Macroplankton and micronekton in the northeast tropical Atlantic: abundance, community composition and vertical distribution in relation to different trophic environments

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Abstract—During the EUMELI 4 cruise in the northeast tropical Atlantic a series of oblique hauls was carried out in the 0–1000 m water column at three different sites: oligotrophic, mesotrophic and eutrophic. Based on the samples obtained, the abundance, community composition and vertical distribution of macroplanktonic and micronektonic groups are described. Data on euphausiids and thecosome pteropods were analyzed at the species or genus level. In both euphausiid and thecosome groups, the number of species decreased from oligotrophic to eutrophic sites with a few clearly dominant species at mesotrophic and eutrophic sites. Therefore, the diversity index increased from eutrophic (1.0 bits) to oligotrophic (3.5 bits) sites. Among vertically migrating species, a general decrease in migration amplitude was observed from the oligotrophic site to the mesotrophic and eutrophic ones, with the organisms often being caught in the upper layers both in the day and at night in the latter two environments. This change of behavior is discussed in relation to the characteristics of the environment (phytoplankton abundance, depth of the euphotic zone, temperature, oxygen concentration). © 1997 Elsevier Science Ltd. All rights reserved

INTRODUCTION

A large amount of information has been gathered on the vertical distribution and migration of macrozooplankton and micronekton in various areas of the world's oceans. Macrozooplankton and micronekton communities have been investigated particularly in the eastern tropical Pacific with transects encompassing several hydrographically distinct structures (Brinton, 1967, 1979; Longhurst, 1967, 1976; Youngbluth, 1976). These transects, performed from coastal areas to offshore waters or along a north–south axis, investigated, using different approaches, interrelationships between zooplankton species distribution, zones of currents and environmental characteristics such as dissolved oxygen concentration and temperature. In the Atlantic Ocean, particularly the eastern tropical Atlantic, most studies on the vertical distribution of macroplankton and micronekton have been conducted in restricted areas or at a single position (Badcock, 1970; Baker, 1970; Pugh, 1974; Casanova, 1980; Roe *et al.*, 1984; Hargreaves, 1985). The studies of Hargreaves and James (1989) and of Wiebe *et al.* (1992) are among the few recent studies performed on larger scales. Hargreaves and James (1989) reported on the geographic and vertical distribution of euphausiid species observed at six stations from 11°N to 60°N in the eastern Atlantic. Wiebe *et al.* (1992) studied the copepod and euphausiid communities in hydrographically distinct areas of a Gulf Stream warm-core ring.

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Within the context of the JGOFS-France program, systematic biogeochemical studies were carried out at three sites in the northeast tropical Atlantic representing typical EUtrophic, MEsotrophic and oLIgotrophic regimes, hence the acronym EUMELI (Morel, 1996). The EUMELI 4 cruise (May–June 1992) provided the opportunity to explore in detail the macroplankton and micronekton communities. The purpose of this paper is to present data on the abundance, composition and vertical distribution of the macroplankton and micronekton communities at the three sites by day and at night in the 0–1000 m water column. Particular attention was paid to euphausiid and pteropod species. Species diversity and occurrence of diel vertical migration (DVM) are discussed in relation to the environmental features of the three distinct sites.

METHODS

Environmental conditions

The EUMELI cruises were carried out in the northeast tropical Atlantic at three stations under different environmental conditions (Fig. 1). These sites strongly differ, highly contrasting phytoplankton abundance during all seasons and wide differences in primary production (see Morel, 1996, for the objectives and background of these studies). The eutrophic site (E: 20°32′N, 18°36′W), located about 130 km off the Mauritanian coast, is in a permanent upwelling area supporting a dense phytoplankton community. The oligotrophic site (O: 21°N, 31°W), located about 1400 km offshore, is at the periphery of the stable North-Atlantic gyre. The mesotrophic site (M: 18°30′N, 21°W), about 400 km offshore, is an intermediate position that is under the influence of extended filaments detached from the upwelling zone.

The average temperature, salinity, oxygen and fluorescence profiles measured during the same period as our zooplankton sampling, leg 2 of the EUMELI 4 cruise (June 92), are plotted in Fig. 2 (Lefèvre, Raunet and Tailliez, personal communication). Temperature was higher at the oligotrophic site, with differences of $\sim 5°C$ between sites O and E and of 2–4°C between sites O and M in the 0–150 m water column. Oxygen profiles presented a clear minimum at sites M and E, 1.25 ml l^{-1} at 450 m and 1.57 ml l^{-1} at 350 m, respectively, while, at site O, the minimum O_2 concentration was ~ 2.81 ml l^{-1} at 690 m. The oligotrophic site was characterized by a deep phytoplankton peak of low values (~ 0.3 mg Chl m^{-3}) at 95–150 m (mean: 125 m), while at sites M and E, chlorophyll was quasi-uniformly distributed in the mixed layer, with a concentration of ~ 1 mg m^{-3} at site M and ~ 3 mg m^{-3} at site E. The three sites were also distinctly different with respect to nutrient availability (Babin *et al.*, 1996) and phytoplankton population composition, with a predominance of diatoms at site E, of cyanobacteria at site M and of picoplanktonic species at site O (Claustre, 1994). At the eutrophic and mesotrophic sites, mixed layer thickness exceeded that of the euphotic zone (50 m vs. 20–25 m, 40 m vs. 27 m, respectively); in contrast, at the oligotrophic site, the euphotic zone, ~ 105 m, extended much deeper than the mixed layer, ~ 60 m (Morel *et al.*, 1996).

Sampling procedure and data analysis

A series of oblique hauls was carried out at these three sites within a period of 11 days (14–24 June 1992) during leg 2 of the EUMELI 4 cruise. All biological samples were taken with
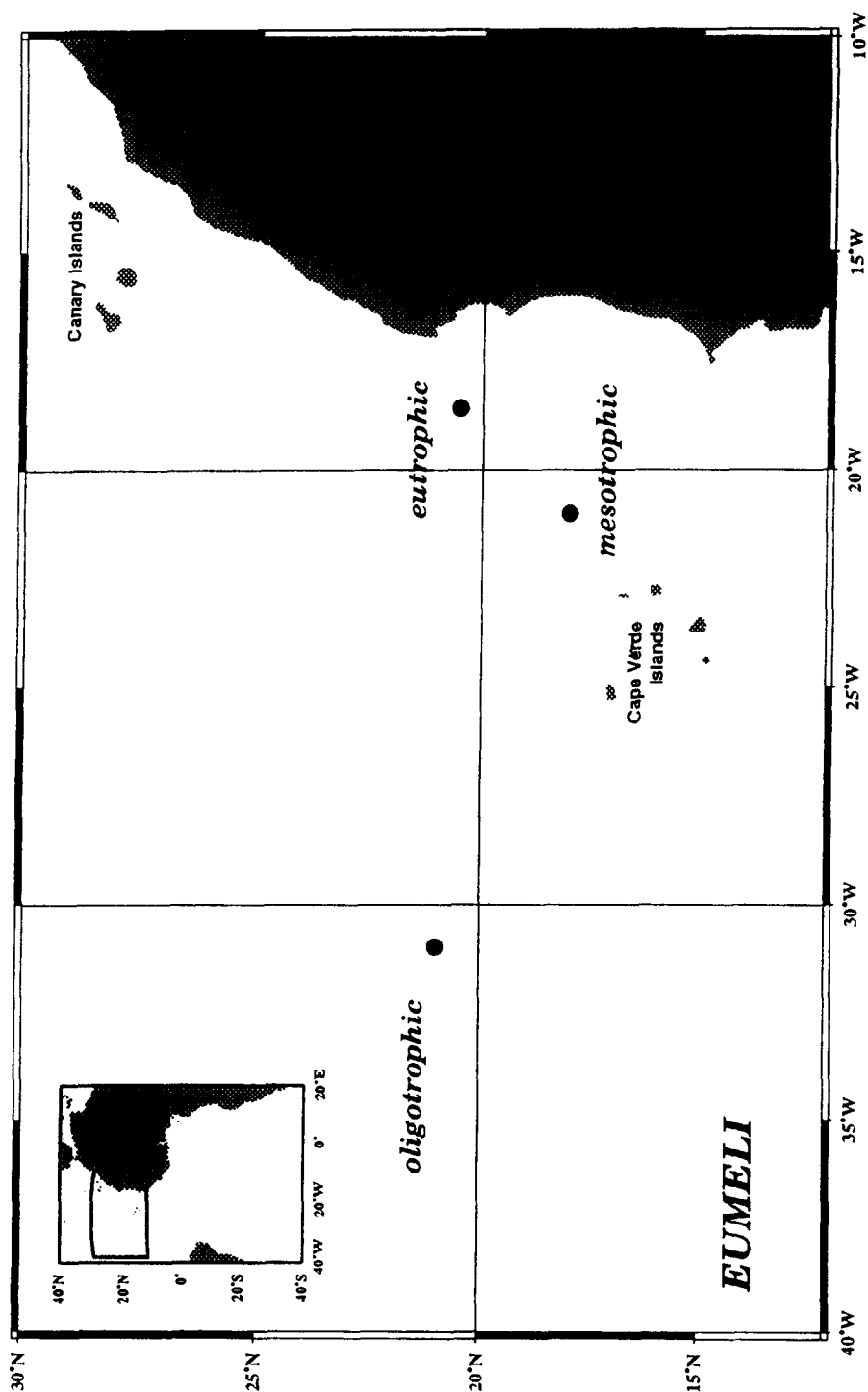
Fig. 1. Location of the three sites selected for the EUMELI program (after Morel *et al.*, 1996).
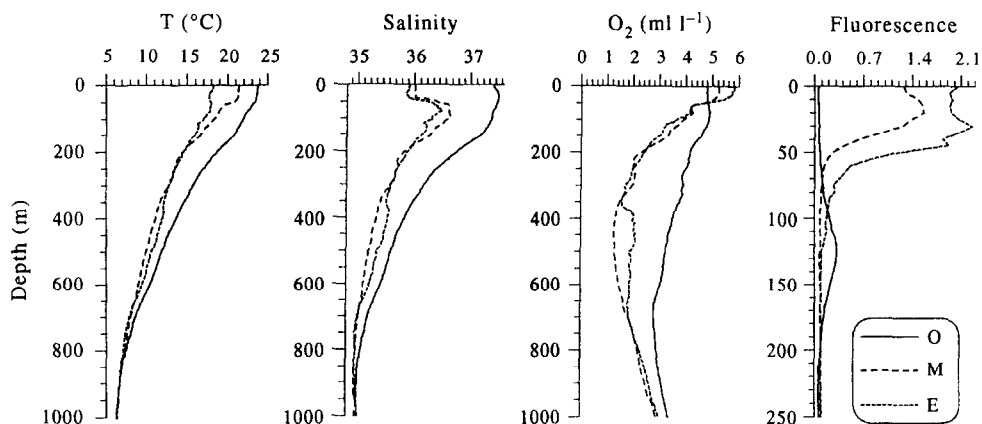
Fig. 2.   Average profiles of temperature, salinity, dissolved oxygen and fluorescence (standard units) observed during the sampling period at the three sites. Temperature, salinity and O_2 data from CTD performed down to 800 m or more (three profiles at sites O and E, four at site M), fluorescence from CTD down to 250 m or more (26, 27 and 14 profiles at sites O, M and E, respectively) (data from Lefèvre, Raunet and Tailliez, personal communication).

