3.42	5.96			
Thalassiothrix frauenfeldii (Grunow) Cleve and Möller	8	7.43	13.29			
Unidentified centric diatoms	12	133.4	95.39			
Pennate diatoms (small)	51	82.1	99.32			
Pennate diatoms (large)	11	5.53	11.85	33	16.84	21.3
Unidentified pennate diatom sp. A						
Dictyocha fibula Ehrenb.	30	73.6	79.75	39	123.61	171.15
Dictyocha speculum Ehrenb.				10	51.71	53.99
Flagellates	127	4811.9	7329.26	107	5742.16	5787.35
Calycomonas spp.	26	728.72	1154.74	10	128.13	36.45
Phaeocystis sp.				16	761.98	821.9
Cryptomonads	22	230.64	134.34	8	145.89	51.58
Leucocryptos?	33	373.07	311.6	42	203.26	121.48
Solenicola setigera	19	1256.17	1306.27	31	1516.35	1650.65
Mesodinium sp.	24	8.91	11.66	15	33.03	65.31
Ciliates	88	179.36	194.77			

small naked gymnodinioids). In general, these two groups were numerically the most abundant. It should be noted, however, that many small cells deteriorate in fixed samples, so that the "flagellate" concentration is likely to be underestimated. Many of the problems associated with the inverted microscope technique and with phytoplankton counts in general have been discussed in several papers (MARGALEF, 1972; 1978; TRAVERS, 1972; VENRICK, 1978). An important consideration in this context is that each technique of phytoplankton enumeration is only able to give a more or less distorted appreciation of a segment of the phytoplankton community. For example, one of the limitations of the inverted microscope technique is its unsuitability for the examination of the organisms in the picoplankton size group. An additional problem, especially in oligotrophic waters such as those studied here, is that the concentrations of most of the relatively large and readily identifiable forms are low and subject to high counting errors in 100 ml samples. This introduces much noise when dealing with the distribution of individual species. However, even considering these limitations, the data should be useful for comparison purposes, provided that the same examination criteria have been used for all the samples.

The characteristics of the data sets used in this paper are summarized in Table I. Mean chlorophyll *a* and phytoplankton concentration values for the upper 100 m (FRONTS 3-85) or 110 m (in the other cruises) of the water column were calculated according to the expression:

$$\overline{X} = \sum_{i=1}^{k} (D_{i+1}-D_i) * (C_{i+1}+C_i)/2/D_k$$

where Ci is the chlorophyll *a* or phytoplankton concentration at depth D_i, is the number of sampling depths and D_k the deeper sampling depth.

Principal component analysis (PCA) was used to summarize the information contained in the phytoplankton lists. A description of the mathematical techniques involved can be found in COOLEY & LOHNES (1971) and LEGENDRE & LEGENDRE (1983). The taxa were selected for the analyses according to their frequency of appearance in the samples (some taxa were excluded because their identification was considered inconsistent). Separate analyses were performed on the correlation matrix among the logarithm-transformed abundance data of the selected species for each cruise. The computer programs were implemented from the IBM Scientific Subroutine Package (IBM, 1969).

RESULTS

The sections of temperature, salinity and chlorophyll along the studied transects are shown in figures 2-5. The distribution of σ_t (not represented) closely followed that of temperature. During FRONTS 3-85, the hydrographical conditions were typical of the mixing period, and temperature and salinity showed little vertical variation. The Catalan front was marked by sharp temperature, salinity and silicate (Fig. 6) gradients in the FRONTS 3-85 and PEP 84 cruises. In the other surveys, carried out later in the season, the upper part of the water column was covered by a layer of warm water; apart from their signature in the salinity distribution, the presence of the fronts and the doming of the isolines in the central zone were apparent only at depth. The distributions (not shown) of nitrate and phosphate (the concentrations of this nutrient were not available for PEP 86) were similar to those of silicate, except that nitrate and phosphate concentrations in the spring cruises were generally undetectable in the surface layers.

During FRONTS 3-85, the highest chlorophyll concentrations were found offshore of the front, in the upper 40-60 m of the water column (Fig. 2). By mid-May

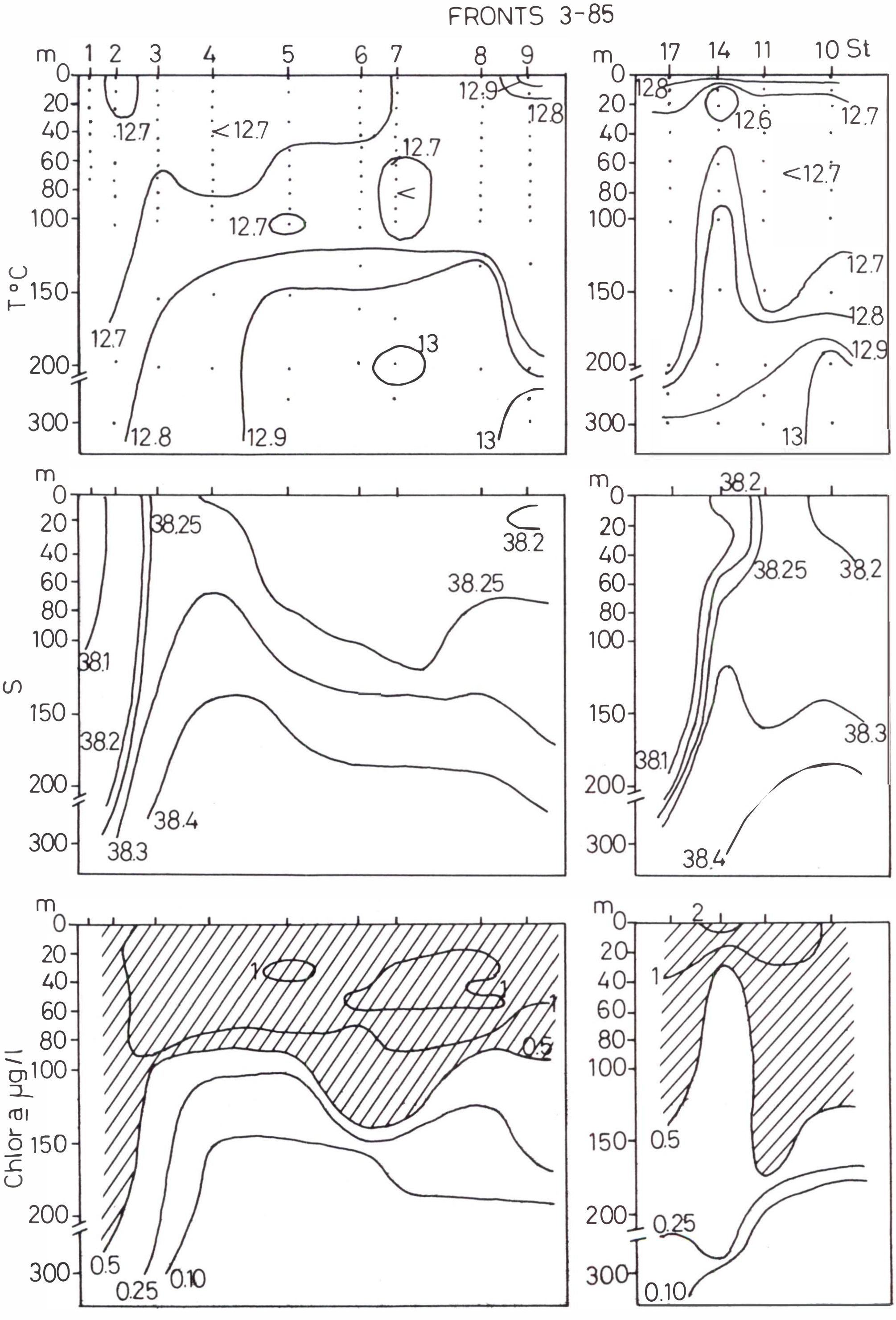


FIGURE 2. Distribution of temperature (T °C), salinity (S) and chlorophyll *a* (chlor. *a*, µg l^{-1}) along the two FRONTS 3-85 transects. The numbers on top on the graph indicate the stations.

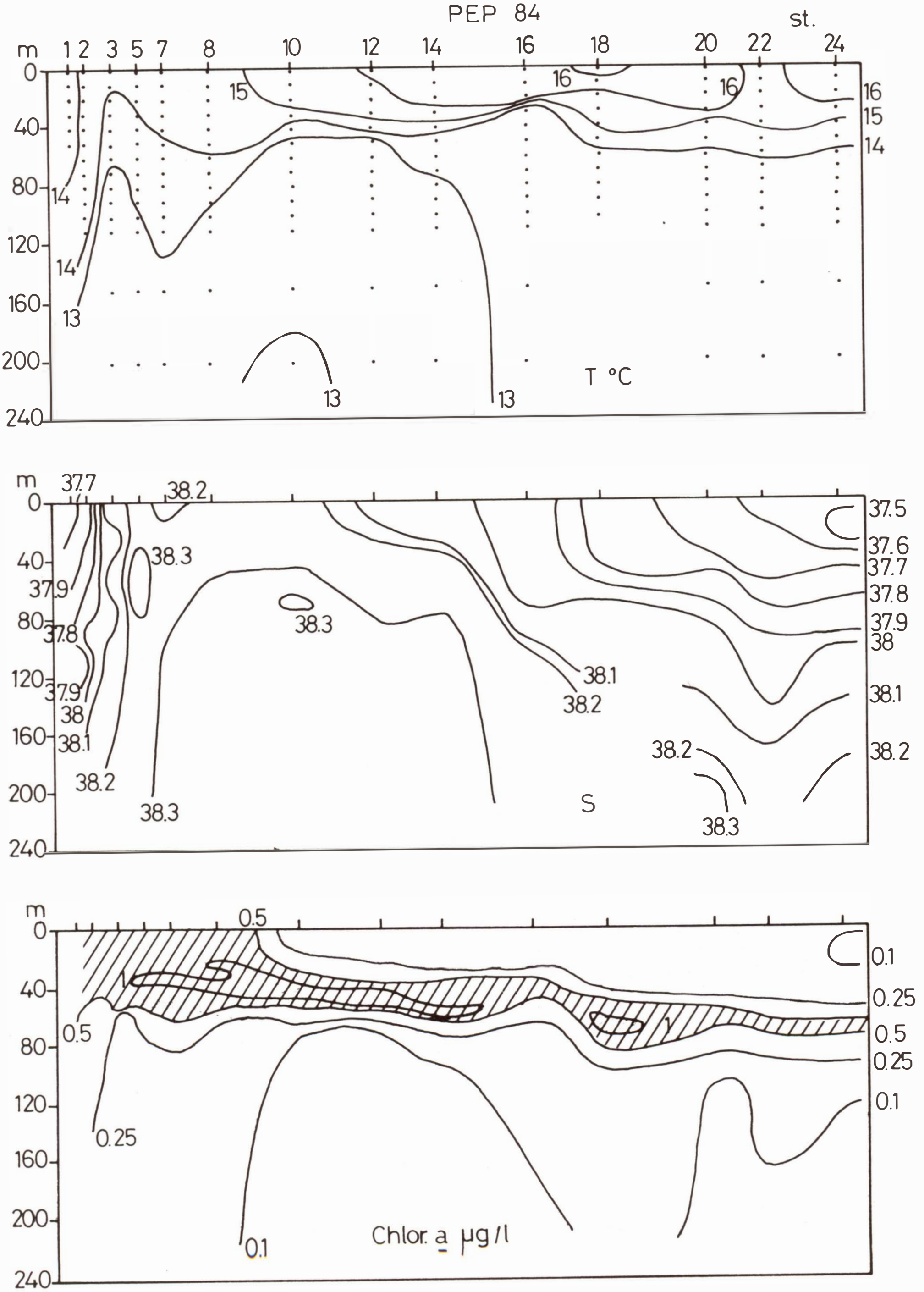


FIGURE 3. Distribution of temperature (T °C), salinity (S) and chlorophyll (chlor *a*, µg l^{-1}) along the PEP 84 transect.

