Seasonal abundance and vertical distributions of macroplankton and micronekton in the Northwestern Mediterranean Sea

Seasonal cycle
Vertical distribution
Macroplankton
Micronekton

Cycle saisonnier
Distribution verticale
Macroplancton
Micronecton

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ABSTRACT

Based on monthly samplings over an entire year, variations of abundance, vertical distributions and diel vertical migrations are described in the 0-1000 m water column in a coastal area of the Northwestern Mediterranean Sea for the main pelagic invertebrates. Detailed results are given for 21 species of macrozooplankton and micronekton. On an annual basis, the most numerous species by numbers comprised the euphausiid *Meganyctiphanes norvegica*, the pteropod *Cavolinia inflexa*, the siphonophores *Abylopsis tetragona* and *Chelophyes appendiculata*, the crustacean decapods *Sergestes arcticus* and *Pasiphaea sivado*, and the salps *Salpa fusiformis* and *Thalia democratica*. Species of the same genus, such as *Sergestes arcticus*, *S. corniculum* and *S. robustus* or *Pasiphaea sivado* and *P. multidentata*, occurred in maximum numbers at different times of the year. Eighteen out of the twenty-one species studied underwent a more or less extensive diel vertical migration. Some species, such as *Meganyctiphanes norvegica* and the pteropods *Cavolinia inflexa*, *Clio pyramidata* and *Cymbulia peroni*, showed monthly variations in their vertical distributions, migrating to deeper depths in certain seasons.

RÉSUMÉ

Variation saisonnière et distributions verticales du macroplancton et du micronecton en Méditerranée nord-occidentale.

Cette étude, basée sur un échantillonnage mensuel pendant une année, présente la variation d'abondance, les distributions verticales et les migrations dans la colonne d'eau 0-1000 m des principaux invertébrés pélagiques d'une zone côtière de Méditerranée nord-occidentale. Une description détaillée est donnée pour 21 espèces de macroplancton et micronecton. Sur une base annuelle, les espèces les plus abondantes sont l'euphausiacé *Meganyctiphanes norvegica*, le ptéropode *Cavolinia inflexa*, les siphonophores *Abylopsis tetragona* et *Chelophyes appendiculata*, les crustacés décapodes *Sergestes arcticus* et *Pasiphaea sivado*, les salpes *Salpa fusiformis* et *Thalia democratica*. Certaines espèces d'un même genre, telles *Sergestes arcticus*, *S. corniculum* et *S. robustus* ou *Pasiphaea sivado* et *P. multidentata*, présentent leur maximum d'abondance à différentes périodes de l'année. Sur les 21 espèces étudiées, 18 effectuent des migrations verticales de plus ou moins grande amplitude. Les distributions verticales de certaines espèces montrent des variations mensuelles ; par exemple, *Meganyctiphanes norvegica* et les ptéropodes *Cavolinia inflexa*, *Clio pyramidata* et *Cymbulia peroni* sont capturés à des niveaux bathymétriques plus profonds à certaines saisons.

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INTRODUCTION

In the Mediterranean Sea, detailed information on the seasonal abundance or vertical distribution of macroplankton and micronekton has often dealt with a particular group of species, such as pteropods (Rampal, 1967; 1975), euphausiids (Casanova, 1974), crustacean decapods (Casanova, 1977), or the Hydromedusa *Solmissus albescens* (Benović, 1973; Mills and Goy, 1988). On the other hand, data on the simultaneous vertical distributions of various species exist, but for restricted periods of time (*e.g.* Castelbon, 1987; Laval *et al.*, 1989; Andersen and Sardou, 1992). Simultaneous studies of various species would provide information on the dynamics of the ecosystem. In the Northwestern Mediterranean, such a study was performed by Franqueville (1971), who described the seasonal variation of abundance and the vertical distributions of the dominant pelagic invertebrates. But his sampling was more or less irregular over a two-year period and performed in a large area, and the results were given on a seasonal basis.

The purpose of this paper is therefore to present, in detail, the monthly variation of abundance and the day and night vertical distributions of the major macroplanktonic and micronektonic invertebrate species in the upper 1000 m of the water column. This study was carried out in a coastal area of the Ligurian Sea (Northwestern Mediterranean), and is based on repeated sampling with an Isaac Kidd Midwater Trawl each month during one year. Monthly variations in the abundance and features of the average annual vertical distribution, and in the diel vertical migration (DVM), when it occurs, are presented for 21 species. Monthly vertical distributions are given for the species, showing variations in their preferred daytime and/or nighttime depth in the course of the year.

METHOD

During 1982, a series of horizontal hauls was performed in the Ligurian Sea (Northwestern Mediterranean) in a coastal area (7° 18' E - 7° 20' E, 43° 34' N - 43° 38' N), 3 to 6 miles off Villefranche-sur-Mer, where the water column is 1100-1300 m deep. The sampling area is at a considerable distance from the Ligurian frontal zone, further offshore (Béthoux and Prieur, 1983). All biological samples were taken with a non-closing IKMT (Isaacs Kidd Midwater Trawl 10 feet), with 1-cm mesh net and a mouth area of 9 m^2; the cod-end, 1 m in diameter, has meshes of 3×5 mm. Each month, horizontal hauls were performed by day and at night at five different depths, 35, 150, 300, 500 and 700 m. A sixth depth of 900 m was sampled by day only. The volume of water filtered during each haul amounted to 16 700 m^3 on average. The dates and depths of the 158 hauls are indicated in Table 1.

A depth recorder (Benthos Depth/Time Recorder) was applied during most of the hauls. This allowed us to estimate the mean depths and depth strata explored, and to calculate the volume filtered at the chosen depth and the volume filtered during the ascent. When reaching the desired depth, the net presented some oscillations around this depth; then the IKMT was towed at a mean speed of 1 m s^{-1} for 30 min. At the end of the sampling, some oscillations occurred again before the ascent to the surface. Due to these oscillations, short in duration, the depth strata corresponding to the six mean levels cited above were 0-75, 75-225, 225-400, 400-600, 600-800 and 800-1000 m. The same strategy was applied for the hauls without depth recorder, taking into account the previously observed relationships between wire length, wire angle and ship speed. Knowing the density of each species in the upper layers, in previous trawls of the same series, it was then possible to estimate the number of organisms caught during the ascent of the net, and to correct the number found for the trawl at the desired depth. Density estimates of the organisms were standardized to individuals per 5000 m^3 for each depth (or depth stratum) sampled. The number of individuals per 100 m^2 for the entire water column was also calculated for each month. All the day samples of each month were combined to give average day distributions in the 0-1000 m water column; the night data were similarly treated to give average night distributions in the 0-800 m water column. To assess the vertical partitioning of the species by day and at night, the weighted mean depth (WMD) of each species in the 0-800 m water column was calculated according to the equation:

$$WMD = \Sigma (ni \times di) / \Sigma ni$$

where di is the depth of a sample i and ni is the number of individuals per 5000 m^3 at that depth. Day WMD was also calculated for the 0-1000 m water column.

Table 1

Sampling data for IKMT. D, day; N, night.

