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Vertical distributions of macroplankton and micronekton in the Ligurian and Tyrrhenian Seas (northwestern Mediterranean)

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Abstract – Vertical distributions and diel migrations at nineteen stations located in the Ligurian and Tyrrhenian Seas (northwestern Mediterranean) are described in detail and compared for the main species of micronekton and macroplankton. Sampling was performed in April 1994 in the 0–700 m water column in most cases, down to 350, 450 or 550 m for the coastal or relatively shallow sites. Most of the twenty species showed similar distributions throughout the sampled area, either non-diel-migrating distributions such as the euphausiid *Stylocheiron longicorne* and the fish *Cyclothone braueri*, or clear diel-migrant behaviour (e.g. the siphonophore *Chelophyes appendiculata* and the euphausiid *Euphausia krohni*). Four species, the siphonophore *Lensia conoidea*, the pteropods *Cavolinia inflexa* and *Clio pyramidata* and the salp *Salpa fusiformis*, showed heterogeneity between distributions, with different preferential daytime depths. For example, moderate or extensive migration and even slight reverse migration were observed in *Lensia conoidea*, depending on the station sampled. The differences in vertical distributions did not appear to be related to hydrological conditions (temperature, salinity); but rather to chlorophyll content (and ambient light) or bottom depth of the station, or to mating behaviour of the species. © Elsevier, Paris

vertical distribution / macroplankton / micronekton / Mediterranean Sea / Tyrrhenian Sea

Résumé – Distributions verticales du macroplancton et du micronecton en mer Ligure et en mer Tyrrhénienne (Méditerranée nord-occidentale). Cette étude présente et compare les distributions verticales et les migrations nycthémérales des principales espèces de macroplancton et de micronecton observées en mer Ligure et en mer Tyrrhénienne (Méditerranée nord-occidentale). Dix-neuf stations ont été échantillonnées, en avril 1994, jusqu'à 700 m de profondeur généralement ou jusqu'à 350, 450 ou 550 m pour les zones côtières ou peu profondes. La majorité des vingt espèces étudiées montre des distributions similaires sur l'ensemble de la zone, avec la même distribution de jour et de nuit (c'est par exemple le cas de l'euphausiacé *Stylocheiron longicorne* et du poisson *Cyclothone braueri*) ou le même comportement migratoire (comme pour le siphonophore *Chelophyes appendiculata* et l'euphausiacé *Euphausia krohni*). Quatre espèces, le siphonophore *Lensia conoidea*, les ptéropodes *Cavolinia inflexa* et *Clio pyramidata* et la salpe *Salpa fusiformis*, présentent des distributions variables, avec des niveaux bathymétriques preférentiels différents le jour. Ainsi, selon la station échantillonnée, on observe chez *Lensia conoidea* une migration modérée ou de grande amplitude, ou même une légère migration inverse. Ces différences de distributions verticales n'apparaissent pas liées aux conditions hydrologiques (température, salinité); elles seraient plutôt associées au contenu en chlorophylle (et à la lumière ambiante) ou à la profondeur du site, ou aussi au comportement reproducteur de l'espèce. © Elsevier, Paris

distribution verticale / macroplancton / micronecton / mer Méditerranée / mer Tyrrhénienne

1. INTRODUCTION

A large amount of information is available on the distribution of the main macroplankton and micronekton species in the western Mediterranean Sea, but these observations often deal either with geographical or vertical distributions. Geographical distributions, covering large areas, have been reported for euphausiids [10, 33], pteropods [27, 28] and various plankton species [26]. Detailed vertical distributions, from opening/closing net systems or submersible dives and with reduced thickness of depth strata, have been provided at a single or a few fixed stations [4, 20]. In the studies performed at numerous sites, either attention was paid to the superficial layer only [16, 26, 33], or results of vertical sampling at different depths were combined and a single average vertical distribution of each species provided for the entire sampled area [9, 10, 15, 28]. The Ligurian Sea is one of the most documented areas of the northwestern Mediterranean. In contrast, information on the macroplankton and micronekton in the Tyrrhenian Sea is scarce, to our knowledge, dealing mainly with geographical distribution with only a few documented vertical distributions [10, 16, 23, 28, 33].

The purpose of this paper is to present and compare the vertical distributions and diel vertical migrations (DVM) at nineteen stations located in the Ligurian and Tyrrhenian Seas for the main species of micronekton and macroplankton. This study is based on day and night sampling down to 700 m or to shallower depths in the coastal or shallow sites in April 1994.

2. METHOD

In April 1994, a series of oblique hauls was made in the northwestern Mediterranean Sea on five transects (*figure 1*) comprising four stations on transects A, B, C and E, and three stations on transect D. Nineteen stations were therefore explored; distance between stations was 10 nautical miles for transects A, B, C and D, and 20 miles for transect E. Biological samples were taken with a multiple opening and closing net, the BIONESS [30], equipped with 500 μm mesh nets of a mouth area of 1 m^2 and towed at a mean speed of 2.2 m s^{-1}. Two oblique hauls were performed at each station, one during the day and one at night, except at stations B1, D2 and D3 where, due to poor meteorological conditions, only the night haul could be performed. The sampling data are summarized in *table I*. In order to perform such a sampling in a relatively short period of time (17 days, 11–27 April), the maximum water column depth was restricted to 700 m (13 stations). In coastal areas or at relatively shallow stations (stations A1 and B1, and transect E along East Corsica), where bottom depth was of 600–900 m, sampling was performed down to 350, 450 or 550 m. During each oblique haul, nine depth strata were fished, the thickness of these strata depending on the type of haul (*table II*). For the 700–0 and 550–0 m hauls, sampling of the superficial layer was made with smaller depth strata at night (0–25, 25–50 and 50–75 m) than during day (0–75 m), in order to better define the depth partitioning of the migrant organisms which concentrate at these depths at night. The volume of water filtered in each layer varied from 110 to 1710 m^3, depending on the depth strata sampled. The tow (nine samples) ranged in length from 5500 to 8845 m, the BIONESS being towed parallel to the coast.

Samples, preserved in 5 % buffered formalin seawater, were analysed further. The following variables were obtained for each species and each haul:

(i) density of the organisms in each depth stratum sampled (ind. per 1000 m^3),

(ii) standing crop of organisms (SC) per unit of area for the entire water column explored (ind. m^{-2}),

(iii) weighted mean depth, WMD = $\Sigma (ni \times zi \times di) / \Sigma (ni \times zi)$, where di is the depth of a sample i (centre of the depth interval), zi the thickness of the stratum and ni the number of individuals per 1000 m^3 at that depth. *t*-tests were performed to test the significance of depth difference between day and night or between transects for a given species. The spatial distributions by day and at night of a given species are presented for each transect as isocontours drawn according to a geometric progression of order 2. Transects are presented from shallow waters to deeper ones, which corresponds to the coast–offshore direction for transects A, B, C and D. The environmental conditions (temperature, salinity, chlorophyll and nutrient concentration) occurring during this study were investigated by means of CTD casts and water samples [1].

3. RESULTS AND DISCUSSION

Seventy-six species of macroplankton and micronekton were identified in the hauls. In the present study, vertical distributions are described for the twenty main species, each of which represented more than 3 % of the standing crop for at least one haul. Average SCs recorded in day and night samples for the entire area are given in *table III*

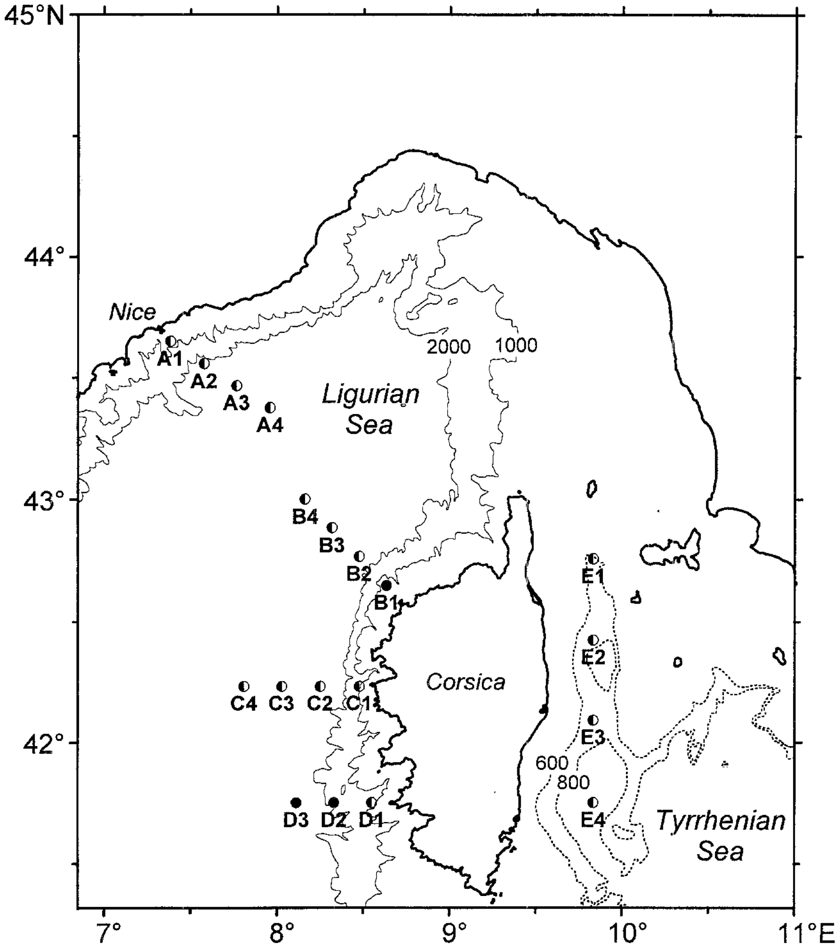


Figure 1. Positions of the sampling stations (◐, day- and night; ●, at night). Isobaths for 600 and 800 m are drawn for the Tyrrhenian Sea only.

for each of these species, values for deep-living species being calculated from 700–0 m hauls only. These twenty species represented 80–95 % of the standing crop for the entire water column. The most abundant species were the fish *Cyclothone braueri* and *Cyclothone pygmaea* (31–48 ind. m^{-2}), then the euphausiids *Meganyctiphanes norvegica* and *Nematoscelis megalops* and the siphonophores *Lensia conoidea* and *Chelophyes appendiculata* (10–16 ind. m^{-2}). High standard deviation reflects a high heterogeneity in the geographical distribution of abundance (e.g. for the salp *Thalia democratica*). This geographical heterogeneity and the differences between day and night catches will be discussed when considering the vertical distributions of each species. As vertical distributions of most of the species studied here have been previously reported for various areas of the world's oceans, discussion of our results will refer essentially to studies performed in the Mediterranean Sea.

