With best wishes

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Small-scale distribution of a cnidarian population in the western Mediterranean

J.M.Gili, F.Pagès[1], A.Sabatés and J.D.Ros[1]

Institut de Ciències del Mar, Passeig Nacional s/n, 08003 Barcelona and [1] Department d'Ecologia, Facultat de Biologia, Universitat de Barcelona, Avd. Diagonal 645, 08028 Barcelona, Spain

Abstract. The neritic area of the coast of Catalonia (north-west Mediterranean) has a continental shelf narrower in the northern half and broader in the southern half. This area is crossed from north to south by a coastal current whose intensity decreases to the south. Both conditions, together with other local geographical and hydrographical features, are thought to be the key factors in determining the distribution of planktonic cnidarian assemblages, along two main variational axes: a north–south axis and a coast–open sea axis. Aiming to find support to this hypothesis, the planktonic cnidarians collected in two seasons of the year 1983 have been studied. The first season (April–May) corresponds to the highest abundance and heterogeneity, and the second (September–October), to the epoch when the cnidarian population is lower, but constant, along the coastal area. In a global principal component analysis the factor that best explains the group distribution in the area is the coastal character, as given by the bottom depth of the sampling station. The number of individuals is greater near the coast (due to the dominance of a euryhaline species, *Muggiaea atlantica*), but the species number increases towards the open sea (due to the addition of more oceanic species, such as Narcomedusae and Trachymedusae and the effect of a permanent hydrographic front at the shelf–slope boundary). The second factor is the latitudinal axis. The northern half of the coast is under the influence of waters favouring a greater number of species and individuals. On the contrary, the southern half shows a less marked influence of the north–south current, their cnidarian assemblages being more constant over time. Although the global cnidarian population follows this general pattern, the most abundant and frequent species (*M.atlantica* and *Aglaura hemistoma*) show a broad distribution over all the studied area because they are rather insensitive to hydrographical variations.

Introduction

On the coast of Catalonia (north-east Spain) the hydrographic system is not homogeneous. Temperature and salinity vary in terms of gradients which, generally speaking, extend from north to south and from the coast to the open sea. These differences have already been indicated in certain hydrographical studies (Furnestin, 1960; Salat and Cruzado, 1981), in which a central water mass of greater density is distinguished, surrounded by two masses of lesser density, one of which hugs the coast. This situation favours the presence of areas of cyclonic circulation in the Catalan Sea (Font, 1986). The dynamics of the superficial water masses are determined by a north–south current (the Catalan current) that occurs all year round and is associated with the vertical of the continental slope (Font, 1986). In association with the shelf–slope boundary there is a permanent hydrographic front in the area (Font *et al.*, 1988).

Similarly, it is possible to distinguish two zones within the geographical area under consideration here. One, on the northern half of the coast, has more typically coastal waters; the other has less typically coastal waters, due to the influence of the north–south current, which is more Mediterranean in nature (Allain, 1960; Hopkins, 1985). This second zone is more important on the southern half of the Catalan coast, where the north–south current periodically diverts the waters of the central zone towards the coast. The structure of the continental shelf clearly influences this diversion since its slope is gentler on the southern coast (Canals *et al.*, 1982).

At the same time, in the zones nearer the coast, local and seasonal phenomena occur, generated by the inflow of continental waters (especially from the Rhone in the north and the Ebro in the south) and by the system of local winds (Hopkins, 1985; Salat and Font, 1985). This geographical differentiation, however, becomes less marked the further out to sea one goes and the more uniform the hydrographical system becomes.

The coastal zooplankton is influenced by the local hydrographic regimes (Raymont, 1983; Gaudy, 1984), and the distribution of the planktonic communities follows, in general, the dynamics of the water masses in each area. On the other hand, the cnidarians are one of the most representative groups of zooplankton, especially of the gelatinous type (Alldredge, 1983); for this reason it can be expected that they will respond to environmental conditions in a way similar to that of the whole zooplanktonic population or as a reflection of this.

The purpose of this article is to ascertain whether the population of planktonic cnidarians studied responds to the hydrographic regime of a medium-sized geographical area such as the Catalan coast (~350 km of linear extension). A further aim is to discover the distribution patterns of the cnidarians in the coastal planktonic community. With regard to this it should be pointed out that on a higher scale (that of the different local seas that form the Mediterranean) notable differences have been found in the zooplanktonic populations, due in part to the hydrographic conditions characteristic of such seas (Furnestin, 1979; Gaudy, 1984).

At the same time the article sets out to observe the level of relationship in the area between the organisms and the environmental conditions, and to ascertain whether this relationship is the same as that encountered on a larger scale, such as that of the Mediterranean Sea as a whole. Few studies of this type have hitherto been published on other areas of the Mediterranean (Goy, 1985; Benovic and Bender, 1987), and in these the influence is noted of local phenomena on the distribution of zooplankton in general and cnidarians in particular.

Materials and methods

In order to study the geographical distribution of the population of cnidarians on the Catalan coast, samples were taken from the ARECES cruises (Gili, 1986). Hauls were taken from 39 stations distributed along the whole of the coast and arranged in 17 radials or cross-shelf lines (Figure 1). Due to the extent of the continental shelf, the southern radials have more than two hauls per radial. The distance between the different hauls of each radial is ~16 km.

The hauls were carried out using a 'bongo'-type plankton net (McGowan and Brown, 1965) with a 40-cm-diameter mouth and with two nets, one of 500 μm and the other of 330 μm mesh size. Samples were collected from near the bottom to the surface, almost always from a maximum depth of 200 m. The descending speed of the net was 1 m s^{-1} and the ascending speed of 10 m min^{-1}. While sampling, the boat travelled at a speed of 2 knots.

All individuals of cnidarians in each sample were counted, without taking aliquot parts. The data were expressed in number of individuals per 100 m^3. To achieve this it was necessary to take into consideration the real volume of water filtered by the net in each sample; this was measured with a flow-meter.

The distribution of planktonic cnidarians in the area studied varies greatly throughout the year, both in number of species and of individuals (Gili *et al.*, 1987b). It is to be expected that this influences the geographical distribution of the group throughout the area studied. For this reason two periods of the year were chosen that are significant for the cnidarians in the area: spring (May and June) and autumn (September and October). Spring corresponds to a state of maximum development and abundance of the group, while autumn might be considered a period of transition, with fewer species and individuals (Gili *et al.*, 1987b).

