In: *Modern trends in the systematics, ecology, and evolution of hydroids and hydromedusae* (eds, J. Bouillon, F. Boero, F. Cicogna, and P.F.S. Cornelius), Oxford University Press, Oxford. (1987)

15. Distribution and ecology of a population of planktonic cnidarians in the western Mediterranean

with best wishes

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ABSTRACT

A population of planktonic cnidarians was sampled between September 1982 and August 1983 off the coast of Barcelona. In nine oceanographic cruises during this period samples of zooplankton were taken from 0–1000 m depth and were used to study vertical and seasonal distribution. 80 per cent of the total number of medusae comprised *Aglaura hemistoma*. Total numbers were at their peak in May. Similarly, *Muggiaea atlantica* comprised 90 per cent of the captured siphonophores; but this species had two peaks, in April and June. The two species tended to concentrate in the superficial region at 0–50 m depth. At the end of June a maximum in the total volume of zooplankton coincided with the maximum density of cnidarians, with the arrival of a new water mass, probably of offshore origin, and with the stabilization of circulating water. On analysing the factors which could have an influence on the distribution of species, it is found that abundance (both absolute and relative, indirectly linked to longevity and fertility) is the more significant factor and, together with trophic relations with other groups of zooplankton, explains the composition of the local cnidarian fauna.

Introduction

The northern Mediterranean zone off the Iberian Peninsula presents special hydrographic characteristics. The area includes the confluence of two currents of different origins. One comes from the north, from the Gulf of Lyon, whilst the other flows into the zone along the northern coast of the Balearic Islands (Allain 1960; Hopkins 1985). The physical characteristics (lower density) of the first current and its aperiodic

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arrival, in relation to seasonal changes, are the main factors in the distribution of zooplankton organisms in the region.

Factors related to the biology of the species (capacity for migration, life cycles, and trophic relations) are also important in explaining the dynamics of different groups of zooplankton (Raymont 1983). The cnidarians, on the other hand, are one of the best represented groups of neritic zooplankton (Alldredge 1983), having a wide bathymetric and seasonal distribution. This is true especially of some coastal species of siphonophores (Bigelow and Sears 1937). From a trophic point of view, their place in the planktonic food webs is influenced by other organisms present (Longhurst 1985).

All these general aspects were considered in the present study during a whole annual cycle. Biological and hydrographic factors were studied during nine cruises, made from September 1982 to August 1983.

Only the fraction of the samples including medusae and siphonophores is considered here. Bathymetric and seasonal distributions are studied, and the relationship with other groups of zooplankton and with physical parameters are ascertained.

Material and methods

The area was located between 10 and 20 miles off Barcelona, on the Catalonian coast (Fig. 15.1).

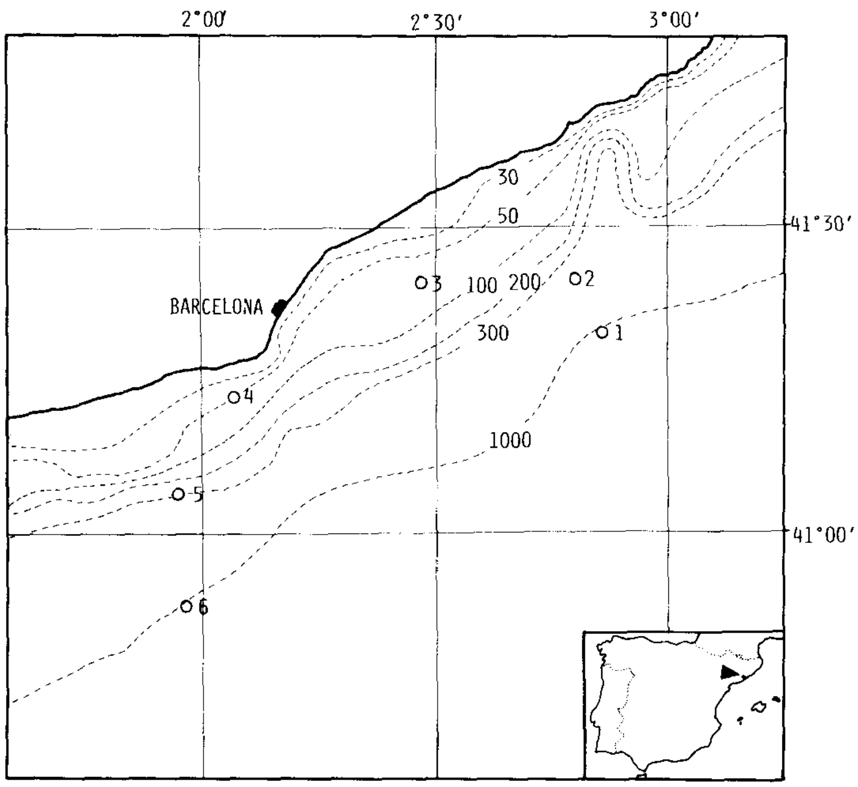

Fig. 15.1. Stations in the survey area (depths in metres).

