Mesoscale coupling between spatial distribution of planktonic cnidarians and hydrographic features along the Galician Coast (Northwestern Iberian Peninsula)*

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SUMMARY: Special circumstances in the hydrodynamic pattern of water masses off the western Iberian Peninsula may create variations in the overall distribution pattern of planktonic cnidarians, leading to a greater degree of heterogeneity. An example of this was observed along the coasts of Galicia during October 1977, when greater concentrations of individuals were detected at some stations further from the coast, even though the major number of the species collected were meroplanktonic. These concentrations were accompanied by a progressive increase in individuals size of the most abundant species. This observed distribution pattern was correlated to a heterogeneous hydrographic pattern which gave rise to the transport of organisms towards specific zones.

Key words: Pelagic cnidarians, spatial distribution, North West Iberian Penninsula.

RESUMEN: ACOPLAMIENTO A MESOSCALA ENTRE LA DISTRIBUCIÓN ESPACIAL DE LOS CNIDARIOS PLANCTÓNICOS Y LAS CARACTERÍSTICAS HIDROGRÁFICAS A LO LARGO DE LAS COSTAS DE GALICIA (NOROESTE DE LA PENÍNSULA IBÉRICA). — Circunstancias especiales que afectan el régimen hidrográfico de la costa noroeste de la Península Ibérica pueden provocar cambios importantes en la pauta de distribución general de las poblaciones de cnidarios planctónicos en el área y dar lugar a un alto grado de heterogeneidad espacial. Un ejemplo de lo descrito se observó durante el mes de octubre de 1977 a lo largo de las costas gallegas donde se detectaron concentraciones elevadas de individuos en estaciones alejadas de la costa. Al mismo tiempo que aumentó la concentración de individuos también se incrementó el tamaño medio de los mismos, especialmente en las especies más abundantes. El grado de heterogeneidad espacial descrito se podía explicar en base al nivel de heterogeneidad hidrográfico observado durante el período estudiado y que generaba un posible transporte, de una manera inusual, de algunas especies hacia zonas alejadas de la costa.

Palabras clave: Cnidarios pelágicos, distribución espacial, noroeste de la Península Ibérica.

INTRODUCTION

Recent reviews attribute the control of spatial heterogeneity of zooplankton to hydrodynamic factors, and the regulation of temporal variability to biological factors (e. g. HAURY *et al.*, 1978; DENMAN and POWELL, 1984). Hydrodynamic mechanisms such as currents running parallel to the coast, displacements of water masses and any other kind of advective mesoscale transport often determine the spatial distribution of zooplankton and the persistence of their distribution pattern. Gelatinous zooplankton are, in particular, abundant in neritic waters and will be quite easily affected by transport processes.

Planktonic cnidarians are often found at high concentrations in coastal areas due to their voracity and rapid growth capacity (e. g. ZELICKMAN, 1972; ALLDREDGE, 1983). These coastal populations may be

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dominated by species of neritic siphonophores or hydrozoan medusae (e.g. VANNUCCI, 1963; GILI *et al.*, 1988). Abundance of these groups is seasonal (e. g. BODO *et al.*, 1965; GILI *et al.*, 1987), and dependent upon suitable temperature and productivity conditions which trigger the species' reproductive processes (RAYMONT, 1983).

The abundance of individual planktonic cnidarians usually decreases gradually with distance from the shore while species diversity changes little (e. g. FURNESTIN, 1957; BERHAUT, 1969; VANNUCCI and NAVAS, 1973; MACKIE *et al.*, 1987; GILI *et al.*, 1988). This general pattern can be drastically altered by local hydrodynamic features which transport littoral species to zones far from, or along an axis parallel to, the coast. Both hydrodynamic processes affect the recruitment of meroplanktonic species, even though the areas where they tend to concentrate coincide with those of maximum production in the studied area (ESTRADA, 1984).

The purpose of this work is to ascertain whether the planktonic cnidarians studied respond to the hydrographic regime which occurred in the Galician coast during October 1977 as a consequence of a peculiar hydrodinamic situation (FRAGA *et al.*, 1982).