3.1. Medusae

By day the hydromedusa *Solmissus albescens* was mainly found between 350 and 550 m (*figure 2*), some individuals being occasionally caught down to 700 m (e.g. at C1 and C2). At night the animals were concentrated in the upper 100 m, performing an extensive DVM of 355 m (*table IV*); they reached concentrations of 380 ind. per 1000 m^3 in the 25–50 m stratum at stations C1 and B3. *S. albescens* is endemic to the Mediterranean Sea and its extensive DVM of 300–600 m has been reported previously by different authors (see [4] for detailed literature references). At night, this species was absent or nearly

Table I. Sampling data for BIONESS tows by day (d) and at night (n). Bottom depths of the sampling stations are given as numbers to the nearest 50. Sunrise around 04.32–04.56 h and sunset around 18.08–18.26 h during this period (●, new moon; ○, full moon).

Haul	Depth Range (m)	Bottom depth (m)	Date April 94	Time (h GMT)	Haul	Depth range (m)	Bottom depth (m)	Date April 94	Time (h GMT)
A1d	450–0	650	12	13.25–14.11	B1n	350–0	700	22	02.06–02.45
n	450–0		12	20.37–21.26	B2d	700–0	2450	22	07.30–08.24
A2d	700–0	2100	13	08.07–08.53	n	700–0		21	23.01–23.54
n	700–0		12	23.02–23.55	B3d	700–0	2600	21	13.29–14.22
A3d	700–0	2350	11	15.16–16.12	n	700–0		21	20.19–21.15
n	700–0		11 ●	21.08–22.05	B4d	700–0	2600	21	10.11–11.06
A4d	700–0	2400	12	08.16–09.09	n	700–0		20	21.05–22.02
n	700–0		12	00.00–00.52	C1d	700–0	1300	22	12.39–13.31
E1d	450–0	600	14	15.21–16.07	n	700–0		23	21.03–22.01
n	450–0		14	20.59–21.45	C2d	700–0	2600	23	13.50–14.43
E2d	550–0	700	16	08.55–09.42	n	700–0		24	00.21–01.15
n	550–0		15	01.02–01.50	C3d	700–0	2700	24	08.57–09.56
E3d	450–0	700	15	08.47–09.42	n	700–0		24	21.02–22.02
n	450–0		16	00.37–01.33	C4d	700–0	2700	24	12.17–13.13
E4d	550–0	900	15	13.09–14.10	n	700–0		25 ○	00.25–01.25
n	550–0		15	20.35–21.17	D1d	700–0	1250	25	09.09–10.02
					n	700–0		26	20.17–21.19
					D2n	700–0	1700	26	23.30–00.26
					D3n	700–0	2500	27	02.35–03.28

Table II. Depth strata sampled during the different tows (9 strata per tow). Results of the 500–550 m stratum of haul A2d and of the 75–150 m stratum of haul A3d have been discarded due to disfunctioning of the net.

Haul 700–0 m		Haul 550–0 m		Haul	Haul
day	night	day	night	450–0 m	350–0 m
0–75	0–25	0–75	0–25	0–25	0–25
	25–50		25–50	25–50	25–50
	50–75		50–75	50–75	50–75
75–150	75–150	75–150	75–150	75–150	75–100
					100–150
150–250	150–250	150–250	150–250	150–200	150–200
				200–250	200–250
250–350	250–350	250–300	250–350	250–300	250–300
		300–350		300–350	300–350
350–400	350–450	350–400	350–400	350–450	
400–450		400–450	400–450		
450–500	450–550	450–500	450–550		
500–550		500–550			
550–700	550–700				

absent from the 0–25 m layer along transects B, C and D, being generally concentrated just beneath that depth (*figure 2*). In contrast, along transects A and E, it was abundant in the 0–25 m stratum at five of the eight stations sampled. This feature appeared to be neither related to the area sampled, Ligurian Sea compared to Tyrrhenian Sea, nor to the coastal/offshore position, nor to the temperature conditions. At that time of the year, the thermocline was not well developed and the temperature gradient between 5 and 25 m was generally <0.8 °C and 1.3 °C at maximum [1]. This feature did not appear to be related to the time of the sampling either, as hauls (D3n excepted) were performed at least two hours after sunset and two hours before sunset (*table I*). The avoidance of

Table III. Average standing crop of organisms for the entire water column and the entire sampled area (ind. m^{-2}), recorded at day and night samples. Results of the incomplete hauls, A2d and A3d, have been discarded. *, calculated from 700–0 m hauls only.

	Day	Night
Medusae		
Solmissus albescens (Gegenbaur, 1856)	4.8 ± 4.7	5.2 ± 4.8
Siphonophores		
Abylopsis tetragona (Otto, 1823)	1.6 ± 1.4	1.4 ± 1.1
Chelophyes appendiculata (Eschscholtz, 1829)	15.9 ± 23.1	9.2 ± 5.1
Lensia conoidea Keferstein and Ehlers, 1861	16.0 ± 11.1	13.7 ± 14.7
Pteropods		
Cavolinia inflexa (Lesueur, 1813)	4.0 ± 3.1	1.7 ± 2.7
Clio pyramidata (Linne, 1767)	2.1 ± 2.6	1.6 ± 0.9
Styliola subula (Quoy and Gaimard, 1827)	0.3 ± 0.8	0.4 ± 1.5
Mysids		
Eucopia unguiculata Willemoes-Suhm, 1875	3.5 ± 2.7*	4.4 ± 3.0*
Euphausiids		
Euphausia brevis Hansen, 1905	1.4 ± 2.0	0.5 ± 0.9
Euphausia hemigibba Hansen, 1910	0.8 ± 1.6	0.5 ± 1.1
Euphausia krohni (Brandt, 1851)	3.1 ± 3.6	3.4 ± 4.5
Meganyctiphanes norvegica (M. Sars, 1857)		
small	10.0 ± 1.2	10.6 ± 5.2
large	18.1 ± 1.6	18.4 ± 4.8
Nematoscelis megalops G.O. Sars, 1883		
small	5.7 ± 4.4	7.7 ± 16.4
large	6.3 ± 2.0	7.3 ± 2.7
Stylocheiron longicorne G.O. Sars, 1883	3.5 ± 3.3	2.7 ± 1.4
Peneideae		
Gennadas elegans (S.I. Smith, 1882)	1.1 ± 1.1*	2.7 ± 1.3*
Salps		
Pegea confoederata (Forskål, 1775)	0.04 ± 0.1	2.9 ± 5.4
Salpa fusiformis Cuvier, 1804	4.1 ± 4.9	4.3 ± 3.7
Thalia democratica (Forskål, 1775)	5.9 ± 10.4	6.9 ± 16.0
Fish		
Cyclothone braueri Jespersen and Tåning, 1926	40.2 ± 13.3*	48.3 ± 10.9*
Cyclothone pygmaea Jespersen and Tåning, 1926	33.3 ± 12.1*	30.7 ± 10.2*

the 0–25 m stratum by *Solmissus albescens* on transects B, C and D could be related to a full moon on 25 April. In fact, night hauls along transects B, C and D were performed in the 20–27 April period, while transects A and E were explored in the 11–16 April period (*table I*). Benović [6] reported that *Solmissus* never reached the 0–100 m level at full moon, while at periods of low moonlight intensity individuals were even found near the surface.

3.2. Siphonophores

The most abundant siphonophore species caught, *Lensia conoidea*, showed a clearly different behaviour along the east Corsican coast compared to the western stations (*figure 3*). By day, at stations A2, A3 and A4 and along transects B and C, a main population was observed in the 0–350 m water column, a few organisms being caught below that. In contrast, along transect E and at station A1, the daytime distribution of *L. conoidea* was clearly bimodal, with a superficial population in the upper 100 m and a deeper population below 250 m. At night, the organisms were concentrated in the upper 200 m, whatever the sampling station. Average WMDs were therefore calculated for the two groups of stations and for two water columns (*table IV*). From these calculations, at stations A1 and E, the deeper population performed a DVM of 210 m as mean amplitude and the superficial population a slight reverse migration of 70 m (from 35 ± 10 m by day to 105 ± 30 m by night). At the other stations, day and night WMDs of the main shallow population were not signifi-

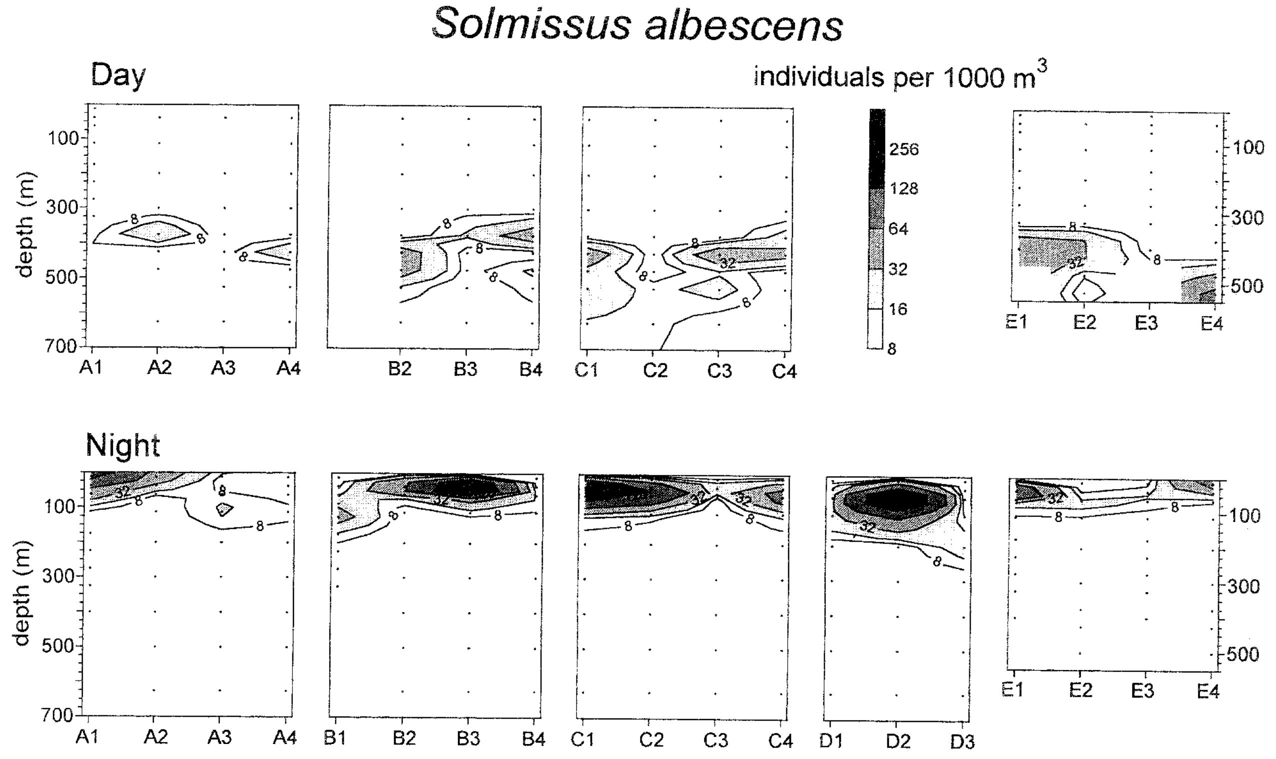


Figure 2. Vertical distributions of the hydromedusa *Solmissus albescens* by day and at night along the sampling transects. Transect D is not represented by day as only one day haul could be performed. Isocontours are drawn according to a geometric progression of 2. Dots correspond to the centre of the depth strata sampled.

cantly different (*table IV*), while the few deeper individuals migrated a distance of 365 m. A slight reverse migration could have occurred at station A2: by day a high number of organisms were caught in the 0–75 m stratum while at night they were very rarely caught. Note that the abundance of *Lensia conoidea* was very variable between stations, with highest concentrations of 800–850 ind. per 1000 m^3 in the upper strata of hauls A1d and B3n, and concentrations often >300 ind. per 1000 m^3 along transect E. Various strategies were observed here for *Lensia conoidea*: moderate to large migration by a distance of 210–365 m, and even slight reverse migration. Results of previous studies also varied widely. Franqueville [15] reported that *L. conoidea* did not appear to undergo a DVM and Patriti [25] caught this species mainly in the 600–1000 m water column and not in the upper 100 m. In a neighbouring site of A3 and A4, in May 1990, Andersen et al. [4] observed a bimodal day distribution with a 200 m migration for the deeper population and a 50 m reverse migration for the shallower population. In contrast, in April 1991, at the same site, *L. conoidea* was concentrated in a single peak by day performing a normal 200 m migration [31].

