Appearance of *Chelophyes appendiculata* and *Abylopsis tetragona* (Cnidaria, Siphonophora) in the Bay of Villefranche, northwestern Mediterranean

Emmanuelle Buecher [*]

*Laboratoire d'Océanographie Biologique et Ecologie du Plancton Marin/CNRS ESA 7076, Station Zoologique, B.P. 28,
06234 Villefranche-Sur-Mer Cedex, France*

Abstract

The vertical and temporal distribution of two calycophoran siphonophores, *Chelophyes appendiculata* (Eschscholtz, 1829) and *Abylopsis tetragona* (Otto, 1823) in the Bay of Villefranche (northwestern Mediterranean) was investigated by an analysis of three different planktonic time series. A daily series (1993–1995) showed seasonal peaks of the nectophores of *C. appendiculata* during spring and particularly in late summer, while the abundance of *A. tetragona* remained similar throughout the year. A weekly series (1994–1995) showed that *C. appendiculata* (nectophores and eudoxids) became concentrated above the thermal discontinuity, in the most stratified and warm waters, whereas *A. tetragona* was collected in large numbers below this discontinuity. A 27-year survey (1966–1993) showed long-term fluctuations of these siphonophore populations, which became abundant in the Bay starting from 1980 and especially after 1984, when the water column grew warm and hypersaline, corresponding to a less rainy period. Temporal (seasonal and long-term) and bathymetric (between 10 and 60 m depth) successions of these two siphonophores were noted in this shallow coastal bay. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Chelophyes appendiculata; *Abylopsis tetragona*; seasonality; vertical distribution; long-term fluctuations

1. Introduction

Gelatinous predators (cnidarians and ctenophores) eat herbivorous zooplankton and fish larvae (e.g. Purcell, 1981a,b; Alvariño, 1985; Arai, 1988; Matsakis and Conover, 1991). Because of their significant consumption in marine pelagic communities and their competition for food with fish, interest in the biology and ecology of these carnivores has increased in the last 20 years (e.g. Alldredge, 1984; Purcell, 1985; Mills, 1995).

Siphonophores (cnidarians) are widely distributed vertically and horizontally in all seas the world over (e.g. Vinogradov, 1970; Alvariño, 1971; Margulis, 1972; Pugh, 1975; Longhurst, 1985). They can represent up to about 20% of the total zooplankton biomass (Longhurst, 1985). In the western Mediterranean, siphonophores represent 45–67% of the total macroplankton in the upper 200 m (Boucher and Thiriot, 1972).

Chelophyes appendiculata (Eschscholtz, 1829) and *Abylopsis tetragona* (Otto, 1823), measuring

* Present address: Zoology Department, University of the Western Cape, Private Bag X17, Bellville 7535, South Africa. Fax: +27 21 959 2266; E-mail: ebuecher@SFRI2.WCAPE.GOV.ZA

about 1 cm, are among the commonest species of calycophoran siphonophores living in the upper layers (Totton, 1965; Pugh, 1974), and they are very dominant throughout the northwestern Mediterranean (Bigelow and Sears, 1937; Trégouboff and Rose, 1957; Casanova, 1970; Franqueville, 1971; Boucher and Thiriot, 1972; Goy and Thiriot, 1976; Laval et al., 1989; Dowidar, 1992).

In the Mediterranean Sea, data on siphonophore seasonality and vertical distribution are plentiful. A good example is the extensive investigations by Bigelow and Sears (1937) during the 'Thor' Expedition (1908–1910) depicting the spatial distribution of siphonophores throughout the Mediterranean and adjacent seas. Their results depict the spatial distribution of siphonophores throughout the Mediterranean. However, seasonal variations were studied only over very large regions (e.g. eastern and western basins) and not at a fixed station; vertical distributions were obtained from hauls made with non-closing nets and without a depth sensor. Other studies have been conducted in smaller areas, for example by Leloup (1935, 1936), Trégouboff and Rose (1957) and Patriti (1964) along the French coast and by Vives (1966) and Gili et al. (1987a, 1987b, 1988) along the Spanish coast. Patriti (1969), Lakkis (1971) and Gamulin and Krsinic (1993a, 1993b) investigated the eastern basin, which is less well known. Lists of siphonophore species have been drawn up from these studies and vertical, horizontal, or temporal distributions of species described, but sampling frequencies and/or material did not allow a detailed description of their vertical distribution or seasonal appearance. Studies designed to investigate nycthemeral migrations of these species (Palma, 1985; Andersen et al., 1992; Sardou and Andersen, 1993) were only performed over short periods of time and hence did not show longer-term (annual and pluriannual) abundance patterns.

None of these previous studies combine vertical distributions with short- and long-term fluctuations. In the present study, seasonal changes, long-term fluctuations, and small-scale vertical distributions of *C. appendiculata* and *A. tetragona* are described from three zooplankton surveys in the Bay of Villefranche-sur-Mer, a shallow coastal area in the northwestern Mediterranean.

2. Material and methods

2.1. Study area

The Bay of Villefranche is a well-sheltered bay in the Ligurian Sea (northwestern Mediterranean). The hydrodynamics of the bay are influenced by the local winds and the Ligurian current which enters at Cap Ferrat and leaves at the Cape of Nice (Gostan, 1968; Béthoux et al., 1988). At its mouth, delimited by these two capes, the bay is 100 m deep.

2.2. Hydrological data

Hydrological measurements (temperature and salinity) were performed weekly in the Bay of Villefranche during the three surveys of siphonophores. Hydrological sampling protocols of the weekly and the long-term series are described in detail in Etienne et al. (1991), Ménard et al. (1994) and Buecher (1997).

2.3. Zooplankton sampling

The anterior nectophores (asexual stage) of *Chelophyes appendiculata* and *Abylopsis tetragona* were examined from each of the time series. To study reproduction in *C. appendiculata*, one of the most abundant siphonophores in the Bay, eudoxids (the sexual stage) were also counted.

Survey-1 (598 samples) was designed to study seasonal patterns and short-term fluctuations of siphonophore populations. From March 1993 to March 1996 (excluding 7 July to 11 October 1993), sampling was carried out at 30 m depth every weekday.

Survey-2 (556 samples) was especially designed to examine small-scale vertical distribution, while also addressing seasonality. From January 1994 to January 1996, samples were collected at intervals of 10 m between 10 and 60 m depth once a week. During these surveys, horizontal tows were made with a Regent net (mouth aperture diameter 1.0 m, filtering length 4.0 m, mesh size 680–700 μm, silk fabric type n°00); all individuals in each sample were counted without taking aliquots. The values were standardised as individuals per 100 m^3 of water.

Survey-3 (1244 samples) consists of vertical hauls from 75 m depth to the sea surface performed with

a Juday–Bogorov net (mouth aperture diameter 0.50 m, filtering length 1.80 m, mesh size 330 μm) twice every weekday from November 1966 to December 1993. Samples from each week were pooled to yield a series of weekly estimates, each sample including a maximum of 10 hauls. Survey-3 animals were counted from subsamples (1/7 of each weekly sample volume) as described in Buecher et al. (1997). To allow comparison with the previous studies based on this long-term series (Buecher, 1997; Buecher et al., 1997), the same abundance classes were used: abundances of *C. appendiculata* and *A. tetragona* were coded according to Frontier's semi-quantitative scale of abundance (Frontier, 1969). Because of the smaller volume of water filtered during Survey-3 hauls, the data were expressed in numbers of individuals per 10 m^3. Further details of sampling and counting methods are given in Buecher et al. (1997).

