Diel variations of the bathymetric distribution of zooplankton groups and biomass in Cap-Ferret Canyon, France

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Abstract

The bathymetric distribution, abundance and diel vertical migrations (DVM) of zooplankton were investigated along the axis of the Cap-Ferret Canyon (Bay of Biscay, French Atlantic coast) by a consecutive series of synchronous net hauls that sampled the whole water column (0–2000 m in depth) during a diel cycle. The distribution of appendicularians (maximum 189 individuals m^{-3}), cladocerans (maximum 287 individuals m^{-3}), copepods (copepods < 4 mm, maximum 773 individuals m^{-3}, copepods > 4 mm, maximum 13 individuals m^{-3}), ostracods (maximum 8 individuals m^{-3}), siphonophores (maximum > 2 individuals m^{-3}) and peracarids (maximum > 600 individuals 1000 m^{-3}) were analysed and represented by isoline diagrams. The biomass of total zooplankton (maximum 18419 µg C m^{-3}, 3780 µg N m^{-3}) and large copepods (> 4 mm maximum 2256 µg C m^{-3}, 425 µg N m^{-3}) also were determined. Vertical migration was absent or affected only the epipelagic zone for appendicularians, cladocerans, small copepods and siphonophores. Average amplitude of vertical migration was about 400–500 m for ostracods, some hyperiids and mysids, and large copepods, which were often present in the epipelagic, mesopelagic, and bathypelagic zones. Large copepods can constitute more than 80% of the biomass corresponding to total zooplankton. They may play an important role in the active vertical transfer of carbon and nitrogen. © 1999 Elsevier Science Ltd. All rights reserved.

1. Introduction

The ECOMARGE (ECOsystem of continental MARgins) operation intends to study the transfer of matter and energy on continental margins. The quantification of

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transfers of matter in the ocean involves taking into account two kinds of fluxes: passive fluxes due to particle sedimentation, and active fluxes caused by living organisms, particularly by migrant zooplankton (Buat-Ménard et al., 1989; Bruland et al., 1989; Noji, 1991; Lane et al., 1994). Two kinds of active fluxes of matter can be distinguished: those related to migrant zooplankton itself and those related to matter transported by migrant zooplankton.

Diel vertical migration (DVM) of aquatic organisms has progressively evolved from direct reaction to light to much more complex patterns (Russell, 1926; Clarke, 1934; Harris, 1953; Longhurst, 1976; Mauchline, 1980; Margalef, 1986; Ohman, 1990; Bollens et al., 1994). Changes in light intensity at dusk and dawn seem to be the major factor controlling vertical migration (Southern and Gardiner, 1932; Harris, 1953; Beeton, 1960; Macquart-Moulin, 1975; Bourdillon, 1989; Checkley et al., 1992; Franck and Widder, 1997). DVM of zooplankton is a well-known phenomenon that transports a substantial quantity of biomass (Angel, 1984,1985,1989; Bourdillon, 1989; Passelaigue, 1989).

The importance of the resulting net fluxes of biomass depends on: (1) the importance of raw fluxes, which relies on population biomass and vertical amplitude of migrations; (2) the mortality and feeding rates or the physiological functions that govern breeding, moulting, defecation, excretion, respiration, as well as the levels at which they occur. The importance of the downward fluxes of respiratory carbon and dissolved inorganic nitrogen associated with diel-migrant zooplankton ("biological pump") has been assessed by numerous workers (Harding et al., 1987; Angel, 1989; Longhurst and Harrison, 1988,1989; Noji, 1991; Dam et al., 1995a). In order to quantify the active raw fluxes attribuable to migrant zooplankton, the first step is to describe the amplitude of zooplankton diel migrations and to quantify the biomass of the concerned populations.

The boundary between neritic and oceanic areas, the continental slope and submarine canyons, can have unique hydrodynamic regimes (Shepard et al., 1974; Slagstad and Tande, 1996). Due to hydrological features occurring in these areas, the coexistence of zooplankton organisms from inshore and offshore areas can result in peculiar zooplankton compositions (Koslow and Ota, 1981; Mackas, 1984; Macquart-Moulin and Patriti, 1993,1996; Vinogradov et al., 1998). Frontal structures defined by strong temperature and salinity gradients are common in these areas, and they actively contribute to the irregular variations of the abundance of inshore and offshore zooplankton. Advective changes may result in changes in the bathymetric distribution of zooplankton organisms, and diel-migrant zooplankton advected from oceanic areas may be trapped in neritic habitats (Isaacs and Schwartzlose, 1965; Genin et al., 1988). The trapping effect of canyons on both shelf and oceanic migrant zooplankton can reinforce this biological accumulation. The present study is the first attempt to delineate the distribution and abundance of zooplankton using synchronous multi-depth opening/closing nets to explore the entire water column in the Cap-Ferret Canyon, France, as such the results may have global significance in defining the sole of changes affecting diel vertical migrations and biomass of zooplankton.

2. Materials and methods

The continental shelf of the Bay of Biscay is a more or less wide flat area extending to depths ranging of 200 m. The continental slope is about 50 km wide, extends to depths of 4000 m in depth and converge into submarine canyons 5–10 km in length.

As a part of the ECOMARGE operation, three ECOFER (Cap-Ferret Canyon Ecology) campaigns took place between 1988 and 1990. The ECOFER 4 campaign was the first one to study zooplankton vertical migration. The ECOFER 4 campaign, in May 1991 in the Bay of Biscay over the Cap-Ferret Canyon (Fig. 1), collected diel cycle samples.

