
The diel migrations and vertical distributions of zooplankton and micronekton in the Northwestern Mediterranean Sea. 2. Siphonophores, hydromedusae and pyrosomids

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Abstract. Vertical distributions and diel migrations in the 0–1000 m water column at a position in the Northwestern Mediterranean Sea are given in detail for the main species of gelatinous macrozooplankton: three siphonophores (*Abylopsis tetragona*, *Chelophyes appendiculata* and *Lensia conoidea*), one hydromedusa (*Solmissus albens*) and one pyrosomid (*Pyrosoma atlanticum*). Extensive diel vertical migration occurred in these five species, particularly in *A. tetragona*, *S. albens* and *P. atlanticum* for which the bulk of the population migrated as a compact unit. *Pyrosoma atlanticum* underwent the largest migration, with a mean amplitude of 515 m. The migration pattern of *L. conoidea* was more complex. Its day-distribution was bimodal and at night part of the population ascended towards the surface, while the other part appeared to undergo a weak reverse migration of ~50 m. Timing of the migrations was observed from horizontal hauls at a given depth around sunset and sunrise, and the migratory cycles presented a clear diurnal symmetry.

Introduction

The present paper describes the vertical distributions and diel vertical migrations (DVM) of the most abundant species of three groups of gelatinous macrozooplankton (siphonophores, hydromedusa and pyrosomids) caught at a position in the Northwestern Mediterranean Sea. It complements the paper of Andersen and Sardou (1992) on the micronekton.

Few studies describe the vertical distributions and DVM of gelatinous macroplankton, although these organisms can be predominant in the macroplanktonic–micronektonic biomass. Detailed information, using opening/closing net systems, is only available for various positions in the North Atlantic, with the studies of Pugh (1974, 1977, 1984) and the review of Mackie *et al.* (1987) for siphonophores, and the studies of Roe *et al.* (1987) and Angel (1989) for pyrosomids.

In the Mediterranean Sea, previous investigations essentially have been made with non-closing nets (e.g. Casanova, 1970; Franqueville, 1970, 1971) and in coastal areas (Palma, 1985), although Franqueville (1971) began some direct observations with a limited number of dives in a manned submarine. The series of eight submersible dives by Laval *et al.* (1989) provides, until now, the most detailed study on DVM of siphonophores in the Mediterranean. The DVM of *Solmissus albens*, the most numerous narcomedusa in the Western Mediterranean (endemic to the Mediterranean Sea), was first described by Benović (1973). In this area, the two existing detailed studies of Mills and Goy (1988) and Laval *et al.* (1989) are based on submersible dives.

The present study, based on repeated oblique and horizontal hauls with a multiple opening/closing net system, reports the features of the vertical

distributions and of the DVM of three siphonophore species, of the narcomedusa *S. albescens* and of the pyrosomid *Pyrosoma atlanticum* in the 0–1000 m water column.

Method

A series of hauls was made at location 43°24'N, 7°52'E in the Ligurian Sea (Northwestern Mediterranean) within a period of 9 days (2–10 May 1990). Biological samples were taken with a multiple opening and closing net, the BIONESS (Sameoto *et al.*, 1980), equipped with ten 500 µm mesh nets and towed at a mean speed of 2.1 m s⁻¹. Two types of hauls were combined: (i) oblique hauls around midday and midnight subdividing the water column into nine strata (980–850, 850–700, 700–550, 550–450, 450–350, 350–250, 250–150, 150–75, 75–0 m); (ii) horizontal hauls at ~230 m around sunrise and sunset, with nets sampling during 20–25 min periods. The sampling data are summarized in Table I; time is given in hours GMT (Greenwich Mean Time). Details on the sampling methods, the environmental conditions (temperature, density and chlorophyll) and the data analyses were provided by Andersen and Sardou (1992). As the hydrological characteristics of the sampling area were stable in time during the period of study, average midday and midnight distributions for each species were estimated by combining the results of the four day hauls or the four night hauls, and corresponding weighted mean depths (WMD) were calculated. Data from the horizontal hauls were pooled in two parts, one around sunrise and the other around sunset.

Results

Day and night distributions

Siphonophores. The average number of individuals per square meter (0–980 m), calculated by vertical integration of their day and night abundance, are presented for each species in Table II. Three species of siphonophores were abundant in the hauls, *Lensia conoidea*, *Chelophyes appendiculata* and

Table I. Sampling data for BIONESS. D, N: oblique tows around midday and midnight, respectively, in the 0–980 m water column; R, S: horizontal tows around sunrise and sunset, respectively, at ~230 m depth. Sunrise and sunset, respectively, at 04.24 and 18.32 h on May 2, and at 04.14 and 18.41 h on May 10

Haul no.	Date May 1990	Time (h GMT)	Haul no.	Date May 1990	Time (h GMT)
N1	2	22.04–23.21	D1	3	08.20–09.39
N2	3	00.47–01.54	D2	5	09.23–10.34
N3	4	21.33–22.46	D3	5	12.19–13.37
N4	5	01.00–02.08	D4	7	09.17–10.39
S1	2	16.09–19.54	R1	3	02.53–06.38
S2	5	14.52–18.12	R2	8	03.53–07.38
S3	7	17.21–20.41	R3	10	03.06–05.46
S4	9	17.20–20.20			

Abylopsis tetragona, and they largely dominated by number the gelatinous macroplankton studied here.