In order to study the distribution of the population, several analyses of principal components were carried out; data were first considered together and then examined separately (every month). The methodology adopted is the normal one for this kind of analysis (Chardy *et al.*, 1976; Legendre and Legendre, 1979). To interpret the factors explaining the axes, two methods were followed. In the first method, the values of the coordinates of the samples obtained as a result of considering the species as variables were transferred to the map of coastal stations. The groups thus obtained demonstrate, through the tracing of isolines, two of the prime factors: distance from the coast and geographical situation. In the second method, the coefficients were calculated of the correlation between the values of the coordinates of the samples for the first three axes, and the values corresponding to:

(i) Maximum depth from which samples were collected (meters).

(ii) Geographical distance. Each sample was given a progressive value of north–south distance using their real geographical latitude.

(iii) Distance from the coast. Samples were grouped by distance from the coast in nautical miles.

(iv) Hydrographical characteristics. Temperature, salinity and the σ_t gradient were considered. So that the values all along the coast should be comparable, values corresponding to a depth of 20 m were chosen in every station. The water samples with which to determine salinity and temperature were taken using Niskin-type hydrographical bottles.

(v) Displacement-volume, using the standard methodology (Omori and Ikeda, 1984) of the entire sample.

(vi) Specific richness. The number of species and individuals of cnidarians was noted, and both parameters were considered characteristics of each sample.

(vii) Abundance of the remaining groups of zooplankton. As a complementary estimate, and owing to the difficulty in counting individuals in many of these zooplanktonic groups, a value of relative abundance was used. This is a logarithmic index from 1 (up to 10 individuals) to 5 (very abundant, >10 000

Table I. Species of Cnidaria collected in the four months studied during the cruises

Species	May			June			September			October		
	n	$\bar{x}$	%	n	$\bar{x}$	%	n	$\bar{x}$	%	n	$\bar{x}$	%
1 *Agalma elegans* (Sars, 1846)	605	15.51	35.8	46	1.17	17.9	2	0.05	2.5	–	–	–
2 *Agalma okeni* Eschscholtz, 1825	–	–	–	10	0.25	2.5	–	–	–	–	–	–
3 *Halistemma rubrum* (Vogt, 1852)	18	0.46	5.1	–	–	–	–	–	–	25	0.64	12.8
4 *Nanomia bijuga* (Delle Chiaje, 1841)	69	1.76	20.5	–	–	–	12	0.30	10.2	–	–	–
5 *Marrus orthocanna* (Kramp, 1952)	–	–	–	6	0.15	2.5	–	–	–	–	–	–
6 *Forskalia edwardsi* Kölliker, 1853	1	0.02	2.5	–	–	–	–	–	–	–	–	–
7 *Hippopodius hippopus* (Forskål, 1775)	1	0.02	2.5	3	0.07	2.5	–	–	–	–	–	–
8 *Lensia conoidea* (Keferstein and Ehlers, 1860)	761	19.51	48.7	183	4.69	43.6	1	0.02	2.5	3	0.07	5.1
9 *Lensia subtilis* (Chun, 1836)	19	0.48	23.1	45	1.15	17.9	467	11.97	87.2	484	12.41	56.4
10 *Lensia subtiloides* (Lens and Van Riemsdijk, 1908)	–	–	–	–	–	–	–	–	–	8	0.20	7.7
11 *Lensia meteori* (Leloup, 1934)	–	–	–	–	–	–	–	–	–	4	0.10	5.1
12 *Muggiaea atlantica* Cunningham, 1892	57 366	1470.92	97.4	14 691	369.45	94.8	787	20.17	94.8	368	9.43	61.5
13 *Muggiaea kochi* (Will, 1844)	4	0.10	7.7	6	0.15	7.7	1024	26.25	100	503	12.89	56.4
14 *Eudoxoides spiralis* (Bigelow, 1911)	1	0.02	2.5	3	0.07	7.7	6	0.15	12.8	90	2.30	38.4
15 *Chelophyes appendiculata* (Eschscholtz, 1929)	70	1.79	51.2	60	1.53	53.8	637	16.33	84.6	1135	29.10	89.7
16 *Abylopsis tetragona* (Otto, 1823)	238	6.10	79.4	269	2.89	89.7	73	1.87	46.2	158	4.05	71.7
17 *Abylopsis eschscholtzi* (Huxley, 1859)	–	–	–	2	0.05	2.5	–	–	–	–	–	–
18 *Sarsia tubulosa* (M. Sars, 1835)	2	0.05	2.5	–	–	–	–	–	–	–	–	–
19 *Hybocodon prolifer* L. Agassiz, 1862	–	–	–	1	0.02	2.5	–	–	–	–	–	–
20 *Euphysa aurata* Forbes, 1841	1	0.02	2.5	1	0.02	2.5	–	–	–	–	–	–
21 *Podocoryne carnea* M. Sars, 1846	42	1.07	7.7	7	0.17	5.1	2	0.05	2.5	–	–	–
22 *Podocoryne minuta* (Mayer, 1900)	21	0.53	5.1	196	5.02	12.8	–	–	–	–	–	–