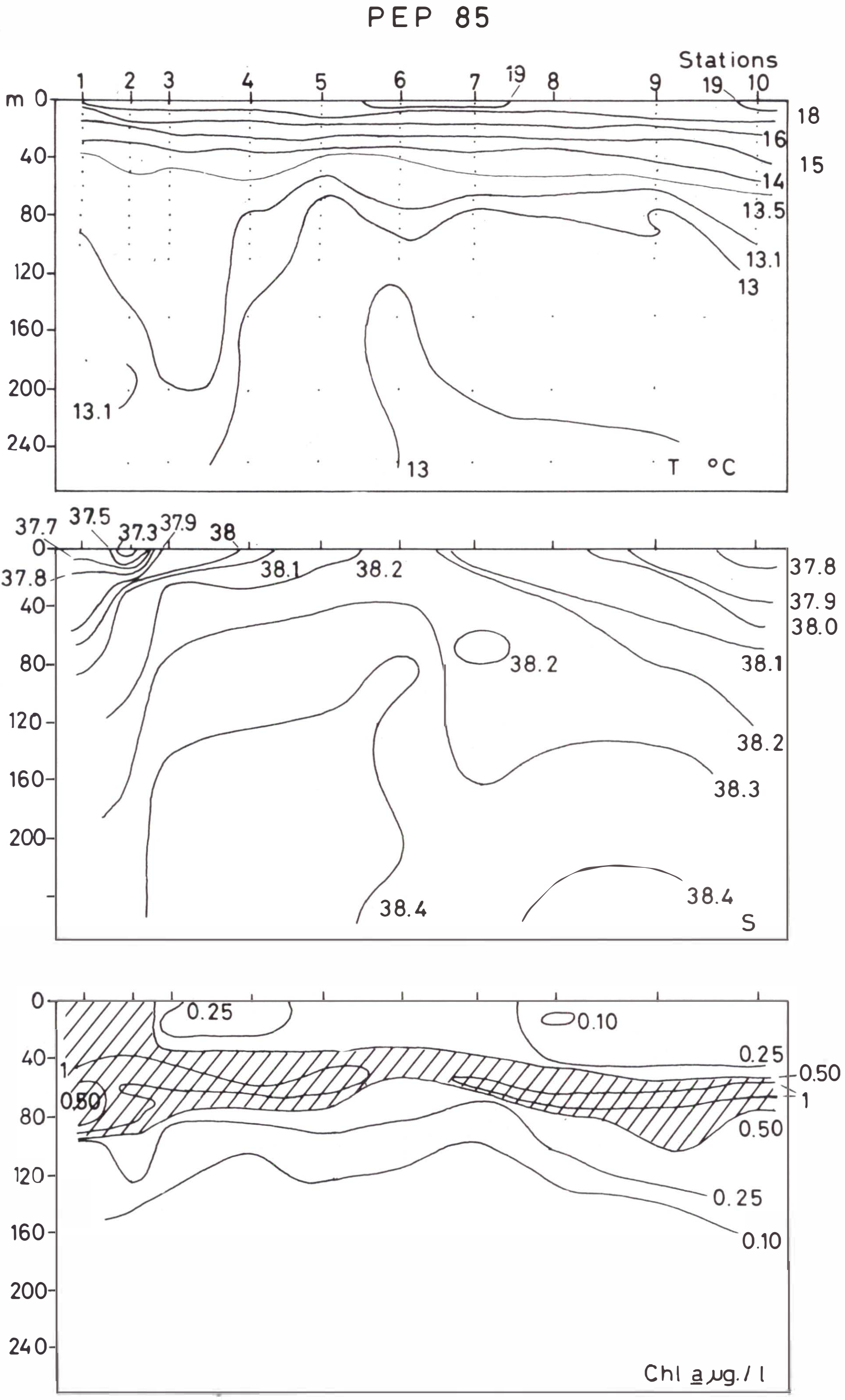


FIGURE 4. Distribution of temperature (T °C), salinity (S) and chlorophyll (chlor. *a*, µg l^{-1}), along the PEP 85 transect.