(i) *Lensia conoidea*. At midday the distribution of *L. conoidea* was bimodal with a maximum in the 0–75 m layer and another, deeper, in the 250–350 m layer; this pattern was maintained in all the four day hauls (Figure 1), although it was less apparent for haul D1 where lower numbers were caught in the superficial layer. At night the individuals were almost exclusively found in the first 150 m and especially in the 75–150 m stratum. Figure 2 shows the resulting average

Table II. Average number of individuals per square meter (from 980 m to the surface), recorded in day and night samples for the most abundant species of gelatinous macroplankton

	Day ($n = 4$)	Night ($n = 4$)
<i>Lensia conoidea</i> Keferstein & Ehlers, 1861	32.7 ± 10.5	29.0 ± 10.7 n.s.
<i>Chelophyes appendiculata</i> (Eschscholtz, 1829)	21.8 ± 7.9	8.4 ± 5.3 *
<i>Abylopsis tetragona</i> (Otto, 1823)	3.0 ± 1.1	2.4 ± 1.3 n.s.
<i>Solmissus albens</i> (Gegenbaur, 1856)	0.9 ± 0.4	3.9 ± 0.6 *
<i>Pyrosoma atlanticum</i> Peron, 1804	0.7 ± 0.3	0.6 ± 0.5 n.s.

Significance of the *t*-test: *, different at the 0.05 level; n.s., no differences at the 0.05 level. \pm , standard deviation.

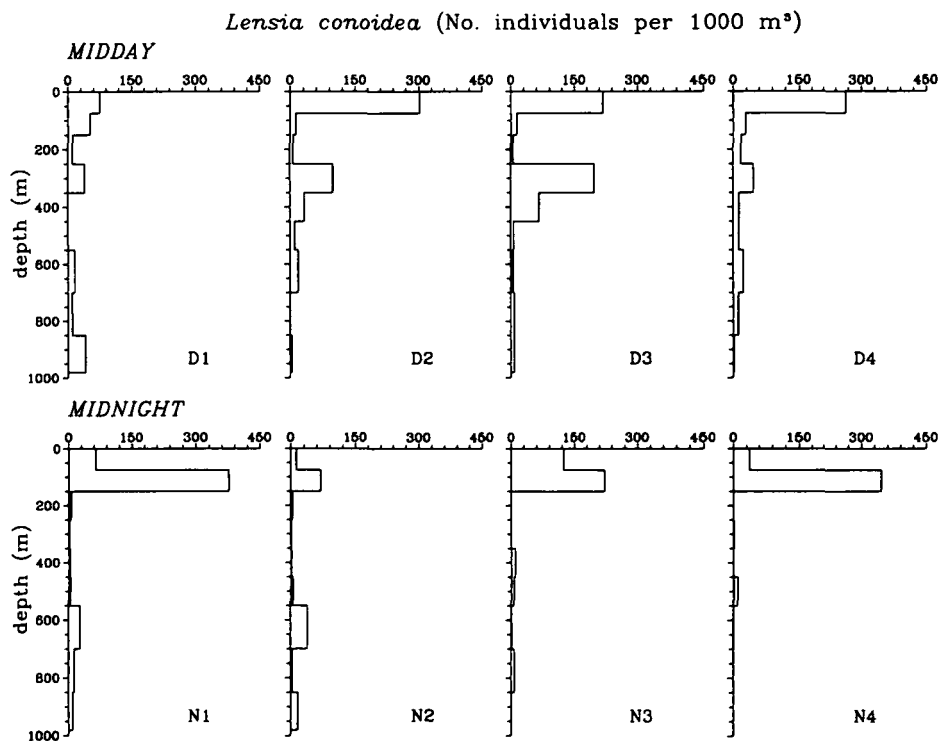


Fig. 1. Vertical distributions of *L. conoidea* during the four day hauls (D1, D2, D3, D4) and the four night hauls (N1, N2, N3, N4).

distributions at midday and midnight. It seemed that two different behaviours existed for this species: the individuals staying in their 250–450 m layer during the day migrated at night to 0–150 m, the others performed a weak reverse migration from the 0–75 m layer during the day to the 75–150 m layer at night. Therefore, as the day distribution of *L. conoidea* was bimodal, we calculated day and night WMDs for each mode (Table III). This gave a mean migration amplitude of 205 m for the deep part of the population and of 50 m for the surface part.

Some individuals were caught down to 850–980 m, both by day and night. No significant differences between total day and night catches over the entire water column (Table II) suggested that this species stayed in the 0–980 m depth range sampled.

