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Mesozooplankton species distribution in the NW and N Iberian shelf during spring 2004: Relationship with frontal structures

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Abstract

We have analysed the mesozooplankton community structure in the southern Bay of Biscay shelf and its relationship with the hydrographic conditions during spring 2004. According to thermohaline characteristics, we observed two frontal zones of distinct origin along the shelf (around 7° and 3°W), that allowed us to differentiate three different hydrographic domains. The westernmost part of the shelf (WC), defined by the presence of relatively warm and salty water related to the presence of the Iberian Poleward Current (IPC), the easternmost region (EC), characterized by colder and fresher water and subject to the influence of freshwater inputs from the Adour river in the French coast, and a region in the Central Cantabrian Sea (CC), where thermohaline characteristics were intermediate between these two extremes. The mixing layer depth (MLD) regime in these areas was also different: the WC region was characterized by a mixed water column, whereas in the EC region the river discharges produces stratification of the upper meters of the water column (<10 m); in the CC region, we found a distinct vertical mixing regime that separated coastal (stratification) from shelf (mixed water column) stations, giving rise to a notorious across-shelf front. We found a good match between the aforesaid hydrographic regions and the distribution of mesozooplankton species composition and community assemblages: the Mantel correlation between physical variables and mesozooplankton distribution was highly significant ($n=63$, $r=0.70$, $\alpha<0.001$). In the WC region, the community was dominated by *Paracalanus parvus*, *Oithona helgolandica*, *Acartia clausi* and *Clausocalanus pergens*, while in the EC region the most dominant species were *Noctiluca scintillans*, *Oncaea media* and *Temora longicornis*. The CC region showed similar composition of copepods than the WC region, but larvaceans (*Oikopleura* spp. and *Fritillaria* spp.) were more abundant in the CC region than in the WC region. Within each zone, the relative abundances of the dominant species differed between coastal and shelf locations.

Keywords: Mesozooplankton; Iberian Poleward Current; River plumes; Frontal areas; Northern Iberian shelf

1. Introduction

The physical environment affects the composition and structure of plankton communities, and therefore modulates ecosystem function and dynamics (Paffenhöfer, 1980; Landry et al., 2001). The mesozooplankton community, as a key component of the food web plankton ecosystem that channels matter and energy from the lower to the higher trophic levels (Longhurst and Harrison, 1989), is strongly controlled by the physical environment, which influence their growth, reproduction and distribution (Mauchline, 1998). This control could propagate up and down different levels of the food web (Kiørboe et al.,

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1988; Munk et al., 1995), including different life stages of commercially important fishes stocks, such as sardine, anchovy, mackerel and horse mackerel (OSPAR, 2000).

Hydrographic conditions in the NW and N Iberian shelf (between 42 and 45°N) show a marked seasonality. Apart from the water column mixing-stratification cycle characteristic of temperate seas (Longhurst, 1998), the development and decay of a warm and saline poleward current flowing along the slope is another salient hydrographic feature. This poleward flow, named Iberian Poleward Current (IPC) (Peliz et al., 2003), Portugal Coastal Counter Current (PCCC) (Ambar and Fiuza, 1994; Álvarez-Salgado et al., 2003) or “Navidad” (Christmas) Current (García-Soto et al., 2002), is a common feature of the winter circulation of eastern ocean margins (Neshyba et al., 1989). In the Iberian shelf, this narrow, upper slope trapped current develops in winter forced by the meridional density gradient, through the ‘Joint Effect of Baroclinicity and Relief’ (JEBAR; Huthnance, 1984, 1986; Pingree and Le Cann, 1989), and decays during the spring–summer period (Peliz et al., 2005; González-Nuevo and Nogueira, 2005).

The NW and N Iberian shelf is located in the inter-gyre zone that separates the subpolar and subtropical gyres of the North-East Atlantic (Pollard et al., 1996). The subpolar gyre is the formation area of the Eastern North Atlantic Central Water Subpolar mode (ENACWsp), while to the south of the inter-gyre zone the formation of the subtropical mode of this water mass (ENACWst) (Pérez and Castro, 2001) takes place. These modes of central waters differ in their thermohaline characteristics being the subtropical, which are warmer and saltier, thus spicier (Flament, 1986), than the subpolar mode waters (Ríos et al., 1992; Pérez et al., 1995).

Fraga (1981) found a sub-surface front between the subtropical and subpolar modes of ENACW off Cape Finisterre (43°N, 9°W), and were the first to suggest a poleward advection of ENACWst along the Iberian margin. Their results were later confirmed by Pérez et al. (1993) using a biogeochemical approach. The presence of relatively warm and salty waters off NW Iberia has been noted since then by different authors (Pingree and Le Cann, 1990; Ríos et al., 1992). These spicy waters enter into the Southern Bay of Biscay moving eastward along the Cantabrian continental shelf and slope (Pingree and Le Cann, 1992; Bode et al., 2002; García-Soto et al., 2002).

Several studies have focused on the influence of the Poleward current on phytoplankton and mesozooplankton biomass and on metabolic rates, both off NW Spain (Castro et al., 1997; Álvarez-Salgado et al., 2003; Huskin et al., 2003; Isla and Anadón, 2004) and in the central Cantabrian Sea (Fernández and Bode, 1991; Fernández et al., 1993; Cabal, 1993). However, information on the mesozooplankton community composition and distribution remains limited (Cabal, 1993; Blanco-Bercial et al., 2006). Besides, most of the studies on mesozooplankton composition in the southern Bay of Biscay were restricted to local (e.g. Alvarez-Marqués, 1980; Valdés et al., 1991; Cabal, 1993; Valdés and Moral, 1998; Villate et al., 2004 and references therein) or meso-scales (e.g. Barquero et al., 1998; Blanco-Bercial et al., 2006).

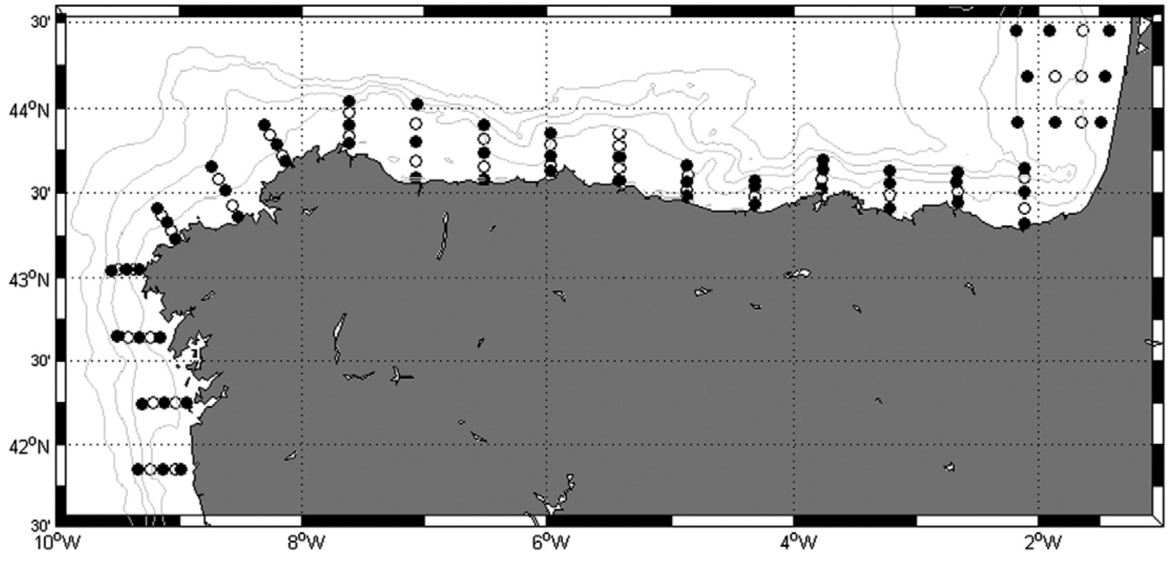


Fig. 1. Position of the hydrographical and biological sampling stations during the *PELACUS 0404* cruise (black dots are biological and hydrographical stations, white dots are hydrographical stations).