3. Results

3.1. Hydrological fluctuations

The long-term and seasonal hydrological fluctuations during the study periods have been described in detail in Buecher (1997) and Buecher et al. (1997). Only typical patterns are presented below.

During the 27 years of monitoring (1966–1993), the years 1967 to 1984 were identified as a 'cold period' (temperatures were generally lower than the average of 17.48ºC at 10 m and 14.15ºC at 75 m); 1975 and 1980 were the coldest years of this series. The years 1985 to 1993 corresponded to a 'warm period' (temperatures were higher than the reference averages) and 1990 was the warmest year. Salinity fluctuations showed similar trends. From 1967 to 1974 and from 1977 to 1979, salinities were generally below the mean values of the entire 27 years (37.91‰ at 10 m and 38.00‰ at 75 m), whereas 1975 to 1976 and 1980 to 1993 were 'hypersaline periods' with higher salinities than the mean reference values.

Annual hydrological variation always presented the same pattern, describing the four seasons: (1) Winter: from mid-January to the end of March, the water column was homogenous. Temperatures were below 14ºC and salinity fluctuations were very small (<0.3‰). (2) Spring: the sea surface temperature rose slowly in April and bottom temperatures were still below 14ºC. A thermocline was induced and consolidated throughout this season. At the same time, surface salinity decreased, inducing haline stratification (salinity differences between sea surface and 75 m were above 0.5‰). (3) Summer: the thermal gradient between sea surface and the bottom (80 m depth) was maximal in August (12ºC). After the highest surface temperature (25ºC) was reached, a slow cooling of sea surface and a gradual warming at depth occurred until the end of October. There was an 'inversion' of the haline gradient particularly due to an increase in the surface salinity. (4) Autumn: the seasonal stratification (thermal and haline) was eroded, mainly due to wind mixing. The water column became homogenous at a temperature of approximately 18ºC and salinity of approximately 38.00‰. It became progressively colder again, reaching 14ºC in January and 13ºC in February, with only minor salinity fluctuations.

3.2. Zooplankton fluctuations

The seasonal occurrences of *Chelophyes appendiculata* and *Abylopsis tetragona* in the Bay were observed in detail from the daily time series of Survey-1. The general trend for the three series, illustrated by the bold line in Fig. 1, was calculated from the moving average method (8-order) (Kendall, 1976).

Nectophores of *C. appendiculata* were observed in 53% of the samples with a mean density of 2.4 individuals per 100 m^3. Nectophores occurred throughout the year but were generally less numerous during the hydrological winter (Fig. 1A). Maximal abundances occurred at the end of the hydrological summer. A second, but smaller, peak of abundance occurred during the hydrological spring. It was prominent in 1994 and appeared earlier in 1995. The greatest abundance of nectophores noted during this three-year survey was 32.5 individuals per 100 m^3 on 24 August 1995. The mean density of eudoxids was 2.7 individuals per 100 m^3. This reproductive stage was less abundant during the hydrological winter and maxima occurred from the middle of spring to the end of summer (Fig. 1B). However, the highest abundance of 42.5 individuals per 100 m^3 was noted on 21 April 1994.
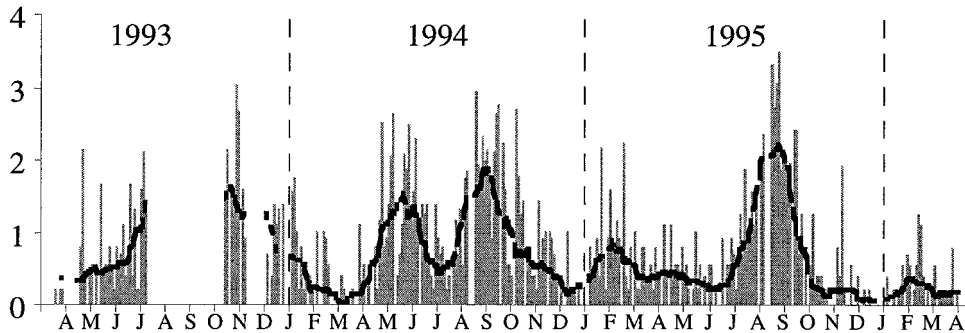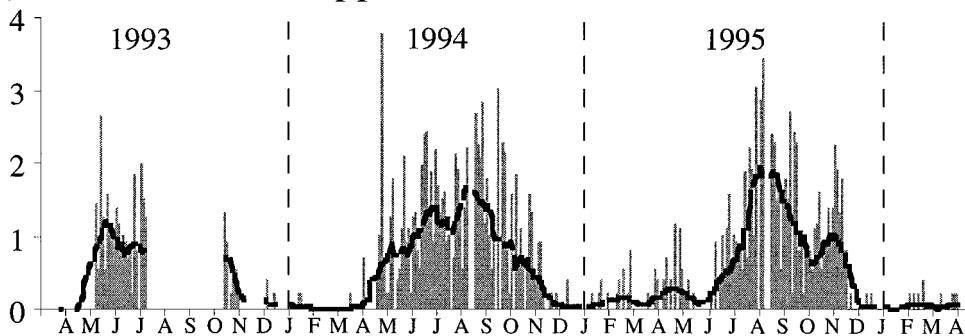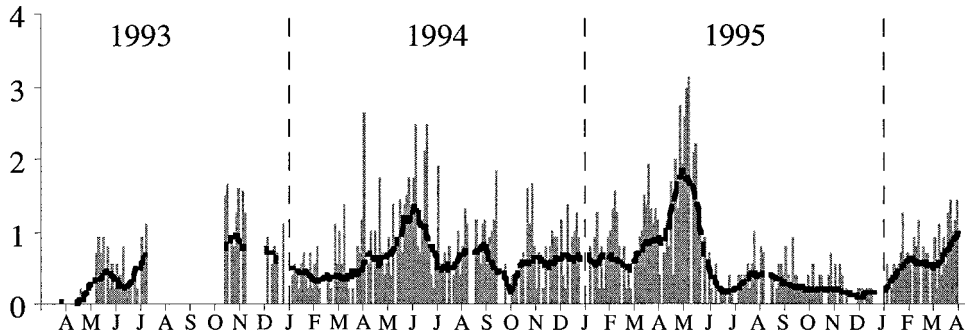
A) Nectophores of *C. appendiculata*

B) Eudoxids of *C. appendiculata*

C) Nectophores of *A. tetragona*

Fig. 1. Daily estimates of abundance of two siphonophores in the Bay of Villefranche from March 1993 to March 1996. Numbers are expressed as ln (individuals per 100 m³) + 1. No samples from mid-July to November 1993. (A) Nectophores of *Chelophyes appendiculata*, (B) eudoxids of *C. appendiculata*, and (C) nectophores of *Abylopsis tetragona*.

A. tetragona was observed in 76% of the Survey-1 samples and the mean density was 1.4 individuals per 100 m³. This siphonophore occurred throughout the year in the bay but animals were less numerous during the hydrological autumn (Fig. 1C). Higher numbers were observed during the spring, especially in 1995. The maximal abundance of 21.8 individuals per 100 m³ occurred on 4 May 1995.