(ii) *Chelophyes appendiculata*. During the day *C. appendiculata* appeared a little scattered vertically, occurring essentially in the 0–350 m water column with maximum numbers between 250 and 350 m (Figure 2). At night all the

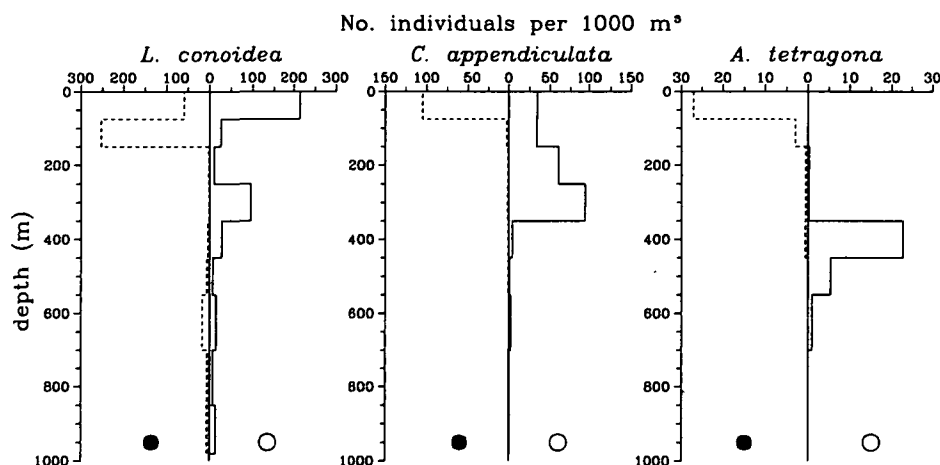


Fig. 2. Average vertical distributions of the three dominant siphonophore species, *L. conoidea*, *C. appendiculata* and *A. tetragona*, at midday (—, ○) and midnight (---, ●).

Table III. Average weighted mean depths (WMD) \pm standard error during the day and at night, and mean amplitude of the migration (dz) when the day–night differences (*t*-test) are significant at the 0.05 level, for the most abundant species of gelatinous macroplankton. Values are given as numbers to the nearest 5

	WMD (day)	WMD (night)	dz
<i>Lensia conoidea</i> 0–150 m	50 \pm 15	100 \pm 10	50
<i>Lensia conoidea</i> 150–450 m	305 \pm 20	—	205 ^a
<i>Chelophyes appendiculata</i>	220 \pm 40	50 \pm 15	170
<i>Abylopsis tetragona</i>	430 \pm 25	60 \pm 20	370
<i>Solmissus albescens</i>	495 \pm 20	85 \pm 20	410
<i>Pyrosoma atlanticum</i>	555 \pm 30	40 \pm 5	515

^a Calculated from the deeper day WMD and the shallower night WMD.

individuals were concentrated in the first 75 m. Although DVM of *C. appendiculata* was clear, all the individuals did not migrate cohesively or synchronously. Calculation of day WMD (220 m) and night WMD (50 m) gave a mean migration amplitude of 170 m (Table III); however, the deeper individuals could have performed a DVM of ~260 m (difference between 300 m by day and 37.5 m at night). Surprisingly the average total numbers of *Chelophyes* caught in the 0–980 m layer were significantly different, and higher, by day than at night (Table II). The standard deviations being low, we do not think that this can be ascribed to patchiness.

(iii) *Abylopsis tetragona*. During the day, *A. tetragona* occurred essentially in the 350–550 m layer, with a maximum concentration in the 350–450 m interval (Figure 2); it extended over a narrower depth range than the two other siphonophore species. *Abylopsis tetragona* appeared to replace *C. appendiculata* as depth increased, these two species not being caught together in significant numbers and therefore partitioning their habitat. At night the bulk of the population of *A. tetragona* appeared to migrate as a compact unit to the 0–75 m interval, very few specimens remaining below. This species therefore performed a strong DVM of 370 m as a mean (WMDs: 430 m, day; 60 m, night; Table III).

Hydromedusae. The most abundant medusa species was *Solmissus albescens* (narco medusae). The other medusa species caught, *Octophialucium funerarium* (leptomedusae) and *Rhopalonema velatum* (trachymedusae), appeared too irregularly or were not abundant enough in the catches to allow a description of their vertical distribution. *Solmissus albescens* appeared in lower numbers in the catches than the three siphonophore species (Table II). It extended over a narrow vertical depth range by day as well as at night (Figure 3). It was almost

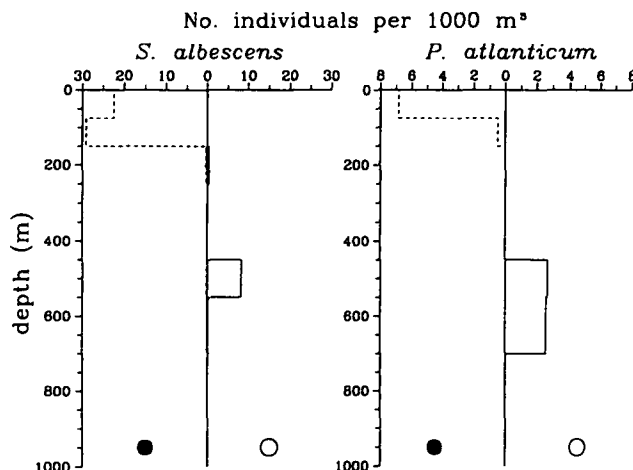


Fig. 3. Average vertical distributions of *S. albescens* and *P. atlanticum* at midday (—, ○) and midnight (---, ●).

exclusively caught in the 450–550 m sampling interval during the day and in the first 150 m at night, therefore showing a large DVM (410 m; Table III). Comparison of the average total numbers of *S. albescens* caught in the 0–980 m layer showed a significant difference, night catches being ~4 times higher than day catches. This phenomenon appeared as a general trend, the standard deviation of the two means being small. As *Solmissus* was never caught at <700 m in all the four day hauls, the migration of animals from below the lower sampling depth (980 m) to the surface did not appear to be a likely explanation. Another explanation could be avoidance of the net by day. In fact, the migration and day-time depth distribution of *S. albescens* appeared light-dependent (Mills and Goy, 1988), although this species has no ocelli.

