Suspended particles
Size distribution
Microplankton
Biochemical composition
Bay of Biscay

Particules en suspension
Distribution de tailles
Microplancton
Composition biochimique
Golfe de Gascogne

Distribution and composition of suspended particulate matter related to a shelf-break saline intrusion in the Cantabrian Sea (Bay of Biscay)

Antonio BODE, Emilio FERNANDEZ, Alfonso BOTAS, Ricardo ANADON
Depto. Biología de Organismos y Sistemas, Unidad de Ecología, Universidad de Oviedo, 33005-Oviedo, Spain.

Received 19/1/89, in revised form 17/10/89, accepted 17/11/89.

ABSTRACT

An intrusion of saline water with relatively high concentrations of nitrite was detected at the Cantabrian shelf-break. Four differentiated particle size distributions (PSD) were recognized in relation to the saline and the adjacent water masses. Small particles dominate in the saline nucleus, with small flagellates as the most abundant cells. Large particles prevailed in both oceanic and coastal waters where a spring bloom of diatoms occurred. Protein to carbohydrate ratio indicated active growth in all water masses, whereas low chlorophyll to protein ratio (CLA : PROT) and primary production characterized the saline water, and was associated with an important heterotrophic component of the microplankton. Size of particles, concentrations of nitrite and the values of the CLA : PROT ratio suggest active regenerative processes inside the saline water mass, in contrast with seston of coastal and oceanic waters where productive processes prevailed.

Oceanologica Acta, 1990. **13**, 2, 219-228.

RÉSUMÉ

Répartition et composition de la matière particulaire en suspension associée à une intrusion d'eau saline près du talus continental de la mer Cantabrique (Golfe de Gascogne)

Une intrusion d'eau saline avec des concentrations en nitrite relativement élevées a été trouvée près du talus continental de la mer Cantabrique. Quatre types de répartitions de taille des particules (PSD) sont associés à la masse d'eau saline et aux masses d'eaux adjacentes. Les petites particules dominent dans le noyau salin et correspondent à une abondance de petits flagellés. Les grandes particules sont plus fréquentes dans les eaux océaniques et côtières en raison du développement d'un « bloom » printanier de diatomées. Le rapport trouvé entre les protéines et les hydrates de carbone indique une croissance active dans toutes les masses d'eau. Les valeurs de la production primaire et du rapport entre la chlorophylle et les protéines (CLA : PROT) pour la masse d'eau saline sont plus basses que celles des eaux adjacentes et elles sont associées à une importante composante microplanctonique hétérotrophe. La taille des particules, les concentrations en nitrite et les valeurs du rapport CLA : PROT suggèrent l'existence de processus régénérateurs dans la masse d'eau saline. Dans les eaux côtières et océaniques les spectres de particules caractérisent des processus productifs.

Oceanologica Acta, 1990. **13**, 2, 219-228.

INTRODUCTION

Different conceptual bases have been used to understand the processes controlling the distribution and composition of particles in the water column, such as the trophic level concept, cyclic flow of carbon, species diversity and several others, with the aim of reducing the original information derived from field studies to a more comprehensible and manageable level. Since the observations by Sheldon *et al.* (1972; 1973), Particle size distribution (PSD) has become an important way to discover regularities in the structure of marine ecosystems. Moreover, the theoretical background developed by Platt and Denman (1977; 1978) permits an approach to size-dependent physiological processes. In addition, the Suspended Particulate Matter (SPM) in euphotic layers is a complex chemical matrix, primarily of biological origin, and the relationship between the biochemical components and the biomass of phytoplankton should reflect its nutritional state (Healey, 1973; Barlow, 1982; Pick, 1987). In this study, both PSD and chemical compositon were used to characterize the SPM in the water masses at the shelf-break in the Cantabrian Sea.

Surface waters of the Bay of Biscay, during the mixing period, are usually considered as a homogeneous water mass with differential characteristics from the oceanic North Atlantic Central Water (Treguer *et al.*, 1979; Fraga *et al.*, 1982; Rios *et al.*, 1987). However, diverse eddies observed in the surface circulations (Pingree, 1979; Dickson & Hughes, 1981) could isolate portions of water for some time, with consequent changes in its physical, chemical and biological properties. High salinity "pockets" in the NE Atlantic result from intrusions of southern water, becoming detached and surrounded by a water of lower salinity (Bary, 1963). Contact between water bodies of different salinity has been recently detected during the spring season off the Cantabrian shelf (Botas *et al.*, 1988). The saline water showed characteristics typical of mixed Atlantic waters off the Galician coast (Fraga *et al.*, 1982), and moved eastwards between coastal and oceanic waters.

The principal objective of this paper is to describe the spatial distribution of SPM and the concentration of some biochemical components in different water bodies near a saline intrusion in the Cantabrian shelf. Characterization of water masses by means of PSD's is attempted and related to the spatial variability in biochemical composition of seston and primary production.

MATERIAL AND METHODS

Water samples were collected from 10 stations off Cape Peñas (N Spain) in April 1987 (Fig. 1). At each station a set of casts with 5 l Niskin bottles equiped with reversible thermometers was made to obtain profiles of temperature, salinity, inorganic dissolved nutrients, phytoplankton and particle abundance at standard depths down to 250 m. The analysis of inorganic nutrients were made with a Technicon AAII autoanalyzer following the methods of Grasshoff *et al.* (1983). Measurements of PSD and abundance were made with a model TAII Coulter Counter on 7.5 ml samples. The aperture size of the counter tube was 140 µm and the range of particles measured is shown in Table 1. Particle volume was computed by multiplying the mean particle volume of each size class by the number of particles belonging to that class. Total chlorophyll (CLA), corrected chlorophyll-*a* (CCLA) and phaeophytin (PHA) concentrations were determined by fluorometry (Yentsch & Menzel, 1963; Holm-Hansen *et al.*, 1965) on particulate material collected on Whatman GF/C filters, that tend to retain particles larger than 0.8 µm (Hickel, 1984). Cell identification and counting were performed in the laboratory on 100 ml samples by the sedimentation technique.

Table 1

Limits of the particle size-classes measured by the Coulter counter. ESD: equivalent spherical diameter (µm). *Mean volume* (µm³).

Class	ESD inferior	ESD superior	Mean Volume
SC2	2.68	3.38	11.32
SC3	3.38	4.25	22.65
SC4	4.25	5.36	45.29
SC5	5.36	6.75	90.58
SC6	6,75	8.50	181.16
SC7	8.50	10.71	362.32
SC8	10,71	13.50	724.64
SC9	13.50	17.01	1 449.28
SC10	17.01	21.43	2 898.56
SC11	21.43	27.00	11 594.24
SC12	27.00	34.02	23 188.48
SC13	34.02	42.86	46 376.96
SC14	42.86	54.00	92 753.92
SC15	54.00	68.04	185 507.84
SC16	68.04	85.72	371 015.68

More detailed sampling on the chemical composition of the SPM was made at stations 21, 23 and 25, using a pumping system at 10 m intervals from the surface to 60 m depth. 2 l of water were filtered through precombusted Whatman GF/C filters for each component immediately after sampling. All filters were kept deep-frozen (−20°C) until analysis in the laboratory some weeks later.

