

Vertical distributions of zooplankton across the Almeria–Oran frontal zone (Mediterranean Sea)

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*The vertical distribution of zooplankton in the upper 700 m of the water column was investigated across the Almeria–Oran front (Alboran Sea) during winter 1997/98 (Almofront 2 cruise). Eight sites corresponding to three hydrodynamic structures (the Atlantic jet, an anticyclonic gyre and the surrounding Mediterranean waters) were explored, by day and at night, using multiple-net sampling. Results are presented for the major species of copepods (>500 µm), macroplankton and microplankton. Species inhabiting the surface layer or occupying it at night extended deeper in the gyre. On the other hand, mesopelagic species (e.g. *Pleuromamma borealis*, *Pleuromamma abdominalis*, *Euphausia krohni* and *Cyclothone braueri*) were found to live deeper, at least by day for the migrants, in the Mediterranean waters compared with the two other structures. These changes in preferential depths across the front are discussed in relation to environmental features, such as light level, abundance of food and mixed layer depth. This study also documented the vertical distribution of some overwintering copepod species (*Calanus helgolandicus*, *Eucalanus hyalinus* and *Eucalanus monachus*).*

INTRODUCTION

Hydrological fronts constitute areas of active exchanges of energy and matter, and harbour specific ecosystems (Sournia *et al.*, 1990). Geostrophic fronts exhibit complex structures and two types of circulation are generally distinguished within them. The primary circulation mainly consists of a horizontal, geostrophically equilibrated flow, while the secondary circulation, ageostrophic, is associated with divergent and convergent regions and with vertical motions (Prieur *et al.*, 1993; Pinot *et al.*, 1996; Allen *et al.*, 2001). Studies carried out over the two last decades in the western Mediterranean Sea have underlined the biological characteristics of frontal areas, such as the Ligurian Sea front and the Almeria–Oran front (Alboran Sea). These frontal areas show higher phytoplankton biomass and primary production than the adjacent waters and a dominance of diatoms (Claustre *et al.*, 1994; Prieur and Sournia, 1994). Secondary producers have been shown to be also influenced by the frontal structure, in terms of biomass as

well as in terms of productivity or specific diversity (Boucher *et al.*, 1987; Seguin *et al.*, 1994; Youssara and Gaudy, 2001). The higher biomass of zooplankton recorded at oceanic fronts is often explained by a physiological response of the organisms to the frontal environment. However, retention or accumulation of organisms at such fronts may also depend on the interaction of the cross-frontal circulations with the differential motion of the organisms (sinking, floating and swimming), as reviewed by Owens (Owens, 1981) and modelled by Franks (Franks, 1992). From studies of sound-scattering layers (SSL) in the Almeria–Oran front region, in the upper 200 m, a zooplankton layer was found coincident with the drawn-down phytoplankton (Fielding *et al.*, 2001), while the depth of the deep SSLs was reported to vary (Baussant *et al.*, 1993) or not (Fielding *et al.*, 2001) either side of the front. However, information at the species level on the vertical distribution of the zooplankton community across frontal areas remains rare in the western Mediterranean, particularly in the Alboran Sea.

A multidisciplinary study, the Almofront 2 cruise, focused on the geostrophic Almeria–Oran front system in December 1997–January 1998. Three main hydrological structures were explored during this survey: the Atlantic jet, an Atlantic anticyclonic gyre and the surrounding Mediterranean waters. This paper focuses on the vertical distribution of the zooplankton community in the different hydrodynamic structures, and considers the occurrence of diel vertical migration (DVM). Results are presented for the main species of copepods ($>500\ \mu\text{m}$), macroplankton and micronekton in the upper 700 m of the water column. Changes in preferential depths and in amplitude of DVM are discussed in relation to the environmental features. As this study was performed in late autumn–early winter, it also allowed a study of the vertical distribution of some overwintering copepod species.

METHOD

Study area, choice and characteristics of the sites

The Almofront 2 cruise was dedicated to the study of winter dynamic and physical properties of the Almeria–Oran geostrophic front and associated biological processes. The first leg (30 November–22 December 1997) was devoted to a synoptic description (dynamic, hydrobiological and biological) of the whole area (Cussatlegras *et al.*, 2001). The second leg (24 December 1997–16 January 1998) was devoted to the study of biological processes associated with the identified physical structures. Eight sites were chosen following an intensive 12 h survey of the area (using continuous thermosalinometer and vessel mounted ADCP RDI 75 kHz). In addition, satellite images focusing on the position of the Atlantic current and associated gyres helped to choose the location of the sites according to the hydrodynamic structure (Figure 1). As the meander jet system moved eastwards about 90 km during leg 2, a schematic view of the positions of the eight sites within the hydrodynamic mesoscale structures is presented in Figure 2. The three main structures visited consisted of: (i) a southern Atlantic water anticyclonic gyre (sites 1, 3 and 6); (ii) the jet of the Atlantic current, with the core (site 4) and the right and left sides of the jet (sites 5 and 7, respectively); and (iii) typical Mediterranean waters (sites 2 and 8).

The process study at each site began with the immersion of a drifting line of two sediment traps, which was subsequently followed by the ship for 36 h (cf. Figure 1). During the 36 h period, repeated CTD casts were carried out, roughly every 3 h. Chlorophyll *a* (Chl *a*) and phytoplankton taxonomic pigment concentrations were determined by HPLC pigment analyses (Claustre *et al.*,

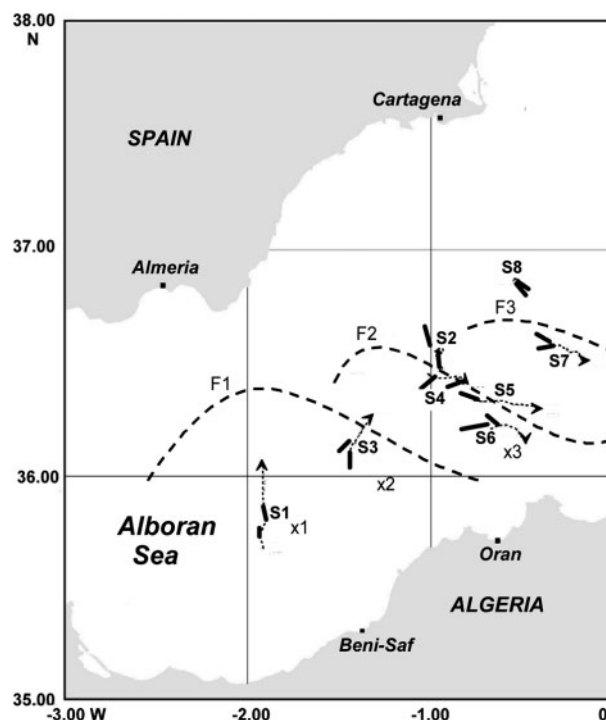


Fig. 1. Geographical locations of the eight sites studied during leg 2 of Almofront 2 cruise. Dotted lines and arrows indicate ship route following the drift of sediment traps during the occupation of one site (36 h), CTD cast being carried along the route. Thick lines correspond to the concomitant BIONESS hauls. During leg 2, the meander jet system moved eastwards about 90 km as indicated by the successive positions of the surface density front (F) and the centre of the anticyclonic gyre (x): F1-x1 stands for 1–20 December (end of leg 1), F2-x2 for 25–30 December (sites 1 to 3 period), F3-x3 for 5–10 January (sites 6 to 7 period).

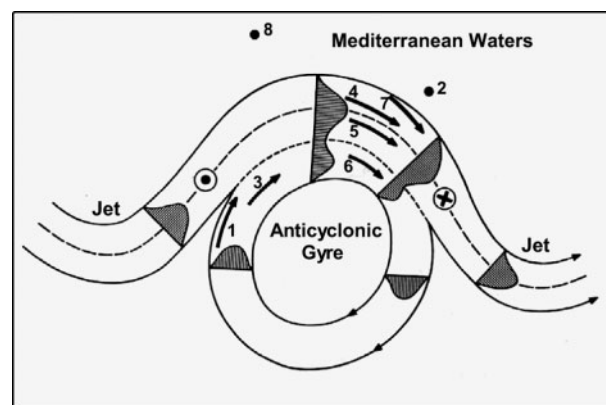


Fig. 2. Idealized scheme of the hydrological structure, positioning sites in relation to the meander of the Atlantic current and the anticyclonic Atlantic gyre. Shaded areas are proportional to the horizontal current velocity.

2000). The depth of the mixed layer clearly increased from the Mediterranean waters (sites 2 and 8) to the Atlantic gyre; it was 120 m at site 6, the more typical gyre site (Figure 3). The Mediterranean waters were