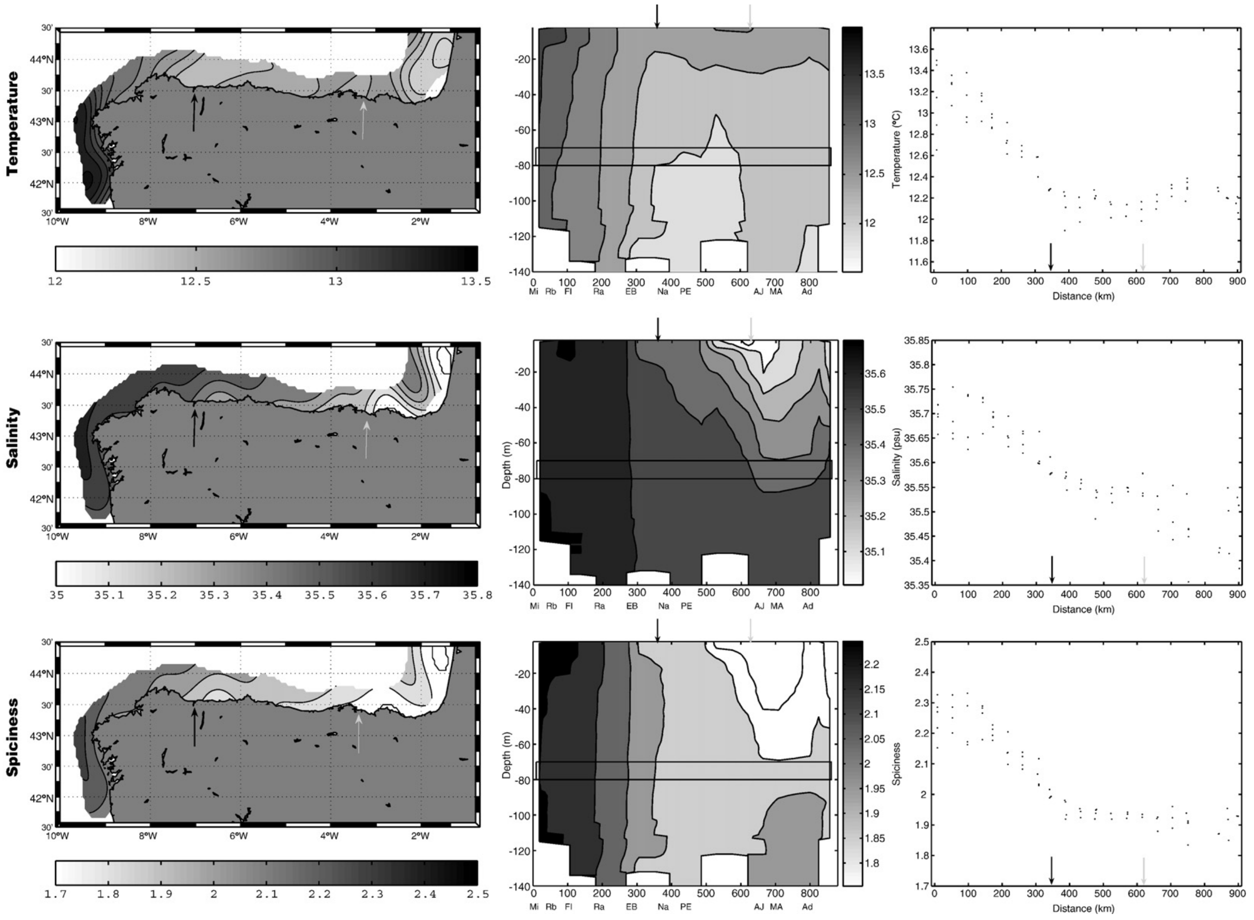


Fig. 2. Spatial (left), vertical (centre) and 70–80 m integrated (right) distributions of temperature, salinity and spiciness. The black arrow represents the limit of influence of spicy waters (IPC_f) and the grey arrow the limit of influence of the Adour river plume.

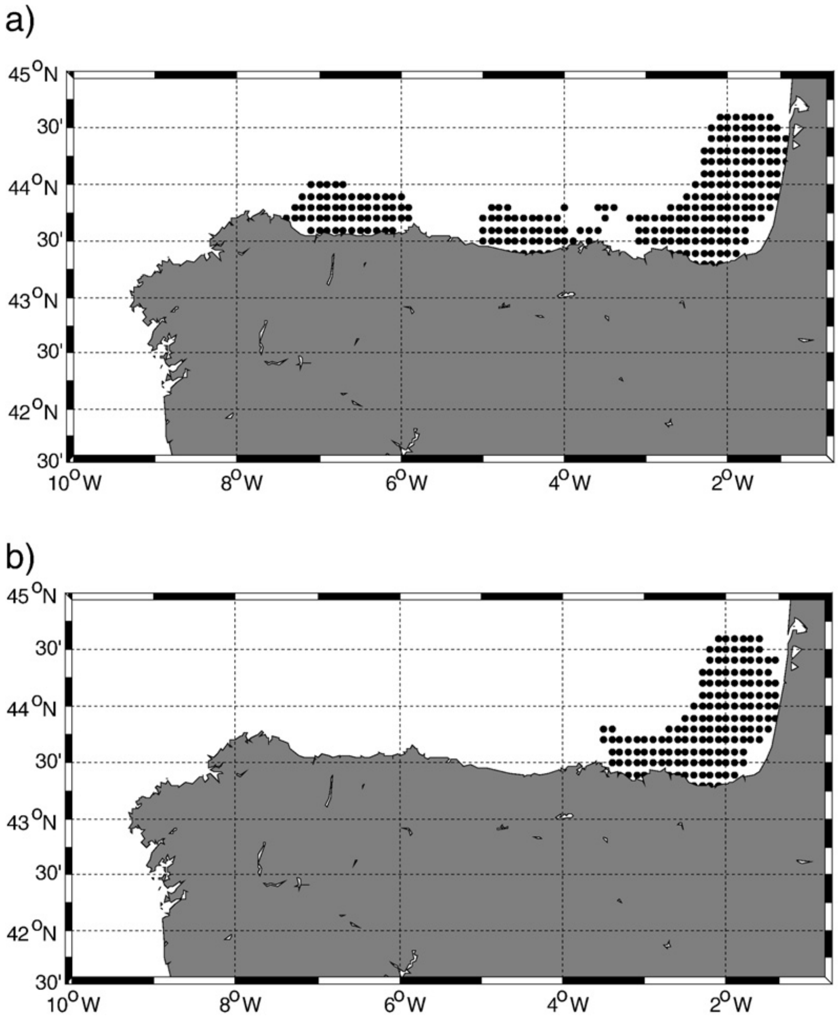


Fig. 3. Distribution of the influence of river plumes for a) 5 m and b) 10 m.

