

Diel activity patterns in deep-living cumaceans and amphipods

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ABSTRACT: Cumaceans and amphipods at 150 m depth in Fanafjorden, western Norway, were studied in April, June, September and December 1979. Samples were collected by sledge at intervals of 0 to 80 cm and 30 to 80 cm above the sediment. Both in cumaceans and amphipods, daytime catches were characterized by low numbers of individuals in the 30 to 80 cm compared to the 0 to 80 cm interval (on average < 5 % of the catch in the 2 levels combined). During darkness, numbers of individuals as well as fraction of total catch increased in the upper level. The first signs of this nocturnal distribution, interpreted as a result of increased swimming activity, were found 1 to 2 h prior to sunset, but the main response came closer to dusk. Swimming activity seemed to decrease towards the end of the night. Enhanced nocturnal activity was found throughout the year. Seasonal variations in diel activity patterns coinciding with fluctuations in population structure were, however, apparent in some species. Consistently high sledge-catches at night indicate that the main part of the population remained relatively close to the substrate during darkness.

INTRODUCTION

Cumaceans and amphipods are abundant components of the hyperbenthos, i.e. the assemblage of animals living in the immediate vicinity of the bottom (Hesthagen 1973, Sainte-Marie & Brunel 1985). Cumaceans and many amphipods are known to burrow into the superficial layer of the sediment, while at times they swim for shorter or longer periods (Forsman 1938, Enequist 1949, Jones 1976). During darkness, many species occur planktonically (e.g. Russell 1931, Fage 1945, Whiteley 1948, Macquart-Moulin 1968, 1984, Corey 1970, Williams & Bynum 1972, Anger & Valentin 1976, Hesthagen & Gjermundsen 1979). Seasonal variations, species-specific patterns, and sexual differences in behaviour have been reported (Brunel 1979, Sainte-Marie & Brunel 1985).

Most studies on diel activity patterns have been carried out at water depths less than 30 m. Specimens in shallow water generally start to migrate into the water column shortly after sunset (Anger & Valentin 1976, Hobson & Chess 1976, Alldredge & King 1980). A continuous interchange of animals between the sediment and the water column may occur during the dark period, or specimens may live pelagically throughout the nocturnal activity period (Alldredge & King 1980). Contrasting observations have been made on the over-

all duration of nocturnal activity. Swimming has both been reported to decrease in the course of the night (Anger & Valentin 1976, Macquart-Moulin 1985) as well as to be maintained until sunrise the next morning (Hesthagen 1973, Alldredge & King 1980).

Results on deep-living cumaceans and amphipods (depths between 85 and 120 m) have confirmed the general trends of increased swimming activity in darkness (Messier & Brunel 1975, Brunel 1979, Cornet et al. 1983, Sainte-Marie & Brunel 1983, 1985). Brunel (1979) found 'twilight-evening swarming' in one gammarid species in light 'considered as diurnal from surface illumination but probably with night or twilight conditions at depth' (115 m). He suggests that this may be a common pattern in cumaceans and amphipods. It has been hypothesized that nocturnal activity in benthic invertebrates may start progressively earlier as light intensities decrease with increasing depth (Chapman et al. 1975). However, there has been little observation on the duration of the nocturnal swimming period in the deep-living cumaceans and amphipods.

In addition to causing an earlier emergence from the sediment in the afternoon, it has been proposed that the weaker light intensities may invoke higher swimming activity in peracarids during the day in deep waters than in shallow environments (Besner 1976, Fosså 1985). Sainte-Marie & Brunel (1983) have, how-

ever, questioned this view, and Fosså (1985) argues that light intensity is not the only factor responsible for different levels of daytime swimming activity between mysids from separate localities.