Total particulate protein (PROT) was determined following the method of Lowry *et al.* (1951) and total glucids (GLU) by the method of Dubois *et al.* (1956). Total lipids (LIP) were extracted by the technique of Bligh & Dyer (1959) and analysed by the method of Marsh & Weinstein (1976). Chlorophyll-*b* (CLB) and carotenoid pigments (CAR) were determined by spectrophotometry (Jeffrey & Humphrey, 1975).

Parallel to chemical determinations, *in situ* incubations were carried out to determine primary production (PROD) by the ^{14}C technique (Steeman-Nielsen, 1952). Samples were incubated for two hours at noon, and immediately filtered on Millipore HA membrane filters (0.8 µm pore size). Filters were decontaminated with 0.5 N HCl acid following the method described by Lean and Burnison (1979). Dark fixation was not substracted.

Differences in chemical composition among water masses were tested by non-parametric Kruskall-Wallis

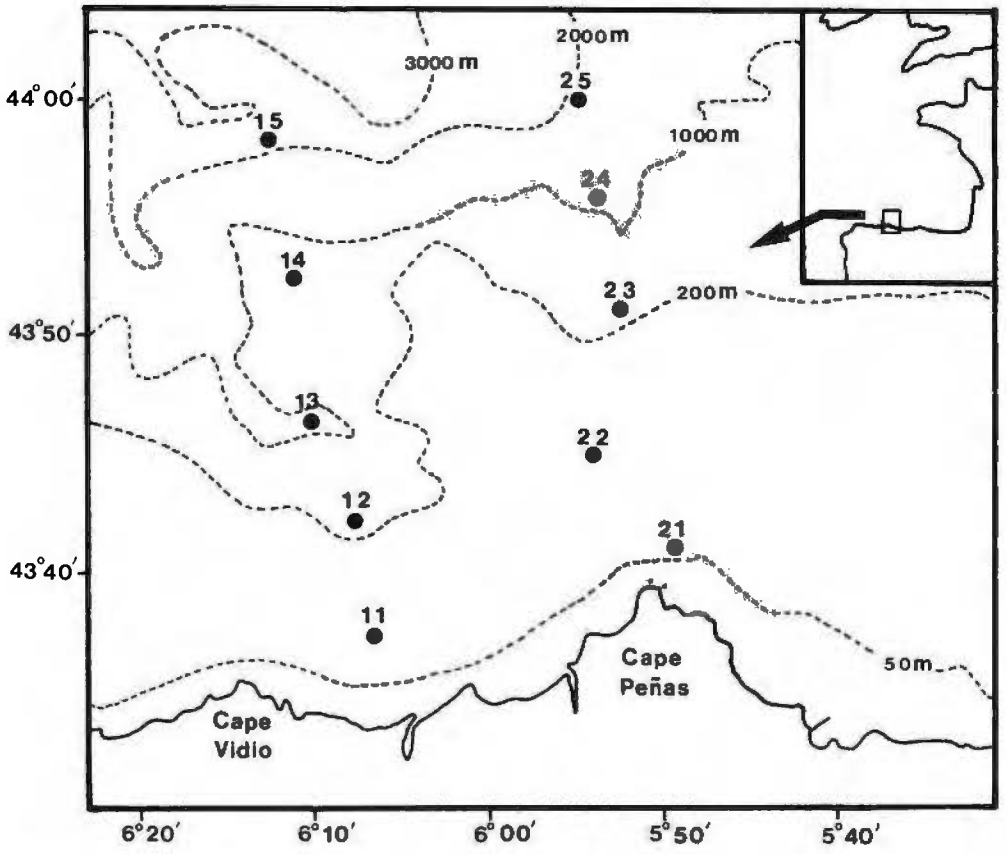

Figure 1
Map of the sampling stations.

analysis of variance (Siegel, 1956). The variability of PSD was analysed with a Principal Components Analysis (PCA) to determine characteristic groups of samples (Kitchen *et al.*, 1975; Flos, 1976, 1984; Mayzaud *et al.*, 1984). The volume concentrations for each size-class were logarithmically transformed before statistical computation to normalize data, and the PCA was made from the correlation matrix. Only the classes SC2 to SC14 were used. Pigments and total particle number and volume concentration were projected on the principal components as auxiliary variables. Samples were grouped according to their projections on the space

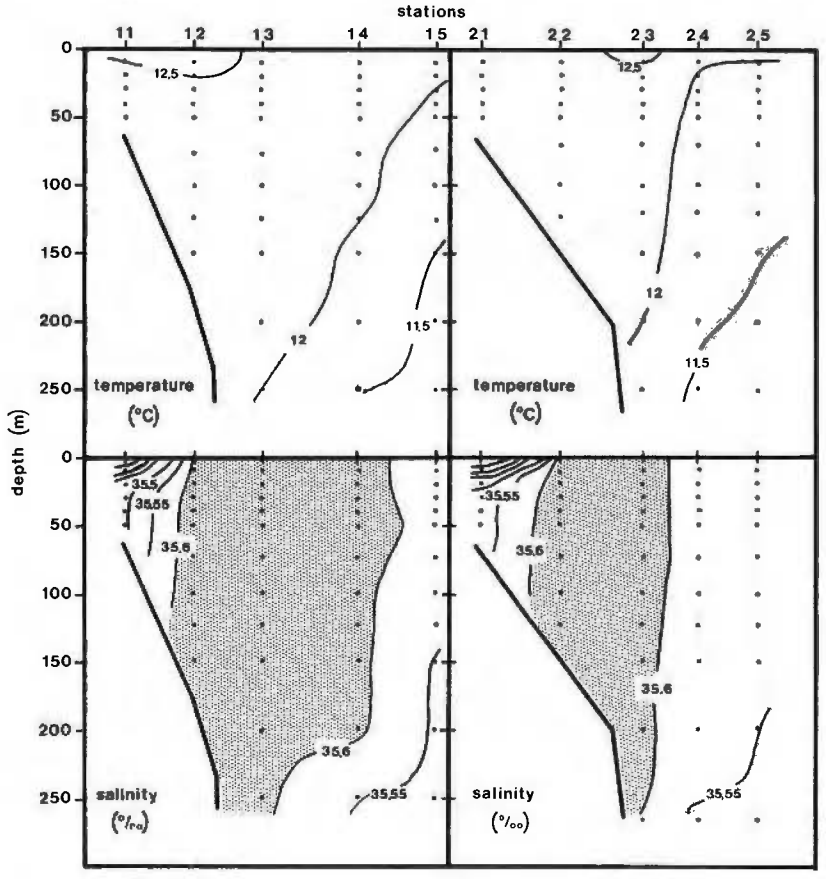

Figure 2
Vertical distribution of temperature and salinity in both sections.

defined by the two first principal components and the signification of the differences between the mean PSD of all the possible pairs of groups tested by means of Kolmogorov-Smirnov two sample test (Siegel, 1956).

