Day-night migrations by deep-sea decapod crustaceans in experimental samplings in the Western Mediterranean sea

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Abstract: Analysis of abundance and size frequency data on decapod crustacean species in two different habitats (inside and outside a submarine canyon) in the Western Mediterranean during two near-continuous 24-h sampling periods using commercial bottom trawls provided an indication of migratory ability and activity of the numerically dominant species. Certain nektobenthic species (e.g. *Aristeus antennatus*) carried out migrations up the slope at night. Mesopelagic species, represented mainly by *Pasiphaea multidentata* and *Pasiphaea sivado*, carried out vertical migrations, more clearly distinguishable in smaller individuals. Diel behaviour tended to differ inside and outside the canyon, and possible causes are mainly discussed in the light of the morphology and feeding ecology of the species considered.

Key words: Day-night migration; Decapod crustaceans; Deep-sea; Mediterranean

INTRODUCTION

The influence of the diel cycle on species composition, density, and community structure is one of the lesser-known aspects of the study of deep-water species. Vertical migrations by the mesopelagic and demersal fauna dwelling close to the bottom have not been studied directly, though they have been discussed by certain authors (Lagardère, 1972; Gordon and Duncan, 1985). Some information is available on some species of mesopelagic crustaceans (Pasiphaeaidae, Sergestidae, Euphausiacea, Mysidacea, etc.), which are relatively dominant in bathyal benthopelagic communities (Abelló et al., 1988; Cartes, 1991) and dwell near the bottom during the daytime and migrate upwards to layers closer to the surface at night (Omori and Ohta, 1981; Lagardère, 1976; Hargreaves, 1984). Conversely, hardly any information exists on the diel cycle of activity of nektobenthic bathyal species (Maurin, 1962; Tobar and Sardà, 1987). Abundance of the species which contribute to benthic communities varies during the diel cycle, either because certain species burrow into the mud (Atkinson and Naylor, 1976; Froglia and Gramitto, 1987) or because they rise off the bottom or move up the slope (Maurin, 1962; Campillo et al., 1990).

The slope in the Western Mediterranean at depths of 400 to 1000 m is character-

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ized by high densities of decapod crustaceans (*Aristeus antennatus, Aristaeomorpha foliacea, Plesionika edwardsi, Plesionika martia, Plesionika acanthonotus,* etc.). These species play important ecological and economic roles (Maurin, 1962; Tobar and Sardà, 1987, Tobar & Sardà, 1992). Environmental light intensities in the deep-sea have been calculated as a function of light extinction in the water (Margalef, 1974) in the Catalan Sea area (Tobar & Sardà, 1992), where a relationship between light intensity and catches in the deep-water shrimp *Aristeus antennatus* has been observed. Generally, daylight is still detectable to 1000 m (Margalef, 1974; Tyler, 1988).

The present study seeks to describe the abundance of numerically dominant decapod crustacean species recorded in samples collected during two near-continuous 24-h sampling periods, one carried out inside a submarine canyon and the other in the external slope region neighbouring this same canyon, on the middle slope in the Catalan Sea, and to relate this to diel behaviour of such species. Size data for several species is also compared.

MATERIAL AND METHODS

Two near-continuous 24-h sampling periods were carried out on the upper middle slope (Table I) using commercial bottom trawls. The first sampling period (DN1) was carried out in the area outside the submarine canyons (Can Pere Negre) at depths between 610 and 728 m. The second sampling period (DN2) was carried out at shallower depths (between 400 and 553 m) inside a submarine canyon (Sant Salvador

TABLE I

Sample data and location (D = daytime; N = nighttime).