the BIONESS (Sameoto *et al.*, 1980), a multiple opening and closing net with ten 500-μm mesh nets, each with a mouth area of 1 m². The BIONESS was towed at a mean speed of 1.9 m s^{-1}. During the oblique hauls performed around midday and midnight, the net fished at nine different levels in the 0–965 m water column: 965–850, 850–700, 700–550, 550–450, 450–350, 350–250, 250–150, 150–75 and 75 m to the surface. The volume of water filtered in each layer varied from 284 to 1782 m³, depending on the depth stratum sampled. The tow (nine samples) ranged in length from 8900 to 10 600 m. The sampling data are summarized in Table 1. Samples were preserved in 5% buffered formalin in seawater. Specimens were identified using taxonomic characters given by Baker *et al.* (1990) for euphausiids and by

Table 1.   *Sampling data for BIONESS*

Haul no.	Date 1992	Time (GMT)	D/N	Start position		End position	
				N	W	N	W
E1	14/6	0056–0214	N	20°34.4	18°35.0	20°38.6	18°35.4
E2	14/6	0942–1053	D	20°33.2	18°34.4	20°37.5	18°34.5
M1	16/6	0103–0209	N	18°31.8	21°06.1	18°35.5	21°06.1
M2	16/6	1443–1550	D	18°32.3	21°07.4	18°36.0	21°06.3
M3	17/6	0132–0240	N	18°37.2	21°06.4	18°41.3	21°05.4
M4	18/6	1413–1529	D	18°32.3	21°07.7	18°36.5	21°08.2
O1	22/6	1506–1620	D	21°04.2	31°08.3	21°06.4	31°04.5
O2	23/6	0111–0230	N	21°08.9	31°03.4	21°11.6	30°59.1
O3	23/6	1523–1638	D	21°02.7	31°06.1	21°05.2	31°02.2
O4	24/6	0141–0257	N	21°03.3	31°03.3	21°06.2	30°59.6

Oblique hauls in the 0–965 m water column by day (D) and night (N). Each haul is numbered at each site:

Boltovskoy (1981) for others. Euphausiids and thecosome pteropods were determined at the species level in most cases. For euphausiids, we did not separate *Nematoscelis atlantica* and *N. microps, Stylocheiron longicorne* and *S. affine*, and *Thysanoëssa gregaria* and *T. parva* because these organisms were more or less unidentifiable due to damage by the net. For thecosomes, species were not differentiated for two genera, caught in small numbers, *Hyalocylis* and *Limacina*. Some abundant genera or species of fishes (*Cyclothone* spp., *Argyropelecus hemigymnus*) and siphonophores (*Chelophyes appendiculata*) were also identified and enumerated.

Density estimates of the organisms were standardized to individuals per 1000 m³ (for each stratum) or m² (for the entire water column, 0–965 m). Since we obtained two day samples and two night samples at sites O and M, for each of these sites, the data for the day samples were combined to give average midday distributions and the night data were similarly treated to give the average midnight distributions. A *t*-test was used to compare the average number of individuals at midday and midnight. In order to compare the vertical partitioning of the taxa, the weighted mean depth (WMD) of each taxon was calculated according to the equation:

$$\text{WMD} = \Sigma(\text{ni} \times \text{di})/\Sigma\text{ni}$$

where *di* is the depth of a sample *i* (center of the depth interval corresponding to the sample) and *ni* is the number of individuals per 1000 m³ at that depth. At sites O and M, the WMD was first calculated for each distribution, then mean WMDs were calculated for day ($n=2$) and night ($n=2$); for non-migrant organisms a mean WMD was also calculated from the four hauls. To test the significance of depth difference between day and night or between sites for a given species or group, and between two species for a given site, *t*-tests were performed.

Data from euphausiids and pteropods were used for plotting day and night rank-frequency diagrams for the entire water column. They were obtained by first ranking the relative frequency of each taxon in decreasing order and then plotting these data in a diagram of rank vs. relative frequency (Frontier, 1976). Logarithmic scales are used for both the *x*- and the *y*-axis, which allows direct illustration of the two fundamental components of diversity: number of species and the regularity in distribution of the individuals within the species (Frontier and Pichod-Viale, 1993). For species richness, we used the diversity index (given in bits) of Shannon (1948) and defined by the equation:

$$H' = -\sum_{i=1}^{s} f_i \cdot \log_2 f_i$$

where f_i is the relative frequency of species *i*, and *s* is the number of species.

ABUNDANCE AND COMPOSITION

Major taxonomic groups of macroplankton and micronekton

Numbers of individuals per square meter from 965 m to the surface, determined for day and for night at the three locations, are presented for each macroplankton and micronekton group in Table 2. Total numbers (TN) increased from ∼263 ind m⁻² at oligotrophic site to 1216 ind m⁻² at site M, i.e. ∼4.6 times higher, and up to 2055 ind m⁻² at site E (or

Table 2. *Number of individuals per square meter (from 965 m to the surface), recorded for the three sites in the daytime and at night for the major taxonomic groups of macroplankton and micronekton*

Group	Oligotrophic					Mesotrophic					Eutrophic		
	Day ($n=2$) (no. m^{-2})		Night ($n=2$) (no. m^{-2})		t-test	Day ($n=2$) (no. m^{-2})		Night ($n=2$) (no. m^{-2})		t-test	Day (no. m^{-2})	Night (no. m^{-2})	N/D
	X	S.D.	X	S.D.	(N/D)	X	S.D.	X	S.D.	(N/D)			
Medusae	0.2	0.2	0.1	0.1	n.s.	0.9	0.6	1.1	0.8	n.s.	0.9	1.1	1.3
Siphonophores	31.7	14.3	6.6	1.1	n.s.	11.3	0.4	17.4	0.1	1.5*	20.2	17.7	0.9
Ctenophores	—	—	0.1	0.1	—	—	—	0.1	<	—	0.1	—	—
Annelids	0.8	<	0.2	0.1	0.2*	0.4	0.4	0.9	1.0	n.s.	—	—	—
Pteropods	3.2	0.3	2.7	2.8	n.s.	131.5	178.7	244.1	7.0	n.s.	901.0	282.9	0.3
Heteropods	0.5	0.1	0.5	0.6	n.s.	<	0.1	—	—	—	—	—	—
Cephalopods	0.6	<	0.7	0.3	n.s.	0.7	0.4	0.1	0.2	n.s.	0.1	0.1	1.2
Amphipods	4.2	0.1	4.0	1.3	n.s.	413.2	80.6	155.0	0.5	0.4*	38.3	18.3	0.5
Mysids	1.4	0.2	0.6	0.6	n.s.	5.0	1.5	5.6	0.7	n.s.	1.5	1.7	1.1
Euphausiids	79.0	27.7	90.5	8.1	n.s.	208.3	4.7	385.8	41.7	1.9*	200.8	563.1	2.8
Euphausiid larvae	—	—	—	—	—	—	—	—	—	—	1651.5	2387.5	1.4
Peneideae	0.4	0.2	0.4	0.1	n.s.	2.1	1.9	2.4	1.2	n.s.	2.8	2.4	0.8
Sergestidae	3.8	0.4	3.1	1.9	n.s.	2.5	0.1	2.5	1.1	n.s.	5.8	2.5	0.4
Caridea	0.8	0.2	0.8	0.9	n.s.	6.4	0.7	13.3	0.8	2.1*	14.6	14.5	1.0
Laomediidae larvae	0.9	1.3	2.2	3.2	n.s.	—	—	—	—	—	—	—	—
Und.crustaceans	0.1	0.2	0.5	0.6	n.s.	0.7	0.4	0.3	0.4	n.s.	—	0.2	—
Chaetognaths	106.7	6.7	118.6	40.3	n.s.	291.5	12.0	412.8	175.5	n.s.	1245.0	694.6	0.6
Salps	0.5	<	0.1	<	0.2*	0.9	0.2	1.1	1.5	n.s.	0.8	0.1	0.2
Pyrosomids	0.3	0.1	0.1	<	0.3*	—	—	—	—	—	—	—	—
Fishes	28.0	2.7	31.0	2.5	n.s.	58.4	0.7	55.4	4.5	n.s.	39.4	39.5	1.0
Total	263.1		262.5			1133.7		1297.9			2471.3	1638.7	

<, lower than 0.05 ind m^{-2}; N/D, ratio night/day; significance of the t-test for day/night difference: *, $P<0.05$; n.s., non-significant at the 0.05 level. Euphausiid larvae are excluded from total numbers.

4075 ind m^{-2} if the numerous euphausiid larvae found at this location were taken into account).

Chaetognaths and euphausiids were numerically dominant at the three sites (respectively 41 and 22% of all sites combined). Their density increased from site O to the other sites: from 107 ind m^{-2} (site O, day), to 1245 ind m^{-2} (site E, day) for chaetognaths, from 79 ind m^{-2} (site O, day), to 563 ind m^{-2} (site E, night) for euphausiids. Fishes and, to a lesser extent, siphonophores were also numerically abundant at the three sites (3.6 and 1.5% of TN) but their densities were of the same order at all sites: mean values of 30–57 ind m^{-2} for fishes, and 14–19 ind m^{-2} for siphonophores. Two other groups were particularly abundant at sites M and E. Pteropods were present in very high densities, 132–244 ind m^{-2} at site M and up to 901 ind m^{-2} (37% of TN) by day at site E, in contrast to site O, where they occurred in low numbers (~ 3 ind m^{-2}). Very large numbers of amphipods were also caught at site M, 155–413 ind m^{-2} (12–36% of TN) and over 91% of which were *Vibilia* sp. Most hyperiid amphipods are parasitoïds of gelatinous zooplankton, and associations of members of the genus *Vibilia* are known only with salps (Laval, 1980). Salps were caught in

small numbers during this period but they occurred in huge swarms 13–15 days before, mainly *Thalia democratica* (Braconnot, personal communication). The high densities of *Vibilia* we recorded might therefore be related to these swarms.

Among the numerically dominant groups, total catches of euphausiids were 2–3 times higher at night than by day, daytime avoidance of nets probably accounting for a large part of this difference as discussed below. Total catches of pteropods, chaetognaths and siphonophores appeared somewhat variable between hauls, with high standard deviations at site M by day for pteropods and at night for chaetognaths. This could be related to spatial heterogeneity or occurrence of swarms.

Fish and siphonophore species

Table 3 gives, for each species, the average number of individuals per square meter from 965 m to the surface and the percentage of each group, recorded by day and at night, marked at the three locations. *Cyclothone* was the most abundant fish genus representing 59% (site O) to 77% (site M) of the fish population, with remarkably similar average day and night total numbers. In a study of the North Atlantic, from 11°N to 60°N along 20°W, Badcock and Merrett (1977) observed that *Cyclothone* contributed 62–70% of the total fish catches. Three species were identified, but we have not separated *C. acclinidens* and *C. microdon*, as organisms were sometimes damaged. Site O was characterized by the dominance of *C. braueri* (87% of the *Cyclothone*), while *C. acclinidens/microdon* largely dominated (79–93%) at sites M and E. *C. braueri* and *C. microdon* are temperate–subtropical species, and *C. acclinidens* is a tropical species. Occurrence of a faunal change in *Cyclothone* around 18°N in the eastern North Atlantic has been suggested by Badcock and Merrett (1977). The dominant species changes observed here are therefore not surprising. *Argyropelecus hemigymnus* was far less abundant, representing 1–10%. *Chelophyes appendiculata*, one of the most common epipelagic siphonophores in the warmer waters of the world's oceans (Roe *et al.*, 1987), represented 12% (site O) to 51% (site M) of the siphonophores. Although its day and night total numbers were not significantly different at sites O and M, they appeared somewhat variable, with a higher value by day at site O and, in contrast, a higher night value at site M. Such differences have also been reported previously: higher numbers at night-time (Pugh, 1974), or in daytime (Andersen *et al.*, 1992; Sardou and Andersen, 1993).