In each of the nine cruises, six stations were visited along transects running from the coast to the open sea. Hydrographic data, especially salinity and temperature, were studied and have been published by other authors (Arias, Sousa, and Delgado, in press). Since there was uniformity between the localities, only the data pertaining to station 1 are shown in Fig. 15.2.

An international closing net WP-2, of mesh-size 250 μm, was used in the vertical tows. These were carried out over four different depth ranges: 0–50 m, 50–200 m, 200–500 m, and 500–1000 m. All animals in the samples were counted. The values were expressed as individuals per 100 m^3 of water over each depth range. In the statistical survey the samples in which no cnidarians were found were also taken into consideration in the average values. The calculation of the biomass of the

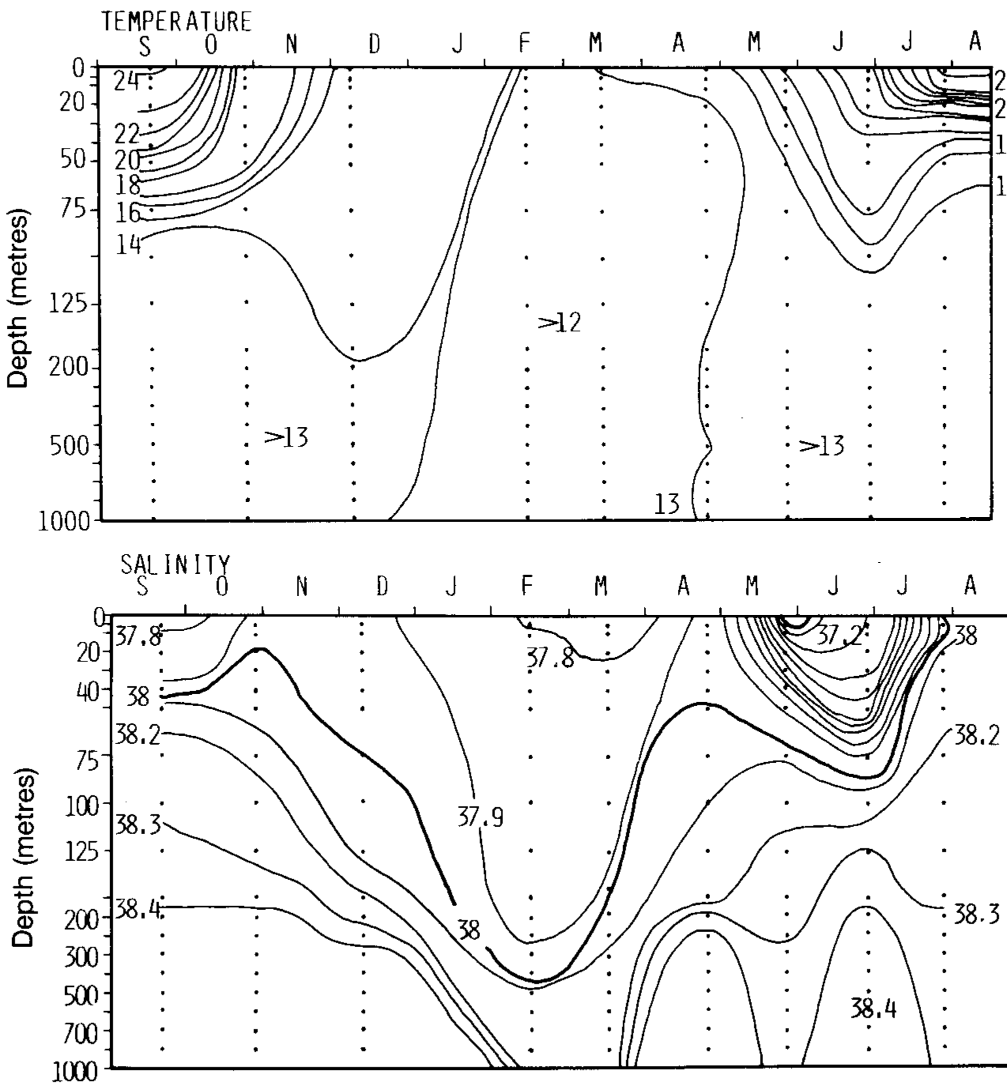

Fig. 15.2. Isothermals and isohalines during the cycle studied. These figures are based on data from station 1, but the rest of the stations were similar. Upper, temperature in °C; lower, salinity in parts per thousand.

different groups was based on the number of individuals, with a coefficient of transformation being applied whereby one copepod is equivalent to one unit mass of organic carbon (Longhurst 1985).

The statistical method used was the analysis of multivariant principal components (Legendre and Legendre 1979; Cuadras 1981). Logarithmically transformed data were used throughout.