HYDROGRAPHIC CONFIGURATION

A heterogeneous hydrographic pattern existed during the month of October 1977 off the coasts of Galicia (FRAGA, 1981; FRAGA *et al.*, 1982). This general pattern, during late summer and early autumm, was characterized by the North-Atlantic anticyclonic gyre which has its northern latitudinal limit on the north-western coast of the Iberian Peninsula (Fig. 1). A number of upwelling phenomena are associated with this anticyclone, one of which commonly occurs on the coast of Galicia. Furthermore, the continental waters out flows from the Rías Baixas in this area were considerable at the time of year when the study was carried out, even though greatest during winter and spring. These three phenomena; distribution of water masses, upwelling regime and runoff, created temperature and chlophyll distributions (ESTRADA, 1984) which are summarized in figures 2 and 3.

The North Atlantic Central Water (NACW) flows in a northerly direction at the surface along the western coast (Fig. 1), while subsurface (below 50 m depth) water flows towards the south. Along the north coast both the surface and the subsurface Central Water of the Bay of Biscay (CWGB) flow in a southwesterly direction. Moreover, during the month studied the Rías Baixas poured a large quantity of continental water into the sea along the west coast. During the summer the phenomenon is reversed, because upwelled shelf waters penetrate into the Rías during this season.

MATERIALS AND METHODS

The study is based on plankton hauls taken between October 7 and 28 1977, during the Galicia IV Cruise, in the area within 45° N 7° W and 41° N 11° W (Fig. 1). Thirty-nine hauls were carried out, either from 200 m to the surface, or from the sea bottom to the surface in shallower water, using paired 60 cm mouth diameter, 500 μm mesh size Bongo-type nets. The dots in figure 4 shows the location of the hauls.

All the species and individuals of jellyfish and siphonophores caught were identified and reported as number of individuals per 100 m^3, based on the theoretical volume filtered by the nets. Plankton samples were collected over a 24-hours period but zooplankton samples were made mainly at night. The sizes of the most abundant species of hydromedusae and siphonophores were measured under the microscope considering the length of the nectophores of siphonophores and the diameter of the umbrella of hydromedusae.

Surface temperature readings and samples for salinity and chlorophyll *a* (by fluorometry) were taken from the hydrographic casts (ESTRADA, 1984). Zooplankton displacement volume (cm^3 100 m^{-3}) was measured by settling in accordance with OMORI and IKEDA (1984). Simplified and objective representation of the general distribution pattern of the cnidarian population in the area was obtained by principal component analysis (PCA). The analysis was based on the matrix of abundance correlations of the species and the sample scores were plotted on the station map for interpretation of factors. The value of such analysis for describing zooplankton distributions has been discussed by, e.g. IBANEZ (1976).

RESULTS

Sixteen species of hydromedusae and seven species of siphonophores were collected (Table 1). Among the hydromedusae, meroplanktonic species accounted for over 90 % of the total number of individuals, and all species had a markedly coastal distri-