In order to sample the entire water column (Fig. 2), two consecutive series of synchronous multi-depth oblique hauls were made: (1) four discrete layers of 100 m between 0 and 400 m, (2) four discrete layers of 400 m between 400 and 2000 m. A surface haul (0 m) was trawled horizontally for each series. Two different kinds of nets were used: for shallow and deep work, ORI (Ocean Research Institute) conical nets (mouth area: 2 m^2, length: 8 m) (Omori, 1965); and for surface work, a rectangular net (mouth area: 1.5 m^2, length: 8 m). This latter net was fitted with a Hydrobios flow-metre. The filtering area of all the nets was Nytrel-TI monofilament polyester gauze of mesh size 335 μm. ORI nets were opened and closed acoustically. The trigger was modified from the one described by Bourdillon et al. (1978) by changing the original mechanic system into an acoustic one. Average duration of hauls was 15 min
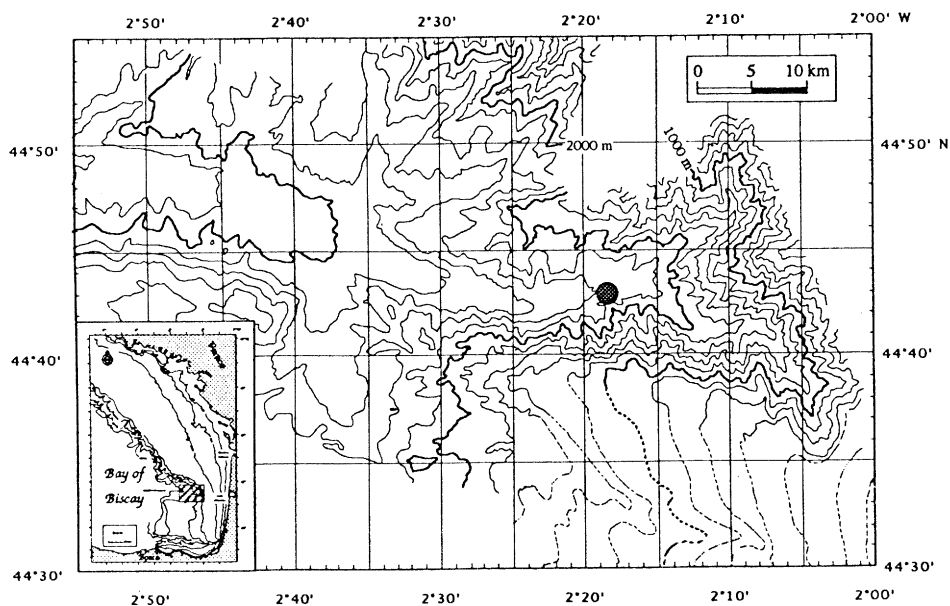

Fig. 1. The study area during ECOFER 4. The Cap-Ferret Canyon is located near the southwestern coast of France, in the Bay of Biscay. The sampling station is indicated by a dot.
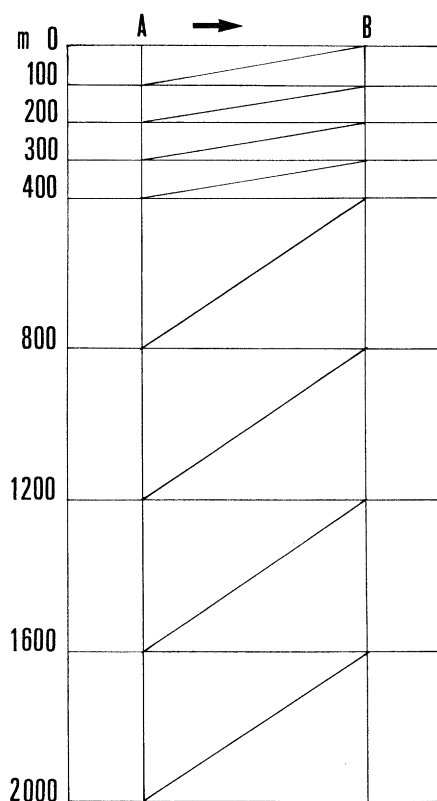
Fig. 2. Layout of nets for the sampling operation. A = net opening position, B = net closing position. Arrow indicates the displacement direction.

for the 400 m hauls, and 7 min for the 100 m hauls. Average distance of hauls was 780 m and 330 m, respectively. Sampling time is given in summer time. Volume calculations were based on the length of the oblique haul and the net mouth area. For the rectangular surface net, volume calculations were made from flow-metre estimations of the distance covered during the haul and the effective net mouth area (1 m^2), since the net was submerged two thirds in height. Forty-eight samples out of 55 were analysed. Samples were split into two in order to determine abundance and biomass.

2.1. Zooplankton distribution

A non-exhaustive inventory of copepod genera and species was worked out from two consecutive series of hauls, a shallow series (0–400 m in depth) and a deep series (400–2000 m in depth). Identifications were made according to Beaudouin (1971,1975) and Vives (1980). Copepods were classified in two size classes: smaller and larger than 4 mm in length (small copepods and large copepods respectively). For appendicularians, cladocerans, copepods and ostracods the abundance was expressed as

individuals m^{-3}. For larger and less abundant organisms (siphonophores and peracarids), it was expressed as individuals $1000\ m^{-3}$. Isoline diagrams were chosen because of the dynamic point of view they introduce in the representation vertical distributions.

2.2. Biomass

The biomass of large copepods and total zooplankton was estimated using dry weight and elementary chemical composition (CHN). Samples were dried in an oven at 50°C to a constant weight and then weighed using a Mettler 240 balance. The drying temperature was chosen according to Lovegrove (1962), Mazza (1964) and Bourdillon (1971) in order to prevent fat evaporation. The elementary chemical composition of large copepods and total zooplankton was measured with a CHN Leco analyser. Aliquots of approximately 10 mg of dry matter were used for each measurement. The carbon and the nitrogen concentration values were both expressed as $\mu g\ m^{-3}$ in isoline diagrams. C/N atomic ratios also were given for large copepods and total zooplankton.