A) Nectophores of *C. appendiculata*

B) Eudoxids of *C. appendiculata*

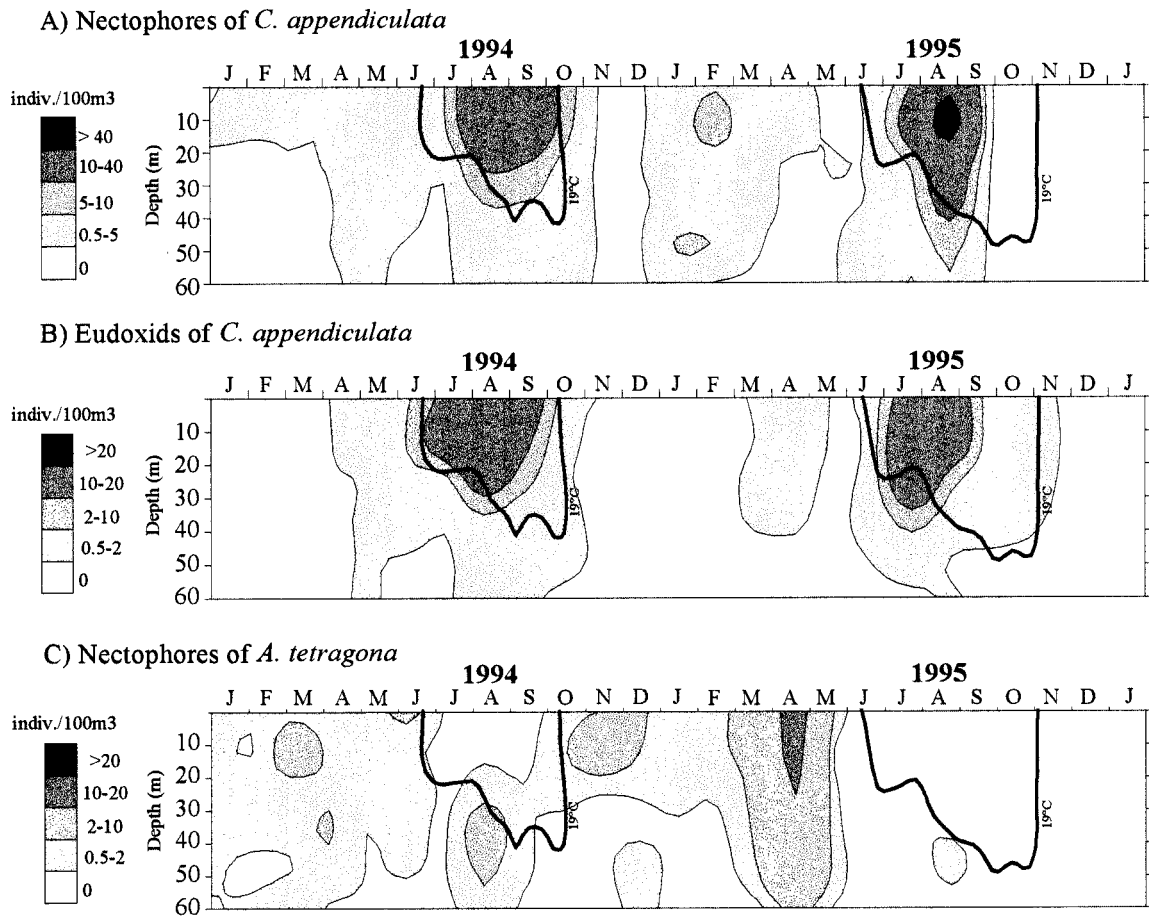

C) Nectophores of *A. tetragona*

Fig. 2. Vertical distribution and seasonal abundance of the two siphonophores between sea surface and 60 m during 1994 and 1995. Abundances (individuals per 100 m^3) are coded in five classes. The isotherm of 19°C (thick line) represents the median temperature in the Bay of Villefranche. (A) Nectophores of *Chelophyes appendiculata*, (B) eudoxids of *C. appendiculata*, and (C) nectophores of *Abylopsis tetragona*.

The vertical distributions of *C. appendiculata* and *A. tetragona* and fluctuations of their distribution as a function of season were analysed from samples collected during Survey-2. The lowest sea surface temperature measured in the Bay was close to 13°C and the highest was close to 25°C. Therefore, 19°C was considered to be the median temperature noted in the Bay. The thermal stratification is represented in Fig. 2, with the 19°C isoline, separating colder (<19°C) from warmer and stratified waters (>19°C).

Both asexual and reproductive stages of *C. appendiculata* showed a similar vertical distribution (Fig. 2A and B). They occurred mainly between 10

and 30 m, with 76.9% of all the nectophores and 88.1% of all the eudoxids found in the upper 30 m. When the thermal stratification was most pronounced (from June to September), abundances were greatest in the upper layers, where temperatures exceeded 19°C. Maxima were observed during summer at 10 m depth: there were 68.4 nectophores per 100 m^3 on 24 August 1995 and 178.8 eudoxids per 100 m^3 on 23 August 1994. From January to May, nectophores were distributed between the sea surface and 60 m depth, conforming to a homothermal and cold or a less stratified water column. Eudoxids were distributed throughout the water column (0–60 m) during this less stratified period.

During this survey, *A. tetragona* was distributed relatively homogeneously through the water column sampled (Fig. 2C): 20.8% were collected at 10 m depth, 21.4% at 20 m, 16.6% at 30 m, 19.3% at 40 m, 13.2% at 50 m and 8.6% at 60 m. However, seasonal fluctuations were noted. Animals were distributed through the sampled water column during the winter months and at the beginning of spring, when the thermal gradient between sea surface and 60 m depth was not established. When the stratification was pronounced, this species was less abundant; individuals occurred only below the 19ºC isotherm in 1994, and were absent from the Bay in 1995.

To detect possible links between environmental factors and animals, as in Buecher et al. (1997) for the Trachymedusae *Liriope tetraphylla*, the method of Perry and Smith (1994) was applied to the Survey-2 data and their corresponding hydrological data. During this period, throughout the water column, temperatures varied from 12.86º to 25.02ºC and salinities from 37.64 to 38.90‰. *Chelophyes* did not display a strong thermal preference (Fig. 3A and B). Asexual nectophores were between 13º and 21ºC and eudoxids from 16º to 25ºC. Their salinity preferences were more limited than their thermal preferences and these two stages were most commonly found at salinities between 37.90 and 38.30‰ (more than 80% of the nectophore population was found in this salinity range, as was more than 70% of the eudoxid population). *Abylopsis* were most frequently collected when temperatures were close to 15ºC (almost 80% of the population was found at less than 15ºC) and when salinities ranged between 37.80 and 38.20‰ (Fig. 3C). Few animals were collected at temperatures above 19ºC. This thermal preference explains the deeper location of *Abylopsis* when the water column was highly stratified.

Nectophores of *C. appendiculata* occurred in 195 out of 1244 weeks in the 27-year Survey-3 (Fig. 4A). In nearly all years, nectophores occurred in the Bay from the end of April to September (from the 17th week to the 40th), but their numbers were relatively low in July and August. In 1967, 1973 and from 1978 to 1980, nectophores were almost absent in the Bay. Conversely, from 1985 onwards, *C. appendiculata* was well represented. The reproductive stage was collected only in 63 weeks in Survey-3. Maximal abundances were still noted from April to May and

in September (Fig. 4B). Eudoxids were almost absent in several years of this survey; maximal abundance occurred in 1981.