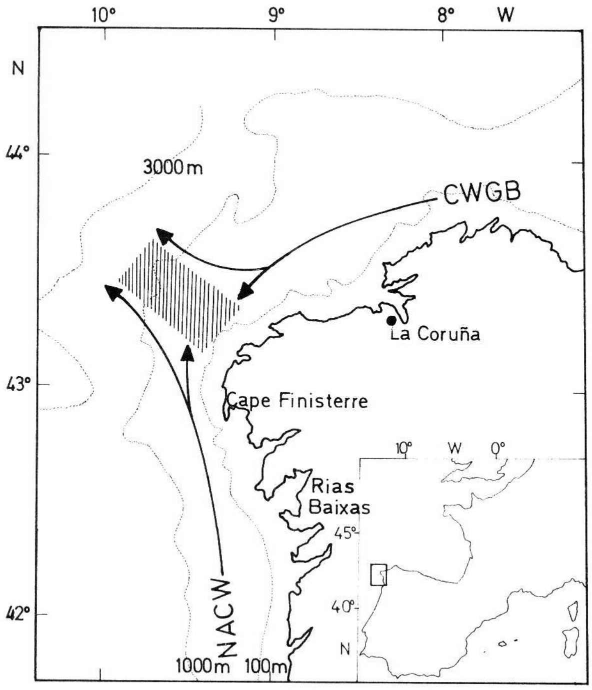

FIG. 1. — Scheme of surface circulation of central water between 100 and 400 m depth. The shaded area is the zone of lateral contact between NACW (North Atlantic Central Water) and the CWGB (Central Water of the Gulf of Biscay). Redrawn from FRAGA *et. al.* (1982).

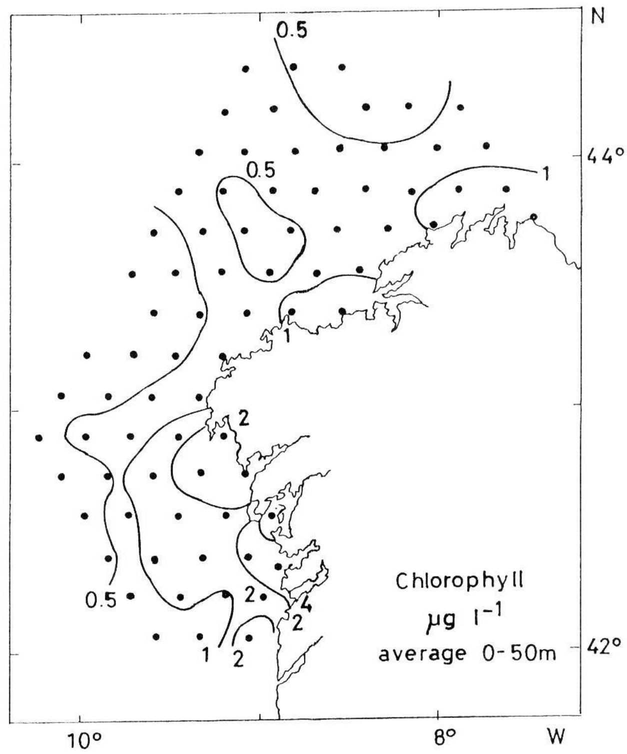

FIG. 3. — Weighted average of Chlorophyll *a* concentration in a layer from 0 to 50 m depth. Redrawn from ESTRADA (1984).