Station	Date	Location	Time (GMT)		D/N	Depth (m)
			Initial	Final		
DN1/1	13.07.1989	41″07′N–02″03′E	17.30	19.45	D	651–710
DN1/2	13.07.1989	41″07′N–02″03′E	21.43	23.51	N	641–706
DN1/3	14.07.1989	41″07′N–02″03′E	01.35	03.46	N	637–655
DN1/4	14.07.1989	41″07′N–02″03′E	05.23	07.26	D	675–728
DN1/5	14.07.1989	41″07′N–02″03′E	08.40	11.05	D	610–646
DN2/1	20.10.1990	41″07′N–01″56′E	19.45	21.00	N	400–550
DN2/2	20.10.1990	41″07′N–01″56′E	22.08	11.23	N	412–553
DN2/3	21.10.1990	41″07′N–01″56′E	00.15	01.25	N	418–546
DN2/4	21.10.1990	41″07′N–01″56′E	02.25	03.30	N	407–544
DN2/5	21.10.1990	41″07′N–01″56′E	04.25	05.30	N	415–559
DN2/6	21.10.1990	41″07′N–01″56′E	06.16	07.30	D	415–546
DN2/7	21.10.1990	41″07′N–01″56′E	08.15	09.35	D	425–553
DN2/8	21.10.1990	41″07′N–01″56′E	10.22	11.37	D	410–546
DN2/9	21.10.1990	41″07′N–01″56′E	12.23	13.40	D	410–546

Canyon). Both sampling locations were situated in closely adjacent areas (less than 4 miles), and were situated on traditional fishing grounds for the red shrimp, *Aristeus antennatus*. Samples were obtained during the daytime and the nighttime. The DN1-1 sample (Table I) must be considered as crepuscular.

The basic features of the specific commercial bottom trawl gear employed in the red shrimp fishery are a vertical opening of 5 m and a horizontal opening between the wings of 25 m. These measurements were estimated with the aid of an acoustic monitoring system (SCANRED) attached to the trawl gear. Codend mesh size was 38 mm. Because the large mesh size used and the scarce catchability of trawls during the up and down of gear, contamination of samples by midwater species must be considered minimal.

Sampling material collected was preserved in 70% alcohol. At the laboratory the specimens in each sample were identified, counted, and weighed. Cephalothorax length (CL) was measured for the most abundant species. Only those species consistently present in the samples were considered in this study. These species comprised the penaeoidean shrimps *Aristeus antennatus* (Risso, 1816) and *Funchalia woodwardi* Johnson, 1868, the sergestid *Sergia robusta* (S.I. Smith, 1882); the pasiphaeids *Pasiphaea multidentata* Esmark, 1886 and *Pasiphaea sivado* (Risso, 1816), the oplophorid *Acanthephyra eximia* S.I. Smith, 1886, and the pandalids *Plesionika acanthonotus* (S.I. Smith, 1882), *Plesionika martia* (A. Milne Edwards, 1883) and *Plesionika edwardsi* (Brandt, 1851) among the natantian species. The polychelid lobster *Polycheles typhlops* Heller, 1862, the anomuran crab *Munida tenuimana* G.O. Sars, 1872, and the geryonid crab *Geryon longipes* A. Milne Edwards, 1881 represented the reptantian group species.

Abundance and biomass data were standardized to 1 h, with a vessel towing speed of 2.6 knots for all hauls. Abundance and biomass of numerically-dominant species in day and night hauls were compared so as to assess the amount of diel migratory activity by species.

Size frequencies of several species were also compared in order to ascertain whether the size structure of specific population varied over the photoperiod. Size frequency distribution data were obtained for *Aristeus antennatus* only in three hauls (DN2-1; DN2-4; DN2-8) during DN2. In *Pasiphaea multidentata* (DN2) and *Plesionika martia* (DN1) day and night size data samples were grouped to achieve a sufficient number of individuals in the size frequencies. The percentage similarity index, used for community analyses by Goodall (1978), and Haedrich et al. (1980) among others, was calculated to determine the overlap values between size-frequency distributions within each species. This index value ranges from 0 to 1 and can be calculated according to either of the following two expressions:

$$2 \frac{[\min(x, y)]}{(x + y)} = 1 \frac{Ix - yI}{(x + y)}$$

where x and y are vectors representing size frequencies to be compared. Thus, the index can be regarded as the proportion of overlap in the size-distributions of the species

TABLE II

Occurrence and abundance (kg/h) of the considered species. DN1: samples collected outside the canyon; DN2: samples collected inside the canyon (D = daytime; N = nighttime).