3. Results

Appendicularians (maximum: 189 individuals m^{-3}), cladocerans (maximum: 287 individuals m^{-3}), copepods (small copepods, maximum: 773 individuals m^{-3}, large copepods, maximum: 13 individuals m^{-3}) and ostracods (maximum: 8 individuals m^{-3}) were the most abundant zooplankton groups. Although they were less abundant, siphonophores (maximum: > 2 individuals m^{-3}) and peracarids (maximum: > 600 individuals $1000\ m^{-3}$) were also taken into account. Euphausiids, pteropods, decapod larvae, chaetognaths, jellyfish and fish (eggs, larvae and adults) were removed before making dry weight calculations for total zooplankton.

3.1. Zooplankton distribution

Appendicularians (Fig. 3) were scarce at the surface at the first noon of the diel study (1 individual m^{-3}) and were absent from surface hauls in the afternoon and around midnight. During the night, two maxima occurred at 22:00 and 03:00. (186 and 189 individuals m^{-3}). Another maximum occurred after dawn (0.7:00, 103 individuals m^{-3}). Values went down to zero thereafter. Appendicularians were only found in the water column in the top 100 m (17–51 individuals m^{-3}). One individual per cubic metre was found at 23:00 in the deepest layer (1600 to 2000 m). This was probably the result of a contamination from the surface layer where they were very abundant at that moment. Intermediate depth levels were free of appendicularians.

Cladocerans were confined to the top 100 m (Fig. 4). Their abundance was low in surface hauls during afternoon, increased around 19:00, and there were two maxima at
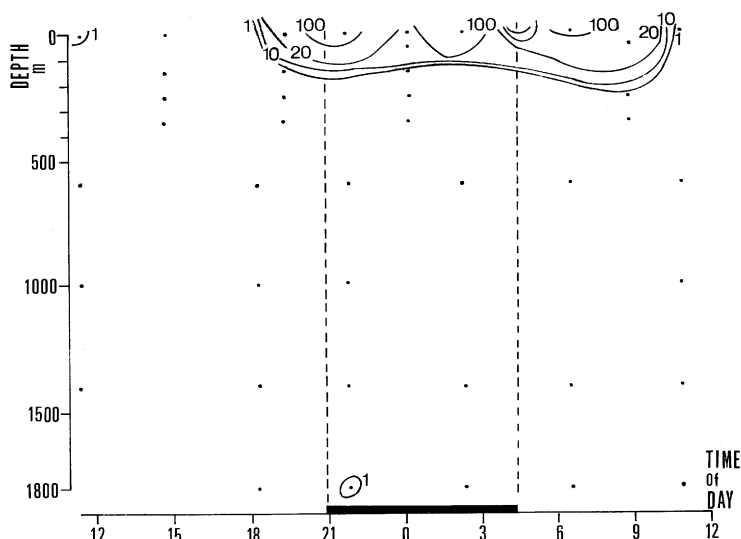
Fig. 3. Time–space variation of appendicularians during a diel cycle. The isoline diagram was drawn according to the number of individuals m^{-3}. The time and the average depth of the samples are indicated by dots. A dark strip indicates the nocturnal period, when the total suface irradiance was less than 0.5×10^{-2} W m^{-2}.

03:05 and 11:45 (absolute maximum: 287 individuals m^{-3}). In the top 100 m, cladocerans ranged from 20 to 40 individuals m^{-3} during the night and increased up to 115 individuals m^{-3} at dawn. They were nearly absent from the rest of the hauls (less than 0.5 individual m^{-3}). They were only present below 100 m between 18:00 and 08:00.

Ostracods were always absent from surface hauls (0 m) (Fig. 5). In the top 200 m, values ranged from less than 1–3 individuals m^{-3} at any time. Ostracods remained between 100 and 1500 m during the daytime (maximum at around 600 m: 6.9 individuals m^{-3}). During the night they concentrated in the 100–600 m layer (average depth at 200 m). After dawn they were found between 300 and 1000 m (maximum at around 400 m). If we consider its distribution at different times, this group accomplished two 400 m migrations, one upward after dusk and another one downward after dawn.

Large copepods included the genera *Rhincalanus*, *Eucalanus* and *Euchirella*. Small copepods of the genera *Calanus*, *Rhincalanus*, *Eucalanus*, *Monstrilia*, *Oncaea*, *Euchaeta*, *Acartia*, *Oithona*, *Euchirella*, *Centropages* were found in the samples. Some individuals of *Temora longicornis*, *Acartia clausi*, *Paracalanus parvus* and *Clausocalanus arcuicornis* also were found.