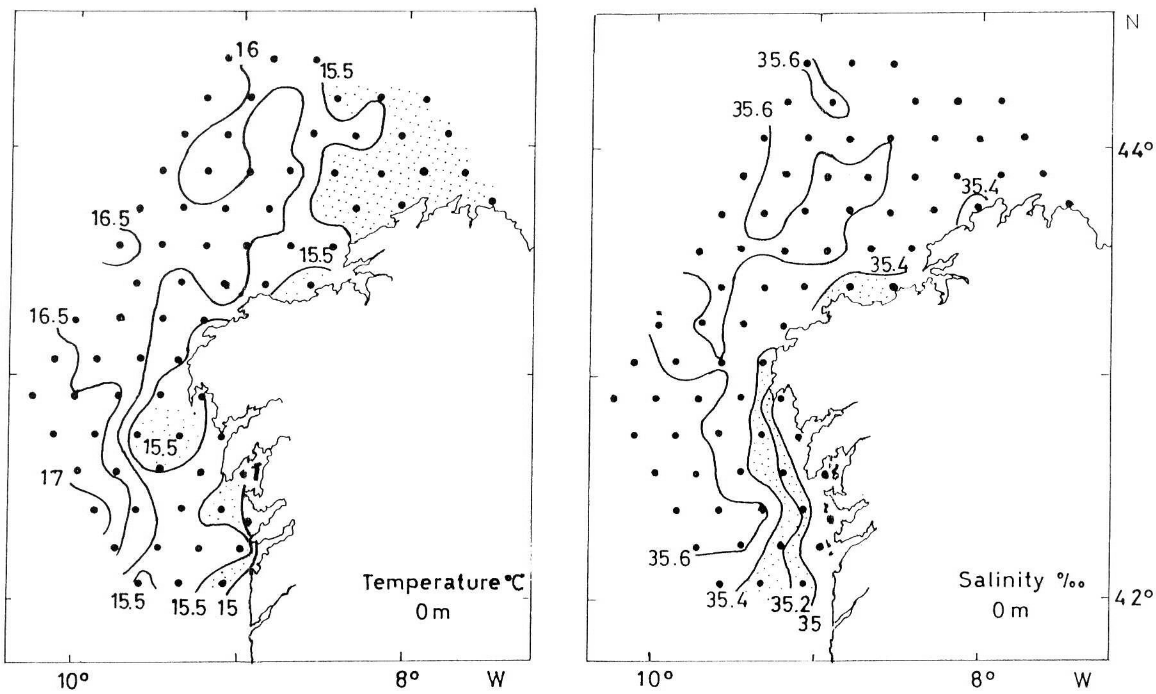

FIG. 2. — Surface Salinity and Temperature during the Galicia IV cruise (October, 1977). Redrawn from ESTRADA (1984).