Euphausiid species

Numbers of euphausiids for which no genus could be identified (due to net-induced damage) represented only 1–6% the total number of euphausiids counted at each site (Table 3). The species percentage is based on the total number of organisms per m² found in the 0–965 m water column and identified at the species level (for example *Euphausia* sp. and *Nematoscelis* sp. are not considered).

Twenty-eight species of euphausiids were identified, 24 at the oligotrophic site, 19 at the mesotrophic site and 14 at the eutrophic one. Species diversity tends therefore to decrease from the oligotrophic site to the eutrophic one. Figure 3 shows the day and night percentages of the numerically dominant species recorded at the three sites; for clarity only those species contributing ≥4% by day and/or at night are given. In addition to the decreasing number of species from site O to site E, some species appeared clearly dominant at the mesotrophic and eutrophic sites. At the oligotrophic site, eight species presented

Table 3. Number of individuals per square meter (from 965 m to the surface) and percentage of total group, recorded for the three sites in the daytime and at night for euphausiids, siphonophores, pteropods and fishes

	Species number			Oligotrophic					Mesotrophic					Eutrophic				
				Day		Night		t-test	Day		Night		t-test	Day		Night		
	O	M	E	no. m^{-2}	%	no. m^{-2}	%	(N/D)	no. m^{-2}	%	no. m^{-2}	%	(N/D)	no. m^{-2}	%	no. m^{-2}	%	(N/D)
Euphausiids	24	19	14															
Undetermined				2.4	—	5.6	—	—	1.7	—	15.9	—	—	—	—	—	—	—
Euphausia (total)		+		24.1	32.3	16	19.7		135.8	65.9	171.2	46.4	n.s.	131.2	65.3	359.5	63.8	—
E. americana	+			16.2	21.6	—	—	—	112.7	54.7	162.9	44.1	—	—	—	—	—	—
E. brevis	+			—	—	5.8	7.1	n.s.	—	—	0.3	0.1	—	—	—	—	—	—
E. eximia	+	+		0.3	0.4	0.1	0.1	n.s.	1.6	0.8	3.2	0.9	n.s.	—	—	1	0.2	—
E. gibboides	+	+	+	—	—	0.1	0.2	—	10.7	5.2	0.3	0.1	—	—	—	7.9	1.4	—
E. hanseni		+	+	—	—	—	—		—	—	—	—		—	—	1.2	0.2	2.5
E. hemigibba	+	+	+	7.4	9.9	9.8	12.1	n.s.	1.9	0.9	1.4	0.4	n.s.	0.5	0.2	—	—	—
E. krohni	+	+	+	0.1	0.1	0.3	0.3		8.9	4.3	3.2	0.9	n.s.	130.7	65.1	349.4	62	2.7
E. tenera	+			0.2	0.3	<			—	—	—	—		—	—	—	—	—
Euphausia sp.				0.2		<			—	—	0.1			—	—	—	—	—
Nematobrachion (total)	+	+	+	0.7	0.9	1.2	1.5	—	1.6	0.8	1	0.3		0.8	0.4	0.8	0.1	—
N. boopis	+	+	+	0.2	0.3	0.1	0.1		0.6	0.3	0.1	<		0.5	0.2	0.3	0.1	0.6
N. flexipes	+	+	+	0.4	0.5	0.9	1.1	n.s.	1	0.5	0.9	0.2	n.s.	0.3	0.2	0.5	0.1	1.5
M. sexspinosum	+			0.1	0.1	0.3	0.3		—	—	—	—		—	—	—	—	—
Nematoscelis (total)	+	+	+	15.1	20.2	15.5	19	n.s.	40.5	19.7	117.3	31.7	n.s.	51.1	25.5	173.1	30.7	—
N. atlantica/microps	+	+	+	10.5	14.1	12.2	15	n.s.	9	4.4	3.7	1	n.s.	1.1	0.5	0.9	0.2	0.8
N. megalops	+	+	+	1.3	1.7	0.7	0.9		30.7	14.9	111.9	30.3	*	47.9	23.8	170.5	30.3	3.6
N. tenella	+	+	+	3.3	4.4	2.5	3.1	n.s.	0.8	0.4	1.7	0.5		2.1	1.1	1.7	0.3	0.8
Nematoscelis sp.				1.5		1.9			0.4		0.3			—	—	—	—	—
Stylocheiron (total)	+	+	+	26.1	35	40.1	49.3	n.s.	16.8	8.2	19.6	5.3	n.s.	6.8	3.4	5.3	0.9	—
S. abbreviatum	+	+		3.2	4.3	6.3	7.8	n.s.	0.5	0.2	1.3	0.3	—	—	—	0.5	0.1	—
S. carinatum	+			9.1	12.1	18.6	22.9	2.1*	—	—	—	—		—	—	—	—	—
S. elongatum	+	+	+	1.8	2.4	2.6	3.2	n.s.	7.4	3.6	6	1.6	n.s.	1.5	0.7	2.1	0.4	1.4
S. longicorne/affine	+	+	+	10.8	14.4	11.5	14.1	n.s.	8.1	3.9	11.1	3	n.s.	5.2	2.6	2.1	0.4	0.4
S. maximum	+			0.1	0.1	<	<	—	0.9	0.4	1.3	0.4	n.s.	0.1	<	0.5	0.1	6
S. suhmi	+			1.2	1.6	1.1	1.3	n.s.	—	—	—	—		—	—	—	—	—
Thysanopoda (total)	+	+		8.7	11.6	8.5	10.4	n.s.	1.1	0.6	0.6	0.2	n.s.	—	—	—	—	—
T. aequalis	+	+		8.0	10.7	5	6.2	n.s.	0.4	0.2	0.5	0.1		—	—	—	—	—
T. cornuta	+			—	—	0.1	0.1		—	—	—	—		—	—	—	—	—
T. cristata	+			0.1	0.1	0.1	0.1	n.s.	—	—	—	—		—	—	—	—	—
T. microphthalma	+	+		—	—	0.4	0.5		0.2	0.1	—	—		—	—	—	—	—
T. monacantha	+	+		—	—	—	—		0.6	0.3	—	—		—	—	—	—	—
T. obtusifrons	+			0.2	0.3	2.2	2.7		—	—	0.1	<		—	—	—	—	—
T. tricuspidata	+			0.4	0.5	0.8	1	n.s.	—	—	—	—		—	—	—	—	—

(Continued)

Table 3. Continued

	Species number			Oligotrophic					Mesotrophic					Eutrophic				
	O	M	E	Day		Night		t-test	Day		Night		t-test	Day		Night		
				no. m⁻²	%	no. m⁻²	%	(N/D)	no. m⁻²	%	no. m⁻²	%	(N/D)	no. m⁻²	%	no. m⁻²	%	(N/D)
Thysanopoda sp.	+	+		0.1	—	1.6	—	—	0.2	—	0.2	—	—	—	—	—	—	—
Thysanoëssa sp.		+	+	—	—	—	—	—	10.2	4.9	59.6	16.1	5.8*	10.9	5.4	24.5	4.3	2.2
Siphonophores																		
Chelophyes appendiculata				4.0	12.6	0.6	9.1	n.s.	4.1	36.6	10.6	61.2	n.s.	7.1	35.1	5.2	29.3	0.7
Pteropods	9	6	2															
Undetermined				—	—	0.2	—	—	0.3	—	0.3	—	—	—	—	0.2	—	—
Gymnosomes																		
Cavolinia inflexa	+	+		0.1	1.3	—	—	—	4	3.1	2.7	—	n.s.	—	—	—	—	—
Cavolinia uncinata	+	+		<	1.9	—	—	—	0.1	0.1	—	—	—	—	—	—	—	—
Clio cuspidata	+	+		0.1	—	—	—	—	—	—	0.1	<	—	—	—	—	—	—
Clio pyramidata	+	+	+	0.8	25	1.7	65.3	—	125.1	96.2	229.4	96.1	n.s.	899.5	99.8	282.2	100	0.3
Cuvierina columnella	+			0.8	26	0.3	11.6	n.s.	—	—	—	—	—	—	—	—	—	—
Diacria sp.				—	—	—	—	—	1.3	—	2.6	—	—	—	—	0.5	—	—
Diacria rampeli		+	+	0.1	4.2	—	—	—	0.8	0.6	9	3.8	n.s.	1.5	0.2	—	—	—
Diacria trispinosa	+			0.1	1.6	—	—	—	—	—	—	—	—	—	—	—	—	—
Hyalocylis sp.	+			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Limacina sp.	+			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Styliola subula	+			0.6	18.6	0.4	14.3	—	—	—	—	—	—	—	—	—	—	—
Cymbulia peroni	+			0.7	21.5	0.2	8.9	—	—	—	—	—	—	—	—	—	—	—
Gleba corda		+		—	—	—	—	—	—	—	0.2	0.1	—	—	—	—	—	—
Fishes																		
Argyropelecus hemigymnus				1.8	6.5	1.5	4.9	n.s.	0.6	1	1.6	2.8	n.s.	4	10.1	0.7	1.8	0.2
Cyclothone braueri				14.7	52.4	15.1	48.9	n.s.	3.3	5.6	2.9	5.3	n.s.	6.4	16.2	4.7	12	0.7
C. acclinidens/microdon				2.5	8.9	1.9	6.1	n.s.	44.8	76.8	37	66.7	n.s.	20.5	51.9	22.3	56.4	1.1

+, the occurrence of the euphausiid or thecosome species at a given site, calculation of percentage being based on these species; <, lower than 0.05 ind m⁻² or 0.05%; N/D, ratio night/day; significance of the t-test of day/night difference: *, $P < 0.05$; n.s., non-significant at the 0.05 level.
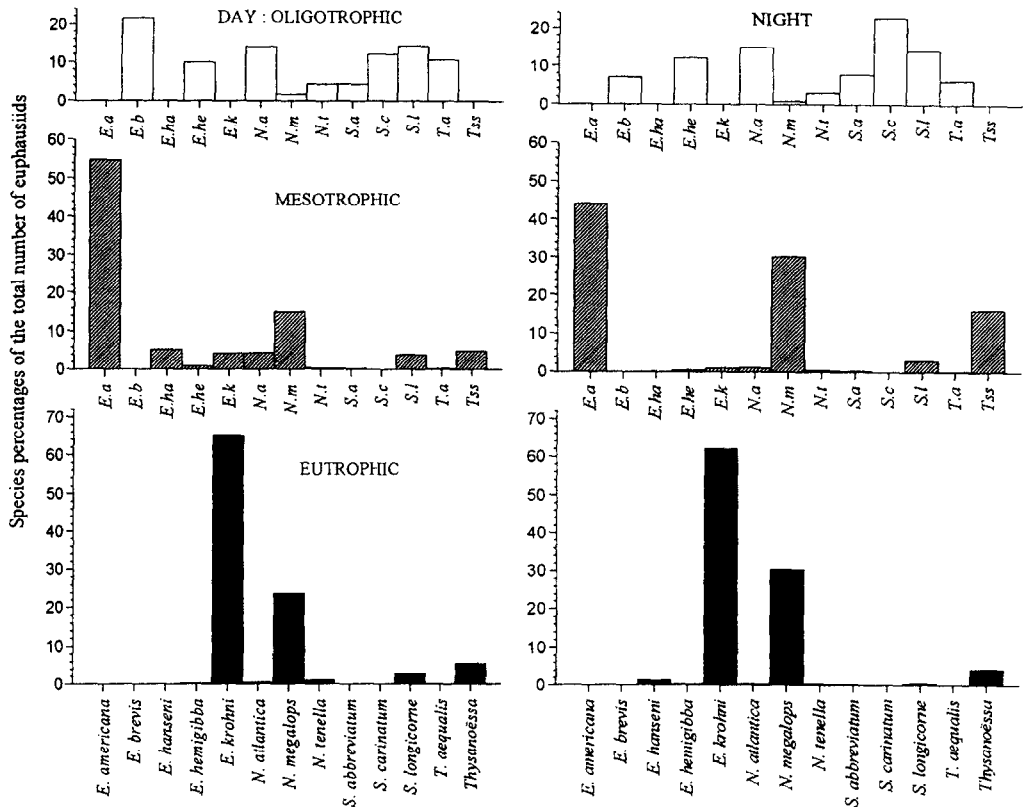
Fig. 3. Numerically dominant euphausiid species expressed as a percentage of the total number of specimens per m² in the 0–965 m water column at the three sites by day and night.

