

Intrusions of eastern North Atlantic central waters and phytoplankton in the north and northwestern Iberian shelf during spring

A. Bode*, M. Varela, B. Casas, N. González

Instituto Español de Oceanografía, Centro Oceanográfico de A Coruña, Apdo. 130, E-15080 A Coruña, Spain

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Abstract

The influence of intrusions of eastern North Atlantic central water (ENACW) in the north and northwestern Iberian shelf on phytoplankton composition and abundance and on particle-size distributions of seston was analyzed using data collected on three extensive cruises during spring 1991 and 1992. Water with temperature and salinity values between 12.20 and 13.86 °C and between 35.66 and 35.98 psu, respectively, characteristics of the subtropical type of ENACW (ENACW_t), was detected in the upper 100 m of the water-column in all cruises, but particularly in the western coast in 1992. The highest salinity values of this water were found near the surface (0–100-m depth) and in early spring 1992, while minimum salinity values, and also minimum geographical extension, were found in late spring in both years. Phytoplankton blooms concentrated in frontal areas between different water types, with maximum intensity and extension in early spring.

Using temperature and salinity characteristics, samples were classified in four groups corresponding to the major water types found in the region: Bay of Biscay central water (BBCW), two segments of ENACW of different salinity and surface water influenced by continental runoff. This classification was significantly confirmed by three independent discriminant analyses using hydrographic and chemical (dissolved nutrients and chlorophyll) variables, phytoplankton species abundance variables and particle-size concentration of seston variables. Phytoplankton blooms related to the presence of saline waters were characterized by the dominance of either chain-forming diatoms or a mixture of diatoms and phytoflagellates and high concentrations of seston. The diatom species dominating in saline waters were typical of upwelling-induced blooms occurring generally during summer. Blooms occurring in waters influenced by runoff also contained diatoms but in lower numbers than those of saline waters. Nutrients were not exhausted in the region, suggesting that phytoplankton populations were still in active growth. These results are interpreted taking into account the known variability in water-mass formation and in the poleward current driving ENACW_t along the shelf, and indicate that saline intrusions are a major feature affecting the distribution and composition of plankton in the spring in the southern Bay of Biscay, thus enlarging to a wider spatial scale their reported influence on the pelagic ecosystem.

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* Corresponding author. Tel.: +34-981-205362; fax: +34-981-229077.

E-mail address: antonio.bode@co.ieo.es (A. Bode).

1. Introduction

The northwestern shelf of the Iberian Peninsula is a region of great hydrologic and biogeochemical activity. The seasonal coastal upwelling, induced by eastern winds between March and October (Fraga, 1981; Blanton et al., 1984), is the main recognized source of phytoplankton production for most of the year (Tenore et al., 1995). A review of published production data (Bode et al., 1994, 1996) confirms that upwelling-related blooms dominated in the western part of the area (Galicia). In contrast, there are significant production pulses during spring and autumn blooms in the northern shelf (Mar Cantábrico) that are not related to upwelling (Flos, 1982; Fernández and Bode, 1991) because the influence of the upwelling in this area is generally restricted to a narrow band near the coast (Dickson and Hughes, 1981; Botas et al., 1990). Mesoscale fronts produced by the separation of water bodies with different temperature and, mainly, salinity are the responsibilities of phytoplankton concentration and increased production leading to spring blooms in the Mar Cantábrico (Botas et al., 1988; Bode et al., 1990; Fernández et al., 1991, 1993).

Several water masses have been recognized in the northwestern Iberian region, as summarized by Rios et al. (1992). Waters above 500 m were dominated by eastern North Atlantic central water (ENACW), of which two subtypes were defined according to their origin and temperature and salinity characteristics. The subtropical subtype (ENACW_t) range from 12.2 to 18.5 °C and from 35.66 to 36.75 psu (Fiuza and Halpern, 1982; Fiuza, 1984; Rios et al., 1992), and its origin was located in a front near the Azores (Fiuza, 1984). The subpolar subtype (ENACW_p) is formed 46°N and corresponds to water between 4 and 12 °C and between 34.96 and 35.66 psu (Harvey, 1982). These two subtypes are separated in summer by a subsurface front at 42°N, near Cape Finisterre (Fraga et al., 1982). Below the salinity minimum near 500-m depth, ENACW gradually mixes with intermediate Mediterranean water, which reaches peak salinity values at approximately 1000-m depth (Parrilla and Morón, 1971; Rios et al., 1992; Diaz del Rio et al., 1998). The upper bathymetric limit of ENACW varies, according to the amount of continental water in the surface, upwelling conditions and other phenomena, but maximum salinity values over the shelf

were found generally between 0- and 100-m depth (Lavín et al., 1992a,b; Cabanas et al., 1992; Pérez et al., 1993). A subtype of central waters with relatively small variations in temperature and salinity (11.8–12.2 °C; 35.53–35.58 psu) was also described in the Bay of Biscay (Treguer et al., 1979; Fraga et al., 1982; Botas et al., 1989) and named Biscay Bay central water (BBCW). Interannual variability in the thermohaline properties of these water masses (notably variations in salinity) was attributed to the intensity of winter cooling in the formation areas (Pollard et al., 1996) and related to regional-scale climatic fluctuations (Pérez et al., 1995, 2000).

While upwelling forces ENACW towards the coast and the surface during most of spring and summer (Fraga, 1981; Cabanas et al., 1992; Tenore et al., 1995; Casas et al., 1997; Castro et al., 2000), downwelling and separation of shelf and oceanic waters prevails during autumn and winter (Castro et al., 1997). In addition, a strong poleward flow of ENACW_t has been described along the Iberian slope during winter and early spring, reaching from south Portugal (Ambar et al., 1984; Frouin et al., 1990; Haynes and Barton, 1990) to the north of the Bay of Biscay (Pingree and LeCann, 1990). This current was detected over the shelf as an intrusion of saline water that generated fronts affecting nutrient concentrations (Botas et al., 1988), seston composition (Bode et al., 1990) and plankton distribution, composition and production (Fernández et al., 1991, 1993). The occurrence and intensity of the poleward current, and therefore the extension of ENACW_t towards the north, is known to vary between years (García-Soto et al., 1991; Pingree and LeCann, 1990; Pingree, 1993, 1994; Lavín et al., 1998).

These hydrologic and hydrodynamic features affect planktonic production on the northwestern Iberian shelf and, in turn, may determine the success in the recruitment of pelagic (García et al., 1992) and demersal fish species (Pereiro and Fernández, 1983) that have recurrent spawning areas in this region. Preliminary information on the food consumed by the North Atlantic sardine in the area (Varela et al., 1988, 1990) indicate that the availability of planktonic cells and particles varies greatly during the spring, the time of peak spawning of sardine (Solá et al., 1992).

The aim of this paper is to show the spatial importance and temporal variability of intrusions of

ENACW along the NW Iberian shelf during the spring periods of 1991 and 1992, along with some of their consequences for plankton distribution and composition. The effect of these intrusions will be compared to those reported for 1987 in a small zone of the shelf (Botas et al., 1988, 1989; Bode et al., 1990; Fernández and Bode, 1991; Fernández et al., 1991, 1993). Using a large number of samples and observations made during three extensive cruises covering the whole continental shelf and shelf-break areas, we demonstrate a large degree of interannual variability in the extent of saline intrusions and the existence of significant differences in nutrients, phytoplankton biomass and composition and particle-size distributions between water bodies of different salinity. This paper complements previous studies of plankton (García-Soto et al., 1991), seston (Robins et al., 1991), sardine-larvae (López-Jamar et al., 1995) and nutrients (Bode et al., 2001) focussed on part of the study period.

2. Methods

Samples were collected during ECOSARP-0491 (April 1991), PROSARP-0392 and PROSARP-0492

cruises on R/V Cornide de Saavedra. On each cruise, more than 80 stations were sampled along the NW Iberian shelf and adjacent oceanic waters (Fig. 1). Stations were arranged in coast to ocean transects and most were visited in every cruise. Water-column temperature and salinity were measured with a CTD Seabird SBE-25 from the surface to 250-m depth in all stations. CTD profiles were extended to 1000-m depth at some stations. Water samples were collected at three to five depths between the surface and 100-m depth at all stations using 5-l Niskin bottles. Details of sampling procedures and part of the raw data employed in this paper can be found in Grupo SARP (1993). In addition to ship-borne measurements, geostrophic wind conditions were summarized in the form of an upwelling index, according to the values provided in Lavín et al. (2000) for a location off the Galician coast (43°N, 11°W). Positive values of the upwelling index are indicative of winds blowing from the north, while negative values indicate winds blowing from the south.