Large copepods were always absent from surface hauls. They were even absent from the top 100 m during the daytime (Fig. 6). Their abundance below 1000 m was less than 1 individual m^{-3} at any time. Most of the individuals remained between 0 and 300 m (average depth at 100 m). The abundance values in this layer were higher at
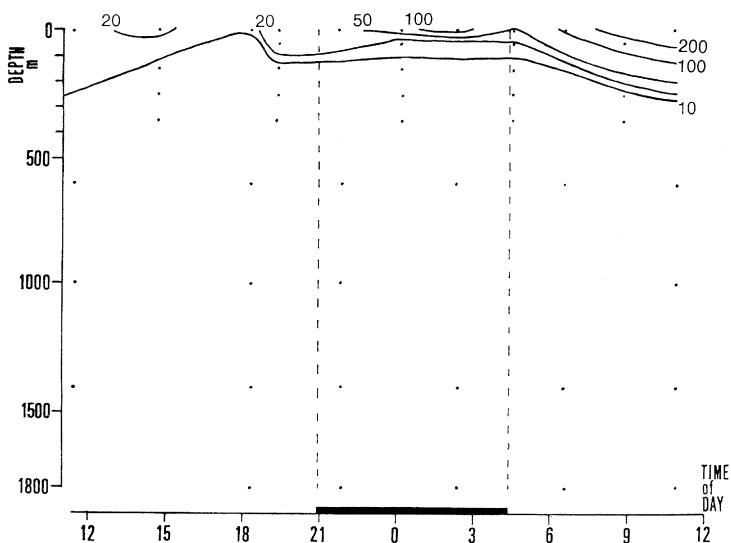
Fig. 4. Time–space variation of cladocerans during a diel cycle. Legend: see Fig. 3.
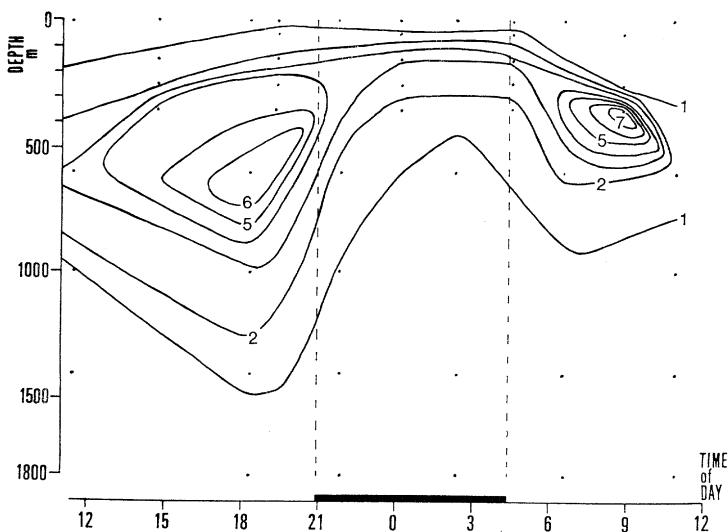

Fig. 5. Time–space variation of ostracods during a diel cycle. Legend: see Fig. 3.

night (maximum: 13 individuals m^{-3}) than during the daytime (maximum: 6 individuals m^{-3}). Night values (maximum: 0.7 individual m^{-3}) were lower than day values (maximum: 7.1 individuals m^{-3}) between 300 and 500 m. After dawn, their average depth was at about 400 m. The values in the rest of the layers remained steady around night values. This reflected their upward migration after dusk and their
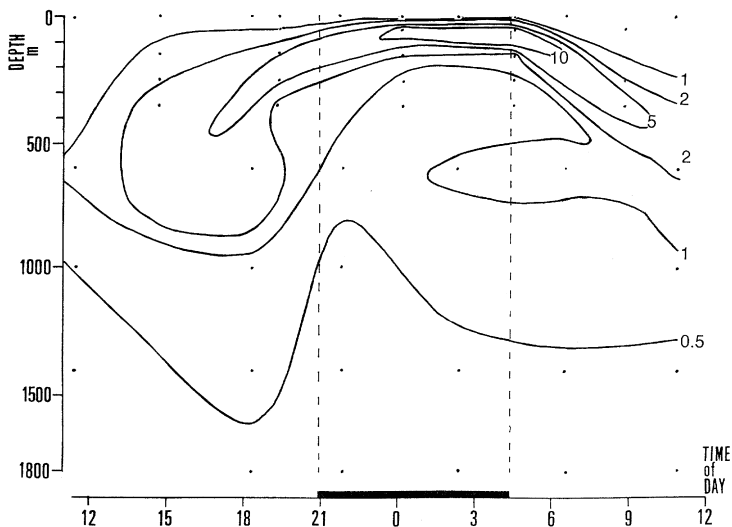
Fig. 6. Time–space variation of large copepods during a diel cycle. Legend: see Fig. 3.
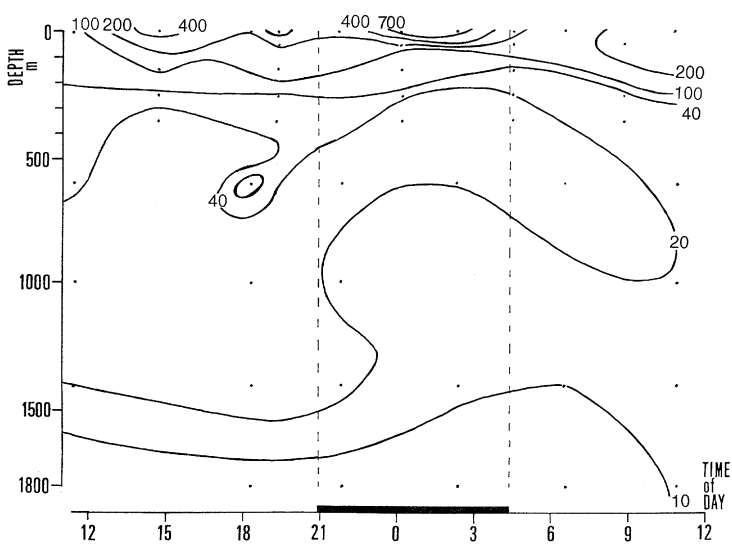
Fig. 7. Time–space variation of small copepods during a diel cycle. Legend: see Fig. 3.

downward migration after dawn. The intermediate layer between 300 and 500 m seemed to be the region of the water column where these copepods passed through without stopping during their migration.