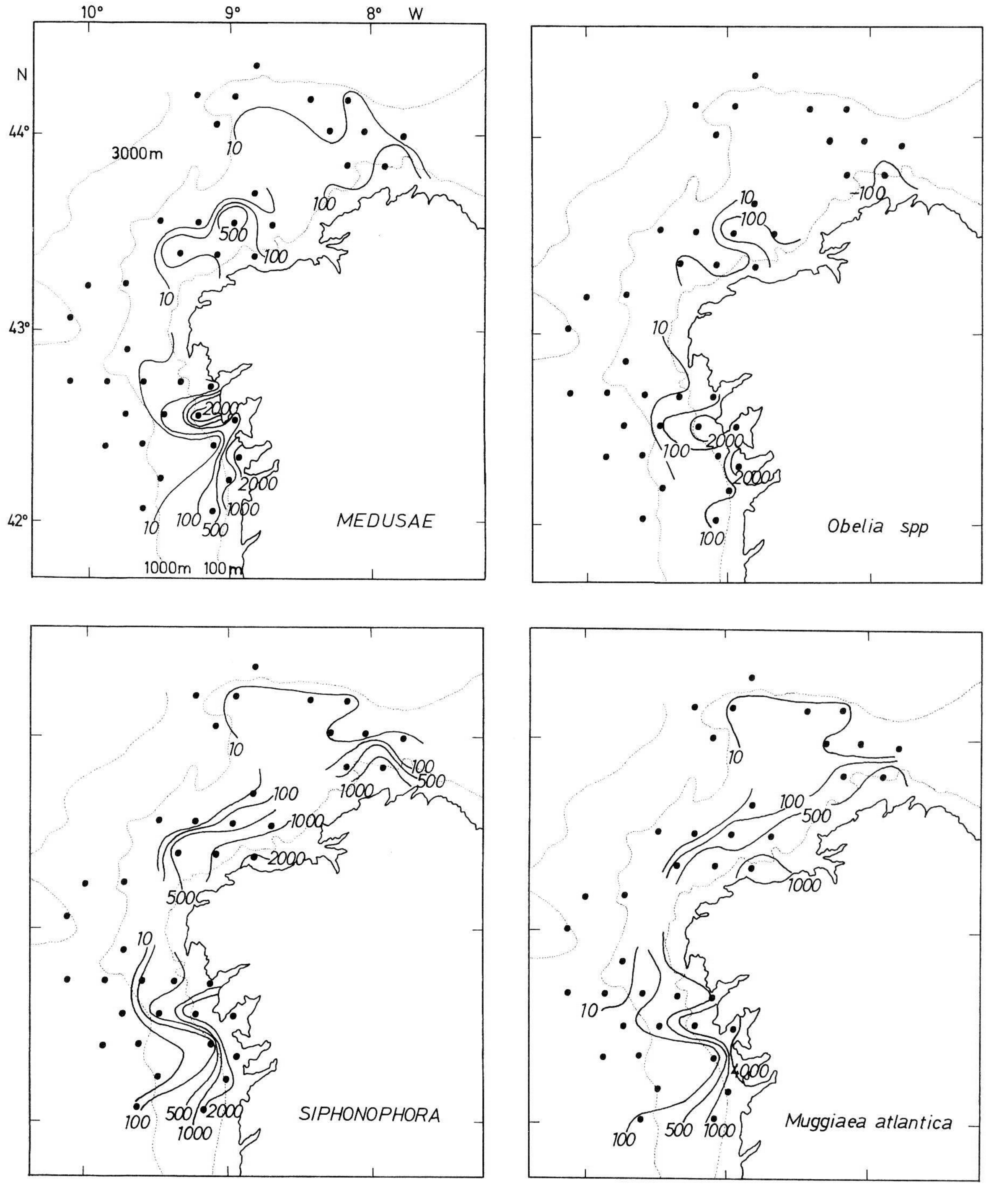

FIG. 4. — Distribution of total number of medusae and siphonophores per 100 m^3 and the most abundant species of each group.

bution. The hydromedusa *Obelia spp. and the siphonophore Muggiaea atlantica* are the most abundant species and their spatial distribution represents the general distribution pattern followed by the total individuals in each group (Fig. 4). A progressive decrease in the number of individuals towards the open sea along the whole coast of Galicia was observed but this general pattern is altered in three zones in the area studied. The most important variation within the general trend can be seen at some stations situated slightly toward the south and the north of the mouth of the Rías Baixas (SW coast). In this zones, some

TABLE 1. — Species of hydromedusae and siphonophores collected during Galicia IV cruise. Total *(n)* and mean *(x)* number of individuals 100 m^{-3} of each species were calculated considering the number of samples *(r)* in which they occurred from a total of 40 samples.

Species	*n*	*x*	*r*
HYDROMEDUSAE			
Velella velella (Linné 1758)	1	1	1
Bougainvillia ramosa (Van Beneden 1844)	1	1	1
Podocoryne hartlaubi Neppi and Stiasny 1911	1	1	1
Euphysa aurata Forbes 1841	1	1	1
Sarsia tubulosa (M. Sars 1835)	5	2.5	2
Amphinema dinema (Péron and Lesueur 1809)	16	3.2	5
Neoturris pileata (Forskal 1775)	5	1.2	4
Leuckartiara octona (Fleming 1832)	1	1	1
Clytia hemisphaerica (Linné 1767)	1427	75.1	19
Obelia spp.	6502	361.2	18
Eutima gracilis (Forbes and Goodsir 1853)	3	1.5	2
Eirene viridula (Perón and Lesueur, 1809)	3	3	1
Laodicea undulata (Forbes and Goodsir 1853)	46	4.2	11
Aglaura hemistoma Perón and Lesueur 1810	54	9	6
Liriope tetraphylla (Chamisso and Eysenhardt 1821)	618	25.7	24
Solmundella bitentaculata (Quoy and Gaimard 1833)	30	2.7	11
SIPHONOPHORES			
Agalma okeni Eschscholtz 1825	5	1	5
Rosacea plicata Quoy and Gaimard 1827	5	1	5
Sphaeronectes gracilis (Claus 1873)	1	1	1
Muggiaea atlantica Cunningham 1892	17614	550.4	32
Muggiaea kochi (Will 1844)	6876	229.2	30
Chelophyes appendiculata (Eschscholtz 1829)	1	1	1
Lensia conoidea (Keferstein and Ehlers 1860)	16	1.2	13