Dissolved nutrients employed in this paper included nitrate, nitrite and phosphate, and were determined in samples stored frozen on board by the autoanalyzer methods described in Grasshoff et al. (1983). Chlorophyll-*a* concentrations (Chl-*a*) were

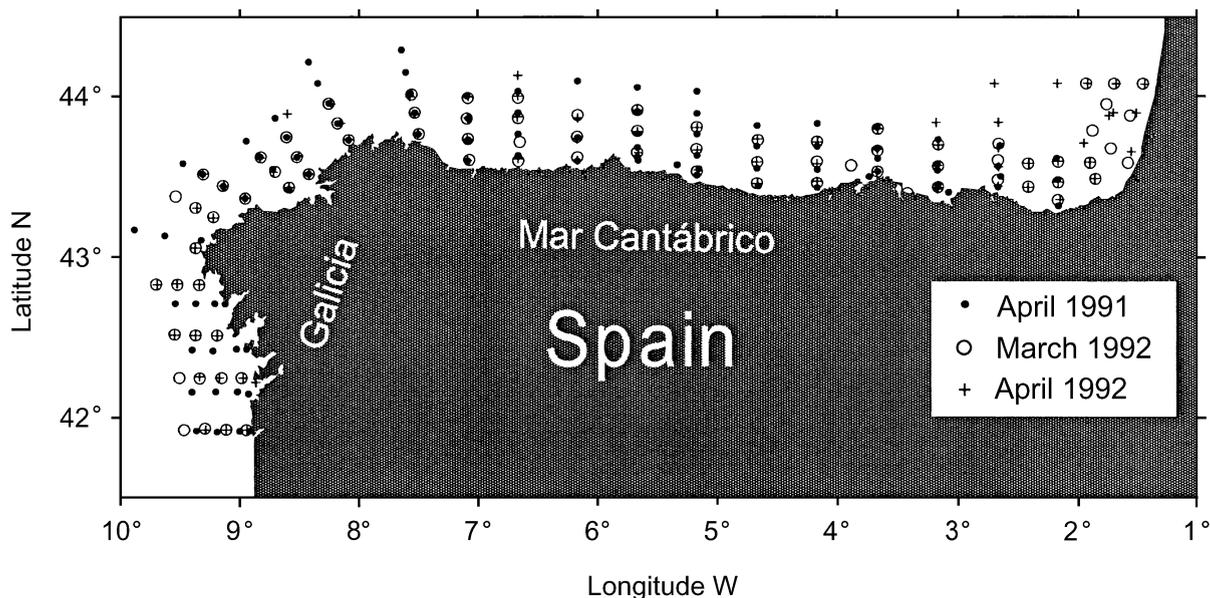


Fig. 1. Map of sampling stations. Different symbols indicate stations sampled in each cruise.

Table 1
Reference temperature and salinity values for the grouping of samples from the study area

Group	Temperature (°C)	Salinity (psu)	Water type	References
1	11.80–12.20	35.50–35.58	BBCW	Treguer et al., 1979; Fraga et al., 1982; Botas et al., 1989
2	12.20–12.50	35.66–35.79	ENACW _t lower segment	Fiuza, 1984; Rios et al., 1992;
3	12.50–18.50	35.80–36.75	ENACW _t upper segment	Fiuza and Halpern, 1982;
4	variable	< 35.50	surface water	Rios et al., 1992; Pollard et al., 1996

BBCW: Biscay Bay central water. ENACW_t: Subtropical eastern North Atlantic central water.

measured on 250-ml samples filtered on board through Nucleopore membrane filters (0.8- μm pore size) and stored frozen. Chlorophyll-*a* was extracted in 90% acetone overnight and its fluorescence measured in a fluorometer (Parsons et al., 1984). Samples for phytoplankton species determination were preserved with Lugol's solution and observed with an inverted microscope. Unidentified forms of dinoflagellates and flagellates were classified by size-groups. Particle-size distributions (only available for cruises in 1992) were measured on board by passing 7.5 ml of seawater through a tube of 140 μm of aperture in a Coulter Counter TAIL on board. The particles counted were grouped in 16 size-classes of doubling volume. To reduce the effect of electronic noise on the counts of smaller particles and the uncertainty in the counts of low numbers of large particles, only results for size-classes 2–12 were employed in this paper, representing a final range of particle-sizes from 2.5 to 25.4 μm of mean equivalent spherical diameter (ESD). Particle concentration in each size-class was reported as particle volume concentration in ml m^{-3} .

Samples (from 0- to 100-m depth only) were classified according to their temperature and salinity values in four groups, using the values of Table 1, based on reported characteristics of the water types described in the region, as reference limits for each group. In practice, the position of each water sample in a T/S diagram was computed and assigned to the nearest group according to the reference limits of Table 1. In general, all samples from the same station were assigned to the same group, except with cases of surface waters of salinity lower than 35.5 psu that were classified in Group 4. Geographical location of samples was also taken into account and, for instance,

samples assigned to Group 1 with thermohaline characteristics close to BBCW were always located to the north of 43°N. The validity of such classification was tested independently by using discriminant analysis on three sets of variables. One set of variables was composed by temperature, salinity, dissolved nutrient and chlorophyll concentrations. Phytoplankton species abundance was used in the second set of variables, and particle concentration by size classes formed the third set. Variables were logarithmically transformed to normalize data before entering discriminant analysis. Differences in mean values of the variables between groups were tested using ANOVA and 'a posteriori' Student–Neuman–Keuls tests (Sokal and Rohlf, 1981).

3. Results

3.1. Distribution of saline intrusions and phytoplankton

The poleward progression of surface waters at the time of the study was restricted by the switch in the average direction of geostrophic winds (Fig. 2). In all cruises, the dominant conditions were of upwelling, as indicated by positive values of the upwelling index caused by winds blowing predominantly from the north and northeast. However, converse conditions were observed in the previous winter months, when the upwelling index maintained negative values as a consequence of winds blowing from the south, thus favouring the poleward flow of surface water (Frouin et al., 1990).

Vertical profiles of salinity revealed that maximum salinity in the upper 500 m was always between the

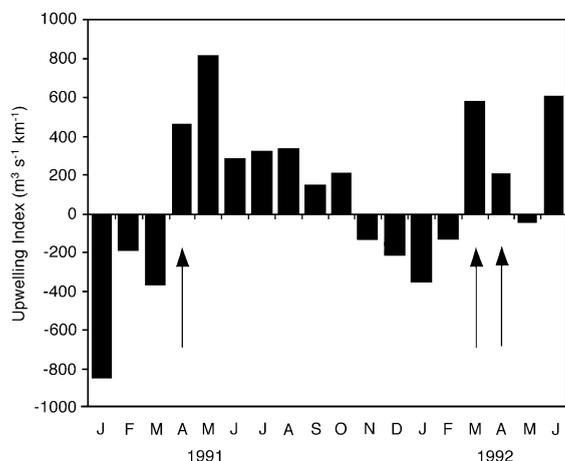


Fig. 2. Monthly mean values of the upwelling index for the Galicia area (see Methods). Arrows indicate cruise dates considered in this study.

surface and 100-m depth (Fig. 3). Therefore, samples from the surface can be used as a measure of the degree of influence of ENACW, as this water type occupies the upper 500 m (Rios et al., 1992; Pollard et al., 1996). The higher variability in salinity profiles in March 1992 compared to the April cruises in both years, particularly in the upper 200 m, must also be noted. Profiles from April cruises displayed a large influence of low salinity water in a narrow layer near the surface, as a consequence of continental runoff,

but most profiles rapidly converged below 200-m depth, particularly in April 1992 (Fig. 3).

The extension of surface waters with salinity values higher than 35.8 psu, was different in each cruise (Fig. 4). The western shelf (Galicia) always displayed higher salinity values than the northern shelf (Mar Cantábrico). Maximum differences appeared when comparing different years, with lower surface salinity values in April 1991 compared to 1992 cruises. The highest salinity values in the surface were measured in March 1992, reaching 35.98 psu. In all cruises, low salinity values (<35.5 psu) were found in surface water at localized areas, particularly near the Galician rias in the western shelf (e.g. March and April 1992) and in the eastern part of the S Bay of Biscay, indicating the influence of continental water. The contact of these low salinity waters with surrounding shelf waters with higher salinity originated marked saline fronts. It must be noted that there was a significant dilution of surface waters near the coast between March and April cruises in 1992.

Phytoplankton biomass, indicated by chlorophyll-*a* concentration (Fig. 5), was generally lower than 1 mg Chl-*a* m⁻³ in the surface in most of the area during April cruises but higher values were found in March 1992. The comparison of surface salinity (Fig. 4) and chlorophyll distributions (Fig. 5) reveals the presence of local patches with more than 3 mg

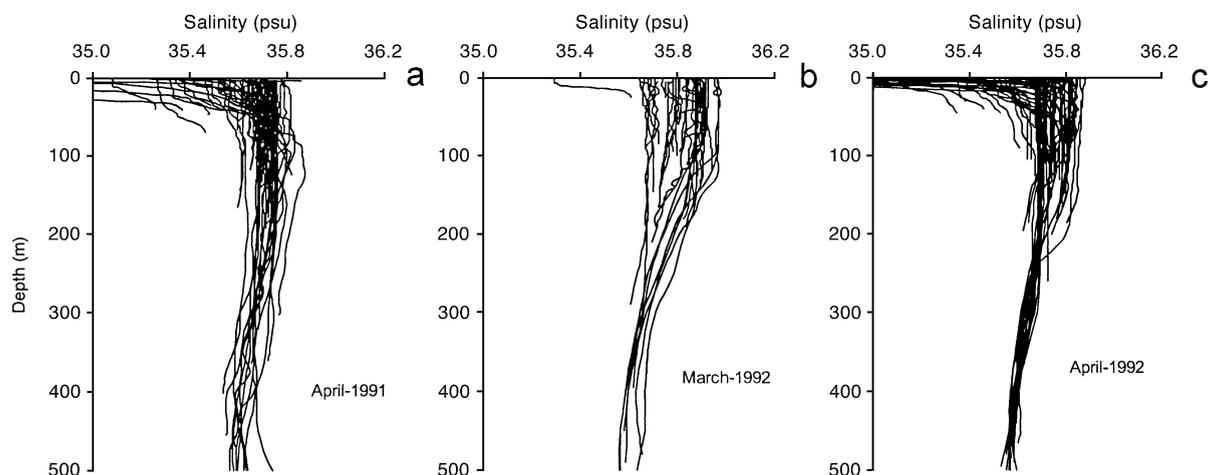


Fig. 3. Salinity depth profiles for individual stations sampled during cruises in (a) April 1991, (b) March 1992 and (c) April 1992.