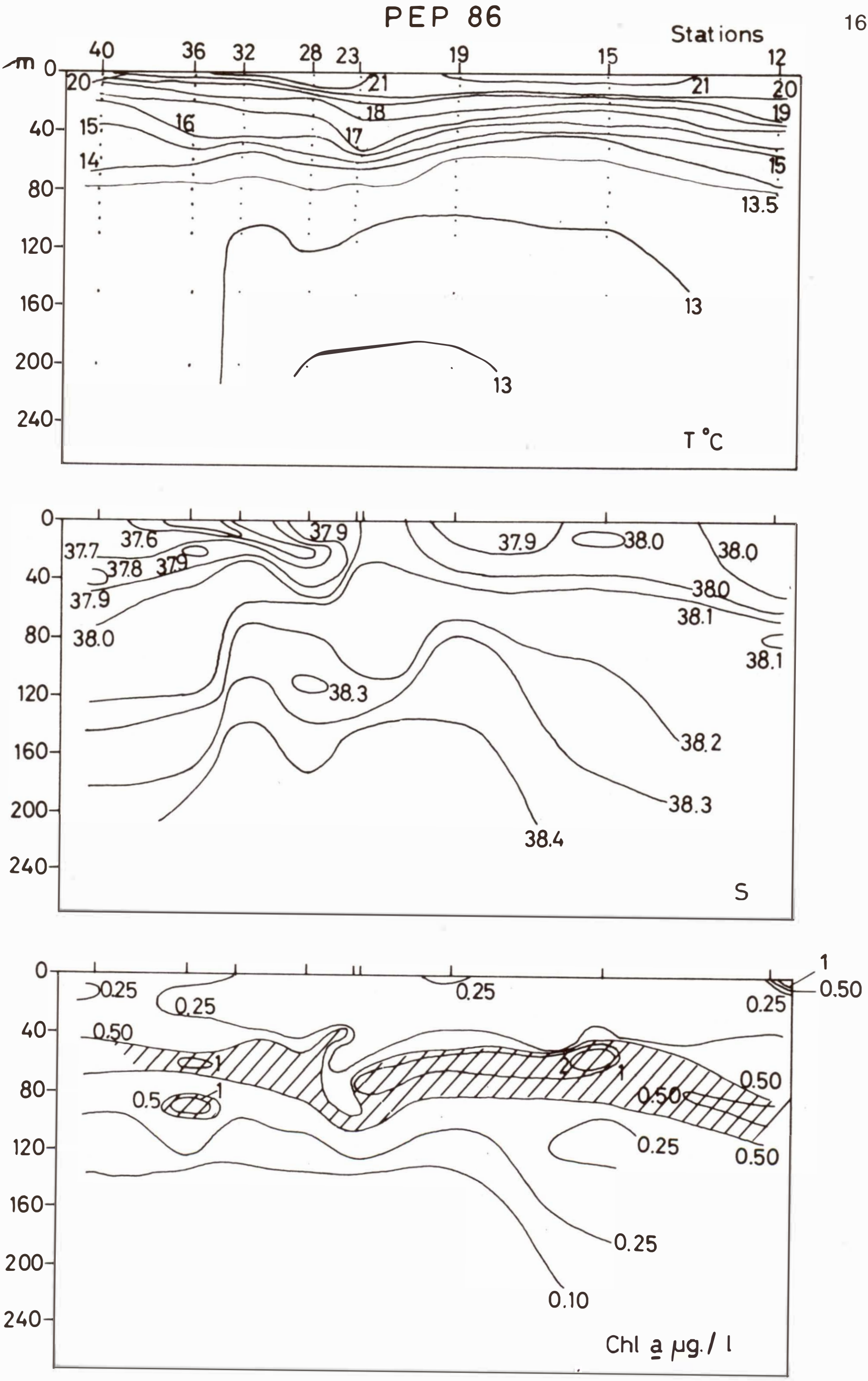


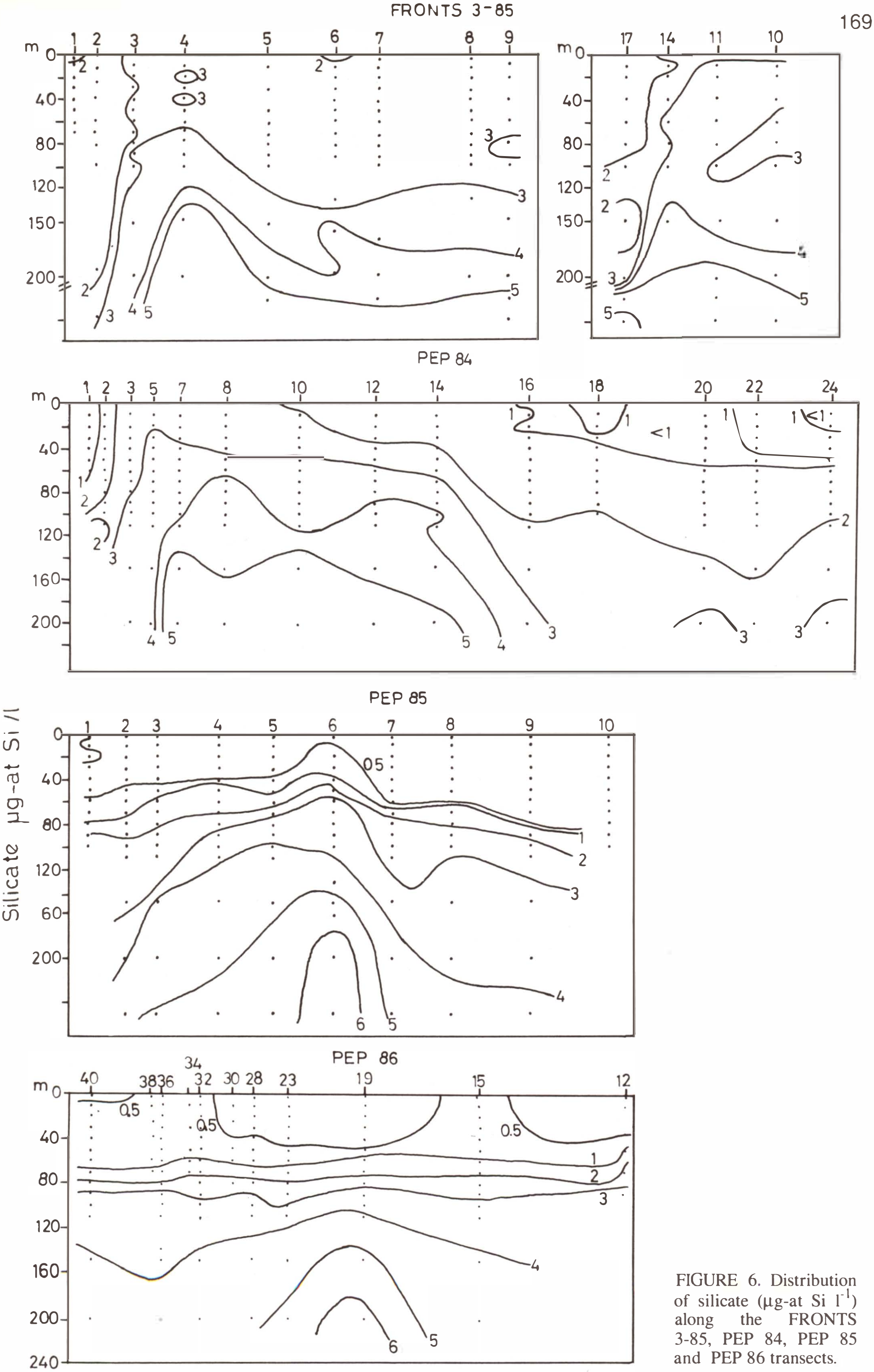
FIGURE 5. Distribution of temperature (T °C), salinity (S) and chlrophyll (chlor *a* µg l^{-1}), along the PEP 86 transect.

(PEP 84), the DCM was well established, with chlorophyll concentrations in some spots exceeding 2 mg m^{-3} (Fig. 3). In this and the other spring cruises (Figs. 4 and 5), the DCM was associated with nitrite and oxygen maxima (not shown) and presented similar global features, although there was a deepening of the chlorophyll maximum with the advance of the season. During PEP 84 and PEP 85, relatively high chlorophyll values (> 0.5 mg m^{-3}) reached the surface, inshore of the Catalan front. A similar situation, although with the front closer to the coast, was found in the first transect of PEP 86 (not shown; see MASÓ & PEPS, 1988); Station 40, in the transect presented here, was too far from the coast to show this feature. No comparable increases of surface chlorophyll concentration were found in the Balearic frontal zone, although high chlorophyll patches were often present at the DCM.

The total phytoplankton abundance showed maxima in the upper euphotic zone, offshore of the Catalan front, in FRONTS 3-85 (Fig. 7). During PEP 84, the highest phytoplankton densities were found offshore, at surface, and in the DCM, at depth (Fig. 8). In the other cruises (Figs. 9 and 10), the higher phytoplankton abundances were found nearshore and at the DCM level. The distributions of flagellates (not shown), which were numerically the dominant group, and of small dinoflagellates tended to show similar features. The distribution of diatoms was much more patchy than that of the other groups. In March 1985 (Fig. 7), diatoms formed the bulk of the phytoplankton community inshore of the Catalan front, while flagellates with a large proportion of haptophytes (including *Phaeocystis*) dominated offshore. In the other cruises later in the season, the diatoms were restricted to the DCM zone, where they formed localized high concentration patches.

The mean chlorophyll *a* concentration for the upper 100 or 110 m of the water column (Fig. 11) exceeded 1 µg l^{-1} for many stations of FRONTS 3-85. During the spring cruises, the mean chlorophyll *a* value was generally lower than 0.6 µg l^{-1}; the higher mean concentrations tended to be found in the frontal zones. The relationship between mean chlorophyll *a* and phytoplankton concentrations (Fig. 11) was very variable, as could be expected from the different size and physiological conditions of the organisms involved; this relation was highest during FRONTS 3-85 and tended to decrease from mid to late spring.

Some statistical data for the most frequent and/or abundant taxa in the four cruises are given in Table I. These lists should be compared with caution, since vaguely defined taxa may represent different species or forms from one cruise to another. As stated before, flagellates and small dinoflagellates were the numerically dominant forms in all cruises. The most common among the thecate dinoflagellate forms were species of *Protoperidinium*, *Prorocentrum*, *Oxytoxum* and *Ceratium*. Coccolithophorids were scarce in all the cruises; it appears that they may be important only at particular times of the year (ESTRADA, 1985a; ESTRADA & SALAT, 1989; and unpublished data). The silicoflagellate *Dictyocha fibula* was present in all cruises but, except in March 1985, was restricted to the lower layers of the euphotic zone, a typical feature of its distribution during the stratification period in the Mediterranean (NIVAL, 1965; TRAVERS & TRAVERS, 1968; ESTRADA, 1985a). *D. speculum* was only appreciably frequent in the PEP 86 cruise. The most abundant diatom genera in all cruises were *Chaetoceros*, *Nitzschia*, *Rhizosolenia* and *Thalassiosira*. *Ditylum brightwelli* was well represented in coastal waters during the FRONTS 3-85 cruise; it was common in the microplankton samples from the July cruises of 1982 and 1983, but had only been found rarely in earlier surveys of the zone (MARGALEF &


FRONTS 3-85

PEP 84

PEP 85

PEP 86

FIGURE 6. Distribution of silicate (μg-at Si l^{-1}) along the FRONTS 3-85, PEP 84, PEP 85 and PEP 86 transects.

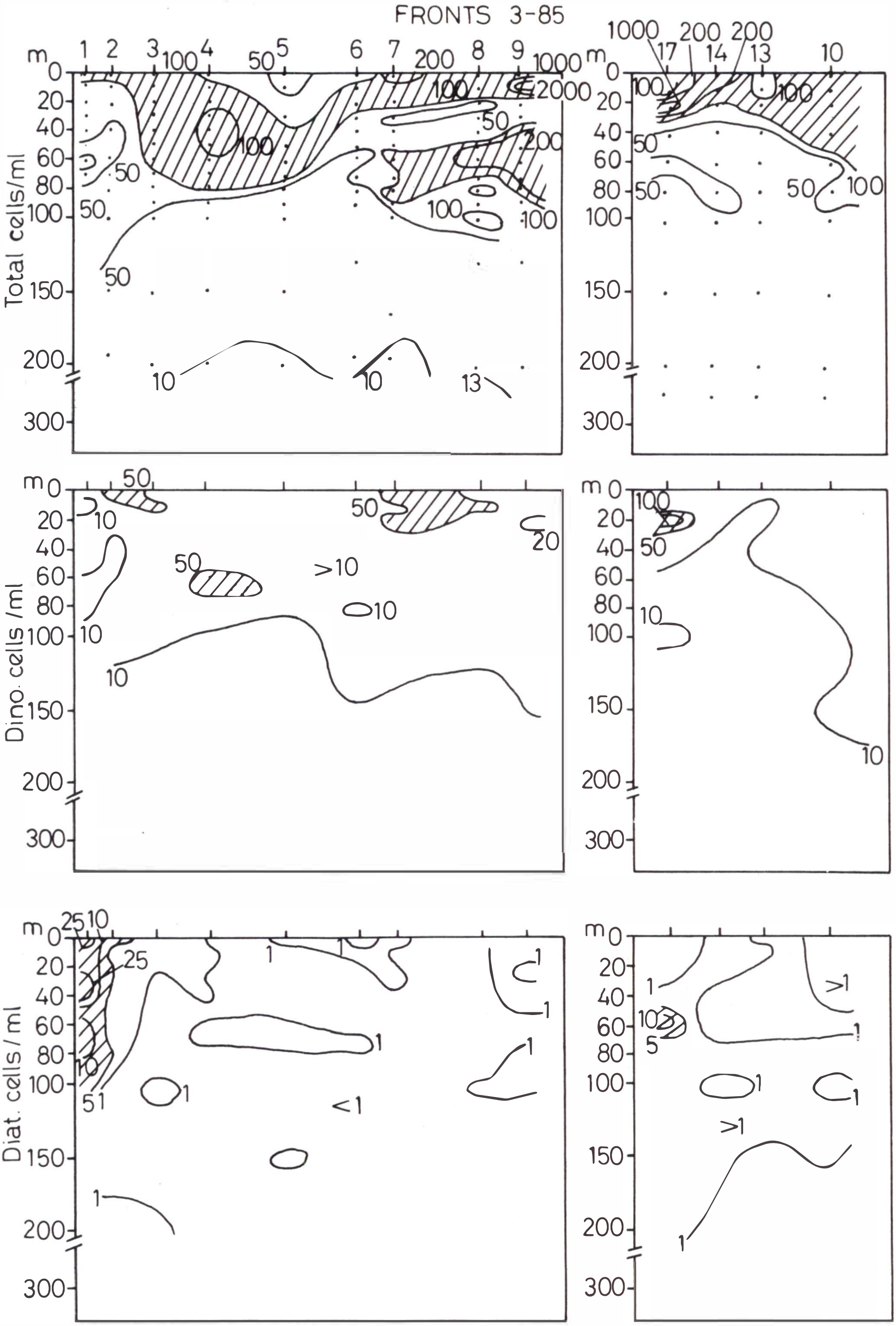


FIGURE 7. Distribution of the population density (cells ml^{-1}) of total phytoplankton, dinoflagellates and diatoms, along the FRONTS 3-85 transects.