RESULTS

The water masses

Figure 2 shows the vertical distributions of temperature and salinity in the two sections. A saline nucleus was associated with the shelf-break forming two marked physical fronts: inshore and offshore. Both variables showed a homogeneous distribution inside the nucleus, and the same occurred for the nutrient concentrations. Table 2 summarizes the mean values of the physical and chemical variables in the water bodies identified in the zone by Botas *et al.* (1988). The mean values of all variables were significantly different for the water bodies considered (Kruskal-Wallis analysis of variance, $p < 0.01$). Stations inside the saline nucleus were characterized by higher concentrations of nitrite.

The vertical stability of the water column is reflected by the Brunt-Väisälä frequency (Table 3). The observed frequencies in section 1 reveal low relative vertical stability near the centre of the saline water, with a minimum at station 13, and more stratification at the oceanic side of the saline water. Fewer differences were found in section 2 where high and low frequencies alternated for neighbouring stations both in saline and oceanic waters.

Table 3

Brunt-Väisälä frequencies for three selected layers in non-coastal stations. Frequencies are $N^2 . 10^6$ (s^{-2}).

Station	0-50 m	0-100 m	0-250 m
12	11.451	7.634	–
13	3.817	0.954	2.672
14	2.863	2.863	4.149
15	15.267	9.542	5.725
22	5.725	3.817	–
23	11.451	6.680	4.199
24	7.634	4.771	5.084
25	11.450	6.679	4.962

Distribution of *SPM* and phytoplankton

High total chlorophyll concentration was detected at oceanic stations close to the offshore thermohaline front (Fig. 3). Station 21 also showed high values, whereas samples inside the saline water body had lower pigment concentration. The distribution of total volume concentration of particles showed a similar trend. Thus the lowest values were measured in the saline water body and the highest ones near the chlorophyll maxima (Fig. 3).

Two components were extracted without axis rotation from the PCA on the volume size distribution of particles, explaining 55.7 and 28% of the original variance respectively. The first component (C1) was positively correlated with all size-classes, with higher values in the intermediate sizes, whereas the second component

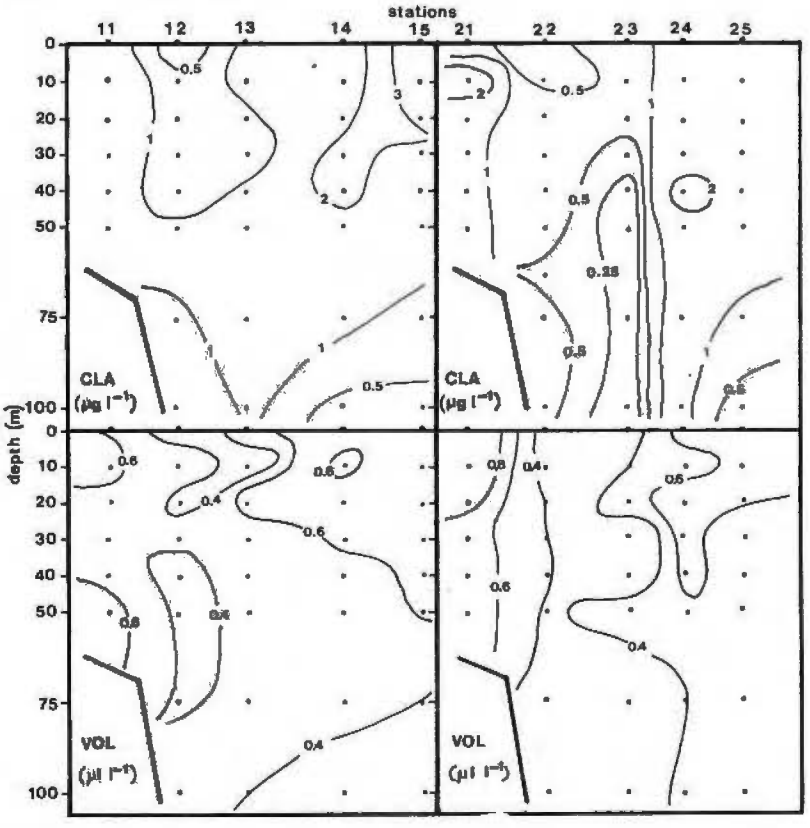

Figure 3

Vertical distribution of Chlorophyll-a and density of particles in both sections.

Table 2
Mean values (± standard error) of the chemical variables measured in the main water masses. N: number of samples. TEMP: temperature. SAL: salinity.

Water body	N	TEMP (°C)	SAL (‰)	Phosphate	Silica	Nitrate	Nitrite	Ammonia
				(µmol kg^{-1})				
Coastal	12	12.33	35.402	0.24	1.26	0.60	0.14	2.01
		(0.09)	(0.202)	(0.09)	(0.23)	(0.35)	(0.07)	(0.54)
Saline nucleus	55	12.28	35.625	0.28	2.15	1.96	0.24	2.09
		(0.20)	(0.014)	(0.09)	(0.42)	(0.73)	(0.07)	(0.73)
Oceanic	35	11.81	35.567	0.23	2.23	2.80	0.17	1.54
		(0.25)	(0.011)	(0.08)	(0.68)	(1.54)	(0.10)	(1.31)

Table 4
Correlation between the size classes of particles and the first and second principal components extracted from PCA on the particle volume size distributions. Variable names appear in the Appendix.

Size classes	Components C1	C2
SC2	0.586	0.743
SC3	0.584	0.776
SC4	0.679	0.703
SC5	0.826	0.543
SC6	0.918	0.287
SC7	0.939	0.017
SC8	0.902	−0.198
SC9	0.858	−0.341
SC10	0.807	−0.457
SC11	0.763	−0.513
SC12	0.773	−0.450
SC13	0.688	−0.345

Table 5
Correlation of some supplementary variables with the two first principal components extracted from PCA on the particle volume size distributions.

Variables	Components C1	C2
CLA	0.620	−0.109
CCLA	0.606	−0.047
PHA	0.536	−0.312
NPAR	0.358	0.803
VOL	0.881	−0.231

(C2) accounted for the variation in small sizes (Table 4). Otherwise, pigments and total particle volume (VOL) were positively correlated with the first component, whereas only NPAR correlated with the second component (Table 5).