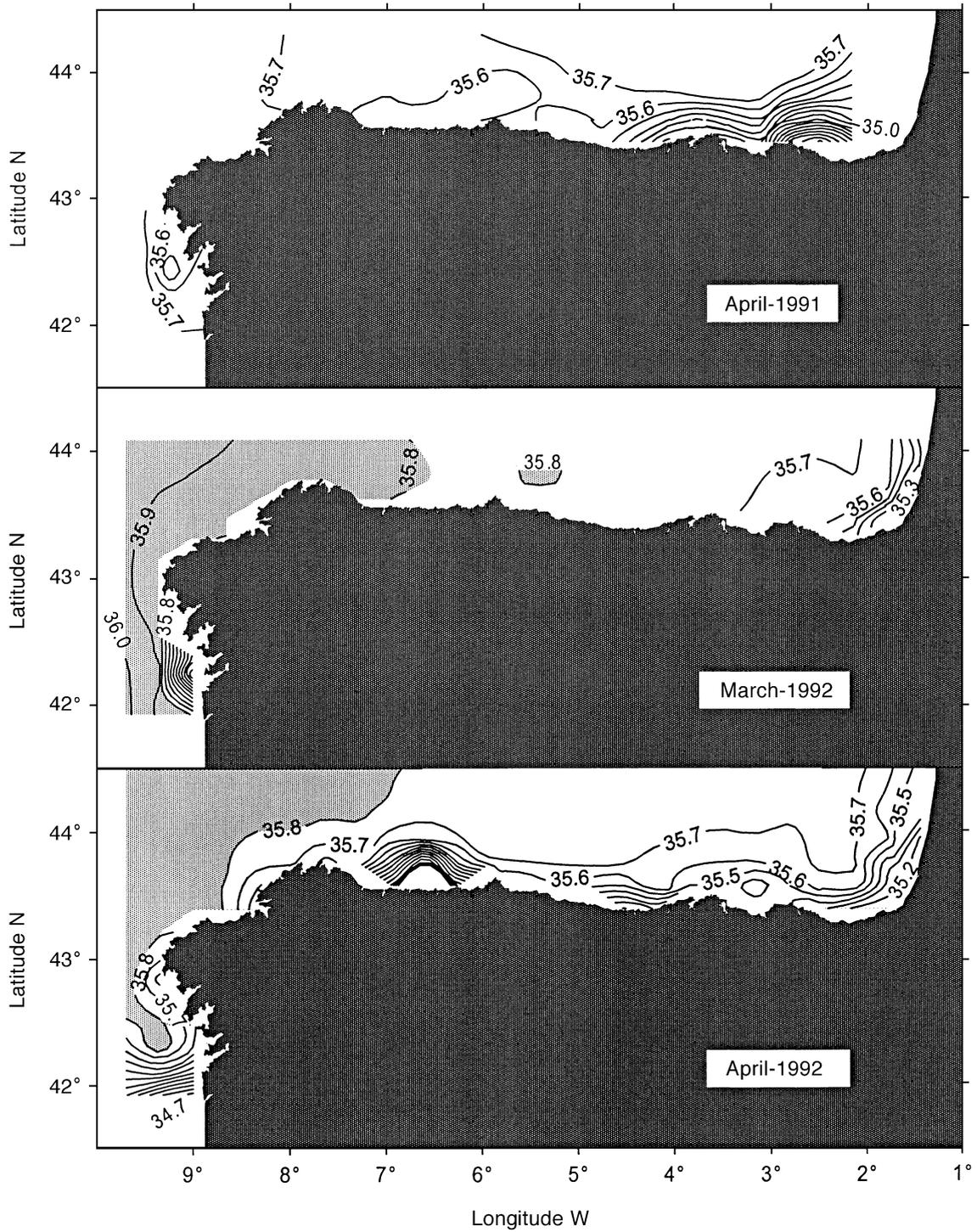


Fig. 4. Distribution of surface salinity (psu) in the NW Iberian region in each cruise. Shaded areas indicate zones with salinity values higher than 35.8 psu.

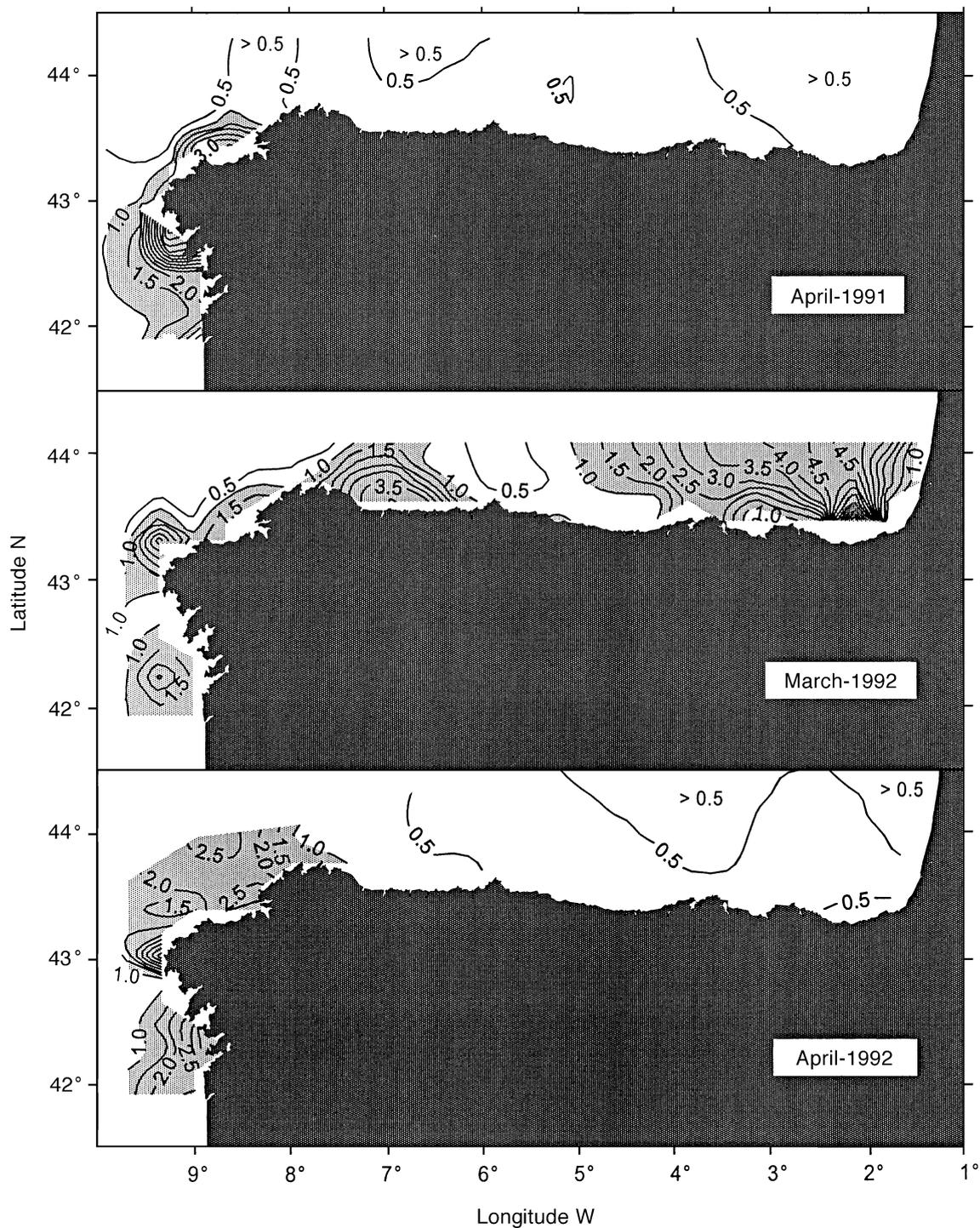


Fig. 5. Distribution of surface chlorophyll-*a* concentration (mg Chl-*a* m⁻³) in the NW Iberian region in each cruise. Shaded areas indicate zones with concentration values higher than 1 mg Chl-*a* m⁻³.

Chl- a m^{-3} , associated with salinity fronts near the western coast (i.e. low salinity water in the mouth of all Galician rias, $8^{\circ}W$) and, in March 1992, also in the eastern part of the Mar Cantábrico (i.e. east of $4^{\circ}W$, with surface salinity lower than 35.7 psu). However, there are also examples of areas in which surface salinity is highly variable but there is no apparent increase in chlorophyll (i.e. the Mar Cantábrico coastal zone in both April cruises).