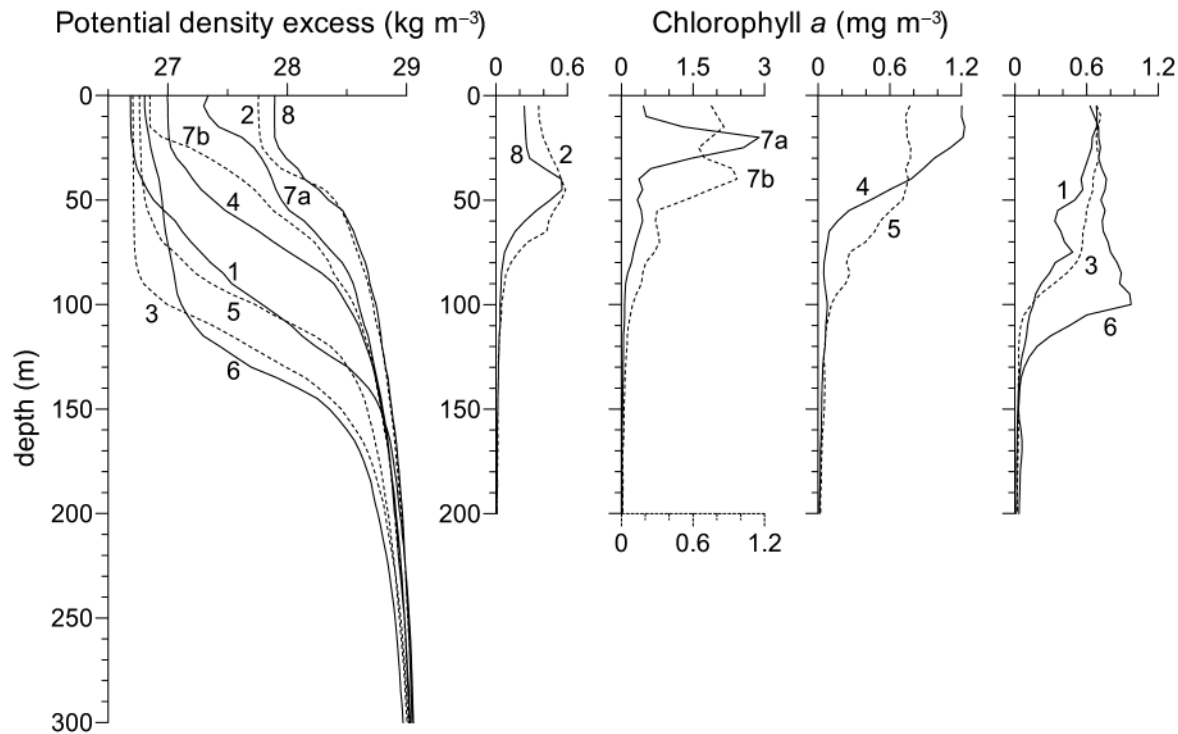


Fig. 3. Average vertical profiles of potential density excess and Chl *a* in the 0–300 m water column at the eight sites. Site 7 was divided into two sub-sites; note the different Chl *a* scale.

characterized by the lowest Chl *a* content and a more or less pronounced sub-superficial peak at ~40–45 m depth, while Chl *a* was homogeneously distributed in the gyre sites down to 80–100 m depth. Site 7, on the left side of the jet core, was divided into two successive sub-sites, according to the CTD-fluorescence profiles.

Zooplankton sampling procedure

A series of oblique hauls was carried out at these eight sites, concomitant with the 36 h surveys. All biological samples were taken with the BIONESS (Sameoto *et al.*, 1980), a multiple opening and closing net with 500 μ m mesh nets. During each oblique haul, generally performed down to 700 m depth by day and at night, nine depth strata were fished. The thickness of these strata depended on the time of the day: 700–550, 550–450 and 450–350 m by day and at night both; 350–300, 300–250, 250–200, 200–150, 150–75 and 75 m to the surface by day; 350–250, 250–150, 150–75, 75–50, 50–25 and 25 m to the surface at night. Narrower strata were then sampled in the 150–350 m water column by day and in the upper 75 m at night. The volume of water filtered in each layer varied from 210 to 2480 m^3 , depending on the depth strata sampled. The sampling data are summarized in Table I and the positions of the hauls indicated in Figure 1.

Table I: Sampling data for BIONESS tows by day (D) and at night (N)

Haul no	Date	Time (UTC)	Bottom depth (m)
S1D-500	25/12/97	13.06–14.00	900
S1N	25/12/97	22.40–00.25	2300
S2D	27/12/97	13.31–15.08	2700
S2N	27/12/97	22.42–00.14	2700
S3D	29/12/97	13.04–14.33	2400
S3N	29/12/97	22.22–23.56	2400
S4D-450	03/01/98	13.55–15.06	2600
S4N	02/01/98	22.34–00.24	2600
S5D	04/01/98	13.30–15.07	2700
S6D	06/01/98	13.10–14.35	2700
S6N	06/01/98	22.17–23.50	2700
S7D	08/01/98	13.15–14.38	2700
S7N	08/01/98	22.28–23.40	2700
S8D	12/01/98	12.50–14.20	2700
S8N	12/01/98	23.28–23.46	2700

Oblique tows were performed in the 0–700 m water column, except hauls S1D and S4D (0–500 and 0–450 m water column respectively). No night haul in site 5. Bottom depths of the sampling sites are given as numbers to the nearest 100. Sunrise around 07.15 h and sunset around 16.50 h during this period. Time is given in h UTC (Universal Time).

Samples, preserved in 5% borax-buffered formalin–seawater, were analysed further. For copepod taxonomy, we have followed the inventory of Razouls and Durand (Razouls and Durand, 1991) for the Mediterranean Sea. The species *Eucalanus hyalinus* (Claus, 1866) found in this study belongs to the *Eucalanus elongatus* group (Fleminger, 1973); comparison of our results with previous studies in the western Mediterranean (Mazza, 1962; Casanova, 1970; Gasser *et al.*, 1998) suggest that this species is the same as *Eucalanus elongatus* reported in these studies. Copepodite stages have been identified for the most abundant species. Sub-sampling, when required for large numbers of copepods or euphausiid juveniles, was generally 1/4 or 1/32th of the whole aliquot and was obtained with a Folsom plankton sample splitter. Size was measured with a precision of ± 0.5 mm for the most abundant euphausiid species, which were separated into size classes of 2 mm width. Density estimates of the organisms were standardized to number of individuals per 1000 m³ (for each stratum) or per m² (for the entire water column explored). We calculated the weighted mean depth for each taxon and haul, $WMD = \Sigma(ni \times zi \times di) / \Sigma(ni \times zi)$, 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 m³ at that depth. When vertical distribution of a given taxon was bimodal, WMD was calculated for two parts of the water column.

Results are presented along a schematic transect from the Mediterranean waters to the Atlantic gyre; sites 2, 7, 4, 5 and 6 can be considered as a horizontal section through the current (cf. Figure 2). Zooplankton concentrations are presented as isocontours drawn according to a geometric progression of order 2 using Surfer® 8.

RESULTS

Vertical distributions of copepods in the 0–700 m water column are described for the 10 main species sampled, each of which represented more than 4% of the total number (TN) of copepods for at least one haul; these 10 species represented 84.5% of the average TN (Table II).

The macroplankton and micronekton organisms (size >3 mm) consisted essentially of euphausiids (45% of the average TN of macroplankton organisms), chaetognaths (32%) and fishes (10%). We consider here only the eight main species, each of which represented more than 2.5% for at least one haul, and the chaetognaths which are the second most abundant group but for which no species determination has been performed (Table II). Two size classes were distinguished for the euphausiid *Nematoscelis*

megalops: small individuals with a total length ≤ 11 mm, and larger individuals.

The temperature profiles recorded with the BIONESS fell in the range of the temperature values recorded with the CTD casts during the same site survey (Figure 4). Then, each haul was performed in one of the typical sites defined from the hydrodynamic and hydrological structures.

Species with heterogeneous vertical distribution

The daytime vertical distribution of the total population of copepods was bimodal at most of the sites, with two peaks in the upper 350 m, except at site S7 where a significant deep peak occurred at ~450–550 m depth (Figure 5). At night most of the copepods concentrated in the upper 100 m; however, the occurrence of a deep peak was observed at S7 as during the day.

Three species of *Pleuromamma* were caught in large numbers: *P. borealis*, the most abundant copepod species, then *P. abdominalis*, and to a lower extent *P. gracilis* (Table II). During the day, these three species tended to live deeper at the Mediterranean sites (S8, S2) and shallower at S6, the typical Atlantic gyre site (Figure 5). At night, they were concentrated in the upper 75 m, except at S6 where they were caught in abundance down to 150–200 m depth. These species exhibited a clear DVM with a mean amplitude of 150–200 m (Table III). The shallower daytime depth and the deeper night-time depth recorded at S6 resulted in a less extensive DVM at S6 than at the other sites.

The second most abundant genus of copepods, *Eucalanus*, consisted mainly of *E. monachus* and *E. hyalinus* (Table II). The copepodites C5 and adults of each of these two species exhibited very different behaviours. C5 *E. monachus* showed a very heterogeneous distribution, both throughout the water column and in the different sampling areas (Figure 6). During the day, they were mainly concentrated around 500 m depth at the Mediterranean sites and at S7; at S7 they constituted more than 90% of the total deep population of copepods. At the other sites, their vertical distribution was bimodal. Surface concentrations increased at night; then, part of the C5s underwent a DVM. By contrast, adults of *E. monachus* did not migrate and were concentrated in the upper 75 m both by day and at night.

On the contrary, in *E. hyalinus*, C5 were non-migrant and concentrated in the superficial layers, while adults generally showed a bimodal vertical distribution both by day and at night (Figure 6) and some of them appeared to migrate (particularly clear at S2). Males were almost exclusively caught in the upper layer, while females were

Table II: Average number of individuals m^{-2} (for the entire water column and the entire sampled area) and percent contribution, recorded for the most abundant species of copepods and macroplankton

Species	no m ⁻²	%	Stages (%)	
TOTAL COPEPODS				
<i>Calanus helgolandicus</i>	146 ± 90	2.9	C5: 65	ad: 35
<i>Centropages chierchiae</i>	118 ± 357	2.3	–	ad: 100
<i>Eucalanus hyalinus</i>	142 ± 123	2.8	C5: 36	ad: 64
<i>Eucalanus monachus</i>	1055 ± 946	21.0	C5: 85	ad: 15
<i>Nannocalanus minor</i>	253 ± 184	5.0	C5: 22	ad: 78
<i>Neocalanus gracilis</i>	67 ± 39	1.3	C2–C5: 64	ad: 36
<i>Pleuromamma abdominalis</i>	819 ± 519	16.3	C2–C5: 63	ad: 37
<i>Pleuromamma borealis</i>	1100 ± 983	21.9	C4–C5: 1	ad: 99
<i>Pleuromamma gracilis</i>	278 ± 146	5.5	C5: 1	ad: 99
<i>Temora stylifera</i>	264 ± 267	5.3	C4–C5: 17	ad: 83
TOTAL MACROPLANKTON				
684.0 ± 308.9				
Siphonophores				
<i>Abylopsis tetragona</i>	8.2 ± 3.4	1.2		
Euphausiids				
<i>Euphausia krohni</i>	155.6 ± 99.7	22.8		
<i>Nematoscelis megalops</i>	128.3 ± 94.0	18.8	small: 85	large: 15
<i>Stylocheiron longicorne</i>	15.3 ± 6.9	2.2		
Peneideae				
<i>Gennadas elegans</i>	5.5 ± 3.1	0.8		
Chaetognaths				
	219.2 ± 142.0	32.0		
Fishes				
<i>Benthoosema glaciale</i>	2.9 ± 2.6	0.4		
<i>Cyclothone braueri</i>	34.5 ± 11.7	5.0		
<i>Cyclothone pygmaea</i>	17.2 ± 9.9	2.5		

The group of Chaetognaths, the second most abundant group of macroplankton, is also included.