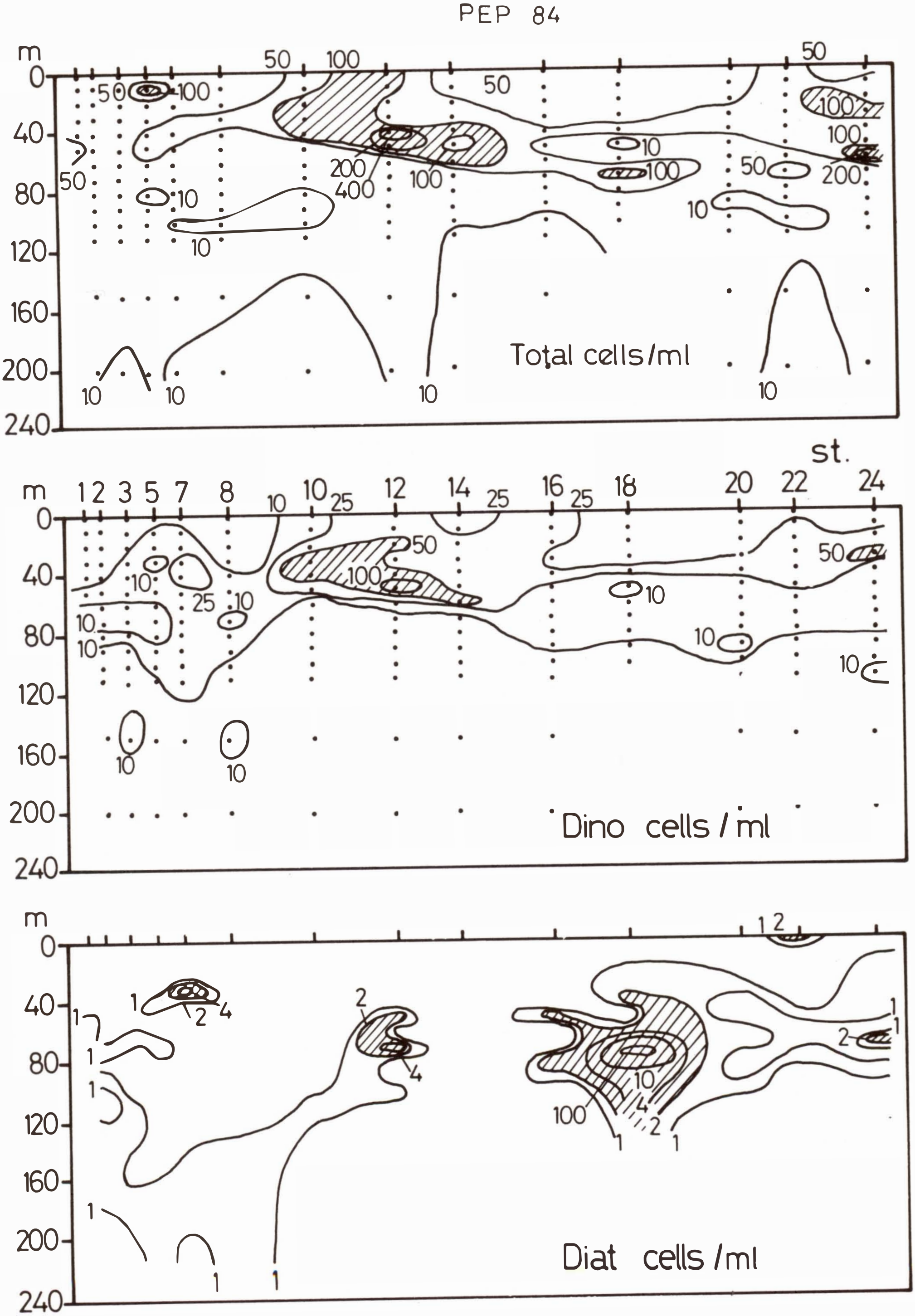


FIGURE 8. Distribution of the population density (cells ml^{-1}) of total phytoplankton, dinoflagellates and diatoms, along the PEP 84 transect.

ESTRADA, 1987). Weakly silicified *Chaetoceros* forms generally contributed the bulk of the high diatom concentration patches in the DCM. In the spring cruises, *Coscinodiscus radiatus* and *Hemidiscus cuneiformis* were typically distributed in the lower part of the euphotic zone; they were found at shallower depths in the winter cruise.

TABLE II. Percentage of variance explained by the first three principal components (PC1, PC2, PC3) of the analyses.

cruise	PC1	PC2	PC3
PEP 84	11.1	7.9	5.3
FRONTS 3-85	10.7	9.2	6.6
PEP 85	11.6	6.8	5.4
PEP 86	11.3	9.3	6.9

The variance explained by the first three principal components (PC) in all the analyses ranged from 29% to 33% (Table II). Examination of the ordination of the species according to their correlations (loadings) with the components (Table III and Fig. 12) showed several regularities. PC2 from FRONTS 85 and PC1 from the remaining cruises presented positive correlations with most of the species and could be considered as generalized "abundance-richness of species" components. Their distribution (Figs. 13-16) was comparable with that of total cell abundances and chlorophyll concentration; this reflects the fact that most taxa tend to coincide in occupying the richer areas and is a general finding in

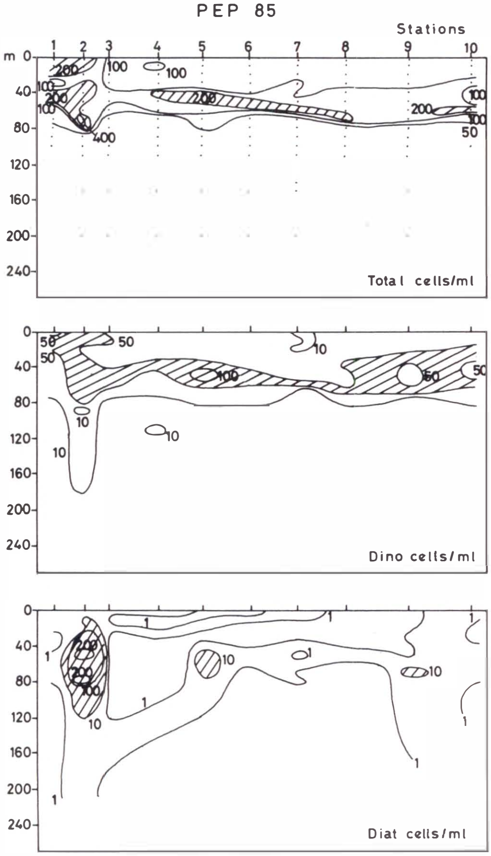


FIGURE 9. Distribution of the population density (cells ml^{-1}) of total phytoplankton, dinoflagellates and diatoms, along the PEP 85 transect.

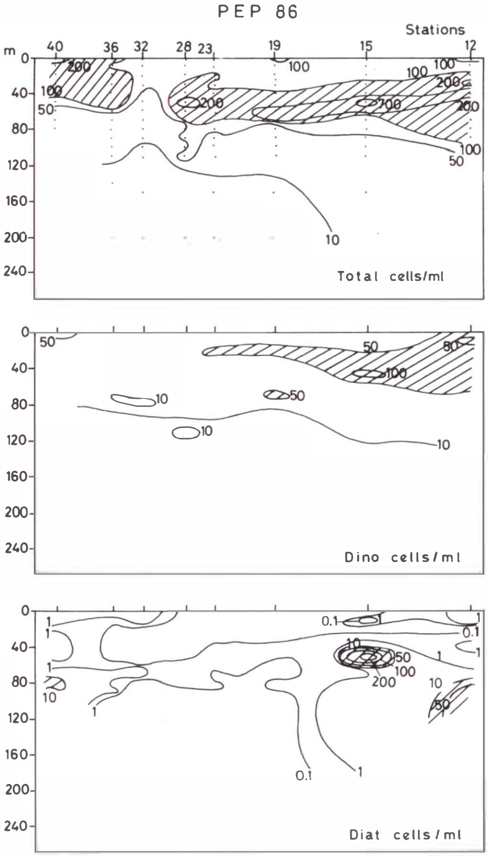


FIGURE 10. Distribution of total population density (cells ml^{-1}) of total phytoplankton, dinoflagellates and diatoms, along the PEP 86 transect.

multivariate analyses concerned with distributions of organisms when there are contrasts in fertility within the area studied.

A comparison of the loading ordinations of PC1 for FRONTS 85 and PC2 for the spring cruises (Fig. 12) showed that these components coincided in expressing a contrast between major taxonomic groups, with diatoms on one side and dinoflagellates and other groups on the other. An estimation of the similarities among these ordinations was carried out by calculating the Spearman rank correlation coefficients (Rs) among the positions of the *n* common taxa in each pair of ordinations. The results indicated significant positive correlations between the PC2 ordinations of the spring cruises (Rs =0.46 between PEP 84 and PEP 85 for *n*=32 common taxa; Rs =0.58 between PEP 85 and PEP 86 for *n*=30, and Rs =0.60 between PEP 84 and PEP 86 for *n*=33). The distributions of the components (Figs. 13-16) presented a clearcut boundary between the phytoplankton populations in the coastal and oceanic side of the Catalan front during the FRONTS 85 and PEP 84 cruises, and reflected the importance of diatoms in the DCM.

The distributions of PC3 in PEP 84 and PEP 86 (Figs. 14-16) consistently showed a marked gradient between the upper and the lower part of the euphotic zone. In both cruises, a group of taxa including *Oxitoxum margalefi*, *Coscinodiscus radiatus*, *Hemidiscus cuneiformis, Dictyocha fibula,* and an unidentified dinoflagellate (sp. D), which were typically distributed in the lower parts of the euphotic zone, characterized one of the extremes of the ordination list, while the highest correlations on the other side corresponded basically to dinoflagellates and flagellates, but also to some diatom taxa. The

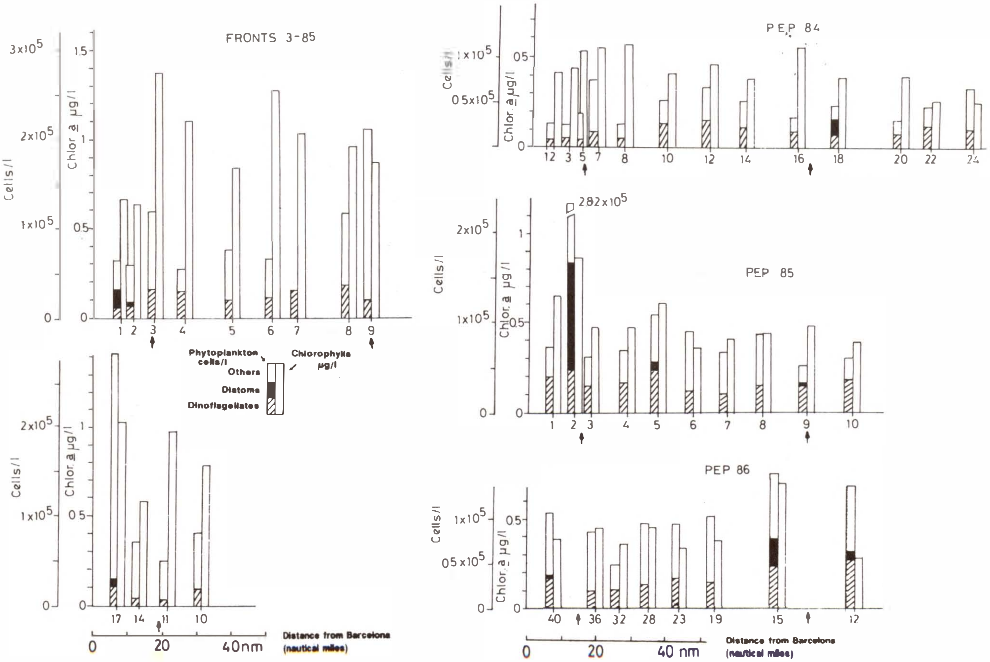


FIGURE 11. Mean values of chlorophyll *a* (chlor. *a* µg l^{-1}) and population densities (cells ml^{-1}) of total phytoplankton, dinoflagellates and diatoms for the upper 100 m (FRONTS 3-85) or 110 m (PEP 84, PEP 85 and PEP 86) of the water column.