3.2. Classification of samples according to temperature and salinity characteristics

The studied stations showed the presence of the main water types described in the region (Fig. 6a). Surface waters, particularly in coastal stations, had variable temperature and salinity values because of the local influence of continental waters. Only in some stations of the northern coast sampled during

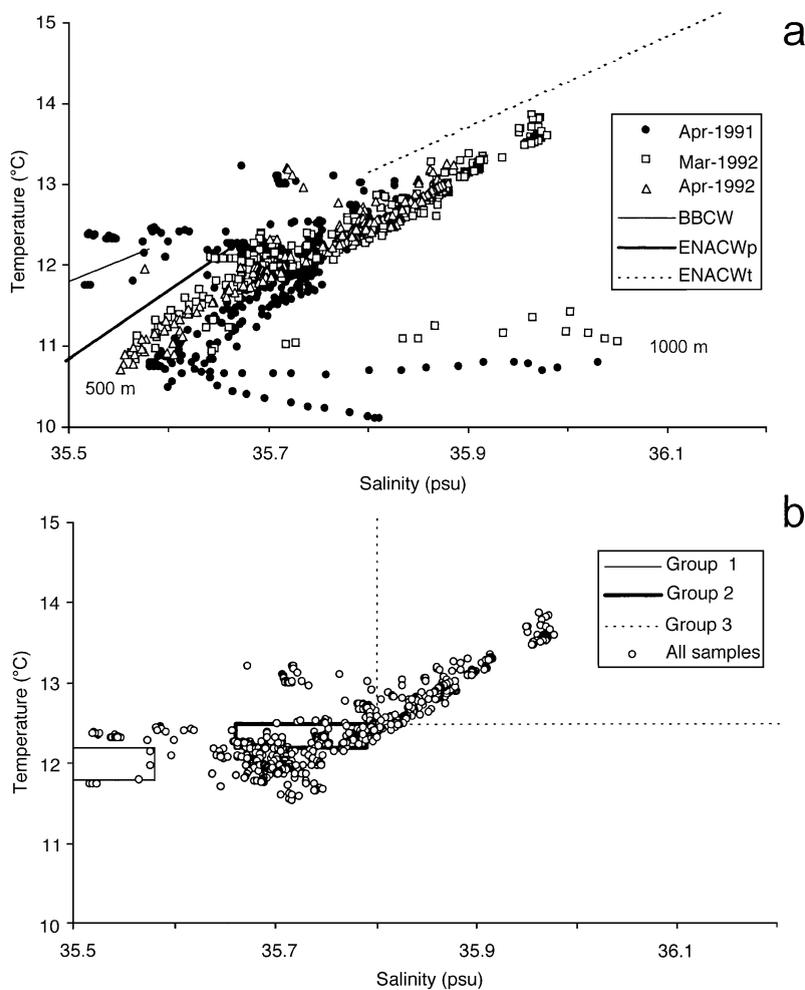


Fig. 6. T/S diagram of observations made at all stations during the study. For clarity, only values with salinity values higher than 35.5 psu and pooled every 5 m for the water layer between the surface and 100-m depth, and every 50 m for the water layer between 100 and 1000 m, were plotted. (a) Observations from the surface to 1000-m depth coded by cruise. The values of the main water types (BBCW, ENACW_p, and ENACW_t) described in the area (see text) were indicated by different lines. (b) Observations from the surface to 100-m depth. The limits of the temperature and salinity values used as a reference for the grouping of water samples for further analysis (see text) were indicated by lines.

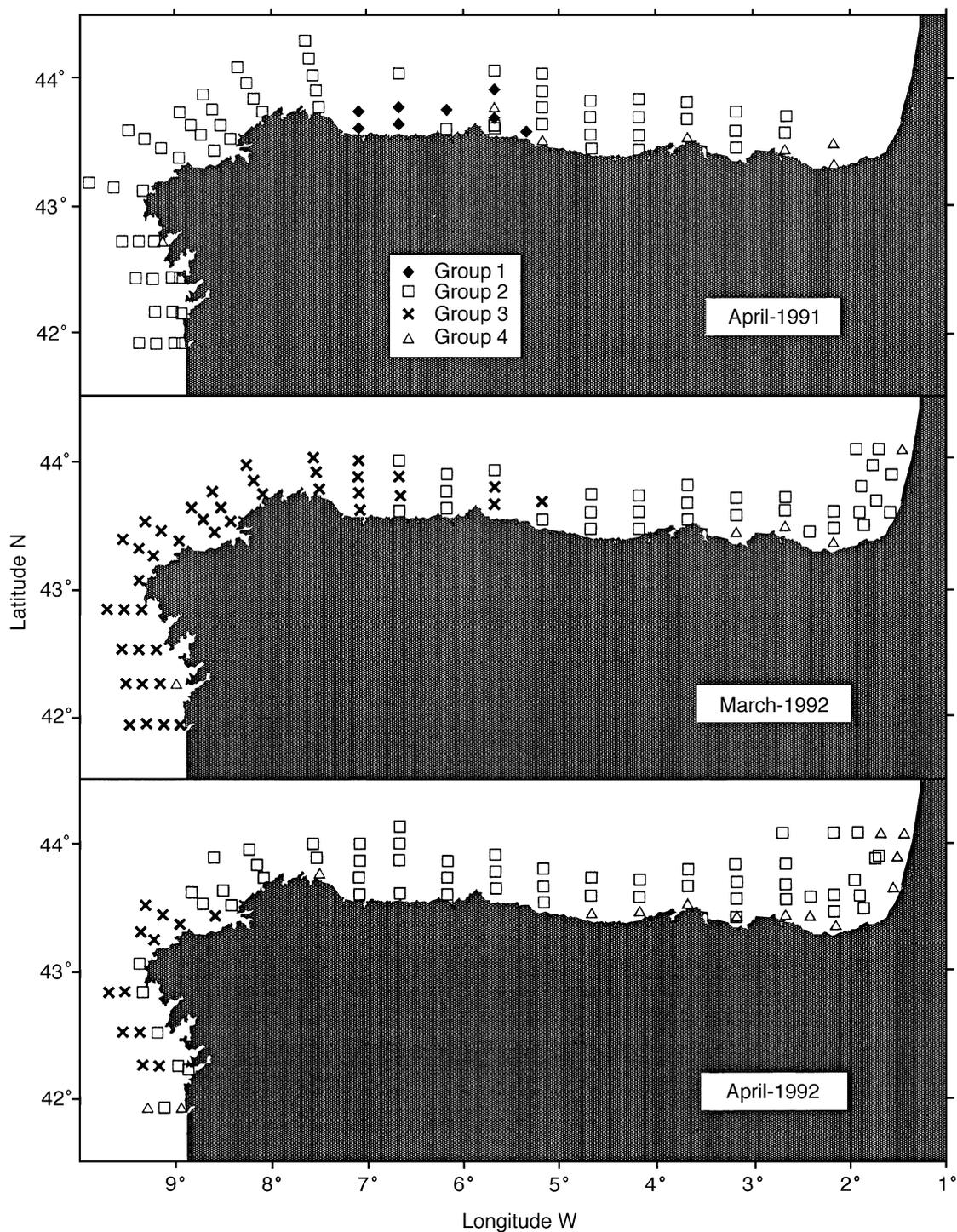


Fig. 7. Distribution of water-type groups during the study. The symbol assigned to each station indicates the median value of water-type considering all water samples collected in this particular station.

April cruises, water with characteristics close to those described for BBCW was found. Water between 20 and 500 m of most stations showed temperature and salinity values corresponding to variable amounts of the main types of ENACW, as indicated by the linear trend of points in the T/S diagram (Fig. 6a). A large number of observations had thermohaline characteristics that fell in the transition between typical subtropical and subpolar subtypes of ENACW (Rios et al., 1992). These observations showed a relatively large variability in temperature values. However, waters with salinity higher than 35.8 psu (that can be assimilated to ENACW_t) and located mostly between the surface and 100-m depth resulted relatively homogeneous in temperature, which reached the highest values in this layer. It should be noted that all observations of waters with temperature and salinity close to ENACW were colder and saltier than the values of ENACW reference lines. Finally, the layer between 500 and 1000 m, measured only at some stations, had water with the characteristic transition between ENACW and Mediterranean water, with a range of temperature of 10.1–11.4 °C and a maximum salinity of 36.05 psu.

Considering only waters in the surface to 100-m depth layer, the observations can be arranged in four groups corresponding to the main water types described in the region (Fig. 6b), using temperature and salinity reference values of Table 1. Group 1 waters had T/S characteristics similar to those of BBCW, although we did not find any particular sample that had T/S values comprised completely between the published values for this water type. Group 2 included waters with salinity higher than 35.66 psu, upper salinity limit for ENACW_p, in the transition zone described for ENACW in the region (Rios et al., 1992). However, temperature and salinity values of these waters did not reach values lying completely within the published limits for ENACW_t and therefore can be considered the lower segment of this water type. Group 3 waters had salinity values higher than 35.8 psu that fit mostly in the line describe for typical ENACW_t. All surface samples with salinity values below 35.5 psu were classified in Group 4. None of the collected water samples had T/S characteristics assimilable to ENACW_p.