	DN1 (Can Pere Negre)					DN2 (Sant Salvador Canyon)								
	1 D	2 N	3 N	4 D	5 D	1 N	2 N	3 N	4 N	5 N	6 D	7 D	8 D	9 D
Benthopelagic species:														
Funchalia woodwardi	–	–	–	0.5	0.4	–	–	–	–	–	–	–	–	–
Sergia robusta	–	0.5	–	1.5	6.3	–	0.8	–	–	1.9	–	–	–	–
Pasiphaea multidentata	12.9	8.9	9.6	23.9	29.6	16.8	19.2	69.8	27.8	12.0	3.2	9.1	8.8	11.8
Pasiphaea sivado	–	–	–	–	–	2.4	–	–	–	–	1.6	0.8	8.0	6.3
Nektobenthic species:														
Aristeus antennatus	120.2	175.5	132.3	223.3	243.4	1901.2	2708.2	3393.9	2752.7	2665.1	2186.3	2054.0	2399.2	1813.1
Acanthephyra exinia	5.8	0.5	4.6	9.3	1.7	–	–	–	–	–	–	–	–	–
Plesionika acanthonotus	0.8	15.0	13.8	2.4	5.8	–	–	–	–	–	–	–	–	–
Plesionika martia	4.9	18.8	24.8	19.0	8.8	3.2	3.2	4.8	4.6	2.8	3.2	2.3	–	3.1
Plesionika edwardsi	–	–	–	–	–	151.2	148.8	50.9	16.7	11.1	0.8	2.9	2.4	2.4
Benthic species:														
Polycheles typhlops	4.9	17.8	16.5	13.7	16.9	–	–	–	–	–	–	–	–	–
Munida tenuimana	1.3	1.9	1.8	7.3	8.7	–	–	–	–	–	–	–	–	–
Geryon longipes	16.4	3.8	3.2	9.3	7.5	–	–	–	–	–	–	–	–	–
Total abundance	168.0	246.4	207.5	312.6	334.2	2082.6	2884.2	3523.7	2803.7	2695.7	2195.9	2075.1	2420.0	1838.3
Total weight	6.1	4.1	3.9	5.0	5.8	17.8	25.7	30.2	22.6	22.5	16.1	15.2	17.7	14.3

being compared, that is, the area of the intersection between size distributions divided by the sum of both the distribution areas, which since the size frequencies represent relative values, the distributions compared must expressed as a percentage.

Finally, the ratio of CL (mm) to wet weight (g) for the species considered was plotted as an estimation of swimming ability. Two different size groups were considered in each species; small individuals, ranging in all the species between 12 and 22 mm CL, and large individuals ranging between 25 and 45 mm CL. Only in *Geryon longipes* range size were higher (35–55 mm CL).

RESULTS

OUTSIDE THE SUBMARINE CANYON (DNI – CAN PERE NEGRE)

Table II sets out the abundance (ind/h) of the species in each sampling period. The mesopelagic species *Pasiphaea multidentata*, *Sergia robusta*, and *Funchalia woodwardi* were more abundant in daytime samples. By night catches of the latter two species were negligible as were those for *Pasiphaea sivado* which was found only inside the canyon (DN2).

Figure 1 represents the size frequency distribution of *Pasiphaea multidentata*. In the nighttime samples (DN1-2, DN1-3) most specimens were in size groups larger than 30 mm CL. Similarity was higher between nighttime frequencies (Table III). In the following daytime hauls (DN1-4, DN1-5) abundance shifted towards smaller modal size

TABLE III

Matrix of percentage of similarity between the size frequency distributions of the different abundant species studied during the two continous 24-h samplings.

		DN1 (Can Pere Negre)					DN2 (Sant Salvador Canyon)	
Benthopelagic species:								
Pasiphaea multidentata		DN1-1	DN1-2	DN1-3	DN1-4		DN2-1/DN2-5	
	DN1-2	62.1				DN2-6/DN2-9	88.7	
	DN1-3	70.8	82.2					
	DN1-4	58.4	75.4	71.4				
	DN1-5	50.9	74.5	64.8	63.2			
Nektobenthic species:								
Aristeus antennatus		DN1-1	DN1-2	DN1-3	DN1-4		DN2-1	DN2-4
	DN1-2	56.2				DN2-4	78.7	
	DN1-3	48.7	76.7			DN2-8	80.5	86.0
	DN1-4	59.0	66.9	57.3				
	DN1-5	59.5	66.7	57.9	78.9			
Plesionika martia		DN1-1/DN1-3						
	DN1-4/DN1-5	90.6						

groups, with a predominance of individuals smaller than 30 mm CL overall. This suggests that the smaller specimens, which are perhaps better able to rise through the water column (Fig. 3), migrated away from the bottom at night.