percentages ≥4%, six of them with percentages ≥10%, and a maximum of 22–23% was obtained for *Euphausia brevis* by day and *Stylocheiron carinatum* at night. In contrast, at the mesotrophic and eutrophic sites, dominance of a few species is clear. At site M, *Euphausia americana* represented about half of the euphausiid population (55% by day and 44% at night), followed by *Nematoscelis megalops* (15–30%) and to a lesser extent by *Thysanoëssa* (5–16%); the other species presented percentages lower than ~5%. The dominance of a small number of species was even more clear at the eutrophic site, with *Euphausia krohni* (62–65%), and secondarily *N. megalops* (24–30%) and *Thysanoëssa* (43%); percentages of the few other species were less than 3%.

These results also show that the dominant species differed by site. *Euphausia brevis* and *Stylocheiron carinatum*, relatively abundant at site O, were absent at sites M and E (Table 3). *Euphausia americana*, dominant at site M, was caught only at this site, and *Euphausia krohni*, dominant at site E, occurred in low numbers at the other locations (0–4%). No *Thysanoëssa* was caught at site O, and no *Thysanopoda* at site E.

Among the most abundant species, total numbers collected at night were often higher than during the day (Table 3), up to 2–5.8 times higher for *Euphausi krohni* (site E), *Nematoscelis megalops* (site E), *Stylocheiron carinatum* (site O) and *Thysanoëssa* (sites M and E). Such differences have been observed for these species in various areas of the world's

ocean (Brinton, 1967, 1979; Baker, 1970; Wiebe *et al.*, 1982, 1992; Andersen and Sardou, 1992) and can be related to daytime avoidance of the net for *S. carinatum* and *T. gregaria*, daytime avoidance or horizontal patchiness for *N. megalops*, and swarming for *E. krohni*. According to the literature and the distributions of the organisms as determined in this study (considered below), higher night catches during the present study can be related to net avoidance by day or swarming of the organisms, and not to the migration of the population down below the lowest sampled stratum by day, except for *Thysanoëssa* as we will see later.

Pteropod taxa

Ten species (belonging to seven genera) and two other genera of thecosomes (*Hyalocylis* and *Limacina*) were identified in the catches (Table 3). Gymnosomes, particularly difficult to identify and caught in very low numbers, were considered as a whole. In the thecosome pteropod group, as in the euphausiid one, a decreasing number of taxa was observed from the oligotrophic to the eutrophic sites, with nine, six and two taxa at sites O, M and E, respectively. An increase in dominance of one particular species was also observed at sites M and E, *Clio pyramidata* representing nearly all the pteropod population (96–100%). At the oligotrophic site, *C. pyramidata* dominated but to a lesser extent (25% by day and 65% at night), and four other taxa had percentages between 9 and 25% (*Cuvierina columnella*, *Limacina* sp., *Styliola subula* and *Cymbulia peroni*). In contrast to the euphausiid group, the same pteropod species, *C. pyramidata*, dominated at the three sites. This species appeared to have a heterogeneous spatial distribution and to form swarms, with densities of 4 and 247 ind m^{-2} for the two day hauls at site M. At site E, the number of organisms in the day haul was three times higher than in the night haul.

VERTICAL DISTRIBUTION AND MIGRATION

The average weighted mean depths (WMD) by day and at night, and mean amplitude of the migration are given in Table 4 for the micronekton and macroplankton groups observed, and in Table 5 for the dominant species. Detailed vertical distributions of the most abundant groups and species are presented in Figs 4–7. For clarity, abundance scales sometimes differ for day and night for the same site or between sites.

Siphonophores, chaetognaths and fishes

At night, siphonophores, and among them *Chelophyes appendiculata*, were concentrated in the 0–75 m layer at the three sites (Fig. 4a,b). By day, they were also concentrated in the upper layer at site E. In contrast, at sites O and M, they were found deeper, down to ~350 m; *C. appendiculata* showed maximum abundance in the 250–350 m layer, with a DVM of ~220 m in amplitude (Table 5). The daytime and night-time depths and the DVM we observed at sites O and M are in agreement with those generally reported to occur in the North Atlantic (Pugh, 1974; Roe *et al.*, 1987) or in the Mediterranean Sea (Andersen *et al.*, 1992). In the North Atlantic, however, Casanova (1980) noted that *C. appendiculata* was essentially caught in the top 100 m. At the three sites, chaetognaths were caught from the surface down to 965 m, with higher concentrations in the top 250 m (Fig. 4c). No migration was detected in this group when considered as a whole (Table 4).

Juvenile fish were caught in non-negligible numbers down to 700–850 m (Fig. 4d). They

Table 4. Weighted mean depths, WMD (m), by day and at night, and amplitude of the migration, dz (m), for the major taxonomic groups of macroplankton and micronekton

	Oligotrophic					Mesotrophic					Eutrophic		
	Day WMD X	WMD S.D.	Night WMD X	WMD S.D.	dz	Day WMD X	WMD S.D.	Night WMD X	WMD S.D.	dz	Day WMD	Night WMD	dz
Medusae	150	—	40	—	(110p)	590	25	610	240	no	685	615	70
Siphonophores	170	50	170	50	(200p)	245	15	85	10	160	80	55	25
Ctenophores	—	—	625	—	—	—	—	450	70	—	40	—	—
Annelids	105	15	40	0	65	255	65	610	230	no	—	—	—
Pteropods	405	25	75	10	330	295	50	45	0	250	125	55	70
Heteropods	150	100	40	0	(110p)	300	—	—	—	—	—	—	—
Cephalopods	130	45	110	50	no	680	220	410	—	(270)	200	40	160
Amphipods	130	5	170	75	no	225	25	50	5	175	145	75	70
Mysids	220	210	320	255	no	400	125	385	55	no	730	470	260
Euphausiid larvae	—	—	—	—	—	—	—	—	—	—	175	40	135
Euphausiids	300	35	120	5	180	105	10	150	0	r45	90	75	15
Peneideae	875	45	325	55	550	630	15	545	70	(440p)	580	315	265
Sergestidae juveniles	140	10	60	30	(80)	490	15	475	115	no	490	470	20
Sergestidae adults	630	35	115	10	510	565	85	400	95	(415p)	360	340	40
Caridea	695	210	325	105	(370)	500	110	345	80	(155p)	455	365	90
Laomediidae larvae	40	—	40	—	(no)	—	—	—	—	—	—	—	—
Chaetognaths	225	0	215	20	no	315	5	305	5	no	190	270	r80
Salps	295	150	75	53	(220)	330	95	40	—	(290)	625	40	585
Pyrosomids	480	15	115	0	365	—	—	—	—	—	—	—	—
Fish juveniles	255	30	190	10	no	460	25	255	45	205	345	255	90
Fish adults	570	5	505	30	no	515	15	530	55	no	615	615	0

Values are given to the nearest 5; r, reverse migration; p, part of the population. For oligotrophic and mesotrophic sites, values of dz are given when the day–night differences are significant at the 0.05 level (*t*-test); values in parenthesis when some migration appeared to occur from the profiles (difference between WMDs or depths of maximum abundance); no, no significant migration.

occurred in the upper layers (0–150 m) at night over the three sites and by day at site O, while adults were essentially restricted to deeper layers, 350–965 m, and did not show any DVM (Fig. 4e). *Cyclothone* species have largely been reported as non-migrant (Badcock, 1970, 1984; Roe and Badcock, 1984; Miya and Nemoto, 1991; Andersen and Sardou, 1992), and in the present case the two *Cyclothone* populations showed the same vertical distributions both by day and at night. *Cyclothone braueri* was caught almost exclusively above 700 m, while *C. acclinidens/microdon* occurred in large numbers down to 965 m, the bottom depth of the sampling (Fig. 4g,h). At each site, mean WMDs of the two populations were significantly different by 160–295 m (Table 5). These two *Cyclothone* species were also found to live significantly deeper at site O than at site M. The depth ranges we found for *C. braueri* are in agreement with previous studies, *C. braueri* being reported to be caught essentially between 400 and 700 m (Badcock, 1970; Badcock and Merrett, 1977; Roe and Badcock, 1984; Andersen and Sardou, 1992). The other two species have been reported as deep-living species: deep mesopelagic for *C. acclinidens*, with maximum abundance between 600 and 900 m (Badcock, 1970, 1984; Badcock and Merrett, 1977; Willis and Pearcy, 1982) and deep meso- to bathypelagic for *C. microdon* with an upper distributional limit of 500 m and broad peaks at 500–1000 m depth and below (Badcock and Merrett, 1976, 1977; Roe *et al.*, 1987).

Table 5. Weighted mean depths, WMD (m), by day and at night, and amplitude of the migration, dz (m), for the different species of euphausiids, siphonophores, pteropods and fishes