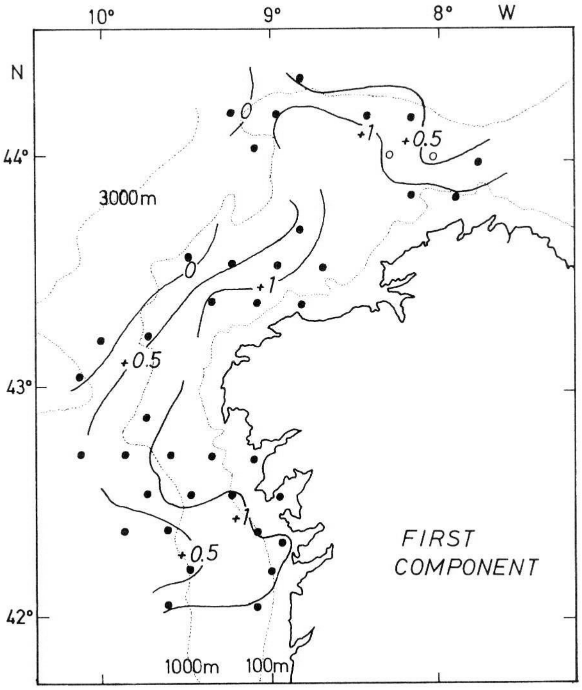

FIG. 5. — Distribution of the f-scores for the first axis in the principal component analysis.

platform stations had similar concentrations of individuals to those detected in stations near the mouth of the Rías.

On the NW coast, especially off La Coruña (Fig. 4), the relatively high concentrations extend more seaward than elsewhere. Furthermore, in the case of some stations situated even further (50 miles) from the coast, isolated individuals of certain meroplanktonic species such as *Clytia hemisphaerica* were observed. Therefore, the aforementioned trend of concentration of individuals in stations close to the coast cannot be applied to the area as a whole. The result is a rather heterogeneous pattern near the coast which is also repeated in some zones further from the coast.

The general pattern of spatial distribution of the total planktonic cnidarian population can be obser-

TABLE 2. — Spearman Rank Correlation between the first factor of the principal component analysis *f*-scores for cnidarian species and the surface Temperature, surface Salinity, Chlorophyll *a* (average of 0-50 m), Zooplankton biomass (displacement volume), number of individuals and species of cnidarian (hydromedusa and siphonophora) collected. Only the significant correlations are shown, and probability is indicated by: $^{**}P \geq 0.99$; or $^{*}P \geq 0.95$.

	PCA 1 axis	*Temperature*	*Salinity*	*Chlorophyll*	*Zooplankton biomass*	*Number species*	*Number individuals*
PCA 1 axis	1						
Temperature	−0.36*	1					
Salinity	−0.43**	0.82**	1				
Chlorophyll *a*	0.44**	−0.52**	−0.61**	1			
Zooplankton biomass	0.44**	−0.42**	−0.36*	0.34**	1		
Number of species	0.56**	−0.56**	−0.66**	0.43**	0.45**	1	
Number of individuals	0.65**	−0.69**	−0.79**	0.59**	0.53**	0.84**	1

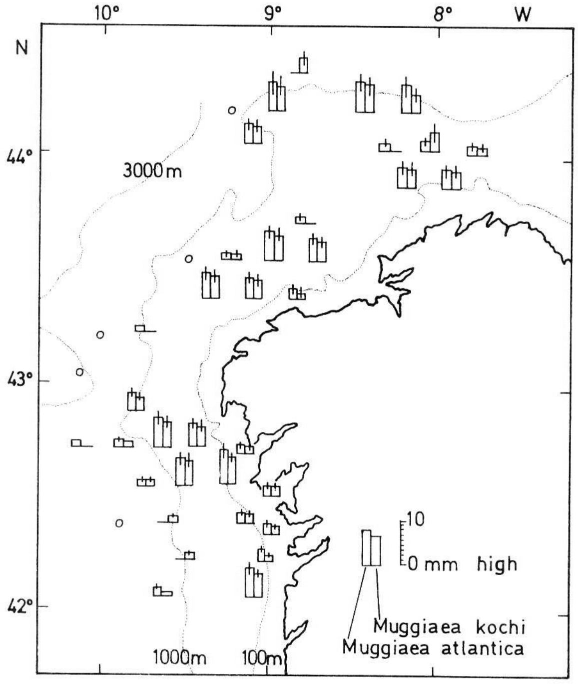

FIG. 6. — Distribution of the total zooplankton biomass (= displacement volume, cm^3 100 m^{-3}) during October 1977.