	Mean depth					
Date (1982)	**35 m**	**150 m**	**300 m**	**500 m**	**700 m**	**900 m**
19 January						D
25 January	D N	D N	D N	D N	D N	D
15 February				D	D	D D
22 February	D N	D N	D N	D N	D N	D
10 March	D			D	D	
19 March		D	D	D	D	D
24 March	N	N	N	N	N	
29 April	D N	D N	D N	D N	D N	D
11 May	N	D N	D N	D N	D N	D
18 May			D			D
28 May	D	D	D	D	D	D
17 June	D N	D N	D N	D N	D N	D
13 July	D	D	D	D	D	D
22 July	N	D N	D N	D N	D N	D
10 August	D N	D N	D N	D N	D N	
20 September	D N	D N	D N	D N	D N	D
27 September			D	D	D	D
2 October	D			D		
15 October	D D					
25 October	D N	D N	D N	D N	D N	D
2 November	D					
18 November	D N	D N	D N	D N	D N	D
13 December	N	D N	D N	D N	D N	D

RESULTS AND DISCUSSION

Sixty-eight species of micronektonic and macroplanktonic invertebrates were identified in the hauls during the year 1982. Seasonal abundance cycles and vertical distributions are presented for 21 species and a group of six euphausiid species which were not counted separately: *Nematoscelis megalops* and *Euphausia krohni* essentially, then *Euphausia hemigibba* and – in small numbers – *Thysanopoda aequalis, Stylocheiron maximum* and *S. abbreviatum*. We call this group "small euphausiids" in comparison with the greater length of the euphausiid *Meganyctiphanes norvegica* described in detail in the study. The other 41 species appeared irregularly or were not abundant enough in the catches to allow description of their seasonal cycle and vertical distribution.

Seasonal abundance cycles

Table 2 gives the average number of individuals per 100 m^2 from 800 m to the surface, recorded in day and night samples over the year. The euphausiid *Meganyctiphanes norvegica* was the most abundant species during the year, with a mean abundance of 94-166 ind. per 100 m^2. It was followed by the pteropod *Cavolinia inflexa* and the group of small euphausiids (55 to 107 ind. per 100 m^2). The next most abundant species, with densities in the range 23-69 ind. per 100 m^2, were the siphonophores *Abylopsis tetragona* and *Chelophyes appendiculata*, the decapods *Sergestes arcticus* and *Pasiphaea sivado*, the salps *Salpa fusiformis* and *Thalia democratica* and, to a lesser extent, the medusa *Pelagia noctiluca*. Present with mean abundances of 10 to 18 ind. per 100 m^2 over the year, by day or at night, were the pteropod *Clio pyramidata*, the decapod *Gennadas elegans* and the thaliacean *Pyrosoma atlanticum*. The other species described here showed values in the range 0.6 to 9.6 ind. per 100 m^2. Some species showed clear differences between day and night total numbers. These differences could be related to: (i) the occurrence of organisms below 800 m during the day, as shown in the higher total numbers for the 0-1000 m water column than for the 0-800 m one (*e.g. Cavolinia inflexa, Gennadas elegans, Salpa fusiformis*); (ii) the tendency of the species to form swarms at night (high N/D ratios, *e.g. Meganyctiphanes norvegica*). This will be discussed when we consider the vertical distributions.

Monthly variations in abundance of species can be classified according to the seasons of maximal abundance. Twelve species showed a marked peak of abundance in spring (Fig. 1). Moreover 5 species, *Salpa fusiformis, Thalia democratica, Cavolinia inflexa, Phronima sedentaria* and *Phrosina semilunata*, were essentially limited to the spring months (Fig. 1*a-e*). In particular, the salps *Thalia democratica* and *Salpa fusiformis* were caught only from March to June, and from January to May, respectively. The absence or presence in low numbers of these five species during the rest of the year would suggest: (i) their occurrence in densities too low to be caught; (ii) the existence of a seasonal migration to deeper layers, as will be discussed later. Four other species, caught nearly all year long, showed a maximum abundance in spring: *Cymbulia peroni, Sergestes corniculum, Abylopsis tetragona* and *Gennadas elegans* (Fig. 1*f-i*). Some other species showed two peaks of abundance in the course of the year, one in spring and a second one during autumn for *Pyrosoma atlanticum* and *Clio pyramidata*, winter (January) for *Chelophyes appendiculata* (Fig. 1*j-l*). The peak of *Pyrosoma atlanticum* observed in autumn was essentially composed of small (< 7 mm) colonies.

The other species were not at a maximum in spring (Fig. 1*m-v*). Their monthly variation showed: (i) one single peak, in the cases of *Sergestes arcticus* and the small euphausiids (summer), *Solmissus albescens* (October), *Sergestes robustus, Pasiphaea multidentata* and *Acanthephyra pelagica* (January); (ii) two peaks, as for *Pelagia noctiluca* (June and November), *Pasiphaea sivado* (sum-

Table 2

Average number of individuals per 100 m^2 (from 800 m to the surface), recorded in day and night samples over the year. Day numbers for the 0-1000 m water column are indicated in parenthesis when they differ by at least 30 % from the values for the 0-800 m water column. N/D, ratio night:day.

Species	Day	Night	N/D
Medusae			
Pelagia noctiluca (Forskål, 1775)	9.9	28.4	2.9
Solmissus albescens (Gegenbaur, 1856)	4.7	8.3	1.8
Siphonophores			
Abylopsis tetragona (Otto, 1823)	68.8	37.4	0.5
Chelophyes appendiculata (Eschscholtz, 1829)	67.2	36.9	0.6
Pteropods			
Cavolinia inflexa (Lesueur, 1813)	63.9 (92.2)	106.9	1.7
Clio pyramidata (Linne, 1767)	11.0 (15.2)	13.6	1.2
Cymbulia peroni de Blainville, 1818	7.0 (10.6)	9.6	1.4
Amphipods			
Phronima sedentaria (Forskål, 1775)	5.6	2.9	0.5
Phrosina semilunata Risso, 1822	1.2	2.4	2.0
Mysids			
Eucopia unguiculata Willemoes-Suhm, 1875	5.6 (9.6)	6.2	1.1
Euphausiids			
Meganyctiphanes norvegica (M. Sars, 1857)	93.7	166.3	1.8
Small euphausiids	95.8	54.5	0.6
Decapods			
Sergestes arcticus Kröyer, 1855	37.7	55.2	1.5
Sergestes robustus (S.I. Smith, 1882)	2.2 (3.5)	5.7	2.6
Sergestes corniculum Kröyer, 1855	1.6 (2.2)	2.5	1.6
Pasiphaea sivado (Risso, 1816)	26.6	41.2	1.6
Pasiphaea multidentata Esmark, 1866	0.6 (0.8)	1.0	1.7
Gennadas elegans (S.I. Smith, 1882)	10.4 (18.2)	17.6	1.7
Acanthephyra pelagica (Risso, 1816)	1.2 (1.9)	1.9	1.6
Salps			
Salpa fusiformis Cuvier, 1804	23.0 (39.7)	56.5	2.5
Thalia democratica (Forskål, 1775)	32.4	43.7	1.4
Pyrosomids			
Pyrosoma atlanticum Peron, 1804	11.1	7.5	0.7