Pyrosomids. Of the five gelatinous macroplanktonic species studied here, *P. atlanticum* was the least abundant (Table II). However, it was caught in the hauls regularly and in sufficient numbers to allow a description of its vertical distribution, unlike the thaliacean species, *Ihlea punctata*, *Pegea confoederata*, *Salpa fusiformis*, *Thalia democratica* and *Doliolum* sp., which were also caught. *Pyrosoma atlanticum* tetrazooids were not taken into account as they were recorded in only three samples and in very small numbers throughout the sampling period (230 m: horizontal hauls, two records; 150–250 m layer: oblique haul, one record). We consider here organisms ranging in length from 8 to 88 mm. During the day *P. atlanticum* was exclusively caught between 350 and 700 m depth, and at night almost all the individuals migrated together to the 0–75 m layer (Figure 3). This species therefore performed the largest DVM observed in the present study, with a mean amplitude of 515 m (Table III).

Relation with environmental conditions. Throughout the study period, the sampling area was characterized by some stratification in the surface 50 m with a thermocline of 1.8–3.1°C between 5 and 25 m, and by a chlorophyll maximum between 40 and 50 m (Andersen and Sardou, 1992). From our results, none of the five gelatinous species appeared to be sensitive to the temperature gradients occurring in the surface layer. By day *L. conoidea* was found in great numbers in the 0–75 m interval, and the other species concentrated at these depths at night. A detailed sampling of the 0–75 m layer would be necessary to verify any correlation between temperature profiles and the vertical distribution of species. At night *P. atlanticum*, a typical filter feeder, therefore aggregated in the rich phytoplankton surface layer.

Timing of the migration

Figure 4 shows the time variations in the abundance of the three siphonophore species at 230 m depth around sunrise and sunset. Crossing this sampling boundary by downward migration around sunrise and upward migration around sunset was clearly detected for the three species, and there was a marked diurnal symmetry of the migratory cycles relative to noon. A marked peak of abundance of *L. conoidea* appeared ~55 min after sunrise and ~1 h 15 min before sunset,

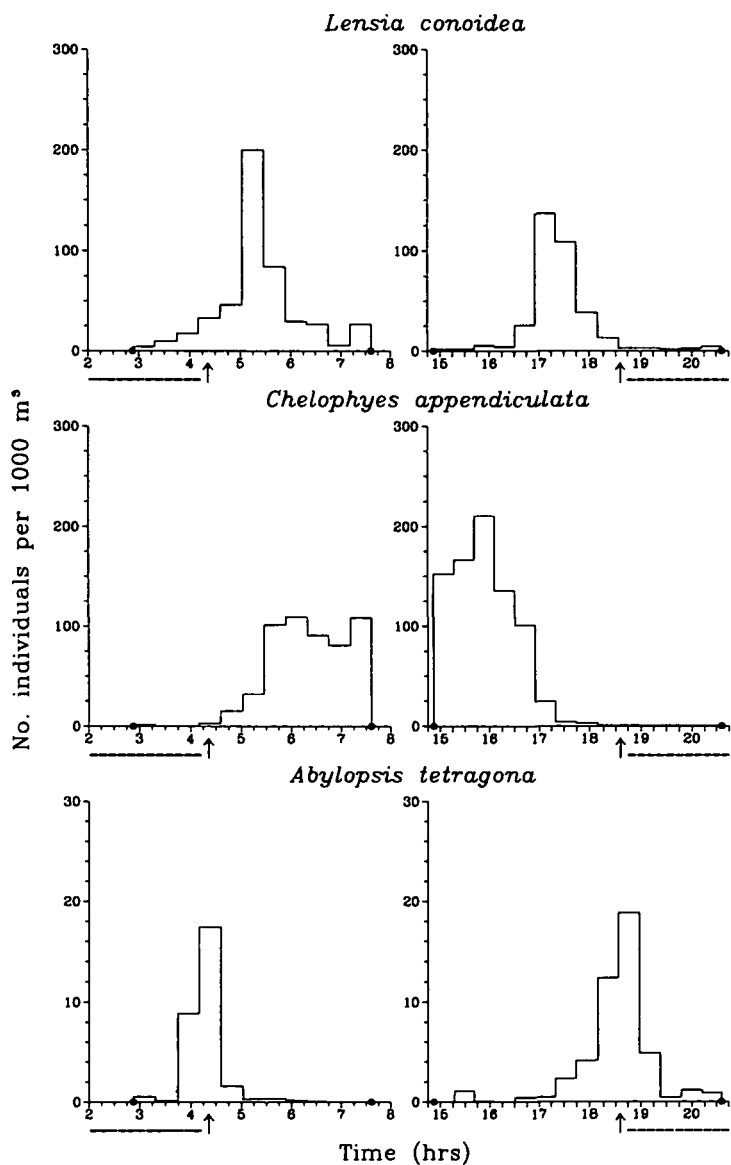


Fig. 4. Variations in the abundance of *L. conoidea*, *C. appendiculata* and *A. tetragona* (horizontal hauls at ~230 m) around sunrise (left) and sunset (right). ↑, sunrise or sunset; ----, night; ●, limit of the sampling period.