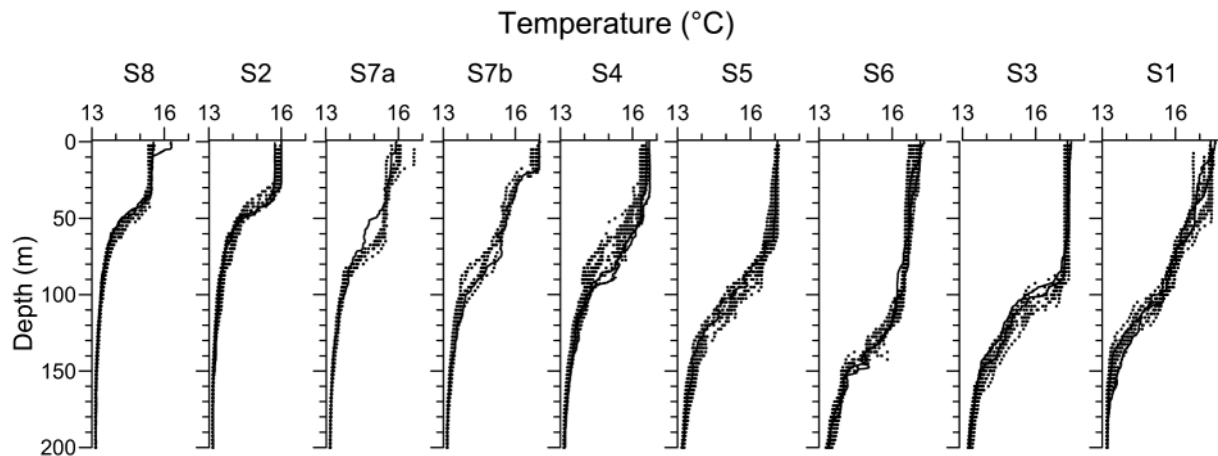


Fig. 4. Temperature profiles recorded with the BIONESS (lines) and temperature values recorded with the CTD casts (dots) during the same site survey. Sites S7a and S7b correspond to the daytime and night-time hauls, respectively.

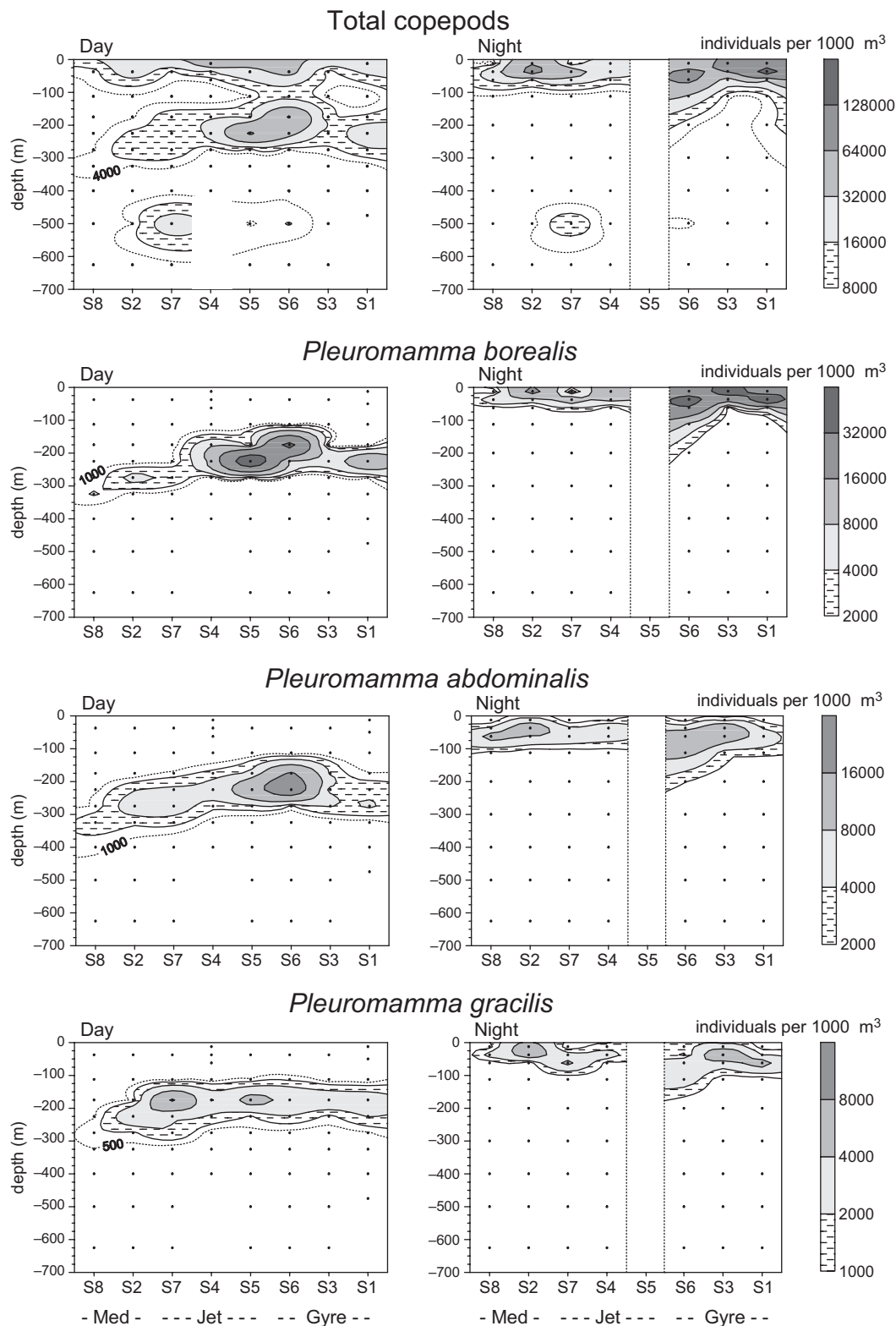


Fig. 5. Vertical distributions of the total copepod population and of the copepods *P. borealis*, *P. abdominalis* and *P. gracilis* along the schematic transect: Mediterranean (S8, S2), frontal (S4, S5, S7) and Atlantic gyre sites (S6, S3, S1). Isocontours are drawn according to a geometric progression of 2. Dots correspond to the centre of the depth strata sampled. Daytime hauls were performed down to 450 and 500 m only at sites S4 and S1, respectively; site S5 was not sampled at night.

Table III: Average weighted mean depths, WMD (m) \pm SD, during the day and at night, and amplitude of the migration, dz (m), for the main taxa of copepods and macroplankton

Taxa	Day WMD	Night WMD	dz
COPEPODS			
<i>Calanus helgolandicus</i>			
C5 0–150 m	50 \pm 30 (8)	40 \pm 30 (7)	435*
150–700 m	475 \pm 30 (6)	470 \pm 45 (7)	
adults 0–150 m	45 \pm 15 (8)		160*
150–700 m	305 \pm 50 (8)		
0–700 m	145 \pm 60 (7)		
<i>Centropages chierchiae</i>	35 \pm 15 (7)	20 \pm 5 (5)	–
<i>Eucalanus hyalinus</i>			
C5	100 \pm 60 (8)	115 \pm 70 (7)	–
adults 0–250 m	80 \pm 25 (8)	70 \pm 25 (7)	490*
250–700 m	560 \pm 30 (6)	560 \pm 50 (7)	
<i>Eucalanus monachus</i>			
C5 0–150 m	50 \pm 15 (8)	45 \pm 10 (7)	355*
150–700 m	400 \pm 90 (7)	410 \pm 100 (7)	
adults	110 \pm 75 (8)	85 \pm 45 (7)	–
<i>Nannocalanus minor</i>	45 \pm 15 (8)	50 \pm 20 (7)	–
<i>Neocalanus gracilis</i>	125 \pm 35 (8)	65 \pm 15 (7)	60
<i>Pleuromma abdominale</i>	255 \pm 40 (8)	105 \pm 30 (7)	155
<i>Pleuromamma borealis</i>	240 \pm 45 (8)	45 \pm 15 (7)	195
<i>Pleuromamma gracilis</i>	210 \pm 35 (8)	55 \pm 25 (7)	155
<i>Temora stylifera</i>	55 \pm 50 (8)	30 \pm 10 (7)	–
MACROPLANKTON			
<i>Abylopsis tetragona</i>			
0–150 m	45 \pm 15 (7)	75 \pm 15 (7)	70**
150–700 m	330 \pm 35 (8)	260 \pm 35 (7)	255*
<i>Euphausia krohni</i>	210 \pm 60 (8)	45 \pm 15 (7)	160
<i>Nematoscelis megalops</i>			
small	40 \pm 5 (8)	60 \pm 15 (7)	–
large 0–250 m	150 \pm 45 (8)	185 \pm 10 (7)	265*
250–700 m	450 \pm 75 (7)	410 \pm 55 (7)	
<i>Stylocheiron longicorne</i>	105 \pm 25 (8)	140 \pm 25 (7)	–
<i>Gennadas elegans</i>	575 \pm 50 (6)	250 \pm 65 (7)	325
Chaetognaths	50 \pm 15 (8)	40 \pm 5 (7)	–
<i>Benthosema glaciale</i>	420 \pm 65 (7)	205 \pm 100 (7)	215
<i>Cyclothone braueri</i>	430 \pm 30 (6)	410 \pm 35 (7)	–
<i>Cyclothone pygmaea</i>	605 \pm 10 (6)	595 \pm 15 (7)	–

Values are given to the nearest 5 (number of samples in parenthesis). Values of dz are given when the day–night differences are significant at the 0.05 level (*t*-test); *, calculated from the deeper day WMD and the shallower night WMD; **, calculated from the deeper day WMD and deeper night WMD.

distributed into two peaks. The deep population of *E. hyalinus* was located deeper than those of *E. monachus*; the highest concentrations were observed down to 700 m, the deepest level sampled here, suggesting that *E. hyalinus* might live deeper. These two species also showed differences in their biogeographical distribution: *E. hyalinus*

was more abundant at the Mediterranean sites and *E. monachus* at the other sites.