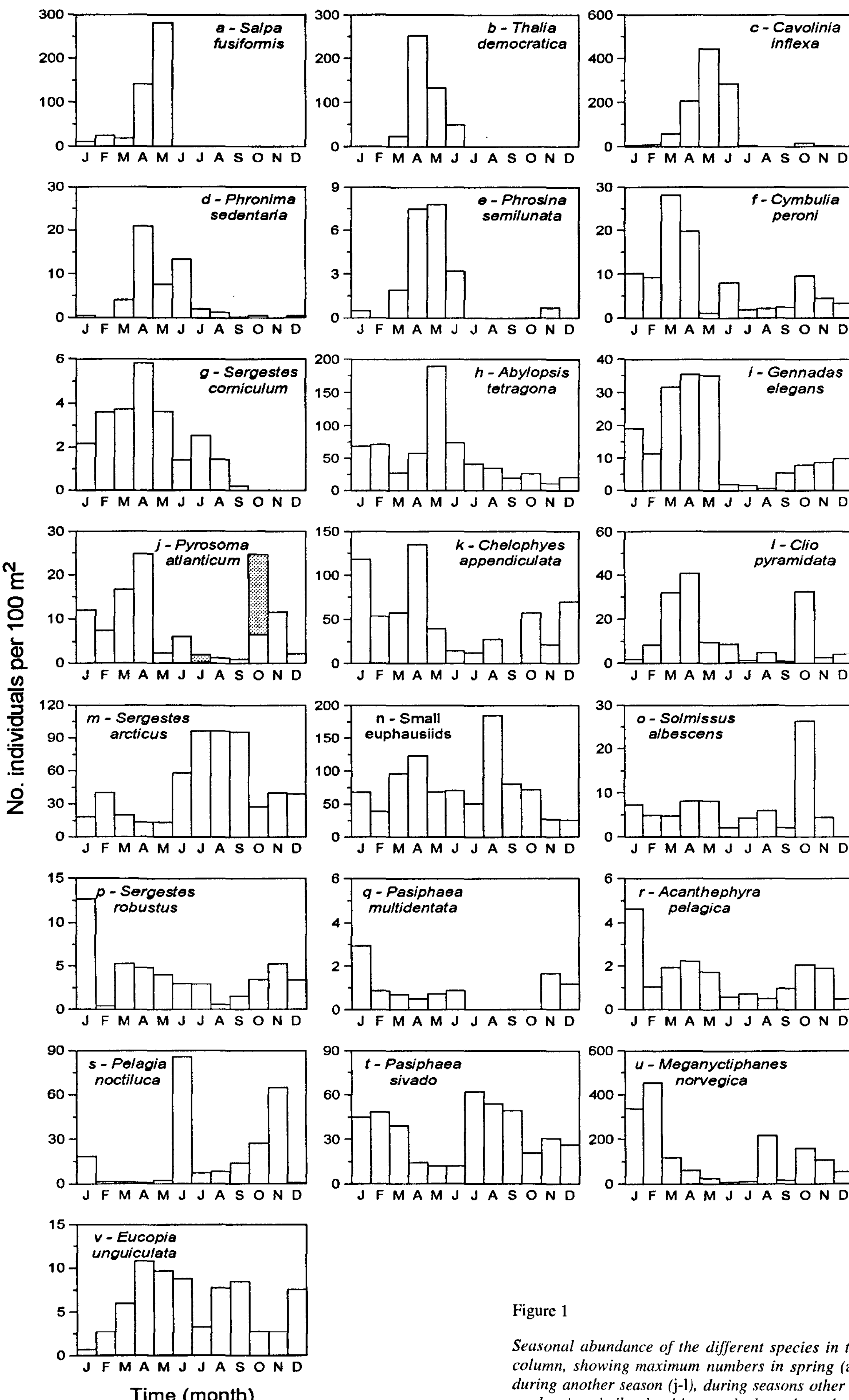

Figure 1

Seasonal abundance of the different species in the 0-800 m water column, showing maximum numbers in spring (a-i), in spring and during another season (j-l), during seasons other than spring (m-u), or showing similar densities nearly throughout the year (v).

mer and winter), *Meganyctiphanes norvegica* (January-February, and to a lower extent August and October); (iii) no marked trend for *Eucopia unguiculata* (formely *E. hanseni, see* Roe, 1984). The three species of *Sergestes* caught here were thus abundant at different times of the year, *Sergestes arcticus* largely dominating, in terms of numbers of animals, the other two. Similarly, when *Pasiphaea sivado* was at its maximum in summer, *Pasiphaea multidentata* was absent from the catches.

The most complete study dealing with the seasonal cycle of various species is that of Franqueville (1971), which allows comparison with our results; Franqueville performed sampling from winter 1967 to autumn 1969. The occurrence or period of abundance of the medusa *Pelagia noctiluca* appears to vary according to the year from these two data sets (absent in 1968 and at a maximum in spring 1969, maximum in summer and autumn in 1982). In fact, *P. noctiluca* is known to have an irregular annual cycle in the Western Mediterranean, occurring in high numbers in various seasons or sometimes absent all year round (Goy *et al.*, 1989*a*; 1989*b*). By contrast, Goy *et al.* (1989*a*) reported that the Hydromedusa *Solmissus albescens* shows a regular annual cycle, with maximum abundance in winter and spring; in this study maximum numbers of this very fragile organism were caught in October. *Abylopsis tetragona* and *Chelophyes appendiculata* were the prevailing siphonophores both in this study and that of Franqueville (1971), with the period of maximum abundance of *C. appendiculata* appearing to vary between years (summer in 1968, spring and autumn in 1969, winter and spring in 1982). The periods of abundance of the pteropods *Cavolinia inflexa* and *Clio pyramidata* are identical in the two considered studies (spring for *C. inflexa*, spring and autumn for *C. pyramidata*), but Franqueville did not observe a spring peak of *Cymbulia peroni*.

The amphipods *Phrosina semilunata* and *Phronima sedentaria* showed a marked peak of abundance in spring. The parasitoid *P. sedentaria*, which depends on salps and pyrosomids for feeding and making its barrel, consequently showed a maximum abundance when these gelatinous organisms are also abundant. *Eucopia unguiculata* is the main mysid species caught in the Mediterranean oceanic waters in the 0-1000 m water column (Casanova, 1970, 1977; Franqueville, 1971; Castelbon, 1987; Andersen and Sardou, 1992; Sardou and Andersen, 1993; present work), and is caught throughout the year. *Meganyctiphanes norvegica* is the most abundant euphausiid species in the Ligurian Sea, accounting for 65 % of the euphausiid population (Casanova, 1974; present data). Differences in the periods of abundance observed and reported by Franqueville (1971) could be explained by the different areas sampled. In fact, large concentrations of adult *Meganyctiphanes norvegica* were frequently observed in winter near the coast in the Ligurian Sea, these high densities being related to breeding behaviour (Casanova, 1974).

In the Northwestern Mediterranean, *Sergestes arcticus* is the most abundant decapod species (Casanova, 1970, 1977; Franqueville, 1971; Castelbon, 1987; present data). In the area covered by our study, *Sergestes arcticus* and *Sergestes robustus* did not show maximum abundance at the same time of the year, in contrast with Franqueville's results. Our results also differ from Franqueville's concerning *Pasiphaea multidentata* and *Pasiphaea sivado*: (i) *P. sivado* was the second most abundant species of decapod in our study whereas it was caught in small numbers by Franqueville; (ii) a discrepancy also exists concerning the season of maximum abundance of the two species. These differences would be particularly important with relation to the role of the carnivorous *P. sivado* in the food web structure. *Gennadas elegans* is among the most abundant decapod species in Mediterranean (Casanova, 1970, 1977; Franqueville, 1971; Castelbon, 1987; Andersen and Sardou, 1992; present data). It was caught in minimum numbers in summer in our own and in Franqueville's study.