due to, respectively, the descent and the ascent of the deep part of the population (cf. Figure 2). *Chelophyes appendiculata* crossed the sampling depth downwards in great numbers ~1 h 10 min after sunrise and upwards it almost disappeared ~1 h 10 min before sunset. *Abylopsis tetragona* went through the sampling depth essentially at sunrise during its descent and at sunset during its

ascent. Some individuals of *L.conoidea* and *A.tetragona* were also caught irregularly at different times all along the two sampling periods, as both species were not completely absent from the 150–250 m interval (cf. Figure 2). As *C.appendiculata* stayed by day in the 150–350 m water column, it was collected in the 230 m sample until the end of the sunrise sampling period and at the beginning of the sunset sampling period.

During its ascent, *S.albescens* became abundant at 230 m ~1 h after sunset (Figure 5). No *Solmissus* were caught during the sunrise sampling period. If this species performed a diurnal symmetrical migratory cycle, it would have crossed the sampling depth at the latest during the 02.55–03.20 h interval, which was covered by our sampling (starting at 02.53 h).

The population of *P.atlanticum* appeared to migrate as a compact unit (cf. Figure 5) and its migratory cycle showed, as for the three siphonophore species, a clear temporal symmetry. The bulk of the population had gone below 230 m 10 min before sunrise and appeared first ~20 min after sunset on its upward migration.

The timing and order of crossing the sampling boundary by the five gelatinous

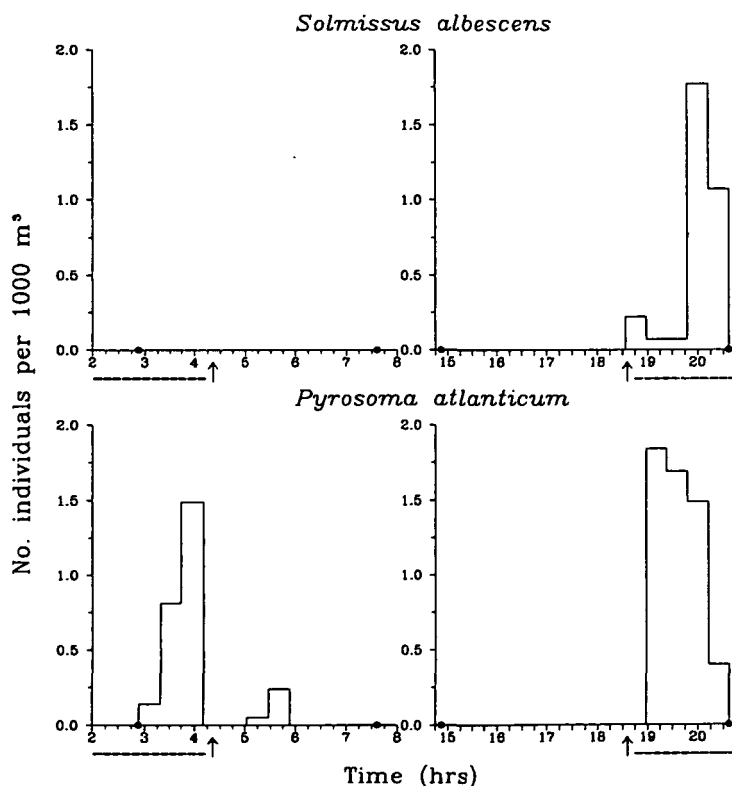


Fig. 5. Variations in the abundance of *S.albescens* and *P.atlanticum* (horizontal hauls at ~230 m) around sunrise (left) and sunset (right). ↑, sunrise or sunset; ----, night; ●, limit of the sampling period.

species studied here was very marked. For example at sunset, during their ascent, they went through 230 m in the following order: *C.appendiculata* followed by *L.conoidea* before sunset, *A.tetragona* at sunset, and after sunset *P.atlanticum* then *S.albescens*. At night they aggregated at nearly the same depth; the chronology of the crossing appeared to be related to their day-depths or migration amplitude. In fact, the deeper they lived by day (cf. Table III), the later they became abundant at 230 m. The rank in day WMDs was the same as the time ranking, with a transportation between *P.atlanticum* and *S.albescens*. In fact, although the pyrosomids generally lived deeper than *Solmissus*, they reached 230 m earlier. This could result from a higher migration speed of the pyrosomids or from a different sensitivity to absolute light intensity or to its rate of change both being possible causes for initiating the migration. An inverse time chronology was symmetrically observed during the sunrise period, except that *S.albescens* was not caught.