TABLE III. Loadings of the selected taxa on the "biomass" component (first principal component, C1, of the analyses of PEP 84, PEP 85 and PEP 86 and second principal component, C2, of the analysis of FRONTS 3-85). Taxa ordained according to decreasing value of the loading

PEP 84

TAXA	Loading on C1
Unidentified dino. sp. B	0.73
Prorocentrum spp. (small)	0.62
Unidentif. pennate diat. sp. A	0.59
Dictyocha fibula	0.54
Nitzschia spp.	0.53
Gonyaulax spp.	0.50
Schröderella delicatula	0.49
Pleurosigma spp.	0.47
Chaetoceros spp. C	0.47
Solenicola setigera	0.47
Cochlodinium spp.	0.43
Unidentified dinoflagellates	0.42
Prorocentrum compressum	0.40
Gyrodinium spp.	0.40
Flagellates	0.38
Oxytoxum scolopax	0.38
Oxytoxum spp. (small)	0.38
Pennate diatoms (small)	0.36
Oxytoxum sp. D	0.35
Mesoporos perforatus	0.34
Leptocylindrus danicus	0.34
Protoperidinium spp. (small)	0.33
Dinophysis spp.	0.31
Unidentified dino. sp. F	0.28
Unidentified dino. sp. D	0.26
Palaeophalachroma unicinctum	0.26
Pronoctiluca sp.	0.25
Rhizosolenia alata	0.23
Torodinium robustum	0.22
Scrippsiella trochoidea	0.21
Oxytoxum variabile	0.17
Oxytoxum margalefi	0.16
Dinophysis (Phalachr.) spp.	0.16
Ceratium fusus	0.15
Calycomonas spp.	0.15
Thalassiosira spp. (small)	0.13
Ceratium furca	0.12
Protoperidinium bipes	0.07
Prorocentrum micans	0.05
Rhizosolenia spp.	-0.00
Unidentified coccolithophorids	-0.00
Mesodinium sp.	-0.03
Hemidiscus cuneiformis	-0.05
Emiliania huxleyi	-0.05
Coscinodiscus radiatus	-0.08
Thalassiosira spp. (medium)	-0.08
Leucocryptos?	-0.09
Torodinium spp.	-0.11

PEP 85

TAXA	Loading on C1
Flagellates	0.75
Unidentif. small dinof.	0.72
Calycomonas spp.	0.59
Gyrodinium spp.(small)	0.56
Prorocentrum spp. (small)	0.56
Protoperidinium spp. (small)	0.50
Leucocryptos?	0.46
Protoperidinium sp. A	0.46
Cochlodinium spp.	0.44
Torodinium robustum	0.44
Ceratium fusus	0.43
Cryptomonads	0.42
Unidentif. centric diatoms	0.40
Syracosphaera pulchra	0.40
Mesoporos perforatus	0.40
Ciliates	0.39
Chaetoceros spp. C	0.36
Unidentified dino sp. B	0.35
Solenicola setigera	0.32
Dinophysis ovum	0.29
Unidentified dino sp. F	0.28
Ceratium furca	0.26
Nitzschia spp. (small)	0.26
Thalassiosira spp. (small)	0.25
Scrippsiella trochoidea	0.24
Rhizosolenia spp.	0.24
Torodinium spp (small)	0.23
Chaetoceros sp. A	0.21
Rhizosolenia alata	0.21
Unidentified dino. sp. D	0.20
Protoperidinium bipes	0.19
Pennate diatoms (small)	0.18
Oxytoxum spp. (small)	0.18
Oxytoxum variabile	0.17
Thalassiosira spp. (medium)	0.16
Dinophysis rotundata	0.16
Nitzschia spp. (large)	0.15
Dictyocha fibula	0.14
Pennate diatoms (large)	0.13
Chaetoceros spp. B	0.13
Oxytoxum margalefi	0.12
Oxytoxum spp. (large)	0.04
Thalassiothrix frauenfeldii	0.02
Mesodinium sp.	0.01
Thalassiosira spp. (large)	-0.01
Protoperidinium spp. (large)	-0.16
Coscinodiscus radiatus	-0.24

Spearman rank correlation coefficient among the ordinations of the 33 common taxa (Rs =0.43) was significant at the 5% level. The PC3 of the FRONTS 85 analysis was more difficult to interpret, but it also appeared to express a contrast in vertical distributions and its positive side was related to the presence of several taxa with

TABLE III (Cont.)

PEP 86

TAXA	Loading on C1
Unidentified dinoflagellates	0.74
Flagellates	0.72
Rhizosolenia alata	0.59
Chaetoceros spp. B	0.57
Chaetoceros spp. C	0.56
Pennate diatoms (large)	0.53
Leptocylindrus danicus	0.49
Solenicola setigera	0.48
Prorocentrum spp. (small)	0.46
Unidentified dino. sp. B	0.45
Rhizosolenia spp.	0.45
Phaeocystis sp.	0.42
Leucocryptos	0.41
Unidentified dino. sp. D	0.41
Goniodoma sphaericum	0.40
Gonyaulax turbynei	0.39
Dinophysis acuta	0.35
Mesodinium sp.	0.35
Protoperidinium spp. (small)	0.35
Gyrodinium spp. (small)	0.30
Goniodoma polyedricum	0.28
Dissodium (*Diplopsalis*) spp.	0.26
Dinophysis rotundata	0.25
Prorocentrum compressum	0.25
Mesoporos perforatus	0.25
Gyrodinium spp. (large)	0.25
Protoperidinium crassipes	0.22
Torodinium robustum	0.22
Cochlodinium spp.	0.20
Protoperidinium spp. (large)	0.19
Ceratium fusus	0.14
Oxytoxum scolopax	0.14
Prorocentrum maximum	0.13
Oxytoxum variabile	0.12
Cryptomonads	0.12
Dictyocha speculum	0.12
Hemidiscus cuneiformis	0.12
Thalassionema nitzschioides	0.12
Oxytoxum margalefi	0.1
Coscinodiscus radiatus	0.09
Dinophysis spp.	0.09
Gonyaulax spp.	0.06
Dinophysis (*Phalachr.*) spp.	0.05
Unidentified dino. sp. F	0.05
Torodinium spp. (small)	0.04
Gonyaulax polygramma	0.02
Calycomonas spp.	0.02
Nitzschia spp.	0.02
Protoperidinium steini	0.00
Dictyocha fibula	-0.02

FRONTS 3-85

TAXA	Loading on C2
Flagellates	0.54
Rhizosolenia imbricata	0.53
Thalassiosira spp. (small)	0.47
Chaetoceros spp. B	0.47
Ditylum brightwelli	0.46
Chaetoceros spp. C	0.45
Nitzschia spp.	0.44
Unidentified dinoflagellates	0.43
Scrippsiella trochoidea	0.41
Pennate diatoms (small)	0.37
Pennate diatoms (large)	0.35
Dictyocha fibula	0.33
Mesoporos perforatus	0.32
Thalassiosira spp. (medium)	0.31
Unidentif. pennate diat. sp. A	0.31
Cryptomonads	0.30
Prorocentrum spp. (small)	0.28
Coscinodiscus radiatus	0.25
Unidentified dino. sp. B	0.22
Ciliates	0.21
Pleurosigma spp.	0.19
Cochlodinium spp.	0.11
Protoperidium spp. (small)	0.08
Torodinium sp. (small)	0.03
Oxytoxum variabile	0.01
Unidentified coccolithophorids	0
Coscinodiscus spp.	-0.01
Phaeocystis sp.	-0.03
Hemidiscus cuneiformis	-0.04
Leucocryptos?	-0.05
Calycomonas spp.	-0.10
Emiliania huxleyi	-0.18
Diploneis sp.	-0.20
Gyrodinium spp. (small)	-0.25

benthic affinities (large pennate diatoms, *Coscinodiscus, Pleurosigma* spp.). These taxa with relatively deep distributions tended to present the lowest correlations with the "abundance-richness of taxa" components, a finding which presumably reflects the segregation of their distribution from the high biomass zones. In contrast, the distribution of the PC3 of PEP-85 appeared mainly to express a difference between the communities neighbouring the Balearic zone and those of the rest of the transect. The taxa showing the highest correlation with this component were several small thecate dinoflagellates.

For simplicity, in the following comments, PC2 of FRONTS 85 and PC1 of the remaining cruises will be referred to as the "biomass component"; PC1 of FRONTS 85 and PC2 of the other cruises will be referred to as the "diatom component" and PC3 of PEP 84 and PEP 86 as the "vertical gradient component".

Considering the loadings of the taxa on the first three components, three main assemblages can be loosely distinguished.

A) A group occupying the upper euphotic zone during stratified conditions, comprising basically dinoflagellates and flagellates presenting negative correlations with the "diatom component", positive correlations with the "vertical gradient component" and more or less positive correlations with the "biomass component". Typical of this assemblage are taxa such as *Torodinium robustum*, *Ceratium furca*, *Ceratium fusus*, *Prorocentrum* spp. (small) and the flagellates.