Small copepods peaked twice, once at 16:00 (424 individuals m^{-3}) and once between midnight and 03:00 (773 individuals m^{-3}) (Fig. 7). This latter peak
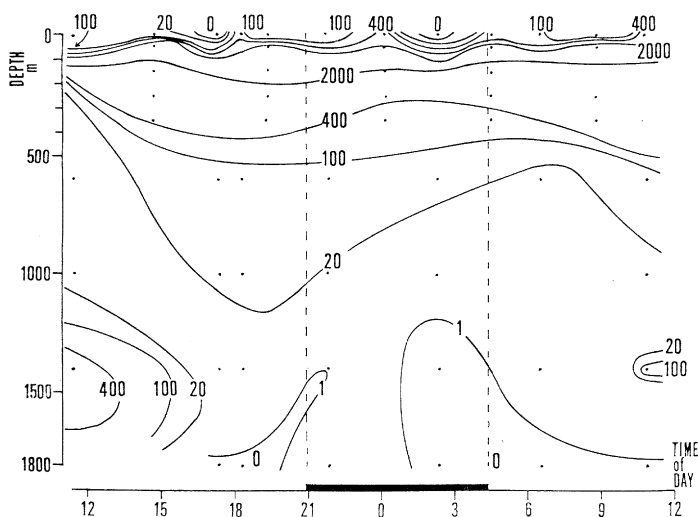
Fig. 8. Time–space variation of calycophores siphonophores during a diel cycle. The isoline diagram was drawn according to the number of individuals 1000 m^{-3}. The time and average depth of the samples are indicated by dots. A dark strip indicates the nocturnal period, when the total suface irradiance was less than 0.5×10^{-2} W m^{-2}.

corresponded to the maximum number of individuals per unit volume for all zooplankton groups. Most of these small copepods remained in the top 200 m at any time. The values below this layer were always lower and remained in an almost steady state. Small copepods seemed to accomplish a very limited migration and to concentrate near the surface throughout the night.

Seven calycophore siphonophores species (adults and eudoxid phases) were mainly caught in the hauls. The epipelagic species *Lensia conoidea* (maximum: 3466 adult individuals 1000 m^{-3}), *Muggiaea kochi* (maximum: 2079 individuals 1000 m^{-3}), *Lensia multicristata* (maximum: 790 individuals 1000 m^{-3}), *Dimophyes arctica* (maxima: 167 adult individuals 1000 m^{-3}; 296 eudoxid phases 1000 m^{-3}) and *Muggiaea atlantica* (maximum: 28 adult individuals 1000 m^{-3}) were mainly located around 100 m. Eudoxid phases were more abundant than adults, and both were located in the same layer. The mesopelagic species *Chuniphyes multidentata* was located around 350 m (maximum: 29 individuals 1000 m^{-3}). *Clausophyes ovata*, a bathypelagic species, was located between 600 and 1800 m (maximum: 13 individuals 1000 m^{-3}). Some rare mesopelagic and bathypelagic species also were caught. As a whole, the most abundant siphonophores were epipelagic (average: 3391 individuals 1000 m^{-3}), which were found between 50 and 150 m. Abundant individuals of mesopelagic species were found between 250 and 350 m (469 individuals 1000 m^{-3}). Siphonophores exhibited a relatively homogeneous distribution in depth and time. Their numbers decreased with depth, but some swarms also were found around 1400 m during the daytime (Fig. 8). If we consider adults and eudoxid phases together, vertical movements were not noticeable.
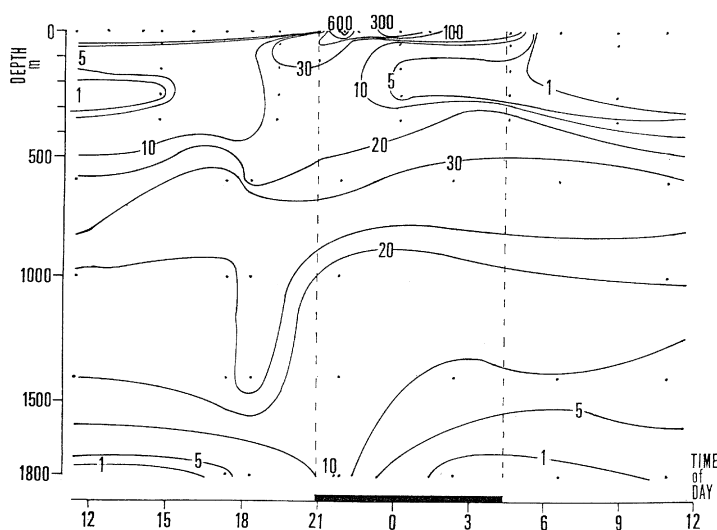
Fig. 9. Time–space variation of peracarids during a diel cycle. Legend: see Fig. 8.

Fourteen peracarid species were regularly caught in hauls: nine mysids, *Eucopia unguiculata*, *E. sculpticauda*, *Boreomysis microps*, *B. arctica*, *B. tridens*, *Gnathophausia zoea*, *G. gigas*, *Meterythrops picta* and *Longithorax fuscus* and five amphipods, the hyperiids *Parathemisto gaudichaudii*, *Scina crassicornis*, *S. borealis* and *Vibilia jean-gerardi* and the gammarid *Cryptocaris anonyx*. All mysids were bathypelagic and mesopelagic species, and only two of them were well-represented in the samples: *Eucopia unguiculata* (maximum: 46 individuals 1000 m^{-3}) and *Boreomysis microps* (maximum: 9 individuals 1000 m^{-3}). The abundance of the rest of the species ranged from 1 to 5 individuals 1000 m^{-3}. The epi- and mesopelagic hyperiid *Parathemisto gaudichaudii* was very abundant (more than 600 individuals 1000 m^{-3}). Some other amphipods were only represented by few individuals. The diel variations of the bathymetric distribution of peracarids (Fig. 9) showed that the nocturnal abundance at the surface was due only to *P. gaudichaudii*. This species, which was scattered between 50 and 600 m during the daytime, rose to the upper layer in the first evening hours and concentrated at dusk and throughout the night in the hyponeustonic surface layer. The bathypelagic species were mainly located in the 500 to 1500 m layer (maximum between 600 and 1000 m). We seldom found individuals below 1500 m. A slight upward migration was evident for *Eucopia unguiculata* juveniles, which could reach the upper part of the mesopelagic zone at night.