A. tetragona was collected in 134 out of 1244 weeks in Survey-3. During the years 1976 to 1984 and also in 1971, it was rare or even absent (Fig. 5). Very high densities were rare and a maximum of 7.6 individuals per 10 m³ was observed at the beginning of May (18th week) in 1980. It was more commonly found in the Bay from April to June (15th to 23rd week), but was always rare in winter.

4. Discussion

Siphonophores are recognised as voracious predators which could have a major impact on the structure and dynamics of the zooplankton (e.g. Alldredge, 1984; Mackie et al., 1987; Matsakis and Conover, 1991). Copepods are the principal types of prey of the calycophoran siphonophores (Purcell, 1981a). The three surveys of the present study provide information on when and where these predators occur.

In the northwestern Mediterranean, previous investigations (e.g. Leloup, 1935; Bigelow and Sears, 1937; Patriti, 1964) have already described seasonality and vertical distribution of *Chelophyes appendiculata* and *Abylopsis tetragona*. However, their samples were taken over a short period and without considering temporal and vertical distribution simultaneously. The combination of the three complementary approaches in the present paper allows a detailed description of the spatio–temporal distribution of these two commonest siphonophores in a fixed shallow Mediterranean station. Moreover, the long-term observations showing the significance of the pluriannual studies and the vertical sampling illustrating biological processes on a small vertical scale were not executed in any of the previous surveys.

Nonetheless, the seasonality of *C. appendiculata* and *A. tetragona* in the Bay of Villefranche can be compared with previous reports, especially with results obtained in the northwestern Mediterranean basin (e.g. Leloup, 1935, 1936; Trégouboff and Rose, 1957). In these previous studies, as in the present work, *C. appendiculata* occurs throughout
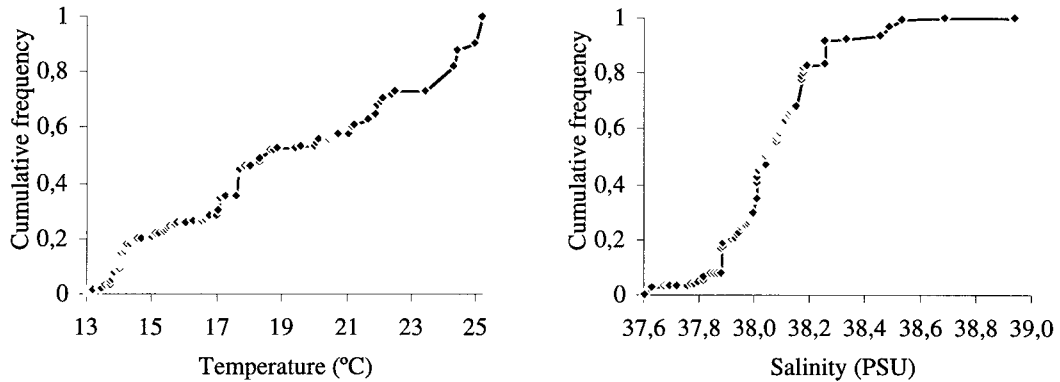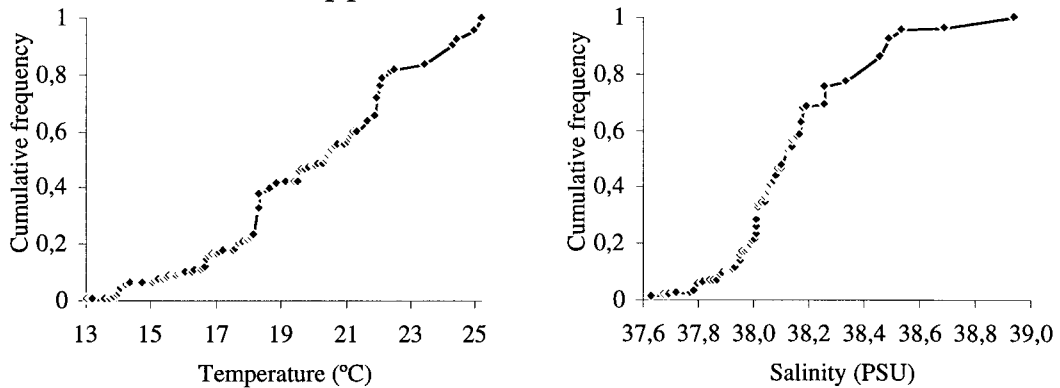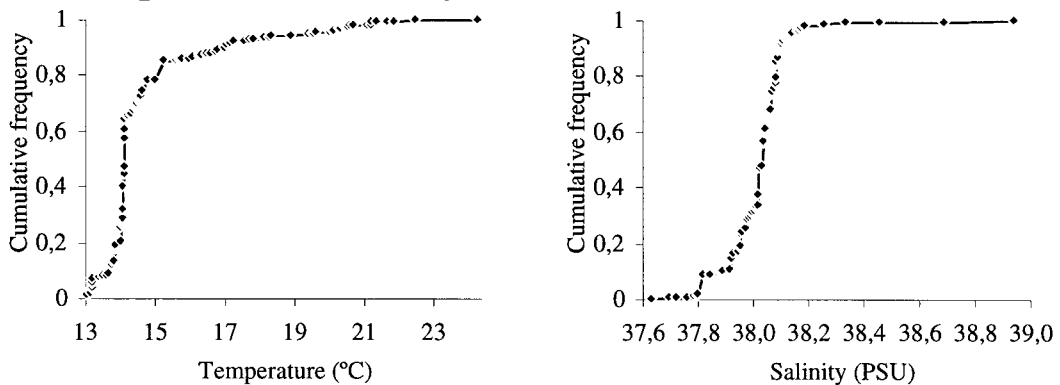
A) Nectophores of *C. appendiculata*

B) Eudoxids of *C. appendiculata*

C) Nectophores of *A. tetragona*

Fig. 3. Cumulative frequency of two siphonophores in relation to temperature (left) and salinity (right). (A) Nectophores of *Chelophyes appendiculata*, (B) eudoxids of *C. appendiculata*, and (C) nectophores of *Abylopsis tetragona*.