Here, we present the results on mesozooplankton species distribution and its relationship with the physical environment from the data acquired during the *PELACUS-0404* cruise, conducted in the continental shelf of the NW and N Iberian Peninsula between March 30 and April 22 of 2004. As far as we know, this is the first

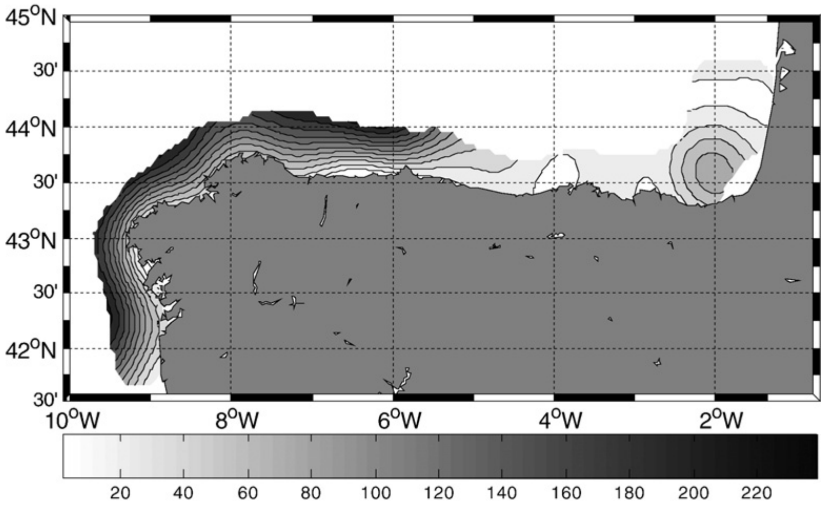


Fig. 4. Spatial distribution of mix layer depth (MLD).

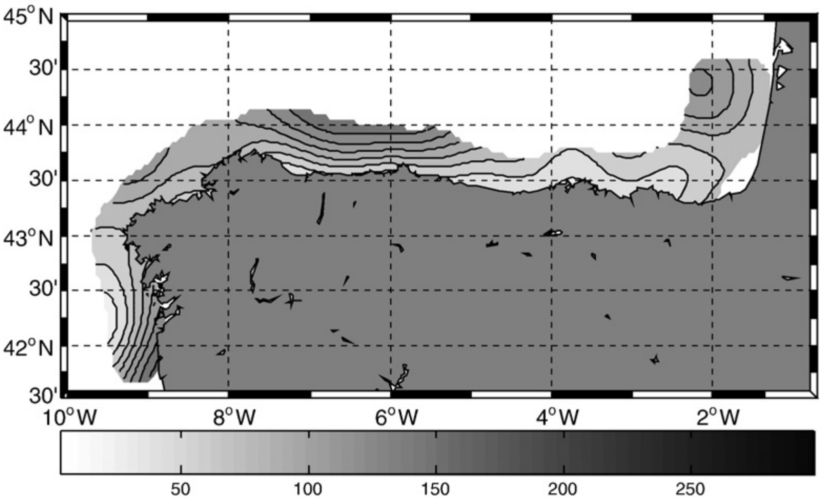


Fig. 5. Spatial distribution of chlorophyll *a* integrated for the first 50 m of the water column (mg m^{-2}).

comprehensive study on the distribution of mesozooplankton during spring covering the entire northern Spanish shelf, from Galicia up to the French border.

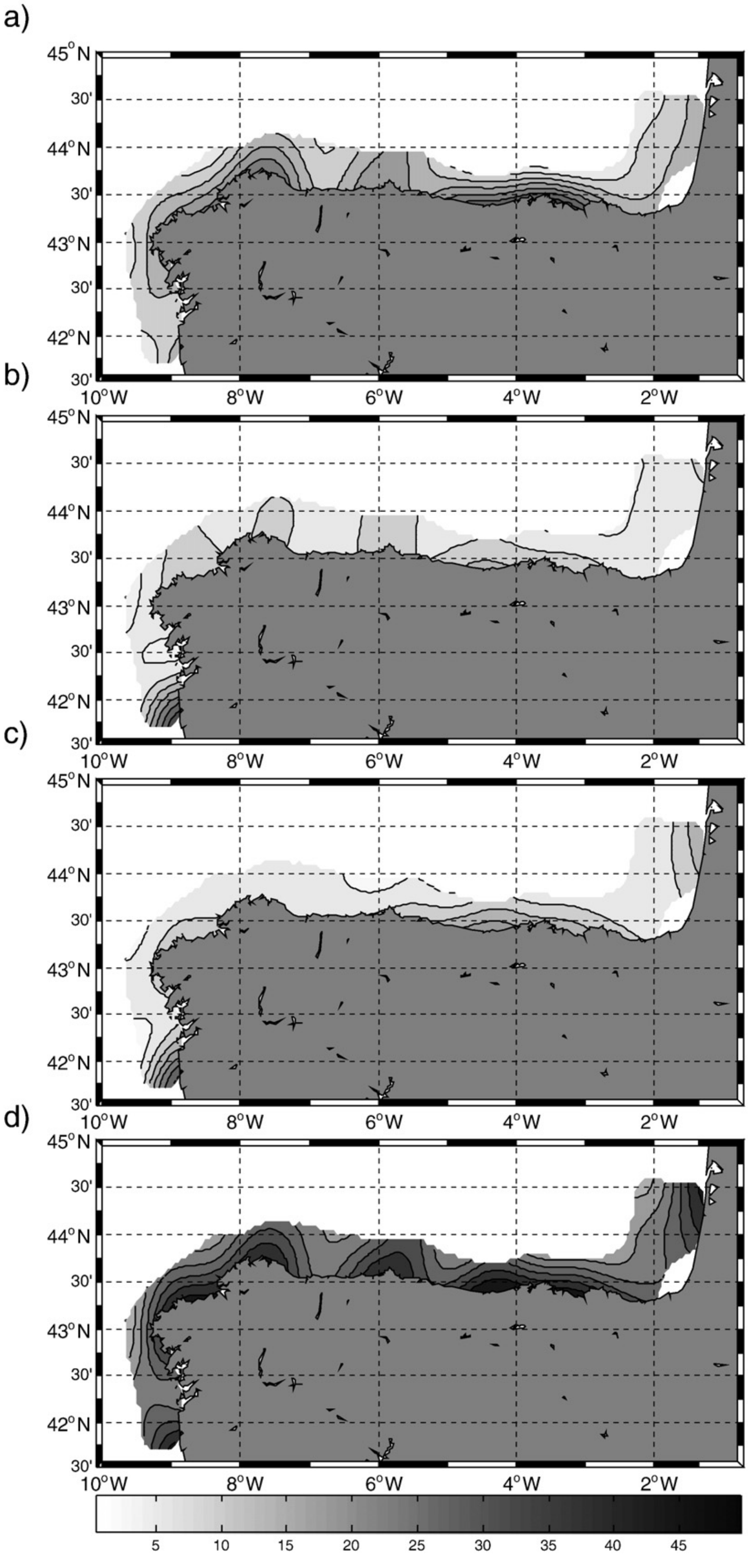
2. Materials and methods

A total of 98 CTDF (conductivity–temperature–depth–fluorescence) casts were recorded all along the NW and N Iberian shelf in the *PELACUS-0404* cruise (30 March–22 April) with a *SeaBird* 25 CTD probe with a *SeaTech* fluorometer. Water column density was derived from temperature and salinity records (UNESCO, 1983). The mixed layer depth (MLD) was calculated using a density gradient criterion of 0.01 m^{-1} (Kara et al., 2000). Fluorescence measurements were transformed into chlorophyll *a* (Chl *a*) concentration (mg m^{-3}) according to the fluorescence/Chl *a* relationships obtained during the cruise (Chl $a = 0.80 * \text{Fluorescence} - 0.11$; $n = 296$, $r = 0.81$, $p < 0.001$). For mapping the distribution of thermohaline characteristics and Chl *a*, we have applied an objective interpolation method (Haagenson, 1982), using a Gaussian variogram model (signal to noise ratio = 0.11, and correlation scale coefficient = 40 km).