The distribution of these water types reveal that Group 1 waters (BBCW) were restricted to a relative small area in the western Mar Cantábrico during April

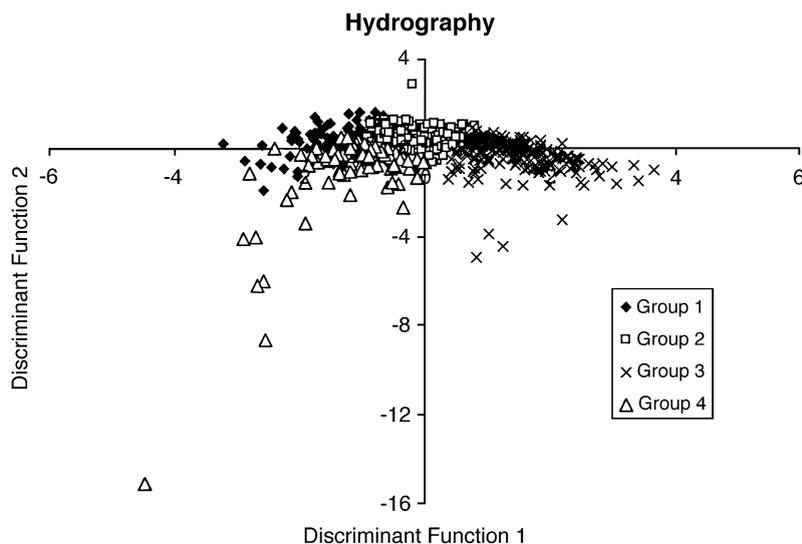


Fig. 8. Plot of samples from all cruises in the space defined by the two first discriminant functions computed to classify samples in the preassigned groups using hydrographic and chemical variables (see text). Observations were coded according to their initial assignment to each group.

Table 2

Standardized canonical discriminant function coefficients and pooled-within-groups correlations between discriminating variables and canonical discriminant functions (DF1 and DF2) computed using hydrographic and chemical variables

Variable	Coefficient DF1	Coefficient DF2	Correlation DF1	Correlation DF2
Temperature	0.702	−0.513	0.790	−0.428
Salinity	0.315	0.833	0.396	0.769
Nitrate	0.500	0.265	−0.129	0.347
Nitrite	−0.158	−0.332	−0.340	−0.048
Phosphate	−0.601	−0.059	−0.509	0.154
Chlorophyll- <i>a</i>	0.104	−0.138	0.243	−0.299

1991 (Fig. 7). Similarly, waters with marked continental influence occurred in scattered locations in all cruises but generally at the eastern limit of the Mar Cantábrico and near the Galician rias. Most of the study area was characterized by Group 2 waters, present in all cruises, while high salinity waters (Group 3) were restricted to Galicia (March and April) and to the western Mar Cantábrico (March) in 1992 cruises, but were not found in April 1991.

3.3. Chemical and biological characteristics of water bodies

The validity of the classification of water samples according to the T/S characteristics was first tested using hydrographic and chemical composition variables of 753 samples in a discriminant analysis that correctly classified more than 80% of samples of Groups 1 and 4, but only ca. 50% of samples

originally attributed to Groups 2 and 3 (Fig. 8). The two first discriminant functions accounted for more than 96% of the variance. Temperature, salinity and chlorophyll had positive correlation values with the first discriminant function, while nutrient concentrations were negatively correlated with this function (Table 2). The second discriminant function was positively correlated with salinity, nitrate and phosphate and negatively with temperature, nitrite and chlorophyll. Samples appeared arranged in the space delimited by these functions from low salinity Group 4 and Group 1 samples (displaying mainly negative values for the first discriminant function) to high salinity samples of Group 3, with samples from Group 2 occupying an intermediate position near the zero value of both discriminant functions. The second discriminant function mostly separates samples from the largely heterogeneous Group 4, with high chlorophyll and temperature samples having low values of the function. Even when the discriminant analysis reconstructed the main characteristics of the ‘a priori’ classification taking into account temperature and salinity, the inclusion of dissolved nutrients and chlorophyll was insufficient to detect a clear separation between samples of both segments of ENACW_t (Groups 2 and 3).

Mean values of temperature from Group 3 samples were significantly higher than those of other groups (Table 3), while mean salinity of all groups (except Groups 1 and 4) was significant (Student–Neuman–Keuls test, $p < 0.05$). Mean nutrient concentrations also varied significantly between groups. Nitrate values in Groups 1 and 2 were higher than

Table 3

Mean and SD values of hydrographic and chemical variables used to classify samples in the preassigned groups by means of discriminant analysis

Variable	Group 1		Group 2		Group 3		Group 4	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Temperature (°C)	12.16*	0.24	12.32*	0.43	12.82+	0.26	12.22*	0.37
Salinity (psu)	35.577*	0.097	35.725+	0.096	35.794×	0.536	35.449*	0.442
Nitrate (mmol N m ^{−3})	4.40*	2.20	3.73*	1.63	3.17+	1.48	3.42+	2.79
Nitrite (mmol N m ^{−3})	0.30*	0.18	0.27*	0.16	0.18+	0.11	0.31*	0.24
Phosphate (mmol P m ^{−3})	0.52*	0.11	0.38+	0.14	0.28×	0.06	0.42○	0.21
Chlorophyll- <i>a</i> (mg m ^{−3})	0.27*	0.19	0.91+	1.00	1.39×	1.36	0.97+	1.29
<i>n</i>	28		401		173		151	

n: Number of samples employed in each group. Symbols after the mean value indicate significance of values between groups. Values of a variable in different groups with the same symbol were nonsignificantly different (Student–Neuman–Keuls test, $p > 0.05$).

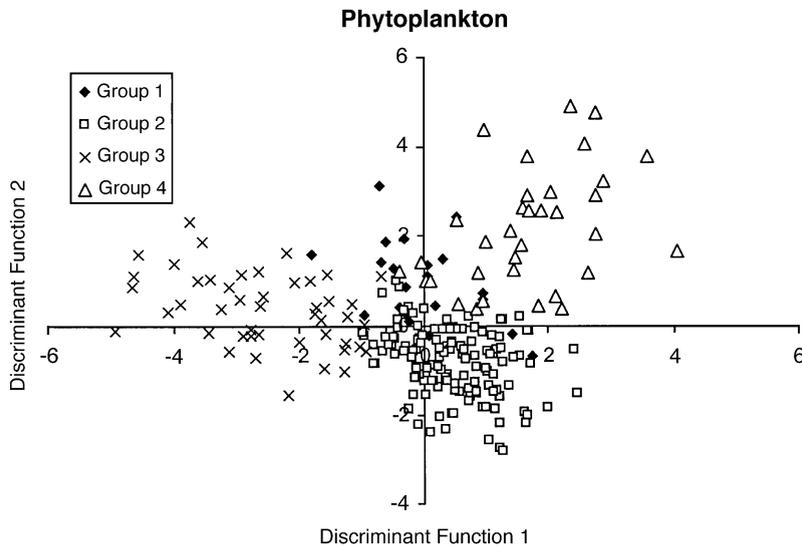


Fig. 9. Plot of samples from all cruises in the space defined by the two first discriminant functions computed to classify samples in the preassigned groups using phytoplankton species abundances (see text). Observations were coded according to their initial assignment to each group.

values in Groups 3 and 4. Nitrite concentration was significantly lower in Group 3 than in all other groups, while phosphate concentrations were significantly different in all groups, with maximum values in samples from Group 1. Similarly, mean chlorophyll concentration was significantly different be-

tween most groups, except between Groups 2 and 4, and the maximum value occurred in Group 3. It should be noted that there was a correspondence between high nutrient concentrations (particularly phosphate and nitrate) and low chlorophyll values and vice versa.

Table 4

Standardized canonical discriminant function coefficients and pooled-within-groups correlations between discriminating variables and canonical discriminant functions (DF1 and DF2) computed using phytoplankton species or taxonomic group abundance values

Species or taxonomic group	Coefficient DF1	Coefficient DF2	Correlation DF1	Correlation DF2
<i>Cachonina hallii</i> Freudentahl and Lee	0.107	0.188	0.191	-0.029
<i>Ceratium lineatum</i> (Ehrenberg) Cleve	-0.125	0.265	0.149	0.299
Dinoflagellates <30 μm	0.389	-0.311	0.256	-0.151
<i>Prorocentrum balticum</i> (Lohmann) Loeblich	0.280	0.304	0.215	0.341
<i>Protoperidinium bipes</i> (Paulsen) Balech	0.063	0.312	0.174	0.007
<i>Scropsiella trochoidea</i> (Stein) Lohmann	0.077	0.212	0.154	0.131
<i>Chaetoceros curvisetus</i> Brightwell	-0.152	-0.042	-0.198	0.005
<i>Chaetoceros danicus</i> Cleve	0.111	-0.310	-0.028	-0.121
<i>Ditylum brightwellii</i> (West) Grunow	0.066	-0.035	-0.043	-0.108
<i>Leptocylindrus danicus</i> Cleve	0.534	0.593	0.229	0.290
<i>Pseudonitzschia delicatissima</i> (Cleve) Heiden	0.077	0.011	-0.162	0.043
<i>Rhizosolenia fragilissima</i> Bergon	-0.648	0.269	-0.307	0.073
<i>Rhizosolenia setigera</i> Brightwell	-0.524	0.355	-0.271	0.067
<i>Rhizosolenia stolterfothii</i> Peragallo	-0.172	0.056	-0.230	0.000
Cryptophyceae	0.190	-0.084	0.243	-0.119

Only species having the highest absolute values of the coefficients were displayed.