Results

A total of 35 species of medusae and 21 of siphonophores were identified (Table 15.1). The medusae had two seasonal maxima: a minor one in April, and a denser one near the middle of June with more than 2000 individuals/100 m^3. Except in the month of March the individuals tended to concentrate in the superficial region at 0–50 m depth (Fig. 15.3). *Aglaura hemistoma* was the most abundant species of the group, and showed a distribution similar to that of the whole group of medusae (Fig. 15.3). The second most abundant species was *Persa incolorata*,

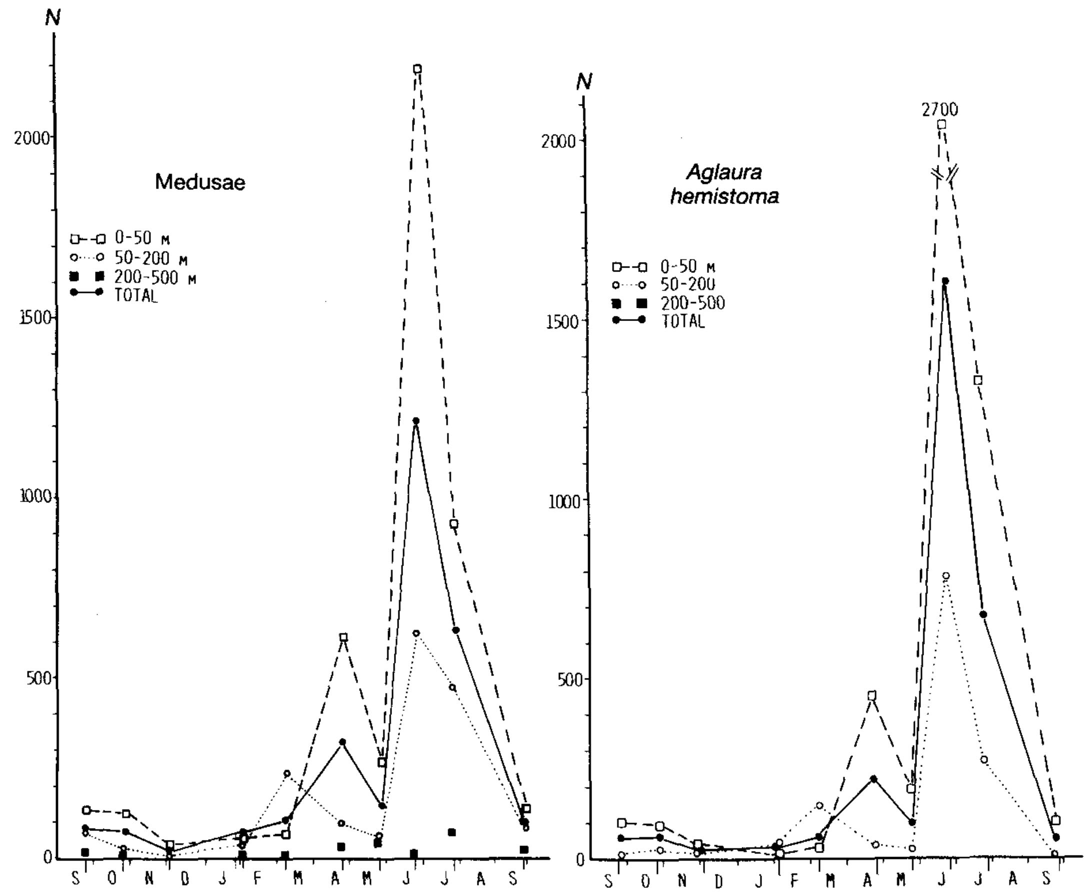

Fig. 15.3. Seasonal distribution of all the medusae and of *Aglaura hemistoma* alone. Average numbers of specimens (N) per 100 m^3 of water.

Table 15.1. List of species collected. Numbers at the left refer to the code used for the species in the representation of the principal component analysis (cf. Fig. 15.6).