The siphonophore *Chelophyes appendiculata* was caught by day between 150 and 250 m (*figure 4*), independently of the station (WMD of 215 ± 25 m, *cf. table IV*). However, its abundance varied strongly between stations, from 4.8 ind. m^{-2} at E2 to 95.2 ind. m^{-2} at C2, with a maximum concentration of 866 ind. per 1000 m^3 in the 150–250 m stratum at C2. At night, *C. appendiculata* was concentrated in the upper 100 m, performing a moderate migration of 135 m as amplitude and generally reaching the surface layer. *Abylopsis tetragona* (*figure 4*) was found ~100 m deeper by day than *Chelophyes appendiculata*, with maximum abundances between 250 and 400 m at every station (WMD of 325 ± 35 m); its preferential depth appeared regular along transect C. In contrast, the night distribution of *Abylopsis tetragona* varied with the sampling station. At the offshore stations and at E3 and E4, *A. tetragona* was concentrated in the upper 100 m, while at the coastal or shallowest stations (A1, B1, C1,

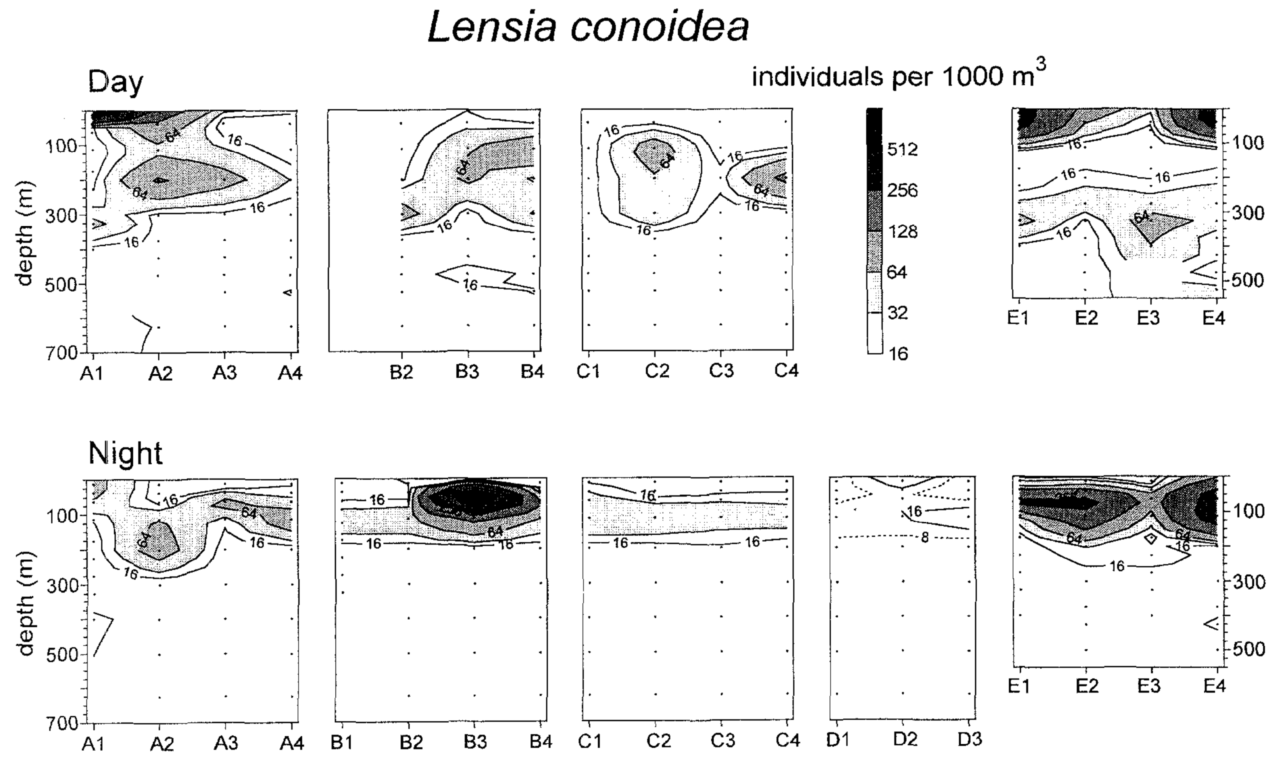


Figure 3. Vertical distributions of the siphonophore *Lensia conoidea* by day and at night along the sampling transects (see caption for *figure 2*).

D1, E1 and E2), the population extended on a deeper water column, down to 250 m, for example at B1 and C1. DVM of this species appeared therefore less cohesive and of smaller amplitude at the coastal stations than at the deeper ones. Note that such a distribution was observed for the five transects. *Abylopsis tetragona* and *Chelophyes appendiculata* are generally reported as diel migrators in the Mediterranean Sea [4, 15, 19]. To our knowledge, only Patriti [25] did not observe DVM for these two species in the Mediterranean Sea, although he performed hauls at 1h30–3h20 intervals over three daily cycles. During the present cruise *C. appendiculata* always reached the surface at night, with maximum concentration in the uppermost stratum (0–25 m) at most of the stations. Zooplankton data with high vertical resolution are rather rare for this species, however in the North Atlantic, Roe et al. [29] also found most of the specimens in the 0–25 m zone at night.

3.3. Pteropods

Three thecosome pteropod species were abundant, *Cavolinia inflexa*, *Clio pyramidata* and to a lesser extent *Styliola subula* (*table III*). The vertical distributions of *Cavolinia inflexa* and *Clio pyramidata* appeared to vary according to the transect (*figure 5*). By day, a constant population of *Cavolinia inflexa* was caught between 150 and 350 m along the four transects, A, B, C and E, particularly regularly along transect C (WMD of 255 ± 20 m). A superficial population was also observed along transect E (at E1 and E2 particularly). At night *C. inflexa* was concentrated in the upper 50 m, and generally in the 0–25 m stratum (WMD of 15 ± 5 m, *cf. table IV*). Therefore, the deep population migrated as a compact unit over a mean distance of 230 m, which agrees with the observations of Castelbon [13] and Sardou and Andersen [31], and even the superficial population of transect E appeared to ascend and concentrate at the surface at night.

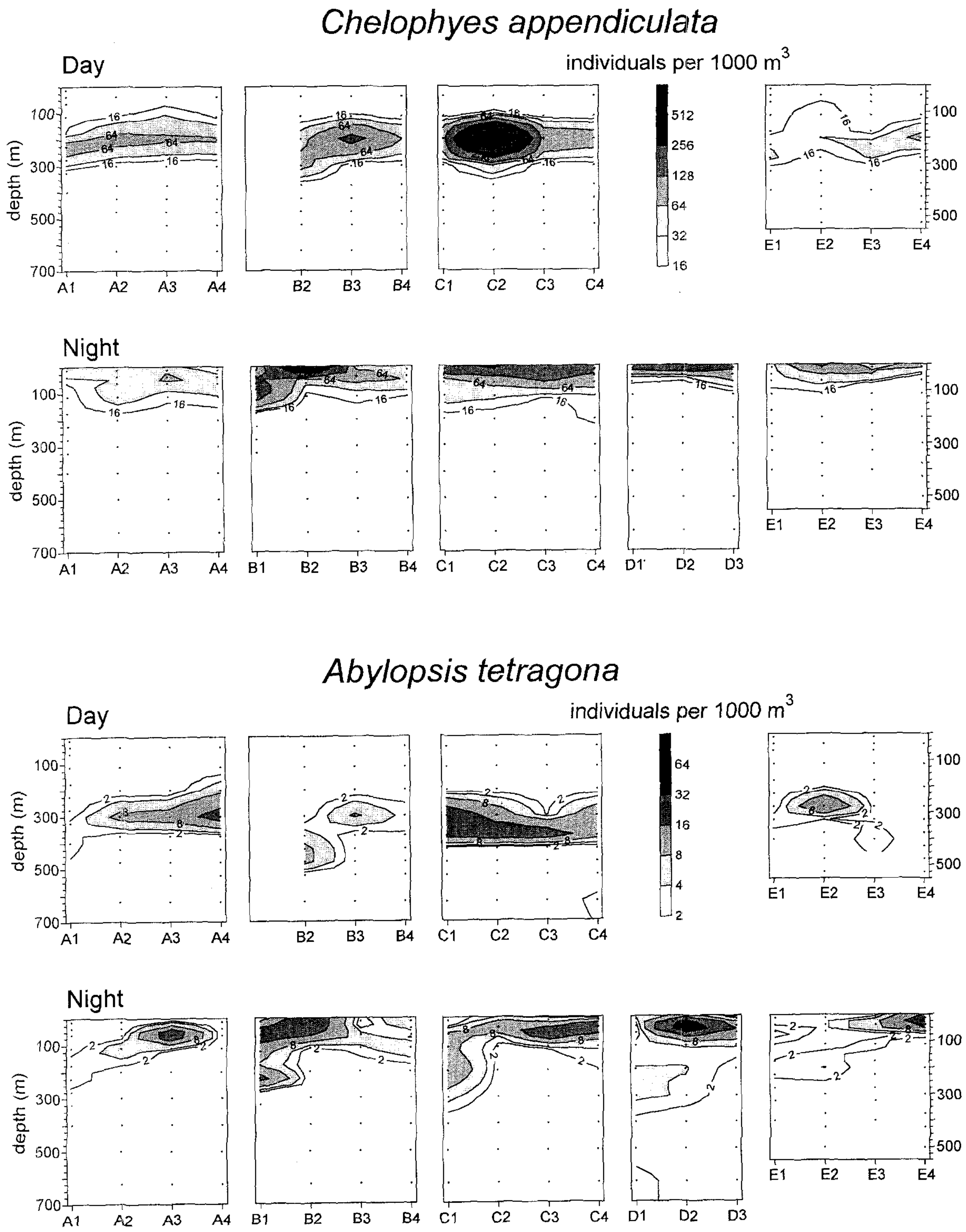
Clio pyramidata showed more heterogeneity in its vertical distribution. By day a deep population was generally caught below 350 m. A shallower population was also observed along transect C, where it appeared to be characteristic of this transect, and at some other stations (A1, E1). At night, both the deeper and upper populations concentrated in the upper 100 m, migrationing by a mean amplitude of 435 and 155 m, respectively. Compared to

Table IV. Average weighted mean depths (WMD) in the entire sampled area ± standard error at day and night, number of samples in parenthesis, and mean amplitude of the migration (dz) when the day-night differences (t-test) are significant at the 0.05 level. Values are given as numbers to the nearest 5. (r): reverse migration.