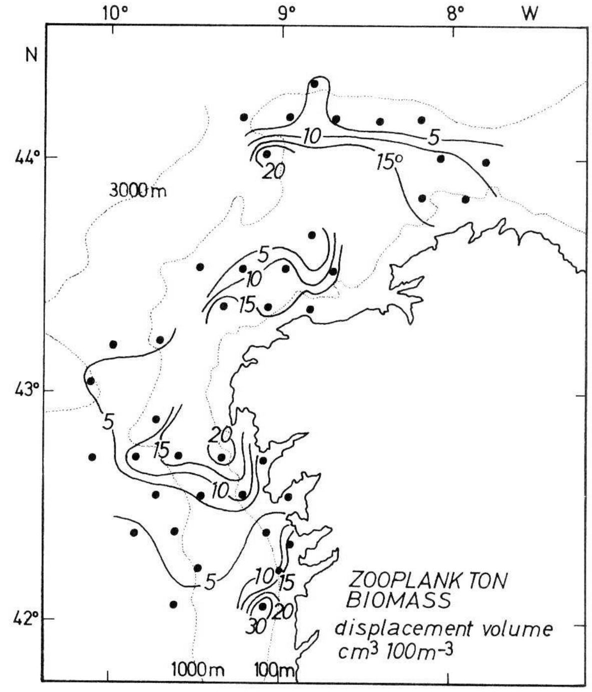

FIG. 8. — Distribution of individual sizes of the most abundant species of siphonophora. Vertical bars represent standard deviation and circles represent stations without specimens.

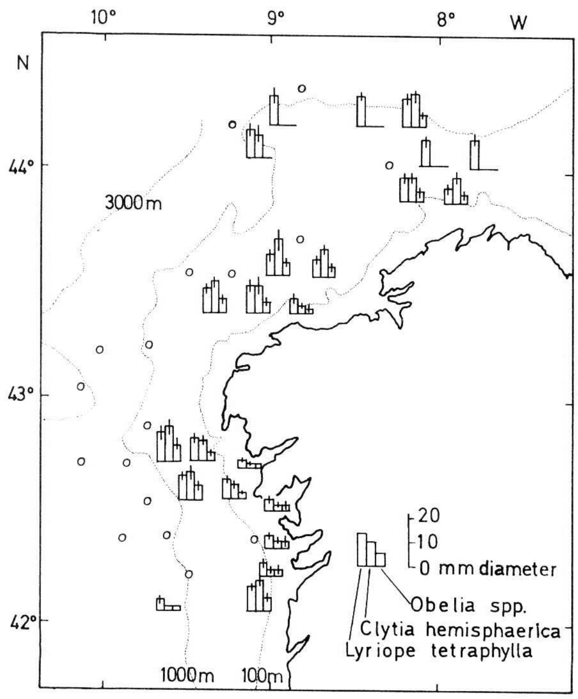

FIG. 7. — Distribution of individual sizes of the most abundant species of medusae. Vertical bars represent standard deviation and circles represent stations without specimens.

ved by plotting on the station map the scores of the first factor of the PCA (which accounts for over 60 % of the total variance) (Fig. 5). Positive values are found in coastal areas, while the negative values are always found far from the coast (Fig. 5).

The positive values in the first factor of the PCA correspond with the highest values of individual concentrations and the major number of species, whereas the negative values correspond with low concentrations of individuals. The spatial distribution pattern of Cnidarian species follow the patterns observed in the area for the physical factors and the total zooplankton biomass (Fig. 6). This last assertion can be corroborated by the high correlation observed between the first PCA factor and the different variables (see Table 2).

Considering the spatial distribution of various sizes of the three most common hydromedusae (*Obelia* spp., *Clytia hemisphaerica* and *Liriope tetraphylla*), the largest individuals of each species are found at stations farther away from the coast (Fig. 7). Note also the presence of some large individuals farthest from the coast in the NW zone. This pattern of increase in the size of individuals belonging to coastal species towards the open sea is also observed in some zones for the two most abundant siphonophores (*Muggiaea atlantica* and *M. kochi;* Fig. 8).

