

# Zooplankton community during the transition from spring bloom to oligotrophy in the open NW Mediterranean and effects of wind events. 2. Vertical distributions and migrations

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*Vertical distribution of zooplankton was investigated over a 3-week period at a fixed station in the open NW Mediterranean during the DYNAPROC cruise (May 1995). The observational period coincided with the transition from spring bloom to oligotrophy in this area. Vertical distribution and migration in the 0–1000 m water column are described in detail for the main species of copepods (>500 µm). Ontogenetic migration is reported for Neocalanus gracilis, Euchaeta acuta and Pleuromamma abdominalis. This study also documented the downwards seasonal migration of Calanus helgolandicus. Short-term changes in the vertical distribution of the small-sized organisms (>50 µm) in the upper 100 m are discussed in relation to the two major wind events that occurred during the cruise. The naupliar stages of copepods and euphausiids appeared unable to counter the upwards vertical advection and the wind-induced mixing, while no marked changes were observed for Oithona spp. and Microsetella spp.*

## INTRODUCTION

Short-term changes in the vertical distribution of zooplankton organisms are related to behaviour, such as diel, ontogenetic and seasonal migration, and to exogenous factors, such as physical forcing and particularly, wind-induced mixing. The selective influence of vertical mixing or advection on the vertical partitioning of zooplankton species or taxonomic categories has been reported in several studies [e.g. (Haury *et al.*, 1990; Lagadeuc *et al.*, 1997)]. However, such *in situ* studies remain rare. On the other hand, detailed data on the vertical distribution and the various migrating behaviours of copepods are limited for the open Mediterranean Sea, compared with other areas of the world's oceans. Previous investigations have essentially been made in surface or shallow waters, or have involved large depth-sampling intervals, such as the

studies of Furnestin (Furnestin, 1960), Mazza (Mazza, 1962, 1963), Vives (Vives, 1978) and Hure and Scotto di Carlo (Hure and Scotto di Carlo, 1968). Furthermore, reports on seasonal migration have been based on monthly sampling [e.g. (Hure, 1955; Vives, 1963; Hure and Scotto di Carlo, 1969)].

The multidisciplinary cruise DYNAPROC, carried out in May 1995 in the open northwest Mediterranean, provided the opportunity to explore the zooplankton community over a 3-week period in an area where currents and horizontal advection were weak. The purpose of this paper is to present data on the vertical distribution of various taxonomic categories of zooplankton (from radiolarians and nauplii up to euphausiids), with the diel and ontogenetic migration of copepods (>500 µm) being described in detail. The short-term changes are discussed in relation to the strong winds that occurred during the cruise and

placed in the context of the seasonal cycle, as the study was conducted during the transition from spring bloom to oligotrophy. The changes in abundance and species composition of the zooplankton community have been presented in the previous paper (Andersen *et al.*, 2001).

## METHOD

### Environmental conditions

The DYNAPROC cruise, devoted to the study of the DYNAmics of the rapid PROCesses that control the vertical flux of matter, was conducted over a 1-month period (1 May–1 June 1995) in the open northwest Mediterranean. Most of the multidisciplinary measurements were performed at the JGOFS-France time-series station DYFAMED [e.g. (Buat-Ménard and Lambert, 1993)], 28 nautical miles offshore (43°25.2'N, 7°51.8'E, depth of 2600 m). Several types of observations, such as ADCP records and CTD casts, confirmed that horizontal advective movements at the time-series station and in its surroundings remained weak throughout the cruise (Andersen and Prieur, 2000).

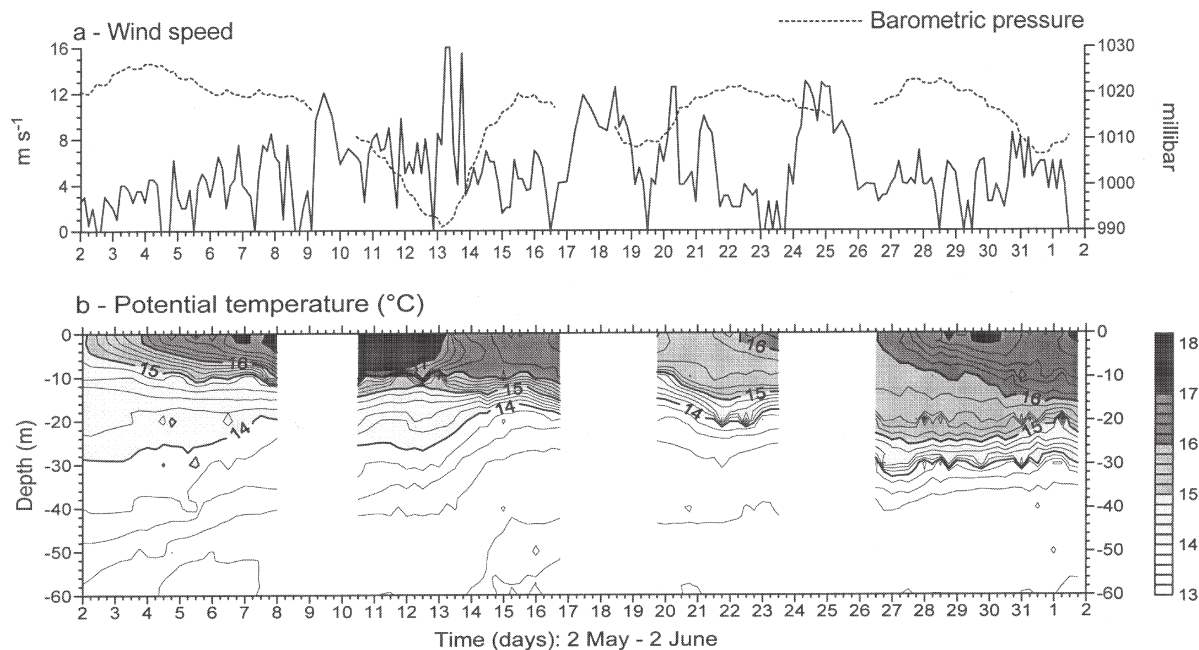
Temporal variation of wind speed was characterized first by a major wind event on 13 May (Figure 1a), associated with a low pressure system, then by several successive wind events of smaller amplitude until 25 May. During

the first wind event, a rapid mixing–cooling of the surface waters and an upwelling of deeper and colder waters, related to Ekman pumping, were observed (Figure 1b). The thermocline slightly deepened from ~10 to 15 m, but became stronger. The upward shift, also observed on the deep nitrate surfaces and the sub-superficial chlorophyll *a* peak, was about 10 m in 3 days. In contrast, direct wind-induced mixing of the upper layer occurred as a result of the wind event of 24–25 May, with a significant increase in depth of the thermocline (from 15 to 25 m).

The changes, observed throughout the cruise, in various properties and processes (biomass and the species composition of phytoplankton, ciliate biomass, the standing stock of suspended particles, POC fluxes and export production etc.) showed that in this area, the month of May corresponded to the transition period from spring bloom termination to an oligotrophic system (Andersen and Prieur, 2000; Goutx *et al.*, 2000; Pérez *et al.*, 2000; Vidussi *et al.*, 2000).

### Zooplankton sampling procedure

The vertical distribution and diel migration of zooplankton and micronekton were investigated with two types of sampling during leg 2 (10–16 May) and leg 4 (26 May–1 June) of the DYNAPROC cruise. Sampling of the small-sized organisms was performed at the time-series station with a 12-bottle rosette at 9–12 depth levels in the upper



**Fig. 1.** Temporal changes in wind speed and barometric pressure (a), and in vertical distribution of temperature in the upper 60 m (b), recorded at the time-series station over the 1-month cruise. Periods with no data correspond to port calls between the four legs of the cruise; wind speeds during the port calls correspond to output of a meteorological model [after (Andersen and Prieur, 2000)].

*Table I: Sampling data for BIONESS: oblique tows by day (D) and at night (N) in the 0–980 m water column*

Leg 2			Leg 4		
Haul no.	Date 1995	Time (UTC)	Haul no.	Date 1995	Time (UTC)
D13	13/05	12.48–13.37	D26	26/05	11.45–12.34
N15	15/05	22.02–22.50	N26	26–27/05	23.18–00.15
D16*	16/05	08.45–09.32	D29	29/05	08.30–09.29
			D32	01/06	08.17–09.18

Sunrise around 03.55–04.5 h and sunset around 18.40–19.05 h during this period. \*Results of the 75–150 m stratum have been discarded due to malfunctioning of the net.

100 m (time and depth of the samples are indicated on the result graphs); the 12 l water samples were filtered through 50  $\mu\text{m}$  mesh. Larger zooplankton were sampled with the BIONESS (Sameoto *et al.*, 1980), a multiple opening and closing net with 500  $\mu\text{m}$  mesh nets. During the oblique hauls, the net fished at nine different levels in the 0–980 m water column: 980–850, 850–700, 700–550, 550–450, 450–350, 350–250, 250–150, 150–75 and 75 m to the surface; the sampling data are summarized in Table I. Note that the daytime haul on 1 June is referred as D32. The series of hauls was achieved within less than 3 miles from the time-series station, i.e. in an area where horizontal advection was negligible (Andersen and Prieur, 2000).