	WMD (day)	WMD (night)	dz
Solmissus albescens	440 ± 55 (16)	85 ± 45 (19)	355
Abylopsis tetragona	325 ± 35 (15)	115 ± 75 (18)	210
Chelophyes appendiculata	215 ± 25 (16)	80 ± 35 (19)	135
Lensia conoidea			
0–350 m (A2 A3 A4 B C D)	190 ± 40 (10)	150 ± 45 (14)[a]	–
below 350 m	515 ± 70 (8)		365
0–150 m (A1 E)	35 ± 10 (5)	105 ± 30 (5)[a]	(r)70
below 150 m	315 ± 30 (5)		210
Cavolinia inflexa			
0–150 m	35 ± 5 (6)	15 ± 5 (16)[a]	20
below 150 m	245 ± 40 (16)		230
Clio pyramidata			
0–350 m	215 ± 45 (12)	60 ± 20 (19)[a]	155
below 350 m	495 ± 65 (11)		435
Styliola subula	170 ± 95 (5)	30 ± 25 (3)	140
Eucopia unguiculata	610 ± 30 (11)	530 ± 70 (15)	80
Euphausia brevis	290 ± 50 (15)	35 ± 30 (13)	255
Euphausia hemigibba	355 ± 60 (10)	55 ± 30 (15)	300
Euphausia krohni	345 ± 60 (16)	50 ± 20 (19)	295
M. norvegica small			
0–250 m	55 ± 20 (14)	35 ± 20 (19)[a]	20
below 250 m	325 ± 25 (6)		290
M. norvegica large	330 ± 100 (13)	55 ± 25 (17)[b]	275
N. megalops small			
0–250 m	85 ± 40 (15)	85 ± 30 (18)[a]	–
below 250 m	355 ± 35 (12)		270
N. megalops large			
0–250 m	140 ± 50 (14)	125 ± 30 (19)	–
below 250 m	420 ± 80 (15)	435 ± 75 (17)	295[c]
Stylocheiron longicorne	175 ± 25 (15)	190 ± 25 (19)	–
Gennadas elegans			
0–350 m	620 ± 10 (9)[d]	160 ± 50 (16)[d]	460
below 350 m		465 ± 65 (13)[d]	155
Pegea confoederata	95 ± 40 (4)	50 ± 50 (9)	–
Salpa fusiformis			
0–250 m	100 ± 70 (11)	90 ± 50 (17)[a]	–
below 250 m	395 ± 60 (10)		305
Thalia democratica	35 ± 10 (8)	25 ± 10 (7)	–
Cyclothone braueri	385 ± 40 (16)[e]	375 ± 45 (18)[e]	–
Cyclothone pygmaea	570 ± 25 (10)[d]	585 ± 30 (13)[d]	–

[a] for the entire water column; [b] results of B3n and C4n excluded (see text for details)
[c] calculated from the deeper day WMD and the shallower night WMD; [d] from 700–0 m hauls
[e] results of B1n (350–0 m) excluded

Cavolinia inflexa, *Clio pyramidata* spread on a larger water column at night with a deeper WMD (60 ± 20 m compared to 15 ± 5 m). These two species are known to form swarms, the effect of this is clear from the catches, for example, along transect A for *Cavolinia inflexa* and along transect E for *Clio pyramidata*. Extensive DVM of *Clio pyramidata* has been generally reported by previous studies in the Mediterranean Sea [13, 15, 28, 31]. In April 1982, Sardou et al. [32] also observed a bimodal day distribution of this species in an area close to A1 and A2. Rampal [28] reported that *C. pyramidata* became eurybathe during the mating period, aggregating in the sub-



Chelophyes appendiculata

Abylopsis tetragona

Figure 4. Vertical distributions of the siphonophores *Chelophyes appendiculata* and *Abylopsis tetragona* by day and at night along the sampling transects. Note that scales of shaded areas are different for the two species (see caption for *figure 2*).

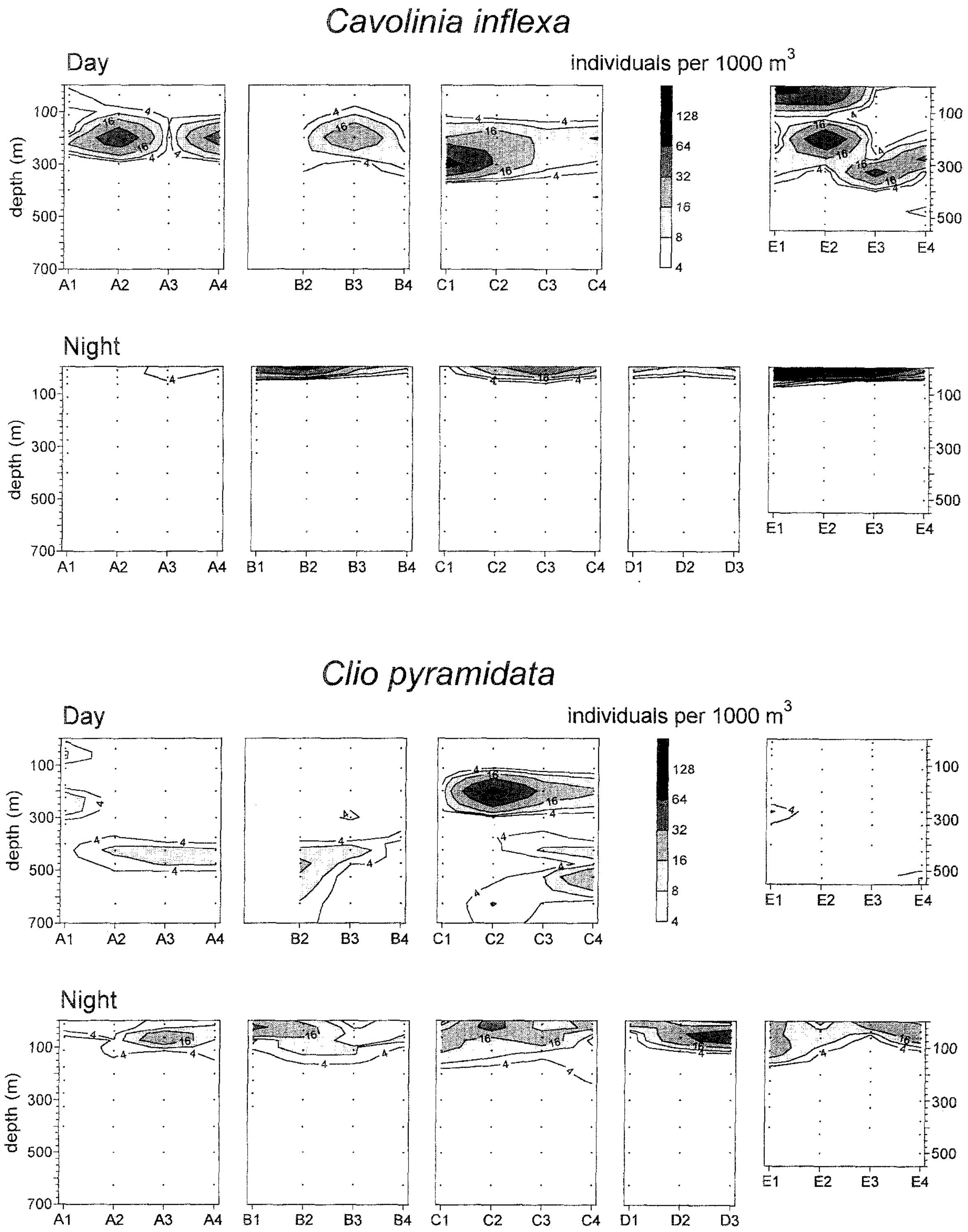


Figure 5. Vertical distributions of the pteropods *Cavolinia inflexa* and *Clio pyramidata* by day and at night along the sampling transects (see caption for *figure 2*).

surface. These results would suggest that the observed bimodal day distribution of *C. pyramidata* could be related to mating behaviour at this time of year.

Styliola subula was caught in only five day hauls and three night hauls, mainly along transect E with a concentration of upto 240 ind. per 1000 m^3 in the 0–25 m stratum of haul E1n. This agrees with previous results on its geographical distribution in the Mediterranean Sea. Menzies [23] observed that *S. subula* was most abundant in the eastern Mediterranean although also occurring in the western basin, and Furnestin [16] caught this species only in the eastern Corsican waters during her study in the western Mediterranean. The daytime distribution of *S. subula* was bimodal along transect E with a superficial population in the upper 75 m and a deeper population below 150 m, while in hauls A1d and A2d it was only caught below 150 m. At night (D2n, E1n, E2n), it was concentrated in the upper 75 m with WMD of 30 ± 25 m (*table IV*), the deeper population undergoing a moderate migration. The variable distribution of *Styliola subula* appeared somewhat similar to those of *Cavolinia inflexa*. *S. subula* has been reported to perform marked DVM, both in the Mediterranean Sea [23, 27] and in the North Atlantic [3, 12, 29, 35]. Greatest abundances of adults were generally found in the upper 50 m at night, as observed here. Along transect E, the deeper peak would correspond to adults performing DVM at night, according to the studies mentioned above; the upper peak would be composed of juveniles which showed maximum numbers in the superficial layers both by day and at night at certain times of the year [27].