23 *Podocoryne minima* (Trinci, 1903)	–	–	–	56	1.43	7.7	–	–	–	–	–	–
24 *Lizzia blondina* Forbes, 1841	454	11.64	25.6	2103	53.92	38.4	–	–	–	–	–	–
25 *Kollikerina fasciculata* (Péron and Lesueur, 1810)	–	–	–	1	0.02	2.5	–	–	–	–	–	–
26 *Amphinema dinema* (Péron and Lesueur, 1809)	–	–	–	2	0.05	5.1	–	–	–	–	–	–
27 *Leuckartiara octona* (Fleming, 1823)	28	0.71	30.7	3	0.07	7.7	–	–	–	–	–	–
28 *Neoturris pileata* (Forskål, 1775)	2	0.05	5.1	–	–	–	–	–	–	–	–	–
29 *Velella velella* (Linné, 1758)	22	0.56	2.5	–	–	–	–	–	–	1	0.02	2.5
30 *Obelia* spp.	349	8.94	28.2	29	0.74	17.9	387	9.69	15.4	66	1.61	17.9
31 *Clytia hemisphaerica* (Linné, 1767)	68	1.74	23.1	9	0.23	10.2	7	0.17	7.7	2	0.05	2.5
32 *Laodicea undulata* (Forbes and Goodsir, 1851)	10	0.25	20.5	–	–	–	–	–	–	–	–	–
33 *Eugymnanthea inquilina* Palombi, 1936	–	–	–	–	–	–	1	0.02	2.5	–	–	–
34 *Eirene viridula* (Péron and Lesueur, 1809)	98	2.51	48.7	11	0.28	17.9	–	–	–	1	0.02	2.5
35 *Helgicirrha schulzei* Hartlaub, 1909	16	0.41	10.2	1	0.02	2.5	2	0.05	2.5	–	–	–
36 *Tima locullana* (Delle Chiaje, 1822)	–	–	–	1	0.02	2.5	–	–	–	–	–	–
37 *Eutima gegenbauri* (Haeckel, 1864)	4	0.10	7.7	–	–	–	–	–	–	–	–	–
38 *Aglaura hemistoma* Péron and Lesueur, 1810	411	10.53	51.2	7383	189.30	92.3	362	9.28	79.5	180	4.61	58.9
39 *Persa incolorata* McCrady, 1857	79	2.02	15.3	148	3.79	17.9	50	1.28	28.2	27	0.69	7.7
40 *Rhopalonema velatum* Gegenbaur, 1856	8	0.02	10.2	13	0.33	25.6	31	0.79	33.3	68	1.74	41.1
41 *Solmundella bitentaculata* (Quoy and Gaimard, 1833)	2	0.05	5.1	12	0.30	15.3	1	0.02	2.5	3	0.07	2.5
42 *Solmissus albescens* (Gegembaur, 1856)	–	–	–	1	0.02	2.5	2	0.05	2.5	–	–	–
43 *Solmaris flavescens* (Kölliker, 1883)	5	0.12	5.1	1	0.02	2.5	–	–	–	2	0.05	2.5
44 *Discomedusa lobata* Claus, 1877	–	–	–	1	0.02	2.5	–	–	–	–	–	–
45 *Pelagia noctiluca* Forskål, 1775	2	0.05	2.5	2908	74.56	43.5	–	–	–	6	0.15	5.1

The numbers in the left margin correspond to the codes of the species in the representation of the analysis of principal components.
n, number of individuals per 100 m^3; $\bar{x}$, mean; %, percentage of samples in which the species occurs.

individuals per 100 m^3). The groups studied were: Salpida, ichthyoplankton, Copepoda, Amphipoda, Chaetognatha, Doliolida, Decapoda larvae, Mollusca and Euphausiacea. A further group was also quantified, consisting mostly of unrecognizable flakes of suspended organic matter, phytoplankton and eggs of different organisms. This group has been classified as 'organic matter'.

Results

A total of 17 species of Siphonophora, 26 of Hydromedusae and two of Scyphomedusae were collected (Table I). The number of species varied greatly between the first two cruises (32 species in May and 34 in June) and the second two (19 species in September and 20 in October). In May the predominant groups are the salps and the copepods; in June the euphausiaceans and the copepods predominate. In September the chaetognaths, copepods and euphausiaceans predominate, as is the case in October, although during this month the chaetognaths were especially abundant.

Two species, *Muggiaea atlantica* and *Aglaura hemistoma*, were the most widespread and abundant during the four months studied. A great number of individuals of both species were found in the analyses and they are representative of the distribution of the population. *Muggiaea atlantica* had a markedly coastal character during the four months studied (Figure 1) as well as a tendency to increase in number of individuals in the northern half of the coast, especially near the coast itself. In May it is abundant along the whole of the littoral. *Aglaura hemistoma* is in a similar situation (Figure 2) and shows an evident tendency to appear near the coast in the northern zone.

Other species which were abundant during some of the four months studied show a slight tendency to appear in coastal waters or definite latitudinal zones. *Lensia conoidea* and *Abylopsis tetragona* increase towards the north, especially in May. The same occurs with *L.conoidea* and *Lizzia blondina* in June. On the other hand, *A.tetragona* and *Chelophyes appendiculata* are distributed very uniformly along and near the coast.

In September the most abundant species, such as *Lensia subtilis*, *C.appendiculata* and *Muggiaea kochi*, do not show a clear geographical preference. In October, however, *L.subtilis* and *M.kochi* tend to increase towards the north, while *Rhopalonema velatum* does so towards the south.

A global analysis of components reveals a variance of 26.1% between the first three axes (I = 9.9%, II = 9.1%; III = 7.1%). This variance is somewhat less than that obtained in any of the four months studied, due only to the fact that more variables (species) were considered. The distribution of the coordinate values of axis I corresponds to a general distribution of the samples going from the coast to the open sea (Figure 3). All the samples near the coast present positive values, while those further out to sea present negative values. On the other hand, in the representation of axis II (Figure 3) it can be seen that the samples or stations with positive values tend to cluster towards the northern half of the coast. Conversely, the negative values are found at a certain distance from the southern part of the coast. This seems to indicate that this second factor