The C5 and adults of *Calanus helgolandicus* also showed different behaviours (Figure 7). The vertical distribution of C5 was generally bimodal by day and at night; some of these organisms migrated at night in the surface layers

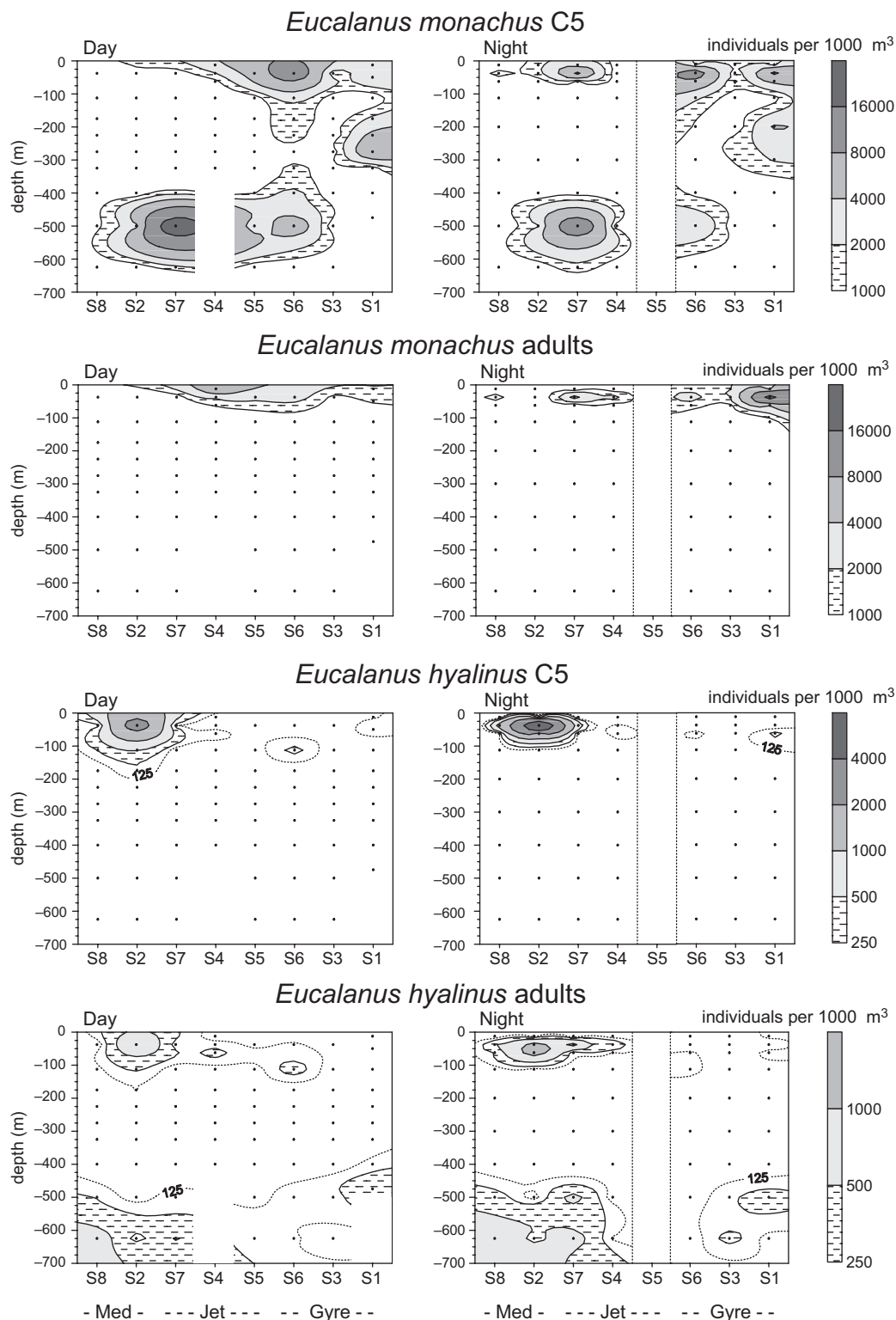


Fig. 6. Vertical distributions of the copepodites C5 and adults of the copepods *E. monachus* and *E. hyalinus* along the schematic transect (see legend for Figure 5).

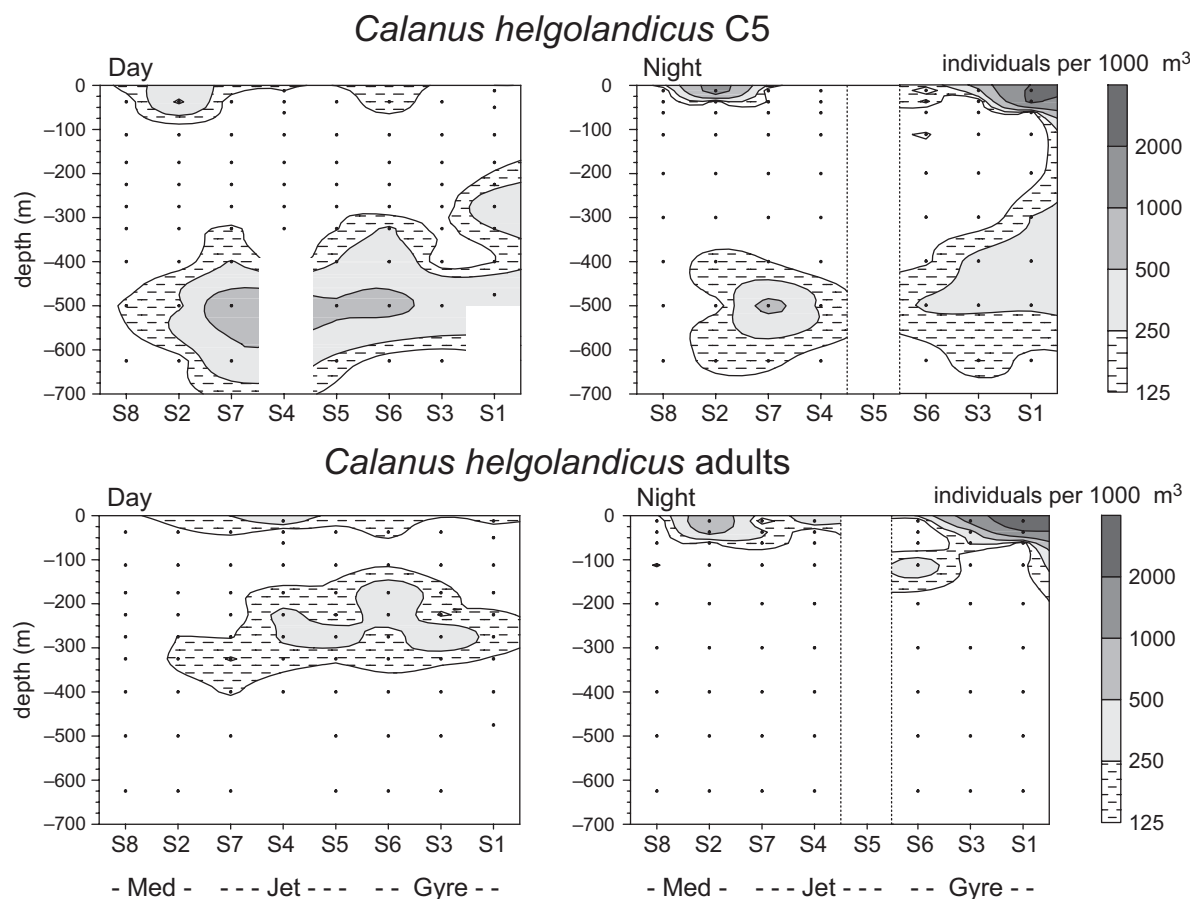


Fig. 7. Vertical distributions of the copepodites C5 and adults of the copepod *C. helgolandicus* along the schematic transect (see legend for Figure 5).

as suggested by the higher concentrations recorded. The adults also showed a bimodal distribution by day, but at night almost all migrated in the upper 150 m; they tended to live shallower by day and deeper by night at S6 than at the other sites, as observed for the migrant *Pleuromamma* species.

Such differences in the preferential daytime depth were also observed in several abundant species of macroplankton and micronekton. They appeared clearly for the whole population of *Euphausia krohni* (Figure 8), of which the maximum concentrations were observed at 250–350 m depth at S8 and S2 (Mediterranean sites) and up to 150 m at S6 (Atlantic gyre). The large individuals of *Nematoscelis megalops* appeared also to live deeper at the Mediterranean sites (Figure 8); some of them migrated at night but avoided the upper 150 m. The small individuals were concentrated in the upper 100 m both by day and at night.

Most of the individuals of *Abylopsis tetragona* were caught between 200 and 450 m depth by day (Figure 9), some individuals were occasionally caught in the surface waters (S4, S6, S3); at night, they were heterogeneously

distributed in the 0–400 m water column, exhibiting various amplitudes of diel migration. *Gemadas elegans* performed an extensive DVM, from 550–700 m by day up to 50 m at night (Figure 9). The non-migrant fish *Cyclothone braueri* showed a tendency to live deeper at the Mediterranean sites than at the gyre sites, both by day and at night (Figure 9).