A)   Nectophores of *C. appendiculata*

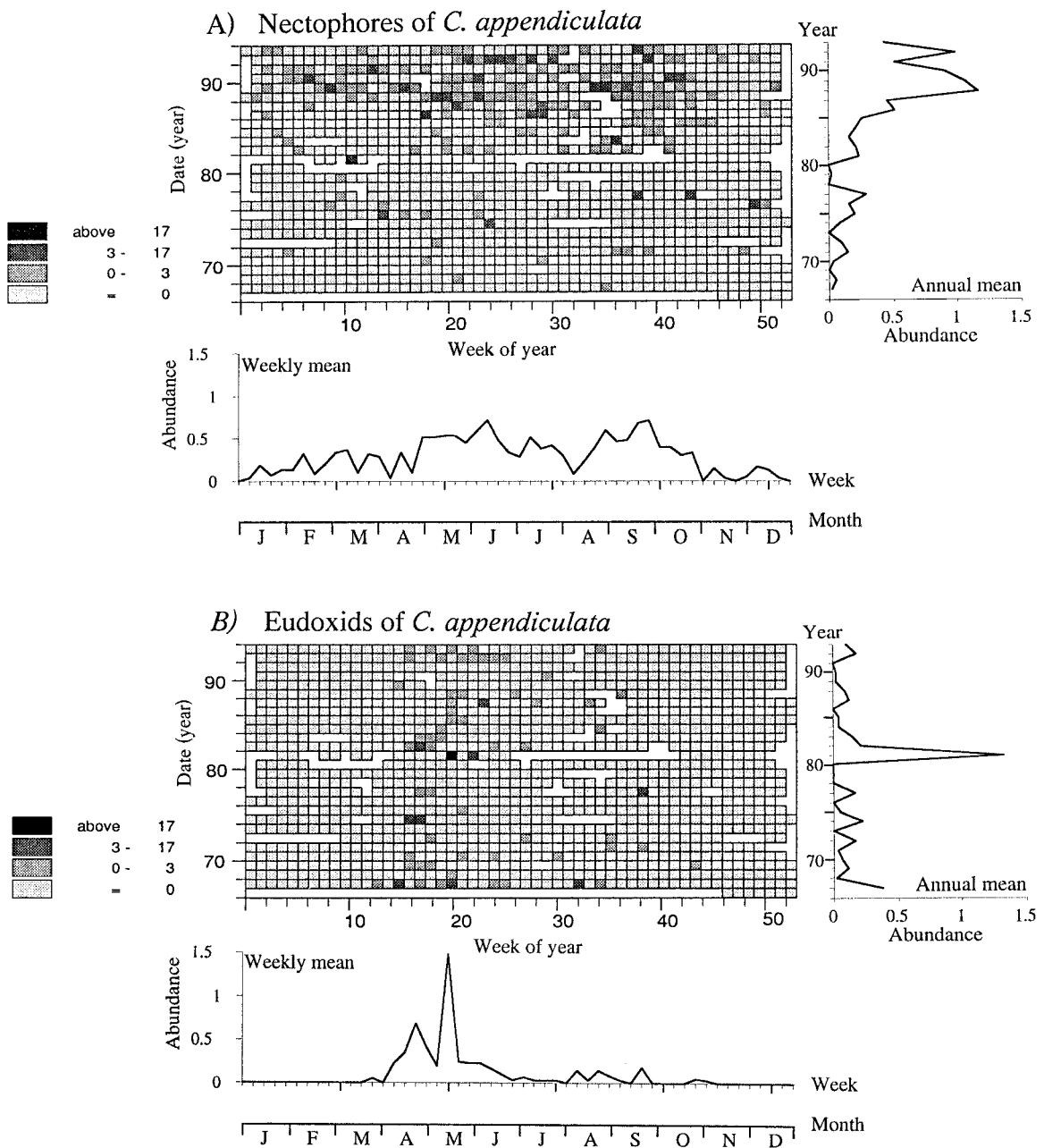## B)   Eudoxids of *C. appendiculata*

Fig. 4. Long-term record of the abundance of *Chelophyes appendiculata* (A: nectophores, B: eudoxids) in the Bay of Villefranche from November 1966 to December 1993. (Centre) Buys-Ballot table: years are in rows and weeks in columns. Abundances (number of individuals per 10 m^3) are represented on a geometric scale (Frontier, 1969). (Right) Annual means. (Bottom) Weekly means (abundances in number of individuals per 10 m^3).
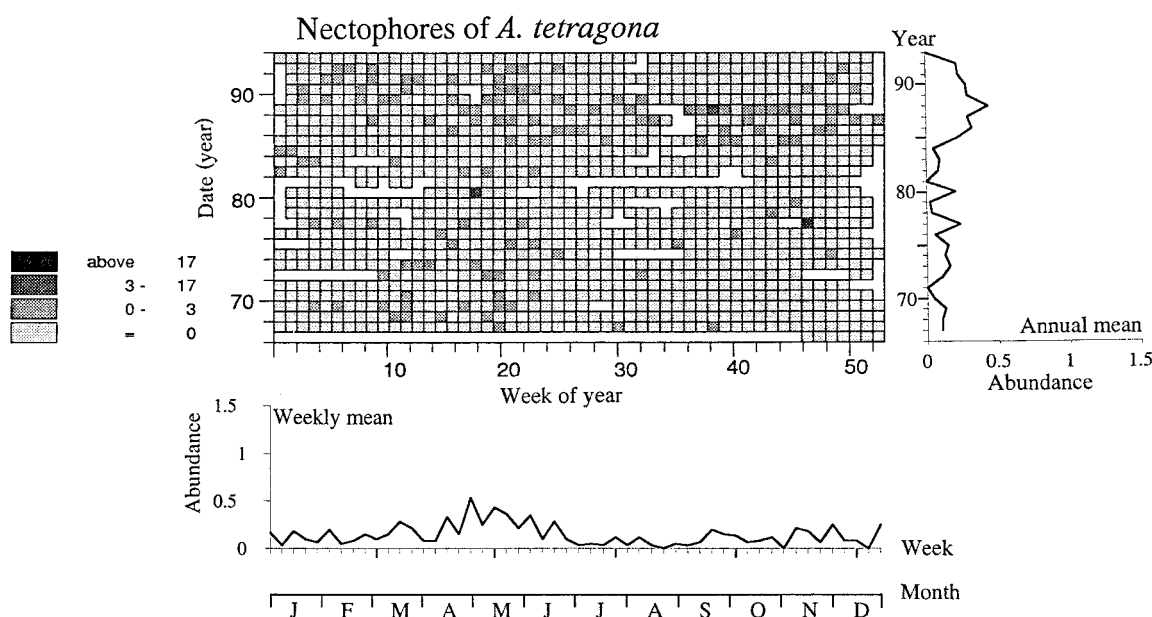
Fig. 5. Long-term records of weekly abundance of *Abylopsis tetragona* in the Bay of Villefranche from November 1966 to December 1993. (Centre) Buys-Ballot table: years are in rows and weeks in columns. Abundances (number of individuals per 10 m^3) are represented on a geometric scale (Frontier, 1969). (Right) Annual means. (Bottom) Weekly means (abundances in number of individuals per 10 m^3).

the year and is always least abundant in winter. Two periods of peak abundance are evident: generally in spring and in autumn (corresponding in fact to the end of the hydrological summer) (Franqueville, 1971; Dowidar, 1992; Sardou et al., 1996). *A. tetragona* also has a wide temporal distribution with minima from October to February and maxima from June to August. However, in the Bay of Villefranche or near its entrance (3–6 miles), greater numbers of *A. tetragona* appear earlier (April to June) (Leloup, 1935; Sardou et al., 1996; the present work). In the Bay of Villefranche, *Abylopsis* is still present between the two peaks of *Chelophyes*. A short time-lag between peak abundances of these two species is demonstrated from Survey-1, as observed by Sardou et al. (1996), illustrating a temporal succession of maximal abundances of these two siphonophores.