3.4. Mysids

Eucopia unguiculata was the largely dominant mysid species caught during this study. By day its distribution was restricted to depths below 500 m; at night, it was caught below 300 m, part of the population performing a moderate DVM (*figure 6*). It was absent or rarely caught at the shallowest stations (A1, B1 and transect E). This species is known as bathypelagic, with the maximum of the adult population occurring below 1000 m [11, 13]. Sampling is generally not deep enough to catch the entire population but, from its upper distributional limits, it

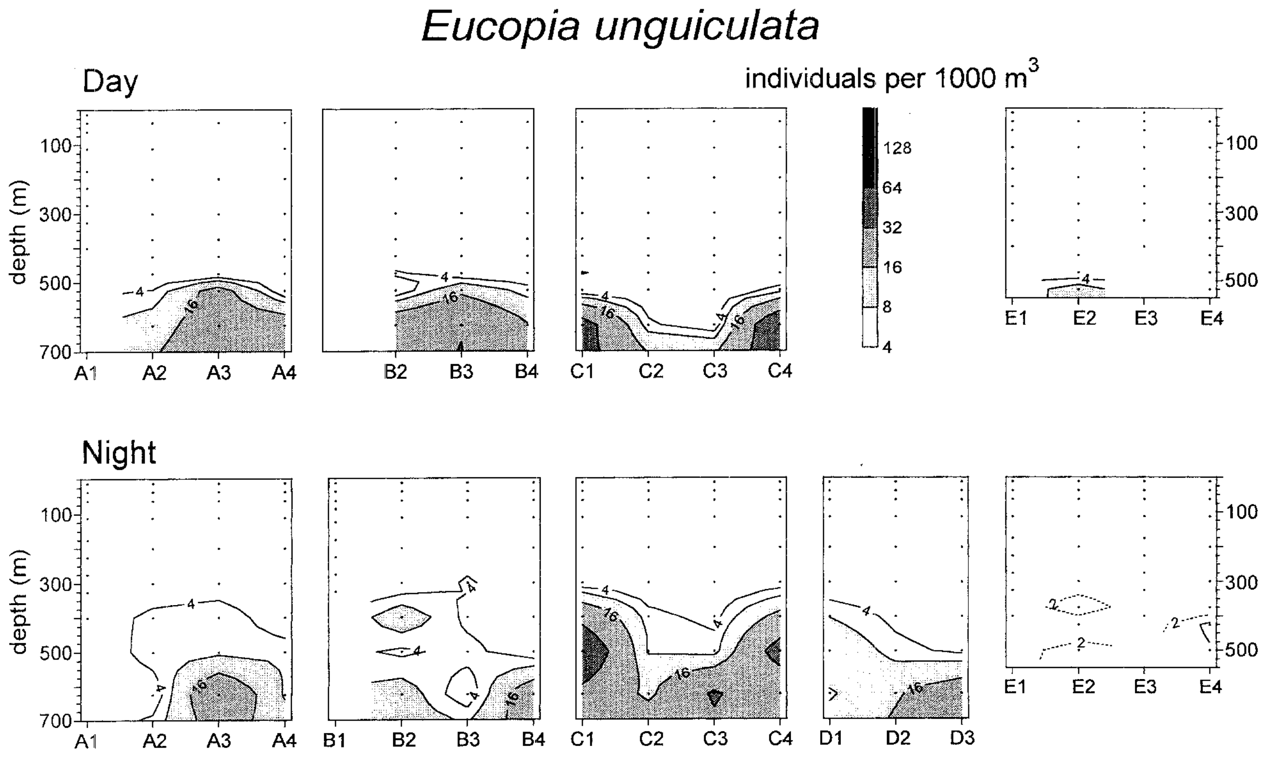


Figure 6. Vertical distributions of the mysid *Eucopia unguiculata* by day and at night along the sampling transects (see caption for *figure 2*).

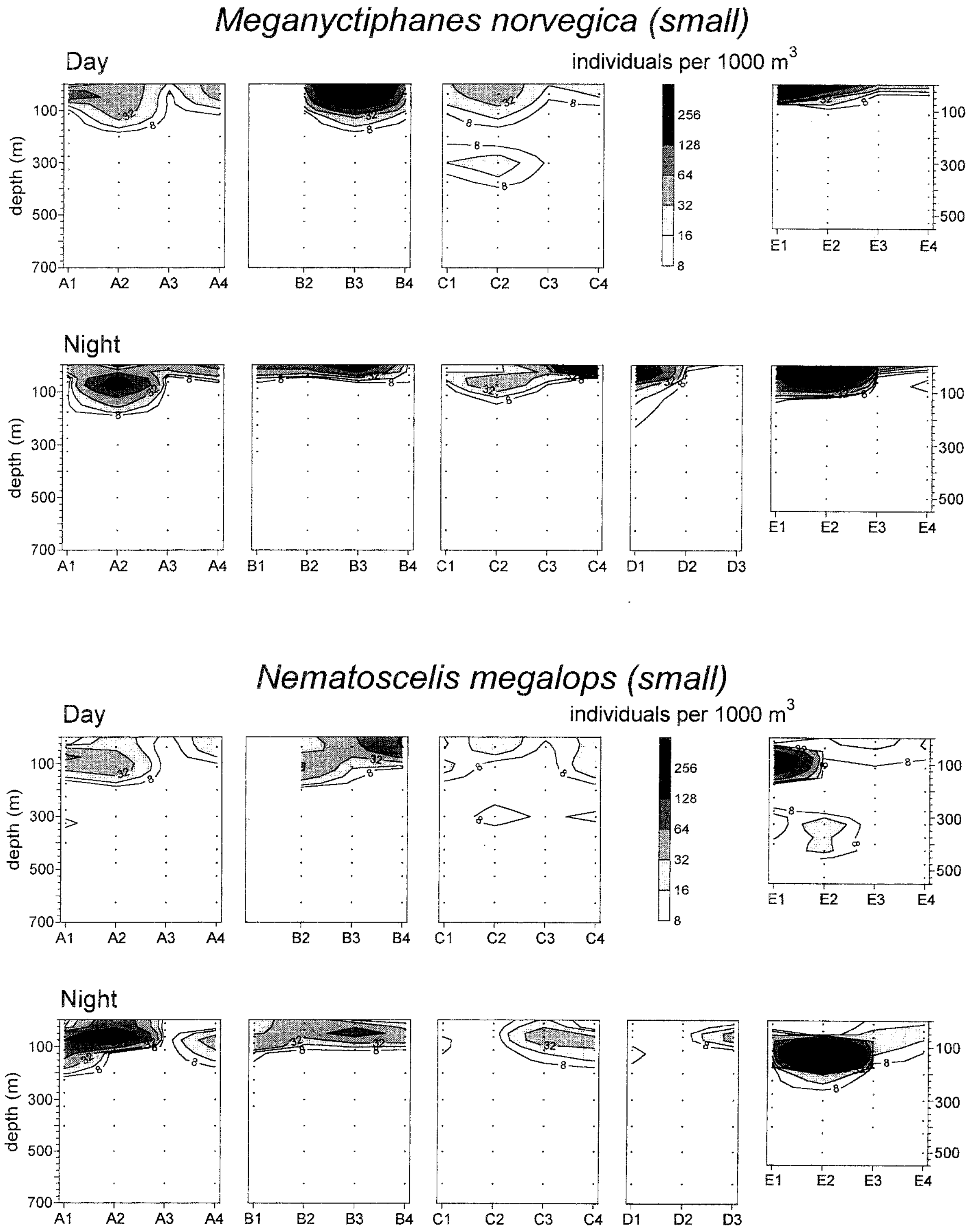


Figure 7. Vertical distributions of the small individuals of the euphausiids *Meganyctiphanes norvegica* (≤ 7 mm) and *Nematoscelis megalops* (≤ 11 mm) by day and at night along the sampling transects (see caption for *figure 2*).

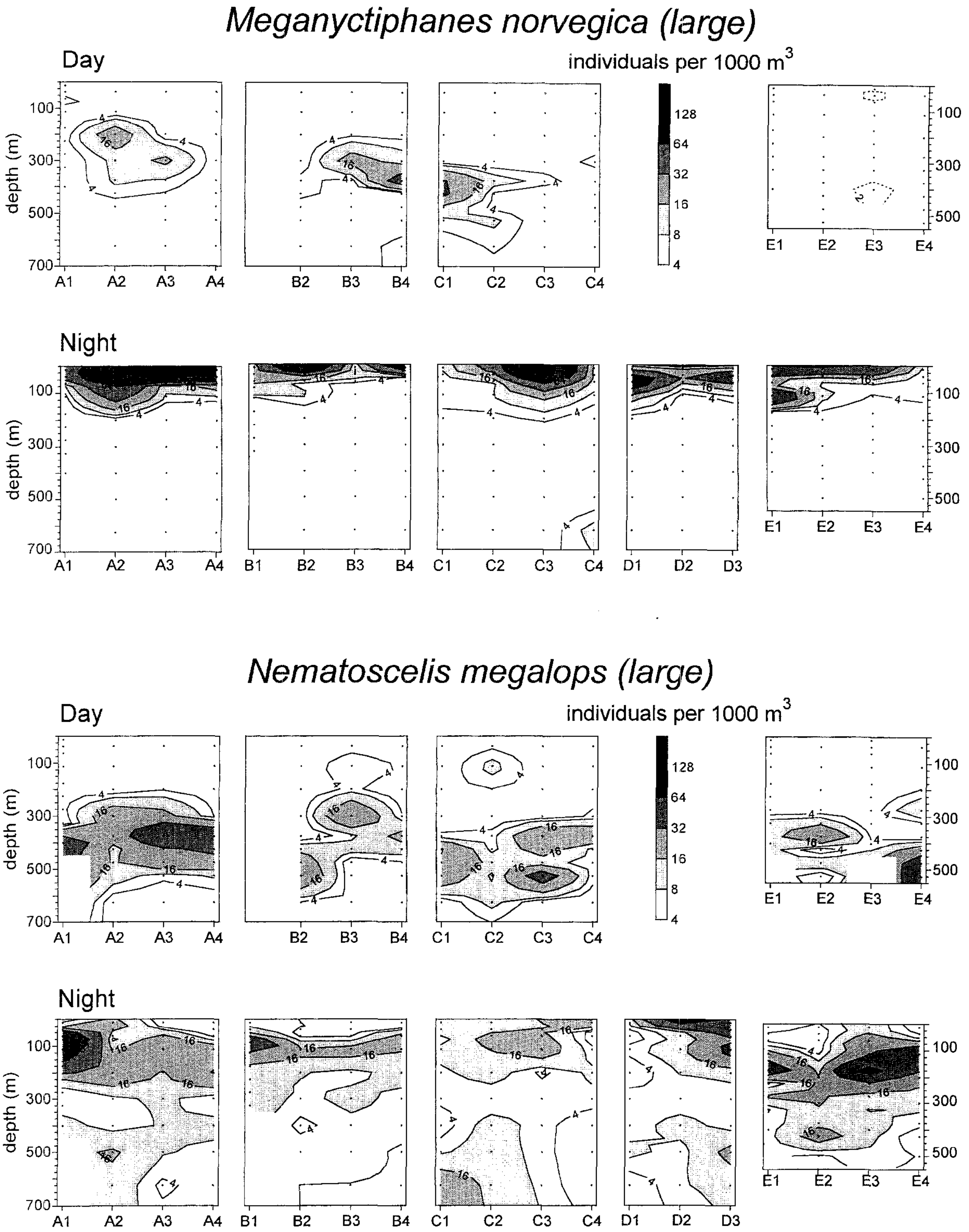


Figure 8. Vertical distributions of the large individuals of the euphausiids *Meganyctiphanes norvegica* and *Nematoscelis megalops* by day and at night along the sampling transects (see caption for *figure 2*).

appears that part of the population undergoes a moderate DVM, *Eucopia* living below 500–700 m by day and some individuals being caught at 250–400 m at night [2, 15, 31].