In order to locate the frontal area that defines the limit of influence of the IPC, which separates bodies of water that are subject to distinct influence of the Subtropical and Subpolar modes of Eastern North Atlantic Central Water ($ENACW_{sp}$ and $ENACW_{st}$ respectively), we analysed the change in the slope of the along-shelf transect of sub-surface (average values in the 70–80 m depth layer) spiciness (Flament, 1986, 2002), according to the method proposed by González-Nuevo and Nogueira (2005). Otherwise, to define frontal areas associated with freshwater inputs we have used salinity data at 5 m and 10 m depth to determine the limit of influence of river plumes. These salinity data were interpolated using objective functions for a grid with 0.1 degrees. These frontal areas associated to river plumes were defined by a difference of 0.10 salinity units in 10 nautical miles (nm).

Mesozooplankton samples were taken by means of vertical hauls from 100 m depth, or from 5 m above the bottom in shallower stations, up to the surface in 61 out of the 98 hydrographic stations with a triple WP2 net of 200 µm mesh-size and 0.125 m^2 of mouth area (Fig. 1). Samples were collected between sunset and sunrise. Samples for taxonomic analysis from one cod-end were preserved in 4% sodium borate-buffered formalin-seawater solution, and later examined under a stereomicroscope to assess the species composition and abundance. Actinopoda and Phoraminiphera were not included in our taxonomic analysis, in spite of their high abundances at some locations, because our sampling method was not adequate for these groups. Similarly, the abundance data of large-sized mesozooplankton (e.g. Euphausiids and Salps) have to be considered with caution because of potential net avoidance or extremely patchy distributions. Other cod-end was used to estimate mesozooplankton fractionated biomass. Cod-end contents were immediately fractionated into three size fractions, 200–500 (small), 500–1000 (medium), and >1000 µm (large), using sieve cups equipped with *Nitex* screens. Samples for biomass analysis were rinsed with 0.2 µm filtered seawater, filtered onto pre-combusted (450 °C, 24 h), pre-

Fig. 6. Spatial distribution of mesozooplankton size fractionated biomass (mg m^{-3}): a) 200–500 µm size fraction, b) 500–1000 µm size fraction, c) 1000–2000 µm size fraction and d) total biomass.


a)
b)
c)
d)
45°N
30'
44°N
30'
43°N
30'
42°N
30'
10°W
8°W
6°W
4°W
2°W
5
10
15
20
25
30
35
40
45

weighted *Whatmann GF/A* filters and dried at 60 °C for 24 h. The dry weight was measured with a *Sartorius* microbalance.

In order to group stations with similar composition of mesozooplankton species, we performed a cluster analysis on the $\log_{10}$ (species abundance + 1) mesozooplankton abundance data, using the Ward's method on the Euclidean distance matrix. Rare species (those present in less than 10% of the samples) were excluded for the analysis. ANOVA and *a posteriori* Student–Newman–Keuls test (Keuls, 1952) were used to assess the significance of the difference between cluster groups. *SPSS+PC* and *Statistica* packages were used for statistical data analysis.

Mantel and partial Mantel correlations among physical, biological and space matrices were calculated to assess the relationship between the biological (response) and physical (explanatory) variables taking into account the common spatial structure (Legendre and Legendre, 1998; Legendre et al., 2005). Both for the physical and the mesozooplankton data, the respective distance matrices were defined assigning 1 when two stations belong to the same physical domain or mesozooplankton cluster, and 0 when two stations belong to different domains or clusters respectively. The spatial matrix was defined as the geographic (i.e. Euclidian) distance among the sampling stations.

3. Results

3.1. Physical characterization

Hydrographic conditions in the southern Bay of Biscay during spring 2004 differed markedly along the shelf, allowing us to differentiate three distinct hydrographic regions. The westernmost part of the shelf (WC region) was characterized by relatively warm (>13 °C) and salty (>35.65), thus spicy, waters that denote the presence of $ENACW_{st}$ advected by the Iberian Poleward Current (Fig. 2). At the extreme of the sampled area, in the cul-de-sac of the Bay of Biscay (EC region), colder and fresher water was found (<12.5 °C and <35.5 respectively) due to the influence of $ENACW_{sp}$ and the continental inputs from the Adour river in the French coast (Figs. 2 and 3). In between these two zones, we observed a transitional area in the Central Cantabrian Sea (CC region), where thermohaline conditions were intermediate between these two extremes. In this region it is also noticeable the influence of freshwater discharges from the small Cantabrian rivers. The river plumes associated to these discharges affect only the upper layers (<10 m depth) of the water column (Figs. 3a).

The separation between the WC and CC regions takes place by a neat frontal area, located around Cape Estaca de Bares (7°W), associated with the limit of influence of the IPC, while the CC and EC regions are separated also by a frontal area located around Cape Machichaco (3°W) that in this case was related with the limit of influence of the Adour river plume (Fig. 3b). The mixing regime in these areas was also different according to the criterion used to define the MLD (Fig. 4). The WC region was characterized by a mixed water column, whereas in the EC region the river discharges produces stratification of the upper meters of the water column (<10 m). In the CC region, we found a distinct vertical mixing regime that separated coastal (stratification) from shelf (mixed water column) stations, giving rise to a notorious across-shelf front (Fig. 4).

3.2. Biological variables: phytoplankton biomass and mesozooplankton biomass and species composition

Spatial distribution of 50 m integrated chlorophyll *a* (Fig. 5) showed maximum values in the shelf-edges located between the WC and the CC regions, and in the northern part of the EC region, associated with the limit of influence of the IPC and the river plume from the Adour river respectively. A spot of high concentration was also found at the coast in the southernmost part of the sampling area (around 42°N). Phytoplankton biomass at 10 m and 30 m depth was low (<1.5 mg m^{-3}) all along the coast, except in the southernmost stations, in the proximity of the frontal area that separates the WC and the CC regions, and in the across-shelf front located in the ECregion, where chlorophyll *a* concentration was 4–5 mg m^{-3}.

Mesozooplankton community was dominated by the small-sized fraction (200–500 μm) (Fig. 6a), which all along the shelf attained average values around 15 mg m^{-3} respectively, thus contributing around 50% to total biomass averaged for the whole sampling area (Fig. 6d). The maximum values for this fraction (around 40 mg m^{-3}) were found in the proximity of the frontal areas associated with the limit of influence of the IPC and the river plume from the Adour river, and also in the CC region off Cape Peñas (around 6°W) (Fig. 6a). The contribution of the medium and large-sized fraction (Fig. 6b and c respectively) to total mesozooplankton biomass averaged for the whole area was of the same magnitude (about 25% each), although high biomass values were found in a spot located in the southernmost part of the sampling area (around 42°N), where biomass in the medium and large-sized fraction reached values around 40 mg m^{-3} each. In this spot, where also chlorophyll *a* concentration was high

Table 1
Mean (number m^{-2}) abundance of zooplankton taxa in each group, between brackets percentage of presence in the samples of each group