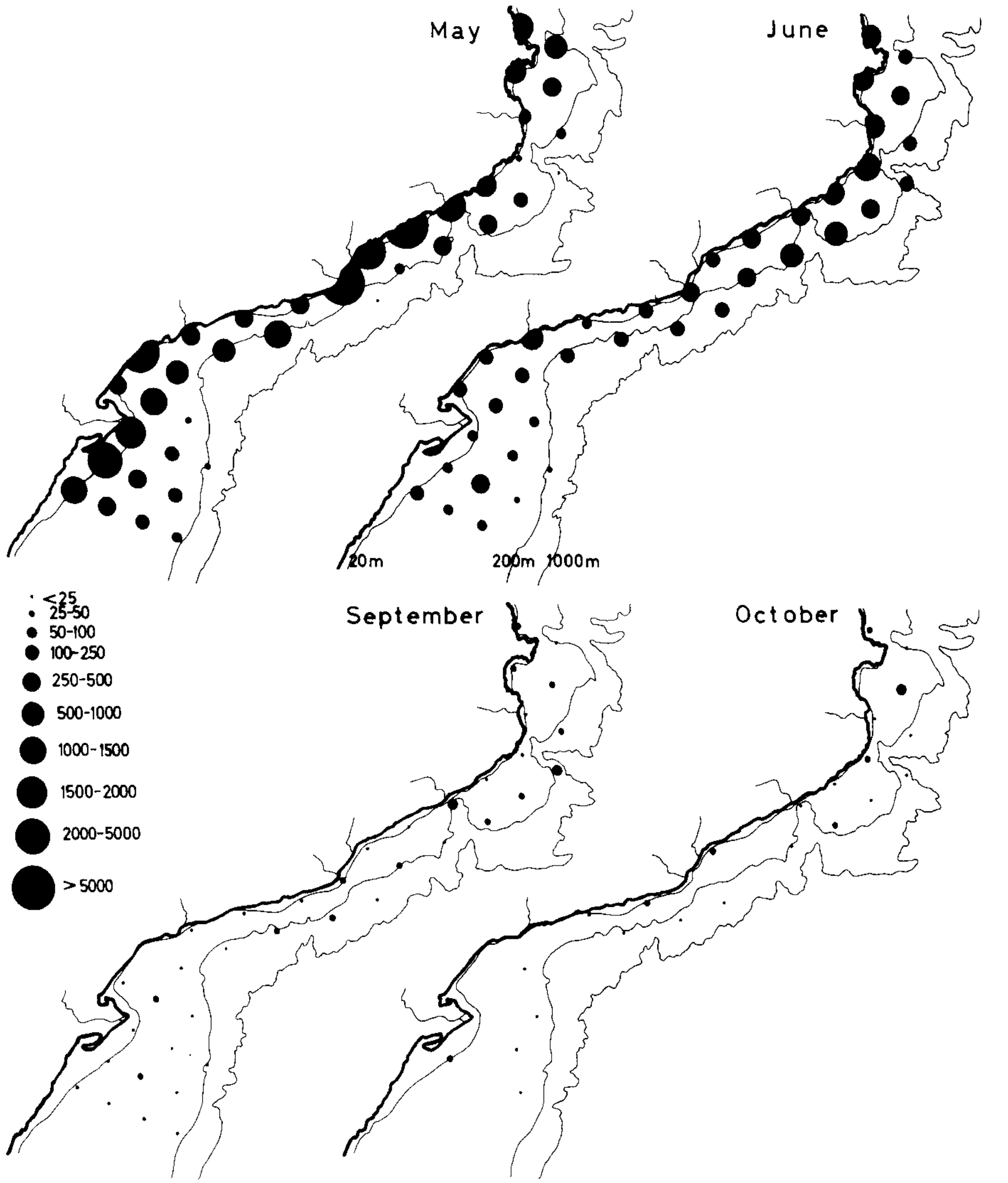

Fig. 1. Distribution of *Muggiaea atlantica* along the Catalan coast during the four months studied. Scale in no. of individuals per 100 m^3.

discriminates between the population in terms of a geographical north–south axis which, however, loses strength the further out to sea it goes. The representation of the species (Figure 4) sketches a tendency similar to the one outlined above. In the positive zone of axis I, most of the species with more coastal characteristics are found, such as *M.atlantica*, *M.kochi* and *Obelia* spp. (Table I, nos 12, 13 and 30 respectively). At the other end of the axis the differentiation is less, due to the fact that the distance from the coast where samples were taken does not allow the presence of species characteristic of the