Discussion

In the western Mediterranean, *C.appendiculata*, *A.tetragona* and *L.conoidea* have previously been reported as the most abundant siphonophore species (Casanova, 1970; Franqueville, 1971; Laval *et al.*, 1989), their order of abundance depending on the area studied and on the sampling period. *Solmissus albescens* is the most numerous narcomedusa (Mills and Goy, 1988; Laval *et al.*, 1989) and *P.atlanticum* appears among the main thaliacean species (Franqueville, 1971). Our results can be compared with those obtained from submersible dives performed in a neighbouring area in April 1986 (Laval *et al.*, 1989) when considering the densities of animals in the stratum of greatest abundance. Concentrations of *C.appendiculata* from the tows and from the dives appear in similar ranges of, respectively, 29–192 and 4–211 individuals 1000 m^{-3} . For *S.albescens*, Laval *et al.* reported concentrations of 15–200 individuals 1000 m^{-3} , while we observed densities of 5–41 individuals 1000 m^{-3} . These relatively lower concentrations could be due to an inadequate sampling of these organisms by the BIONESS or even to their collapse in the net. It must also be noted that because of their fragility some gelatinous animals are not adequately sampled (if sampled) by nets, which is the case in the ctenophores, observed at maximum densities of 31–416 individuals 1000 m^{-3} by Laval *et al.*

Vertical distributions and amplitude of the DVM

Although the five macroplanktonic species studied here are frequently observed in various regions, relatively few studies have been performed on their vertical distributions and migrations. Table IV gives the average day and night population depths, and the existence or range of DVM recorded in the literature. In the present study the vertical distribution of *L.conoidea* is bimodal during the day, with part of the population performing a mean upward migration of 205 m and another part a reverse migration of ~ 50 m at night. Franqueville (1971) found that in the Mediterranean *L.conoidea* did not seem to perform DVM, but his sampling was inappropriate (horizontal hauls with a non-closing

Table IV. Daytime depths, night-time depths and the existence of DVM or its range. Day- and night-time depths correspond to the layers where the abundance is maximum

Daytime depth (m)	Night-time depth (m)	Migration range (m)	Area	Reference
<i>Lensia conoidea</i>				
250–350	0–150	200 (p)	NW Mediterranean	present work
0–75	75–150	50 reverse (p)		
300–600	300–600	no	NW Mediterranean	Franqueville, 1971
100–200	0–200	100 ^b (p)	North Atlantic	Pugh, 1984
300–400 ^a	50–200 ^a	225 ^b	North Atlantic, 60°N	Mackie <i>et al.</i> , 1987
200–300 ^a	50–200 ^a	125 ^b	53°N	
0–100 ^a	0–100 ^a	yes (p) ^a	49°30'N	
200–1500 ^c	0–900 ^c	400 ^b	42°N	
1000–1250 ^a	1250–1500 ^a	250 ^b reverse	40°N	
<i>Chelophyes appendiculata</i>				
150–350	0–75	≥170	NW Mediterranean	present work
250–300 ^a	0–50 ^a	250 ^b	NW Mediterranean	Franqueville, 1970
200–800	0–150	425 ^b	NW Mediterranean	Franqueville, 1971
100 ^g	0	≥100	NW Mediterranean	Palma, 1985
150–250 ^a	50–150 ^a	100–150	NW Mediterranean	Laval <i>et al.</i> , 1989
250 ^f	70 ^f	≥200	North Atlantic	Pugh, 1974
250 ^c	–	yes	North Atlantic	Roe, 1974
250 ^c	–	yes	North Atlantic	Pugh, 1977
48,74 ^h	–	5,48	Florida Current	Moore, 1949 and 1953
75	–	87	Bermuda	in Pugh, 1974
74,221 ^h	–	–	Florida Current	Moore and Corwin, 1956
<i>Abylopsis tetragona</i>				
350–450	0–75	370	NW Mediterranean	present work
400–600	0–150	425 ^b	NW Mediterranean	Franqueville, 1971
85,104 ^h	–	70,80	Florida Current	Moore, 1949 and 1953
55	–	89	Bermuda	in Pugh, 1974
104,188 ^h	–	–	Florida Current	Moore and Corwin, 1956
<i>Solmissus albescens</i>				
450–550	0–150	410	NW Mediterranean	present work
400–700	0–100	500 ^b	NW Mediterranean	Mills and Goy, 1988
460–560	25	485 ^b	NW Mediterranean	Laval <i>et al.</i> , 1989
500 ^d	100 ^d	≥400	Adriatic, full moon	Benović, 1973
400 ^d	0–100 ^d	≥300	new moon	
<i>Pyrosoma atlanticum</i>				
450–700	0–75	515	NW Mediterranean	present work
400–600?	0–250 ^e	yes	NW Mediterranean	Franqueville, 1970
500–900	0–150	625 ^b	NW Mediterranean	Franqueville, 1971
700–800	0–200	650 ^b	North Atlantic	Roe <i>et al.</i> , 1987
500–900 ^a	0–100 ^a	650 ^b	North Atlantic	Angel, 1989

^a Estimated from figures. ^b Estimated from middle of day- and night-time depths. ^c Horizontal hauls at 250 m depth. ^d Upper limit of occurrence. ^e Occurrence. ^f Horizontal hauls at discrete depths.