B) A group of taxa with negative loadings on the "biomass" and the "vertical gradient" components, occupying the lower parts of the euphotic zone, within the

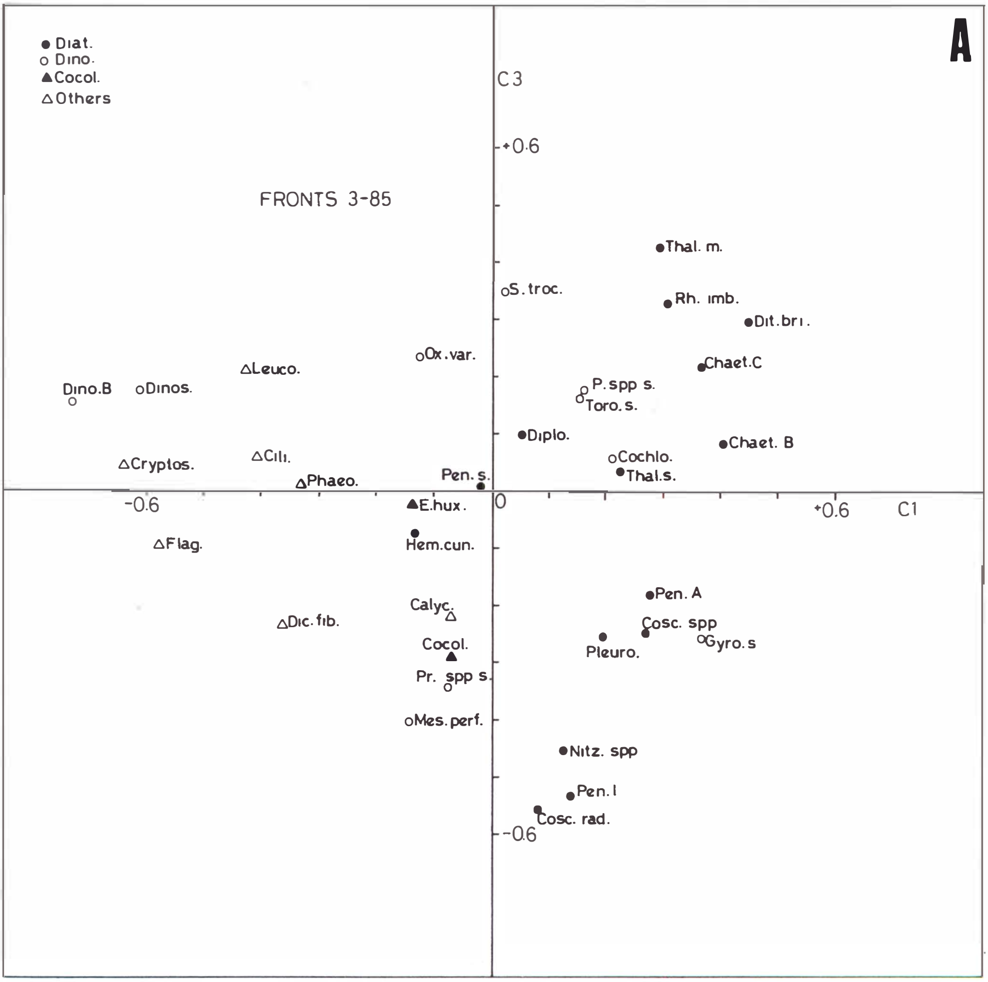


FIGURE 12. Position of the extremes of the taxa vectors in the space determined by the "diatom" component (first principal component, C1, of FRONTS 3-85 and second principal component, C2, of PEP 84, PEP 85 and PEP 86) and the third principal component, C3 (which represents the "vertical gradient" component for PEP 84 and PEP 86). The scale of the third principal component of PEP 85 has been reversed to facilitate comparison with the other graphs. The key for the codes is given in Table I.

DCM, but not being important contributors to the high chlorophyll patches in it. Characteristic of this group are *Oxytoxum margalefi*, *Coscinodiscus radiatus*, *Dictyocha fibula*, *Hemidiscus cuneiformis* and the unidentified dinoflagellate sp. D.

C) Practically all the diatoms (the exceptions being mainly *C. radiatus* and *H. cuneiformis*), characterized by positive loadings on the "diatom component" and high or medium loadings on the "biomass component", were distributed as an assemblage in each cruise, in the coastal zone inside the Catalan front in winter, and in the DCM in spring. However, given the differences in the diatom species present in the different cruises (especially when comparing winter and spring surveys) and the fact that many of the taxa identified to the genus level could include different species in each cruise, it is not possible to ascertain precisely the similarities between the diatom assemblages present in each cruise.

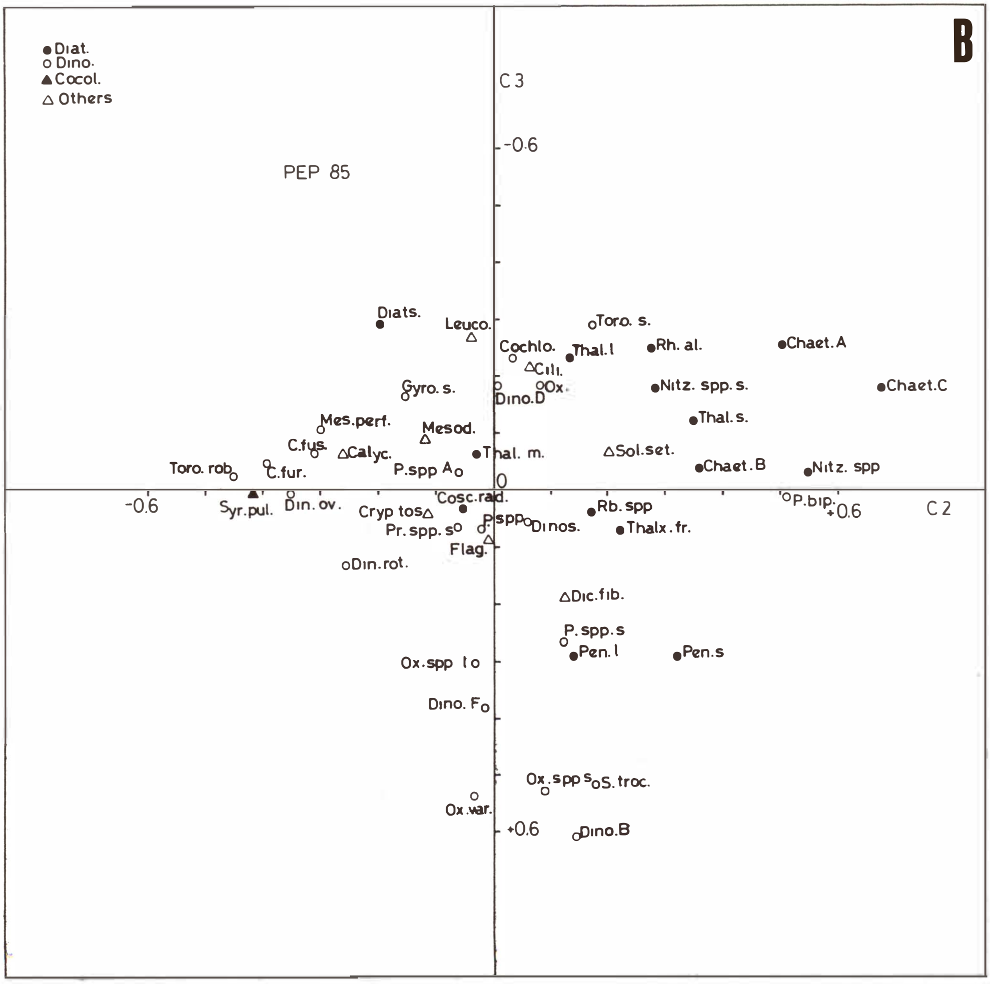


FIGURE 12. (Cont.).

DISCUSSION

Comparison of the phytoplankton and chlorophyll distributions showed overall similarities, although there were some exceptions, for example in the upper 30 m of the water column in the stations of the Catalan coast side of the PEP 84 cruise, where relatively high chlorophyll *a* concentrations corresponded to relatively low phytoplankton densities. Apart from the possibility of certain artifacts, such as differential deterioration of cells in the fixed samples, this could be due, for example, to a lower proportion of heterotrophic forms, larger average cell volume or increased chlorophyll content per cell (which could be a result of the higher nutrient concentrations) in the coastal zone.

During March 1985, although diatoms were more abundant in the coastal zone inshore of the Catalan front, chlorophyll concentrations were higher offshore, coinciding with high flagellate concentrations. This finding stresses the importance of the contribution of frontal instabilities to the fertility of the central zone of the Catalan Sea. Both the coastal