Samples, preserved in 5% borax-buffered formalin-seawater, were analysed further. Density estimates of the organisms were standardized to number of individuals  $\text{m}^{-2}$  for the entire water column explored, or  $\text{m}^{-3}$  or 1000  $\text{m}^{-3}$  for each depth level sampled. From the BIONESS data, we calculated the weighted mean depth for each species and haul,  $\text{WMD} = \sum(n_i \times z_i \times d_i) / \sum(n_i \times z_i)$ , where  $d_i$  is the depth of a sample  $i$  (centre of the depth interval),  $z_i$  the thickness of the stratum and  $n_i$  the number of individuals 1000  $\text{m}^{-3}$  at that depth. Average day time and night time distributions have been calculated for species for which the vertical distributions did not appear to vary throughout the sampling period. The 75–150 m stratum of D16 was excluded to calculate average concentrations, due to malfunctioning of the corresponding net. In the following sections, the terms ‘weak migrant’ or ‘extensive migrant’ are applied to organisms for which the amplitudes of migration are relatively short or large, respectively; these terms do not denote whether part or all of the population is concerned.

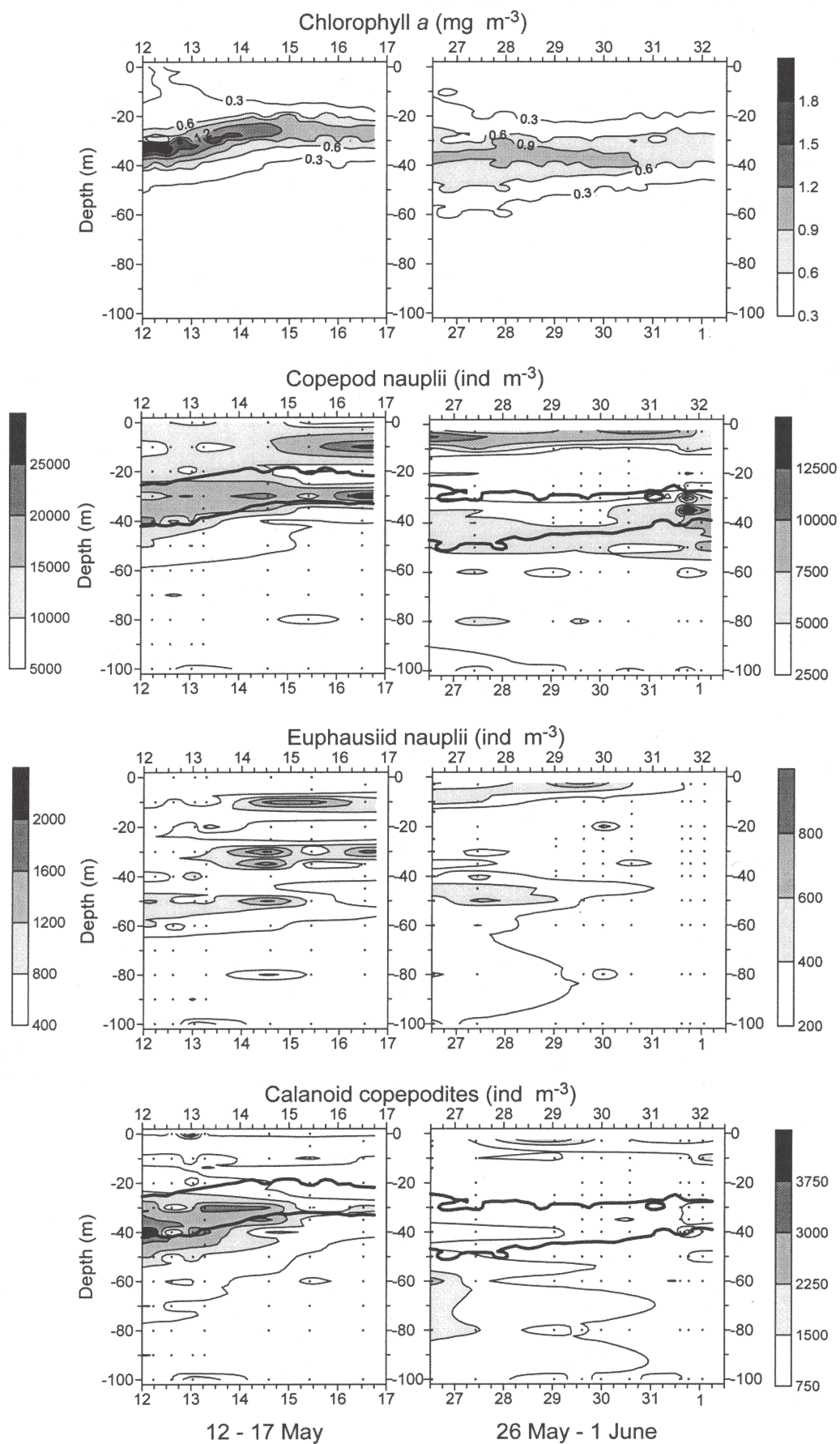
## RESULTS

### Time–depth distributions of small-sized zooplankton

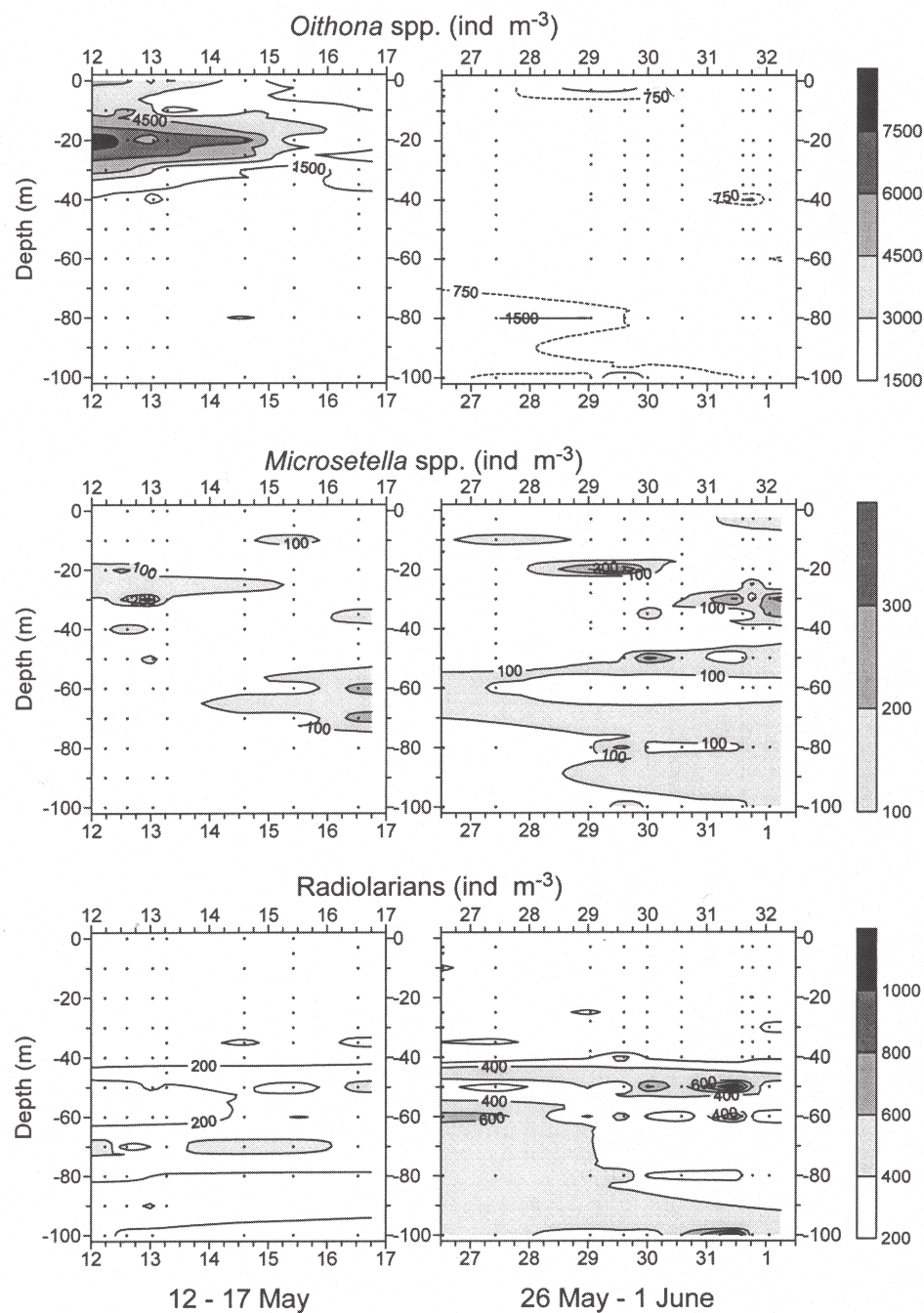
The small-sized zooplankton ( $>50 \mu\text{m}$ ), recorded in the bottle samples in the upper 100 m, were assigned to six taxonomic categories. These categories, in order of decreasing density, consisted of copepod nauplii (71% of the total standing stock), *Oithona* spp. and calanoid copepodites (10–13% each), and *Microsetella* spp., euphausiid nauplii and radiolarians (1–3% each). While no diel vertical migration (DVM) was apparent in the six categories, three of these categories showed marked changes in their vertical distribution throughout the sampling period (Figure 2).