	Oligotrophic					Mesotrophic					Eutrophic		
	Day WMD X	WMD S.D.	Night WMD X	WMD S.D.	dz	Day WMD X	WMD S.D.	Night WMD X	WMD S.D.	dz	Day WMD	Night WMD	dz
Euphausiids													
E. americana	—	—	----	—	----	45	5	80	10	r35	—	—	---
E. brevis	390	45	55	10	335	—	----	—	---	----	----	----	—
E. eximia	—	—	40	----	—	—	—	40	—	—	—	—	----
E. gibboides	350	70	115	0	235	255	25	55	5	200	—	115	---
E. hanseni	—	---	—	---	—	40	0	40	---	(no)	---	45	—
E. hemigibba	490	25	80	5	410	370	40	230	240	(140)	390	125	265
E. krohni	625	—	—	—	—	170	35	180	200	(160p)	80	40	40
E. tenera	440	—	115	----	(325)	—	---	—	—	—	—	---	---
N. boöpis	560	—	500	—	(60)	475	110	350	—	(125)	415	425	r10
N. flexipes	450	210	165	70	(285)	220	5	270	110	no	200	335	r135
N. sexspinosum	450	—	255	205	(190p)	—	—	—	—	—	—	—	—
N. atlantica/microps													
0–965 m						435	20	375	15	(60)	280	365	r85
0–450 m	40	0	170	55	—								
450–965 m	530	0	605	30	360*								
N. megalops	300	---	140	—	(160)	60	10	140	20	r80	55	115	r60
N. tenella	440	35	185	10	255	465	40	345	70	(120)	445	510	r65
S. abbreviatum	165	10	140	10	no	110	85	200	105	(r90)	—	115	—
S. carinatum	45	5	45	5	no	—	---	—	—	---	----	---	—
S. elongatum	330	0	275	65	(55)	205	5	185	20	no	215	210	5
S. longicorne/affine	190	10	195	20	no	195	10	200	5	no	215	180	35
S. maximum	500	—	625	—	(r125)	420	25	345	35	no	500	525	r25
S. suhmi	115	5	115	15	no	—	—	—	—	—	—	---	----
T. aequalis	530	5	100	20	430	400	0	180	30	220	—	----	---
T. cornuta	---	—	400	—	---	—	—	—	—	—	—	—	—
T. cristata	300	—	115	—	(185)	—	---	----	---	—	—	—	—
T. microphthalma	—	---	200	0	—	400	0	—	—	—	---	----	—
T. monacantha	—	---	----	---	—	535	190	40	0	(495)	—	—	—
T. obtusifrons	625	—	155	60	(470)	—	—	—	—	—	—	—	—
T. tricuspidata	335	235	70	5	(265p)	—	—	—	---	—	—	----	—
Thysanoëssa sp.	—	—	—	—	—								
0–350 m	—	—	—	---	---	45	5	180	35	r135	50	85	r35
350–965 m	—	—	----	---	—	545	60	665	40	365*	815	895	no*
Siphonophores													
C. appendiculata	275	5	50	—	(225)	255	20	40	5	215	40	40	0
Pteropods													
Gymnosomes	175	—	—	---	—	560	95	235	235	(325)	—	—	—
Cavolinia inflexa	300	—	—	—	—	200	—	—	—	—	—	---	—
Cavolinia uncinata	115	—	—	—	--	240	---	—	—	—	—	—	—
Clio cuspidata	—	---	----	---	—	—	—	40	—	—	---	---	---

(Continued)

Table 5.   Continued

	Oligotrophic					Mesotrophic					Eutrophic		
	Day WMD X	WMD S.D.	Night X	WMD S.D.	dz	Day WMD X	WMD S.D.	Night X	WMD S.D.	dz	Day WMD	Night WMD	dz
Clio pyramidata	530	40	65	—	(465)	345	115	40	0	(305)	125	55	70
Cuvierina columnella	400	0	110	5	290	—	—	—	—	—	—	—	—
Diacria sp.	—	—	—	—	—	40	—	225	145	(r185)	—	115	—
Diacria rampeli	—	—	—	—	—	120	115	155	60	no	40	—	—
Diacria trispinosa	400	—	—	—	—	—	—	—	—	—	—	—	—
Hyalocylis sp.	500	—	—	—	—	—	—	—	—	—	—	—	—
Limacina sp.	—	—	75	55	—	—	—	—	—	—	—	—	—
Styliola subula	480	75	115	—	(365)	—	—	—	—	—	—	—	—
Cymbulia peroni	300	0	—	—	—	—	—	—	—	—	—	—	—
Gleba corda	—	—	—	—	—	—	—	160	—	—	—	—	—
Fishes													
A. hemigymnus	480	30	450	60	no	340	30	300	15	(40)	205	240	r35
Cyclothone braueri	535	5	540	5	no	375	5	370	10	no	465	475	r10
C. acclinidens/ microdon	855	10	810	45	no	510	5	550	65	no	690	695	r5

Values are given to the nearest 5; r, reverse migration; p, part of the population. For oligotrophic and mesotrophic sites, values of dz are given when the day–night differences are significant at the 0.05 level (*t*-test); values in parentheses denotes cases when some migration appeared to occur from the profiles (difference between WMDs or depths of maximum abundance); no, no significant migration; *, calculated from the deeper day WMD and the shallower night WMD.

We found similar results at site O and, to a lesser extent, at site E. However, at site M, large numbers of organisms were caught up to the 350–450 m layer. Part of this difference could be related to the size of the organisms, about 20% being juveniles in this layer, as a size–depth relationship is known to occur in *Cyclothone* (Badcock and Merrett, 1976; Badcock, 1984). As discussed below, other groups or species tended to live higher in the water column at site M compared to site O.

The fish *Argyropelecus hemigymnus* did not show any clear diel movement in the water column, although it occurred higher in the water column at night than by day at site M (Fig. 4f); its WMDs tended to decrease from site O (450–480 m) to site M (300–340 m) and E (205–240 m). Occurrence of a consistent migratory behavior in *A. hemigymnus* is not clear. This species has been reported as non-migrant (Roe and Badcock, 1984), but also to present some migratory activity (Badcock and Merrett, 1976) or to perform clear DVM with an amplitude of 150–200 m (Badcock, 1970; Andersen and Sardou, 1992).

Amphipods, mysids and crustacean decapods

At site O, amphipods were caught essentially in the 0–250 m water column both by day and at night (Fig. 5a). In contrast, at sites M and E they performed DVM with an amplitude of 175 and 70 m, respectively (Table 4). These differences between the three sites are related to the occurrence of different species. In fact, *Vibilia* sp. represented 71–91% of the
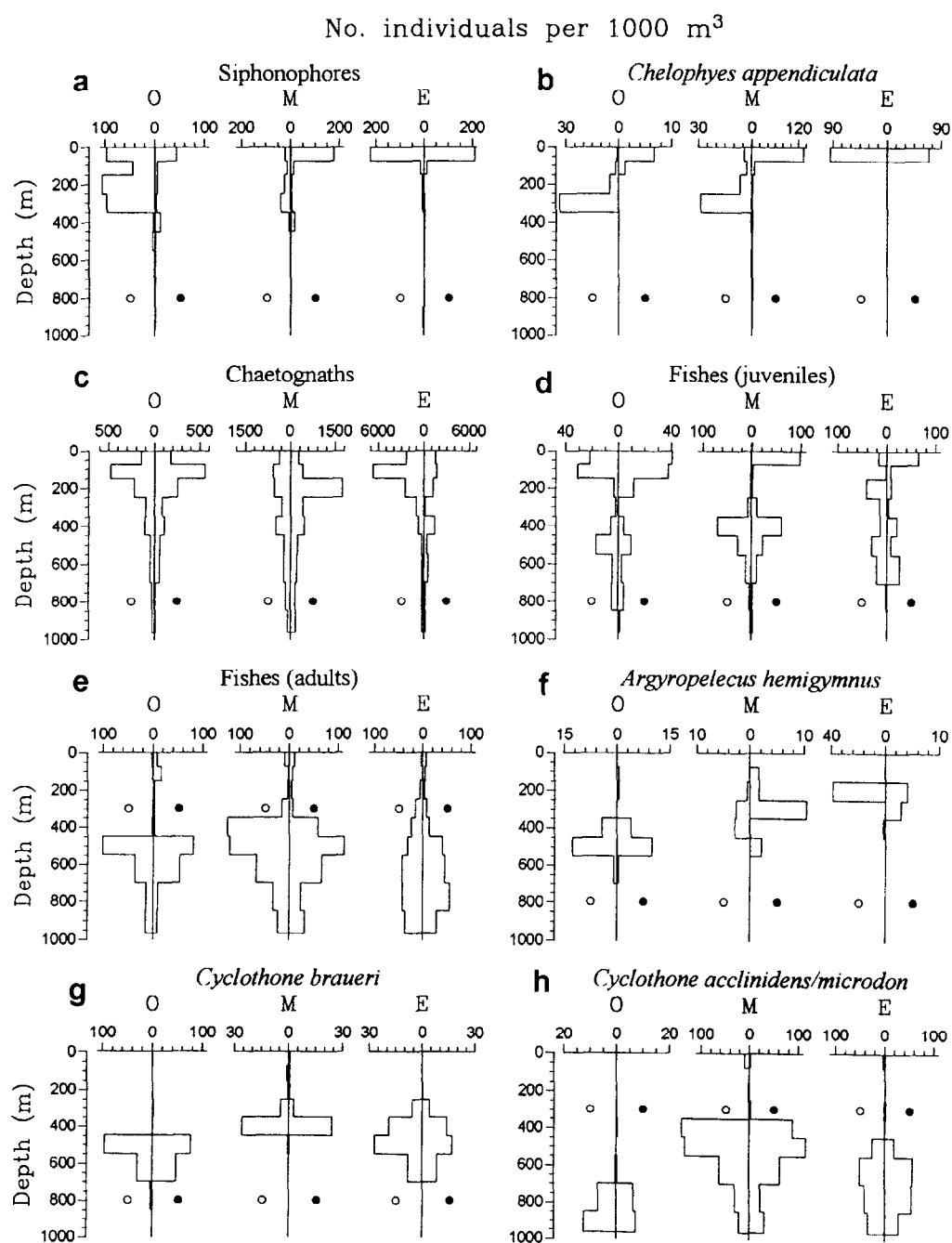
No. individuals per 1000 m^3

a Siphonophores

b *Chelophyes appendiculata*

c Chaetognaths

d Fishes (juveniles)

e Fishes (adults)

f *Argyropelecus hemigymnus*

g *Cyclothone braueri*

h *Cyclothone acclinidens/microdon*

Fig. 4. Siphonophores (a, b), chaetognaths (c) and fishes (d–h): vertical distributions of the total populations and of some numerically dominant species at midday (○) and midnight (●) at the three sampling sites (O, M and E).
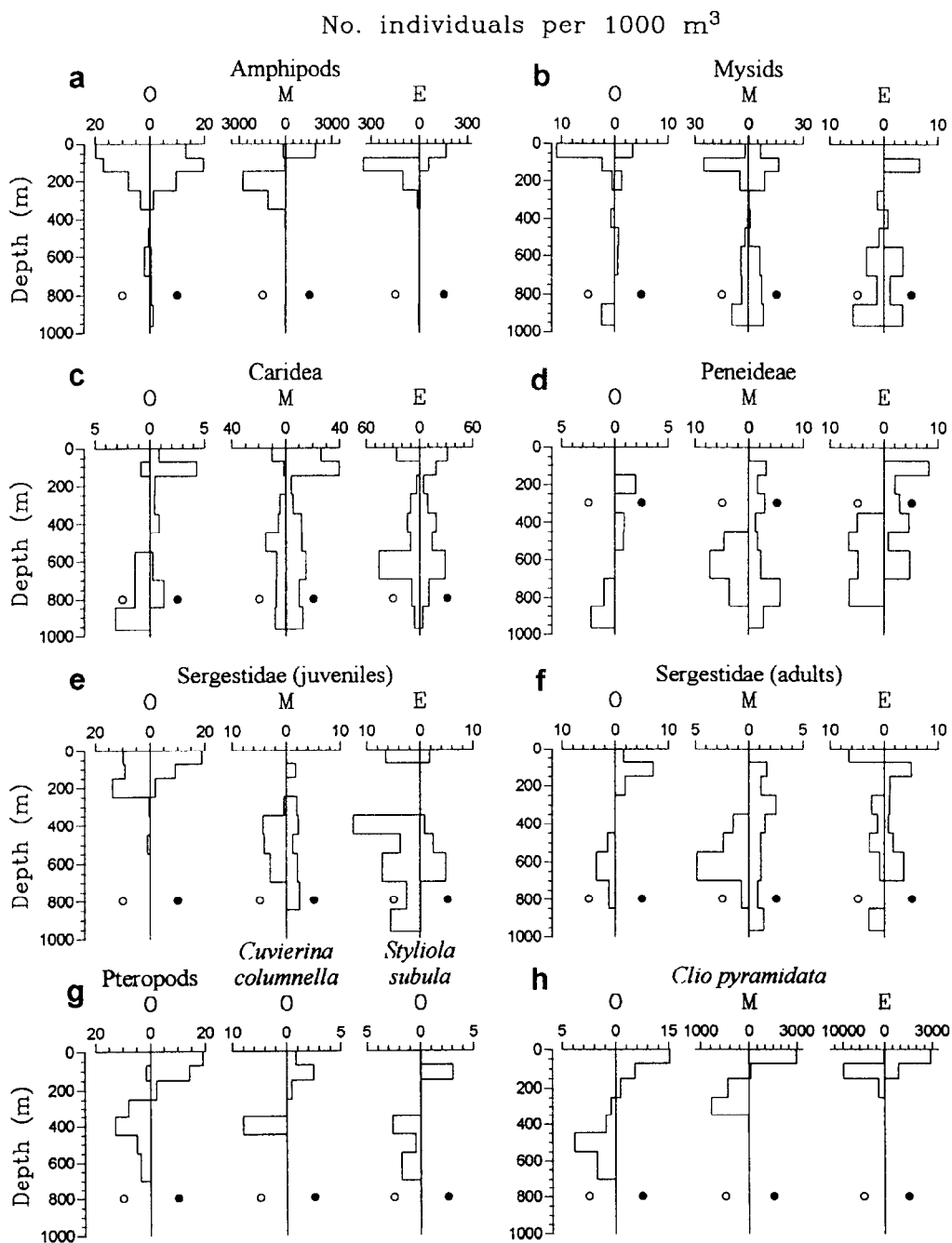
No. individuals per 1000 m³