^g Maximum sampling depth of 150 m, bottom of the water column between 100 and 200 m. ^h Two stations. p: part of the population.

Isaacs Kidd Midwater Trawl). The results of Pugh (1984) and Mackie *et al.* (1987), who used a RMT8 net, are therefore more reliable. From the vertical distributions given for six stations in the North Atlantic (cf. Table IV), it appears that *L. conoidea* performed a 100–400 m amplitude DVM at four stations. At the 40°N station, Mackie *et al.* (1987) observed a reverse migration of deep *L. conoidea* living at <1000 m by day and at night. Concerning the superficial layers, a neighbouring species (*Lensia subtilis*) has been reported to perform a slight reverse migration in the 0–100 m water column (Musayeva, 1976, in Mackie *et al.*, 1987), as we observed here. *Lensia conoidea* appears to extend over a large water column; it has been observed from the surface down to 1000 m in the present study and by Pugh (1984), and down to 2000 m by Mackie *et al.* (1987), with 1000 and 2000 m being the lower sampling limit in each case.

The day and night depths reported for *C. appendiculata* in the Mediterranean Sea (Franqueville, 1970; Laval *et al.*, 1989) and the North East Atlantic (Pugh, 1974) are similar to those observed in this study (see Table IV). *Chelophyes appendiculata* has been reported as a migrator in various areas. It performs a relatively large migration in the Mediterranean Sea and the North East Atlantic, ranging from 100 to 425 m, or 100 to 250 m if we except Franqueville's (1971) data. Available data for the Northwestern Atlantic (Moore, 1949, 1953, in Pugh, 1974) show a small migration of 5–87 m. This could be due either to the different areas sampled or to the different sampling strategies (Moore's strategy being less efficient than the multiple opening/closing net systems used more recently). Previous reports of the day and night vertical distribution of *A. tetragona* are rare, but all show the existence of DVM in this species (cf. Table IV). Moore (1949, 1953, in Pugh, 1974) again reported a small migration for this species.

The study of Benović (1973) was the first to report the large DVM of the narcomedusa *S. albescens*. Our results confirm the previous observations made in the Mediterranean and Adriatic Seas. During the day, *S. albescens* is abundant between 400 and 700 m (cf. Table IV), and at night it reaches the superficial layers, performing a DVM of 300–500 m. Mills and Goy (1988) noted, as observed here, that this species migrated as a population into the upper water layers at night. Casanova (1970) classified *S. albescens* among the weak or non-migrators, but his sampling was inappropriate. Palma (1985) also reported no migration for this organism, but his sampling was not deep enough.

Among the five macroplanktonic species described here, *P. atlanticum* is the organism which lives the deepest by day (cf. Table IV) and performs the largest DVM, 515–650 m of amplitude. The existence of its DVM has also been noted by less detailed studies: Franqueville (1970) found it in the upper 250 m only at night and Goy (1977) observed its aggregation at night around 100 m depth. Only Casanova (1970) classified it among the weak or non-migratory species. Our results, as well as the figures of Roe *et al.* (1987) and Angel (1989), suggest that at night the population migrates as a compact unit towards the surface layers. According to Kampa and Boden (1956) and Boden *et al.* (1965), *P. atlanticum* would be associated with the migrating deep-scattering layer (DSL). They found that the intensities of luminescence of *P. atlanticum* and the euphausiid *Euphausia pacifica* were compatible with the range of intensities

encountered in the measurements of light generated in the DSL. Few tetrazoid stages were caught, but their exclusive presence in the 150–250 m stratum suggests that they may not migrate, confirming the report by Palma (1985) from samples in the 0–200 m water column.

Moore (1955) and Moore and Corwin (1956) observed a good correlation between the depth of the 15°C isotherm and the lower daytime limit of a specific population of siphonophores such as *A.tetragona* and *C.appendiculata*; however, they also showed that light played a part in the regulation of depth, Daniel (1977) found that *A.tetragona* and *C.appendiculata* were not influenced by the thermocline. Concerning *S.albescens*, local temperature conditions apparently exerted no significant effects on its DVM (Benović, 1973). In the present study, the thermocline occurs between 5 and 25 m (with the 15°C isotherm between 5 and 20 m). The depth range of the shallower sample (0–75 m) is therefore too large to decide on the effect of temperature on the species.

Timing of the migration

Pugh (1977) distinguished three patterns in the DVM of siphonophores: (i) apparently no migration; (ii) slow vertical migration, sinusoidal pattern; (iii) rapid migration around sunset and sunrise. Roe (1974) and Pugh (1977) classified *C.appendiculata* among the second migrator type from the results of a series of hauls made over a 24 h period at 250 m depth. From our observations, the animals entered the sampled layer at 230 m after sunrise, disappeared from it before sunset and remained absent during the night. Roe (1974) and Pugh (1977) observed that, after sunrise, the density of animals at 250 m gradually increased to a peak some hours later and then declined fairly slowly until sunset. In our study, the sampling period extended for 3 h 20 min after sunrise and began ~3 h 45 min before sunset. During these daytime periods, the numbers of organisms remained relatively constant because part of the population occurs in the 150–250 m stratum, as indicated by the daytime vertical distribution.