To illustrate the environmental conditions and the food distributions of some of these organisms, we also present the time–depth distribution of chlorophyll *a* (Chl *a*). This distribution was characterized by: (i) an upward shift of the sub-superficial peak from  $\sim 32$  to  $\sim 23$  m between 12 and 15 May, the time of the first major wind event, with some decrease in the thickness of the peak, and (ii) a deepening to 30–35 m and a dilution of the peak on 26–28 May, as a result of wind-induced mixing.

Copepod nauplii showed changes in their vertical distribution both during the first sampling period and between the two sampling periods. On 12 May their maximum abundance was found between 25 and 40 m, at the same depth as the Chl *a* peak and below the thermocline. Then, their population presented an upward shift, as observed in isotherms and Chl *a* isocontours; their vertical distribution became bimodal, with a superficial peak at 5–15 m, above the thermocline, and a deeper one at the depth of the Chl *a* maximum and below the thermocline.







**Fig. 3.** Time–depth distributions of *Oithona* spp., *Microsetella* spp. and radiolarians in the upper 100 m over the two sampling periods. Dots correspond to the depth levels sampled.

**Fig. 2.** Time–depth distributions of chlorophyll *a*, copepod nauplii, euphausiid nauplii and calanoid copepodites in the upper 100 m over the two sampling periods. Dots correspond to the depth levels sampled. Note the two shade scales for copepod nauplii and for euphausiid nauplii. To facilitate interpretation, the 0.6 isocontour for chlorophyll is superimposed on two zooplankton graphs.

Table II: Average number of individuals  $m^{-2}$  (from 980 m to the surface) and percentage contribution, recorded for the most abundant species or genera of copepods and macroplankton

Genus or species	no. $m^{-2}$	%	Stages (%)			
			C2–C3	C4	C5	f-m
Total copepods	3546					
<i>Calanus helgolandicus</i>	1012	28.5	–	+	96	4
<i>Centropages typicus</i>	45	1.3	–	–	+	100
<i>Chiridius</i> spp. ( <i>C. poppei</i> )	36	1.0	–	2	48	50
<i>Euchaeta acuta</i>	350	9.9	21	31	27	21
<i>Euchirella rostrata</i>	53	1.5	–	–	4	96
<i>Gaetanus kruppi</i>	41	1.2	5	11	49	35
<i>Heterorhabdus</i> spp.	225	6.3	–	3	14	83
<i>Mesocalanus tenuicornis</i>	43	1.2	–	–	6	94
<i>Monacilla typica</i>	159	4.5	–	+	91	9
<i>Neocalanus gracilis</i>	235	6.6	8	25	40	27
<i>Pleuromamma abdominalis</i>	145	4.1	–	40	35	25
<i>Pleuromamma gracilis</i>	949	26.8	–	+	4	96
Total macroplankton	317.5					
Siphonophores						
<i>Chelophyes appendiculata</i>	11.0	3.5				
<i>Lensia conoidea</i>	68.6	21.6				
Pteropods						
<i>Cavolinia inflexa</i>	19.9	6.3				
Amphipods						
<i>Vibilia armata</i>	39.4	12.4				
Euphausiids						
<i>Euphausia krohni</i>	10.0	3.1				
<i>Meganyctiphanes norvegica</i>	19.3	6.1	small (61), large (39)			
<i>Nematoscelis megalops</i>	24.1	7.6	small (34), large (66)			
Fishes						
<i>Cyclothone braueri</i>	45.1	14.2				
<i>Cyclothone pygmaea</i>	40.5	12.7				

C, copepodite; f-m, adult

This bimodal distribution persisted until the end of the cruise. However, during leg 4, the upper peak was shallower (upper 10 m) and the second peak deeper than during leg 2. The copepod nauplii therefore appeared distributed over a larger depth interval, as observed for the Chl *a* maximum. It should be noted that the standing stock of copepod nauplii was greatly reduced between legs 2 and 4, as were those of euphausiid nauplii and calanoids.

Euphausiid nauplii showed changes in vertical distribution similar to those observed for copepod nauplii, i.e. upwards shift of their population maximum between 12 and 15 May, with the appearance of a bimodal distribution that persisted until the end of the cruise but extended through a larger water column during leg 4. The shallower and deeper peaks were respectively above and

below the thermocline, as for copepod nauplii. At the beginning of the sampling, the peak was located below the Chl *a* maximum, differing from the peak of copepod nauplii, but the three naupliar stages of euphausiids are non-feeding. Calanoid copepodites also showed an upward shift of their population at the time of the first wind event but with a drastic decrease in their density, contrary to nauplii. Their bimodal distribution was therefore less marked and they were mainly located deeper during leg 4 than during leg 2.

The three other taxonomic categories did not present marked changes in vertical distributions throughout the observational period (Figure 3). The peak in abundance of *Oithona* spp. was found around 20 m throughout leg 2; it slightly narrowed between 12 and 15 May. During leg 4,

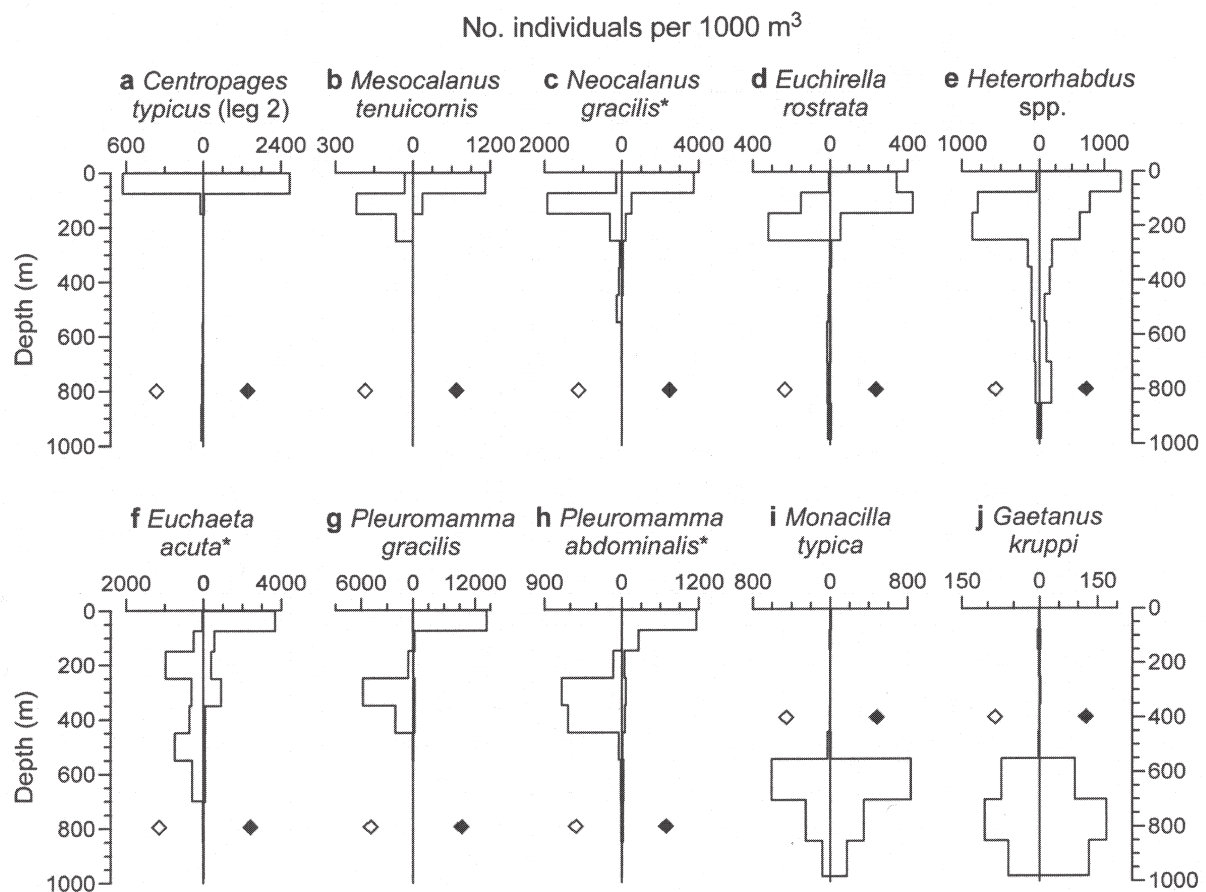
*Oithona*, caught in much lower numbers, appeared evenly distributed in the water column. *Oithona* was generally found below or above the Chl *a* maximum, which is consistent with its carnivorous diet. *Microsetella* spp. appeared evenly distributed in the water column, with some trend to live deeper during leg 4. Radiolarians were almost exclusively caught below 40 m, with maximum numbers at 50 and 70 m during leg 2, and down to 100 m during leg 4.