Fig. 5. Amphipods (a), mysids (b), crustacean decapods (c–f) and pteropods (g, h): vertical distributions of the total populations and of the numerically dominant pteropod species at midday (○) and midnight (●) at the three sampling sites (O, M and E). Note the different abundance scales at midday and midnight for *Clio pyramidata*.

No. individuals per 1000 m^3
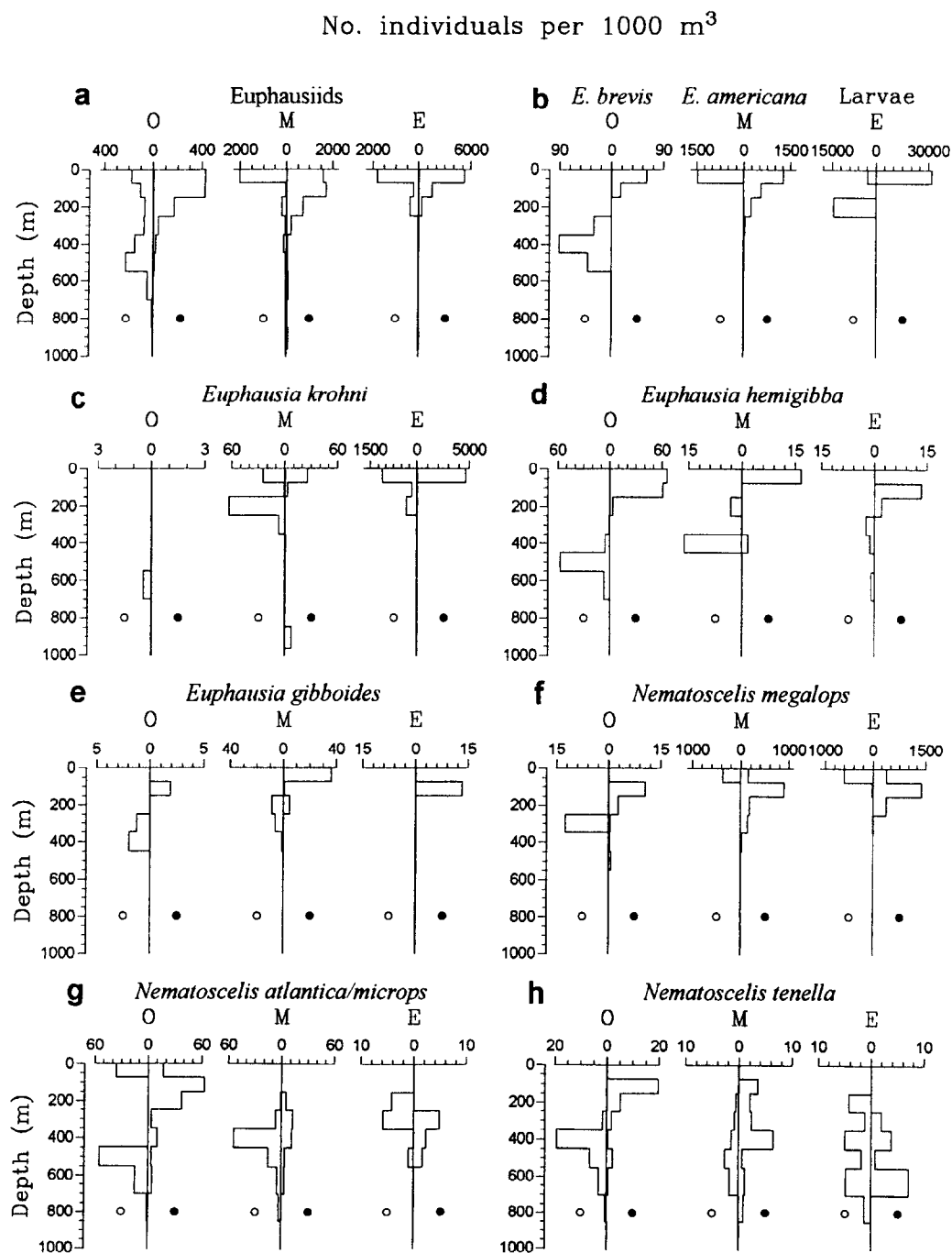
Fig. 6. Euphausiids: vertical distributions of the total population (a) and of the numerically dominant species of *Euphasia* (b–e) and *Nematoscelis* (f–h) at midday (○) and midnight (●) at the three sampling sites (O, M and E). Note the different abundance scales at midday and midnight for euphausiids (total), larvae, *E. krohni* and *N. megalops* at site E.

No. individuals per 1000 m³

Fig. 7. Euphausiids: vertical distributions of *Stylocheiron* species (a–e) and of *Nematobrachion* (f), *Thysanopoda* (g) and *Thysanoëssa* (h) genus at midday (○) and midnight (●) at the three sampling sites (O, M and E). Note the different abundance scales at midday and midnight for *Thysanöessa* at site M.
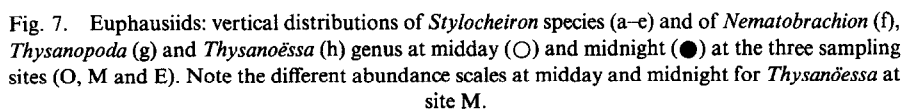
amphipod population at sites M and E and is known to undergo extensive migrations in excess of 400 m (Laval, 1974; Thurston, 1976; Roe *et al.*, 1984). The various genera caught at site O, such as *Phronima*, *Phrosina* and *Primno*, have been reported as epipelagic organisms, occurring in the upper 200 m, where some species perform weak DVM (Thurston, 1976; Roe *et al.*, 1987).

Except for euphausiids and amphipods, we did not identify the different species or genera of crustaceans; their vertical distributions therefore reflect populations composed of organisms that probably showed different behavior. Mysids appeared widely distributed throughout the water column both by day and at night (Fig. 5b), with a high standard deviation of WMD, particularly at site O (Table 4). Two parts could be distinguished, a shallower one in the 0–150 m stratum and a deeper one below 450–550 m.

Vertical profiles of Caridea tend to show that these organisms (or some of them) underwent large DVM (Fig. 4c): higher numbers were caught in the 0–150 m layer by night, and at site O part of the population performed a DVM of ∼370 m in amplitude. By day Caridea appeared to live higher in the water column at sites M and E compared to site O. Adult Sergestidae underwent a large and compact DVM with an amplitude of 510 m at site O (Fig. 4f, Table 4); at site M part of the population appeared to migrate over a distance of at least 275 m. Peneideae were large migrators at the three sites (Fig. 4d): at site O, they migrated as a compact unit with a migration amplitude of 550 m and at sites M and E part of the population migrated over distances of about 375 and 265 m, respectively. Peneideae tended therefore to live higher in the water column from site O to site E, with significantly different day WMDs at sites O and M (Table 4).

Pteropod taxa

DVM of *Clio pyramidata*, the most abundant pteropod species and almost the only one at sites M and E, was very clear at the three sites (Fig. 5h). By day it was abundant below 450 m at site O and at shallower depths at site M (150–350 m) and O (75–150 m), and at night organisms were essentially concentrated in the 0–75 m layer. Therefore, the mean migration amplitude of *C. pyramidata* decreased from site O to site E (from 465 to 305 and 70 m, Table 5), due to shallower daytime depths. Behavior of *C. pyramidata* at the eutrophic site differs from what has previously been observed in various areas. Generally this species has been observed below 250–300 m by day and concentrated in the top 100 m at night, performing an extensive DVM of 200–500 m in amplitude (Rampal, 1967; Spoel, 1973; Casanova, 1980; Wormuth, 1981; Roe *et al.*, 1987; Sardou and Andersen, 1993). The two other relatively abundant species at site O, caught by day and at night, *Cuvierina columnella* and *Styliola subula*, also performed DVM with mean amplitudes of 290 and 365 m, respectively (Fig. 5g), in agreement with the previous observations of Casanova (1980), Wormuth (1981) and Roe *et al.* (1987) in the North Atlantic. At site M, the second most abundant species (∼3% only), caught by day and at night, *Diacria rampeli*, showed no significant migration (Table 5). Depths of occurrence of the other taxa, occasionally caught by day or at night, agree with literature data: the migrant species *Cavolinia inflexa*, *Diacria trispinosa* and *Cymbulia peroni* were caught between 150 and 450 m by day, and *Clio cuspidate* and *Limacina* sp. were caught in the top 100 m at night.

Euphausiid group and Euphausia *species*

Euphausiids were essentially caught in the upper layers (0–150 m) at sites M and E both by day and at night (Fig. 6a). In contrast, at site O, they were caught down to 700 m by day and a large part of the population performed an extensive DVM. This heterogeneous daytime distribution is associated with different species as shown in detail below.

Euphausiids of the genus *Euphausia* were the most abundant at sites M and E and among the most abundant at site O. At site O, *Euphausia* species constituted most of the deep maximum (350–550 m) of the euphausiid population, with *E. brevis*, *E. hemigibba* and, to a far lesser extent, *E. gibboides* and *E. tenera*, performing DVM with a mean amplitude of 235–410 m (Fig. 6b,d–f and Table 5). In contrast, the largely numerically dominant *Euphausia* species at site M (*E. americana*, Fig. 6b) and at site E (*E. krohni*, Fig. 6c) did not appear to undergo DVM. If they did, it would concern a small part of the population and would be of small amplitude (35 m for the reverse migration of *E. americana* and ∼ 100 m for the normal migration of *E. krohni*). The other much less abundant species at sites M and E showed no DVM or a reduced one of 140–265 m in amplitude, often involving only part of the population. The numerous euphausiid larvae, probably larvae of *E. krohni*, migrated generally at night from 150–250 m to 0–75 m (Fig. 6b).