Code	Medusae	Code	~~Medusae~~ Siphonophores
	Hybocodon prolifer L. Agassiz		
1	*Euphysa aurata* Forbes	21	*Agalma elegans* (Sars)
2	*Corymorpha nutans* M. Sars	22	*Halistemma rubrum* (Vogt)
3	*Zanclea costata* Gegenbaur	23	*Cordogalma cordiformis* Totton
4	*Podocoryne carnea* M. Sars		*Marrus orthocanna* (Kramp)
	Koellikerina fasciculata (Péron and Lesueur)	24	*Nanomia bijuga* (Delle Chiaje)
5	*Lizzia blondina* Forbes		*Physophora hydrostatica* Forskal
	Leuckartiara octona (Fleming)	25	*Hippopodius hippopus* (Forskal)
	Neoturris pileata (Forskål)		*Sulculeolaria biloba* (Sars)
6	*Laodicea undulata* (Forbes and Goodsir)	26	*Lensia meteori* (Leloup)
	Mitrocomella brownei (Kramp)	27	*Lensia conoidea* (Keferstein and Ehlers)
7	*Obelia* spp.	28	*Lensia subtilis* (Chun)
8	*Clytia hemisphaerica* (Linnaeus)		*Lensia subtiloides* (Lens and van Riemsdijk)
9	*Octocanna funeraria* (Quoy and Gaimard)	29	*Muggiaea kochi* (Will)
10	*Eirene viridula* (Péron and Lesueur)	30	*Muggiaea atlantica* Cunningham
11	*Octorchis gegenbauri* Haeckel	31	*Chelophyes appendiculata* (Eschscholtz)
12	*Haliscera bigelowi* Kramp	32	*Eudoxoides spiralis* (Bigelow)
13	*Aglaura hemistoma* Péron and Lesueur		*Sphaeronectes bougisi* Carré
14	*Persa incolorata* McCrady		*Abyla haeckeli* (Lens and van Riemsdijk)
15	*Persa incolorata* f. *lucerna* Haeckel	33	*Abylopsis tetragona* (Otto)
16	*Rhopalonema velatum* Gegenbaur	34	*Abylopsis eschscholtzi* (Huxley)
	Rhopalonema funerarium Vanhöffen		*Enneagonum hyalinum* Quoy and Gaimard
	Ransonia digitale (O. Müller)	35	(adult) (Pelagia noctiluca)
	Aglantha krampi (Ranson)		
	Sminthea eurygaster Gegenbaur		
17	*Solmundella bitentaculata* (Quoy and Gaimard)		
	Solmaris solmaris (Gegenbaur)		
18	*Solmaris flavescens* (Kölliker)		
	Solmissus albescens (Gegenbaur)		
	Cunina globosa Gegenbaur		
	Atolla sp.		
	Periphylla periphylla (Péron and Lesueur)		
	Paraphyllina intermedia Mass		
19	*Nausithoe punctata* Kölliker		
	Pelagia noctiluca (Forskål)		
20	(ephyra)		

which was found in samples at all depths but especially at medium depths (Fig. 15.4). The medusa fauna was characterized by these two common species which represented nearly 90 per cent of the total number of individuals. These species showed seasonal changes in abundance. *A. hemistoma* was more surface-dwelling than *P. incolorata*, which was a deep-water species associated with others regularly present throughout the year.

Species with a low density but normally observed with an irregular distribution all the year round were *Clytia hemisphaerica* and *Rhopalonema velatum*. *R. velatum* was distributed over a large bathymetric