### Copepods with similar vertical distribution throughout the sampling period

Vertical distributions of copepods in the 0–1000 m water column are described for the 11 main species and one genus sampled with the BIONESS, each of which represented more than 1% of the average total number of copepods (Table II). About 88% of the genus *Chiridius* were identified as *Chiridius poppei*, and, when identified, the species for *Heterorhabdus* spp. was *H. papilliger*. Proportions

of copepodite stages and adults varied according to the species (Table II).

The vertical distribution of most of these copepod taxa did not appear to vary throughout the sampling period; their average day time and night time distributions are therefore given in Figure 4 according to their preferential day time depth. Table III presents for each taxon the weighted mean depths (WMD) by day and at night. *Centropages typicus* was typically epipelagic, being almost exclusively caught in the upper 75 m both by day and at night (Figure 4a). Slightly deeper, *Mesocalanus tenuicornis* and *Neocalanus gracilis* showed similar preferential depths. They were caught in maximum numbers in the 75–150 m stratum by day and in the upper 75 m at night (Figure 4b,c) and appeared therefore to perform a weak migration. However, the stages of *N. gracilis* were characterized by different preferential depths, as will be seen below. *Euchirella rostrata* also appeared to be a weak migrant, from 75–250 m by day to 0–150 m at night (Figure 4d); the



**Fig. 4.** Average vertical distributions, by day  $\diamond$  and at night  $\blacklozenge$ , of the most abundant species and genera of copepods for which the vertical distribution did not vary throughout the cruise. \*, species for which the ontogenetic migration is presented in Figure 5. Note different abundance axes. *Centropages typicus* was almost exclusively caught during leg 2.

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 different species or genera of copepods

Genus or species	Day WMD	Night WMD	dz
<i>Calanus helgolandicus</i>			
0–150 m	50 $\pm$ 15 <sup>b</sup>	40 $\pm$ 0	–
150–980 m	655 $\pm$ 55	660 $\pm$ 30	–
<i>Centropages typicus</i>	40 $\pm$ 5 <sup>a</sup>	40 <sup>+</sup>	–
<i>Chiridius poppei</i>			
0–550 m	375 $\pm$ 15	275 $\pm$ 30	100
550–980 m	775 $\pm$ 30	840 $\pm$ 45	–
<i>Euchaeta acuta</i>			
C2–C4	195 $\pm$ 60 <sup>b</sup>	90 $\pm$ 10	(105)
C5 0–350 m	–	40 $\pm$ 0	410
350–980 m	450 $\pm$ 45	340 $\pm$ 30	110
f-m 0–350 m	–	45 $\pm$ 5	500
350–980 m	545 $\pm$ 40	420 $\pm$ 10	125
<i>Euchirella rostrata</i>			
0–350 m	135 $\pm$ 40 <sup>b</sup>	80 $\pm$ 35	(55)
350–980 m	690 $\pm$ 25	690 $\pm$ 85	–
<i>Gaetanus kruppi</i>	755 $\pm$ 50	775 $\pm$ 5	–
<i>Heterorhabdus</i> spp.			
0–250 m	160 $\pm$ 30 <sup>b</sup>	105 $\pm$ 5	(55)
250–980 m	510 $\pm$ 35	565 $\pm$ 35	–
<i>Mesocalanus tenuicornis</i>	140 $\pm$ 35 <sup>b</sup>	45 $\pm$ 10	95
<i>Monacilla typica</i>	690 $\pm$ 45	690 $\pm$ 5	–
<i>Neocalanus gracilis</i>			
C2–C4	125 $\pm$ 10 <sup>b</sup>	55 $\pm$ 5	70
C5	185 $\pm$ 75 <sup>b</sup>	65 $\pm$ 25	(120)
f	220 $\pm$ 40 <sup>b</sup>	120 $\pm$ 60	(100)
m	465 $\pm$ 20	205 $\pm$ 10	260
<i>Pleuromamma abdominalis</i>			
C4	295 $\pm$ 45	85 $\pm$ 5	210
C5	345 $\pm$ 45	195 $\pm$ 95	150
f-m	385 $\pm$ 30	175 $\pm$ 40	210
<i>Pleuromamma gracilis</i>	310 $\pm$ 20	60 $\pm$ 5	250

Values are given to the nearest 5. Values of dz are given when the day–night differences are significant at the 0.05 level (*t*-test); values in parentheses denote cases when some migration appeared to occur from the profiles. <sup>a</sup>, <sup>b</sup>, WMD values calculated for leg 2 only or from 4 day profiles (results of D16 discarded) respectively. C, copepodite; f, female; m, male.

population consisted essentially of adults (96%, Table II). We have calculated WMD values for this species for two water columns, 0–350 and 350–980 m (Table III), due to the occurrence of a few organisms down to 980 m both by day and at night.

Vertical distributions of *Heterorhabdus* spp. and *Euchaeta acuta* extended over a large water column, down to

700–850 m, even 1000 m for *Heterorhabdus*. Most of the *Heterorhabdus* were caught in the upper 250 m, 75–250 m by day and 0–250 m at night, suggesting a weak migration of some of these organisms (Figure 4e). The clear bimodal distribution of *Euchaeta acuta* by day (Figure 4f) is described in detail in the next section when considering stages. *Pleuromamma gracilis* and *P. abdominalis* exhibited a clear vertical



migration of 210–250 m as mean amplitude (Figure 4g,h). The catches of *P. gracilis* consisted essentially of adults (Table II) and the migration was very cohesive. As the main species of deep copepods, we found *Monacilla typica* and *Gaetanus kruppi*, clearly non-migrant (Figure 4i,j). They were caught in abundance below 550 m both in the day time and at night time, *G. kruppi* living preferentially deeper than *M. typica* (WMD of ~765 m and 690 m, respectively, Table III).

### Ontogenetic migration of copepods

The different developmental stages of three species were caught in sufficient numbers to discern ontogenetic vertical migration (Figure 5, Table II). The copepodites (C2–C4, C5) and females of *N. gracilis* underwent a weak migration, from 75–150 m mainly by day to the upper 75 m at night (Figure 5a). Their day WMDs were not significantly different, except when comparing C2–C4 and females (Table III). However, vertical distributions showed that depth of occurrence increased with age of the organisms. Males of *N. gracilis* displayed a very different behaviour. By day they lived between 350 and 550 m depth, significantly deeper than the copepodites and females. At night, they performed a large DVM of 260 m as mean amplitude, but they were absent from the upper 75 m, contrary to the other stages. The different behaviour of these stages was observed throughout the sampling period (from 13 May to 1 June). A small portion of the female population was caught at the same depth level as the males in the day time and fertilization of these females was therefore possible. However, the occurrence of a shallow and large peak of females, at different depths to the males both by day and at night, is rather puzzling. We can suggest two possible explanations. (i) These females are fertilized when the males migrate upwards at night; this would imply that males reach the 75–250 m layer before the females have migrated to the upper 75 m. (ii) The females only migrate to deep layers by day to be fertilized and remain thereafter in the upper layers.

As expected, the younger stages of *Pleuromamma abdominalis* (C4) lived at significantly shallower depths than the adults by day (Figure 5b; WMDs of 295 and 385 m, respectively). At night, the C4, C5 and adults were concentrated in the upper 75 m. The amplitude of the DVM increased with age of the organism, although it was not clear from the WMD values due to the occurrence of a few deep C5 and adults at night. It should be noted that adults of *P. abdominalis* lived significantly deeper, by ~75 m, than adults of *P. gracilis* (Table III). The increase in day time preferential depth with age of the organism was very clear in *Euchaeta acuta* (Figure 5c), with significantly different WMDs of 195 m (C2–C4), 450 m (C5) and 545 m (adults). At night, the C2–C4 concentrated in the upper 75 m, while the C5 and

adults presented a bimodal distribution, a shallower peak at 0–75 m and a deeper one at 250–350 m. Nearly all the C5 and adults appeared to migrate at night, with the amplitude of the migration up to 400–500 m for some.