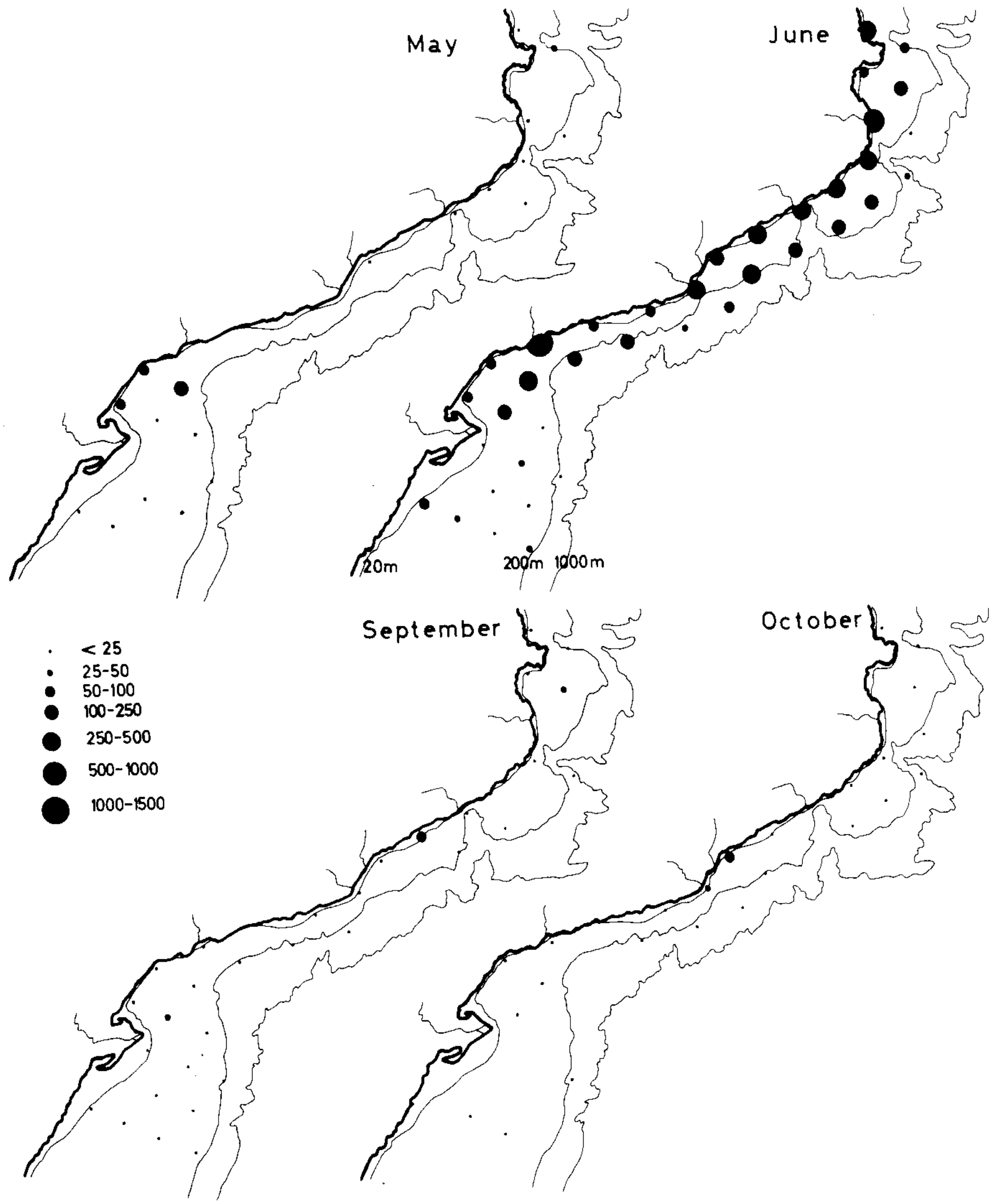

Fig. 2. Distribution of *Aglaura hemistoma* along the Catalan coast during the four months studied. Scale in no. of individuals per 100 m^3.

open sea. On the second axis, within the positive values species of almost exclusively northern presence are found, such as *Euphysa aurata* and *Podocoryne minima* (Table I, nos 20 and 23 respectively), while within the negative values some species of preferably southern distribution are found, such as *Rhopalonema velatum* and *Eudoxoides spiralis* (at least during the time of year when they are most abundant).

In May, the variance explained by the three first axes is 35.5%. Samples from the southern half of the coast, as well as some from the middle zone, present the

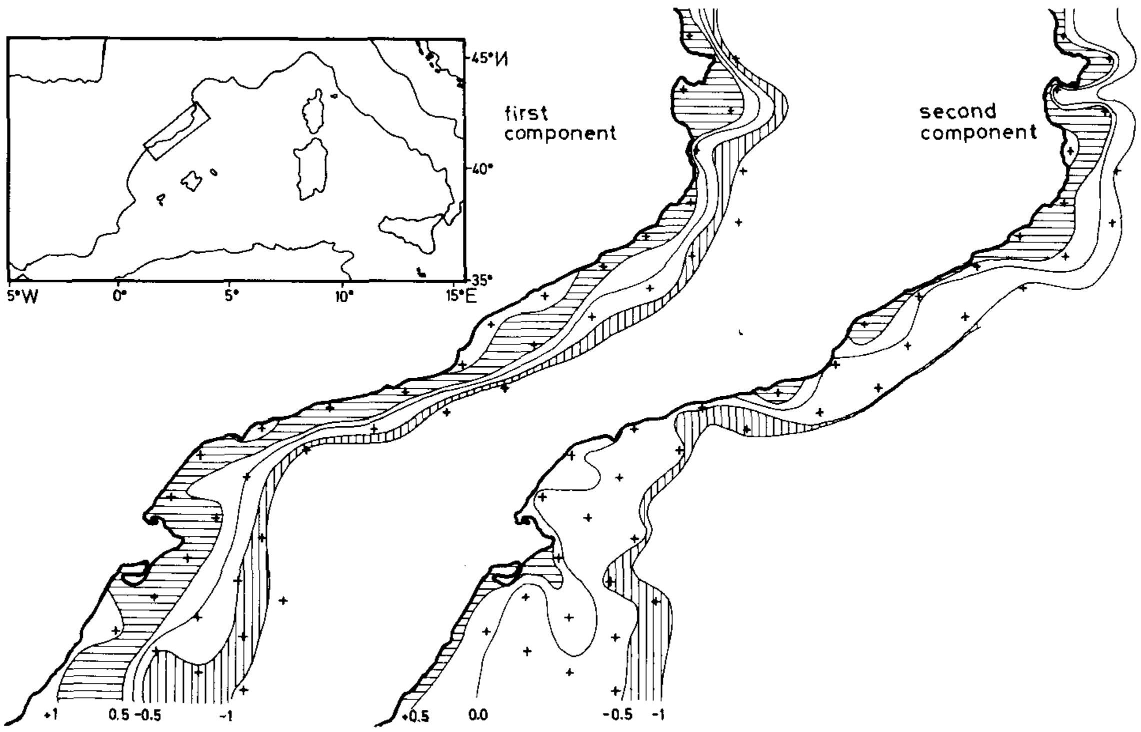

Fig. 3. Representation of the curves calculated with the values of the factor scores in of all the samples of Cnidaria for the first axis (left) and the second axis (right) in the principal component analysis.

highest positive values, while those from further away from the coast (in the northern half) present the highest negative values (Figure 5). The factor that best explains the first axis is the geographical distribution and the depth of the station (Table II). On the second axis, the stations segregate into two bands parallel to the coast; the factors that explain a greater correlation are depth and number of species (Table II). In the latter case, the samples with the greatest number of species were taken from offshore stations, while those richest in individuals are taken from inshore. This coincides with the global zooplankton biovolume, the highest values being those of the offshore stations (Figure 6).

In June, the variance explained by the first three axes is 33.8%. The distribution of the values of the stations in the first factor follows a curve almost parallel to the coast; for this reason, distance to the coast and depth are the factors that best explain the distribution of this first axis. In the second factor the stations with highest positive values correspond to the inshore samples in the northern half. The geographical distance is, therefore, the most representative factor of this second axis (Table II).