In order to examine possible differences in preferential daytime depths between the sites, day WMDs of each of the species presented above have been plotted along the transect (Figure 10). Variability in daytime depths was very clear for the migrant species, *Pleuromamma gracilis*, *P. borealis* and *P. abdominalis* (Figure 10a) and *E. krohni* (Figure 10b), which were concentrated in layers of 200 m thickness at a maximum. These species showed a similar trend: highest WMD values were recorded at S8 (Mediterranean site), then WMDs decreased, more or less regularly, from S8 to S4, and then remained rather constant from the right site of the front to the gyre (S4 to S1); the lowest value was often found at S6. For example, WMDs ranged from 350 to 220 m for *P. abdominalis* and from 330 to 130 m for

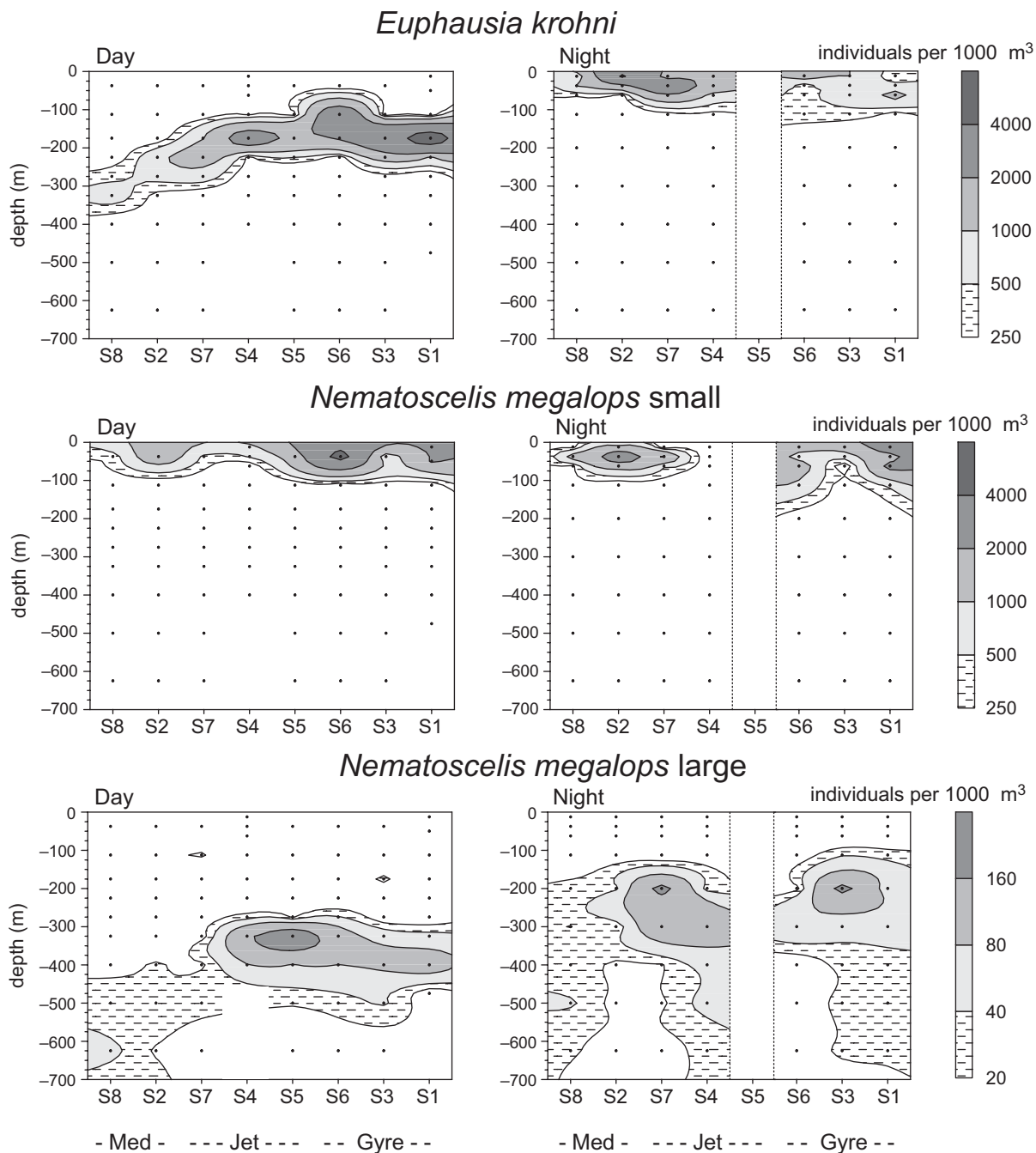


Fig. 8. Vertical distributions of the euphausiids *E. krohni* and *N. megalops* (small, ≤ 11 mm, and large individuals) along the schematic transect (see legend for Figure 5).

E. krohni. The other species showed a similar general trend, sometimes not so regular. In fact, five of these species displayed a bimodal daytime distribution and WMDs have therefore been calculated for two portions of the water column; the choice of the depth limits for these parts could have induced some artefact. On the other

hand, the whole population of the deep-living *G. elegans* and of the adults of *E. hyalinus* would not have been entirely sampled (Figure 10c). Changes in preferential depths of *C. braueri*, observed both by day and at night, appeared less marked (Figure 10d) than for all the other species or stages which were diel migrators.

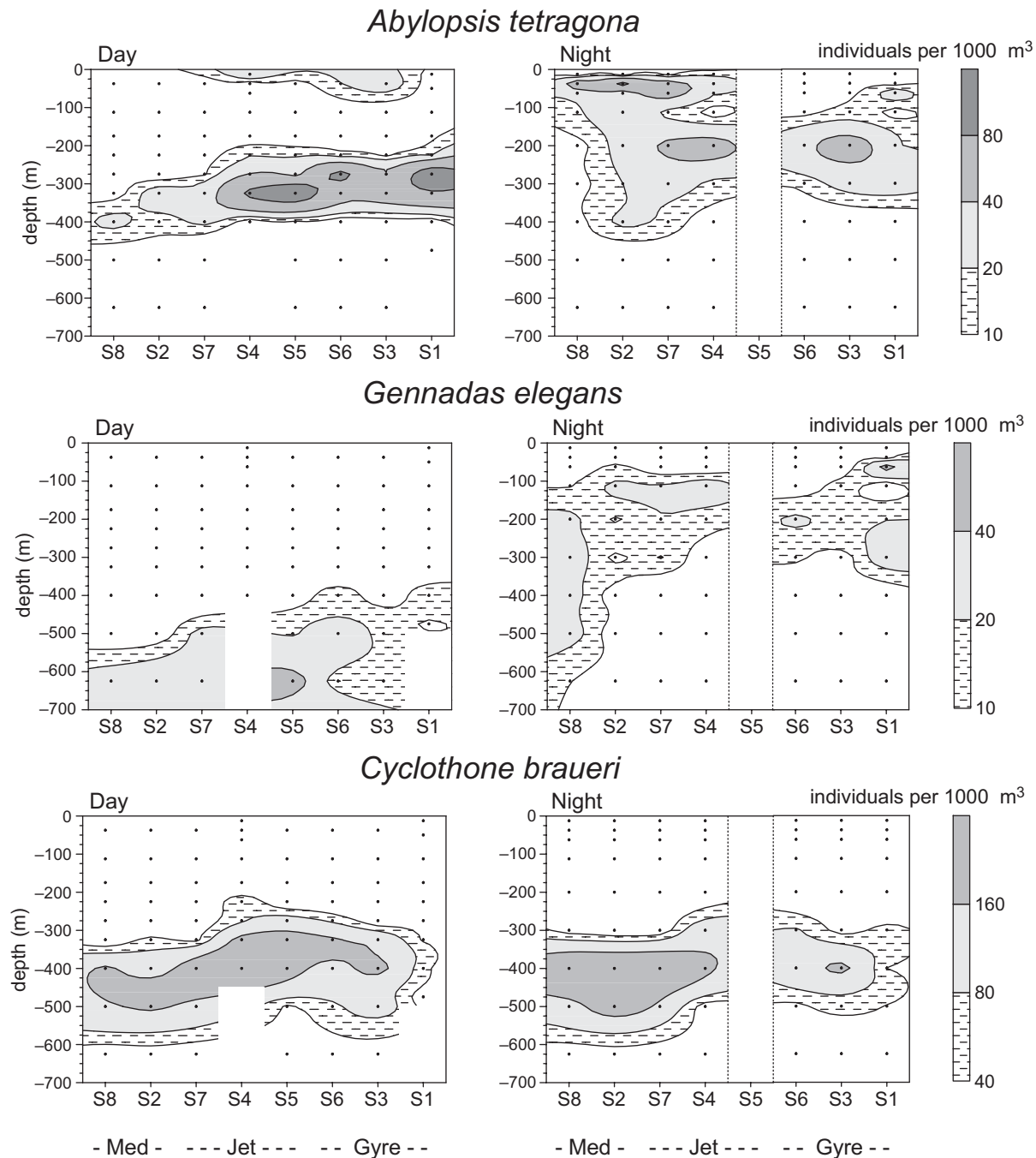


Fig. 9. Vertical distributions of the siphonophore *A. tetragona*, the Peneidae *G. elegans* and the fish *C. braueri* along the schematic transect (see legend for Figure 5).

Ontogenetic migration

Plots of day WMDs of the developmental stages of *P. abdominalis* along the transect clearly show the different daytime depths of the stages, depth increasing with age of the individuals (Figure 11a). The more interesting phenomenon is that changes in day WMD along the transect

showed a similar trend for the three groups, C2–C4, C5 and adults, as presented above for the whole population. Such changes in day WMD were also observed for the different size classes of *E. krohni*, which were more or less regularly spaced out (Figure 11b).