In coastal waters off Villefranche-sur-Mer, the salp *Thalia democratica* is regularly observed in large numbers in spring, as in our data, a peak of secondary importance appearing in some years in autumn (Braconnot, 1971; Ménard *et al.*, 1994). The main appearance of *Salpa fusiformis* during the spring months is also well documented (Braconnot, 1971; Franqueville, 1971; Ménard *et al.*, 1994), while *Pyrosoma atlanticum* shows a regular maximum of large colonies in spring and a peak of young colonies in autumn (Franqueville, 1971; present data).

Day and night vertical distributions

The vertical partitioning of the species is presented according to their preferential daytime depths. The species showing monthly variable vertical distributions are described at the end of this section. Table 3 presents for each species

Table 3

*Average weighted mean depths (WMD) at day and night, and existence of DVM or its range in the 0-800 m water column. Day WMDs in the 0-1000 m water column are indicated in parenthesis for the species which are deep-living species by day throughout the year. Values are given as numbers to the nearest 10. * indicates monthly variable depths (see text for details).*

Species	WMD day	WMD night	Migration range (m)
Pelagia noctiluca	540	180	360
Solmissus albescens	570	290	280
Abylopsis tetragona	320	150	170
Chelophyes appendiculata	220	150	70
Cavolinia inflexa	*330	180	150
Clio pyramidata	*520	110	410
Cymbulia peroni	*530	*250	280
Phronima sedentaria	350	100	250
Phrosina semilunata	380	230	150
Eucopia unguiculata	630 (740)	620	no
Meganyctiphanes norvegica	*440	110	330
Small euphausiids	420	240	180
Sergestes arcticus	*410	50	360
Sergestes robustus	660 (750)	290	370
Sergestes corniculum	540 (640)	340	200
Pasiphaea sivado	340	60	280
Pasiphaea multidentata	570 (670)	250	320
Gennadas elegans	610 (730)	280	330
Acanthephyra pelagica	600 (710)	330	270
Salpa fusiformis	*460	610	-
Thalia democratica	60	50	no
Pyrosoma atlanticum (large)	380	170	210

the weighted mean depths (WMD) by day and at night, calculated from the average annual vertical distributions in the 0-800 m water column.

Epiplanktonic species, weak or non-migrants

The salp *Thalia democratica* was typically epiplanktonic (Fig. 2), being concentrated in the upper layer by day and at night, as also observed by Braconnot (1971) and Palma (1985). The siphonophore *Chelophyes appendiculata* occurred essentially in the 75-225 m stratum by day, although it was caught throughout the water column. At night, part of the population reached the upper layer, performing a weak migration of ~70 m in amplitude (*cf.* Tab. 3).

Species with maximum numbers at 300 m during the day

The decapod *Pasiphaea sivado* occurred almost exclusively in the 225-400 m layer by day and was concentrated in the 0-75 m layer at night (Fig. 2), migrating as a compact population over a mean distance of 280 m. The siphonophore *Abylopsis tetragona* was caught over a large water column by day, with maximum numbers at 300 m. At night, it was concentrated in the upper 200 m, performing a migration with an amplitude of ~170 m (*cf.* Tab. 3). Such migratrory behaviour of *A. tetragona* has previously been observed by Franqueville (1971), Andersen *et al.* (1992) and Sardou and Andersen (1993). The vertical distributions of the amphipod *Phrosina semilunata* also extended over large depth ranges, although showing a mean displacement of 150 m upwards at night.

Species with maximum numbers at 500 m during the day

The amphipod *Phronima sedentaria* showed a bimodal day distribution (Fig. 2), with a primary maximum of abundance at 500 m and a secondary one at 150 m, this bimodality being unrelated to variations in the depth of maximum abundance with time. At night, *P. sedentaria* was concentrated in the upper layer. From these vertical distributions it appeared that the deeper part of the population performed an extensive migration of 450 m as amplitude, and the upper part a weak migration with an amplitude of ~100 m. The bimodal day distribution of the group of small euphausiids is related to the different preferential daytime depths of the different species pooled in this group (Franqueville, 1971; Casanova, 1974; Andersen and Sardou, 1992).

Solmissus albescens and *Pelagia noctiluca* were absent from the upper 400 m by day and showed a maximum of abundance at 500 m (Fig. 2). At night, most of the *Pelagia* were caught in the 0-75 m layer, performing a migration of 360 m as mean amplitude (*cf.* Tab. 3). In contrast, only part of the population of *Solmissus* reached the shallow layers, undertaking a mean displacement of 280 m. The extensive DVM of *Solmissus* has been previously reported (Benović, 1973; Castelbon, 1987; Mills and Goy, 1988; Laval *et al.*, 1989; Andersen *et al.*, 1992; Sardou and Andersen, 1993). Mills and Goy (1988), summarizing the year-round daytime vertical distribution of *S. albescens*, reported that this