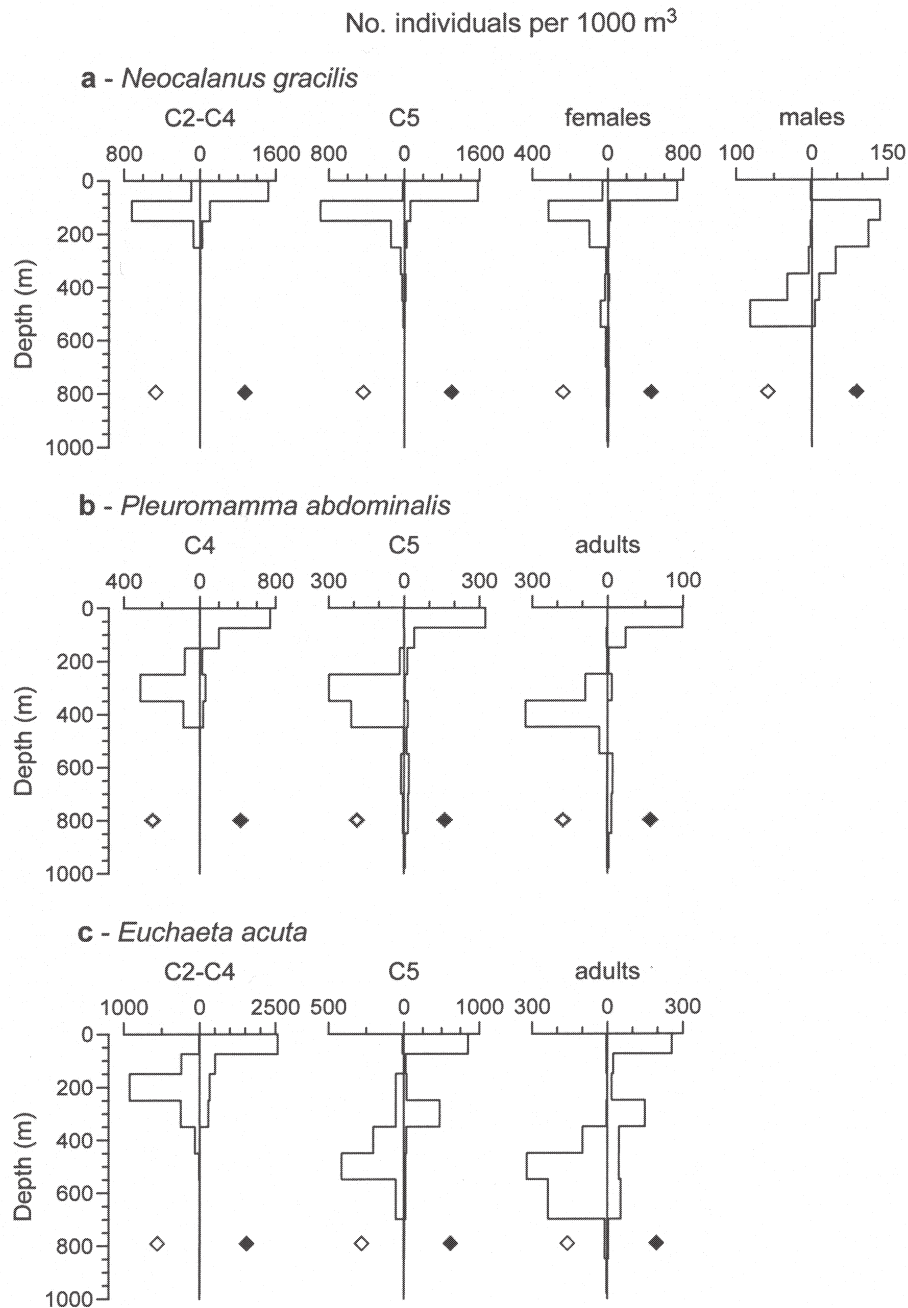
### Changes in copepod vertical distribution over the sampling period

Two copepod species exhibited changes in vertical distributions during the sampling period of the cruise. The bulk of the population of *Chiridius poppei* was concentrated in the 350–450 m stratum in the day time and was caught essentially between 150 and 450 m at night time, performing a moderate DVM (Figure 6). However, a deep peak was observed between 550 and 980 m, both by day and at night. Its density clearly increased during leg 4, while the density of the shallow peak was similar over the two sampling periods. The occurrence of the deep population did not appear to be related to the deepening of a given stage, copepodites (C4, C5) or adults.

Changes in the vertical distribution of *Calanus helgolandicus* were even more marked (Figure 7). A peak in abundance was observed in the 0–75 m stratum during leg 2, both by day and at night, while during leg 4, individuals were exceptionally caught in the upper 75 m (and even in the upper 450 m). The preferential depth of the deep population appeared to increase throughout the sampling period, as can be seen from the profiles and from the graph of deep WMD versus date of sampling, with deep WMDs calculated for the 150–980 m water column. The average WMD calculated for leg 4 was significantly deeper, by about 70 m, than that for leg 2 ( $685 \pm 25$  m compared with  $615 \pm 45$  m). The population of *C. helgolandicus* consisted essentially of copepodites C5 (96%, Table II); this deepening could have corresponded to the seasonal downward migration of overwintering stages.

### Macroplankton and micronekton

Nine species represented 88% of the total number of macroplankton individuals in the 0–980 m water column, each of them representing at least 3% (Table II). Two size classes were distinguished for *Meganycitophanes norvegica* and *Nematoscelis megalops*: (i) small individuals with a total length  $\leq 7$  mm for *Meganycitophanes* and  $\leq 11$  mm for *Nematoscelis*; (ii) larger individuals. No change in the vertical distribution of these nine species was clearly discernible throughout the sampling period. Figure 8 presents the average day time and night time distributions and Table IV, the corresponding weighted mean depths (WMD). Three species showed an upward migration at night of the whole population, the siphonophore *Chelophyes appendiculata*, the amphipod *Vibilia armata* and the euphausiid *Euphausia krohni* (Figure 8a,d,e), with an amplitude of migration of 250–600 m (Table IV). The fishes *Cyclothone braueri* and



**Fig. 5.** Average vertical distributions, by day  $\diamond$  and at night  $\blacklozenge$ , of the stages of the three copepod species that exhibited a clear ontogenetic migration.

*C. pygmaea* were clearly non-migrant (Figure 8j,k). The other species displayed intermediate behaviours. We could not detect any migration in small individuals of *M. norvegica* and *N. megalops*, which concentrated in the upper 75 or 150 m both by day and at night; by contrast, large *Meganyctiphanes* and some large *Nematoscelis* underwent an extensive DVM (Figure 8f-i).

The day time vertical distribution of the pteropod

*Cavolinia inflexa* was bimodal, the deeper organisms undergoing a DVM with an amplitude of 400 m (Figure 8c). The shallow peak was observed on D16 and D29, in similar or higher concentration than those of the deep peak; the occurrence of the shallow peak did not appear, therefore, to be related to the date of the sampling. The siphonophore *Lensia conoidea* presented a bimodal distribution both in the day time and at night time throughout

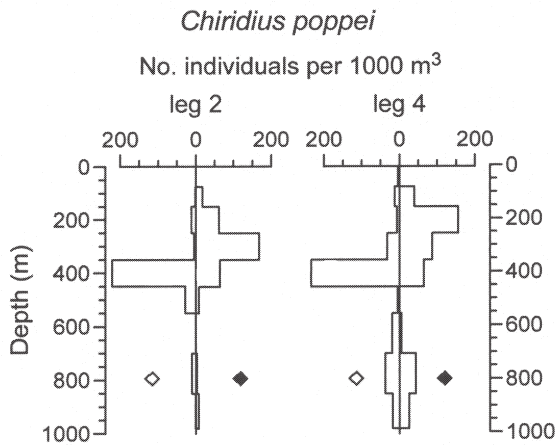


Fig. 6. Vertical distributions of *Chiridius poppei* during the two sampling periods, by day  $\diamond$  and at night  $\blacklozenge$ .

the sampling period (Figure 8b). The shallow day organisms appeared to concentrate in the 75–150 m stratum at night, performing a weak DVM. Higher numbers were recorded at night than by day, both in the 0–450 and

450–980 m water columns (cf. values in Figure 8b). This suggests an extensive DVM of the deep day organisms up to the upper 150 m and also, migration of organisms below the lowest depth sampled by day.