Of the nektobenthic species, the pandalids *Plesionika martia* and *Plesionika acanthonotus* were more abundant in nighttime samples (Table II). The size frequencies of *Plesionika martia* in the nighttime and daytime samples did not differ (Table III).

The results for *Aristeus antennatus* indicated that peak catches were made in the daytime. A comparison of the size frequencies (Fig. 2) yielded greater affinities between daytime samples DN1-4 and DN1-5 on the one hand and nighttime samples DN1-2 and DN1-3 on the other (Table III).

The only appreciable differences in abundance for the benthic species were recorded in the catches of *Geryon longipes*, which were larger in the daytime (Table II).

INSIDE THE SUBMARINE CANYON (DN2 – SANT SALVADOR CANYON)

On the whole, the pattern for the results in this area was the reverse of that outside the canyon (Table II). The highest abundance values for *Pasiphaea multidentata*, *Pasiphaea sivado*, *Plesionika edwardsii*, and *Aristeus antennatus* were recorded at night. Abundance levels for *Plesionika martia* remained relatively constant over the entire sampling period.

Nearly all *Pasiphaea multidentata* individuals were large (CL > 30 mm), and there were no differences in the daytime and nighttime size frequencies (Fig. 1; Table III). In contrast to the results from DN1, *Aristeus antennatus* was more abundant inside the canyon at night. Smaller individuals were by far the more predominant (Fig. 2), and there was a high degree of similarity between daytime and nighttime size frequencies (Table III).

Figure 3 shows that CL/wet weight values were higher for mesopelagic species than for more markedly benthic species. The difference in the values for this relationship was most pronounced for adult and juvenile *Pasiphaea multidentata*.
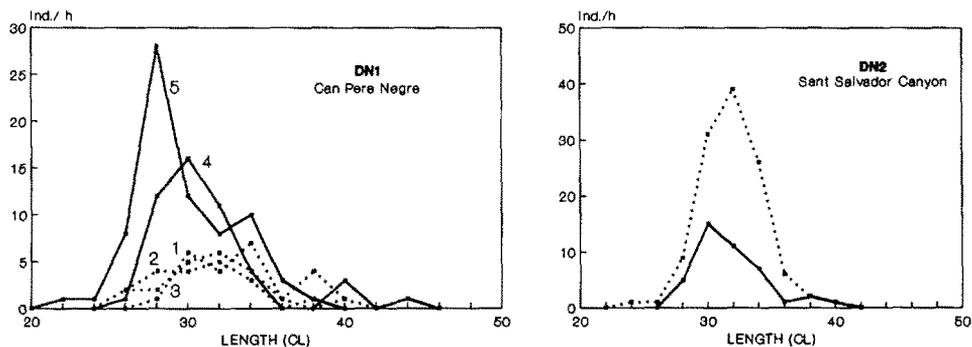

Fig. 1. Size frequency distribution (absolute values per hour) of *Aristeus antennatus* samples (day, continuous lines; night, discontinuous lines). Nos. 1–5 = hauls 1–5.
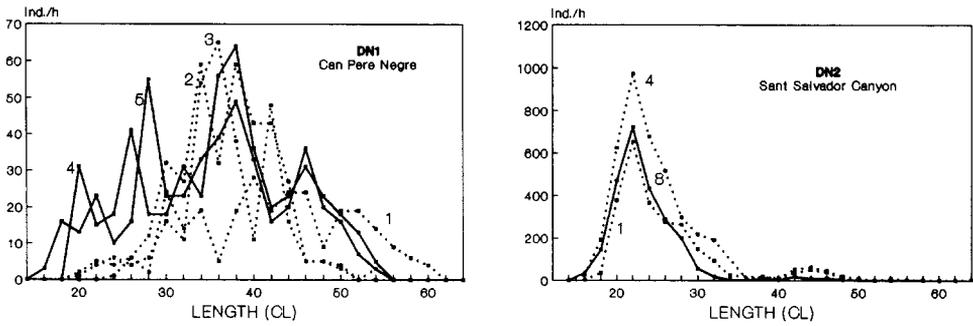
Fig. 2. Size frequency distribution (absolute values per hour) of *Pasiphaea multidentata* samples (day, continuous lines; night, discontinuous lines). Nos. 1–5 = hauls 1–5.