Bigelow and Sears (1937) note that the breeding season of *Chelophyes* in the Mediterranean is spring and early summer. This reproductive period is similar elsewhere, for instance near the Canary Islands (Pugh, 1974). In the Bay of Villefranche, the breeding season was determined by successions between higher abundances of the asexual and the sexual

stages, suggesting that the period separating maximal abundances corresponded to successive generations. Calycophoran siphonophores have two alternating pelagic generations: the asexual (nectophore) and the reproductive (eudoxid) stages. Eudoxids, released by abundant nectophores in autumn, grow and after maturation produce new larvae. Seven months separate numerous autumn eudoxids from spring adult nectophores. These newly released eudoxids are numerous in April and May. The second peak of nectophores in October is explained by reproduction of the spring eudoxid population. The lowest temperatures from January to March induce a two-month difference between duration of the fall–winter generation and the spring–summer one. These results agree with the two generations of *Chelophyes* observed by Patriti (1964) in the Gulf of Marseilles and by Gili et al. (1987a) on the Catalan coast. No reproductive stages of *Abylopsis* were analysed in this study, but Bigelow and Sears (1937) and Gili et al. (1987b) report a spring (April to June) breeding season for this siphonophore.

The results of Survey-1 demonstrate some variations in population dynamics between the years

of observation, especially between 1994 and 1995, which complicates generalisation of the annual cycle of these species. On the Catalan coast, Vives (1966) noticed the same type of fluctuations with *C. appendiculata* between 1955 and 1957 (when abundances were high) and 1961 (when abundances were low). A survey over several years appears to be essential to identify a characteristic seasonality; the long-term series strengthens the description of this typical cycle, without considering interannual fluctuations of abundances. On the other hand, it also shows the long-term fluctuations of these populations. The results of Survey-3 show that *Chelophyes* and *Abylopsis* were more abundant starting from 1980 and especially after 1984. The long-term hydrological series reveals important changes in temperature and salinity fluctuations in the Bay (Buecher et al., 1997). These hydrological changes correspond to the beginning of the hypersaline period in 1980 and of the warm period in 1984. At the same time, years with maximal abundances of these calycophoran siphonophores correspond to one of the most important climatic events of the last 30 years noted in this area, viz. the dry period from 1980 to 1990 described by Fromentin and Ibañez (1994). Thus *C. appendiculata* and *A. tetragona* were mainly present when the water column was warm and hypersaline, coinciding also with less rainy years.

Animals collected during the 27-year survey were less numerous than in the other two series, especially when abundances of 1993 (a year included in Survey-1 and Survey-3) are compared. These lower concentrations could be due to inadequate sampling by the Juday–Bogorov net, which filters only 10 m^3 per haul and which has a small mesh size. Indeed, Patriti (1964) has demonstrated that the Juday–Bogorov net is inappropriate to study siphonophores. However, even if this 27-year series appears unsuitable to give quantitative information, the long-term data from it are qualitatively valuable.

Long-term fluctuations of *Chelophyes* and *Abylopsis* from this study are compared with those of other species from the same long-term series (Beck, 1993; Ménard et al., 1994; Buecher, 1996). Changes in the zooplankton composition have been observed in the Bay of Villefranche from long-term studies since 1966, as is also the case in the English Channel (e.g. Cushing and Dickson, 1976; Southward, 1980,

1984; Southward et al., 1988). Overall, the zooplankton diversity was low until the 1980s; *Lensia subtilis*, *Muggiaea kochii*, *Sagitta minima* and *Sagitta setosa* are the most frequently collected species (Beck, 1993). This period also corresponds to a less salty and cold water column. Then the diversity increased, especially after 1985. *Muggiaea kochii* was progressively replaced by *Muggiaea atlantica*, *Sagitta minima* decreased, whereas *Thalia democratica* and *Centropages typicus* increased (Beck, 1993; Ménard et al., 1994). The increase of gelatinous carnivores (such as the hydromedusae *Rhopalonema velatum* and *Solmundella bitentaculata* and siphonophores *C. appendiculata* and *A. tetragona*) since 1985 also corresponds to the long-term warming up of the water column. Some authors (e.g. Raymont, 1983; Gili et al., 1987a) have demonstrated that temperature is one of the factors with which seasonal presence of many species in the zooplankton best correlates. It appears that environmental conditions, especially long-term fluctuations, control the plankton diversity and allow successions of species of the same trophic level. Some biological successions were noted in the English Channel as well: for example, *Aglantha digitalis* (Trachymedusae) was replaced by *Liriope tetraphylla* (Trachymedusae), or *Sagitta elegans* (chaetognath) was replaced by *Sagitta setosa* (chaetognath) (Southward, 1980, 1984). In the Bay of Villefranche, previous studies of other coelenterates such as *Liriope tetraphylla* (Trachymedusae), ephyrae of *Pelagia noctiluca* (Scyphomedusae) (Goy et al., 1989b; Morand, 1989; Buecher et al., 1997) or *Leucothea multicornis* (ctenophore) (Morand and Dallot, 1985; Goy et al., 1989a), salps such as *Thalia democratica* or *Salpa fusiformis* (Ménard et al., 1994) or copepods such as *Calanus helgolandicus* or *Calanus minor* (Beck, 1993) have also shown that some biological successions occur at the same trophic level, and that the whole pelagic ecosystem is influenced by the long-term environmental fluctuations, especially rising sea temperature in the Bay. I suspect that these changes describing zooplankton successions or specific compositions correspond to competitive exclusions at the same trophic level. Further studies are needed to prove this statement. Continuation of this long-term survey may also confirm repetition of all of these successions.

Previous investigations of vertical distribution in

the Mediterranean have identified *C. appendiculata* and *A. tetragona* as epipelagic species occurring almost exclusively between 0 and 300 m (Casanova, 1970; Ianora and Scotto di Carlo, 1981; Gili et al., 1987b). Numerous studies of siphonophores in this area have typically been carried out during a restricted period of time and most of them describe diel vertical migration (DVM) (Franqueville, 1970; Palma, 1985; Laval et al., 1989; Andersen et al., 1992). Various surveys have demonstrated the existence of variations in vertical distributions according to the season. Thus, during summer, *Chelophyes* has a distribution closer to the surface (above 40 m as stated Bigelow and Sears, 1937), while *Abylopsis* penetrates to greater depths (Bigelow and Sears, 1937; Gili et al., 1987b). At our shallower sampling stations, this contrasting distribution between the two species is also observed in summer. As Lo and Biggs (1996) found at Bermuda, the present study shows high numbers of *C. appendiculata* throughout a thermally stratified water column. It also shows that *A. tetragona* occurs essentially in a mixed and cold column and becomes less numerous when the seasonal thermocline develops.

On a larger depth scale, the same type of vertical segregation was also noted offshore in the Ligurian Sea, reinforcing the conclusion of temporal and spatial partitioning between the two siphonophores (Andersen et al., 1992). Andersen et al. (op. cit.) summarised the distribution of the most numerous species of siphonophores: the DVM of *C. appendiculata* ranged from 100 to 450 m (corresponding to the distance between day and night distributions) and this species was distributed in the upper 75 m at night. DVM of *A. tetragona* was about 400 m and this species occurred in the upper 100 m at night.

However, in coastal waters the behaviour of these siphonophores is different from the offshore observations. During the day, animals are mostly abundant near the sea surface (Baussant, 1993). In *Chelophyes*, DVM is limited to less than 100 m and that of *Abylopsis* is negligible (Palma, 1985).