The graphical representation of the samples on the reduced space of the two principal components (Fig. 4) shows several groups clustered according to similarity in shape of the PSD's, and the relative position of samples in the sea. Four types of water were distinguished: Type 1 included surface samples down to 50 m depth of both coastal and oceanic stations off the saline mass; Type 2 included samples down to 100 m depth of stations 23 and 24, belonging to the saline water mass; Type 3 contained samples from depths below 100 m of all stations and both surface and bottom samples of stations 12, 13 and 14; finally, samples of station 11 and the surface of station 12 (down to 10 m depth) were classified in Type 4.

The mean PSD of each group was plotted (Fig. 5), and all possible pairs were tested to be significantly different (Kolmogoroff-Smirnoff two sample test, $p < 0.01$). The PSD of Type 1 showed the mode in larger size classes,

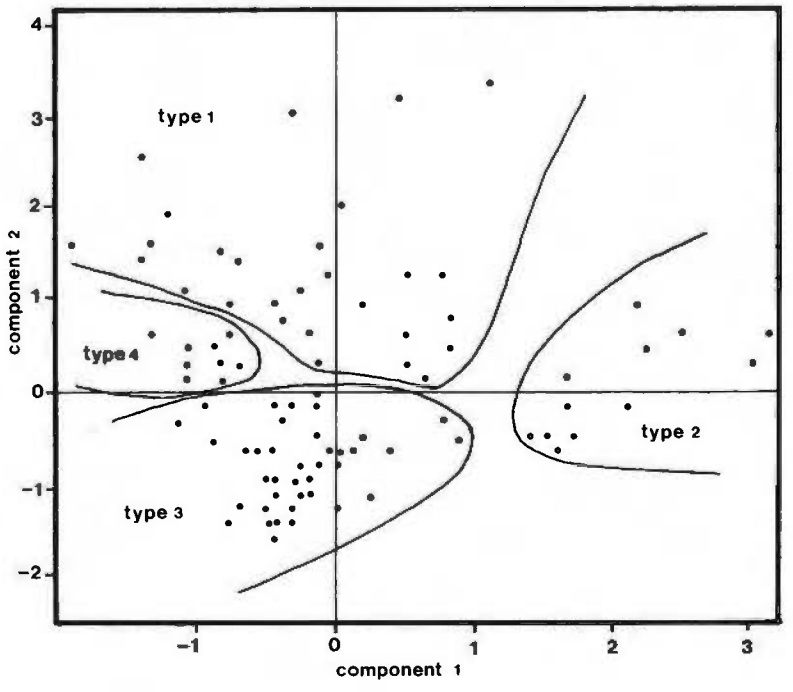

Figure 4
Plot of samples on the two first principal components of the ACP on the particle size variables. Four particle types are shown:
Group 1. – *Surface samples* (0-50 *m*) *from the coastal and oceanic stations* 15, 21, 24 *and* 25.
Group 2. – *Samples down to* 100 *m from stations* 13 *and* 14.
Group 3. – *Deep samples from all the stations studied, and surface samples* (0-100 *m*) *from stations* 22, 23 *and* 24.
Group 4. – *Coastal station* 11 *and surface samples* (0-10 *m*) *from station* 21.

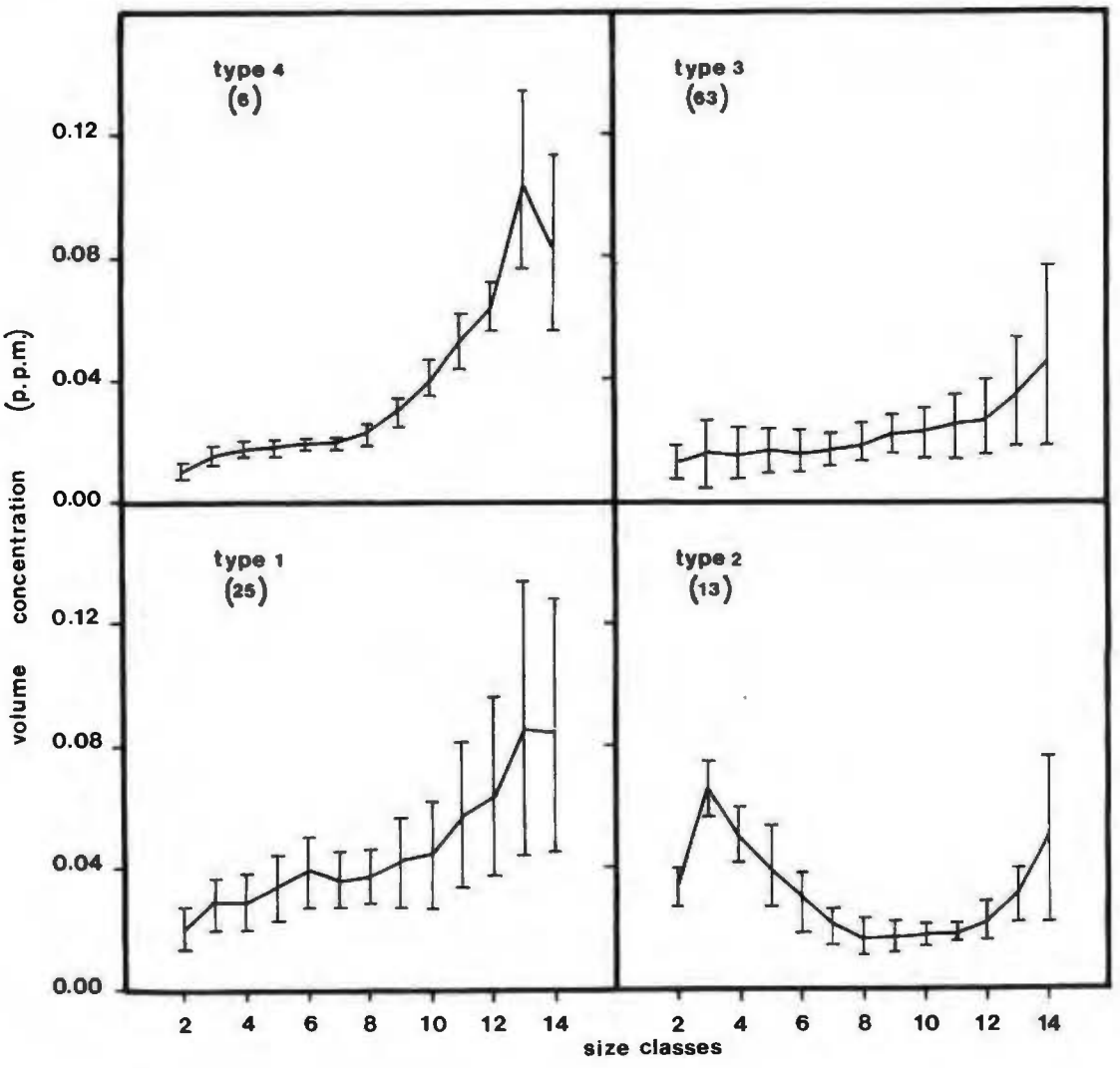

Figure 5
Mean (± standard error) PSD of the different water types. Number of samples is shown in brackets.

also the most variable. The PSD of Type 2 displayed modes at both extremes of the measured range. The mean PSD of Type 3 was rather flat, and the total particle concentration was lower than the other types. Type 4 samples had PSD's similar to samples of Type 1 but with higher values for the mode (Fig. 5). Therefore, we can only differenciate three well-defined types of spectra: a Type 1 spectra characterized by large particles, a Type 2 spectra where small particles prevailed and a flat Type 3 spectra.