DISCUSSION

Mesopelagic species exhibited the most pronounced differences between daytime and nighttime samples. *Pasiphaea multidentata*, *Funchalia woodwardi*, and *Sergia robusta* were more abundant in the daytime samples taken outside the canyon. Large individuals of *Pasiphaea multidentata* (CL > 30 mm) remained on the bottom at night, where they even fed on benthic resources such as gammarids, the burrowing decapod *Calocaris macandreae* Bell 1864, and polychaetes, while smaller individuals moved away. Conversely, during the day smaller individuals were also present on the bottom and
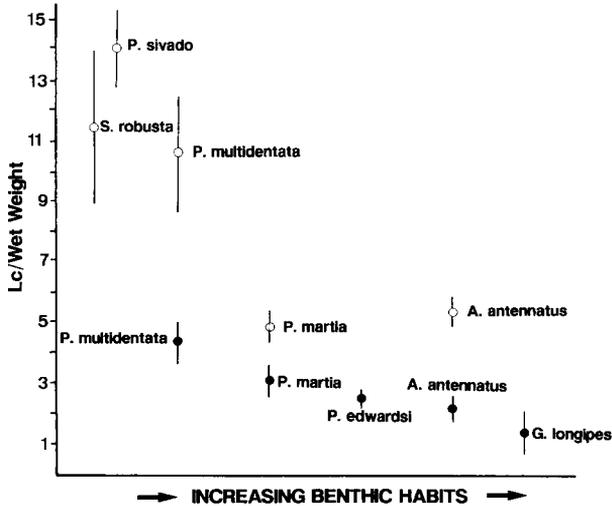
Fig. 3. Relationship between CL/wet weight (mean value and standard error) and benthic habits of different species considered (○, small individuals, CL between 15–20 mm; ●, adult individuals, CL between 25 and 35 mm).

predominated. Planktonic prey (mesopelagic fishes, euphausiids, etc.) in an advanced degree of digestion predominated in the stomach contents of these size classes (Cartes, 1991). These results were therefore indicative of vertical migration, primarily by juveniles, at night. In contrast, the behaviour of larger *Pasiphaea multidentata* (> 30 mm CL) more closely resembled that of nektobenthic species (Figs. 3 and 4).

The differences between day and night catches of nektobenthic species were not as marked. Catches of the pandalids *Plesionika edwardsi*, *Plesionika acanthonotus*, and *Plesionika martia* were more variable, with an increase in catches seen at night. Lower daytime ocurrences of *Plesionika martia* in the net samples were consistent with its daytime diet based on mobile mesopelagic prey (*Pasiphaea* spp.) (Cartes, 1991) for which *Plesionika martia* would exhibit a higher natatory activity. Catches rose at night, when passive feeding on benthic resources took place. Even so, the high proportion of full stomachs containing food in this species were not suggestive of a vertical migration to superficial water levels during the daytime. Rather, the shoals seemed to disperse, making irregular movements towards the Benthic Boundary Layer located a few metres above the bottom (Wishner, 1980; Hargreaves, 1984, Angel, 1990), or they spread out along the bottom towards shallower or deeper areas of the slope. *Aristeus antennatus* also appeared to follow a similar pattern. The highest catches of this species are taken early in the daylight hours (Maurin, 1962; Tobar and Sardà, 1992), suggesting that at night the bulk of the population migrates to shallower areas of the slope or upwards to layers of the water column farther away from the bottom (Maurin, 1962; Lagardère, 1972; Campillo et al., 1990). The present findings would be consistent with migration up the slope, in this case towards submarine canyons. The high nighttime catches of *A. antennatus* found in the shallower part of the canyon might result
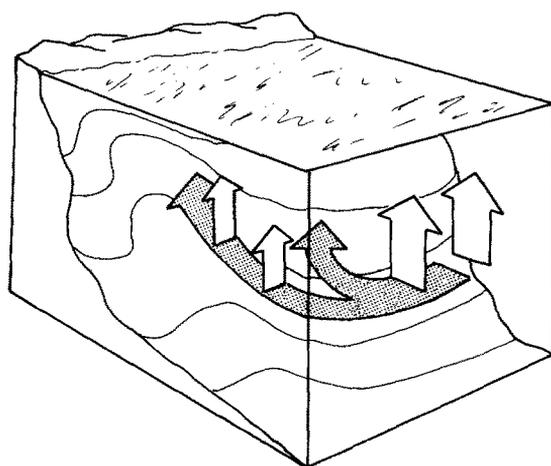