Taxon	Cluster A	Cluster B	Cluster C	SNK
Copepods				
Rhincalanus nasutus				
Calanus helgolandicus	1780 (96)	4157 (94)	2848 (100)	n.s.
Mesocalanus tenuicornis	974 (96)	1640 (94)	1715 (71)	n.s.
Calanoides carinatus	1108 (96)	1163 (88)	733 (94)	A=B>C
Neocalanus gracilis	69 (11)	515 (19)	344 (24)	n.s.
Nannocalanus minor				
Subeucalanus elongates				
Subeucalanus monachus	0 (0)	207 (13)	0 (0)	C>A=B
Ischnocalanus tenuis				
Paracalanus parvus	49979 (100)	33775 (100)	8393 (100)	A=B>C
Calocalanus contractus	1078 (18)	1061 (19)	0 (0)	n.s.
Calocalanus styliremis	2371 (89)	3694 (88)	1507 (71)	n.s.
Pseudocalanus elongatus	4746 (93)	9425 (100)	1506 (88)	B>A>C
Clausocalanus arcuicornis	2650 (93)	4095 (100)	2057 (82)	B>C
Clausocalanus farrani	646 (25)	3820 (6)	0 (0)	n.s.
Clausocalanus jobei	1106 (7)	359 (13)	669 (29)	n.s.
Clausocalanus lividus	1416 (93)	4333 (81)	1181 (88)	n.s.
Clausocalanus paululus	700 (14)	668 (6)	1592 (6)	n.s.
Clausocalanus pergens	16082 (96)	7272 (100)	1872 (76)	A>B>C
Ctenocalanus vanus	4245 (100)	4628 (100)	3958 (88)	A=B>C
Aetideus armatus	62 (14)	272 (44)	66 (35)	B>A=C
Euchirella rostrata				
Euchirella curticauda				
Euchaeta hebes	1082 (96)	799 (81)	645 (65)	A>B=C
Paraeuchaeta norvegica				
Paraeuhaeta tonsa				
Phaenna spinifera	914 (18)	1124 (25)	0 (0)	n.s.
Scolecithrix ovata	7 (4)	318 (6)	301 (24)	n.s.
Scolecithricella bradyii				
Diaxis pigmea				
Diaxis hibernica	674 (11)	292 (19)	465 (18)	n.s.
Temora longicornis	1098 (36)	621 (25)	7842 (100)	C>A=B
Temora stylifera	0 (0)	191 (13)	205 (24)	n.s.
Heterorhabdus robustus				
Heterorhabdus papilliger				
Heterostylites longicornis				
Metridia lucens	595 (86)	1317 (88)	938 (76)	n.s.
Pleuromamma gracilis	366 (36)	284 (56)	308 (35)	n.s.
Pleuromamma robusta				
Pleuromamma abdominalis				
Centropages chierchiae	2311 (96)	1241 (75)	249 (65)	A>B=C
Centropages typicus	711 (43)	799 (81)	214 (35)	B>A=C
Isias clavipes				
Candacia armata	293 (21)	540 (69)	321 (71)	B>A=C
Anomalocera pàtersoni				
Acartia clausi	28041 (100)	41074 (88)	7224 (94)	A=B>C
Oithona helgolandica	28886 (100)	37646 (94)	22277 (100)	A=B>C
Oithona plumifera	1042 (25)	1924 (75)	914 (29)	B>A=C
Oithona nana				
Microsetella rosea	840 (29)	1716 (50)	419 (71)	n.s.
Microsetella novergica				
Euterpina acutifrons	921 (25)	359 (6)	852 (47)	n.s.
Clitemnestra rostrata				
Oncaea media	1491 (43)	2368 (88)	14995 (94)	C>A=B
Oncaea subtilis				
Ditrichocorycaeus anglicus	668 (4)	509 (19)	1510 (94)	C>A=B
Ditrichocorycaeus brehmi				

(continued on next page)

Table 1 (*continued*)

Taxon	Cluster A	Cluster B	Cluster C	SNK
Copepods				
Sapphirina angusta				
Copepod nauplii	2306 (64)	1114 (69)	1340 (76)	n.s.
Other holoplankton				
Noctiluca scillitans	0 (0)	398 (6)	97998 (100)	C>A=B
Flatworms				
Hydromedusae	682 (11)	749 (56)	344 (29)	B>A=C
Podocoryne spp.				
Solmundella bitentaculata				
Obelia spp.				
Liriope spp.				
Siphonophora Calicophora	336 (25)	1430 (100)	3229 (100)	C>B>A
Beroe cucumis				
Ctenophora larvae	68 (7)	979 (19)	368 (35)	n.s.
Pteropoda	103 (14)	64 (6)	0 (0)	n.s.
Tomopteris helgolandica	72 (4)	356 (19)	849 (18)	n.s.
Podon intermedius	1617 (36)	3919 (94)	1896 (59)	B>A=C
Evadne nordmanni	1094 (25)	2783 (94)	2049 (88)	C>A=B
Evadne spinifera	0 (0)	438 (19)	716 (6)	n.s.
Ostracoda	0 (0)	519 (31)	52 (12)	B>A=C
Nauplius of Euphausiacea				
Calyptopis larvae	772 (54)	544 (44)	493 (88)	n.s.
Furcilia larvae				
Meganyctiphanes norvegica	503 (68)	550 (81)	597 (76)	n.s.
Stylocheiron				
Tessarabrachion oculatum				
Thysanoesssa viana				
Mysidacea	322 (25)	46 (13)	426 (41)	C>A=B
Amphipoda				
Isopoda (Microniscus)				
Sagitta spp.	72 (7)	299 (25)	292 (88)	C>A=B
Salpa fusiformis	143 (21)	0 (0)	0 (0)	n.s.
Pegea coefedarata				
Doliolida	0 (0)	189 (13)	141 (18)	n.s.
Oikopleura fusiformis	1632 (68)	4750 (81)	2231 (76)	B>C
Oikopleura longicauda	3641 (50)	3913 (56)	2766 (47)	n.s.
Fritilaria borealis	0 (0)	0 (0)	609 (18)	n.s.
Fritilaria pelucida	1695 (7)	8903 (94)	7206 (71)	B=C>A
Brachiostoma lanceolatum	0 (0)	0 (0)	427 (71)	n.s.
Meroplankton				
Gastropoda larvae	733 (39)	740 (69)	682 (88)	n.s.
Bivalvia larvae	716 (4)	597 (31)	477 (41)	n.s.
Nemertea larvae				
Polychaeta larvae	586 (21)	372 (31)	465 (35)	n.s.
Ceriantharia larvae				
Ectprocta larvae				
Cirripedia larvae	5788 (71)	1081 (56)	558 (65)	n.s.
Decapoda larvae	265 (86)	503 (88)	434 (76)	n.s.
Echinodermata larvae	843 (43)	568 (56)	1092 (94)	C>A=B
Anchovies eggs				
Sardine eggs				
Fish eggs				
Fish larvae				

White spaces indicate species that were not included in the distance matrix. Comparison of variables between cluster groups (A, B, C) according to a multiple range SNK test (Note “>” significance ($p > 0.05$) difference, “=” and “n.s.” non-significance ($p > 0.05$) difference).