Over the entire temperature and salinity range measured in the Bay of Villefranche (from 12.86° to 25.2°C and from 37.64 to 38.90‰), both species of siphonophores were always present, but they were rarer at extreme values. The thermal and salinity preferences observed in the Bay are in the same range of those noted in the Mediterranean by Bigelow and Sears (1937), Vives (1966) and Gili et al. (1987b). From all these results *C. appendiculata* and *A. tetragona* can be defined as eurythermal and euryhaline. This statement is reinforced by the gradients they cross during their diel migrations. Even so, their populations are likely to be sensitive to general changes of the environment rather than to short-term and local hydrological changes. Long-term fluctuations of these populations show that warm and hyperhaline periods are favourable for these species.

5. Conclusion

Many previous studies of *Chelophyes appendiculata* and *Abylopsis tetragona* conducted in the Mediterranean include spatio–temporal distribution of these two siphonophores, but they do not combine short-term with long-term fluctuations and with small-scale vertical distribution. The three different time series analysed in the present study allow a description of the occurrence of these two common species in the Bay of Villefranche. Species successions in the siphonophore populations, similar to those suggested by Gili et al. (1987b), are noted for *Chelophyes* and *Abylopsis* both seasonally and through the water column. According to their occurrence and their vertical distribution, these two species are characterised as eurythermal and euryhaline. However, the abundance of *Chelophyes* and *Abylopsis* shows the same pattern as the long-term fluctuations in temperature and salinity, with maximal numbers when temperature and salinity are above the long-term average. During their periods of occurrence in this shallow and coastal area, these two calycophoran siphonophores follow each other in time and space, indicating the omnipresence of this trophic level during the year and between the sea surface and 80 m depth.

References

Alldredge, A.L., 1984. The quantitative significance of gelatinous zooplankton as pelagic consumers. In: Fasham, M.J.R. (Ed.), Flow of Energy and Materials in Marine ecosystems. Plenum Press, New York, pp. 407–433.

Alvariño, A., 1971. Siphonophores of the Pacific with a review of the world distribution. Bull. Scripps Inst. Oceanogr. 16, 1–432.

Alvariño, A., 1985. Predation in the plankton realm: mainly with reference to fish larvae. Invest. Mar. Cicimar 2, 1–122.

Andersen, V., Sardou, J., Nival, P., 1992. The diel migrations and vertical distributions of zooplankton and micronekton in the North-western Mediterranean Sea. II. Siphonophores, hydromedusae and pyrosomids. J. Plankton Res. 14, 1155–1169.

Arai, M.N., 1988. Interactions on fish and pelagic cœlenterates. Can. J. Zool. 66, 1913–1927.

Baussant, T., 1993. Analyse saptio-temporelle du macroplancton et du micronecton observés par echosondage en mer Ligure (Méditerranée Nord-Occidentale). Ph.D. thesis, P. and M. Curie Univ., Paris, 144 pp.

Beck, O., 1993. Les variations planctoniques et climatiques en Méditerranée Nord-Occidentale. DEA Rep., P. and M. Curie Univ., Paris, 33 pp.

Béthoux, J.-P., Prieur, L., Bong, J.-H., 1988. Le courant Ligure au large de Nice. Oceanol. Acta Special Issue 9, 59–67.

Bigelow, H.B., Sears, M., 1937. Siphonophorae. Rep. Dan. Oceanogr. Exped. 1908–1910, Mediterr. Adjac. Seas, II (Biology). Copenhagen, pp. 1–144.

Boucher, J., Thiriot, A., 1972. Zooplancton et micronecton estivaux des deux cents premiers mètres en Méditerranée Occidentale. Mar. Biol. 15, 47–56.

Buecher, E., 1996. Etude écologique des carnivores gélatineux — Hydroméduses, Scyphoméduses, Siphonophores et Cténophores — dans la rade de Villefranche-sur-Mer. Ph.D. thesis, P. and M. Curie Univ., Paris, 183 pp.

Buecher, E., 1997. Distribution and abundance of *Pleurobrachia rhodopis* (Cydippid Ctenophore) in the Bay of Villefranche-sur-Mer (Northwestern Mediterranean) from three different planktonic time series. Ann. Inst. Océanogr. Paris 72, 173–184.

Buecher, E., Goy, J., Planque, B., Etienne, M., Dallot, S., 1997. Long-term fluctuations of *Liriope tetraphylla* in Villefranche Bay between 1966 and 1993 compared to *Pelagia noctiluca* populations. Oceanol. Acta 20, 145–158.

Casanova, J.-P., 1970. Essai de classement bathymétrique des formes zooplanctoniques en Méditerranée. Rev. Trav. Inst. Pêches Marit. 34, 45–58.

Cushing, D.H., Dickson, R.R., 1976. The biological response in the sea to climatic changes. Adv. Mar. Biol. 14, 1–122.

Dowidar, M.M., 1992. Biométrie et croissance des Siphonophores et Méduses de la rade de Villefranche-sur-Mer et étude au laboratoire de deux espèces de méduses. Ph.D. thesis, P. and M. Curie Univ., Paris, 104 pp.

Etienne, M., Corre, M.C., Dallot, S., Nival, P., 1991. Observations hydrologiques à une station côtière méditerranéenne.

Point B — Rade de Villefranche-sur-Mer (43°41′10″N–7°19′00″E). Ifremer, Campagnes Océanogr. Fr. 14, 1–89.

Franqueville, C., 1970. Etude comparative du macroplancton en Méditerranée Nord-Occidentale par plongées en soucoupe SP 350 et pêches au chalut pélagique. Mar. Biol. 5, 172–179.

Franqueville, C., 1971. Macroplancton profond (invertébrés) de la Méditerranée nord-occidentale. Tethys 3, 11–56.

Fromentin, J.M., Ibañez, F., 1994. Year-to-year changes in meteorological features of the French coast area during the last half-century. Examples of two biological responses. Oceanol. Acta 17, 285–296.

Frontier, S., 1969. Sur une méthode d'analyse faunistique rapide du zooplancton. J. Exp. Mar. Biol. Ecol. 3, 18–26.

Gamulin, T., Krsinic, F., 1993a. On the occurrence of calycophores (Siphonophora) in the southern Adriatic and Tyrrhenian Sea: a comparison of the annual cycles off Dubrovnik and Naples. J. Plankton Res. 15, 855–865.

Gamulin, T., Krsinic, F., 1993b. Distribution and abundance of calycophores (Siphonophora, Calycophorae) in the Mediterranean and Adriatic Sea. Mar. Ecol. 14, 97–111.

Gili, J.-M., Pagès, F., Vives, F., 1987a. Distribution and ecology of a population of planktonic cnidarians in the Western Mediterranean. In: Bouillon, J., Boero, F., Cicogna, F., Cornelius, P.S.F. (Eds.), Modern Trends in the Systematics, Ecology, and Evolution of Hydroids and Hydromedusae. Clarendon Press, Oxford, pp. 157–170.

Gili, J.M., Pagès, F., Riera, T., 1987b. Distribución de las especies más frecuentes de sifonóforos calicóforos en la zona norte del Mediterráneo occidental. Inves. Pesq. 51, 323–338.

Gili, J.M., Pagès, F., Sabates, A., Ros, J.D., 1988. Small-scale distribution of a cnidarian population in the western Mediterranean. J. Plankton Res. 10, 385–401.