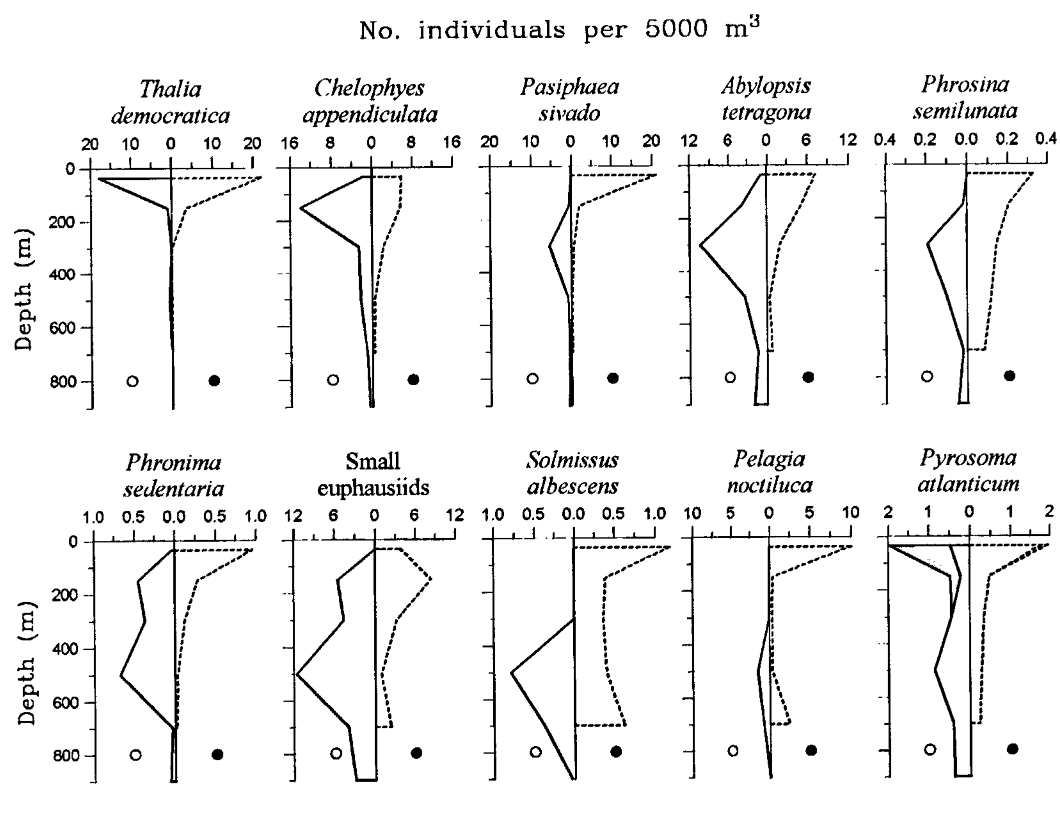

Figure 2

Average annual vertical distribution by day (—, ○) and at night (---, ●) of the species caught in maximum numbers at 500 m or above. Mean lower sampling depth was 900 m by day and 700 m at night. For Pyrosoma atlanticum *shading correspond to small (< 7 mm) colonies.*

species formed throughout the year a more or less continuous layer of 100-200 m thick between 400 and 700 m. We also observed such a constant daytime distribution throughout the year.

By day, the population of *Pyrosoma atlanticum* showed a shallower peak consisting essentially of small colonies with length less than 7 mm and a deeper peak of large colonies at 500 m. WMD values gave a mean migration amplitude of 210 m for the large pyrosomids, but from the vertical profiles, it appeared that some colonies could have performed larger migration of at least 450 m. This extensive DVM of *P. atlanticum* has previously been reported by Franqueville (1971), Andersen *et al.* (1992) and Andersen and Sardou (1994) for the Mediterranean Sea. Andersen and Sardou (1994) showed from samples taken with a Bioness that amplitude of the migration increased with the size of the colonies, from 90 m for the 3 mm-length colonies up to 760 m for the 51 mm-length ones.

Deep-living species during the day

The six species belonging to this category occurred in large numbers at 500 m and below by day and were absent or rarely caught in the upper 400 m (Fig. 3). Their day WMDs for 0-1000 m were also greater by at least 100 m than those for the 0-800 m (*cf.* Tab. 3), indicating that these species were abundant below 800 m by day. The decapod *Sergestes corniculum* did not reach the shallow layer at night (maximum at 300 m), performing a relatively moderate DVM (200 m as amplitude). In contrast, the decapods *Pasiphaea multidentata, Gennadas elegans* and *Sergestes robustus* underwent extensive DVM, performing a mean displacement of 320-370 m (*cf.* Tab. 3). At night, their maximum abundance occurred at 150 m, few organisms being caught at 35 m. The two species of *Pasiphaea* caught during this study appeared more or less partitioned in the water column. By day, *P. multidentata* lived at a greater depth than *P. sivado* (*cf.* Fig. 2), as also observed by Franqueville (1971). At night, *P. sivado* was concentrated at 35 m and *P. multidentata* at 150 m, these two species performing large DVM of ~300 m. The night distribution of the decapod *Acanthephyra pelagica* was bimodal with an upper peak at 150 m and a deeper one at 500 m, in all likelihood composed of organisms living deeper than 800 m by day. Furthermore, *A. pelagica* appeared as an extensive migrator: from at least 500 m by day to the shallow stratum 0-75 m at night, *i.e.* a migration amplitude of ~450 m. *Gennadas elegans* and *Acanthephyra pelagica* have been reported to occur in large numbers at 1000 m and below (Casanova, 1970; 1977, Castelbon, 1987).

The mysid *Eucopia unguiculata* appeared clearly as nonmigrant. Its day and night vertical distributions presented a minimum at 300 m, followed by a clear increase down to 500 or 700 m (Fig. 3). Below these depths, the concentration of the organisms remained the same down to the limit of the sampling (1000 m). Franqueville (1971) reported that at night *E. unguiculata* migrated in the upper layers but not above 400 m. Two other studies performed in the 0-1000 m water column (Andersen and Sardou, 1992; Sardou and Andersen, 1993) concluded that only a few individuals performed a migration amplitude of about 200 m. Results from

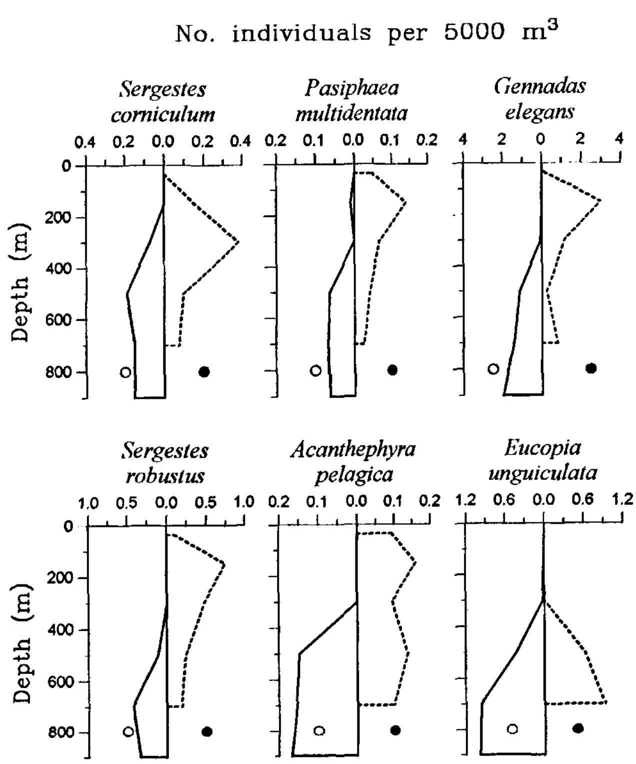

Figure 3

Average annual vertical distribution by day (—, ○; down to 900 m) and at night (----, ●; down to 700 m) of the deep-living species during the day.

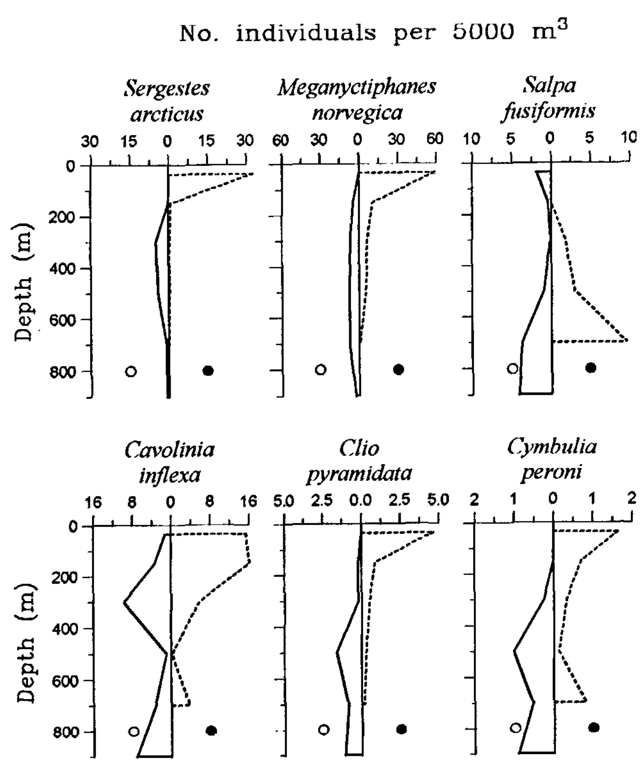

Figure 4

Average annual vertical distribution by day (—, ○; down to 900 m) and at night (----, ●; down to 700 m) of the species showing monthly variable daytime depth.

hauls below 1000 m do not agree with each other: Casanova (1970, 1977) described the vertical distributions of *E. unguiculata* as barely affected by diel variations, while this species appeared to perform a DVM in the abysso- and bathypelagic areas according to Castelbon (1987); but these samplings below 1000 m lacked depth resolution, as they concerned broad strata (600 to 1000 m thick).