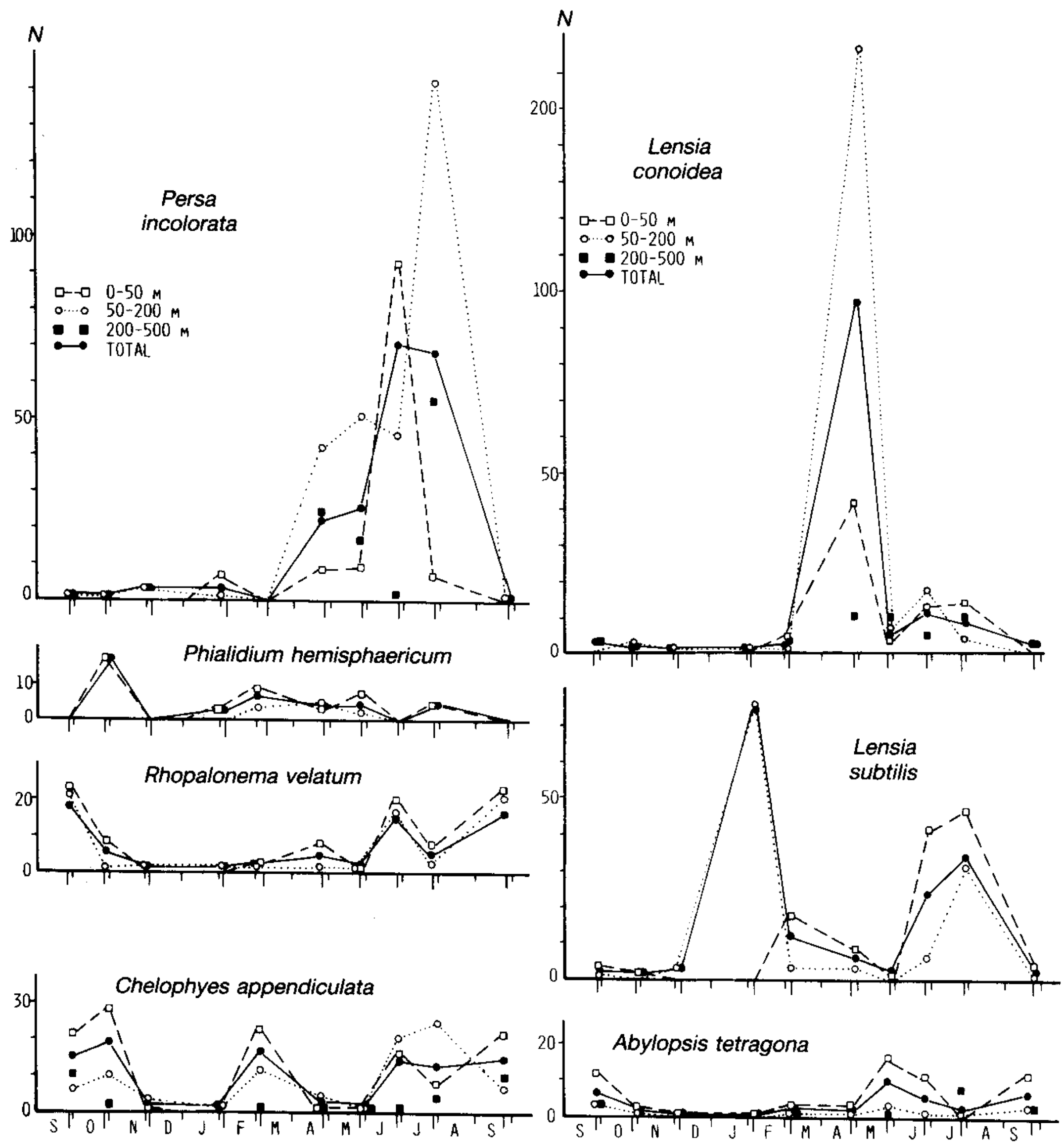

Fig. 15.4. Seasonal distribution of certain important species of medusae and siphonophores. Average numbers of specimens (N) per 100 m^3 of water.

range, while *C. hemisphaerica* was more restricted to the surface layers in accordance with Kramp's (1959) observations.

The seasonal distribution of siphonophores was characterized by a maximum between April and July. There were two peaks of abundance, one late in April (with 2500/100 m^3) and the other late in June. During the year the concentration of these animals was greatest in the surface layers, between 0 and 50 m (Fig. 15.5). One species, *Muggiaea atlantica*, represented nearly 90 per cent of the total number of siphonophores, and its distribution was similar to that of the total population (Fig. 15.5). *M. atlantica* was abundant in the superficial zone (0–50 m). Two other species, *Lensia conoidea* and *L. subtilis*, presented a more seasonal distribution but occupied moderate depths (50–200 m) and formed the peaks of abundance in these layers. Other species, less abundant but occurring regularly throught the year, also presented regularly distributed minor peaks (*Abylopsis tetragona* and *Chelophyes appendiculata*). These other species, though not important quantitatively, had a uniform distribution throughout the area. Comparable distributions have

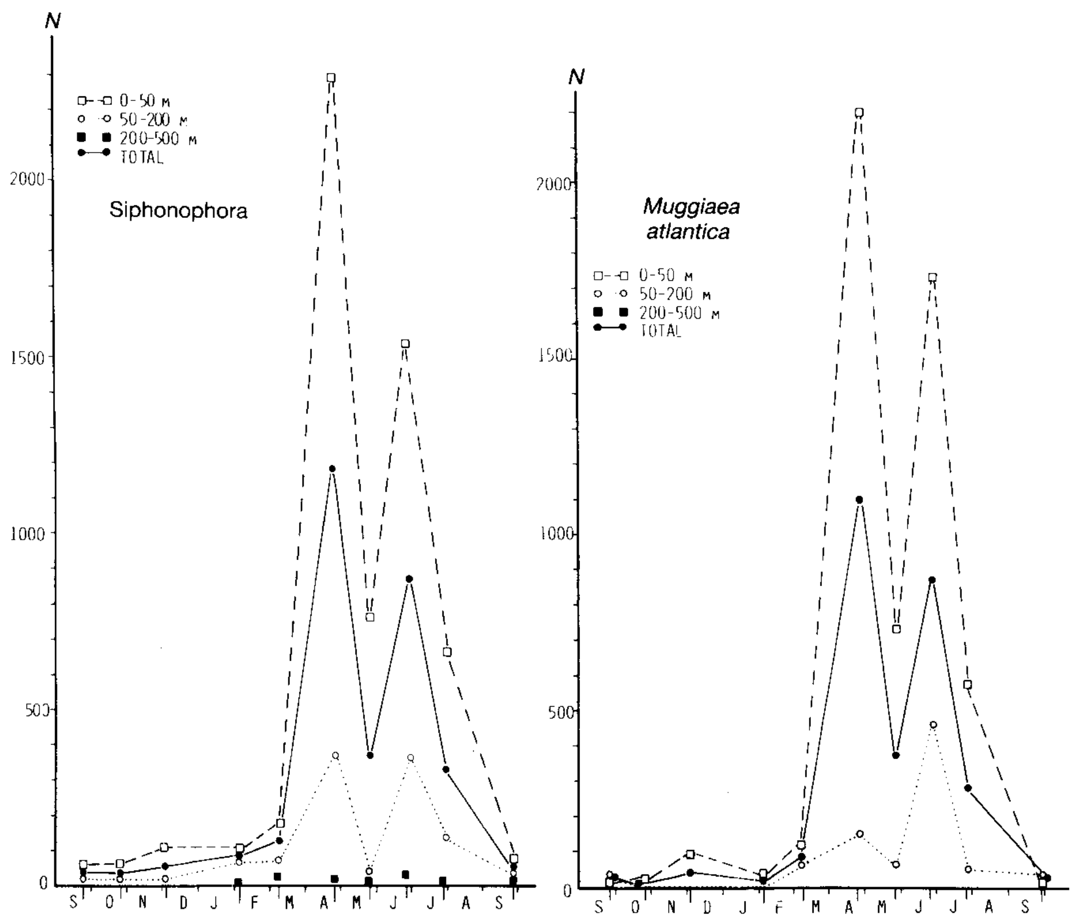

Fig. 15.5. Seasonal distribution of all the siphonophores and of *Muggiaea atlantica* alone. Average number of specimens (*N*) per 100 m^3 of water.

been reported by other authors from neighbouring waters [e.g. Razouls and Thiriot (1968) in the Gulf of Lyon].