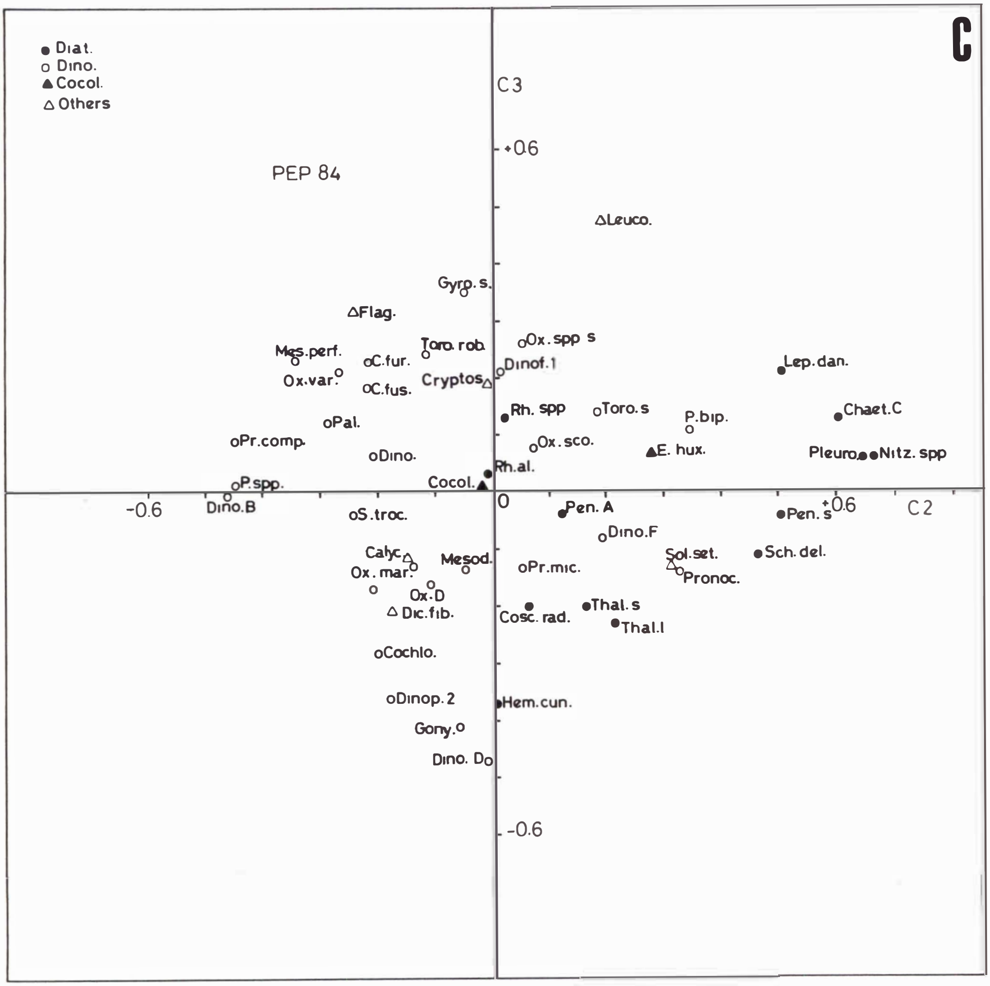
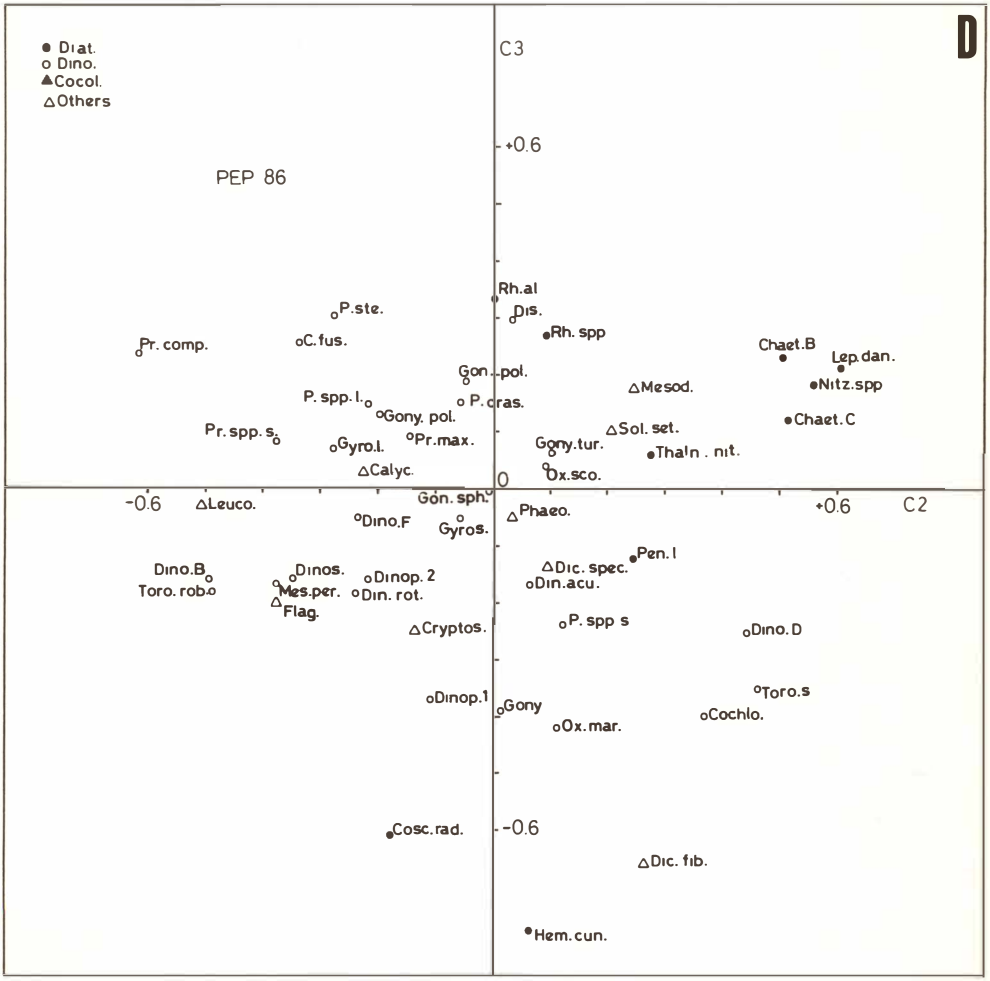


FIGURE 12. (Cont.).

and offshore assemblages included taxa cited by MARGALEF (1969) as typical of the winter-spring bloom in coastal waters of the Catalano-Balearic sea. MARGALEF & BALLESTER (1967) and MARGALEF & CASTELLVÍ (1967) had pointed out the variable contribution of diatoms and flagellates (including a large number of organisms now included within the haptophytes) to the spring bloom; however, as earlier data were restricted to littoral stations (depths < 1000 m), it is difficult to make comparisons with the inshore and offshore assemblages found in the present study.

The global features of the phytoplankton distribution during the cruises studied showed a major change from winter to spring, in correspondence with the hydrographical transition from a mixing to a stratified situation. All the spring cruises showed the presence of a well established DCM. In general, this DCM was associated with a peak in cell numbers and there was good correspondence between high chlorophyll spots at the DCM and patches of high diatom abundance. However, as shown by other studies (ESTRADA, 1985a; VANDEVELDE *et al.*, 1987; GOULD, 1988), comparison of chlorophyll and cell



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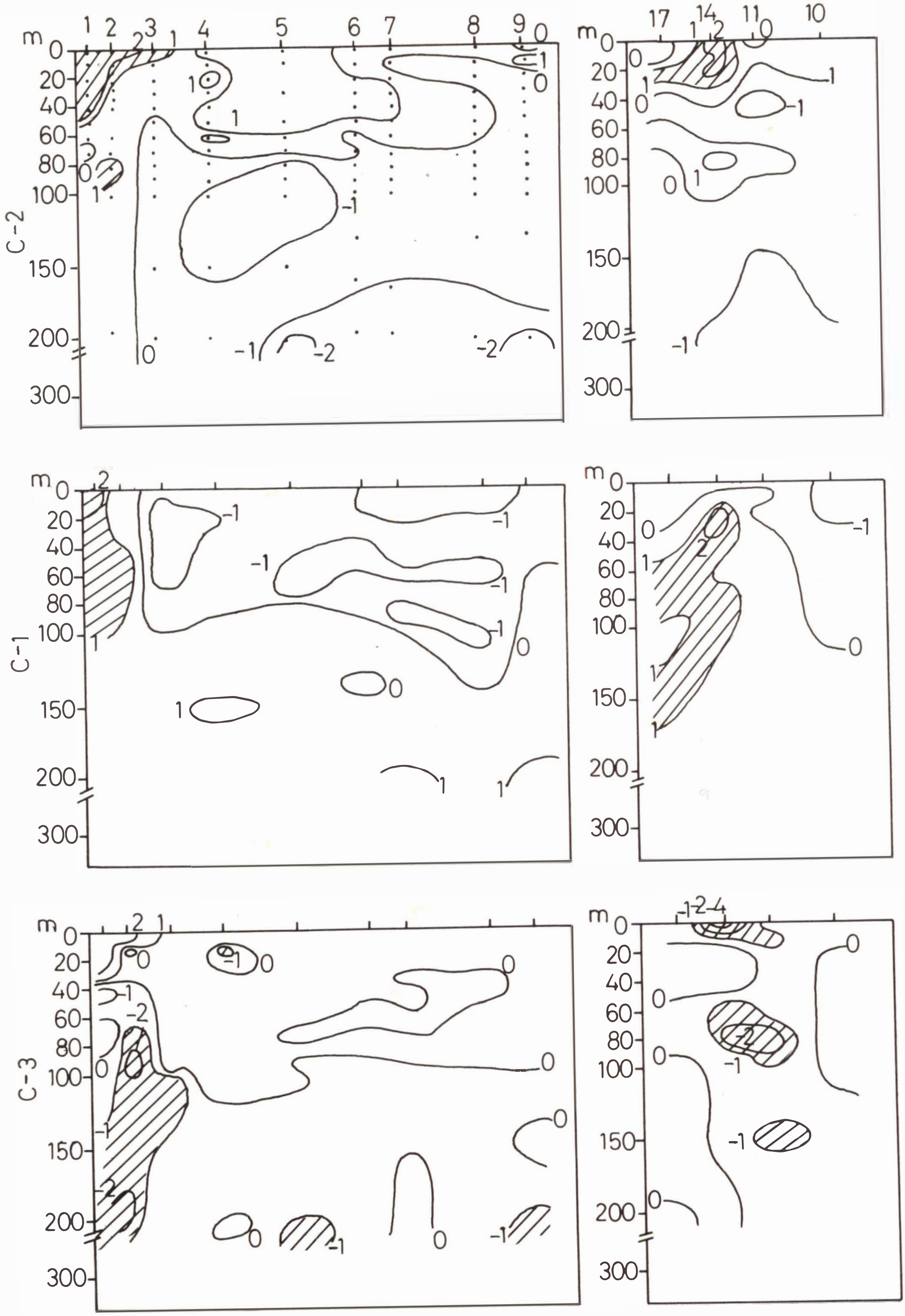

FIGURE 13. Distribution of the first three principal components (C2, C1 and C3) along the FRONTS 3-85 transects. C2 represents the "biomass" component for this cruise and is shown in the upper graph.