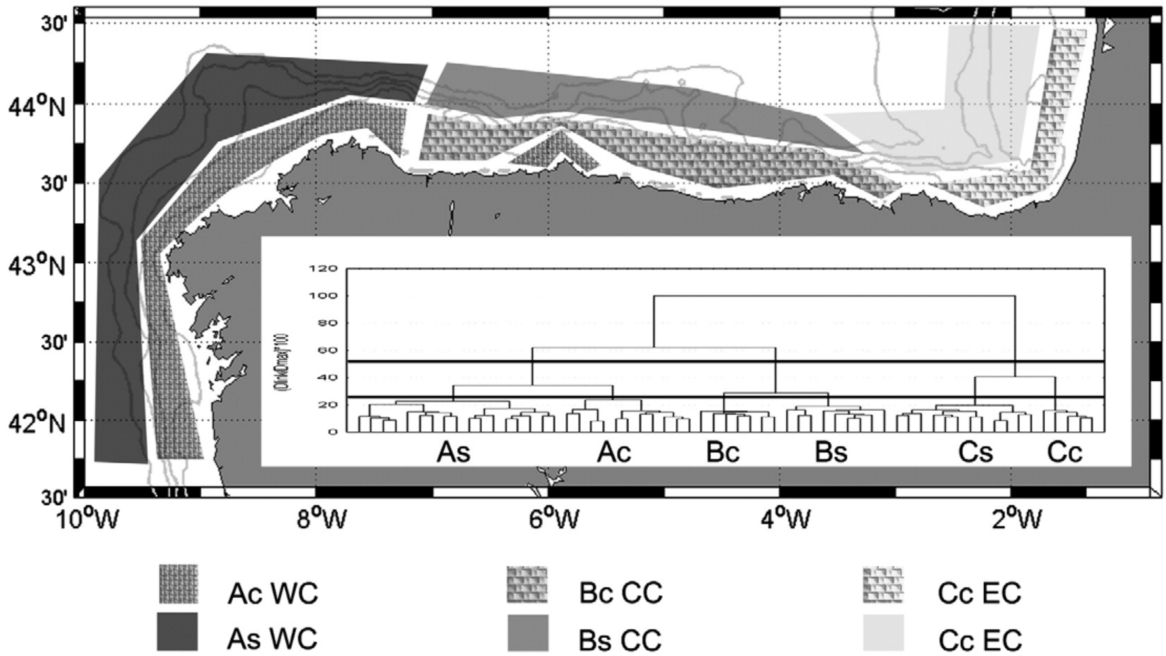


Fig. 7. Geographical distribution of station groups (A, B, and C, 'c' and 's' subscript refer to coastal or shelf station) defined by cluster analysis (insert graph) on mesozooplankton species composition. WC, CC and EC refer to the zonation based on hydrography.

(150 mg m^{-2}), total mesozooplankton biomass attained the highest values of the whole sampled area (around 140 mg m^{-3}).

Mesozooplankton abundance varied between $2.4 \cdot 10^4$ and $50 \cdot 10^4$ individuals m^{-2}. A total of 107 mesozooplankton taxa were found, of which 63 were retained for further analysis (Table 1). Holoplankton organisms are the major constituent of mesozooplankton taxa, despite the high relative abundance of meroplankton organisms (cirripedia, echinodermata and gastropoda larvae) in coastal areas.

Cluster analysis on the mesozooplankton species abundance matrix (log individuals m$^{-2}+1$) allowed us to discriminate three major (distance level 50%) groups of stations (Fig. 7, insert): cluster groups A, B and C (Table 1). These cluster groups matched the zonation based on hydrographic conditions. Group A corresponded with the WC region, characterized by the presence of the IPC; group B, with the transitional CC region; while group C related to the EC region, where colder and fresher water was found. The Mantel analysis of the relationship among the matrices that define the physical domains, the zooplankton clusters and the spatial structure are shown in Table 2. The simple Mantel correlations were highly significant ($p<0.001$) for all the possible pairs of matrices, although the highest correlation corresponded to the pair physical-mesozooplankton ($r=0.70$, $p<0.001$, $n=63$). However, when the effect of the common spatial structure is taken into account (partial Mantel correlations, Table 2), only the physical-mesozooplankton relationship remains highly significant ($r=0.56$, $p<0.001$, $n=63$).

In group A, *Paracalanus parvus* (24.4%), *Oithona helgolandica* (14.1%), *Acartia clausi* (13.7%), *Clausocalanus pergens* (7.8%), *Pseudocalanus elongatus* (2.3%), *Ctenocalanus vanus* (2.1%),and larva of Cirripedia (2.8%) were the dominant species. Group B share with group A these dominant species, but with different relative abundance (*A. clausi* 20.5%, *O. helgolandica* 18.8%, *P. parvus* 16.9%, *P. elongatus* 4.7%, *C. pergens* 3.6%) and also the distinctive relative high abundance of *Calanus helgolandicus* (2.1%), *C. arcuicornis* (2%), *C. lividus* (2.2%), larvaceans (*O. fusiformis* 2.4%, *O. longicauda* 1.9% and *F. pelucida* 4.5%) and cladocerans (*Evadne nordmanni* 1.4% and *Podon intermedius* 1.9%). Group C was defined by the

Table 2
Mantel analysis of the relationship between matrices representing physical variables, zooplankton distribution and space

	Space	Physical	Mesozooplankton
Space	–	0.57*	0.58*
Physical	0.27	–	0.70*
Mesozooplankton	0.31	0.56*	–

Above the diagonal: simple Mantel test statistics; below diagonal: partial Mantel statistics controlling for the effect of the third matrix. Asterisks indicate significance at the 0.01 α-level.