Gostan, J., 1968. Contribution à l'étude hydrologique du bassin liguro-provençal entre la Riviera et la Corse; distribution et variations saisonnières de la température, de l'oxygène et des phosphates minéraux dissous dans les masses d'eau superficielles, intermédiaires et profondes. Ph.D. thesis, P. and M. Curie Univ., Paris, 206 pp.

Goy, J., Thiriot, A., 1976. Conditions estivales dans la divergence de Méditerranée Nord-Occidentale. II. Macroplancton et micronecton. Etude qualitative et estimation quantitative des Cnidaires et des Euphausiacées. Ann. Inst. Océanogr. Paris 52, 33–44.

Goy, J., Dallot, S., Morand, P., 1989a. Les proliférations de la méduse *Pelagia noctiluca* et les modifications associées de la composition du macroplancton gélatineux. Océanis 15, 17–23.

Goy, J., Morand, P., Etienne, M., 1989b. Long-term fluctuations of *Pelagia noctiluca* (Cnidarian, Scyphomedusae) in the western Mediterranean Sea. Prediction by climatic variables. Deep-Sea Res. 36, 269–279.

Ianora, A., Scotto di Carlo, B., 1981. The distribution and annual cycles of Siphonophora Calicophora in the Gulf of Naples and adjacent waters. Arch. Oceanogr. Limnol. 20, 51–65.

Kendall, M., 1976. Time-Series, 2nd ed. Griffin, London, 197 pp.

Lakkis, S., 1971. Contribution à l'étude du zooplancton des eaux libanaises. Mar. Biol. 11, 138–148.

Laval, P., Braconnot, J.-C., Carré, C., Goy, J., Morand, P., Mills,

C.E., 1989. Small-scale distribution of macrozooplankton and micronekton in the Ligurian Sea (Mediterranean Sea) as observed from the manned submersible Cyana. J. Plankton Res. 11, 665–685.

Leloup, E., 1935. Les Siphonophores de la rade de Villefranche-sur-Mer (Alpes Maritimes, France). Bull. Mus. R. Hist. Nat. Belg. 11, 1–12.

Leloup, E., 1936. Siphonophores récoltés dans la région de Monaco. Bull. Inst. Océanogr. Monaco 703, 1–15.

Lo, W.T., Biggs, D.C., 1996. Temporal variability in the night-time distribution of epipelagic siphonophores in the North Atlantic Ocean at Bermuda. J. Plankton Res. 18, 923–939.

Longhurst, A.R., 1985. The structure and evolution of plankton communities. Prog. Oceanogr. 15, 1–35.

Mackie, G.O., Pugh, P.R., Purcell, J.E., 1987. Siphonophore biology. Adv. Mar. Biol. 24, 97–262.

Margulis, R.Y., 1972. Factors determining the large-scale distribution of Siphonophores of suborders Physophorae and Calycophorae in the Atlantic Ocean. Oceanology 12, 420–425.

Matsakis, S., Conover, R.J., 1991. Abundance and feeding of Medusae and their potential impact as predators on other zooplankton in Bedford Basin (Nova Scotia, Canada) during spring. Can. J. Fish. Aquat. Sci. 48, 1419–1430.

Ménard, F., Dallot, S., Thomas, G., Braconnot, J.C., 1994. Temporal fluctuations of two Mediterranean salp populations from 1967 to 1990. Analysis of the influence of environmental variables using a Markov chain model. Mar. Ecol. Prog. Ser. 104, 139–152.

Mills, C.E., 1995. Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. ICES J. Mar. Sci. 52, 575–581.

Morand, P., 1989. La méduse *Pelagia noctiluca* en Méditerranée Occidentale: de la dynamique de population aux variations à long terme. Ph.D. thesis, Univ. Paris VII, 191 pp.

Morand, P., Dallot, S., 1985. Variations annuelles et pluriannuelles de quelques espèces du macroplancton côtier de la mer Ligure. Rapp. Comm. Int. Mer Méditerr. 29, 295–297.

Palma, S.G., 1985. Migración nictemeral del macroplancton gelatinoso de la bahía de Villefranche-sur-Mer, Mediterráneo Noroccidental. Invest. Pesq. 49, 261–274.

Patriti, G., 1964. Les Siphonophores Calycophores du Golfe de Marseille. Rec. Trav. St. Mar. End. Bull. 35 (51), 185–258.

Patriti, G., 1969. Apperçu sommaire sur la distribution des Siphonophores dans le Golfe de Gabes et dans les eaux cotières de Tripolitane. Campagne de la 'Calypso', Avril–Mai 1965. Tethys 1, 249–254.

Perry, R.I., Smith, S.J., 1994. Identifying habitat associations of marine fishes using survey data: an application to the Northwest Atlantic. Can. J. Fish. Aquat. Sci. 51, 589–602.

Pugh, P.R., 1974. The vertical distribution of the siphonophores collected during the SOND cruise, 1965. J. Mar. Biol. Assoc. UK 54, 25–90.

Pugh, P.R., 1975. The distribution of the siphonophores in a transect across the North Atlantic Ocean at 32ºN. J. Exp. Mar. Biol. Ecol. 20, 77–97.

Purcell, J.E., 1981a. Dietary composition and diel feeding patterns of epipelagic siphonophores. Mar. Biol. 65, 83–90.

Purcell, J.E., 1981b. Feeding ecology of *Rhizophysa eysenhardti*, a siphonophore predator of fish larvae. Limnol. Oceanogr. 26, 424–432.

Purcell, J.E., 1985. Predation on fish larvae by pelagic cnidarians and ctenophores. Bull. Mar. Sci. 37, 739–755.

Raymont, J.E.G., 1983. Plankton and Productivity in the Oceans. Int. Ser. Monogr. Pure and Applied Biology. Pergamon Press, Oxford, 660 pp.

Sardou, J., Andersen, V., 1993. Micronecton et macroplancton en Mer Ligure (Méditerranée): migrations nycthémérales et distributions verticales. Oceanol. Acta 16, 381–392.

Sardou, J., Etienne, M., Andersen, V., 1996. Seasonal abundance and vertical distributions of macroplankton and micronekton in the Northwestern Mediterranean Sea. Oceanol. Acta 19, 645–656.

Southward, A.J., 1980. The western English Channel — an inconstant ecosystem? Nature 285, 361–366.

Southward, A.J., 1984. Fluctuations in the 'indicator' chaetognaths *Sagitta elegans* and *Sagitta setosa* in the Western Channel. Oceanol. Acta 7, 229–239.

Southward, A.J., Boalch, G.T., Maddock, L., 1988. Fluctuations in the herring and pilchard fisheries of Devon and Cornwall linked to change in climate since the 16th century. J. Mar. Assoc. UK 68, 423–445.

Totton, A.K., 1965. A Synopsis of the Siphonophora. British Museum, London, 230 pp.

Trégouboff, G., Rose, M., 1957. Manuel de Planctonologie Méditerranéenne. Vols. I, II. CNRS, Paris, 587 pp.

Vinogradov, M.E., 1970. Vertical Distribution of the Oceanic Zooplankton (Vertikal'noe Raspredelenie Okeanicheskogo zooplanktna). Keter Press, Jerusalem, 339 pp.

Vives, F., 1966. Zooplancton nerítico de las aguas de Castellón (Mediterraneo occidental). Invest. Pesq. 30, 49–166.