3.5. Euphausiids

The two dominant euphausiid species were *Meganyctiphanes norvegica* and *Nematoscelis megalops* (*table III*). Numbers of individuals caught were high enough to differentiate two size classes for these species: (i) small individuals with a total length ≤ 7 mm for *Meganyctiphanes* and ≤ 11 mm for *Nematoscelis*, which correspond respectively to larvae and post-larvae according to Casanova [10], (ii) larger individuals. Andersen and Sardou [2] and Sardou and Andersen [31], defining the same size classes, observed that migrating behaviour varied according to the size class at a station near A3 and A4. The small individuals of these two species showed similar vertical distributions (*figure 7*). By day, a main peak of abundance was observed in the upper 150 m, a secondary one being observed between 250 and 400 m, along transect C for the two species and along transect E for *Nematoscelis megalops*. At night, maximum numbers were caught in the upper 100 m, although small *Nematoscelis* lived, on an average, 50 m deeper than small *Meganyctiphanes* (WMDs of 85 ± 30 m and of 35 ± 20 m, *cf. table IV*). This agrees with the general observation of Casanova [10] on euphausiid larvae: most of the larvae are concentrated at 25–50 m while the oldest lived deeper, down to 100 and 200 m.

In contrast to small individuals, the behaviour of large individuals largely differed between the two species. By day, large *Nematoscelis* lived generally deeper than large *Meganyctiphanes* (*figure 8*). At night, large *Meganyctiphanes* were concentrated in the upper 150 m (rare individuals being caught deeper at B3 and C4), while large *Nematoscelis* spread throughout the entire water column, forming a main peak above 250 m and a secondary one below 350 m (particularly visible at stations A2, C1, C2, D3 and E2). Therefore an extensive DVM was observed for the entire population of large *Meganyctiphanes*, but for only part of the large *Nematoscelis* and this behaviour was observed in all the transects. Previous studies have reported the occurrence of a main upper population of *Nematoscelis* at 75–250 m at night [2, 9, 10, 13, 15, 31, 33].

Stylocheiron longicorne was caught between 75 and 350 m during the day and at night at all the sampled sites and was a non-migrant species (*figure 9, table IV*). This feature was also observed in spring 1990 and 1991 near stations A3 and A4 by Andersen and Sardou [2] and Sardou and Andersen [31]. *S. longicorne* has also been reported as a weak migrant living between 500 and 2000 m by day [9, 10] or between 250 and 2000 m with a maximum around 500 m [13]. Mauchline [22] found in his review on euphausiids based on various areas for *S. longicorne* characteristics similar to ours: non-migrant, with average day and night depths of 100–300 m and 100–400 m, respectively.

In contrast, *Euphausia krohni* performed an extensive DVM of 295 m as mean amplitude, migrating as a compact unit from 250–400 m by day to the upper 75 m at night (*figure 9*). *Euphausia brevis* and *Euphausia hemigibba* were less abundant than *Euphausia krohni* (*table III*) and caught mainly along transect E with maximum densities of 5.3–6.5 ind. m^{-2} compared to 0.3–0.9 ind. m^{-2} for the other transects. This is in accordance with previous geographical investigations which report that these species are very common in the eastern Mediterranean and Tyrrhenian Seas and rare in the other areas of the western basin [9, 10, 33]. *E. brevis* and *E. hemigibba* showed similar migrating behaviour to *E. krohni*, migrating as a compact unit on large distances of 255 and 300 m respectively (*table IV*). By day, *E. hemigibba* and *E. krohni* were found at the same depth but *E. brevis* lived significantly higher in the water column (~60 m). At night the three *Euphausia* species aggregated at the same depth. *E. krohni* is well known as an extensive migrator. The large DVM we observed for *E. brevis* and *E. hemigibba* has been reported by Casanova [9, 10] and Castelbon [13] for the Mediterranean Sea, but it has also been observed in various areas of the North Atlantic, [3, 5, 17, 34]. In the North Atlantic, *E. hemigibba* was also reported as living slightly deeper by day than *E. brevis*, as observed here.

3.6. Decapods

Among the eight decapod species identified in the hauls, the Peneidea *Gennadas elegans* was largely the most abundant species. By day, it was caught below 500 m and no specimen was observed at the shallowest stations (*figure 10*). At night, the vertical distribution was bimodal with an upper peak around 100–200 m and a deeper one, often less pronounced, in the 450–550 m stratum. Average WMDs give amplitudes of migration of 460 and 155 m (*table IV*). The average standing crop was significantly higher at night than by day (*table III*). This sug-

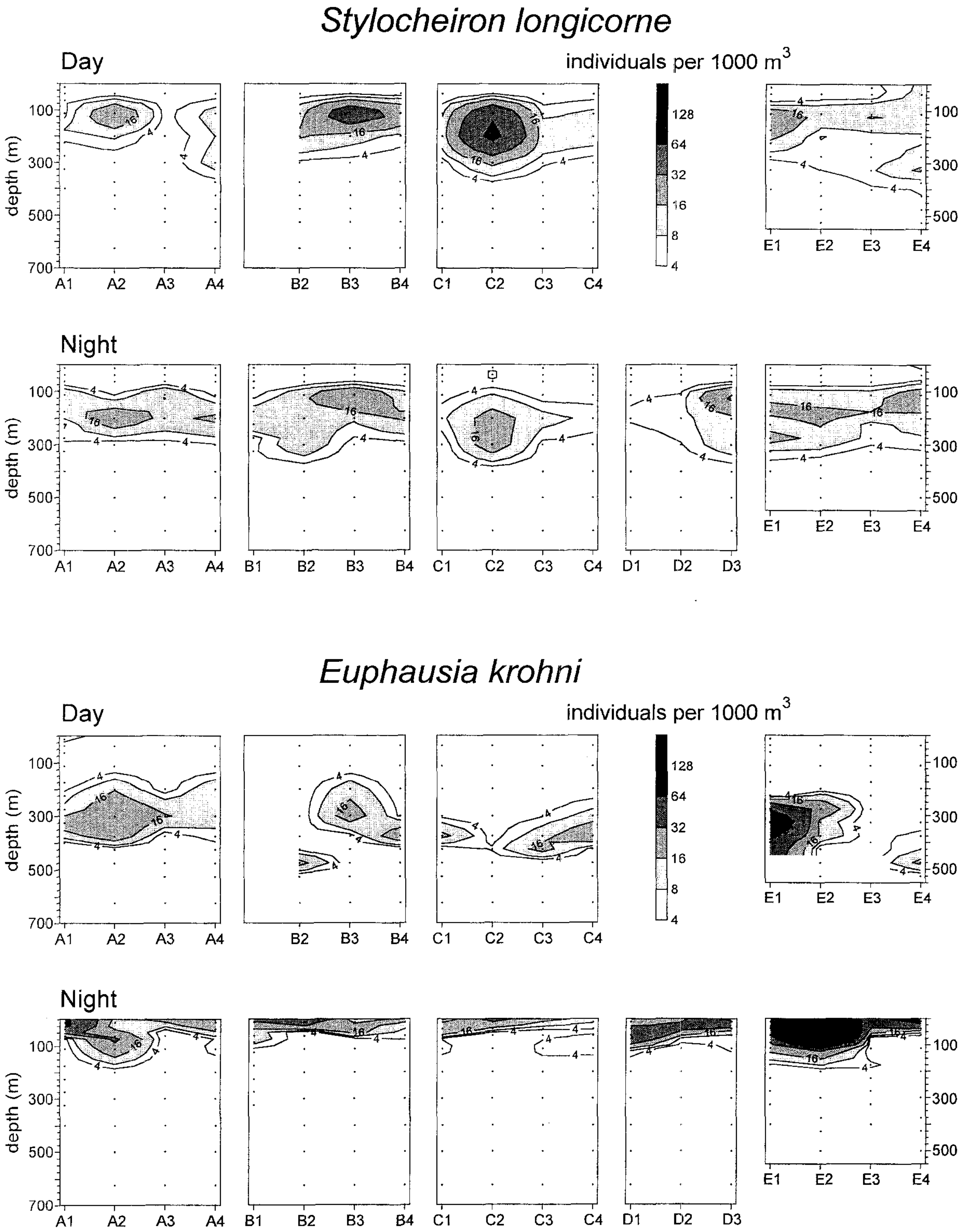


Figure 9. Vertical distributions of the euphausiids *Stylocheiron longicorne* and *Euphausia krohni* by day and at night along the sampling transects (see caption for *figure 2*).

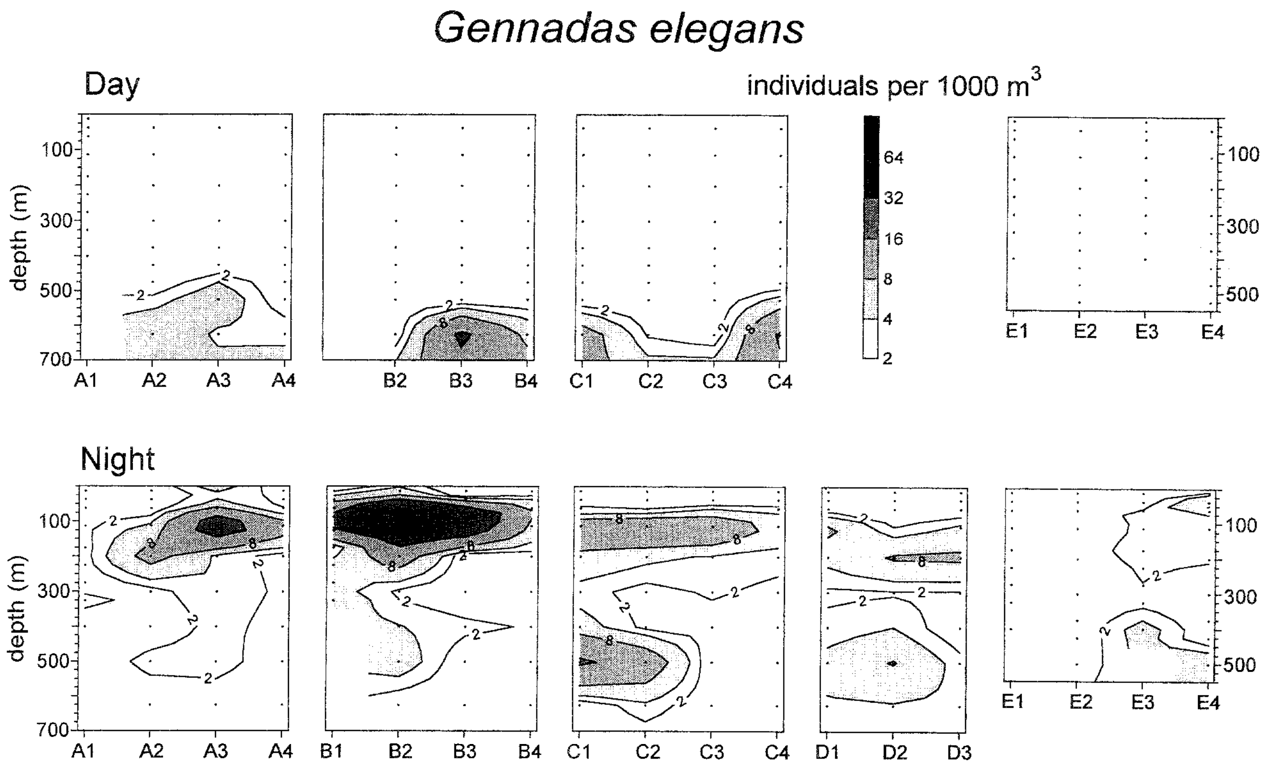


Figure 10. Vertical distributions of the decapod *Gennadas elegans* by day and at night along the sampling transects (see caption for *figure 2*).