The principal component analysis shows in three dimensions the distribution of the species as a function of the three factors (axes) which have the most influence on their distribution. Because of the relative homogeneity of the pelagic environment we might expect gradients in the positions of species rather than well-defined and discontinuous groups.

In the first analysis, which included all species taken two or more times (listed in Table 15.1), the total variance explained by the three first factors was 26.5 per cent. This is considered normal in natural communities (Margalef 1974). The first axis with a higher demonstrated variance (11.4 per cent) segregated the species as a function of the dominance, especially in the total number of specimens of each species. The second, with a demonstrated variance of 8 per cent, segregated the species as a function of season, separating autumn and winter species from spring and summer ones. The third axis segregated species especially as a function of depth, contributing 7 per cent to the variance, separating surface species (0–50 m) from those of moderate depths (50–200 m) (Fig. 15.6).

When we repeated the analysis without the more abundant species the variance found was a little less (25 per cent), but the factors-distribution was similar. With the elimination of these species, the ordination of the remaining species in space was also very similar in the two analyses (Fig. 15.6).

The cnidarians appeared to form a different percentage of the total plankton according to whether they were estimated by number of individuals or by biomass (Fig. 15.7). As number of individuals their proportion was not higher than 10 per cent, copepods being the dominant group with more than 80 per cent throughout the year. As biomass (see previous section) the percentage seemed greater at 20–25 per cent, especially from March to June when it was augmented by the siphonophores. When expressed as percentage of the biomass the importance of copepods is diminished, and that of amphipods increased.

Discussion

Temperature is one of the factors with which the seasonal presence of many species in the zooplankton correlates best (Raymont 1983). But seasonal abundance can depend on other factors. This can be observed when cycles are compared in neighbouring areas of similar hydrographic conditions, comparing different species.

Aglaura hemistoma is the commonest medusa in Mediterranean superficial waters (Berhaut 1969; Albertini-Berhaut 1979). It has shown seasonal changes in abundance in spring and summer in consecutive