Species with monthly variable preferential depth

The decapod *Sergestes arcticus* and the euphausiid *Meganyctiphanes norvegica* were clearly concentrated in the 0-150 m layer at night (Fig. 4), although some individuals of *M. norvegica* were caught below this layer. On the other hand, by day they occurred between 225 and 600 m for *S. arcticus* and 75-800 m for *M. norvegica*. The monthly vertical distributions of *S. arcticus* by day (Fig. 5) suggested the occurrence of a seasonal shift in the daytime depth of this species. In fact, *S. arcticus* was at a maximum at 300 m from January to April, and then appeared to deepen in May and June, at 500 m and down to 900 m. Later the population became abundant once more at shallower depths, 500 m in July and August, 300 and 500 m from September to December. At night, *S. arcticus* was concentrated in the upper layer throughout the year. It therefore performed DVM with mean amplitudes of 270 m (*e.g.* in January) to 600 m (in June). *S. articus* has previously been reported as a strong migrant by Franqueville (1971), Casanova (1977) and Castelbon (1987). The three species of *Sergestes* caught here, which were not at their maximum abundance during the same period of the year, also appeared to be more or less partitioned in the water column. By day, *S. arcticus* was generally abundant at 300 and 500 m (*cf.* Fig. 5), whereas *S. corniculum* and *S. robustus* lived at

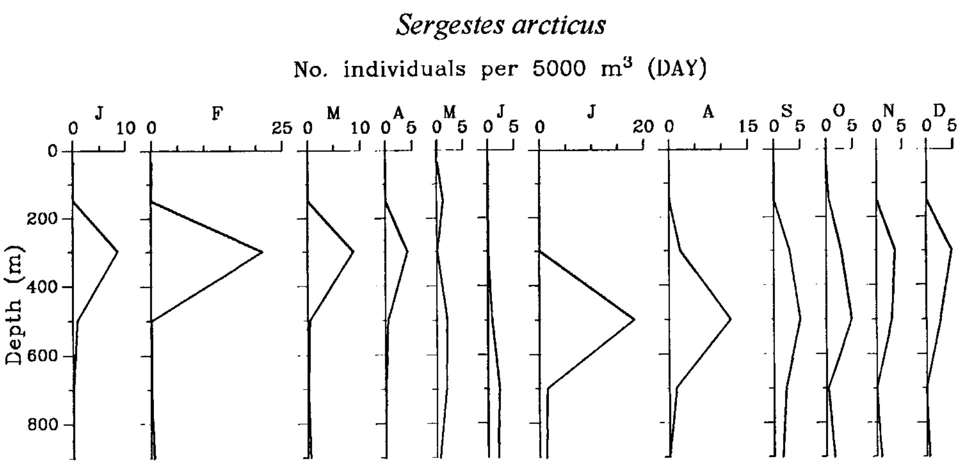

Figure 5

Monthly vertical distribution of the decapod Sergestes arcticus *by day.*

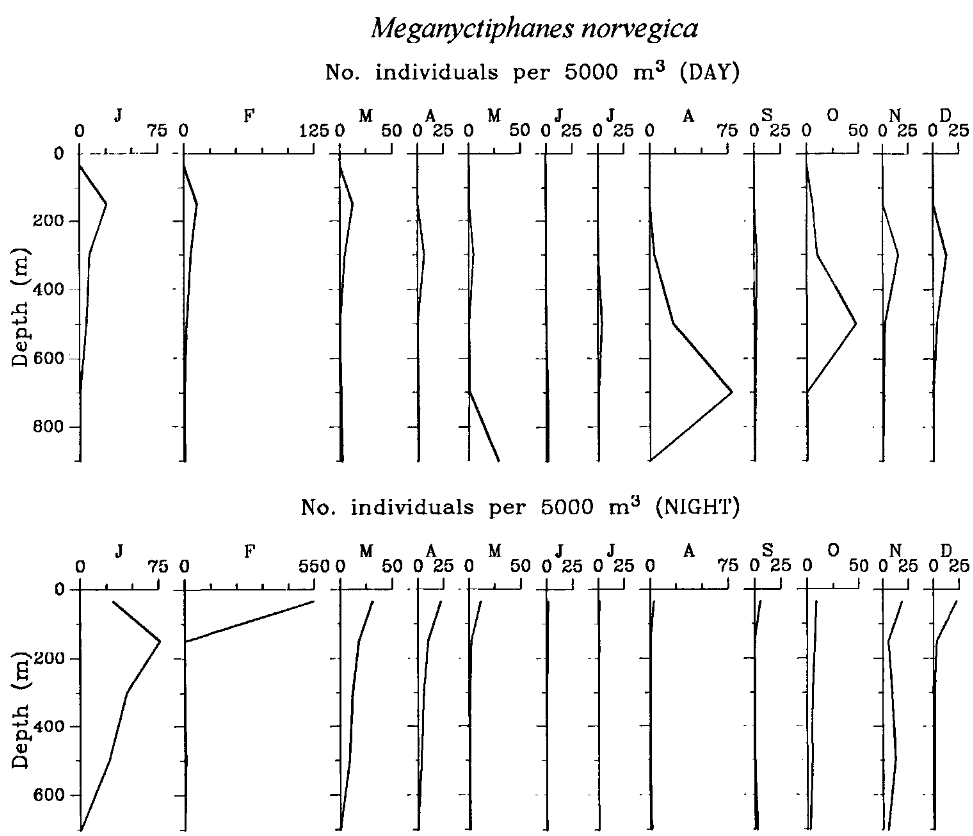

Figure 6

Monthly vertical distribution of the euphausiid Meganyctiphanes norvegica *by day (above) and at night (below). Note that the night scale for February is 4.4 times the scale for the other graphs.*

greater depths, below 500 m and below 700 m respectively (*cf.* Fig. 3). At night, *S. arcticus* was the highest in the water column (maximum at 35 m), followed by *S. robustus* (maximum at 150 m) and *S. corniculum* (maximum at 300 m). *S. corniculum* performed the smallest migration (200 m), while the two others migrated over distances of ~350 m.