gested that the deep night population comprised migrant organisms living below our deepest stratum sampled by day. In fact, *Gennadas elegans* is typically bathypelagic, living below 500 m by day [15] and generally at 1000 m and below [11, 13], and performing an extensive DVM at night. The present study and the studies of Andersen and Sardou [2] and Sardou and Andersen [31], performed with relatively narrow depth strata, showed that *G. elegans* did not appear to migrate as a compact unit, as its night distribution was bimodal in the 0–700 m water column.

3.7. Salps

Thalia democratica was the most abundant salp species in the total sampled area (*table III*), although it was caught in only eight day hauls and seven night hauls and almost exclusively along transects A, D and E. It tended to form swarms at the shallowest or coastal stations (A1, transect E) with concentrations >300 ind. per 1000 m^3 and up to 1200 ind. per 1000 m^3 in the 0–25 m stratum of haul E2n. By day as well as at night, and independently of the sampling station, it was concentrated in the upper 50 m (*table IV*). It was clearly a non-migrant epiplanktonic species, as reported, for the Mediterranean Sea, by Braconnot [7], Palma [24] and Sardou et al. [32].

Salpa fusiformis was more regularly caught than *Thalia democratica*, forming swarms of up to 575 ind. per 1000 m^3 in the 0–25 m stratum of haul A1d (*figure 11*). In contrast to *T. democratica*, it was only occasionally caught along transect E and its vertical distributions appeared very variable. In fact, the day distribution showed either one superficial peak (A1), either a deep peak (e.g. B2) or two peaks (e.g. A2, C1, C3), and was variable along a given transect (for example, two maxima at C1 and C3 and a single shallower maximum at C2 and C4). At night, *Salpa fusiformis* was almost exclusively caught in the upper 250 m, and upper 150 m more particularly. The day deep population would have migrated a mean distance of 305 m (*table IV*). The large differences observed in daytime distributions during the present study neither appear related to the position of the

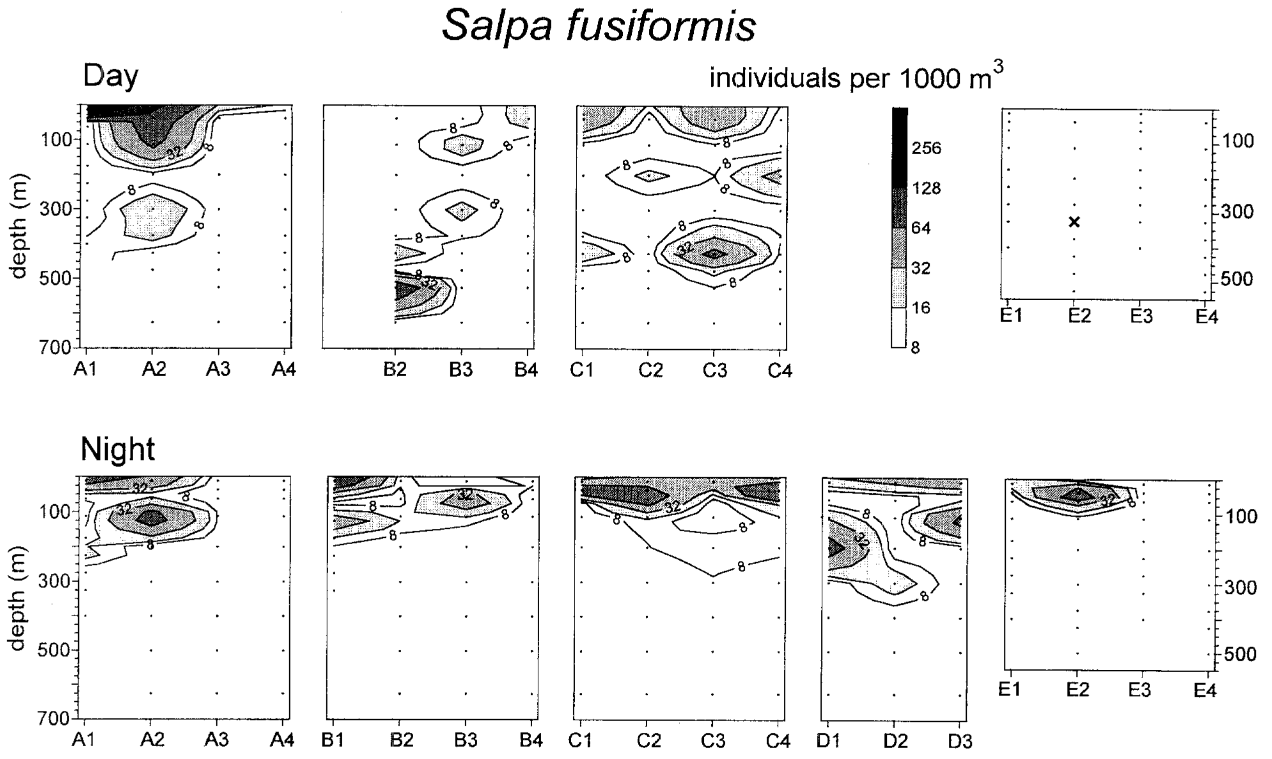


Figure 11. Vertical distributions of the salp *Salpa fusiformis* by day and at night along the sampling transects (see caption for *figure 2*). × occurrence in very small numbers.

transects nor to the coastal-offshore position of the stations. Such a diversity appears from previous observations. In Mediterranean waters, Laval et al. [20] observed a bimodal day distribution while Castelbon [13] reported the absence of a superficial maximum by day. According to Franqueville [15] *S. fusiformis* underwent an extensive DVM while data of Laval et al. [20] and of Sardou et al. [32] did not show evidence of a clear DVM. In the Atlantic, off Bermuda, Madin et al. [21] caught large numbers of *S. fusiformis* at night in the 0–200 m water column but only a few specimens by day. The migrant behaviour of this species therefore remains a debated subject.

Pegea confoederata was caught in very small numbers by day compared to at night (*table III*) and it was present in only four day hauls. The few individuals caught by day were observed in the upper 150 m. At night, the WMD was of 50 ± 50 m (*table IV*), with swarms >400 ind. per 1000 m^3 encountered in the 0–25 m stratum. These results suggest an extremely patchy distribution or occurrence of organisms below 700 m (limit of our sampling) during the day. In that case, *P. confoederata* would be a very extensive migrator, performing DVM of at least 600 m. To our knowledge, vertical distribution of this species has received little attention and has been occasionally mentioned in physiological studies. So, Caron et al. [8], studying salp faecal pellets, noted that *P. confoederata* was caught in surface waters during both day and night in the North Pacific. Further investigations are therefore needed.

3.8. Fish

Maximum abundance of *Cyclothone braueri* was observed between 250 and 450 m during the day and the night (*figure 12*), lowest densities occurring along transect E. Its preferential depth was particularly regular along transect C (WMD of 365 ± 20 m by day and 365 ± 25 m at night). Going deeper, *C. braueri* was progressively replaced by *Cyclothone pygmaea* which was also non-migrant, with maximum abundance below 450 m (*figure 12; table IV*). *C. pygmaea* was exceptionally caught at the shallowest stations (e.g. transect E).

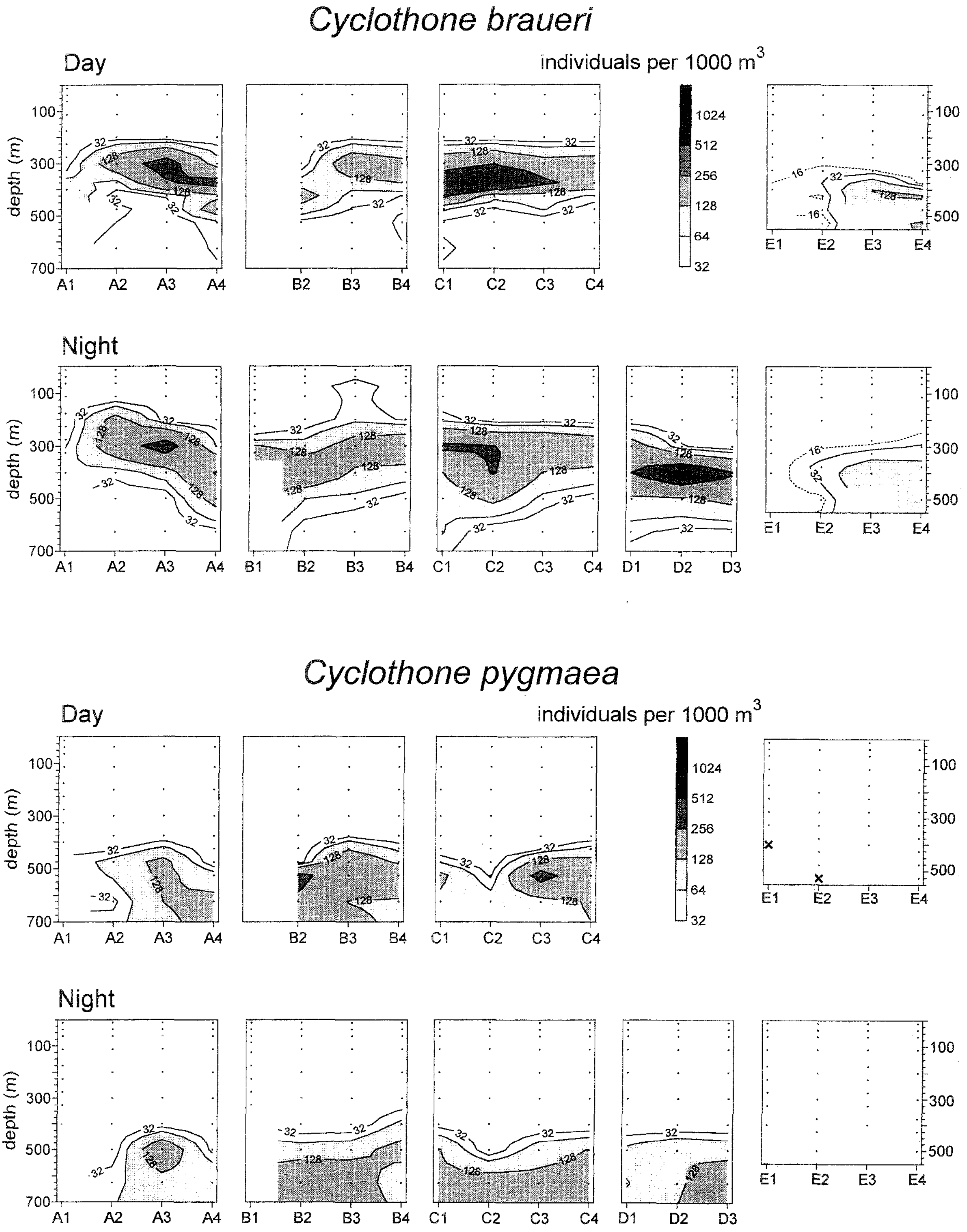


Figure 12. Vertical distributions of the fish *Cyclothone braueri* and *Cyclothone pygmaea* by day and at night along the sampling transects (see caption for *figure 2*). ×: occurrence in very small numbers.