## DISCUSSION

### Vertical distribution, diel and ontogenetic migration of copepods

Most of our results from BIONESS hauls confirm the previous observations made by different authors in various areas of the world's oceans. However, concerning the Mediterranean Sea, this study is one of the most detailed on the vertical distribution and the diel and ontogenetic migration of large-sized copepods ( $>500 \mu\text{m}$ ). To our knowledge, previous detailed results are limited to those of Weikert and Trinkaas (Weikert and Trinkaas, 1990) for the eastern Mediterranean, and Gasser (Gasser, 1995) and Gasser *et al.* (Gasser *et al.*, 1998) for the north-western Mediterranean, which are based on repetitive sampling with a multiple opening/closing net system (BIONESS or MOCNESS) at a fixed station or in a

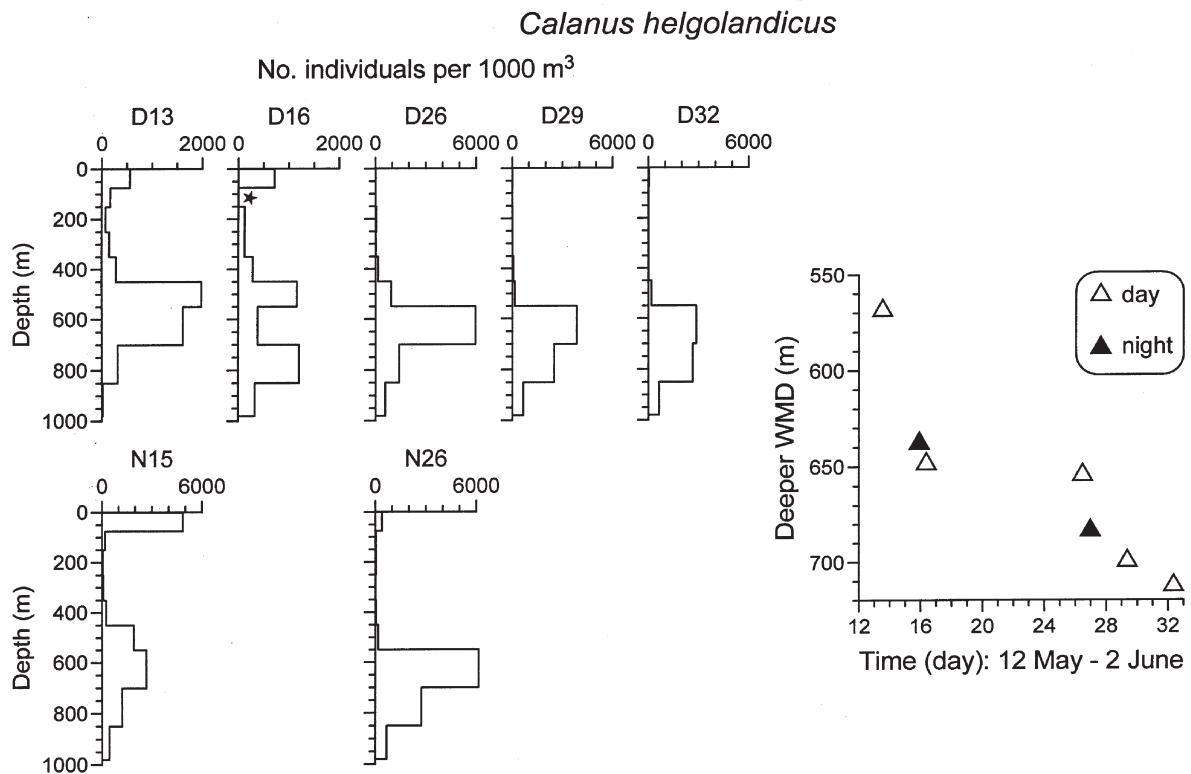
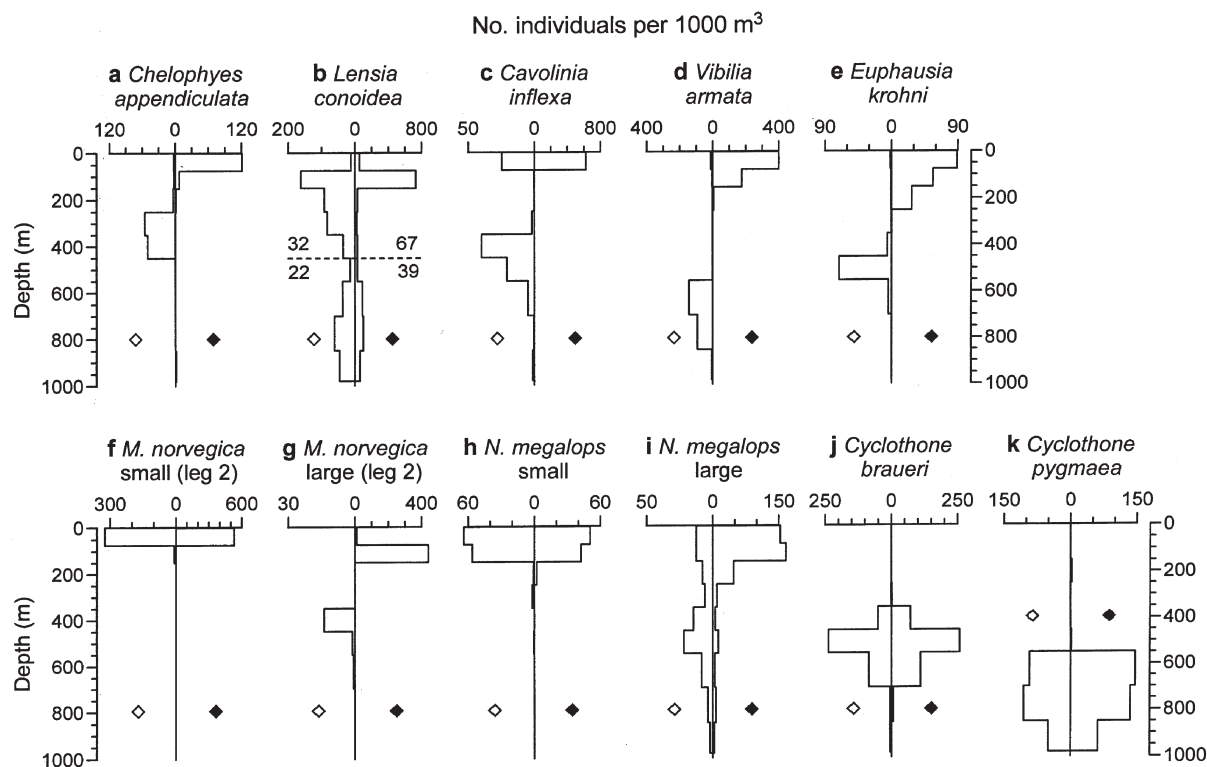


Fig. 7. Vertical distributions of *Calanus helgolandicus* during the five day hauls and the two night hauls (left), and corresponding weighted mean depths of the deep population (WMD in the 150–980 m water column) throughout the cruise (right). \*, Absence of results for the 75–150 m stratum.



**Fig. 8.** Average vertical distributions of the most abundant species of macroplankton and micronekton, by day  $\diamond$  and at night  $\blacklozenge$ . Values on the graph of *Lensia conoidea* correspond to number of individuals  $m^{-2}$  for the 0–450 and 450–980 m water columns. Note the different abundance axes.

restricted area. Table V summarizes the day and night-time depths and existence of DVM or its range recorded in the literature and in the present work.

*Centropages typicus* (typically epipelagic), *Mesocalanus tenuicornis* and *Euchirella rostrata* (literature data are rather rare for *E. rostrata*) appear as non- or weak migrators, with an amplitude of migration lower than 50–100 m (Table V). In the present study, the peak of abundance of *Heterorhabdus* spp. in the upper 250 m would have consisted essentially of *H. papilliger* while most of the deeper organisms would have corresponded to *H. abyssalis* if we compare our results with those of Scotto di Carlo *et al.* (Scotto di Carlo *et al.*, 1984). These authors also reported *H. papilliger* to be a weak migrant. Studies on the DVM of *C. poppei* are rather scarce; it appears that if DVM occurs, it would be weak or concern only part of the population.

Males of *Neocalanus gracilis* have been found to live significantly deeper than copepodites and females in the day time in both this study and in those of Ambler and Miller (Ambler and Miller, 1987), Gasser (Gasser, 1995) and Gasser *et al.* (Gasser *et al.*, 1998), although Gasser's studies are less detailed (Table V). Ambler and Miller concluded

that there was no apparent DVM in this species; however, their vertical profiles suggested the occurrence of a DVM for the males (Ambler and Miller, 1987). The present study shows a weak DVM of copepodites and females and a rather large one for males. The different reports on the migrant behaviour of *N. gracilis* suggest a need for detailed studies of different stages based on narrow depth strata.

As deep and non-migrant species, we found *Monacilla typica* and *Gaetanus kruppi*, in agreement with previous studies. It should be noted that *G. kruppi* is reported to live in abundance below 1000 m, our deepest depth sampled. Our results on the diel and ontogenetic migration of *E. acuta* confirm previous, generally less detailed studies concerning ontogenetic migration. It is notable that Longhurst and Williams (Longhurst and Williams, 1979) reported an age–depth differential distribution, especially in the day time, for *Euchaeta norvegica*. The present results on the extensive diel migration of *Pleuromamma abdominalis* and *P. gracilis*, their partitioning in the water column in the day time and the ontogenetic migration of *P. abdominalis*, are in general agreement with the abundant literature data available for various areas.