From site O to sites M and E, there was therefore a trend towards the disappearance of DVM in the *Euphausia* population and a decrease in the amplitude of migration of a given species (e.g. *E. hemigibba*). All these species have been reported as extensive migrators with the lowest migration amplitude (about 200 m) for *E. gibboides* and up to 500 m for the others (see the review by Mauchline, 1980; Roe *et al.*, 1984; Hargreaves, 1985; Sameoto *et al.*, 1987; Hargreaves and James, 1989; Andersen and Sardou, 1992; Wiebe *et al.*, 1992). *Euphausia krohni* and *E. americana*, in particular, have been observed to perform migrations of 200–400 m and 330–500 m, respectively. The behavior of these species at sites M and E was therefore unusual.

Nematoscelis *species*

The small number of *Nematoscelis megalops* caught at site O seemed to undergo a normal migration of 160 m, while, at sites M and E, where they were very abundant, they showed a slight reverse migration of 60–80 m in amplitude (Fig. 6f and Table 5). *Nematoscelis atlantica/microps*, the most abundant *Nematoscelis* species at site O, presented a bimodal distribution at day: an upper peak in the 0–75 m stratum and a deeper one below 450 m, this part of the population performing a large DVM with an amplitude of 360 m (Fig. 6g). This pattern was observed for the two day and the two night hauls. In contrast, at sites M and E, no clear DVM was found for this species. *Nematoscelis tenella* was also found as a clear and extensive migrator at site O and a weak or non migrator at the two other sites (Fig. 6h). As for the *Euphausia* species, the migratory behavior of a given *Nematoscelis* species appears to change according to the site. The extensive migrations observed at site O agree with those generally reported (review by Mauchline, 1980; Hargreaves, 1985; Sameoto *et al.*, 1987; Hargreaves and James, 1989; Andersen and Sardou, 1992; Wiebe *et al.*, 1992; Sardou and Andersen, 1993), as does the incomplete migration of populations of *N. megalops* and *N. microns*.

Stylocheiron *species*

These species were, in general, non-migrant at the three sites (Fig. 7a–e and Table 5). At site O there was a marked tendency towards the vertical segregation of these species, with, in order of increasing depth, *S. carinatum* (45 ± 5 m), *S. suhmi* (115 ± 10 m), *S. abbreviatum* (150 ± 15 m) and *S. longicorne/affine* (190 ± 15 m), and then *S. elongatum* (305 ± 50 m). Among these five species, only *S. longicorne/affine* and *S. abbreviatum* did not show significantly different WMDs. *Stylocheiron maximum* was caught deeper, below 450 m, in very low numbers, and only once at night and once by day. At site M, *S. elongatum* occurred at significantly shallower depths (195 ± 15 m) than at site O (305 ± 50 m). Therefore habitat-partitioning was reduced compared to site O: (i) *S. longicorne/affine*, *S. elongatum* and *S. abbreviatum* at similar upper depths, and (ii) *S. maximum* living significantly deeper. These *Stylocheiron* species have generally been reported as non-migrant (review by Mauchline, 1980; Sameoto *et al.*, 1987; Hargreaves and James, 1989; Wiebe *et al.*, 1992), with a possibility of short migration being occasionally noted for *S. carinatum*, *S. elongatum* and *S. maximum*. In the present study, *S. carinatum* appeared as a non-migrant, but the upper stratum sampled, 0–75 m, would be too thick to detect very short migration; at site O, part of the *S. elongatum* population appeared to have migrated slightly. The habitat-partitioning of the different *Stylocheiron* species had been clearly identified at site O, and this confirms previous observations, more or less detailed, areas of high population density being reported as mutually exclusive for different species (Brinton, 1967, 1979; Baker, 1970; Youngbluth, 1976; Griffiths, 1979; Hargreaves and James, 1989; Wiebe *et al.*, 1992).

Nematobrachion, Thysanopoda *and* Thysanoëssa *genera*

As very few *Nematobrachion* were caught, evidence of DVM was difficult to judge (Table 5). From the profiles of the three species pooled (Fig. 7f), it seems that these organisms performed a migration of 200 m or more at site O, being caught below 250 m by day and concentrated in the 75–250 m layer at night. These species are generally scarce, and previous reports on their migrating behavior vary widely (Brinton, 1967, 1979; Baker, 1970; Longhurst, 1976; Youngbluth, 1976; Hu, 1978; Mauchline, 1980; Roe *et al.*, 1984; Hargreaves, 1985; Sameoto *et al.*, 1987; Hargreaves and James, 1989). *Nematobrachion flexipes* is generally shown to perform migrations of amplitude 100–275 m although reported as non-migrant by Baker (1970). *Nematobrachion böopis* and *N. sexspinosum* have been reported as non-migrant, weak or large migrants.

DVM with an amplitude of 200–500 m occurred in all the five *Thysanopoda* species caught both by day and at night at sites O and M (Fig. 7g and Table 5), which is in agreement with previous studies reporting these species, except *T. cristata*, as extensive migrants (Mauchline, 1980; Hargreaves and James, 1989; Andersen *et al.*, 1992; Wiebe *et al.*, 1992). The dominant *Thysanopoda* species, *T. aequalis*, showed a decrease in its migration amplitude from site O to site M, 430 and 220 m, respectively, as has been noted above for other migrating euphausiid species.

At site E, *Thysanoëssa* appeared distinctly distributed in two different populations, one in the 0–250 m layer and the other below 700 m, neither of the populations showing DVM (Fig. 7h). As individuals were damaged we did not differentiate between *T. gregaria* and *T. parva*. Previous studies showed that *T. parva* lived below 500 m and *T. gregaria* higher in the water column, most often in the upper 200 m (Mauchline, 1980; Hargreaves and James,

1989; Barange, 1990). Therefore at site E, the upper peak might correspond to *T. gregaria* and the deeper one to *T. parva*. As we saw before, night total numbers were more than two times higher than day concentrations, in both the 0–350 and 350–965 m layers. This pattern could be related to (i) daytime avoidance of net by *T. gregaria* in the upper layers and (ii) migration of *T. parva* from depths below the lowest stratum sampled (850–965 m). At site M, vertical segregation of the two species was not so clear, although each daytime and night-time distribution presented two maxima, separated by the 250–350 m layer. These results suggest various behaviors (Table 5): (i) reverse migration of 135 m as mean amplitude by the organisms of the upper day peak, (ii) normal migration on a mean distance of 365 m by part of the deep day population and (iii) migration of organisms living by day below 965 m as the mean total number of individuals was ∼6 times higher at night than by day (again with daytime avoidance of net by *T. gregaria*). In a neighboring area of site M, 18°N–25°W, Hargreaves and James (1989) reported migration of *T. gregaria* from 410–500 m by day to 110–200 m at night, which agreed well with one of the behaviors we observed. On the other hand, in his review, Mauchline (1980) did not provide a definite conclusion on the occurrence of a regular DVM in *T. gregaria*. Observations of populations of this species occurring in the upper 200 m have not described migrations, or described a reversed one, as observed here (Brinton, 1967, 1979; Youngbluth, 1976; Griffiths, 1979; Barange, 1990).

DISCUSSION

Species diversity

Since euphausiids and pteropods were mainly determined to species level, the species composition at each of the three sites could be compared. The number of species encountered decreased from the oligotrophic to the eutrophic site (cf. Table 3). The distribution of individuals within the species present was also more even at site O than at site E. Several species contributed equally at site O, whereas site E was characterized by a few largely dominant species, the other species showing low (<2%) percentage numbers.

Species number and distribution of individuals within species (regularity) are key features of the diversity of an ecosystem (Frontier and Pichod-Viale, 1993). This can be illustrated by rank-frequency diagrams and the associated diversity indices, which we computed for two sets of data: euphausiids and euphausiids and pteropods combined (Fig. 8). Indices ranged from 1.0 (eutrophic site) to 3.5 bits (oligotrophic site). Species diversity at the oligotrophic site was high considering that an index of 4.5 bits is a maximum normally found in natural systems (Frontier and Pichod-Viale, 1993). There was only a slight difference between day and night indices except for the euphausiid–pteropod group at site E. This difference was due to the abundance of *Clio pyramidata*, which showed great variation between day and night samples (Table 3). The difference between the sites is confirmed by the shape of the curve of the rank-frequency diagrams. Both the day and night diagrams of the oligotrophic site showed a fairly high number of similar relative frequencies of individuals in the top ranks, thus indicating high regularity. This convex shape is much less marked at site E. The regularity is low with over 99% of all individuals distributed within less than five species.

Frontier (1976) used rank–frequency diagrams to describe ecological succession in a newly populated habitat. In the beginning, the community is characterized by dominant pioneer species capable of rapidly invading a new space or a given space under new environmental conditions. The rank–frequency diagrams of such a juvenile community are
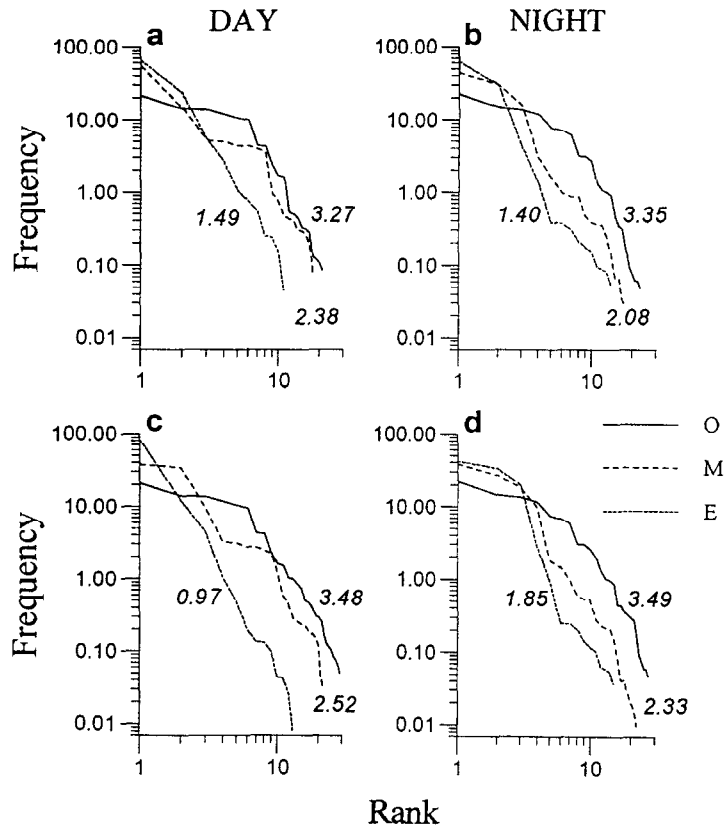
Fig. 8.   Rank–frequency diagrams for euphausiid population (a, b) and for combined euphausiid and pteropod populations (c, d) at the three sites by day and at night. For each curve, the diversity index is plotted.

concave in their upper left part and represent the dominance of only a few species. After an inflection, the lower right part of the curve becomes convex due to the low number of rare species. As the ecosystem matures, it shows a progressive modification with new species and niches occurring. The convex shape of the rank–frequency diagrams extends towards the upper left and the whole curve becomes convex as a consequence of high regularity. Such a curve represents a stable and resilient community with a high diversity index.

Our results do not refer to the development in time of a community at a given site, but rather refer to three different sites with communities ranging from a juvenile to a mature stage. In fact, the three sites were selected as being typical of the three trophic regimes, eutrophic, mesotrophic and oligotrophic. Throughout the whole year, climatic conditions at all sites are similar, but the sites differ strongly in phytoplankton abundance; the periphery of the North Atlantic gyre (site O) always shows low standing stocks while in the Mauritanian upwelling area (site E) standing stock is always high (Morel, 1996). As Frontier and Pichod-Viale (1993) stated, the juvenile stage of an upwelling system is maintained by a constant nutrient input leading to high phytoplankton standing stock at almost any given time.