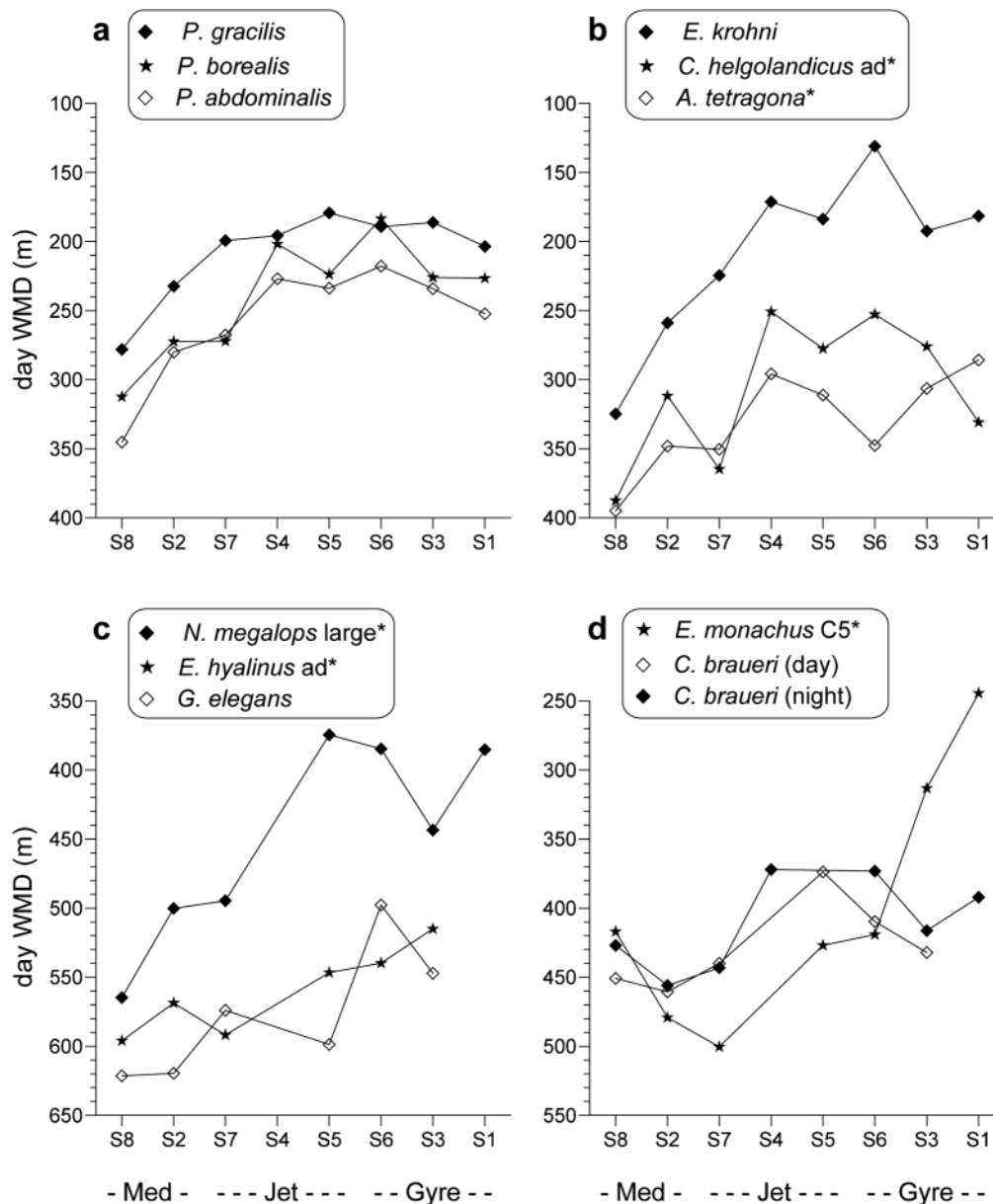


Fig. 10. Day WMDs along the transect for the species with variable preferential daytime depths. Night WMDs are also plotted for the non-migrant fish *C. braueri*. *, deeper day WMD considered.

To examine the ontogenetic migration of *E. krohni* and *N. megalops*, plots of their daytime and night-time WMDs versus size (classes of 2 mm width) are presented in Figure 11 for sites S2 and S7, which showed large size ranges and relatively high concentrations for these species. Day WMD of *E. krohni* clearly increased with size of the organisms (Figure 11c); difference in WMD was of about 200 m between the 3–4 mm class and the 17–18 mm class. At night, the smaller individuals appeared to live shallower than the larger ones; however, differences in night WMDs were slight. It is noteworthy that all the *E. krohni* identified

in the hauls, even the smallest ones, performed a DVM (with amplitude from 210 m for the 3–4 mm individuals to 345 m for the 17–18 mm ones at S2).

Day WMD of *N. megalops* also clearly increased with size of the organisms (Figure 11d). However, by contrast to *E. krohni*, the smaller organisms did not migrate. Day and night WMDs were very similar for the 3–8 mm individuals and clearly different by 250–300 m for the organisms longer than 15 mm. Between these size limits, day WMDs were generally lower than night WMDs, suggesting occurrence of a slight reverse migration; but

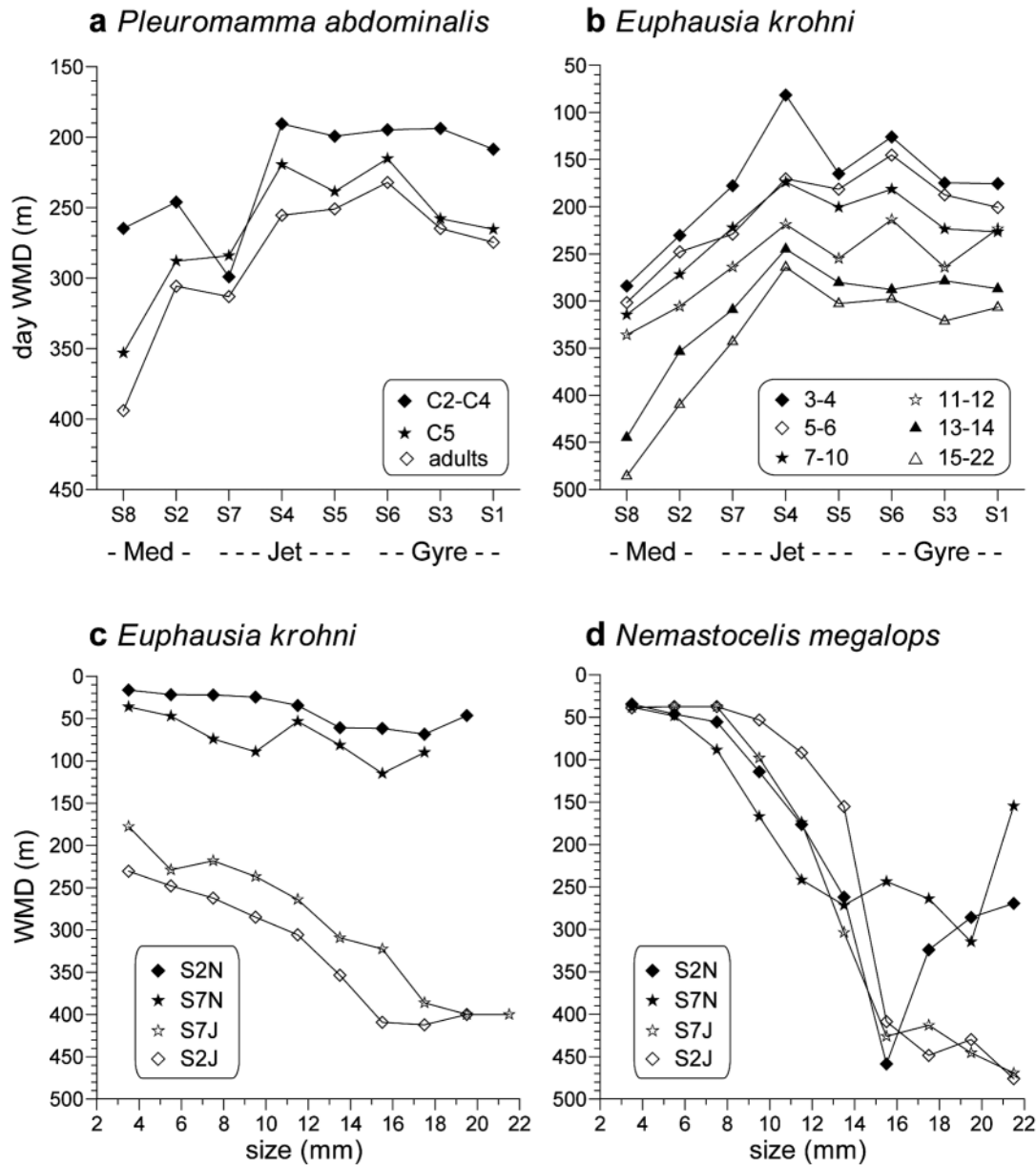


Fig. 11. Ontogenetic vertical distributions. Day WMDs along the transect for (a) the different developmental stages of *P. abdominalis* and (b) size classes of *E. krohni*; day WMDs versus size of animals for (c) *E. krohni* and (d) *N. megalops*.

this could be an artefact, related to the different thickness of the strata sampled by day and at night.

Species with similar vertical distribution throughout the sampling area

No change in the vertical distribution throughout the sampling area was discernible for the other main species of copepods, macroplankton and micronekton. These copepod species were essentially caught in the upper 75 m (Figure 12a–d). No DVM was discernible in *Temora stylifera*,

Centropages chierchiae and *Nannocalanus minor*, the slight difference between their day- and night-time distributions being related to the sampling proceeding, while *Neocalanus gracilis* appeared to perform a weak DVM in the upper 200 m. The other main taxa of macroplankton and micronekton were caught at different depths in the water column (Figure 12e–h). The chaetognaths were concentrated in the upper 75 m both by day and at night. The non-migrant euphausiid *Stylocheiron longicorne* was essentially caught in the 0–250 m water column. The fish *Benthosema glaciale* showed