3.2. Biomass

The diel variation over depth of carbon concentration for large copepods (Fig. 10) showed the same trends as their abundance. The average depth of biomass decreased after dusk, remained steady near the surface during the night and increased after dawn
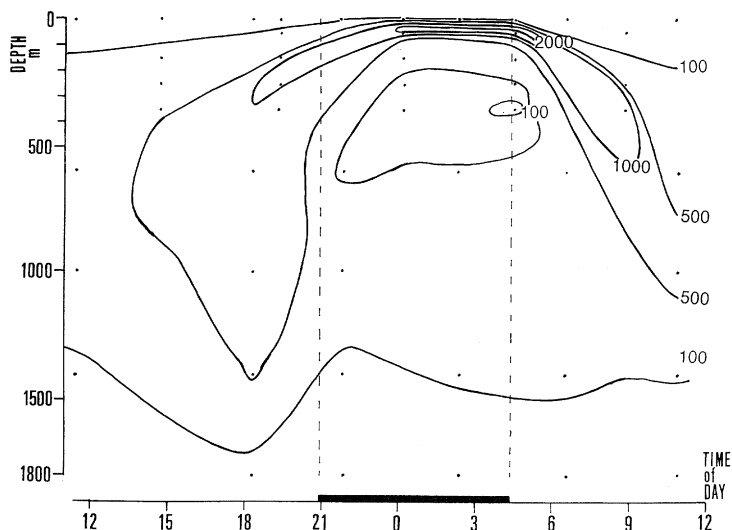
Fig. 10. Time–space variation of carbon contents in $\mu g \, m^{-3}$ for large copepods during a diel cycle. Legend: see Fig. 3.

organic carbon values near the surface (0–100 m) were zero during the daytime and rose to 2256 $\mu g \, C \, m^{-3}$ during the night. Between 300 and 500 m, night values (119 $\mu g \, C \, m^{-3}$) were lower than day ones (1114 $\mu g \, C \, m^{-3}$). As already observed for abundance values, this mid-depth minimum seemed to be the region where migrating copepods passed without stopping both during ascent and descent. The diel variation over depth in nitrogen concentration (Fig. 11) showed values that could be up to ten-fold lower but showed the same feature. Due to the absence of large copepods at any time in the surface layer (0 m) and during the daytime in the 0–100 m layer, nitrogen concentration values were negligible during the daytime and rose to 425 $\mu g \, N \, m^{-3}$ during the night.

The diel variation over depth of carbon and nitrogen concentration for total zooplankton (Figs. 12 and 13) showed very interesting general features. Values in the top 300 m were always high, but they increased nearly ten-fold at the surface during the night (day maximum: > 2000 $\mu g \, C \, m^{-3}$, 500 $\mu g \, N \, m^{-3}$; night maximum: > 18000 $\mu g \, C \, m^{-3}$, 3780 $\mu g \, N \, m^{-3}$). Before dusk and after dawn the 300 m to 1200 m layer showed a steady state in carbon and nitrogen values (around 1000, 200 $\mu g \, N \, m^{-3}$). The upper part of this layer (300–500 m) showed a decrease in both series of values, which remained constant during the night (while values increased in the 0–300 m layer). This phenomenon was mainly due to the migration of large copepods.

According to analyses of our samples, C/N atomic ratios ranged from 3.4 to 9.66. C/N values increased with depth at any time. C/N values for large copepods ranged from 3.43 to 7.75. C/N values for total zooplankton ranged from 4.11 to 9.66, and their bathymetric distribution was consistent with that of large copepods.
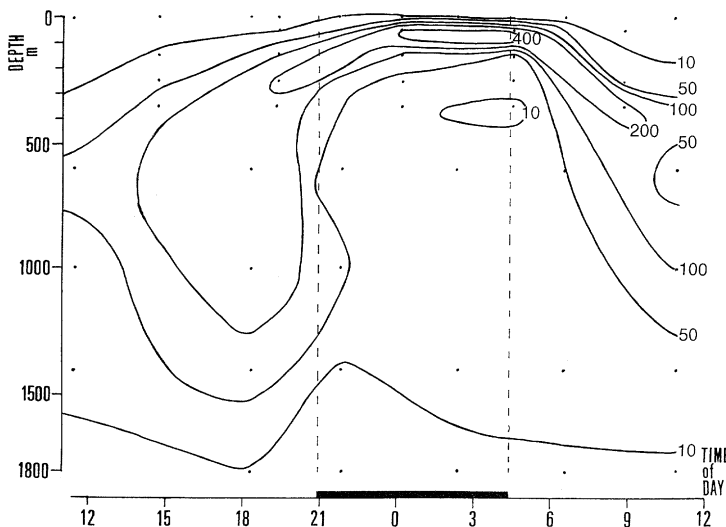
Fig. 11. Time–space variation of nitrogen contents in µg m^{-3} for large copepods during a diel cycle. Legend: see Fig. 3.

Fig. 12. Time–space variation of carbon contents in µg m^{-3} for total zooplankton during a diel cycle. Legend: see Fig. 3.