These water types also showed different numeric microplanktonic composition in the upper 50 m (Fig. 6). Only three cell types were considered: diatoms, dinoflagellates, and microflagellates; the remaining phytoplankton, Coccolithophorids and Chrysophyceae, were less than 1% in number.

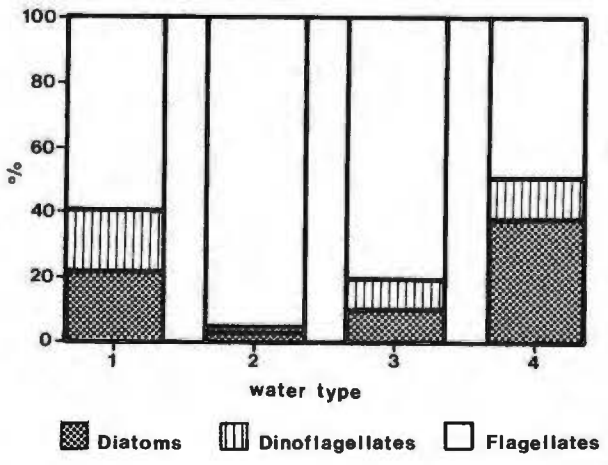

Figure 6
Relative cell abundance of the main taxonomic microplankton groups in the four water types.

Microflagellates were the most abundant cells in all types, but stations belonging to the saline water had higher values (up to 95% of the cells in water Type 2). It should be noted that the composition for Type 3 in Figure 6 corresponds only to the upper 50 m of stations 22, 23 and 24, all of them included in the saline nucleus (Fig. 2). Diatoms dominate the remaining cell classes at some coastal stations (Types 1 and 4).

Chemical composition

We attempted a different approach to characterize onshore, saline and offshore waters by means of the chemical composition of SPM at three selected stations of section 2.

The profiles of biochemical components and primary production were different for the stations considered (Fig. 7). The coastal station had maximum chlorophyll values near the surface, while the depth profiles for the other stations were more uniform. Station 23, in the saline water mass, showed the lowest values of these components. The values of primary production were higher at stations off the saline water, with the maximum at the surface of the coastal station. Microplankton populations of station 23 presented chlorophyll-specific production rates (CSPR) similar to those in the other stations. The ratios of protein to carbohydrate were rather homogeneous in the water column, except at station 23 where a maximum was reached at 40 m depth due to a relative decrease in the glucid content of the SPM. More differences appear when chlorophyll to protein (both in $\mu g\ l^{-1}$) ratios were considered (Fig. 7). Station 23 showed the lowest values due to a sharp decrease in chlorophyll-a concentration, while stations 21 and 25 contained more pigments per unit of protein. These differences can be explained by the relative dominance in cell number of microplankton groups (Figure 8). The coastal station had a large proportion of diatoms, whereas dinoflagellates dominated at station 25. Station 23 was dominated by microflagellates.

DISCUSSION

In this study the main physical sources of variability of PSD's are the saline intrusion at the outer shelf, and the opposition between the euphotic and deep layers at stations outside the saline water. Horizontal variation parallel to the coast also accounts for changes in PSD's. Thus, saline waters in section 2 and the deepest waters had flat distributions of particles, typical of poorer "steady-state" oceanic areas (Sheldon *et al.*,

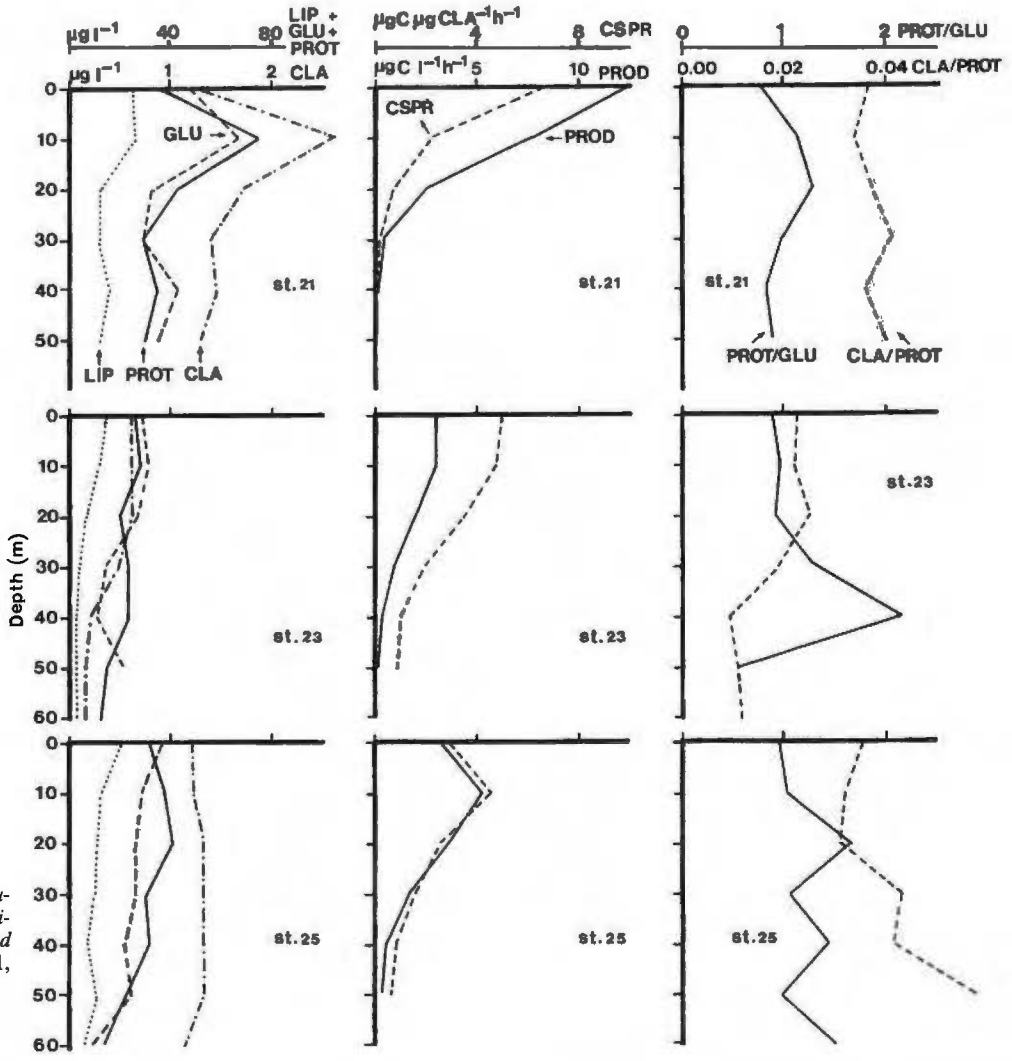

Figure 7
Vertical profiles of lipids, proteins, glucids, chlorophyll, primary production, assimilation number and protein: glucid and chlorophyll: protein ratios, at stations 21, 23 *and* 25.