Table 5

Mean and SD values of phytoplankton species and taxonomic groups (cells ml⁻¹) used to classify samples in the preassigned groups by means of discriminant analysis

Species or taxonomic group	Group 1		Group 2		Group 3		Group 4	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<i>Cachonina hallii</i> Freudentahl and Lee	0.83*	1.76	0.80*	1.37	0.11+	0.39	0.89*	1.81
<i>Ceratium lineatum</i> (Ehrenberg) Cleve	0.14*	0.34	0.02*	0.08	0.01*	0.05	0.38+	1.18
Dinoflagellates <30 µm	5.75*	1.25	6.87*	1.59	2.31+	1.49	5.52*	1.72
<i>Prorocentrum balticum</i> (Lohmann) Loeblich	0.74*	0.71	0.21+	0.59	0.07+	0.23	1.29*	2.35
<i>Protoperidinium bipes</i> (Paulsen) Balech	0.04*	0.16	0.17*	0.55	–	–	0.26*	0.00
<i>Scropsiella trochoidea</i> (Stein) Lohmann	–	–	0.10*	0.43	0.02*	0.11	0.36+	0.94
<i>Chaetoceros curvisetus</i> Brightwell	–	–	0.10*	0.53	0.48+	1.22	0.05*	0.27
<i>Chaetoceros danicus</i> Cleve	–	–	0.14*	0.50	0.12*	0.41	0.03*	0.16
<i>Ditylum brightwelli</i> (West) Grunow	–	–	0.05*	0.21	0.05*	0.22	–	–
<i>Leptocylindrus danicus</i> Cleve	–	–	0.39*	1.67	0.16*	0.63	3.17+	4.25
<i>Pseudonitzschia delicatissima</i> (Cleve) Heiden	–	–	0.21*	0.55	0.78+	2.24	0.25*	0.95
<i>Rhizosolenia fragilissima</i> Bergon	–	–	0.07*	0.33	0.91+	2.19	0.07*	0.31
<i>Rhizosolenia setigera</i> Brightwell	–	–	0.04*	0.17	0.52+	1.47	0.04*	0.20
<i>Rhizosolenia stolterfothii</i> Peragallo	–	–	0.11*	0.42	0.47+	0.93	0.06*	0.22
Cryptophyceae	4.44*	2.55	14.10+	3.81	3.69*	3.25	13.79+	4.13
<i>n</i>	15		128		51		42	

n: Number of samples employed in each group. Empty cells indicate that the species did not appear in a particular sample group. Symbols after the mean value indicate significance of values between groups. Values of a variable in different groups with the same symbol were nonsignificantly different (Student–Neuman–Keuls test, $p > 0.05$).

Sixty different phytoplankton species or taxonomic groups were recognized in the 236 samples analyzed, including 36 diatoms, 13 dinoflagellates and 11 categories of other flagellated phytoplankton. All the categories entered the discriminant analysis of phytoplankton composition (Fig. 9), those listed in Tables 4 and 5 having the highest correlation values with the computed discriminant functions. The two first functions accounted for 76% of the variance in the data and allowed for a correct classification of 81% of samples in the preassigned groups. More than 87% of samples from Groups 1 and 2 were correctly classified, whereas only 67% of samples of Group 4 were assigned to this group after the analysis. The first discriminant function was positively correlated with dinoflagellates, particularly with those of small size like *Prorocentrum balticum*, with Cryptophyceae and with the diatom *Leptocylindrus danicus*, while most other diatoms had negative correlations with this function (Table 4). The second function was positively correlated mainly with the dinoflagellates *P. balticum* and *Ceratium lineatum* but also showed relatively high positive correlation with the diatom *L. danicus*. Small unidentified dinoflagellates and the diatoms

Chaetoceros danicus and *Ditylum brightwelli* showed the highest negative correlations between this function and phytoplankton groups. Using these functions, samples from Group 3 were clearly

Table 6

Standardized canonical discriminant function coefficients and pooled-within-groups correlations between discriminating variables and canonical discriminant functions (DF1 and DF2) computed using particle-size concentration variables

Size-class mean diameter (µm)	Coefficient		Correlation	
	DF1	DF2	DF1	DF2
2.5	0.793	0.372	0.752	0.450
3.2	–0.042	0.278	0.337	0.674
4.0	–1.156	1.667	0.077	0.695
5.0	1.065	–1.606	0.361	0.433
6.4	–0.443	–0.279	0.423	0.310
8.0	1.096	0.490	0.429	0.229
10.1	–1.585	–0.622	0.268	0.147
12.7	1.110	1.165	0.242	0.190
16.0	–0.420	–0.238	0.207	0.145
20.2	0.199	0.356	0.208	0.104
25.4	–0.164	–0.517	0.237	–0.021

The mean equivalent spherical diameter of particles in each class is given (µm).

separated from those of Group 2, the latter having most samples with positive values in the first discriminant function and negative in the second function (Fig. 9). Also, samples from Group 4 showed positive values in both functions and could be clearly identified using these functions. Group 4 samples had generally high abundance values of most phytoplankton species, mainly of small dinoflagellates and *L. danicus* (Table 5). Differences between Groups 2 and 3 were mostly due to significantly higher abundances of Cryptophyceae in the former and diatoms like *Chaetoceros curvisetus*, *Pseudonitzschia delicatissima* and various species of *Rhizosolenia* in the latter. Group 1 samples displayed a phytoplankton composition clearly different from the rest, lacking most diatoms present in other groups.

The discriminant analysis considering particle-size concentration variables employed the 270 samples analyzed from 1992 cruises. The two first discriminant functions accounted for more than 99% of variance, but only 64% of samples were classified correctly in the preassigned groups using these functions. The first discriminant function was positively correlated with concentration in all size-

classes, but the smaller size-class considered had the highest correlation value (Table 6). The second correlation function was also positively correlated with most size-classes but showed negative correlation with the largest size-class. Consequently, samples from Group 4 reached relatively high positive values in the first discriminant function, and Group 2 and Group 3 samples showed values with opposite sign in the second function (Fig. 10). Mean particle-size distributions in all groups were quite similar in shape, generally displaying increasing concentrations from the smallest class (2.5 μm of mean diameter) to particles of 6.4 μm in diameter (Fig. 11). In all groups, particles with mean diameter larger than 10 μm reached equivalent concentrations in all classes considered. However, significant differences were found when comparing the concentration of each size-class between groups (Student–Neuman–Keuls test, $p < 0.05$). For instance, all size-classes of Group 3 samples had mean concentration values significantly higher than concentrations of those classes in other groups, with the exception of the size-class with mean diameter of 4 μm of Group 2. Furthermore, particle concentrations of samples of Groups 2 and 4 were non-

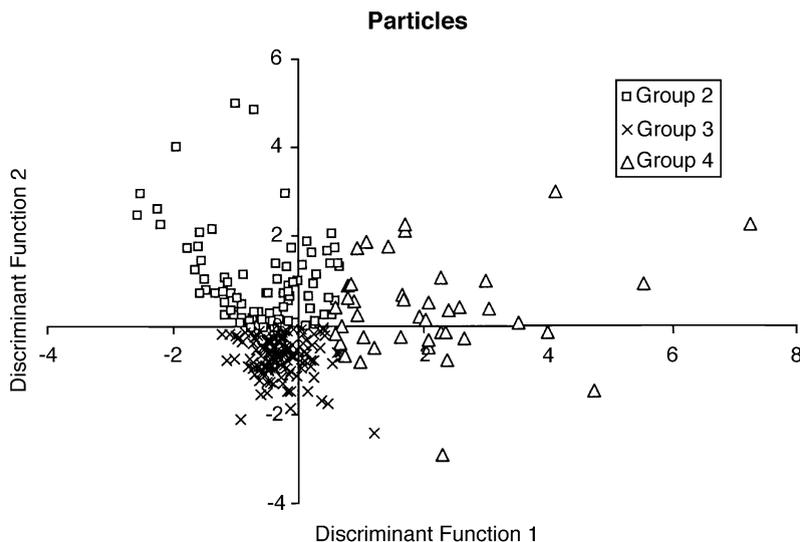


Fig. 10. Plot of samples from all cruises in the space defined by the two first discriminant functions computed to classify samples in the preassigned groups using particle-size variables (see text). Observations were coded according to their initial assignment to each group.