*Table IV: Average weighted mean depths, WMD (m)  $\pm$  SD, during the day and at night, and amplitude of the migration, dz (m), for the main species of macroplankton and micronekton*

Species	Day WMD	Night WMD	dz
<i>Chelophyes appendiculata</i>	330 $\pm$ 40	65 $\pm$ 25	265
<i>Lensia conoidea</i>			
0–450 m	205 $\pm$ 25 <sup>b</sup>	130 $\pm$ 0	75
450–980 m	750 $\pm$ 50	730 $\pm$ 20	620 <sup>d</sup>
<i>Cavolinia inflexa</i>			
0–150 m	45 $\pm$ 10 <sup>c</sup>	40 $\pm$ 0	–
150–980 m	475 $\pm$ 70	–	435 <sup>d</sup>
<i>Vibilia armata</i>	655 $\pm$ 60	75 $\pm$ 40	580
<i>Euphausia krohni</i>	495 $\pm$ 20	90 $\pm$ 40	405
<i>Meganyctiphanes norvegica</i>			
small	45 $\pm$ 5 <sup>a</sup>	40 <sup>+</sup>	–
large	420	110 <sup>+</sup>	310
<i>Nematoscelis megalops</i>			
small	90 $\pm$ 40 <sup>b</sup>	60 $\pm$ 35	–
large			
0–250 m	115 $\pm$ 75 <sup>b</sup>	100 $\pm$ 15	–
259–980 m	525 $\pm$ 30	555 $\pm$ 50	425 <sup>d</sup>
<i>Cyclothone braueri</i>	540 $\pm$ 30	525 $\pm$ 25	–
<i>Cyclothone pygmaea</i>	745 $\pm$ 35	735 $\pm$ 40	–

Values are given to the nearest five. Values of dz are given when the day–night differences are significant at the 0.05 level (t-test). <sup>a</sup>, <sup>b</sup>, <sup>c</sup>, WMD values calculated for leg 2, from 4 day profiles and from 3 day profiles, respectively (results of D16 discarded or absence of organism); <sup>d</sup>, calculated from the deeper day WMD and the shallower night WMD.

### Seasonal migration of *Calanus helgolandicus*

*Calanus helgolandicus* was the most abundant copepod species recorded in the present hauls and consisted essentially of copepodites C5 (Table II). We have observed its disappearance from the surface waters (0–75 m) between the two sampling periods, while its main peak, below 450 m, tended to deepen as time proceeded (Figure 7). WP-II hauls (200  $\mu$ m mesh), performed during the same cruise in the upper 200 m, provided similar information, i.e. disappearance between legs 2 and 4 and dominance of C5 [77% (Andersen *et al.*, 2001)]. *Calanus helgolandicus* is known to overwinter primarily as stage C5 [e.g. (Williams and Conway, 1988; Stöhr *et al.*, 1996) for deep waters]. Our results therefore suggest that our sampling corresponded with the time when *C. helgolandicus* underwent its seasonal downwards migration.

In the detailed study of Williams and Conway (Williams and Conway, 1988) performed in the northeast Atlantic, *C. helgolandicus* is reported to show its maximum concentration in the upper 70 m in May and June, and

below 400 m in July, where it remains till the following spring. Seasonal migration of this species has been less documented in the Mediterranean Sea. Sampling has often been performed in surface waters or in coastal and shallow waters (Hure, 1955; Vives, 1963; Hure and Scotto di Carlo, 1968); in general, these studies report the absence or quasi-absence of *C. helgolandicus* in surface waters in summer (July to September), and a maximum abundance in this layer in winter and early spring (January to April). From deeper hauls, *C. helgolandicus* is reported as living below 500 m in late May, June and July while in April, it included a surface population (0–200 m) and a deeper-living one (Scotto di Carlo *et al.*, 1984). Gasser *et al.* also observed maximum abundance of *C. helgolandicus* below 700 m in June, with the population consisting almost exclusively of C5 (Gasser *et al.*, 1998). Our results and literature data suggest that *C. helgolandicus* would begin its downwards seasonal migration in May at the latest, C5 being the primarily overwintering stage, while in the North Atlantic this migration occurs later (Williams and Conway, 1988). The main peak appeared to deepen from



Table V: Day time depths, night time depths and existence of DVM or its range. Day and night time depths correspond to the layers where the abundance is maximum. Migration range has been estimated from middle of day and night time depths when not indicated by the authors. Only studies performed in the Mediterranean Sea are cited, when available, and observations made in shallow waters are not considered

Day time depth (m)	Night time depth (m)	Migration, range (m)	Area	Reference
<i>Centropages typicus</i>				
0–75	0–75	no	NW Med	present
0–75	0–75	no	NW Med	7
50–100	0–50	weak 50	W Med	20
epiplanktonic			W Med	6, 10, 14, 15
<i>Chiridius poppei</i>				
350–450 (I), 550–1000 <sup>a</sup> (II)	150–450 (I), 550–1000 <sup>a</sup> (II)	part 100	NW Med	present
125–350	below 50 m	no/weak	W Med	20
50 to 1000–1500 <sup>b</sup>			W Med	20, 22
spp. 150–450 (I), 550–850 (II)			W Med	8
150–205, 570–625 (625 <sup>c</sup> )	150–250, 550–600 (150 <sup>c</sup> )	yes?	NE Atl	16
<i>Euchaeta acuta</i>				
C2–C4 150–250	C2–C4 0–75	C2–C4 (105)	NW Med	present
C5 450–550, ad 450–700	C5, ad 0–75 (I), 250–350 (II)	C5 110–410, ad 125–500	W, E Med	11
C 230, 260, ad 465, 495 <sup>e</sup>			NW Med	8
C5 spp. 150–250, ad 450–550			W, E Med	12
450–480	150–180	300	W, E Med	4, 9
	250	yes	NE Atl	18
500		250		
<i>Euchirella rostrata</i>				
150–250	0–150	weak part (55)	NW Med	present
mesoplanktonic		no/weak	W Med	4
450 <sup>d</sup>	up to 100 m <sup>d</sup>	part	NE Atl	19
<i>Gaetanus kruppi</i>				
550–1000 <sup>a</sup>	550–1000 <sup>a</sup>	no	NW Med	present
700–1000 <sup>a</sup>	700–1000 <sup>a</sup>	no	NW Med	7
1600–2500			W Med	20, 21
bathypelagic			W Med	14, 15, 22
780–950 <sup>a,b</sup>	910–960 <sup>a,b</sup>	no	NE Atl	16

Table V: continued

Day time depth (m)	Night time depth (m)	Migration, range (m)	Area	Reference
<i>Heterorhabdus</i> spp.				
75–250	0–250	weak part (55)	NW Med	present
0–150 (in June), 75–250 (in May)	0–150	no	NW Med	7
0–100 (I), 200–900 (II)	0–100 (I), 200–900 (II)	no	E Med	23
<i>H. papilliger</i> 100–300		weak	W Med	20
<i>H. abyssalis</i> 500–850		?		
<i>Mesocalanus tenuicornis</i>				
75–150	0–75	weak 95	NW Med	present
0–75	0–75	no	NW Med	7
50–100	0–50	weak 50	W Med	20
50–75	50–75	no	NW Atl	24
75–150	75–125	weak 25–50	NW Atl	2
25–60	5–40	weak	E Pac	13
<i>Monacilla typica</i>				
550–700	550–700	no	NW Med	present
550–1000 <sup>a</sup>	550–1000 <sup>a</sup>	no	NW Med	7
700–1300		no	W Med	20
500–1000 <sup>a</sup>			W, E Med	11, 22
<i>Neocalanus gracilis</i>				
C2–C4, C5 75–150, f 75–250, m 350–550	C 0–75, f 0–75, m 75–250	C2–C4 70, C5 (120), f (100), m 260	NW Med	present
C 0–150, m 450–550			NW Med	7, 8
50–100	up to the surface	weak	W Med	20
below 100 m	0–100	yes	W Med	14
40–85 (II), 350–780 (I)	up to the surface	yes	NE Atl	17
0–200	0–200	no	NW Atl	2
C2, C3, C4, C5, f 75–100, m 200–300	C2–C5, f 75–100, m 75	C2, C3, C4, C5, f no, m 175?	N Pac	1
100–150, 560–675 <sup>b</sup>	0–440 <sup>b</sup>	yes ?	E Pac	5