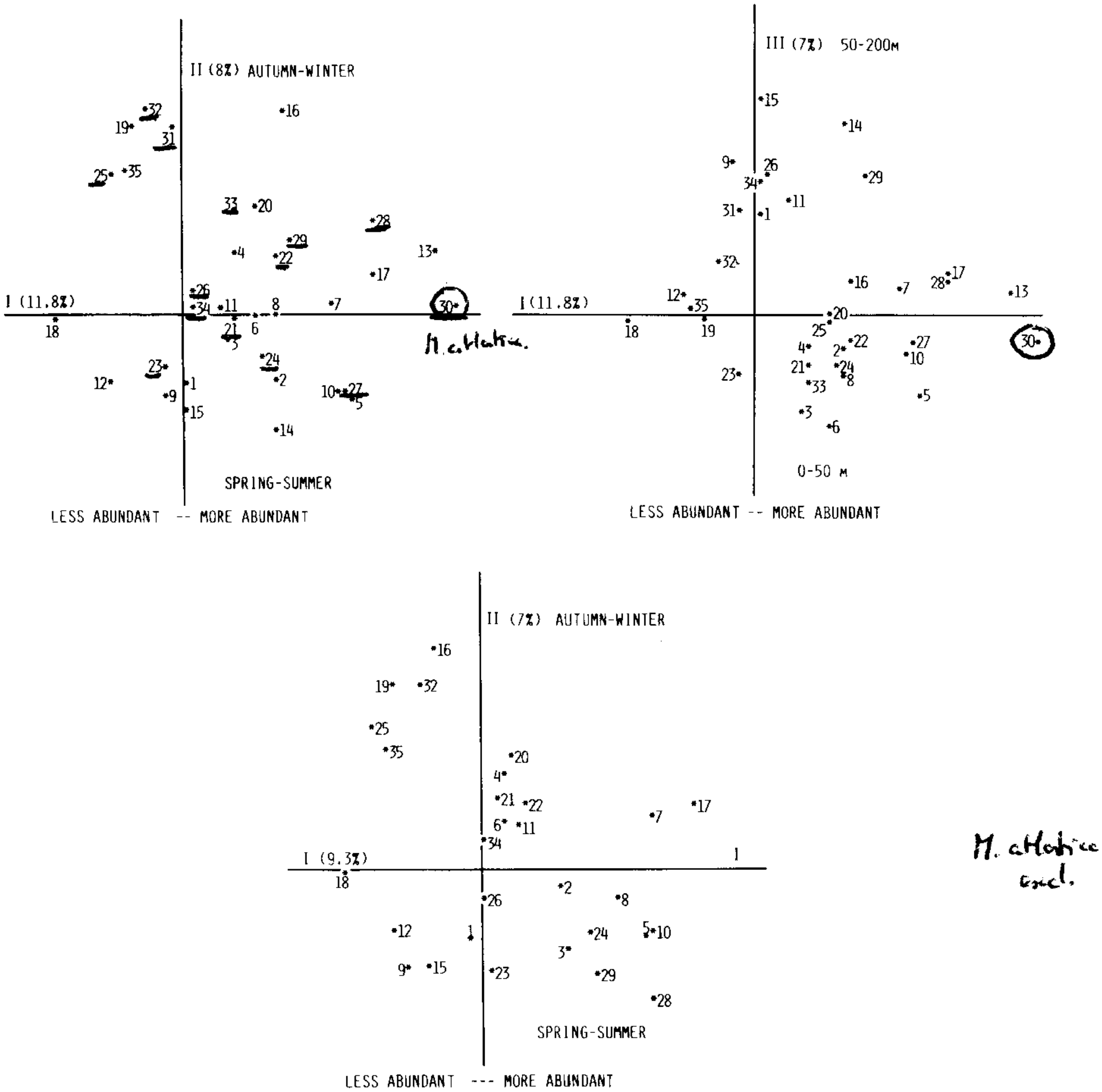

Fig. 15.6. Positions of species in the space of the principal component axes. Above, analysis with all the studied species; below, excluding the six most frequent. Code of the species as in Table 15.1.

years (Goy 1985). This is due principally to local hydrographic conditions, as discussed later. A similar situation has been observed in *Persa incolorata* during the annual cycle (Goy 1964; Benović 1977) but not in superficial waters. Similarly, the more regularly collected species of siphonophores are frequent in Mediterranean superficial layers throughout the year. *Muggiaea atlantica* has been found above the thermocline (Alvariño 1980) and its day–night migration is remarkable (Southward and Barrett 1983). At the same time this species has a more littoral distribution due to its euryhaline behaviour (Moncaleano and

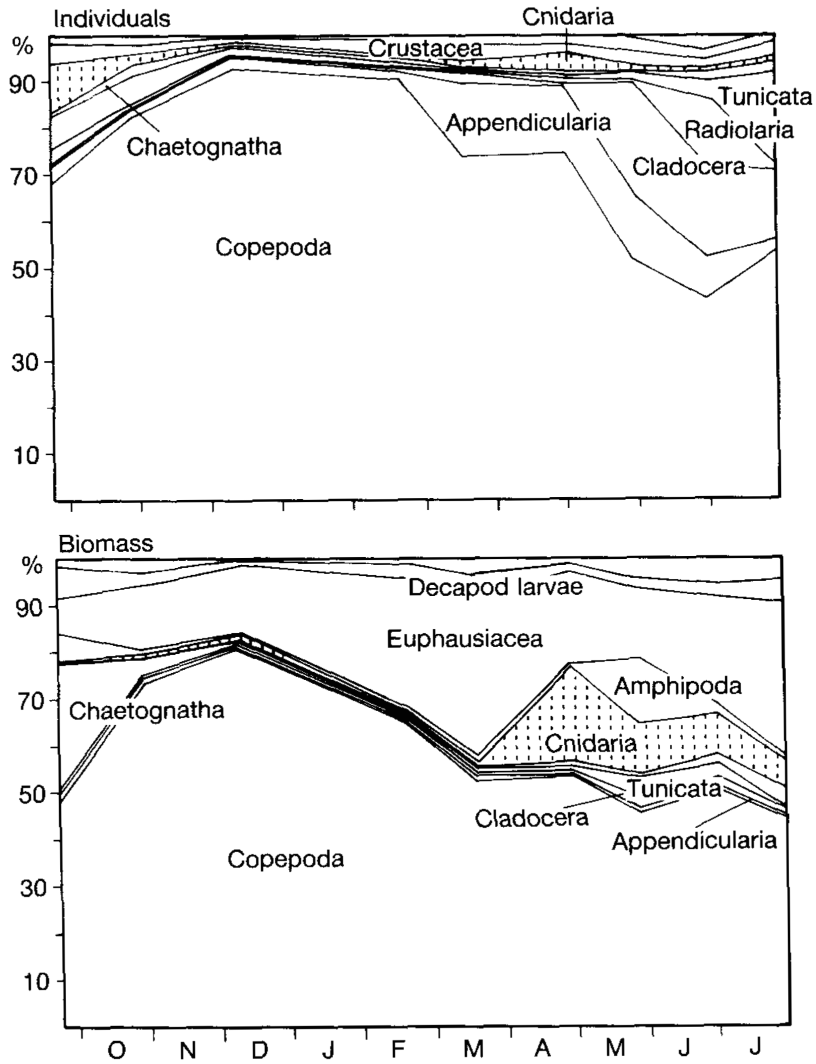

Fig. 15.7. Percentages of the main groups of zooplankton in terms of numbers of individuals and of biomass. (After Vives 1985.)