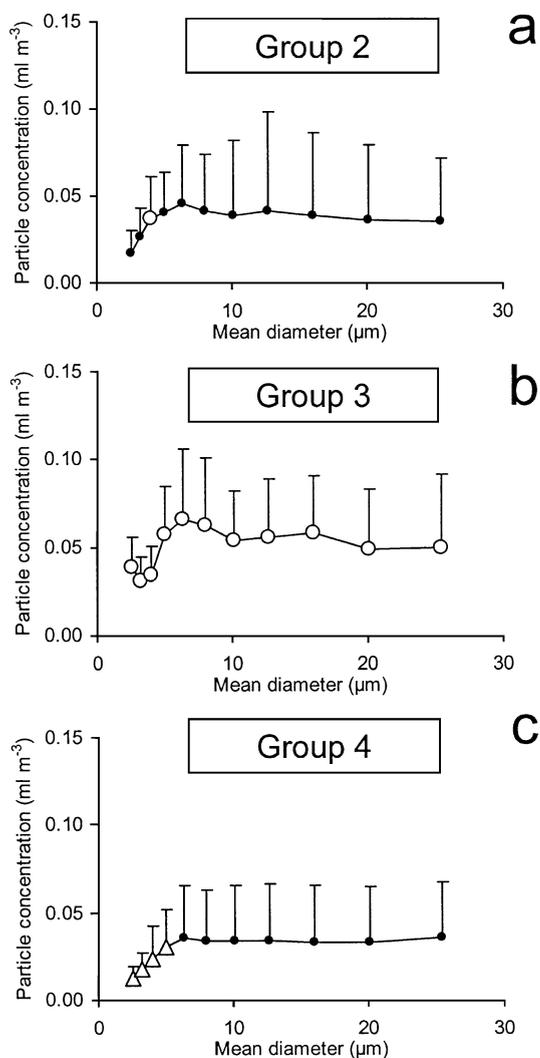


Fig. 11. Mean (+SD) volume concentration (ml m^{-3}) of particles from the different size-classes measured (indicated as the equivalent mean spherical diameter of each class) in each group. No particle samples were available for Group 1 waters. Number of samples averaged for Groups 2, 3 and 4 were 128, 96 and 46, respectively. Different symbols indicate significant differences in mean concentration of each size-class when comparing different groups (Student–Neuman–Keuls test, $p < 0.05$).

significantly different for size-classes of particles between 6.4 and 25.4 μm of mean diameter, but samples of Group 4 had significantly lower concentrations than those of other groups when considering smaller classes (Fig. 11).

4. Discussion

As shown by recent studies, salinity of ENACW can be affected by decadal, large-scale changes in the water mass formation (Pérez et al., 1995; Pollard et al., 1996; Pérez et al., 2000) and by variations in the poleward current (García-Soto et al., 1991; Pingree and LeCann, 1990; Pingree, 1993, 1994; Lavín et al., 1998). Water masses found during the study coincide in general with those previously described in the region (Fraga et al., 1982; Botas et al., 1989; Rios et al., 1992), however, salinity values resulted higher in comparison with earlier studies. For instance, nearly all observations in the T/S diagrams of Fig. 7 are displaced to the right of the reference lines for each water type drawn according to literature values, indicating an increase in salinity (Pérez et al., 2000). For this reason we have in fact broadened the criteria based on temperature and salinity values for classifying our observations in salinity groups (see Methods). Despite this increase in salinity, different water masses can still be recognized in Fig. 7, even when new salinity and temperature reference values that take into account climatological changes were still not defined for the region (Pérez et al., 1995, 2000; Pollard et al., 1996).

On the other hand, the variability in the poleward current may influence the extension of the more saline ENACW_t in the study area (Frouin et al., 1990). This current would increase during the reinforcement periods of the Azores High through an increase of northerly winds, cooling of surface waters and the subsequent increase in thermohaline circulation and advection of warm and saline waters northwards (Pérez et al., 1995). Our results agree in part with those of Castro et al. (2000) that did not find ENACW_t in Galicia in May 1991 (but some of our observations in S Galicia in April 1991 showed T/S characteristics of ENACW_t, cf. Fig. 6a). Satellite imagery during that period show that the warm surface poleward current was lessening as the coastal upwelling increased from April to May (García-Soto et al., 1991). In contrast, our results for 1992 clearly show the presence of surface waters with salinity exceeding 35.8 psu and T/S properties within the limits described for ENACW_t (cf. Figs. 3, 4 and 6). Also, the average wind-stress during previous winter months (expressed as the upwelling index, Fig. 2) is

indicative of northward transport of surface waters (negative values of the upwelling index). Furthermore, the presence of the poleward current in winter 1992 was noted by Pingree and LeCan (1992) analyzing satellite images until March–April 1992, and the surface salinity and temperature distributions along the NW Spanish coast in five cruises between March and June 1992 showed by López-Jamar et al. (1995) illustrate the relaxation of the poleward flow and the increasing importance of the southward, upwelling-induced flow from spring to summer. Therefore, we conclude that the high salinity of waters found in 1992 cruises were the consequence of both higher salinity during water mass formation (Pollard et al., 1996) and also of the poleward transport of southern ENACW_t in the previous winter.

One of the consequences of the increasing salinity was the apparent reduction in the amount of BBCW in the southern Bay of Biscay, as this water type was well represented in the area prior to 1991 (Treguer et al., 1979; Fraga et al., 1982; Botas et al., 1989) but was barely detected in our study, and only during 1991 cruise. The increase in salinity of ENACW at the time of water-mass formation (Pollard et al., 1996) would also affect BBCW, which is a subtype of ENACW influenced by the presence of continental water in the Bay of Biscay (Treguer et al., 1979; Fraga et al., 1982; Botas et al., 1989). Also, this water type was displaced from the surface layer as a consequence of advection of more saline ENACW types from the west during spring (Botas et al., 1989). Both effects would cause that most points in Fig. 6 close to BBCW reference limits were displaced to the right in the T/S diagram. At the same time, our results illustrate the influence of local factors on the extension of ENAW over the shelf. For instance, a period of heavy rain between March and April 1992 cruises was the responsibility of the dilution of saline waters near the coast because of enhanced runoff of the Cantabrian rivers and an increase in the formation of salinity fronts and stratification in the upper 50 m layer (López-Jamar et al., 1995).

Another consequence of the presence of saline waters was the separation of waters with different nutrient, phytoplankton and particle concentrations. Our classification of samples using thermohaline characteristics was confirmed by each of the discriminant analyses on chemical and biological variables,

although the differentiation of some water types was more evident using certain combinations of variables. Previous studies in the northern Iberian shelf during spring, but on a much reduced spatial scale, also found a differentiation of water bodies with characteristic nutrient and plankton composition in close relation with saline intrusions (Botas et al., 1988; Bode et al., 1990; Fernández et al., 1991; Lavín et al., 1992a,b; Fernández et al., 1993). In these studies, high salinity waters showed in general higher nutrient concentrations than coastal and, sometimes, oceanic waters (e.g. nitrate). Botas et al. (1988) suggested that high nitrite and low oxygen concentrations in saline waters were indicative of a dominance of remineralization processes in these waters, a hypothesis also supported by studies of plankton composition (Bode et al., 1990; Fernández et al., 1991, 1993). In a more general context, Pérez et al. (1993) showed the importance of remineralization along the northward progression of ENACW_t, but particularly in waters below 100-m depth. In contrast, we found relatively low nutrient concentrations in saline waters (i.e. Group 3, Table 3), but particularly those of phosphate and nitrite. Our findings can be interpreted as the result of a general bloom development in saline waters, especially in those of highest salinity (Group 3). Mean nitrate and phosphate concentrations in ENACW_t waters (Groups 2 and 3) were lower than those reported by Pérez et al. (1993) at the salinity maximum (35.815 psu, 5.6 mmol N–NO₃⁻ m⁻³, 0.32 mmol P–PO₄³⁺ m⁻³). Nitrate was more depleted than phosphate in all waters, indicating that in situ remineralization of nitrate was insufficient to account for phytoplankton demand. This is further supported by the low nitrite concentrations in saline waters, as nitrite accumulation is known to occur during nitrification (McCarthy et al., 1984). In addition, significantly higher chlorophyll concentrations and the large diversity of diatom species in saline waters compared with other water types are typical characteristics of spring blooms in temperate regions (e.g. Legendre, 1990).

The different phytoplankton assemblages found in this study provide an additional proof of the occurrence of several blooms in temperate waters, instead of a single bloom, typical of high latitudes (Legendre, 1990; Ducklow and Harris, 1993; Townsend et al., 1994). Some of them displayed characteristics of other

spring-blooms reported in the area, either considering chlorophyll concentrations (Flos, 1982; Fernández and Bode, 1991; Casas et al., 1997) and general species composition (Estrada, 1982; Varela, 1992a,b; Fernández and Bode, 1994; Casas et al., 1999). However, the dominance of particular species in waters with high salinity in our study allows for a differentiation of blooms occurring in these waters in our study and those reported in earlier studies. Since the cruises were made in different years and sampling of the entire area was accomplished in 3 or 4 weeks during each cruise, in this study no attempt was made to establish a sequence between these blooms, but the environmental and planktonic characteristics of the recognized water bodies are interpreted in relation to the available information on the NW Iberian shelf instead. Phytoplankton species characteristic of Group 1 waters, found in the northern shelf in April 1991, were typical of late-winter, having low cell abundances and being small dinoflagellates and flagellates the only noticeable groups (Fernández and Bode, 1994; Casas et al., 1999). Low chlorophyll and relatively high nutrient concentrations also indicate that the bloom was not initiated in these waters, with a low degree of vertical stratification (López-Jamar et al., 1995). In contrast, phytoplankton blooms were well developed in all other groups recognized.

The two types of saline waters were characterized by the presence of a larger number of species than Group 1 waters. Both saline groups were separated mainly by a dominance of Cryptophyceae in Group 2 (lower salinity segment of ENACW_t), while both shared most diatom species. Such dominance of phytoflagellates is similar to the bloom described in April 1987 by Fernández et al. (1993) and was also observed in other areas where large numbers of microflagellates accompany or follow diatom blooms (Nielsen and Richardson, 1989). The mixotrophic nutrition of many marine flagellates (e.g. Riemann et al., 1995), along with the favourable conditions provided by stabilization of the water-column near frontal zones between saline and coastal or oceanic waters (Fernández et al., 1991, 1993), may explain this dominance. Moreover, time-series studies of phytoplankton composition noted an increase in microflagellate abundances between 1989 and 1992 in the coast of NW Spain (Casas et al., 1999), a general trend attributed to increasing eutrophication near the

coast also found in other North Atlantic regions (Hickel et al., 1993).