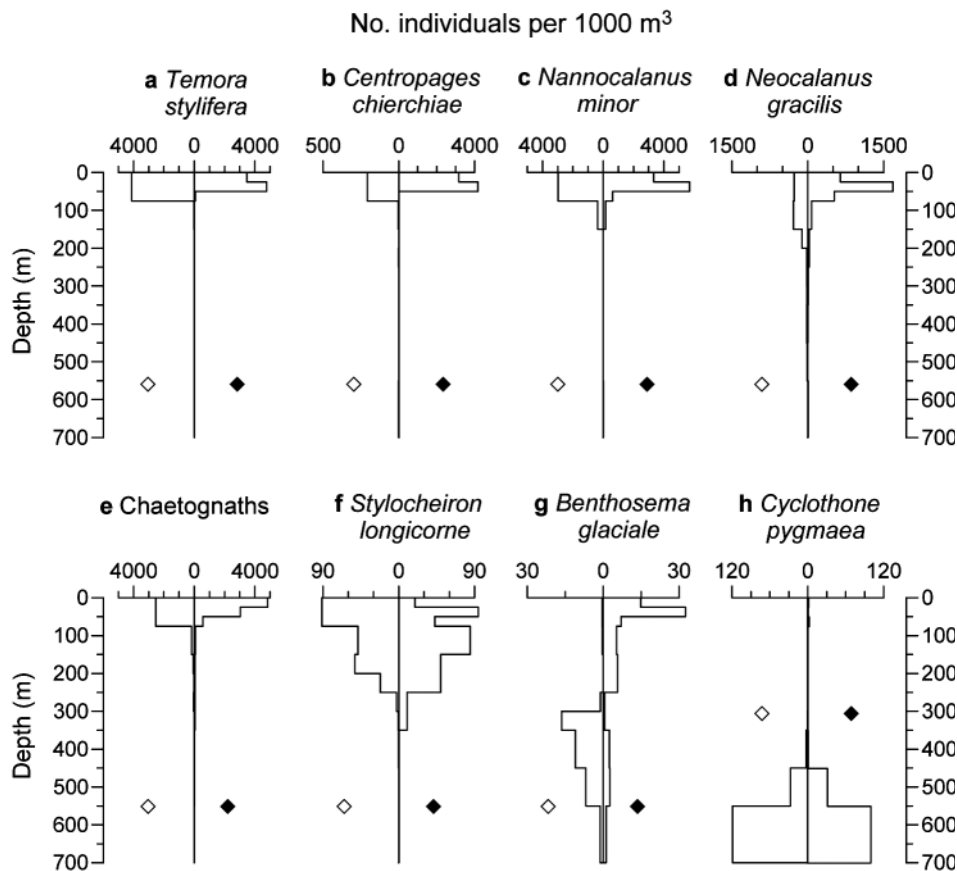


Fig. 12. Average vertical distributions, by day (\diamond) and at night (\blacklozenge), of the most abundant taxa for which the vertical distribution did not vary with the sampling sites.

an extensive DVM with a mean amplitude of 215 m (Table III). The non-migrant fish *Cyclothone pygmaea* was caught in abundance in the deepest sampled stratum, 550–700 m.

DISCUSSION

Vertical distribution and migration of the different main taxa in the Alboran Sea

The general features of the vertical distribution and migration of most of the taxa considered here have previously been documented by different authors in the Mediterranean Sea or in various areas of the world's ocean. However, concerning the Mediterranean Sea, this study is one of the most accurate as it was based on sampling with a multiple opening/closing net system over relatively narrow strata.

In the present study, three copepod species, *Temora stylifera*, *Centropages chierchiae* and *Nannocalanus minor*, were found to be epipelagic and non-migrant, agreeing with the observations made in various areas of the western

Mediterranean (Furnestin, 1960; Mazza, 1962; Giron, 1963; Casanova, 1970; Vives, 1978). The weak migration of *Neocalanus gracilis* and the extensive migration of *P. abdominalis* and *P. gracilis* are well documented (Andersen *et al.*, 2001). Occurrence of ontogenetic migration in *P. abdominalis*, as observed here, has previously been reported for the Mediterranean Sea (Andersen *et al.*, 2001) and other areas of the world's ocean (Ambler and Miller, 1987; Bennett and Hopkins, 1989).

Data on the DVM of *P. borealis* are sparse for the Mediterranean Sea. In fact, *P. borealis* is a cold water Atlantic species whose extent in Mediterranean waters is more or less limited to the Alboran Sea (Giron, 1963; Vives, 1978). In accordance with its Atlantic origin, we caught it in greater numbers at the frontal and gyre sites than at the Mediterranean sites. In the present study, its daytime WMD varied from 180 to 310 m and at night it was concentrated in the upper 75 m. Reported depths of maximum abundance were similar in the NE Atlantic, maximum abundances at 350 m by day and at 100 m by night, with specimens reaching the surface (Roe, 1972b), but deeper in the NW Atlantic, 550–700 m by day and 150–175 m at night (Ashjian and

Wishner, 1993). The three *Pleuromamma* spp. observed here were vertically segregated by day, in order of increasing depths, *P. gracilis*, *P. borealis* and *P. abdominalis*, as previously reported (Roe, 1972b).

The vertical distributions of the macroplankton and micronekton taxa considered here, the fish *B. glaciale* and the chaetognaths excepted, have previously been documented in the NW Mediterranean (Andersen and Sardou, 1992; Andersen *et al.*, 1992); the present results are in agreement with these previous studies and the literature data summarized in them. In the present study, most of the *B. glaciale* individuals showed an extensive DVM from 300–550 m by day to the upper 50 m at night. Similar preferential depths have been observed in different sites in the Mediterranean Sea (Goodyear *et al.*, 1972). *Benthosema glaciale* has also been reported to be an extensive migrant in various areas of the Atlantic Ocean, with, as observed here, a more or less important part of the population which did not migrate (Badcock and Merrett, 1977; Kinzer, 1977; Roe and Badcock, 1984).

During the present cruise (December–January), chaetognaths were found highly concentrated in the upper 75 m both by day and at night and the population did not display obvious DVM. Previous observations performed in the upper 200 m in the Alboran Sea during the cold season showed that *Sagitta enflata* was the dominant species of chaetognaths and that the specific composition of the carnivore population was very slightly affected by DVM (Dallot *et al.*, 1988). Even if some chaetognath species are known to migrate, the present results agree with previous observations in the eastern Mediterranean, such as occurrence of *S. enflata* between 0 and 50 m depth mainly (Kehayias *et al.*, 1994) and a maximum abundance of chaetognaths in the upper 100 m, both by day and at night (Weikert and Trinka, 1990).

We have presented in detail the different patterns of migration of the euphausiids *E. krohni* and *N. megalops* according to the body size of the animals. Occurrence of ontogenetic migration has been reported for several euphausiid species (Mauchline, 1980) with detailed vertical layering of size classes of *Meganyctiphanes norvegica* (Mauchline and Fisher, 1969). However, to our knowledge, such detailed results have not been previously provided for *E. krohni* and *N. megalops*, which are among the most abundant species in the western Mediterranean. For example, previous reports dealt with only two categories, adolescents and adults, or with mean body length at large depth intervals (Mauchline and Fisher, 1969; Baker, 1970).

Overwintering copepod species

The vertical distributions of *E. monachus*, *E. hyalinus* and *C. helgolandicus* observed here appear to result mainly

from their seasonal downwards migration. Seasonal migration of *E. monachus* has been observed in various areas, such as the Tyrrhenian Sea (Hure and Scotto di Carlo, 1969), NW Atlantic (Deevey and Brooks, 1977) and east equatorial Atlantic (Binet, 1983); in general, the organisms descend from the surface waters to greater depths (400–900 m) in summer to autumn, and rise to the shallower waters in winter and spring. Stage C5 would be the primarily overwintering stage (Binet, 1983; Weikert and Koppelman, 1993). *Calanus helgolandicus* is also known to overwinter primarily as stage C5 (Williams and Conway, 1988; Stöhr *et al.*, 1996) and presented similar timing of seasonal migration, at least in the Mediterranean Sea (Andersen *et al.*, 2001). During summer and fall, C5 *C. helgolandicus* have been reported to contribute to more than 95% of the total population (Vives, 1978; Williams and Conway, 1988; Gasser *et al.*, 1998; Andersen *et al.*, 2001).

Our data show that in the winter (25 December–12 January), populations of *E. monachus* and *C. helgolandicus* exhibit similarities in their stage composition and vertical distribution. C5 dominated, 85% for *E. monachus* and 65% for *C. helgolandicus*, and showed a bimodal distribution by day and at night, with the shallow peak in the surface waters. This suggests that part of the C5 population had completed its overwintering, in agreement with the literature data cited above, and had given rise to a population of adults.

By contrast, in *E. hyalinus*, the C5 represented only 35% and were concentrated in the upper 100 m, as well as the males, while the females (57%) showed a bimodal distribution by day and at night, with the deeper peak below 500 m. Seasonal migration of *E. hyalinus* is poorly documented. The same seasonal behaviour as for *E. monachus* was reported, but no information on stages was provided (Deevey and Brooks, 1977). Our results suggest that in this species the adult female could also be a dormant stage, as C5, and that stage C5 would have finished its overwintering at this period of the year. Another species of *Eucalanus*, *E. californicus*, has been reported to be dormant as both adult females and C5s (Ohman *et al.*, 1998). The study of the dormancy cycle of these three species merits further investigation, such as those by Ohman *et al.* in the California Current System which showed that copepod dormancy responses differed appreciably with the species of copepod considered.

Part of the population of these three copepod species appeared also to perform DVM. A small part of the C5 of *E. monachus* migrated for distances of 150–350 m, while adults were non-migrant; this species has been reported to be a non- or weak migrant in the few studies dealing with its DVM (Casanova, 1970; Weikert and Koppelman, 1993). DVM in *E. hyalinus* populations appeared to concern

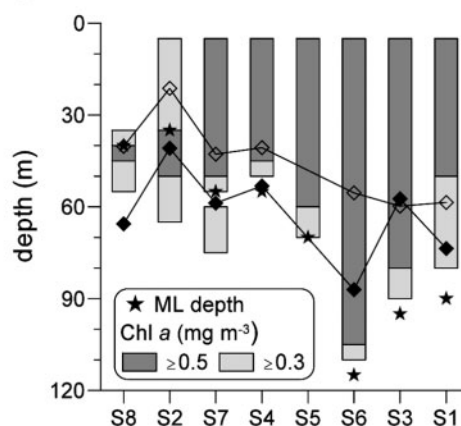
a small part of the females; it would explain why previous reports differ, from little evidence of DVM (Roe, 1972a) to large DVM (Casanova, 1970). As in the present study, *E. hyalinus* has been caught at greater depth than *E. monachus* in the Mediterranean Sea (Mazza, 1962; Casanova, 1970; Gasser *et al.*, 1998).