4. Discussion

From these results, two different situations can be identified. Firstly, either no vertical migration or a very limited migration was observed for appendicularians,
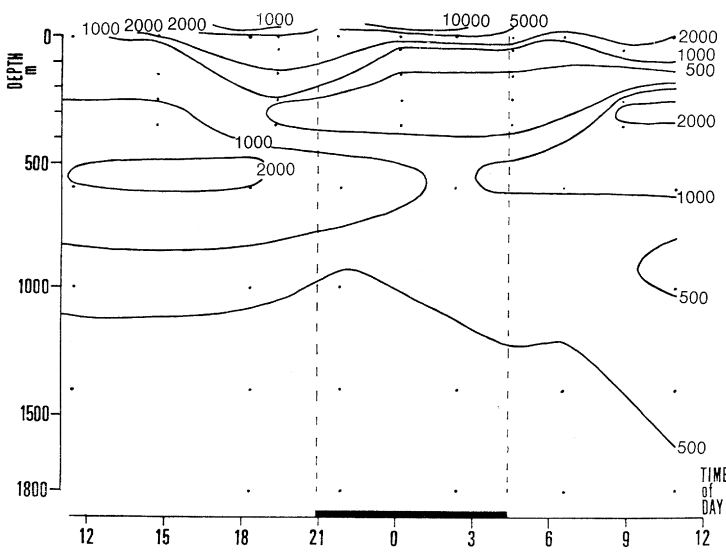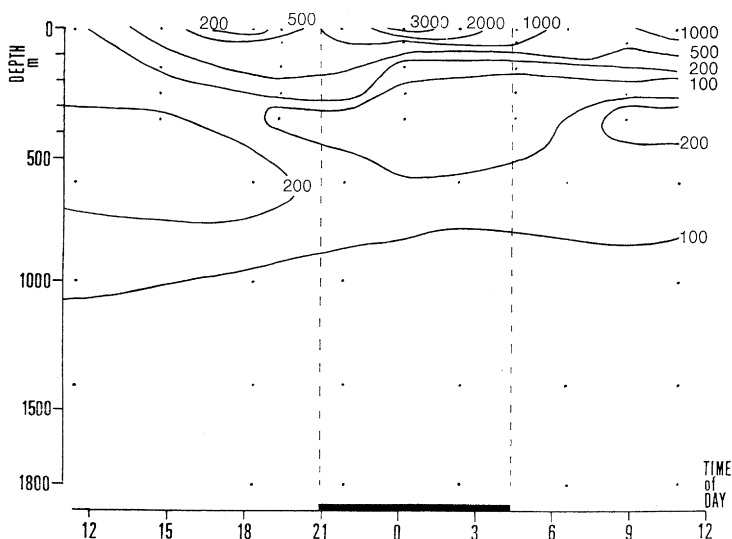
Fig. 13. Time–space variation of nitrogen contents in µg m^{-3} for total zooplankton during a diel cycle. Legend: see Fig. 3.

cladocerans, copepods smaller than 4 mm in length, siphonophores and some peracarids. Secondly, a sufficiently large migration was observed for ostracods, copepods larger than 4 mm in length, as well as the peracarids *Parathemisto gaudichaudii* and *Eucopia unguiculata*. The abundance of larger organisms in near surface waters generally exhibited greater day/night variations (related to DVM) than small ones, similar to that reported by Roman et al. (1995) for several size classes of net zooplankton at the equator.

Diel variations of zooplankton in the epipelagic zone (0–200 m) may have eluded our investigation since only one oblique haul and a surface haul were made in the top 100 m of the water column. Appendicularians, cladocerans, small copepods and siphonophores are abundant in this layer, and many authors have studied their DVM. For example, many calycophores siphonophores undergo DVM has slow sinusoidal movements with little bathymetric amplitude (Pugh, 1977; Mackie et al., 1987). Three species of Mediterranean siphonophores with different migratory behaviours nevertheless show extensive diel vertical migration (Andersen et al., 1992). Vertical migration may or may not be noticeable, depending on the environmental conditions or on the sampling methods used (time and space sampling-scales) (Pearre, 1979). However, our sampling methods could make evident the sub-superficial distribution of ostracods and large copepods, which were absent from surface hauls but were found in the top 100 m. Results concerning ostracods agree with those found by Alcaraz (1981). Onbé and Ikeda (1995) observed the epipelagic distribution of several cladoceran species in the Sea of Japan, although they did not detect a clear sub-surface distribution. By towing very thin layers in the uppermost water column, they made clear a "reverse" DVM for *Evadne* and *Podon* species and a normal DVM for other cladoceran species.

Our results also should be used with care since they are obtained for only one 24-h period and the last samples were probably taken before the end of the downward migration. This is more obvious near the surface, since the settlement of biological components in the surfacial mixed layer can be disturbed by fronts characterized by strong temperature or salinity gradients, causing changes in the surface water mass and thus in zooplankton abundance and species composition (Onbé and Ikeda, 1995; Bergstrom and Stromberg, 1997; Vinogradov et al., 1998); this advective change can be wrongly interpreted as the result of a vertical movement. In a study of vertical mixing and the vertical distribution of copepods, Lagadeuc et al. (1997) report that vertical changes in adult distribution was not result from advection, as for nauplius stages, but active migration. Advective changes, however, occurred at the surface during the afternoon of our sampling. Their effect on the epipelagic fauna (appendicularians and cladocerans) can be clearly identified from the diel variations of the abundance of these groups. The S and SE surface currents during the cruise (Castaing et al., 1999) brought in continental shelf waters that could have created this phenomenon. Hitherto, the influence of bathymetric features in the vertical migrations of epipelagic zooplankton has not been demonstrated. Rather, the distribution and migration of epipelagic organisms are controlled by local illumination (implying a seasonality) moonlight and water turbidity. Therefore, their abundance also depends on variations in primary production, the advective movements caused by prevailing winds (offshore and inshore advection), frontal structures, the presence of an upwelling or particular hydrological conditions in slope waters (Bailey, 1981; Cooney and Coyle, 1982; Gardner and Howell, 1983; Smith and Jossi, 1984; Macquart-Moulin, 1993). The diel variations of the distribution and abundance of zooplankton differ with environments, depending upon abiotic and biotic factors (Frost, 1988; Bollens and Frost, 1989; Ohman, 1990; Checkley et al., 1992). Nevertheless, mesopelagic and bathypelagic species are less subject to advection because of their bathymetric distribution. Their distribution may be affected by internal waves at depth, but these variations are slower than those related to vertical migration.