Fig. 4. Schematic representation of the hypothesis proposed for nocturnal migrations by mesopelagic species (white arrows) and nektobenthic species (black arrows).

from such migratory behaviour. Such is the upper depth distribution of this species in the Catalan Sea (Tobar & Sardà, 1987; Demestre, 1990). According to available data for this area, seasonality does not appear to be responsible for the changes in abundance observed for *A. antennatus* during the two sampling periods described herein (Tobar and Sardà, 1987). Moreover, vertical migration into the water column above would seem to be an unlikely explanation, in view of the small share of planktonic prey items in the nocturnal diet of this species (Cartes, 1991).

Mesopelagic species such as *Pasiphaea multidentata*, *Pasiphaea sivado*, and *Sergia robusta* displayed more pronounced migratory behaviour. All these species exhibit marked morphological differences with respect to the other species: carapace and pereiopods laterally compressed and with dorsal keels present, rostrum rudimentary, all of which seem to be common adaptations to a pelagic existence exhibited by a high number of pelagic species. Thus, although certain bathypelagic oplophorid species (e.g. some *Acanthephyra*, and *Systellapsis* spp.) have relatively long rostra, the rest of morphological features after cited prevailed among them. The presence of a long rostrum in pandalids and *Aristeus antennatus* has been related to a more benthic behaviour related to orientational mobility and balance with respect to the sea-floor (cf. Burukovsky, 1972; Sardà and Demestre, 1989). These species may be less adapted for extensive vertical migrations, partly because of their lower CL/wet weight ratio (Fig. 3). In fact, these latter species were not caught in the water column (planktonic hauls). Furthermore, part of their feeding strategy appears to be based on exploitation of mesopelagic species when the latter descend close to the bottom during their own diel migrations. However, occasional penetration by these nektobenthic species into the Benthic Boundary Layer cannot be ruled out and in fact has been reported for *Aristeus antennatus* (Campillo et al., 1990).

In conclusion, it is suggested that there may be two different patterns responsible for diel migrations by deep-water decapod crustaceans a schematic view of which is illustrated in Fig. 4. Shoals of certain nektobenthic species seem to undergo migrations along the bottom to shallower areas of the slope at night. This might account for the relatively high biomass recorded in the canyons in the present study. The submarine canyons possibly serve as areas of aggregation at night, an aspect already confirmed for planctonic organisms (Koslow & Ota, 1981). Particular hydrographic conditions such as up and downcanyon flows (Shepard et al., 1974; Monaco et al., 1990) or favourable food-resources (Haedrich et al., 1980; Houston & Headrich, 1984 and references cited) occurring in the canyons perhaps could be correlated with orientation and aggregation of shoals in these areas. Thus, several species (i.e. *Pasiphaea multidentata*, *Aristeus antennatus*, and *Plesionika martia*) showed higher foregut fullness index in specimens taken inside rather than outside the submarine canyons in the Catalan Sea (Cartes, 1991). On the other hand, mesopelagic species apparently carried out major vertical migrations which in the present study were more discernible in small individuals.

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