1972), whereas small (ca. 5 µm ESD) and large particles (ca. 40 µm ESD) were equally abundant in volume in section 1. The PSD's of the euphotic layer of both coastal and oceanic stations were similar, and representative of a spring diatom bloom.

Fronts could affect the described particle populations by passive accumulation of materials (Holligan, 1981; Jordan & Joint, 1984) and also by *in situ* growth stimulated by the accumulation and current induced nutrient enrichment (Yentsch & Phinney, 1985). Probably both mechanism occurred. The main water circulation in spring is predominantly eastwards, producing an accumulation of coastal waters nearshore, while intense mixing occurs in the central stations of section 1 (Rios *et al.*, 1987; Botas *et al.*, 1988). Active processes seemed to occur in that section as revealed by the sharp changes observed in the Brunt-Väisälä frequencies at both sides of the saline water mass linked to different particle characteristics. High densities of small cells (in our case microflagellates) and low phytoplankton biomass would be expected in areas of active regeneration (*e.g.* Newell & Linley, 1984) and high vertical mixing (Malone, 1980) as occurred at station 14. Larger cells concentrate in nutrient-rich areas producing high biomass values (Margalef, 1974, 1978; Flos, 1976; Varela & Costas, 1987) as occurs in station 15.

The components of SPM reached maximum values near the surface in the coastal station because of the lower degree of mixing (higher Brunt-Väisälä frequencies) and the light-enhanced biological production in that layer. The differential role of light and vertical mixing is revealed by the shape of the production when compared to the biomass profiles at the stations considered (Fig. 7). In this season, primary production seems to be determined to a greater extent by the level of radiation, whereas the distribution of biomass varies according the mixing forces, as noticed by Marra (1980).

The observed biochemical composition agrees in general with phytoplankton (Parsons *et al.*, 1961; Moal *et al.*, 1987) and seston (Poulet *et al.*, 1986) composition data, but some minor changes might be expected depending on the dominant species and physiological status. Healey (1973) suggested that the ratio PROT : GLU could be used as indicator of nutrient deficiency both in field and laboratory populations of phytoplankton. Ratios lower than 0.7 would indicate extreme nutrient deficiency whereas ratios higher than 1.2 indicate no deficiency (Healey, 1973). In our case no severe nutrient deficiency was found as the values of the ratio PROT : GLU were mostly greater than 1, indicating active growth (Barlow, 1982).

Although cell number and volume concentrations cannot be directly compared, we can associate a taxonomic composition to a size spectrum when a given cell group with a small range of sizes relative to the whole range covered by the size spectrum dominates, and the corresponding volume spectrum has a mode just at that size. So, the shape of the PSD from group 2 indicates a major contribution of small particles to the total particle number in accordance with microplanktonic composition at station 23, where microflagellates formed the bulk of the total number of cells. Moreover, the CLA : PROT ratio, usually considered as an index of photosynthetic plankton (Dortch, 1987), showed higher values at both sides of the saline water mass, related to large cells, whereas the lowest values were observed inside the saline water. Sharp variations in this ratio, associated with different oceanographic regimes, have been previously described by Packard and Dortch (1975) comparing upwelled and oceanic stations in North Atlantic surface waters. They found lower CLA : PROT ratios at oceanic stations, and they calculated that at this stations, only 20% of the sestonic protein was related to phytoplankton biomass. In our case, the homogeneous distribution of CLA in the water column unable us to calculate the percentage of heterotrophic protein. Nevertheless, the dominance of small flagellates and dinoflagellates, many of them recognized as heterotrophs (Fenchel, 1982 *a*, *b*, *c*; Gaines & Elbrätcher, 1987), are responsible for the lower values observed at station 23. Furthermore, the high nitrite concentration inside this water body could be originated by a mechanism similar to the one reported by Rault *et al.* (1988) in microcosm experiments. They suggested that the active grazing of microflagellates on bacteria enhanced the nitrite release to the water.

Lower concentrations of planktonic protein have been associated with oligotrophic areas (Dortch, 1987). This is in relation to the predominance of heterotrophic microflagellates that are considered as an important compartment in the microbial food loop described by

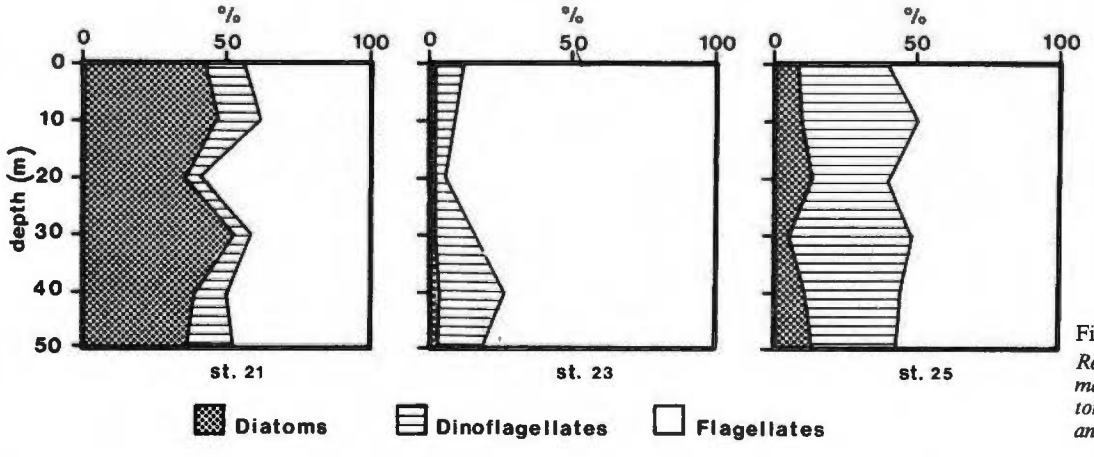

Figure 8
Relative cell abundance of the main taxonomic microplankton groups, at stations 21, 23 *and* 25.

Azam *et al.* (1983), tranferring energy from bacteria and small diatoms to ciliates. Both PSD and chemical composition of SPM testify to the existence of different food chains in the water bodies described.