Shifts in the monthly vertical distributions by day of *Meganyctiphanes norvegica* (Fig. 6) showed a similar trend to those of *Sergestes arcticus. Meganyctiphanes norvegica* showed a maximum at 150 m from January to March, and reached 300 m in April. The data suggest that in May a population was living deeper than our maximum sampling depth (1000 m). The small numbers of organisms caught in June and July suggest that the population could have been below the lower depth sampled or was at a minimum during summer. A peak of abundance was again observed in August at 700 m and became shallower with time, 500 m in October, 300 m in November and December. Our results agree with the general remarks made by Casanova (1974) for the Ligurian Sea: (i) during summer, *Meganyctiphanes* lives below 500 m and even 1000 m; and (ii) by contrast, in winter, it is found in abundance up to 200 m depth. At night, most individuals were caught in the upper layers, with a maximum at 35 m generally and at 150 m in January, and with particularly high concentrations in February (~550 ind per 5000 m^3 at 35 m). But at certain times of the year, moderate numbers were observed throughout the water column, especially during January. Therefore *M. norvegica* appeared to perform DVM of variable amplitude according to the time of the year, with low amplitudes in winter (~100 m in February) and higher ones in summer (~600 m in August).

The behaviour of *Salpa fusiformis* was more difficult to interpret from its mean annual distributions (*cf.* Fig. 4). Figure 7 gives the monthly vertical distributions of *S. fusiformis* from January to May, the restricted period during which it was caught by the net. From January to March, a small population was concentrated in the superficial layer by day and very few individuals were caught in all the 0-800 m water column at night. On the other hand, the greatest populations of April and May occurred at 700 m or below both by day and at night, no individual or very few being caught in the superficial layer. The upper limit of the distribution appeared shallower at night; this would suggest an upward migration of some individuals at night. The occurrence of DVM in *Salpa fusiformis* appears to be controversial. According to Franqueville (1971), *S. fusiformis* undergoes a large migration, from 300-800 m by

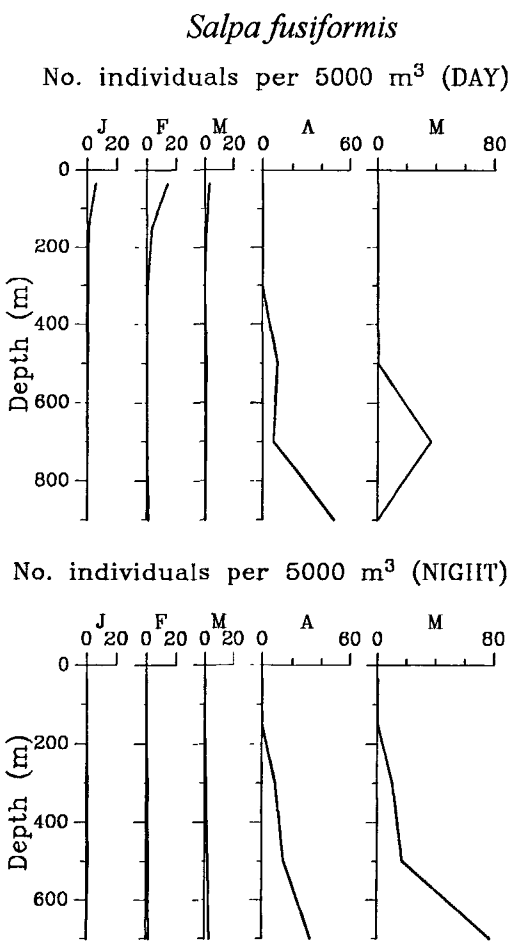

Figure 7

Monthly vertical distribution of the salp Salpa fusiformis *by day (above) and at night (below) during its restricted period of occurrence in the catches,* i.e. *from January to May.*

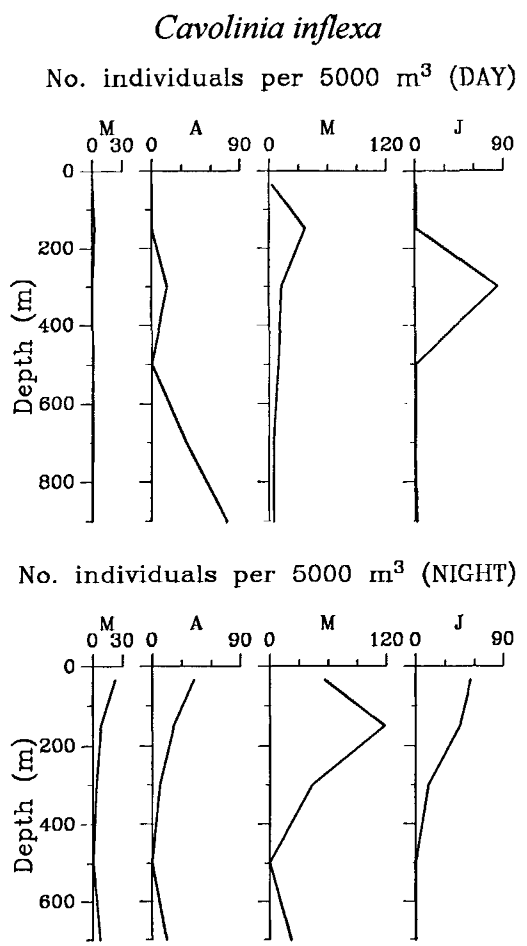

Figure 8

Monthly vertical distribution of the pteropod Cavolinia inflexa *by day (above) and at night (below) during its period of abundance,* i.e. *from March to June.*

day up to the surface at night. On the other hand, Laval *et al.* (1992) reported results similar to ours. During most of their eight submersible dives, they observed a surface population (0-200 m) and a deep population (400-600 m) both by day and night, and concluded that the bulk of the population did not move up and down on a nycthemeral basis. In the Northwestern Pacific, sampling down to 600 m also indicates *S. fusiformis* as a non- or weak migrant (Tsuda and Nemoto, 1992).

The three pteropod species caught during this study showed monthly variable vertical distribution. *Cavolinia inflexa* was almost exclusively caught during the spring months and its monthly day vertical distribution was highly variable (Fig. 8). During April, there was a small maximum at 300 m and the occurrence of a deep population at 900 m or below; maximum abundances subsequently occurred at 150 m in May and at 300 m in June. At night, *C. inflexa* was essentially concentrated at 35 and 150 m, irrespective of the month. In April and June, the upper day population appeared to perform a DVM of 150-250 m as amplitude. By day, maximum concentrations of *Clio pyramidata* (Fig. 9) and *Cymbulia peroni* (Fig. 10) were often observed at 500 m, but deep populations also occurred at 700 m or below at different times of the year (*e.g.* March and April). During winter, the vertical range of *C. peroni* extended higher in the water column, up to 225 m. At night, *C. pyramidata* was concentrated in the 0-75 m layer irrespective of the month, performing a DVM of 250-450 m as amplitude; *C. peroni* was essentially caught in the shallow layer, except in April, and appeared as an extensive migrant.

The three pteropod species caught here, *Cavolinia inflexa*, *Clio pyramidata* and *Cymbulia peroni* are known to perform more or less extensive migration (Rampal, 1967, 1975; Franqueville, 1971; Castelbon, 1987; Sardou and Andersen, 1993; present data). Rampal (1967, 1975) previously observed that the vertical distribution of these pteropods varied in the course of the year. Pooling the results of hauls performed in various areas of the Mediterranean, she found that adults occurred between 600 and 1000 m and deeper by day during the non-breeding periods; during the breeding period, they became concentrated in the upper layers. In the Ligurian Sea, *Cavolinia inflexa* was observed only in the upper 300 m in April 1986 (Laval *et al.*, 1989) or almost exclusively caught between 250 and 450 m in April 1990 (Sardou and Andersen, 1993). Our results concerning only the adults, as young individuals were not caught by our net, would lead to the following conclusions: (i) the breeding period extends from April to June; and (ii) during the other months, these organisms live below 1000 m, the lower limit of our sampling. These results contrast with Rampal (1975) who concluded that the breeding of *C. inflexa* north of 42° N is essentially important in autumn and winter (November to March), with adult populations in the upper layers in autumn and at the beginning of spring.