The number of individuals is closely related to the first factor, since the inshore samples have the highest abundances. The correlation with the number of individuals is also high in the case of the second factor, because the stations in the northern half are the richest ones (Table II). On this second axis the correlation with the number of species should also be emphasized, since some offshore stations in the southern zone have a great number of species. During this month the salinity is closely related to the first factor (Table II). This fact is

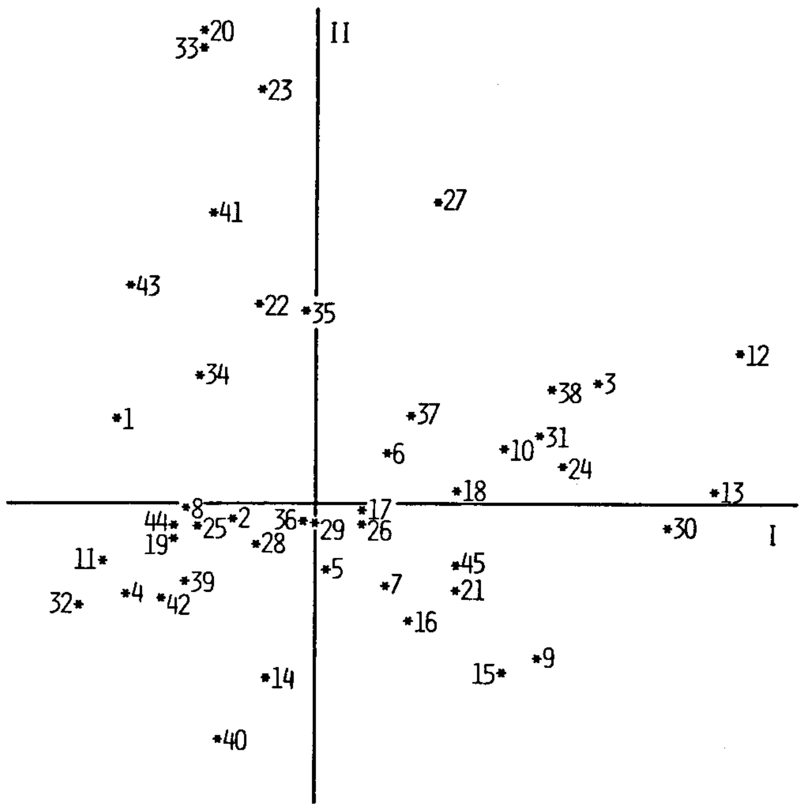

Fig. 4. Representation in the space of the first two axes, of the 45 species of Cnidaria collected over the four months studied. The variance explained by the first axis is 9.9% and by the second 9.1%. The first discriminates the species in terms of their distribution with regard to the distance from the coast, and the second on a geographical north–south axis. (For the code, see Table I.)

worth noting, since though the axis discriminates the population of cnidarians geographically, the distribution of salinity is uniform all along the coast (except for the more coastal waters which are slightly less saline), and does not seem to influence the north–south segregation of the population.

In September, the variance explained by the first three axes is 39.4%. Depth is the parameter most closely related to the first axis (Table II). At the same time, the northern offshore stations show the highest values of biovolume and number of Cnidarian species. In the second axis, although there is a slight tendency towards segregation in a north–south direction, with quite a number of stations with positive values in the southern zone and negative in the north, the meaning of this factor does not seem to be clear. On the other hand, it presents a good correlation with the number of species, due to the fact that, in general, stations in the northern half present a greater number of species than the remainder. In the case of this latter factor, the correlation with temperature is significant (Table II). Although certain northern stations present a slightly lower temperature, and a few southern ones a temperature slightly higher than that of the remainder, the distribution of temperature along the coast is quite even in September, a similar phenomenon to that of salinity in June.

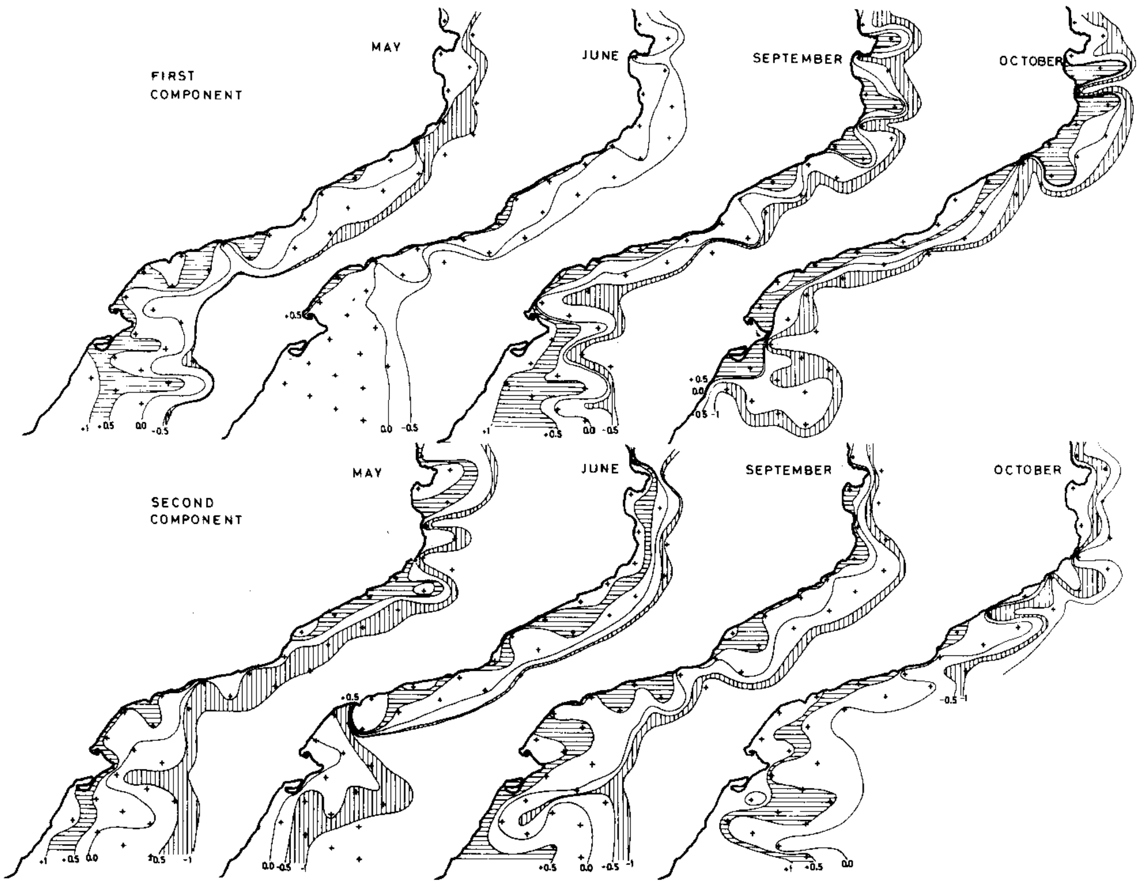

Fig. 5. Representation of the factor score values of the samples of Cnidaria collected over the four months studied. First axis (above) and second axis (below). The curves have been adjusted according to the nearest values, both positive and negative.