In coastal waters, high CLA : PROT ratios suggest high cell division rates and low respiratory activity (Chan, 1978) characteristics coupled to a proliferation of large and medium-size diatoms. In this water, energy would be transfered through the traditional food chain, based on mesozooplankton, mostly copepods, as the main grazers. Thus, coastal areas where the spring bloom takes place have high values of primary production that would be in a large proportion unused by heterotrophs (Walsh, 1983; Malone *et al.*, 1983). The presence of a thermohaline front would prevent the export of primary production to the deep ocean, giving rise to an oxidation of the produced SPM *in situ* on the shelf, as has been recently reported in the Western Atlantic by Falkowski *et al.* (1988).

In contrast, particles inside the saline nucleus are small, as a result of the proliferation of heterotrophic microflagellates after a previous bloom. It should be expected that high nutrient regeneration rates associated with the microbial loop, between 50 and 90% depending on the number of trophic levels (Goldman *et al.*, 1985), would be characteristic of this water body.

In conclusion, our results suggest that a thermohaline front separates water bodies where different food chains became dominant as a consequence of the different age, and therefore, "life history" of these water bodies. Size of particles, microplankton composition, nitrite concentration and the values of the CLA : PROT ratio suggest active regenerative processes within the saline water body, in contrast with SPM of coastal and oceanic waters where productive processes prevailed.

Acknowledgements

We wish to thank Hidroelectrica del Cantábrico S.A. for financial support and Dr. J. Flos and Dr. E. Anadón for valuable criticism of the manuscript. We are also grateful for the critical comments by two anonymous reviewers, which notably improved the original manuscript.

Appendix: Abbreviations and variable names cited in the text, tables and figures.

Abreviation	Explanation	Units
CAR	Carotenoid pigments	m-SPU ($\mu g\ l^{-1}$)
CCLA	Corrected Chlorophyll-*a*	$\mu g\ l^{-1}$
CLA	Total Chlorophyll-*a* and Phaeophytin	$\mu g\ l^{-1}$
CLB	Chlorophyll-*b*	$\mu g\ l^{-1}$
Cn	n-th component extracted from PCA	–
CSPR	Chlorophyll Specific Production Rate	$\mu gC\ h^{-1}\ \mu gCLA^{-1}$
D	Depth	m
ESD	Equivalent spherical diameter	μm
GLU	Total particulate glucids	$\mu g\ l^{-1}$
LIP	Total particulate lipids	$\mu g\ l^{-1}$
NPAR	Total number of particles	n° part. ($\times 10^3\ ml^{-1}$)
PCA	Principal Components Analysis	–
PHA	Phaeophytin	$\mu g\ l^{-1}$
PSD	Particle size-distribution	–
PROD	Production	$\mu gC\ l^{-1}\ h^{-1}$
PROT	Total particulate protein	$\mu g\ l^{-1}$
SCn	Volume concentration of particles in size-class *n*	p.p.m. ($mm^3\ l^{-1}$)
SPM	Suspended particulate matter	–
VOL	Total volume of particles	p.p.m. ($mm^3\ l^{-1}$)

REFERENCES

Azam F., T. Fenchel, J. G. Field, J. S. Gray, R. A. Meyer Reil and F. Thingstad (1983). The ecological role of water column microbes in the sea. *Mar. Ecol. Prog. Ser.*, **10**, 257-263.

Barlow R. G. (1982). Phytoplankton ecology in the Southern Benguela Current. I. Biochemical composition. *J. Exp. Mar. Biol. Ecol.*, **63**, 209-227.

Bary B. McK. (1963). Temperature, salinity and plankton in the eastern North Atlantic coastal waters of Britain, 1957. I. The characterization and distribution of surface waters. *J. Fish. Res. Bd. Canada*, **20**, 3, 789-814.

Bligh E. G. and W. J. Dyer (1959). A rapid method of total lipid extraction and purification. *Can. J. Biochem. Physiol.*, **37**, 911-917.

Botas J. A., A. Bode, E. Fernández and R. Anadón (1988). Descripción de una intrusión de agua de elevada salinidad en el Cantábrico Central: Distribución de los nutrientes inorgánicos y su relación con el fitoplancton. *Inv. Pesq.*, **52**, 4, 559-572.

Chan A. T. (1978). Comparative physiological study of marine diatoms and dinoflagellates in relation to irradiance and cell size. *J. Phycol.*, **14**, 396-402.

Dickson R. R. and D. G. Hughes (1981). Satellite evidence of mesoscale eddy activity over the Biscay abyssal plain. *Oceanologica Acta*, **4**, 43-46.

Dortch Q. (1987). The biochemical composition of plankton in a subsurface chlorophyll maximum. *Deep Sea Res.*, **34**, 5/6, 705-712.

Dubois M., K. A. Gilles, J. K. Hamilton, P. A. Rebers and F. Smith (1956). Colorimetric method for determination of sugars and related substances. *Anal. chem.*, **28**, 350-356.

Falkowski P. G., C. N. Flagg, G. T. Rowe, S. L. Smith, T. E. Whitledge and C. D. Wirick (1988). The fate of a spring phytoplankton bloom: export or oxidation? *Cont. Shelf Res.*, **8**, 5-7, 457-484.

Fenchel T. (1982 a). Ecology of heterotrophic microflagellates. II. Bioenergetics and growth. *Mar. Ecol. Prog. Ser.*, **8**, 225-231.

Fenchel T. (1982 b). Ecology of heterotrophic microflagellates. III. Adaptations to heterogeneous environments. *Mar. Ecol. Prog. Ser.*, **9**, 25-33.

Fenchel T. (1982 c). Ecology of heterotrophic microflagellates. IV. Quantitative occurrence and importance as bacterial consumers. *Mar. Ecol. Prog. Ser.*, **9**, 35-42.

Flos J. (1976). Seston superficial de la zona de afloramiento del NW de Africa. *Oecologia Aquatica*, **2**, 27-39.

Flos J. (1984). Variability of Coulter counter data and their relationship with other oceanographical parameters. *P.S.Z.N.I.: Marine Ecology*, **5**, 3, 197-216.

Fraga F., C. Mouriño and M. Manríquez (1982). Las masas de agua en la costa de Galicia: junio-octubre. *Res. Exp. Cient.*, **10**, 51-77.

Gaines G. and M. Elbrächter (1987). Heterotrophic nutrition. In: *The biology of Dinoflagellates*. Edited by F. J. R. Taylor, Blackwell, London, p. 224-268.

Goldman J. C., D. A. Caron, O. K. Andersen and M. R. Dennett (1985). Nutrient cycling in a microflagellate food chain: I. Nitrogen dynamics. *Mar. Ecol. Prog. Ser.*, **24**, 231-242.