We did not obtain a clear concave curve of a juvenile community at site E, but compared to site O, there was a strong dominance of three to four species, which led to a rapid drop on

the left side of the rank–frequency diagrams and to a low diversity index (cf. Fig. 8). The community structure of the upwelling system relies on external control by physical forces and on interactions between a few dominant species. Such a system is generally unstable due to the lack of internal control mechanisms (Frontier and Pichod-Viale, 1993). El Niño events are striking examples of such instability. Longhurst (1967) discussed the contrast between the low diversity of the upwelling community of the California Current and the offshore communities situated in Central Pacific and Tropical Surface Water, which were marked by high diversity. He related this contrast to external forces being generally absent in permanently stratified waters of low latitude areas, but present in upwelling regions of the same areas, and compared this latter event with the autumnal breakdown of the thermocline in high latitude areas, where plankton generally shows low diversity. He concluded that the relative stability of energy input from the environment into the biological system determines the degree of diversity. The low diversity coupled with upwelling conditions at site E confirms this theory, as do the convex shape of the rank–frequency diagrams and the high diversity index at site O, typically oligotrophic. The constantly very low phytoplankton standing stock indicates the absence of nutrient input. The energy in this system is mostly recycled, and high diversity suggests a great number of possible trophic links with internal control mechanisms. The system has matured; it depends on internal forces and is characterized by great stability (Frontier and Pichod-Viale, 1993).

A step-like shape of the curve was found at the mesotrophic site (cf. Fig. 8). It can be attributed to the superposition of several sub-communities or to a bias due to mixing of night and day samples (Frontier, 1985). We have treated separately the euphausiid and the euphausiid–pteropod community, as well as the day and night samples. As all the diagrams of site M show steps, we may exclude both cases and explain our results by the third theory invoked by Frontier (1985), which relates the steps to a transitory stage of a system with strong fluctuations in the abundance and specific composition of the community. We believe that this is the case at the mesotrophic site. The transitory characteristics of this site apply not only to biological but also to physical properties. During the study period, the site is normally exposed to the merging of the Canary Current and a southern current carrying South Atlantic Central Water (SACW), the latter being quite variable in time and space (Mittelstaedt, 1991; Fiekas et al., 1992). Van Camp et al. (1991) reported a "giant filament" of relatively high chlorophyll-like pigment concentration spreading offshore somewhat north of site M. Bricaud et al. (1987) mentioned the seasonal variations of such structures, which were confirmed in a more detailed manner by Berthon (1992). The site is also exposed to the highly variable Cape Verde Frontal Zone (CVFZ) separating SACW and Northern Atlantic Central Water (NACW) (Zenk et al., 1991). Considering these physical and biological aspects, the mesotrophic site can be characterized not as a site of intermediate (meso) trophic status but rather as a site fluctuating between oligotrophy and eutrophy.

It is therefore not surprising to encounter a quite peculiar community structure of the macroplankton and also to find the only presence of Euphausia americana at this site. This would mean that this species is related to the nutrient rich and poorly oxygenated SACW (Zenk et al., 1991). It does not cross the CVFZ to reach site E, nor does it appear at site O, as it is not well adapted to oligotrophic conditions. Similar features of habitat separation have also been reported for euphausiids by Hargreaves and James (1989) and for fish by Badcock and Merrett (1977) and Zelck (1993).

Vertical distributions and migrations

Overall vertical distribution of most of the species reported here has been established previously. The present work precisely describes their day and night distributions together with migrating behavior in sites of different trophic state. We also complete previous information on pteropods, which is far less abundant than on euphausiids. It was of particular interest to observe that diel vertical migration was reduced at eutrophic and mesotrophic sites compared to the oligotrophic site. This was reflected in a decrease in the migration amplitude of a given species (e.g. the pteropod *Clio pyramidata*) or the absence of migrant behavior in species largely reported as extensive migrants in the literature (e.g. the euphausiids *Euphausia americana* and *Euphausia krohni*). This behavioral change could be related to characteristics of the environment, such as dissolved oxygen concentration, temperature, phytoplankton concentration or depth of the euphotic layer.

In contrast to site O, sites M and E presented a clear O_2-deficient layer below 250 m, with a minimum concentration of 1.2–1.6 ml l^{-1} (cf. Fig. 2). This layer could have acted as a barrier to the vertical distribution of most of the euphausiid species. In fact, at sites M and E, the most abundant euphausiid species (*E. krohni*, *E. americana*, *Nematoscelis megalops*) were restricted to the upper 250 m (and highly concentrated in the upper 75 m) both by day and at night, while at site O, by day, euphausiids (except the non-migrant *Stylocheiron*) were caught in abundance below 350 m. In the eastern tropical Pacific, where O_2-deficiency is more extreme than in the present study, Sameoto *et al.* (1987) observed that the O_2 minimum layer appeared to act as a barrier to the vertical distribution of all euphausiid species. Brinton (1979) reported *Thysanoëssa gregaria* to disappear where O_2-deficiency was < 1.0 ml l^{-1} within its vertical range. The thermocline has also been reported as a distribution boundary for several species (Youngbluth, 1976). In the present study, the slope of the thermocline appeared relatively weak (cf. Fig. 2) and our sampling strata were too thick to relate vertical distribution of the organisms and depth of the thermocline. However, as temperature was sensibly higher at the oligotrophic site, by $\sim 5°C$ compared to site E and by 2–4°C compared to site M in the 0–150 m water column, we can hypothesize that at site O organisms lowered their energy expenditure by reduced activity in deep cooler waters during the day.

The three sites differed also and mainly in their chlorophyll content and consequently in euphotic layer depth. The oligotrophic site was characterized by a deep peak of low value (cf. Fig. 2) and a euphotic layer depth of ~ 105 m, while the euphotic zone was reduced to 27 and 20–25 m at sites M and E, respectively (Morel *et al.*, 1996), due to their high chlorophyll concentration in the upper 30 m. According to the review by Forward (1988) on DVM, light is generally agreed to be the most significant external factor influencing migration. If we consider the Preferendum Hypothesis, the change in daytime depth of a species between the three sites would be related to the depths of its preferential isolume. To test this we considered the light irradiance at the top of the maximum abundance layer of the different migrant species at the three sites (e.g. at 75, 150 and 450 m at sites E, M and O, respectively for *Clio pyramidata;* cf. Fig. 5h). Morel *et al.* (1996) measured irradiance down to ~ 40 m at sites E and M and down to ~ 130 m at site O. We performed extrapolations to calculate irradiance at the greater depths inhabited by the organisms, irradiance at the surface being equal to 500 W m^{-2}: (i) the attenuation coefficient has been considered to be constant below 100 m for the three sites, and equal to the minimum value calculated by Morel *et al.* (1996) at site O (0.027 m^{-1}); (ii) at sites M and E, attenuation coefficients have been linearly
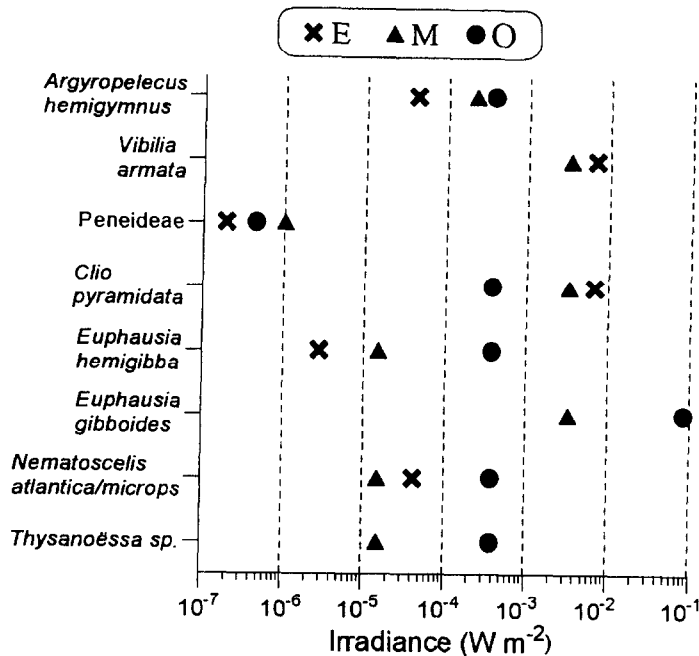
Fig. 9.   Irradiance at midday at the top of the maximum abundance layer for different migrant species at the three sites.

extrapolated between the deepest measurement and 100 m. Figure 9 presents such calculated values of light for different migrant species (or groups) for which some relationship appears between depth of occurrence of the organisms and light intensity. The calculated light range is the smallest for Peneideae, $\sim 2 \times 10^{-7}$ W m^{-2} (site E) to $\sim 1 \times 10^{-6}$ W m^{-2} (site M); for six species, such as *Argyropelecus hemigymnus* and *Clio pyramidata*, this range did not encompass two orders of magnitude. Although these calculations are rough, light could be considered as a factor influencing the daytime depth and consequently the amplitude of the migration of some of the present species.

Such a phenomenon has been reported in various studies. For example, Isaacs *et al.* (1974) observed that the depth of the Deep Scattering Layers increased with the surface water transparency, and they proposed that "In areas of low standing crops of phytoplankton, daylight penetrates further into the ocean causing the migrating animals to descend deeper. In the turbid water associated with high standing crop, the migrating forms remain closer to the surface." Youngbluth (1976) observed such a phenomenon in one euphausiid species in the central region of the California Current: DVM of the *Euphausia pacifica* population tended to be more pronounced in the clearer oligotrophic offshore waters than in the coastal turbid areas. Decreases in the extent of DVM from offshore to coastal areas have also been reported by Brinton (1967) in the eastern tropical Pacific, but he did not give any information on phytoplankton abundance. More recently, Dodson (1990) found a linear relationship between amplitude of DVM of *Daphnia* and Secchi disk depth in various lakes, and Kaartvedt *et al.* (1996) reported that the distribution of scattering layers of fish and krill along a transect off northern Norway changed markedly in concert with fluctuating fluorescence in upper waters. In contrast, in the study of Roe (1983), for

example, none of the five species of euphausiids and of the six species of fishes studied was restricted to an isolume. In fact, light is part of a complex of environmental factors that interact to control the vertical distributions of zooplankton; it is difficult to precisely isolate the influence of a given factor when the importance also varies among species.

DVM is generally explained as a means of avoiding predators (Zaret and Suffern, 1976; Stich and Lampert, 1981). Visual predation at a given depth would be reduced by the more turbid waters (sites M and E in the present cases). On the other hand, for the organisms that were concentrated both by day and at night in the rich phytoplankton upper layers, such as *Euphausia americana* at site M and *Euphausia krohni* at site E, the loss due to predation would have been compensated by the plentiful food.

The present study relates the trophic state of an environment and the structure of macroplankton and micronekton communities. The community structure at the eutrophic site is characterized by a few largely dominant opportunistic species. These species depend on external forces reflected by the upwelling system that provides a more or less constant nutrient input. This was not the case at the oligotrophic site, where a great number of equally but sparsely abundant species lived in low nutrient conditions and represented high diversity; the community structure was mostly regulated by internal mechanisms. High migration amplitudes at the oligotrophic site contrasted with low or non-detectable amplitudes at the meso- and eutrophic sites. This most likely appears related to the sensitivity of migrators to different light conditions, forcing them to dive deeper during daylight at site O than at the other sites to avoid visual predators.

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