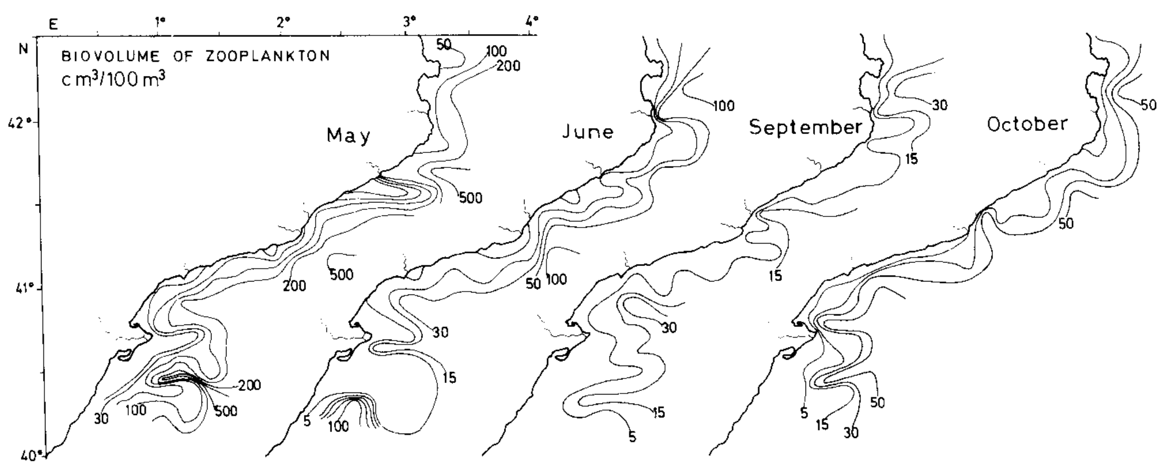

Fig. 6. Biovolume (displacement-volume) of all zooplankton groups over the four months studied in cm^3 $100\ m^{-3}$.

In October, the variance explained by the three first axes is 41.1%. The distribution of stations in the first factor follows curves quite parallel to the coast (Figure 6). Distance from the coast and depth are the factors that best correlate

Table II. Correlation factors between the principal component analysis *f*-scores for cnidarian species and the considered physical and geographical parameters and the abundance estimates of the remaining zooplankton groups (see text)

	May			June			September			October		
	1 axis	2 axis	3 axis	1 axis	2 axis	3 axis	1 axis	2 axis	3 axis	1 axis	2 axis	3 axis
Depth	−0.47***	−0.29**	0.12*	−0.37**	0.51***	0.25	0.34**	0.39**	−0.51***	−0.32**	0.33**	−0.09
Geographical distance	0.31**	−0.20	−0.32**	−0.47***	−0.36***	−0.41***	−0.04	−0.36**	0.11	−0.19	−0.65***	0.22
Distance from the coast	−0.16	−0.05	−0.15	−0.68***	0.08	−0.22	0.14	0.03	−0.35**	−0.36**	−0.12	0.06
Temperature	−0.17	−0.24	0.05	0.02	−0.35**	−0.22	−0.08	−0.22	0.14	−0.18	−0.55***	0.16
Salinity	0.22	−0.18	−0.24	−0.46***	−0.10	−0.24	0.01	−0.06	−0.02	0.23	0.12	−0.01
Density (σ_t)	0.12	−0.13	−0.30**	−0.33**	0.13	0.10	0.11	0.15	−0.16	0.21	0.53***	−0.14
Salpida	−0.35**	−0.35**	0.01	−0.20	−0.17	−0.15	−0.05	−0.15	−0.28	−0.10	0.44**	−0.12
Ichthyoplankton	−0.06	0.30**	−0.03	0.33**	0.44***	0.10	0.33**	−0.08	−0.04	−0.16	−0.06	0.15
Copepoda	0.51***	−0.10	−0.16	−0.26	0.35**	−0.07	0.13	0.10	0.05	0.29	0.20	0.33**
Amphipoda	−0.14	−0.39**	−0.06	−0.29	0.36**	0.03	0.39***	0.23	−0.01	0.28	0.01	0.25
Chaetognatha	0.38***	−0.18	−0.04	0.19	0.03	0.22	0.67***	0.06	0.04	0.42***	0.43***	−0.07
Doliolida	−0.04	−0.07	0.04	0.40***	−0.10	−0.01	0.32**	0.40***	−0.09	−0.09	0.49***	−0.31**
Decapoda larvae	0.31**	−0.01	−0.04	0.20	0.08	0.37**	0.08	0.08	−0.23	0.18	−0.15	0.26
Mollusca	0.21	−0.13	0.01	0.30**	0.13	0.31**	0.17	−0.24	0.10	0.15	0.10	−0.12
Euphausiacea	−0.10	−0.30	−0.16	−0.20	0.38***	0.13	0.53***	0.19	0.02	0.02	0.10	0.32
Number of species	0.28	0.60***	0.20	0.21	0.41***	0.21	0.75***	0.22	−0.10	0.75***	0.17	−0.07
Number of individuals	−0.35**	0.53***	−0.08	−0.48***	0.63***	−0.01	0.21	−0.29	0.38***	0.78***	0.12	−0.23
Displacement-volume	−0.44***	−0.03	0.28	−0.03	0.05	0.05	0.23	0.38***	0.13	−0.01	0.02	−0.03

Only the significant correlations coefficients are shown, and probability is indicated by: ** $P = 0.95–0.98$; or *** $P = 0.99–1.00$.

to the distribution of the first axis (Table II). On the second axis, the southern stations present the highest positive values while the northern ones present the highest negative values. Geographical distance is thus the most significant factor, with a high correlation with axis. Furthermore, the temperature also correlates well with this second factor. In this case a slight north–south segregation does exist, superimposed on the distribution of the surface temperature. Both the number of species and of individuals are well correlated with the first axis. This is due to the fact that the greatest number of individuals are found in the coastal stations, while the greatest number of species are found out the sea (Table II).

Certain groups of zooplankton have a good correlation with the distribution of cnidarians in the area studied. In May, the copepods and the chaetognaths tend to be distributed along the north–south axis, and both are more abundant in the southern half of the studied coast (Table II).