DISCUSSION

The spatial heterogeneity of planktonic cnidarians in our study area can be largely explained by hydrodynamic patterns. Mesoscale hydrodynamic mechanisms can have a marked effect on zooplanktonic populations (e. g. ALLDREDGE and HAMNER, 1980; PUGH and BOXSHALL, 1984). The generally accepted opinion is that the accumulation of many zooplankton in specific zones cannot be explained without considering the hydrodynamic mechanism that generates them (MACKAS *et al.*, 1985). In fact, the observed distribution patterns on the coast of Galicia during October 1977 would be incomprehensible if we did not take into consideration the distribution on the same scale of water masses.

The surface current that flows in a northernly direction parallel to the coast probably transports meroplanktonic individuals from the Rías Baixas area that are carried seaward by the continental waters, north-west towards the zone off Cape Finisterre. In contrast, towards the south of the area studied some concentrations of individuals have also been observed; these were probably transported further south by a process of advection caused by the subsurface current that flows southwards (FRAGA *et al.*, 1982), from the Rías Baixas.

In the NW zone, important concentrations of individuals were collected at stations at a considerable distance from the coast. In this case it seems to be the current east from the Bay of Biscay that caused the transport.

The high concentration of hydromedusae and siphonophores south of Cape Finisterre may be caused by the northward advection of these meroplanktonic organisms which have intense recruitment in the Rías or close to the coast. At the same time, in this zone there is a less intense continuation of the effects of the upwelling which occurs during late summer and early autumn (FRAGA, 1981). Moreover, in this zone a major accumulation of phytoplankton (ESTRADA, 1984) and zooplankton biomass (MARTÍN, 1982 and Fig. 6) has been observed.

Individuals of the most abundant species increase in size as they are transported offshore (Figs. 7, 8). This information leads one to conclude that these species are carried by a water mass that is sufficiently productive in itself so that they are able to feed and grow. Nevertheless, few individuals reach offshore stations which means that the mortality of the species is high during their drift. The two collected species of the genus *Muggiaea* exemplify the same trend in relation to their size distribution. One point worthy of note is that these two species, *M. atlantica* and *M. kochi,* live together in the area studied, in similar numbers, in contrast to the situations described in the Atlantic (RUSSELL, 1934) and in the Mediterranean (RIERA *et al.*, 1986) where the two species are mutually exclusive in space and time.

Transport towards the open sea can diminish the recruitment capacity of meroplanktonic species as the larvae are removed from suitable benthic habitats. Although some authors indicate that meroplanktonic species such as *Clytia hemisphaerica* have long enough life cycles to allow them to travel considerable distances and then return to their place of origin (VANNUCCI and NAVAS, 1973; MILLS, 1987), a lot still remains to be learned about this kind of process. Thus, in hydrodynamic situations such as the one described in the studied area, the probably high mortality can be compensated, in some species, by a high production rate such as observed in *Obelia spp.* (BODO *et al.*, 1965; BERHAUT, 1969). On the other hand, this meroplanktonic species has several generations through the year. Probably when lots of larvae or medusae are produced during periods when offshore transport does not occur, the survival of species is guaranteed. Other species such as *Liriope tetraphylla* tends to occur near the coast in areas of upwelling (FURNESTIN, 1957) since it is a holoplanktonic species.

The passive transport, such as the one described for medusae and siphonophora, which give rise to a heterogeneous spatial distribution pattern also seems to occur in other zooplanktonic organisms. The concentrations of cnidarians observed both to the south and to the north of the area studied respectively, coincide with the accumulation of cells of phytoplankton (ESTRADA, 1984), of other zooplankton organisms such as chaetognaths (ANDRÉU, 1982), decapod larvae (FUSTÉ and GILI, 1990), fish larvae (CHESNEY and ALONSO-NOVAL, 1989), and general zooplankton biomass (Fig. 6). This general coincidence probably means that all zooplankton organisms were involved in the advection processes which, including the upwelling regime and the continental runoff.

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