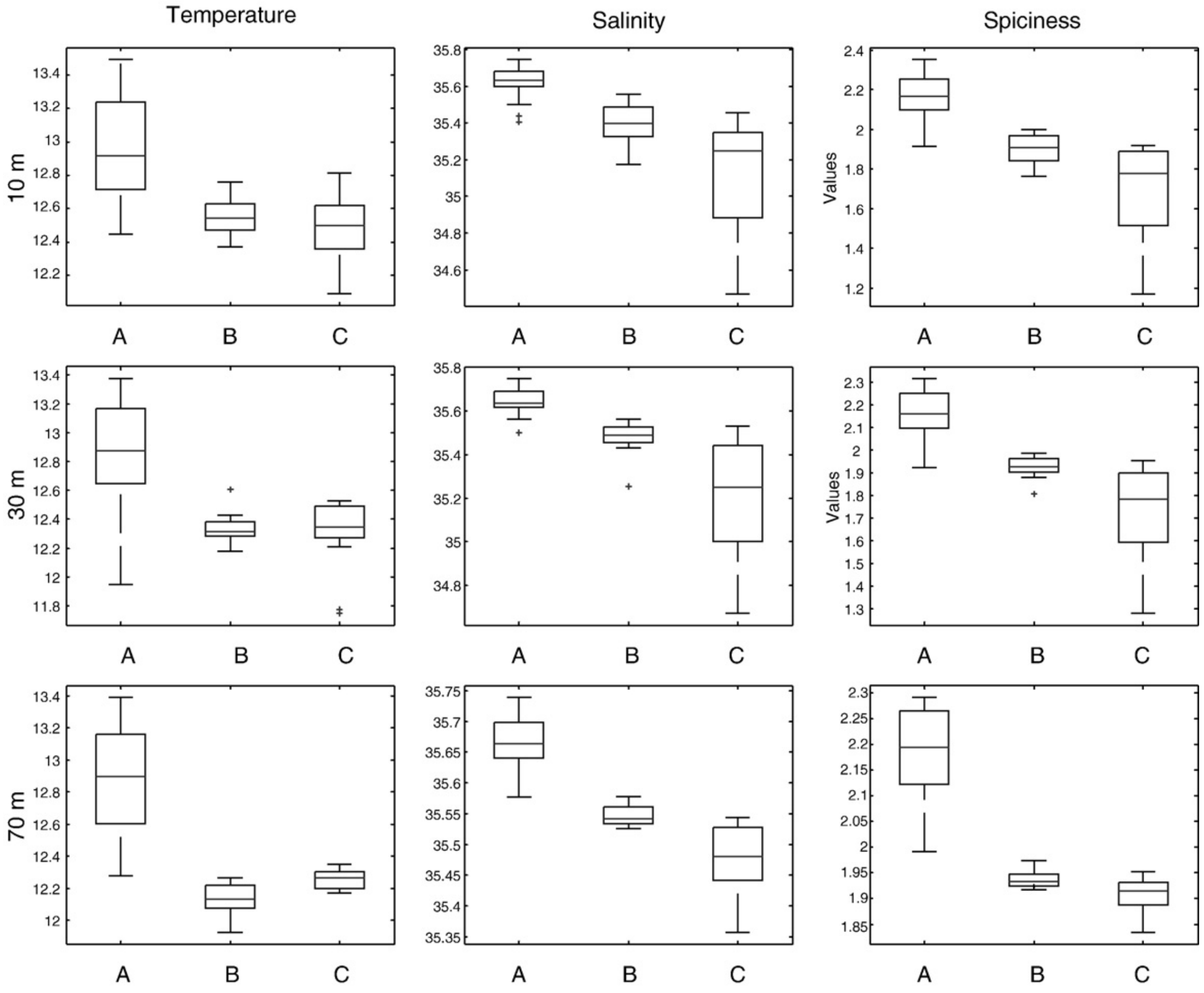


Fig. 8. Box and whiskers representation of temperature, salinity and spiciness at 10 m, 30 m and 70 for the groups of stations (A, B and C) obtained from the cluster analysis on mesozooplankton data. The box has lines at the lower quartile, median and upper quartile values and the whiskers represent 1.5* inter-quartile range.

dominance of *Noctiluca scintillans* (45%) coupled with relative high abundances of *O. helgolandica* (10.2%), *Oncaea media* (6.9%), *Temora longicornis* (3.60%), *Ditrichocorycaeus anglicus* (0.7%), and the presence of species as *P. parvus* (3.9%), *A. clausi* (3.3%)and *F. pelucida* (3.3%) (Table 1).

The distribution of values of the environmental variables (temperature, salinity and spiciness) for each of these groups is shown in Fig. 8. Groups differed significantly in temperature a 10 m ($F_{2,60}=25.089$; $p<0.001$), 30 m ($F_{2,59}=28.259$; $p<0.001$) and 70 m ($F_{2,40}=38.675$; $p<0.001$), which were ranked A>B=C by the post hoc SNK test. Salinities were significantly different a 10 m ($F_{2,60}=4\ 3.214$; $p<0.001$), 30 m ($F_{2,59}=47.637$; $p<0.001$) and 70 m ($F_{2,40}=73.229$; $p<0.001$), resulting in the rank A>B>C. Spiciness were also significantly different ($p<0.001$) among these three groups at 10 m, 30 m and 70 m ($F_{2,60}=54{,}292$; $F_{2,59}=55.246$;$F_{2,40}=72.043$), resulting in a rank at 10 m and 30 m A>B>C and at 70 m, A>B=C. In summary, the group A presented the highest values of temperature, salinity and spiciness at all the depths; group C presented the lowest values of salinity; while group B was characterized by temperature and spiciness equals to C (lower than A) and salinity with intermediate values between A and C.

Each of the cluster groups could be further sub-divided (distance level 25%, Fig. 7 insert) in two sub-groups that separate coastal and shelf stations. The sub-division of each of the major groups in a coastal and shelf sub-groups ('c' and 's' respectively) reflects the higher species densities found in the shelf that environment in the coastal. Thus, the costal sub-groups showed higher relative abundance of neritic species such as *A. clausi*, *Evadne nordmanni*, *P. intermedius* and meroplankton larvae (e.g. Cirripedia), while the shelf sub-groups

Table 3
Mean and standard error, *F* of the ANOVA test and SNK post hoc analysis

Variable	Depth	A_s	A_c	B_s	B_c	C_s	C_c	Total	*F*	SNK
Temperature	10	13.06±0.07	12.79±0.08	12.51±0.03	12.57±0.04	12.53±0.05	12.41±0.09	12.72±0.04	25.09	$A_s > A_c > B_s = B_c = C_s = C_c$
	30	12.99±0.08	12.68±0.11	12.33±0.03	12.34±0.04	12.37±0.03	12.14±0.16	12.57±0.05	28.26	$A_s > A_c > B_s = B_c = C_s = C_c$
Salinity	10	35.67±0.01	35.55±0.02	35.46±0.03	35.33±0.04	35.28±0.05	34.73±0.09	35.42±0.04	43.21	$A_s > A_c = B_s > B_c = C_s > C_c$
	30	35.68±0.01	35.59±0.01	35.50±0.01	35.46±0.03	35.34±0.04	34.87±0.07	35.48±0.03	47.64	$A_s = A_c > B_s = B_c > C_s > C_c$
Chl *a*	Inegrated 50 m	103±8	93±13	109±14	49±5	91±10	82±9	90±5	13.37	–

Note: "$>$" significance ($p > 0.05$) difference, "$=$" non-significance ($p > 0.05$) difference) for the different clusters using temperature, salinity and chlorophyll *a* variables.

Table 4
Comparison of variables between cluster groups according to a multiple range SNK test

Taxon	SNK test
Paracalanus parvus	$A_s = B_s > A_c = B_c > C_s = C_c$
Acartia clausi	$A_c = B_c = B_s > A_s = C_s = C_c$
Centropages chierchiae	$A_c = A_s > B_s = B_c > C_s = C_c$
Pseudocalanus elongatus	$A_c = B_s = B_c > A_s = C_s = C_c$
Oithona helgolandica	$B_s > A_s > A_c = C_s > B_c = C_c$
Temora longicornis	$C_c > C_s > A_c > A_s = B_c = B_s$
Noctiluca scintillans	$C_c = C_s > A_s = A_c = B_s = B_c$
Oncaea media	$C_c = C_s > A_s = A_c = B_s = B_c$
Ditrichocorycaeus anglicus	$C_c > C_s = A_s = A_c = B_s = B_c$
Euterpina acutifrons	$C_c > C_s = B_s = B_c = A_s = A_c$

Note: "$>$" significance ($p > 0.05$) difference. "$=$" non-significance ($p > 0.05$) difference.

showed the presence of oceanic or mesopelagic indicator species, such as *Mesocalanus tenuicornis*, *Metridia lucens*, *Pleuromamma gracilis* and *Diaxis hibernica*. The sub-groups presented significantly differences between the mean values of temperature, salinity and spiciness for the different depths (Table 3). Thus, sub-group Ac had low values of surface (10 m) temperature and salinity than sub-group As, but presented the same values at 30 m. Sub-group Bc did not present significantly differences of temperature with Bs at any of the analyzed depths. Salinity at the surface was always lower in the 'coastal' (Ac, Bc, Cc) than in the 'shelf' sub-groups (As, Bs, Cs. In the case of the Cc, the values of temperature were equal to those of Cs, while salinity in the coast was lower than in the shelf at 10 and 30 m depth.

At the species level, some of them characterize the aforesaid spatial distribution (Table 4). Thus for example, *N. scillitans* and *O. media* were characteristic species of sub-groups Cs and Cc, stressing the singularity of the group defined by the river plume from the Adour, while *D. anglicus* and *E. acutifrons* characterized the coastal environment of group C. Besides, *T. longicornis* characterized areas influenced by river discharges corresponding to sub-groups Cc, Cs and Bc, while on the contrary *P. parvus* showed higher abundances on the shelf sub-groups of A and B than in the coastal, and these were higher than in the C sub-groups. *C. chierchiae* decreased significantly from group A to C. Abundances of *P. elongatus* and *A. clausi* were significantly different in the coastal area of the A and B groups and in the shelf of the group B (Table 4).