In June, the correlation with molluscs, ichthyoplankton and amphipods is good. The first two groups are more abundant in the northern zone of the coast, while the third is abundant all along it, especially in the offshore stations (Table II).

In September, the correlation is significant with the amphipods, euphausiids and chaetognaths. These groups are abundant along the whole of the coast, but while the amphipods are more abundant in the stations where there are fewer cnidarians, the chaetognaths are more abundant precisely where there is also an abundance of cnidarians. Euphausiids are more abundant in the offshore stations (Table II).

In October, the correlation is high with the same groups of the previous month: amphipods and chaetognaths, and also with doliolids (Table II). The distribution is similar to that of September.

Discussion

The four months studied correspond to two different seasonal situations; the spring months (May and June) are characterized by a greater number of species than the autumn months (September and October). Both situations are characteristic of the distribution of the planktonic cnidarians on the Catalan coast (Razouls and Thiriot, 1968; Gili *et al.*, 1987b), in which the abundance peaks occur at the end of the spring and beginning of the summer, in the case both of siphonophores and hydromedusae.

In autumn and winter the population is maintained with fewer species and individuals and without notable abundance peaks.

The overall analysis shows that there is a clear tendency for the population to be distributed from the coast to the open sea. This distribution is particularly marked in June, when there is a maximum abundance of species and individuals. In general, it can be observed that this distribution pattern is repeated in the four months studied, but it should be pointed out that a second factor, the north–south segregation of the population, could carry considerable weight when it comes to explaining the distribution of cnidarians in the studied zone.

This second factor is more evident nearer the coast, especially in the northern half. The wide distribution of the most abundant species along the coastal area makes it impossible to give a clearer indication of this geographical segregation.

This geographical differentiation is accompanied by a slight increase in salinity and temperature in the southern zone, especially during June. This phenomenon, together with the lower salinity in the northern zone, can be explained both by the geographical situation itself and by the inflow of dense waters from the middle zone of the Catalan Sea.

In September and October the latitudinal differences of the geographical parameters are more accentuated, especially the σ_t gradient. This is reflected in a greater north–south segregation in October, but more significant is the richness in numbers of species and individuals in the coastal stations in the northern half.

As a whole, a geographical, latitudinal differentiation of the population of cnidarians in the studied zone can be observed in the sense that the northern coastal region is richer in species and individuals. Furthermore, this region is less affected by the current that flows along the Catalan coast in a north–south direction; certain northern stations are constantly richer in species through the four months studied. The coastal character of this northern zone is similarly affected by the considerable continental inflows, which differentiates it from the southern zone. In general, this tendency is maintained in the four months studied irrespective of whether the period is suitable or not for the cnidarian population. In the less saline inshore waters *M.atlantica*, an euryhaline species (Moncaleano and Niño, 1979), is favoured. Because this species is the most abundant its numbers have a great influence on those of the group as a whole.

Uniformity in the distribution of species is also observable, especially in the most abundant ones, along the whole of the coast, irrespective of whether a segregation of the population exists. It is the rare or less frequent species that collaborate towards a differentiation of the population in geographical terms.

Planktonic cnidarian species in general are highly adaptable to fluctuating geographical conditions (Colebrook, 1964; Zelickman, 1972; Mills, 1984). For this reason, in small and definite areas of the Mediterranean the most abundant cnidarian species are uniformly present, but the individual populations have differences characteristic of the local conditions of each area (Gili *et al.*, 1987a).

A situation like the one observed on the Catalan coast, with a gradient in the distribution of the cnidarian population overlying a hydrographical gradient, is also to be seen in the open Atlantic (Pugh, 1975) and in a coastal area in the Indian Ocean (Vanucci and Navas, 1973). The most abundant species are uniformly distributed, while the less abundant ones tend to be found associated with particular hydrographic features.

The differences observed can be partially explained by the inflow of continental waters, especially from the Rhone and from the rivers all along the Catalan coast, which contribute to the decrease of salinity of the more coastal waters and towards an increase of the euryhaline species in the zooplankton population (Alvariño, 1972). Among the cnidarians this is reflected in an increase in the number of individuals belonging to the most abundant species.

Further from the coast, where this inflow hardly reaches, the increase is in the number of species of cnidarians and in the biovolume of all zooplankton. The explanation for this is the presence of a shelf–slope permanent front that favours the zooplankton concentration (Olson and Backus 1985; Boucher *et al.*, 1987).

A phenomenon such as the one that occurs offshore can be explained by the arrival of allochthonous species, such as certain narcomedusae whose normal habitat is the open sea. Similarly, these stations further away from the coast are exposed to the influence of the Catalan current (Font, 1986) which, while enriching the local population with other species, does not increase the number of individuals of the species already present. The increase in number of individuals near the coast would seem to be a direct consequence of the abundance of *M.atlantica*, as stated above.

The possible trophic relation of cnidarians with other groups was considered, although there are difficulties involved in drawing conclusions about the ways in which these are interrelated, particularly when such trophic relations are probably indirect (Pugh and Boxshall, 1984; Arai, 1987). The crustaceans and the molluscs are important prey and predators of siphonophores (Purcell, 1981) and hydromedusae (Zelickman, 1972). Some of these groups have high correlation with cnidarians in the studied zone. These groups are most abundant in stations where cnidarians are scarce (i.e. where amphipods act as predators) or abundant (i.e. where copepods act as prey).

In short, the totality of the population best reflects the distribution of the cnidarians in the studied zone (which, it must be remembered, is of relatively small dimensions: ~350 km in a north-east–south-west direction; see Figure 4), in response to the local hydrographic conditions. The distribution of the species, on the other hand, is not so significant. It could be said that the cnidarian population responds as a group to local environmental changes, while the populations of the most abundant species are relatively unaffected by such changes. This is understandable if one remembers that the most variable environmental conditions in the coastal area studied (and in general in littoral environments in seas everywhere) are the hydrographical ones—conditions to which species are already adapted to a greater or lesser extent. These general adaptations or, which is the same thing, the relatively low sensitivity to changes that do not have a hydrographical basis, favours the spreading capacity of planktonic cnidarian species and their capacity to remain in a specific geographical area. On the small scale at which the population has been studied, the variation-generating mechanisms are mobility and physical accumulation (Mackas *et al.*, 1985), which are closely dependent on local hydrography.

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