The present results are in agreement with the preferential depths reported for these species in the Mediterranean and Tyrrhenian Seas by different authors [2].

3.9. Environmental conditions influencing the vertical distribution of the species

During this study, the vertical temperature gradient was weak (~1.7 °C at a maximum) with no well developed thermocline, and salinity values are in the range 37.9–38.6 [1]. Such small differences in temperature and salinity would not have influenced the distributions of the species. However, it can be noted that transect C, which is influenced by a mesoscale eddy and showed the smallest differences between stations in its hydrological structure (temperature, salinity and density) compared to the other transects in the Ligurian Sea, also presented the smallest differences in preferential daytime depth for several species (e.g. *Cavolinia inflexa*, *Abylopsis tetragona* and *Cyclothone braueri*).

The stations sampled here largely differed in their content in Chlorophyll *a* (Chl), from 10.2 mg m^{-2} at E1 to 118.7 mg m^{-2} at A4 in the 0–200 m layer. A sub-superficial peak was observed at 20–40 m depth at most of the stations with values of 1.3–2.2 mg m^{-3} (e.g. A3, A4, B3, B4, C2, C3, C4, E4), while distributions were more or less homogeneous down to 50–100 m depth at some others stations with Chl concentration <0.6 mg m^{-3} (A1, A2, E1, E2, E3). Absorption of light by phytoplankton changes the light distribution in and beneath the euphotic layer. Total chlorophyll per square meter can be used as an index of the relative irradiance encountered by the organisms, with the bottom of the euphotic layer shallowing when Chl increases. Light is generally considered to be the most significant external factor influencing DVM [14]. If we consider the Preferendum Hypothesis, the daytime depth of a species would be related to the depth of its preferential isolume, and, as hypothesized here, to the Chl content. To test this hypothesis, day WMD of a species was plotted versus Chl content in the 0–200 m layer for each station, two WMDs being considered when the distribution showed two maxima (*table IV*). A significant relation was found for *Euphausia brevis*, *Meganyctiphanes norvegica* adults and *Clio pyramidata* (deeper peak), day WMD decreasing as Chl content increased (*figure 13*).

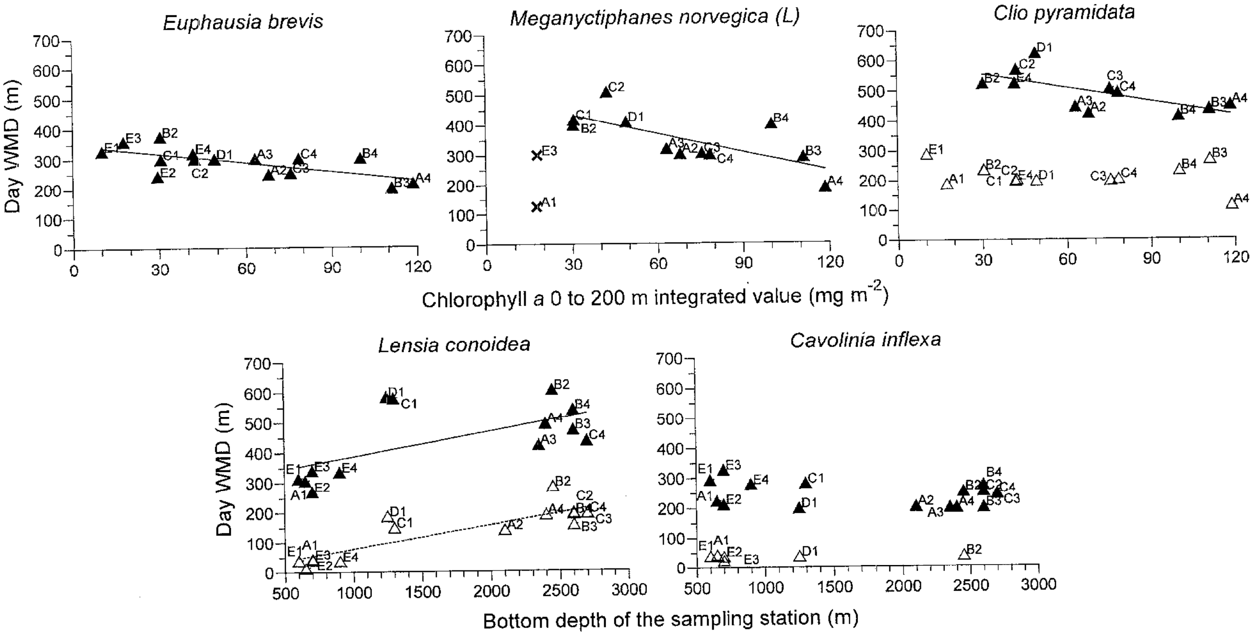


Figure 13. Day WMDs versus chlorophyll *a* content in the 0–200 m water column for different species showing trend (above) and day WMDs versus bottom depth of the sampling stations (below). WMD was calculated for two water columns (Δ, shallower peak; ▲, deeper peak) when the day distribution of the organisms was bimodal. ×, results excluded from the calculation of the regression line.

Above: *E. brevis*: $Y = -1.02\,X + 348.45$, $n=15$, $r^2=0.491$, $p<0.01$; *M. norvegica*: $Y = -2.07\,X + 494.92$, $n=11$, $r^2=0.529$, $p<0.05$; *C. pyramidata*: $Y = -1.53\,X + 601.17$, $n=11$, $r^2=0.471$, $p<0.05$;

Below: *L. conoidea* shallower peak: $Y = 0.08\,X + 0.28$, $n=15$, $r^2=0.729$, $p<0.01$; *L. conoidea* deeper peak: $Y = 0.08\,X + 304.35$, $n=13$, $r^2=0.385$, $p<0.05$.

The highest variation of day WMD with Chl content was found in *M. norvegica* adults, 190 to 510 m (excluding results of stations A1 and E3 where shallow peaks of small density were observed). Day WMD ranges of the deep population of *Clio pyramidata* and of *Euphausia brevis* were less extended, 415–625 m and 200–375 m, respectively. It therefore appeared that light could be the dominant factor influencing the daytime depth of these species. The study of Isaacs et al. [18] was, to our knowledge, among the first to highlight such a relationship, depth of deep scattering layers being observed to increase with water transparency. Recently, in the tropical Atlantic, Andersen et al. [3] observed a decrease in the preferential daytime depth of migrant euphausiids and pteropods from oligotrophic location to mesotrophic and eutrophic ones, these sites differing in their chlorophyll content and in their euphotic layer depth, which was calculated independently. Casanova [10] suggested that, by day, *Euphausia brevis* lived deeper or extended throughout a larger water column in the Tyrrhenian Sea than in the other areas of the western basin, which corresponds to our observations (transect E, *cf. figure 13*). The preferential daytime depth of *M. norvegica* was reported to deepen with bottom depth during summer [9]; our sampling, performed in spring, did not suggest such a variation.

We also considered bottom depth as a global index of ecosystem characteristics, coastal waters being more diluted, less dense and poorer in nutrients in the superficial layers than offshore waters. Some trends appeared between day WMD and bottom depth for the siphonophore *Lensia conoidea*; both its shallower and deeper peaks appeared to deepen when bottom depth of the station increased (*figure 13*). To our knowledge no such a relationship has previously been shown. Concerning the most abundant pteropod species, *Cavolinia inflexa*, no trend could be seen between WMD of its peaks and Chl content or bottom depth. Our data showed that the shallowest stations (≤1300 m) were characterised by the occurrence of two peaks while the deepest stations were characterised by a single peak (if we except station B2 where the superficial peak was weak). It therefore suggests that the distribution of *C. inflexa* is related to bottom depth in this area of the Mediterranean Sea. Rampal [28] reported a variation in the depth distribution of this species according to its reproductive cycle. At the beginning of the mating period (November), part of the population ascended to the surface and maxima were observed at the surface and at 200 m depth. At the end of spring, *C. inflexa* descended to depths of 300 m and below. The bimodal distribution observed in the present study along transect E and in station A1 might be related to mating strategy.

4. CONCLUSIONS

This study allows the day and night distributions of the main macroplankton and micronekton species at different Mediterranean sites to be described in detail, with narrow depth strata of 25 m by night in the upper layer and of 50 m between 350 and 550 m during daytime. It completes previous information for the northwestern Mediterranean Sea and particularly for the North Tyrrhenian Sea where studies on macroplankton and micronekton are scarce. These results show that, depending on the species, the migration strategy differs in its amplitude, day- and night-time depths, and that, in some species, these characteristics could be controlled by environmental or biological factors. Among the twenty species studied, four were non-migrant (e.g. *Cyclothone braueri* and *C. pygmaea*), one was weakly migrant (*Eucopia unguiculata*), six were synchronous migrants, represented by the three *Euphausia* species, and seven showed a heterogeneous migration pattern, such as *Nematoscelis megalops* (distribution of the two remaining species being too patchy to see a clear pattern). Most of the species had similar distribution throughout the sampled area. However migration of three of these species appeared to be influenced by light absorption in the surface layers. Ascent at night of *Solmissus albescens* could have been restricted by moonlight. Distributions of some species were influenced by unknown factors related to distance from the coast or more precisely to bottom depth. Differences were also observed between Tyrrhenian Sea and north or west of Corsica. In some species, such as *Cavolinia inflexa*, the pattern of distribution and migration, which might be related to reproduction, should also change according to the seasons.

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