For ostracods, large copepods, an amphipod and a mysid, which were mainly located in the mesopelagic zone, vertical migration was rather clear. An important daily vertical transfer of organic and inorganic matter can be attributed due to feeding, excretion and defecation by these animals. Large copepods are particularly interesting given their large vertical migration (500 m in average) and their large biomass. In fact, below 100 m in depth, the carbon and nitrogen contents of large copepods were only slightly less than for total zooplankton. Furthermore, carbon and nitrogen variations with depth for both large copepods and total zooplankton show strong similarities (Figs. 10–13): nocturnal enrichment that occurs next to the surface corresponds to an impoverishment in the 300 m to 500 m layer. These results show the importance of the role played by large copepods in controlling upward and downward carbon and nitrogen transfers. These large copepods, which elude the surface layer, are essentially carnivorous copepods that can feed and produce fecal pellets throughout the water column. A depth segregation related to size was reported by Andersen and Sardou (1992) in Mediterranean euphausiids and by Roman et al. (1995) for net zooplankton. In our study, large copepods were generally found deeper

than the smaller ones, which performed a more limited migration than the larger ones, or even none.

Several authors have reported that the C/N ratio remains relatively constant within different species of copepods and other crustaceans, varying from 3.6 to 5.2 (Boucher et al., 1976; Champalbert and Kerambrun, 1978; Dawirs, 1980). This may be the case for papers in which only one or two species were studied, but our study of large copepods and total zooplankton at specific time and depths suggest otherwise. Data from Omori (1969) support our results, since he observed C/N ratio values ranging from 3.5 to 11.0 for different zooplankton. According to his paper, the highest values come from the animals with high fat content. Our results suggest that zooplankton with high C/N ratio values never reached the surface, since surface values ranged from 4.11 to 4.87.

The distribution and abundance of bathypelagic and mesopelagic zooplankton can present special features on the slope and in canyons. Due to the depth of their preferred diurnal biotope, these oceanic species can accumulate near the bottom in slope waters and concentrate in canyons. Near-bottom diurnal accumulation of mysids has been observed and discussed by Hargreaves (1985) and Macquart-Moulin (1993). The range of depths studied in the Cap-Ferret Canyon, however, did not enable us to observe this suprabenthic accumulation, as maximum densities were located around 1000 m. Nevertheless, Elizalde et al. (1991) noticed the accumulation of mysids on a 1000 m bottom near the head of the Cap-Ferret Canyon.

Two main phenomena can be considered to explain the accumulation of deep species in canyons: (1) animals which swim to the continental shelf, the continental slope or canyon during their morning descent below 200 m (behaviour filmed by Omori in the Sergestidae in Koslow and Ota, 1981), (2) animals scattered near the head of the canyon in the top of the continental slope can be dragged into the canyon by prevailing bottom currents (Shepard et al., 1974; Castaing et al., 1999). Such accumulations have been observed for two copepod species, *Calanus pacificus* and *Rhincalanus nasutus*, as well as for the euphausiid *Euphausia pacifica* in La Jolla Canyon (California) (Koslow and Ota, 1981) and for several peracarids in northwestern Mediterranean canyons (Macquart-Moulin and Patriti, 1993). These phenomena could explain the relative abundance of the bathypelagic mysid *Eucopia unguiculata* in the Cap-Ferret Canyon, which was ten-fold greater than levels reported by Hargreaves (1985) for the same depths in Irish slope waters. They also may explain the high biomass of large copepods found in our study.

The passive fluxes measured at 250 m in April 12 and June 4 in the sampling zone were 58 and 11 mg C m^{-2} d^{-1}, respectively (Etcheber et al., 1999). The values were 26 and 39 mg C m^{-2} d^{-1} at 1350 m. Primary production measured during our study was 1200 mg C m^{-2} d^{-1} (Laborde et al., 1999). The upward active fluxes of large copepods as measured at 250 m and 1350 m in May 11 were 357 and 80 mg C m^{-2} d^{-1}, respectively (Bourdillon, personal communication). This raw flux is 6–32 times the passive flux at 250 m and twice to three times the passive flux at 1350 m. Thus, even if the net active flux is only a small percentage of the gross flux, it would be about the same level as the passive flux. It is noteworthy that large copepods could elude advective changes at the surface because of their distribution, and

the diel variations of their bathymetric distribution were the result of diel vertical migration.

Up to now there have been few attempts to quantify biologically induced fluxes: Harding et al. (1987) compared the active raw fluxes to the passive fluxes due to particle sedimentation. Longhurst and Harrison (1988), active net fluxes of C/N to excretion and respiration. Longhurst and Harrison, 1988; Longhurst et al., 1989,1990 and Dam et al., 1995b show that active fluxes due to the zooplankton vertical migration are not negligible, and may be about the same level as passive fluxes.

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