Niño 1979). *Lensia conoidea* also presents a superficial distribution, with few migratory fluctuations (Pugh 1984).

On the other hand, the maximum abundance of cnidarians is seen when the water column is homogeneous, or when stratification begins at the end of May. In the two observed peaks, siphonophores, especially *Muggiaea atlantica*, form a major part. The first peak, late in April, is composed mainly of this species. The fact that the maximum siphonophore density is observed before that of the medusae can be explained as a consequence of a higher growth rate (Purcell 1982). The presence of polymorphic colonies, particularly with specialized reproductive individuals, may explain such capacity in comparison with medusae.

The second peak of siphonophores is a second generation coming from the eudoxias produced during the first period. In general, if siphonophores show more peaks of abundance than medusae, this may be accounted for by differences in their modes of reproduction.

The second maximum of abundance of cnidarians is associated with the yearly maximum of all zooplankton (Vives 1985). Only *Muggiaea atlantica* is more abundant during the first cycle of siphonopores, when it represents about 20 per cent of the total zooplankton population.

The stability of the water masses may promote the increase of zooplankton populations, especially in shallow waters where there are accumulations of plankton. But the entry of off-shore water can also lead to an increase of zooplankton. In this case a larger population might result from the addition of individuals from other areas more than from a local increase due to reproduction. The two phenomena together might explain the large concentration of cnidarians observed. Increases in other zooplankton groups will increase the prey available to cnidiarians (Möller 1979). When copepods increase it is to be expected that the populations of the predators will follow suit, among them the cnidarians. *Muggiaea atlantica* is a great predator of copepods and other small crustaceans (Purcell 1982). The population of siphonophores is reduced when the Amphipoda increase, and the latter can limit the growth of the siphonophore population (Laval 1980). Medusae can hunt a whole range of prey (McCormick 1969), but this varies greatly with the species. But siphonophores seem more specialized in feeding on certain groups of zooplankton populations.

Taking the results of the statistical analysis, the absolute or relative abundance of species can explain the distribution and composition of the cnidarian fauna of the region. So, the first factor probably also corresponds to the richness of life and to general fertility, as an indirect idea of species abundance.

On the other hand, it is normal for a population of planktonic cnidarians to be dominated by some of the more frequent species (Williams and Conway 1981; Pugh 1984). Therefore, the distribution of these species will have a large influence on the total population. But when we leave out these species in our statistical study, relative abundance is still an important factor in the distribution of the population.

Seasonality and abundance are not independent, and consideration of them helps to understand the distribution of the different species (Fig. 15.7). Appropriate temperatures at certain seasons permit the development of certain zooplankton populations. For planktonic cnidarians in the western Mediterranean rather narrowly defined conditions are the most favourable; for example, a temperature above 14°C. Further thermal variation, during the year, has less significance. This is reflected in the analyses. Two tendencies are seen. The first occurs during spring and early summer, when the temperature is at first in the whole water column and later from 50 m depth over 14°C. Above this temperature maximal abundances are recorded. The species in this group include the most abundant. The second tendency occurs during autumn and winter when other species, which show a more regular distribution all the year round, are dominant.

We have observed some significant differences in size among individuals of the same species in the same sample but not in different periods of the year. This leads us to suppose that the surveyed population is continuously changing and that the peaks of abundance show an increment of the total population but do not indicate a clear pattern of seasonal growth.

Depth-related factors get only third place in the ranking of descriptors of the behaviour of the population. This results from the importance of the surface layers, from 0–50 m, where the largest part of the sampled population occurs. On the other hand, some species of medusae (Benović 1973) and siphonophores (Pugh 1984) carry out daily vertical migrations. This phenomenon may be significant when we wish to define vertical distributions of the species during longer periods. Vertical migration is more noticeable in the open sea than near the coast. Since the samples were collected usually at the same hour (the first hour of the afternoon) it is possible that vertical migration quite often escaped our notice. In the sense that we discuss it in this work, it is also known that some cnidarians follow a night–day feeding cycle (Purcell 1981), which corresponds to a bathymetric distribution consequent on the search for food.

Even though physical environmental conditions are important in the distribution of planktonic cnidarians, the trophic relations between them and other zooplankton groups (Arai 1987) are the most important factors governing the composition and distribution of populations in different areas. It is a biological structure not perfectly in step with hydrological conditions (R. Margalef, pers. comm.) in which species can resist non-ideal environmental conditions but closely follow trophic opportunities.

Acknowledgements

Thanks are due to Prof. R. Margalef for comments on the manuscript and for his helpful suggestions during the preparation of this work. Also, to Dr M. N. Arai for revision of the manuscript and to her and to Dr J. Goy for their comments on the original manuscript during the workshop in Ischia.

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