So far as we know, the timing of the migration of *A.tetragona* has not previously been reported, although Franqueville (1971) noted that it began its downward migration before sunrise. From the present data, this species follows the third pattern described by Pugh (1977): it migrated rapidly through the 230 m zone at sunset and sunrise. Pugh (1984) observed the population of *L.conoidea* at a shallower daytime depth (100–200 m) than we did (250–350 m). Although obtained at a depth of 100 m (Pugh, 1984) and 230 m (our data), the two sets of data can be compared. Our results show that *L.conoidea* behaves as the second category, instead of the third as Pugh (1984) suggested.

Submersible dives (Laval *et al.*, 1989) have been performed in a neighbouring area at about the same period as our study (22–27 April compared to 2–10 May) and therefore with similar hours of sunrise and sunset (~15 min difference). Their data concerning *S.albescens* are shown with ours in Figure 6. They are generally in good agreement, showing similar depths of maximum density around midday and midnight. However, they differ in two respects: (i) between 19.00 and 20.30 h, *S.albescens* was found abundant between 213 and 310 m

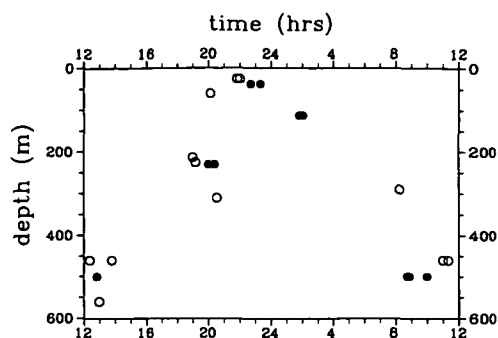


Fig. 6. *Solmissus albescens*. Depth of maximum density plotted against time. ●, results of the present study (four night hauls, four day hauls and pooled horizontal hauls around sunset); ○, results of Laval *et al.* (1989).

during three dives and our horizontal hauls, but surprisingly at 60 m during one dive; (ii) our oblique hauls show that this species is abundant at 500 m as early as 08.40 and 08.50 h, while Laval *et al.* found it shallower at the same time (290 m; 08.15 h). This comparison clearly shows the lack of data in the late afternoon and just after sunrise. The time spent in the surface layer by *Solmissus* needs also to be evaluated precisely. Laval *et al.* estimated it to be 4 h (the interval between two observations), but our data suggest that *Solmissus* spends a shorter time in the surface layer. In fact, maximum abundance was found in the 0–75 m interval on hauls 1 and 3 (sampled around 22.45–23.15 h) and in the 75–150 m interval on hauls 2 and 4 (sampled around 01.45–02.00 h); these results suggesting that at 01.45 h *Solmissus* had already begun its descent from the 0–75 m level.

Laval *et al.* (1989) noted that *Solmissus* (maximum density layer) migrated from its daytime depth to its night-time depth at a speed of 45–50 m h⁻¹. As foreseeable from the data of Figure 6, we find a similar value of 47 m h⁻¹. Benović (1973) also reported a mean speed of 50 m h⁻¹, but these values are estimated from relatively large time intervals, hence the migration speed may be greater. Enright (1977) has shown that underestimates of migration speed occur when time intervals in sampling are too large. In fact, in the present work, migration from 230 to 37.5 m takes ~2 h, i.e. a speed of 84 m h⁻¹. Mills and Goy (1988) also estimated higher migration speeds, 50–125 m h⁻¹, when they considered the movement of the upper or lower boundary of the population during 2 h intervals, their results concerning the same dives as Laval *et al.* (1989).

The few literature studies reporting the DVM of *P. atlanticum* did not give a lot of information on the timing of its migration. Franqueville (1971) noted that these organisms began their descent towards their daytime depth before sunrise, as observed here. In the report of Goy (1977), adult pyrosomids appeared to be aggregated around 60 m between midnight and 02.00 h, assuming that they were associated with the sonic-scattering layer.

Conclusion

Extensive DVM is observed in the five gelatinous macroplanktonic species studied here, with a mean amplitude from 170 m for *C.appendiculata* to 515 m for *P.atlanticum*. These organisms follow three patterns: (i) the bulk of the population migrates as a compact unit (*A.tetragona*, *S.albescens* and *P.atlanticum*); (ii) most of the animals migrate, but not cohesively or synchronously (*C.appendiculata*); (iii) only part of the population migrates (*L.conoidea*). The existence of a reverse migration of weak amplitude (50 m as a mean) is also observed for part of the population of *L.conoidea*. Concerning the Western Mediterranean Sea, this study gives the most detailed vertical distributions for *L.conoidea*, *A.tetragona* and *P.atlanticum*, and it complements the previous data based on submersible dives for *C.appendiculata* (Laval *et al.*, 1989) and *S.albescens* (Mills and Goy, 1988; Laval *et al.*, 1989).

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