Occurrence of DVM in *C. helgolandicus* was obvious from our data. Part of the C5 living at depth by day migrated at night for distances of ~400 m; adults showed a bimodal daytime distribution and were concentrated at night in the surface layer. To our knowledge, information on DVM of *C. helgolandicus* is very scarce. During the dormant period, when the bulk of the population is concentrated at 500–600 m and below, no or only a slight migration has been observed (Roe, 1972a; Andersen *et al.*, 2001), while, in spring (April), DVM from 250 m to the upper 100 m has been reported (Roe, 1984).

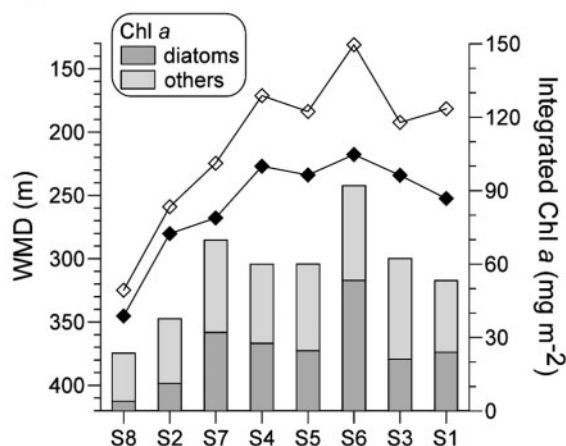
Changes in preferential depths across the front

We found that many of the species encountered exhibited changes in their preferential depths across the front, by day and at night. To show these changes in the context of environmental conditions, we have superimposed in Figure 13 a summary of this behaviour for two abundant migrant species, *P. abdominalis* and *E. krohni*, and data on phytoplankton distribution and standing stock and depth of the mixed layer. Night WMDs of *P. abdominalis* and *E. krohni* tended to be greater at the gyre sites than at the other sites (Figure 13a). The same trend (particularly in S6) has also been observed for other mesopelagic species migrating at night to the surface layers, such as *P. borealis*, *P. gracilis* and adults of *C. helgolandicus*, or for some non-migratory species inhabiting the surface layer, such as *E. monachus* (cf. Figures 5, 6 and 7). Site 6, a typical gyre site, showed the deepest mixed layer of the eight sites and a homogeneous Chl *a* distribution down to ~100 m depth, resulting from the high turbulence regime. As the copepod species sampled during this study are of relatively large size, the deeper WMD and extended vertical distribution at night at S6 would not have been related to vertical turbulent diffusivity (and moreover for euphausiids). However, as it is parallel to the Chl *a* distribution, it would rather have been a result of behaviourally mediated concentration driven by the presence of abundant food. *Pleuromamma abdominalis* and *E. krohni*, chosen as examples here, are omnivores; however, herbivores such as *C. helgolandicus* also showed such a behaviour. The thickness of the strata sampled did not permit detection of a causal relationship between Chl *a* profile and vertical distribution of zooplankton. However, in the same area and at the same season (December 1996), Fielding *et al.* have

a night WMD: ◆ *P. abdominalis*; ◇ *E. krohni*



b day WMD



c migration amplitude

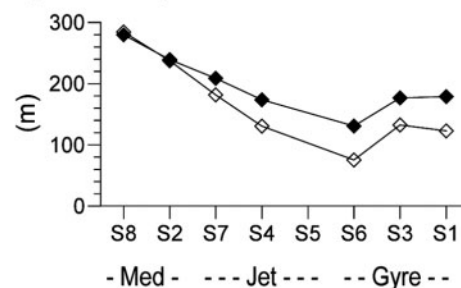


Fig. 13. Overview of the characteristics of vertical distribution of two abundant migrant species, *P. abdominalis* and *E. krohni*, and data on the environmental features at the eight sites. (a) Night WMD of the zooplankton species, mixed layer depth and concentration of Chl *a*. (b) Day WMD of the zooplankton species, integrated Chl *a* content (0–200 m) and contribution of diatoms to total Chl *a*. (c) Amplitude of the diel migration.

observed at ~150–200 m depth a sound-scattering layer (38 kHz echosounding data) concurrent with the tongue of subducted phytoplankton (Fielding *et al.*, 2001).

On the other hand, the species living below 250–350 m, by day (migratory species) or both by day and night (e.g. the fish *C. braueri*), showed variability in their preferential depths (WMD) across the front: (i) deeper WMDs at the Mediterranean sites, (ii) intermediate ones on the left side of the jet and (iii) shallower ones in the core and the right side of the jet and in the gyre, with the lowest WMD often recorded at the typical gyre site, S6 (cf. Figures 10 and 13b). These vertical distributions can be compared with the SSLs observed in the same area in spring 1991 during a similar cruise Almofront 1 (Baussant *et al.*, 1993) and in December 1996 (Fielding *et al.*, 2001), this latter study dealing with day and night observations. These two studies reported the occurrence of two main SSLs below 250 m (38 kHz data particularly).

The deeper SSL was dominated by non-migratory fish *Cyclothone* and was permanent, although its intensity decreased at night. The present results concord with these observations; at the depth of this SSL, we have found *C. braueri* in large numbers, migratory decapoda crustacea (*G. elegans*) and euphausiids (adults of *N. megalops*). These species were found deeper, by at least 50 m, in the Mediterranean sites than at the gyre and frontal sites (cf. Figure 10), in accordance with the observations of Baussant *et al.* (Baussant *et al.*, 1993) but contrary to that reported by Fielding *et al.* (Fielding *et al.*, 2001) who did not observe any change in the depth of this SSL either side of the front.

The second main SSL below 250 m moved to the surface at night (Fielding *et al.*, 2001) and would correspond, in the present study, to acoustic scattering species, such as the myctophid fish *Benthosema glaciale*, and other groups, less or not detected by sound-scattering, such as euphausiids (*E. krohni*), siphonophores (*A. tetragona*) and copepods (*Pleuromamma* spp.). This SSL was also reported to occur deeper by about 50 m in the Mediterranean zone than in the other ones and an additional SSL, rather diffuse on the echograms, was found around 180 m in the frontal zone by Baussant *et al.* (Baussant *et al.*, 1993); the present results (cf. Figure 10) would reinforce these observations.

The variability in preferential depths of the migrant organisms, both by day and at night, resulted in a large range of migration amplitude for a given species. For example, it varied from 80 and 130 m at the gyre site S6 for *P. abdominalis* and *E. krohni*, respectively, and up to 280 m at the Mediterranean site S8 (Figure 13c).

The daytime vertical distribution of the mesopelagic communities sampled here did not appear to be directly correlated to the physical processes in this area. In fact, the front is limited to the upper 200 m and physical parameters of the water masses below 200 m do not show significant variations (Prieur *et al.*, 1993; Allen

et al., 2001), as illustrated by the profiles of potential density excess (cf. Figure 3) and of temperature (cf. Figure 4). Moreover the mesoscale vertical motions, which can reach 20–25 m day⁻¹ in the front in the upper 200 m (Allen *et al.*, 2001; L. Prieur, unpublished results), are relatively weak compared with the ability of zooplankton to migrate at greater speeds. However, the vertical distribution of the mesopelagic organisms could be indirectly affected by the production in the euphotic layer. For example, absorption of light by phytoplankton changes the light distribution in and beneath the euphotic layer and if migratory organisms follow a preferred isolume (Forward, 1988), their daytime depth would be related to the vertical distribution of light and, as hypothesized here, to the chlorophyll content. In fact, the profiles of photosynthetically available radiation (PAR) were performed only down to the 1% PAR level (40–65 m depending on the site) during the present cruise, while phytoplankton occurred in relatively high concentration well below this level in the gyre and at site S5 (cf. Figure 3). Although a direct and accurate relationship could not be established between day WMD of a given species and Chl *a* content in the 0–200 m water column, some trends were visible (Figure 13b). The deepest WMDs coincided with the lowest values of Chl *a* content (Mediterranean sites) and the shallowest WMD was found at the richest site in phytoplankton (S6).

However, the changes in the vertical light distribution across the front would not be large enough to explain entirely the large difference in preferential daytime depth. In fact, the trophic state of the system and abundance of food would play a significant role in the vertical partitioning of the organisms observed here. The gyre sites, S6 particularly, and the Mediterranean sites (S2 and S8) corresponded to two very contrasting systems. The highest chlorophyll content and contribution of diatoms, optimal prey for large herbivorous copepods, were recorded at S6, the lowest values at S2 and S8 (cf. Figure 13b). Zooplankton biomass, recorded with 80 and 200 µm mesh nets in the upper 200 m during the same cruise, was also highest in the gyre and lowest in the Mediterranean waters (Youssara and Gaudy, 2001). At the typical gyre site, large concentrations of food were therefore available to the organisms of different diets reported here, which could partly explain why the migrant species appeared to remain in or just below the layer of abundant food over the diel cycle.

It has been shown that DVM in interaction with cross-frontal circulation can give rise to patchiness of zooplankton at frontal and eddy systems (Owens, 1981; Franks, 1992). For example, zones of higher organism concentrations in daylight would become rarified at night, as the migrators would be dispersed by horizontal

flows. During the present work, the highest day catches of the migrant euphausiid *E. krohni* were recorded at the gyre sites. They were more than two times higher than the night catches performed on the same dates (cf. Figure 8), which would suggest a lateral displacement of this species when it was in the superficial layers at night. But, an inverse pattern was observed at these gyre sites for the migrant copepod *P. borealis*, of which the day catches were more than two times lower than the night ones (cf. Figure 5). These features are rather striking as the swimming ability of euphausiids is much larger than that of large copepods, but the type of sampling performed during this study does not allow for isolation of the causal effects of these two opposite patterns.

In summary, this study is one of the most detailed, at the species level, on the vertical distributions of zooplankton (>500 m) in the Alboran Sea and its permanent frontal area. It also documents ontogenetic migration of the two main euphausiid species and seasonal migration of three abundant copepod species. The changes in day-time and night-time distributions observed across the front did not appear directly correlated to the physical processes; they would be related to light distribution, and to food abundance and trophic state of the system, which were related to the patterning circulation. These observations underline the need for further detailed studies, with data taken concurrently on both physical and biological parameters, in order to differentiate better the effects of mesoscale physical processes and biological behaviours. Particularly, refined zooplankton sampling should combine more or less discrete observations with hauls of various meshes that allow species identification, and continuous records (echosounder, OPC).

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