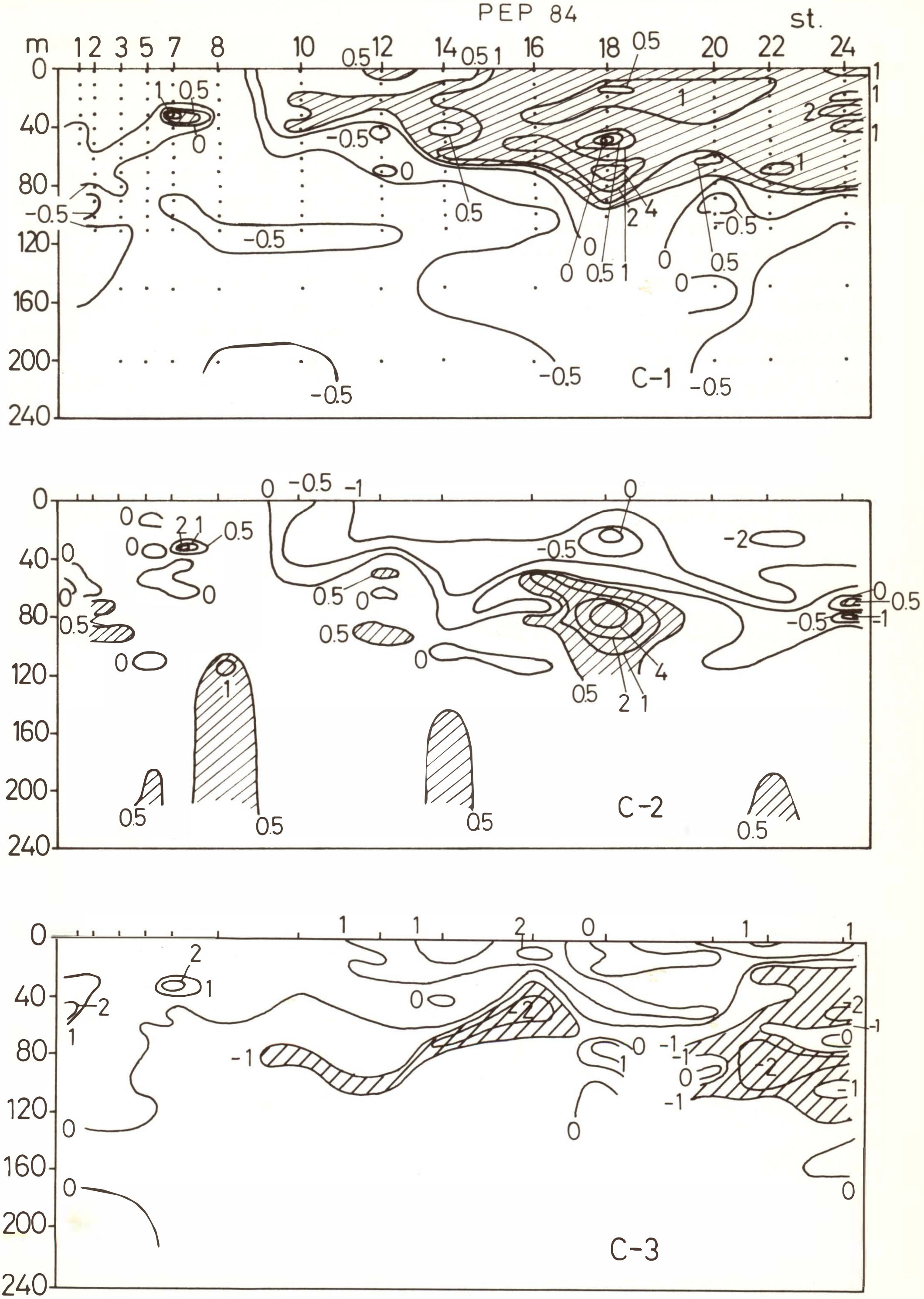

FIGURE 14. Distribution of the first three principal components (C1, C2 and C3) along the PEP 84 transect.

distributions indicated that increased chlorophyll content per cell was also a factor. Concerning mean chlorophyll a and phytoplankton concentration in the euphotic zone, the most striking feature is the high chlorophyll to phytoplankton ratio in FRONTS 3-85, when compared to that of other cruises. Apart from artifacts such as those mentioned above and differences in cell size, a likely explanation is higher chlorophyll *a* content of actively growing cells during the bloom period.

An important difference between PEP 84 and the cruises carried out later in the season was the presence, in the later cruises, of a surface layer of low density water which covered the coastal zone and the disappearance of the strong surface signatures characterizing the Catalan front. This is closely related with major features of the phytoplankton distribution. As can be seen comparing figures 15 and 16, the main change between mid May (PEP 84) and early June appears to be the extension inshore, across the Catalan front, of the phytoplankton assemblage (Group A) which, during May, occupied the upper part of the euphotic zone, offshore of the front. In the two early June cruises, PEP 85 and PEP 86, this assemblage extends along the entire transect. Whether these changes represent expansion of offshore surface waters and their resident phytoplankton or the response of phytoplankton to local stratification remains to be clarified. In the first case, the phenomenon could be related to the spring invasion of surface waters from the east which had already been noted

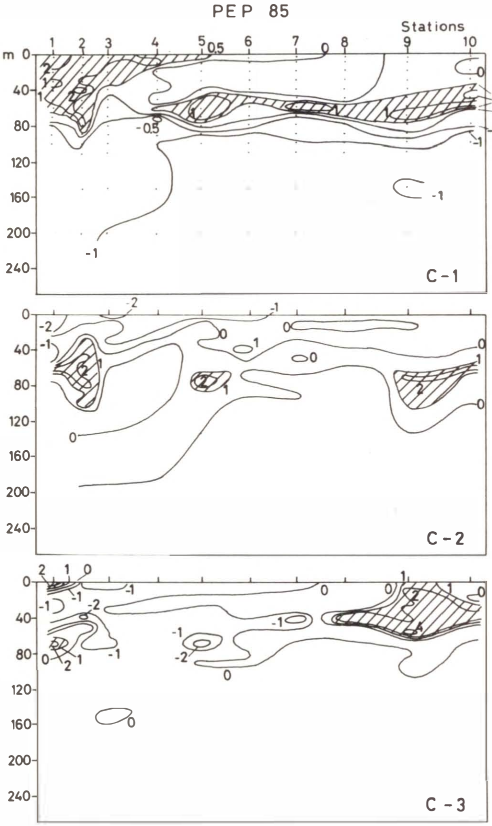

FIGURE 15. Distribution of the first three principal components (C1, C2 and C3) along the PEP 85 transect.

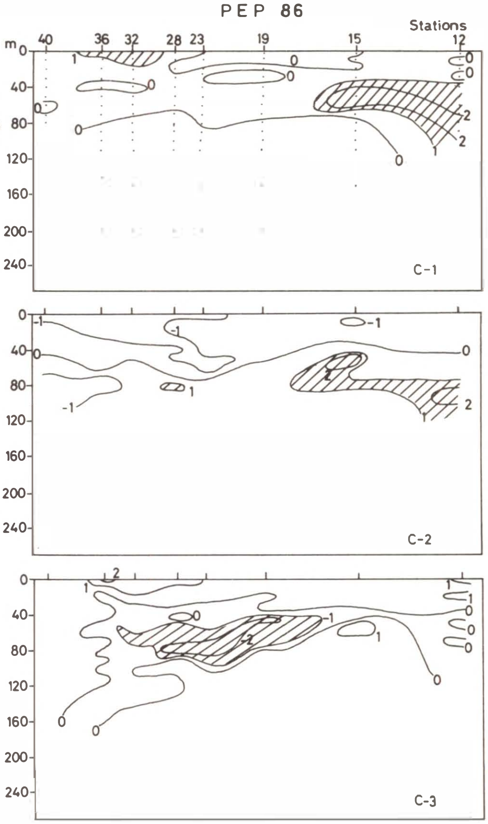

FIGURE 16. Distribution of the first three principal components (C1, C2 and C3) along the PEP 86 transect.

by MARGALEF (1963) and whose consequences were reflected in local fishing traditions.

With respect to the deepening of the front, the diatom assemblages (C), which in winter occupied the upper part of the water column in the nearshore waters, become restricted to patches within the DCM, in the lower part of the euphotic zone. At the same time, another assemblage (Group B) tends to constitute a background population within the DCM.

The distribution of the assemblages can be related to different trophic conditions within the water column. The high phytoplankton abundances in March 1985 were associated with the supply of nutrients to the upper layers caused by winter mixing. This situation led to diatom dominance inshore and flagellate dominance offshore. These differences may have been related to hydrological differences or to a different timing in the initiation of the bloom inshore and offshore; the lack of an adequate temporal sequence of sampling prevents clarification. During a recent cruise in February 1990, in the same area (Estrada, unpublished data), it was noted that diatom blooms appear offshore in response to hydrographic perturbations, but they may be relatively short-lived.

During the stratification period, the community of the upper euphotic layer, where nutrients are generally undetectable, is probably associated with a predominance of regenerated production. Irradiance does not constitute a limitation in this zone, and assimilation numbers may be relatively high, although biomasses remain low, perhaps due to a close equilibrium between production and predation. It is important to note in this context that many flagellates and dinoflagellates typical of this zone are likely to be heterotrophic.

The presence of localized high population densities of diatoms in the DCM suggests that they are the result of *in situ* growth and low diffusion losses, as had been noted in previous studies (ESTRADA, 1985a). Diatoms are typically associated with situations of high "new" production (MARGALEF, 1978; CUSHING, 1989) and the association of the Mediterranean DCM with the nutricline (ESTRADA, 1985a, b) indicates the importance of the supply of "new" nutrients. However, irradiance levels at the DCM (1-3% of surface irradiance during the spring cruises studied here) are generally too low to allow for high productivity indices (ESTRADA, 1985b). Increased production at the DCM could occur in pulses, when hydrographic perturbations expose nutrient rich water bodies to higher irradiances in shallower levels. The presence of the fronts and the lower stability of the central zone are likely to be very important for the origin of these perturbations. This would explain why the high biomass patches of the DCM tend to appear in the vicinity of the frontal zones.

In contrast to the distribution of most diatoms, the taxa of Group B are widely distributed within the DCM, but generally in low concentration. They could belong to a "shade flora" adapted to low irradiance conditions. However, these taxa were present in upper water levels during the winter cruise; as noted by SOURNIA (1982), it should be taken into account that the occurrence of algae at depth can be related to factors such as nutrient availability and water circulation in addition to light conditions. It is possible that the Group B taxa are part of a successional sequence following blooms occuring at depths above or within the DCM.

Comparison of these results with those from the previous summer cruises (PEP 82 and PEP 83) shows similar patterns, but also some differences (ESTRADA, 1985a; ESTRADA & SALAT, 1989). Both an upper euphotic zone assemblage (A) and a diatom assemblage were also present during the summer cruises, but the contribution of Group B was less clear. In July 1983, a tongue with high chlorophyll concentration (up to 4 mg m^{-3} of chlorophyll), probably due to local enrichment by coastal runoff, occupied the waters of the coastal zone. The corresponding phytoplankton community presented an important contribution of large dinoflagellates (such as *Ceratium furca*, *C. fusus* and *Protoperidinium brochi*) typical of stratified situations with adequate nutrient supply (ESTRADA & SALAT, 1989). A similar assemblage appeared to be present throughout the PEP 82 section, although the transect did not cross any high chlorophyll tongues near the coast (ESTRADA, 1985a). As shown by these studies and those of MARGALEF (1985) and MARGALEF & ESTRADA (1987) concerning the microplankton distribution during the PEP 82, PEP 83 and PEP 84 cruises, an assemblage of large thecate dinoflagellates is typical of the summer conditions in the top 10-20 m of the water column. This suggests that a segregation of phytoplankton also occurs within the upper part of the euphotic zone. The analysis by MARGALEF & ESTRADA (1987) also indicated a contrast between the upper layers and those of the lower and more productive levels and noted the presence of a "shade flora", although in this case it was characterized by large taxa such as *Ceratium platycorne*, *Amphisolenia globifera* and *Planktoniella sol*, which were not adequately sampled with the techniques used here.

Although fragmentary, the available data on the Northwestern Mediterranean ecosystem illustrate how fronts and gradients provide opportunities for enhanced biological activity and play a role in maintaining ecological boundaries. Superimposed on the general effects of the seasonal changes, the interplay of physical and chemical factors produces a mosaic of environmental situations which allows the coexistence of phytoplankton assemblages in different successional phases. In this context, it is interesting to note that repeatable patterns in the composition of phytoplankton assemblages can be found in different years, in spite of high environmental variability. However, more information is needed to complete a basic picture of the seasonal changes and to evaluate regularities and patterns of fluctuation at different temporal and spatial scales.

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