4. Discussion

The study showed the spatial coherence between the main hydrographic features off the N-NW Iberian shelf and the composition of the mesozooplankton community in spring. The main hydrographic features that modulate the regional scale distribution of thermohaline properties in this area during the spring of 2004 were the progression of the seasonal thermocline, the intrusion of $ENACW_{st}$ into the Cantabrian Sea advected by the IPC, and the presence of river plumes generated by enhanced river flows due to spring precipitations and melting of the winter snow. The areas of distribution of the 3 groups obtained by the cluster on the mesozooplankton species composition matched the physical zonation. The group A was found in the area of influence of the IPC (WC), the group C was related to the Adour River plume (EC). Between these two distinctive areas, group B corresponded with the Central Cantabrian (CC) Sea region, which is a transition area influenced by both the IPC and the plume from the Adour but also by local river discharges from small Cantabrian rivers. The Mantel analysis supported a causal model according to which the distribution of zooplankton is controlled by the hydrographic environment, and not by the common spatial structure of these two variables (Legendre, 1993).

Biomass of mesozooplankton was relatively high in relation to previous studies (Valdés et al., 1991; Cabal and Alvarez-Marqués, 1995; Villate et al., 2004), and was dominated by small-sized organism. These high values of biomass of mesozooplankton in the small size fraction, the low values of phytoplankton biomass and the mix of the water column (MLD), show a situation of post-bloom in the study area during the cruise *PELACUS 0404*, except in the areas where chlorophyll *a* concentration was high (around 5 mg m^{-3}) localized in the southernmost stations, in the across-shelf front located in the EC region and in the proximity of the frontal area that separates the WC and the CC regions. These maximum were related to continental freshwater inputs, which in turn influence local currents and salinity patterns allowing a stratification of the water columns that produces a bloom of phytoplankton, and to frontal systems linked to intrusions of saline waters. These types of processes were described in previous works in this area (Fernández and Bode, 1991, 1994; Fernández et al., 1993).

Small sized copepods (200–500 µm) were very abundant in the area of study, (Fig. 6A and Table 1). This size fraction was constituted in the WC and CC region mainly by widespread copepod species such as *O. helgolandica*, *P. parvus* and *A. clausi*, while in the EC region were more abundant *O. media* and *O. helgolandica*. Species such as *A. clausi*, *O. helgolandica* and *O. media* are linked to coastal spring bloom (Turner and Granelli, 1992; Atkinson and Shreeve, 1995), but could also feed on small phytoplankton and they were present in great number. Head et al. (2002) also found that communities dominated by *Oithona* spp. and *Oncaea* spp. wherever flagellates and picoplankton accounted for 86% of phytoplankton biomass. *A. clausi* showed higher values of abundance in coastal areas than in the shelf areas, and could be a characteristic species of the environment with a wide range of variation in salinity (Rodriguez et al., 1985; Paffenhöfer and Stearns, 1988).). Opportunistic species (such as *T. stylifera*, *O. media* and *D. anglicus*) have advantage if the environment changes towards stratification conditions whereas other species characteristic of cold waters and blooms of phytoplankton formed by large-sized cells are in clear disadvantage if this type of change occurs.

Large-sized copepod Calanidae (*C. helgolandicus* and *C carinatus*) linked to high phytoplankton concentrations were more abundant in the CC region. These species are considered residents in the northern Iberian shelf with two types of overwintering strategies (diapause at deep waters and reside in the coast waters during the winter) (Cabal, 1993) and that can take advantage of spring blooms in temperate latitudes (Laabir et al., 1998; Weikert et al., 2001; Bonnet et al., 2005), responding with high reproductive activity. Mesozooplankton composition are also affected by topography, the shelf of the N-NW Iberian Peninsula is very narrow, so shelf edge or even oceanic species may penetrates into coastal area and mix with neritic species. In fact the near shore presence of species with deep and oceanic affinity has been reported in several studies (Valdés et al., 1991; Cabal, 1993; Villate et al., 2004). Thus the penetration of such water masses might account for the occasional occurrence of species as other copepod *M. lucens*, *P. gracilis* and *D hibernica* in the coastal area.

The influence of the Poleward current in the NW Iberian shelf has been investigated in relation to the plankton communities distribution (Botas et al., 1988; Fernández et al., 1993; Fernández and Bode, 1994; Poulet et al., 1996; Bode et al., 2002), or fish populations (Sánchez and Gil, 2000). Besides, related to intrusions of IPC waters have been described the presence of subtropical species of phytoplankton (Fernández and Bode, 1994) and copepods (Cabal, 1993) in the central Cantabrian sea. In the present study, several species that were not very abundant in the samples, but its relative distribution concerns them an indicator character. *Clausocalanus farrani*, *Phaenna spinifera* and *Calocalanus contractus*, only were collected in the WC region related to IPC current and in the transition region CC, and not in the EC domain. These copepods are considered tropical/subtropical species (Frost and Flemiger, 1968; Bradford-Grieve et al., 1999), which would likely prefer the warm, saline poleward current that was found here. *Salpa fusiformis* only was collected in the samples belonging to the WC region, and the relatively high temperature and salinity observed in the IPC would also favour this species because it seems to have an affinity for warm saline water (Lavaniegos et al., 2002).

On the contrary, *N. scintillans*, *Scolecithrix ovata*, and *Temora stylifera* was restricted to EC domain and in the coastal area of CC region related saline stratification in the upper meters of the water column, derived from the input of freshwater from Adour River and Cantabrian rivers respectively. In this study *N. scintillans* average abundance ranged from $89 \cdot 10^3$ to $323 \cdot 10^3$ cell m^{-3}, with maximum abundances in the EC region. These dense swarms of *N. scintillans* are comparable to others that reported in the literature (Le Fèvre and Grall, 1970; Sekiguchi and Kato, 1976; Daan, 1987; Quevedo et al., 1999), related to water column stability and under calm conditions (Lefèvre, 1986; Gaines and Elbrachter, 1987; Huang and Qi, 1997). The predation of *N. scintillans* on eggs of broadcast spawning copepods, such as, *Acartia* and *Temora* suggesting that this mechanism could be highly relevant to population dynamics of neritic mesozooplankton. (Kimor, 1979; Daan, 1987; Quevedo et al., 1999), and could be one of the cause of the lower abundance of species linked to lower salinity in the EC domain, such as *A. clausi*.

T. stylifera is considered in the northern Iberian shelf as a summer–autumn species related to water column stratification (Valdés et al., 2007) and it is a copepod species typical of subtropical and Mediterranean areas (Razouls, 1995), however *T. stylifera* was not collected in the WC region related to intrusions of ENACst, and it was present in the EC region related to the saline stratification produced from the discharges of the river plume.

5. Conclusions

Three different hydrographic zones along the shelf were obtained according to the distribution of thermohaline properties. These zones are separated by neat frontal areas and presented significantly different thermohaline characteristics.

Three major groups of stations were obtained according to the composition of mesozooplankton species. These major zonation could be further subdivided to take into account the difference between coastal and shelf stations.

There was a highly significant spatial correlation (Mantel test) between the hydrographic zones and the distribution of mesozooplankton species assemblages. The resulting causal model is indicative of the hydrographic control exerted on the distribution of mesozooplankton.

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