Our results suggest that *Clio pyramidata* performs a seasonal migration to depths greater than 1000 m during summer, before becoming abundant again in the 400-1000 m water column in October. Franqueville (1971) deduced a similar behaviour: in his study, *C. pyramidata* was infrequently caught above 900 m in summer while it occurred in great numbers in autumn. This agrees with the observations of Rampal (1975) that, in the Ligurian Sea, reproduction of *C. pyramidata* occurs essentially in autumn, but also at the end of the summer and winter. Rampal (1975) reported that the reproduction of *Cymbulia peroni* was intensive in spring and summer. However, our results suggest that in 1982, in the Ligurian Sea, breeding would have occurred in January and February. Organisms caught in the sub-superficial layers, and the peaks at 500 m in March, April and June would then correspond to young individuals before they reach the deeper layers in summer and autumn. As the annual cycle presented by Rampal (1975) is based on results of various locations and our sampling not deep enough, further investigations will have to be performed to test these hypotheses.

Comparison of the present results with previous investigations points to the need for further *in situ* studies on macroplanktonic and micronektonic invertebrates in the Mediter-

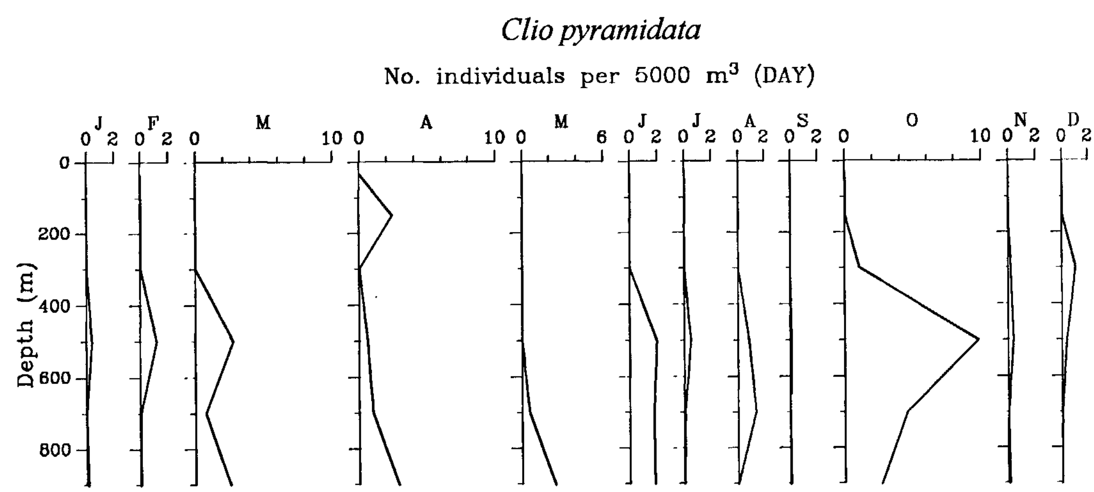

Figure 9

Monthly vertical distribution of the pteropod Clio pyramidata *by day.*

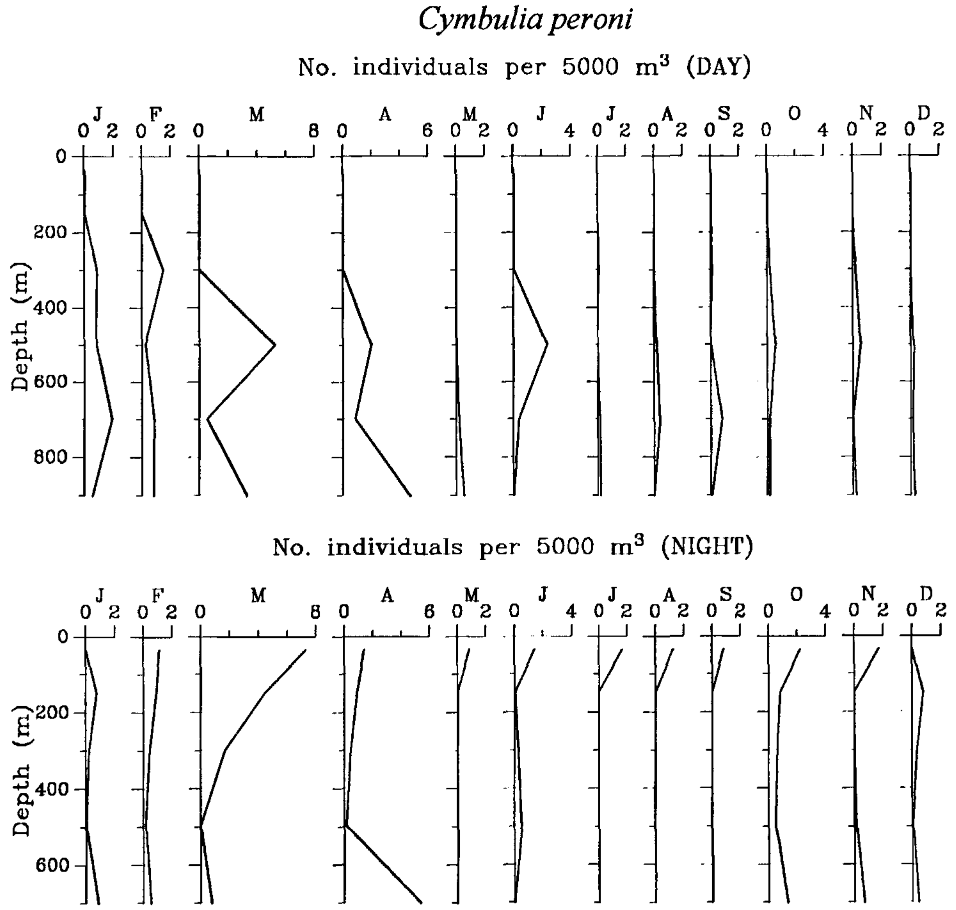

Figure 10

Monthly vertical distribution of the pteropod Cymbulia peroni *by day (above) and at night (below).*

ranean. The seasonal variation of abundance of some species remains insufficiently documented (*e.g.* the siphonophore *Chelophyes appendiculata* and the decapod *Pasiphaea sivado*). Sampling to depths greater than 1000 m and with relatively small depth strata have to be performed regularly in order to obtain a better understanding of the vertical distributions of deep-living species such as the decapods *Gennadas elegans* and *Acanthephyra pelagica* and the mysid *Eucopia unguiculata*, or of species characterized by seasonal migration, such as the pteropods *Cavolinia inflexa*, *Clio pyramidata* and *Cymbulia peroni*. In the case of pteropods, it would be useful to consider size data as these organisms perform ontogenic migration. At the least, sampling with multiple opening/closing nets would provide more accurate information on the limits of the vertical distribution of the species.

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