Table V: continued

Day time depth (m)	Night time depth (m)	Migration, range (m)	Area	Reference
<i>Pleuromamma abdominalis</i>				
C4 250–350, C5 250–450, ad 350–450	C4–C5, ad 0–75	C4 210, C5 150, ad 210	NW Med	present
C4–C5 250–350, ad 250–450			NW Med	8
C 330, 360, ad 380, 455 <sup>e</sup>			W, E Med	11
C 200–450, ad 350–450			E Med	23
C3 275, C4 300 <sup>e</sup>	C, ad 0–100	C 275, ad 350	W Atl	3
C5 325 <sup>e</sup> , ad 375 <sup>e</sup>	C3 50, 300, C4 44, 330 <sup>e</sup> C5 55, 370 <sup>e</sup> , ad 65 <sup>e</sup>	C3 part 225, C4 part 256 C5 part 270, ad 310		
C4 250–275, C5 380–405, ad 450–490	C4–C5, ad 50–75	C4 part 200, C5 part 330, ad 400	N Pac	1
<i>Pleuromamma gracilis</i> adults				
250–350	0–75	250	NW Med	present
250–350	0–75	265	NW Med	7
315, 380 <sup>e</sup>		strong > 200	W, E Med	11
300–400	50–75	290	W, E Med	20, 23
		strong > 200	W Atl	3
			NE, NW Atl	18, 24
300	25	275	N Pac	1

C, copepodite; f, female; m, male; ad, adult. I, II: Primary, secondary peak. Med, Mediterranean; Atl, Atlantic; Pac, Pacific. <sup>a</sup>Deepest depth sampled. <sup>b</sup>Limits of occurrence. <sup>c</sup>Depth of maximum abundance. <sup>d</sup>Horizontal hauls at 100, 250, 450 and 600 m depth. <sup>e</sup>Weighted mean depth or mean level. References: 1. (Ambler and Miller, 1987); 2. (Ashjian and Wishner, 1993); 3. (Bennett and Hopkins, 1989); 4. (Casanova, 1970); 5. (Chen, 1986); 6. (Furnestin, 1960); 7. (Gasser, 1995); 8. (Gasser *et al.*, 1998); 9. (Giron, 1963); 10. (Hure and Scotto di Carlo, 1968); 11. (Hure and Scotto di Carlo, 1969); 12. (Hure and Scotto di Carlo, 1974); 13. (Longhurst, 1985); 14. (Mazza, 1962); 15. (Mazza, 1963); 16. (Roe, 1972a); 17. (Roe, 1972b); 18. (Roe, 1972c); 19. (Roe, 1984); 20. (Scotto di Carlo *et al.*, 1984); 21. (Scotto di Carlo *et al.*, 1991); 22. (Vives, 1978); 23. (Weikert and Trinka, 1990); 24. (Wiebe *et al.*, 1992).

450–700 m on 13 May to 550–850 m on 1 June during the present study. As this peak has been found between 700 and 1000 m in June in a neighbouring area by Gasser *et al.* (Gasser *et al.*, 1998), it would suggest that *C. helgolandicus* has not finished its downwards migration at the end of May. A bimodal distribution of *Chiridius poppei*, such as those recorded here during leg 4 (Figure 6), has been reported by Gasser *et al.* (Gasser *et al.*, 1998) and Roe (Roe, 1972a). However, to our knowledge, no previous detailed study is available to confirm whether or not the descent of the population observed here corresponded to a seasonal downwards migration.

### Macroplankton and micronekton: behaviour of *Lensia conoidea*

The vertical distributions of the macroplankton and micronekton species considered here, *Vibilia armata* excepted, have previously been documented by some of us at the same time-series station or in its vicinity and with the same sampling device [in May 1990 (Andersen and Sardou, 1992; Andersen *et al.*, 1992); in April 1991 (Sardou and Andersen, 1993); in April 1994 (Andersen *et al.*, 1998)]. The present results are in good agreement with these previous studies. Concerning *V. armata*, its extensive migration, in excess of 400 m, has been reported in studies performed in the North Atlantic [e.g. (Thurston, 1976; Roe *et al.*, 1984)].

With regard to the vertical distribution of *L. conoidea*, in April 1991, April 1994 and May 1990, the bulk of the population was caught in the upper 350 m, as during the present cruise. However, deeper individuals were caught exceptionally in April 1991 and 1994, in small but non-negligible numbers in May 1990 (2–7 May), and contributed to a large part of the total standing crop during the present study (13 May–1 June). This would suggest a descent of *L. conoidea* as the season proceeded. Franqueville (Franqueville, 1971) noted that in summer, *L. conoidea* was almost absent above 650 m, which is consistent with our hypothesis. The DYNAPROC cruise would therefore have been performed during a transition period in the seasonal cycle of this species.

### Short-term changes and effects of wind events

The vertical distribution of small-sized zooplankton, sampled in the upper 100 m, appeared to be greatly influenced by wind events. The upward shift by 10–15 m, observed between 12 and 15 May, in the population primarily of copepod nauplii and euphausiid nauplii and secondarily of calanoid copepodites (Figure 2), appeared to be related to the strong wind event and the Ekman pumping of deeper waters that occurred at this time. These organisms were also distributed in a larger water

column during leg 4 than during leg 2; this extended distribution could be attributed to the wind event, which occurred just before leg 4, that induced a deepening of the mixed layer and a dilution of the phytoplankton biomass in the water column.

From the isothermal and isopycnal lines, Andersen and Prieur (Andersen and Prieur, 2000) estimated that the upward shift occurred at a speed of about 3 m day<sup>-1</sup> (shift of 10 m in 3 days); they also noted that in steady state, the estimated wind stress curl would induce a vertical pumping velocity as high as 11 m day<sup>-1</sup> at the bottom of the Ekman layer. Buskey *et al.* reported mean speeds of 0.11–0.55 mm s<sup>-1</sup> (9.5–47.5 m day<sup>-1</sup>) for copepod nauplii, but nauplii would certainly not maintain such speeds during 3 days (Buskey *et al.*, 1993). *Clausocalanus* was the largely dominant genus of calanoids in the WP-2 hauls done during the same cruise (Andersen *et al.*, 2001); it can therefore be assumed that the calanoids of the bottle samples consisted essentially of *Clausocalanus* spp. Mazzocchi and Paffenhöfer reported a mean speed of 10 mm s<sup>-1</sup> for females of *C. furcatus* (Mazzocchi and Paffenhöfer, 1999). The present results on vertical distribution appear consistent with these swimming speeds. The naupliar stages of copepods and euphausiids were unable to counter the vertical advection and wind-induced mixing, while calanoid copepodites were less influenced and no marked changes were observed in vertical distributions of *Oithona* spp., *Microsetella* spp. and radiolarians.

The vertical distribution of nauplii became bimodal just after the major wind event, and this distribution persisted until the end of the cruise. Such a feature would also be related to physical forcing; the population was distributed in similar concentrations above and below the strong thermocline. The deeper peak of the copepod nauplii was at the depth of the Chl *a* maximum, while the superficial peak was 10–20 m above (Figure 2). However, the surface population of nauplii may have found a sufficient concentration of prey to persist; for example, the maximum of zeaxanthin (cyanobacteria and prochlorophytes) was at and above the Chl *a* peak (Vidussi *et al.*, 2000), and nanociliates concentrated between the surface and 30 or 40 m during leg 2 and leg 4, respectively (Pérez *et al.*, 2000).

Literature data on the influence of wind events on the vertical distribution of zooplankton remain rather scarce. Ortner *et al.* noted that changes in the centroid of zooplankton biomass approximately paralleled changes in the mixed layer depth, but they did not provide information on the specific composition of zooplankton sampled with 63 µm and 333 µm mesh nets (Ortner *et al.*, 1984). The results of Mackas *et al.* (Mackas *et al.*, 1993), concerning species of the genera *Neocalanus* and *Eucalanus* that are of greater size than the present ones, suggest that zooplankton actively select their preferred depth range

using turbulence intensity as a direct environmental cue. Haury *et al.* reported that weakly swimming organisms, such as *Oithona* spp., were unable to counter wind-induced mixing (Haury *et al.*, 1990); this was not obvious in the present study but it depends on the level of turbulence encountered. The study of Lagadeuc *et al.* (Lagadeuc *et al.*, 1997) was more analogous to the present one as it was based on the vertical distribution of small-sized organisms (64 µm mesh) before and during homogenization of the water column due to wind. The authors observed a homogeneity of nauplii over the water column after the wind event, while the adult stages of *Oithona similis* and of *Microsetella norvegica* exhibited the same distribution in stratified and unstratified columns, which agrees with our observations.

## CONCLUSION

The present study has two main features. On the one hand, it provides detailed information on the vertical distribution, ontogenetic and diel migration of major copepod species in the open northwest Mediterranean, an area for which such data were rather lacking. On the other hand, it documents short-term changes in the vertical distribution of organisms, changes related to (i) the behaviour of the organism, such as the seasonal downwards migration of *Calanus helgolandicus*, and (ii) the occurrence of wind events and their influence or otherwise on small-sized organisms. Bimodal distributions have been observed for a variety of organisms during the present study. These distributions could be attributed to various causes, such as physical forcing in the superficial layers for copepod nauplii, and ontogenetic or seasonal migration for distances of several hundred metres for large-sized copepods and macroplankton. The various assumptions made in this context underline the need for further detailed studies.

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