Dominance of several species of small-sized and chain-forming diatoms was noticed for phytoplankton blooms in the study area (Fernández and Bode, 1994; Casas et al., 1999). *Chaetoceros socialis* is always the dominant diatom species in spring blooms in the Galician shelf (Casas et al., 1999), while spring blooms reported in the Mar Cantábrico included other species such as *L. danicus* and *P. delicatissima* that reach higher abundances than *Chaetoceros* spp. (Fernández and Bode, 1994). In this context, our results show that the more saline waters (Group 3) contained significantly higher abundances of species like *L. danicus*, *P. delicatissima* and *Rhizosolenia stolterfothii* than other groups. These species, of widespread distribution in the Atlantic, are reported to increase their abundances during blooms occurring in oceanic and warm waters (e.g. Guillard and Kilham, 1977 and references therein). This feature, along with the reduced importance of *C. socialis* in our study (although present in the results and entered the discriminant analysis, this species was not one of the main discriminant species, Table 4), allows us to relate blooms occurring in these waters to blooms produced later in the season as a consequence of the upwelling (Casas et al., 1999). The codominance of similar species, also found in other shelf regions (Holligan, 1987; Legendre, 1990), was probably due to the existence of zones with frequent mixing and stabilization processes that create favourable conditions for the simultaneous growth of several species, while monospecific blooms often occur as a response to a single major environmental change like freshwater runoff or coastal eutrophication (Holligan, 1987). Summer blooms caused by upwelling in the northwestern Iberian shelf are also multispecific, and several species of dinoflagellates increase their abundances along with diatoms, particularly *L. danicus* (Varela, 1992a; Casas et al., 1999). The upwelling-favourable wind conditions during the cruises considered in this study would explain the production of blooms in saline waters with a species composition similar to those of summer, particularly in Galicia. However, one of the main characteristics of the studied spring blooms is the mixture of typical bloom-forming diatoms along with flagellates and small dinoflagellates, the latter being present all year

round (Casas et al., 1999). This diversity of groups originates large differences in sestonic particles, which has important trophic implications.

On one hand, diatom chains and colonies form the bulk of netphytoplankton ($>12\ \mu\text{m}$, as in Bode et al., 1994) and are a significant food source for pelagic fish like sardine (Varela et al., 1988, 1990), with the resulting shortening in the food chain and increase in efficiency in energy transfer (Blaxter and Hunter, 1982). Fernández et al. (1993) reported a differential distribution of sardine larvae near the coast in the northern Iberian shelf associated with diatom-dominated phytoplankton populations. Our results extend the importance of saline waters in the whole NW Iberian shelf for the increasing availability of large phytoplanktonic particles, as indicated by the abundance of chain-forming diatoms, although the particle-size data presented here did not show a specific shape in the distributions of particles in these waters because only sizes smaller than $25.4\ \mu\text{m}$ ESD were considered. However, Robins et al. (1991) found clear differences in particle-size distributions of seston during April 1991 cruise. In their study, a large size range of particles was employed ($1\text{--}170\ \mu\text{m}$ ESD) and the signal of chain-forming diatoms was clearly seen in waters of the western shelf (Galicia).

On the other hand, flagellate-dominated communities tend to be organized around microbial food chains, with longer pathways and low efficiency of energy transfer, although they are important for nutrient remineralization (Glibert, 1993). Previous studies of local blooms in the area also reported flagellate dominance in fronts related to saline intrusions (Bode et al., 1990; Fernández et al., 1991, 1993). In our case, the high abundance of Cryptophyceae in Group 2 and Group 4 waters (low salinity ENACW_t and surface water, respectively) may be explained by the existence of frontal zones caused by the salinity gradient between ENACW_t and surface waters with low salinity since these areas would provide enough stability to the water column for flagellate growth and accumulation (Holligan, 1987). Although we do not provide detailed depth distributions of variables in this study, other papers concerning some of the cruises analyzed here reveal that high chlorophyll areas occurred in zones near large horizontal gradients of temperature and salinity (García-Soto et al., 1991; Robins et al., 1991; Bode et al.,

2001). Phytoflagellates lower than $10\ \mu\text{m}$ may be a significant food source for planktonic copepods known in the region (Cabal et al., 1990; Barquero et al., 1998; Valdés and Moral, 1998), which in turn may be consumed by the spawning sardine populations (Varela et al., 1988, 1990; Varela, 1992b). Indirect support for this hypothesis was provided by Barquero et al. (1998) when reporting large abundances of herbivorous copepods with daily grazing rates equivalent to 12% of primary production for a coastal zone dominated by phytoflagellates in the western Iberian shelf during spring. In addition to phytoplankton, the increased availability of all sestonic particles in saline waters found in our study may be an important nutritional resource for spawning adults and larvae of pelagic fishes in the region. In this way, several studies have related the distribution of sardine eggs and larvae with suitable feeding areas (e.g. Robins et al., 1991; Varela, 1992b). However, the survival of the fish larvae would ultimately depend not only on the availability of suitable food particles but also from their retention in nursery areas by hydrographic processes, like the currents associated with saline intrusions (Fernández et al., 1993) and upwelling (López-Jamar et al., 1995).

This study confirms the importance of intrusions of saline waters of subtropical origin along the northern and northwestern shelf of the Iberian Peninsula during spring, when these intrusions affect the development of phytoplankton blooms mainly by the generation of hydrodynamic discontinuities, such as fronts and jet currents, which stabilize the water-column. The main consequence for the pelagic ecosystem is the production of a large degree of heterogeneity in plankton composition, biomass and distribution that would occur if these intrusions were not produced. On a shelfwide scale, the occurrence of waters with different salinity during the spring is critical for the development and composition of phytoplankton blooms in this region of NW Spain, as the large hydrodynamic changes made by the seasonal switch in the dominant surface currents affect the retention and transport of planktonic organisms (Fernández et al., 1993; López-Jamar et al., 1995). First, the accumulation of surface water and plankton towards the coast is favoured by predominantly northward flow, such as in winter and early spring, generally associated to well-mixed water-columns and low phytoplankton biomass and

production (e.g. Bode et al., 2001). Second, offshore transport of surface low-salinity waters occurring near the coast as a consequence of the increasing importance of upwelling during the spring season would favour stabilization of the upper water-column and phytoplankton development (e.g. López-Jamar et al., 1995).

The broad spatial and temporal coverage of this study suggests that the effects caused by saline intrusions on the composition, distribution and production of plankton and pelagic fishes described in previous studies at lower space and time scales (Bode et al., 1990; Fernández et al., 1991, 1993) may determine biogeochemical fluxes and the success of fish populations at annual or even larger time scales in the southern Bay of Biscay. In contrast, earlier studies of this region only considered the seasonal upwelling in the northwestern part of the area as the major source of nutrients and hydrodynamic forcing affecting the pelagic shelf ecosystem even during spring (Robins et al., 1991; Varela, 1992a,b; Tenore et al., 1995). However, a large variability on the effects of saline intrusions on plankton could be expected given the evidences on the interannual variability of the salinity of ENACW (Rios et al., 1992; Pérez et al., 1995; Pollard et al., 1996; Lavín et al., 1998; Pérez et al., 2000) and in the intensity of the poleward current which can affect these intrusions (Pingree and LeCann, 1992). For instance, salinity of ENACW in the study area increased in late 1980s (Pérez et al., 1995; Pollard et al., 1996), reaching a maximum in 1992 and decreased until 1995 (Lavín et al., 1998; Pérez et al., 2000). At the same time, Valdés and Moral (1998) detected a decrease in copepod species diversity between 1991 and 1995 in a coastal station in the northern Iberian shelf.

It must be noted that the situation described in our study corresponds to a period when salinity in the southern Bay of Biscay reached their maximum intensity recorded in almost 20 years, and that the composition and distribution of plankton may be very different from those of years with low-intensity or nonexistent intrusions. Therefore, the results provided here can be used as a reference for comparison of values obtained in other years. The main difference between the results reported here and those described for 1987 in the central Cantabrian Sea (Botas et al., 1988, 1990; Bode et al., 1990; Fernández and Bode,

1991; Fernández et al., 1991, 1993) is the absence of a jet-like structure of the intrusions in spring 1991 and 1992, when ENACW of higher salinity than those of previous years washed large shelf areas, thus preventing the formation of BBCW and limiting the formation of salinity fronts when meeting runoff water. In late 1990s, a decrease in the recruitment of sardine populations has been noted in this region (ICES, 1999), but the possible links between these changes and those in the water masses or in the pelagic ecosystem were not known. Long-term fluctuations in the characteristics of water masses and currents found along the Iberian shelf are probably linked to large-scale climatic processes since their formation is affected by variations of atmospheric pressure and winds (Frouin et al., 1990; Pérez et al., 1995, 2000). Further studies in this region would need to take into account the large-scale variability in hydrology and planktonic populations along with small-scale processes in order to understand the implications of these sources of natural variability for the sustainability of the shelf ecosystem.

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