Grasshoff K., M. Ehrhardt and K. Krembling (1983). *Methods of seawater analysis*. 2nd. Ed. Verlag Chemie, Weinheim. 419 pp.

Healey F. P. (1973). The inorganic nutrition of algae from an ecological point of view. *CRC Critical Rev. Microbiol.*, **3**, 69-113.

Hickel W. (1984). Seston retention by Wathman GF/C glass fiber filters. *Mar. Ecol. Prog. Ser.*, **16**, 185-191.

Holligan P. M. (1981). Biological implications of fronts on the northwest European continental shelf. *Phil. Trans. R. Soc. Lond.*, **A302**, 547-562.

Holm-Hansen O., C. J. Lorenzen, R. W. Holmes and J. D. H. Strickland, 1965. Fluorometric determination of chlorophyll. *J. Cons. perm. int. Explor. Mer.*, **30**, 3-15.

Jeffrey S. W. and G. F. Humphrey (1975). New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. *Biochem. Physiol. Pflanz.*, **167**, 191-194.

Jordan M. B. and I. R. Joint (1984). Studies on phytoplankton distribution and primary production in the western English Channel in 1980 and 1981. *Cont. Shelf. Res.*, **3**, 25-34.

Kitchen J. C., D. Menzies, H. Pak and J. R. V. Zaneveld (1975). Particle size distributions in a region of coastal upwelling analyzed by characteristic vectors. *Limnol. Oceanogr.*, **20**, 775-783.

Lean R. S. and B. K. Burnison (1979). An evaluation of errors in the ^{14}C method of primary production measurement. *Limnol. Oceanogr.*, **24**, 5, 917-928.

Lowry M., N. J. Rosenbrough, A. L. Fara and J. R. Randall (1951). Protein measurement with the folin phenol reagent. *J. Biol. Chem.*, **193**, 265-275.

Malone T. C. (1980). Algal size. In: *The physiological ecology of phytoplankton*. Edited by I. Morris. Blackwell. Oxford. p. 433-464.

Malone T. C., P. G. Hopkins, P. G. Falkowski and T. E. Whitledge (1983). Production and transport of phytoplankton biomass over the continental shelf of the New York Bight. *Cont. Shelf Res.*, **1**, 305-337.

Margalef R. (1974). Distribution du seston dans la région d'affleurement du Nord-Ouest de l'Afrique en mars 1973. *Thétys.*, **6**, 1-2, 77-88.

Margalef R. (1978). Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanologica Acta*, **1**, 493-509.

Marra J. (1980). Vertical mixing and primary production. In: *Primary productivity in the sea*. Plenum press. New York. 531 pp.

Marsh J. B. and D. B. Weinstein (1976). Simple charring method for determination of lipids. *J. of lipids research*, **7**, 571-576.

Mayzaud P., S. Taguchi and Ph. Laval (1984). Seasonal patterns of seston characteristics in Bedford Basin, Nova Scotia, relative to zooplankton feeding: A multivariate approach. *Limnol. Oceanogr.*, **29**, 745-762.

Moal J., V. Martin-Jezequel, R. P. Harris, J.-F. Samain and S. A. Poulet (1987). Interspecific and intraspecific variability of the chemical composition of marine phytoplankton. *Oceanologica Acta*, **10**, 3, 339-346.

Newell R. C. and E. A. S. Linley (1984). Significance of microheterotrophs in the decomposition of phytoplankton: estimates of carbon and nitrogen flow based on the biomass of plankton communities. *Mar. Ecol. Prog. Ser.*, **16**, 105-119.

Packard T. T. and Q. Dortch (1975). Particulate protein-nitrogen in North Atlantic surface waters. *Mar. Biol.*, **33**, 347-354.

Parsons T. R., K. Stephens and J. D. H. Strickland (1961). On the chemical composition of eleven species of marine phytoplankters. *J. Fish. Res. Board. Can.*, **18**, 1001-1016.

Pick F. R. (1987). Carbohydrate and protein of lake seston in relation to plankton nutrient deficiency. *Can. J. Fish. Aquat. Sci.*, **44**, 2095-2101.

Pingree R. D. (1979). Baroclinic eddies bordering the Celtic Sea in the late summer. *J. Mar. Biol. Ass. UK.*, **59**, 689-698.

Platt T. and K. Denman (1977). Organisation in the pelagic ecosystem. *Helgol. Wiss. Meeres.*, **30**, 575-581.

Platt T. and K. Denman (1978). The structure of pelagic marine ecosystems. *Rapp. P.-v. Réun. Cons. int. Explor. Mer.*, **173**, 60-65.

Poulet S. A., D. Cossa and J.-C. Marty (1986). Combined analyses of the size spectra and biochemical composition of particles in the st. Lawrence estuary. *Mar. Ecol. Prog. Ser.*, **30**, 205-214.

Rault P. L., Sohier L. P., Rivier A. M. and R. A. Daumas (1988). Dark bacterial-protozoan culture: acidification, nitrite accumulation and protozoan inhibition in absence of phytoplankton. *J. Exp. Mar. Biol. Ecol.*, **116**, 273-291.

Rios A.$_2$ F. Fraga, F. G. Figueiras, R. Prego and F. F. Pérez (1987). Campañas oceanográficas "Asturias I, II, III y IV". *Datos informativos Inst. Inv. Marinas.*, **22**, 1-140.

Sheldon R. W., A. Prakash and W. H. Sutcliffe (1972). The size distribution of particles in the ocean. *Limnol. Oceanogr.*, **17**, 327-340.

Sheldon R. W., W. H. Sutcliffe and A. Prakash (1973). The production of particles in the surface waters of the ocean with particular reference to the Sargasso Sea. *Limnol. Oceanogr.*, **18**, 5, 719-733.

Siegel S. (1956). *Nonparametric statistics for the behavioral sciences*. McGraw-Hill Kogakusha, Tokyo, 312 pp.

Steeman-Nielsen E. (1952). The use of radioactive carbon (^{14}C) for measuring organic production in the sea. *J. Cons. perm. int. Explor. Mer.*, **18**, 117-140.

Treguer P., P. Le Corre and J. R. Grall (1979). The seasonal variations of nutrients in the upper waters of the Bay of Biscay region and their relation to phytoplankton growth. *Deep Sea Res.*, **26A**, 1121-1152.

Varela M. and E. Costas (1987). Distribución del tamaño de las especies del fitoplancton en un área de afloramiento. *Inv. Pesq.*, **51**, 1, 97-105.

Walsh J. J. (1983). Death in the sea: enigmatic phytoplankton losses. *Progress in Oceanography*, **13**, 1-16.

Yentsch C. S. and D. W. Menzel (1963). A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. *Deep Sea Res.*, **10**, 221-231.

Yentsch C. S. and D. A. Phinney (1985). Rotary motions and convection as a means of regulating primary production in warm core rings. *J. Geophys. Res.*, **90**, 3237-3248.