The present paper analyses diel activity patterns in cumaceans and amphipods in deep water. The following cumaceans were studied: *Leucon nasica* (Krøyer), *Campylaspis costata* G. O. Sars, and *Diastylodes* spp. G. O. Sars. The latter genus was represented by *D. biplicata* G. O. Sars and *D. serrata* G. O. Sars of which the juveniles were difficult to separate. The amphipods studied were *Monoculodes packardi* Boeck, *Westwoodilla caecula* (Bate), *Bathymedon longimanus* (Boeck), *Bruzelia typica* Boeck, and *Pardalisca tenuipes* G. O. Sars.

MATERIAL AND METHODS

Sampling was performed at 150 m depth in Fanafjorden, western Norway, on 4–5 April, 18–19 June, 12–13 September and 10–11 December 1979. A description of Fanafjorden is given by Lie (1978) and Wassmann (1984). Hyperbenthic samples were collected by a modified version of a Beyer epibenthic sledge, the 'Three net sledge' (Fig. 1 in Oug 1977). The lower edge

of each net opening is located 30 cm above the bottom, but a concave sloping plate in front of one of the nets facilitates sampling down to the sediment surface. Usually this 'lower net' also takes some sediment with epi- and infauna. 2 'upper nets' sample the depth interval 30 to 80 cm above the bottom. Animals from the upper net are thus interpreted to have been caught swimming above the sediment (see 'Discussion'). The sledge was towed a fixed distance of about 600 m at about 1 knot. Samples were preserved in 5 % neutralized formaldehyde. Individuals were identified and grouped as juveniles, mature males and mature females. In *Pardalisca tenuipes*, for methodological reasons, only the total number was noted.

Light was measured by a Li-Cor 190 quantum sensor. Surface values were continuously registered. Light transmission was recorded twice a day down to 50 m which was the maximum depth obtainable with the equipment at hand. Transmission to the sampling depth was estimated by extrapolation of a regression line based on measurements from 40, 45, and 50 m. Light conditions during sampling are given in Table 1.

For statistical treatment, the samples were grouped with respect to whether they originated from day or night hauls (Tables 2 & 3). From each survey, the 3 (2)

Table 1. Sampling schedule, cloud cover, and light conditions during sampling in Fanafjorden

Date	Time of sampling	Cloud cover	Light intensity surface ($\mu\text{E m}^{-2} \text{s}^{-1}$)		Estimated transmission at 150 m (%)
			Start of haul	End of haul	
4 Apr	1140 – 1156	Cloudy	960	1140	1.5×10^{-7}
	1810 – 1831	Clear	168	150	
	1942 – 2003		34	4	
	2304 – 2324				
5 Apr	0530 – 0550			3	
	0759 – 0819		230	430	
18 Jun	1236 – 1256	Cloudy	340	260	7.2×10^{-6}
	2004 – 2024		420	440	
	2158 – 2218		–	0.4	
	2325 – 2343				
19 Jun	0231 – 0250	Partly cloudy		2	
	0430 – 0450		36	71	
12 Sep	1726 – 1747	Cloudy	68	76	1.3×10^{-8}
	1922 – 1941		1	0.1	
	2121 – 2141				
13 Sep	0520 – 0538			0.2	
	0726 – 0745		66	96	
10 Dec	1130 – 1150	Clear	150	144	2.7×10^{-5}
	1356 – 1416		86	70	
	1608 – 1627		0.7	0.1	
	1833 – 1853				
11 Dec	0818 – 0839		130	150	
	1105 – 1127				

Table 2. Catches of cumaceans in day and night samples from Fanafjorden (N = number of samples). Numbers of individuals (n) summed for the 2 upper nets are represented by upper figures and numbers in the lower net by lower figures. Fraction (%) of total catch in the upper nets (based on mean from the 2 nets) is given in parentheses. Level of significance for differences between day and night catches in the upper nets: ** p < 0.01; * p < 0.05; Ns = not significant

Species	Apr		Jun		Sep		Dec		Total		Significance
	Day N = 3	Night N = 3	Day N = 3	Night N = 3	Day N = 2	Night N = 2	Day N = 3	Night N = 3	Day N = 11	Night N = 11	
<i>Leucon nasica</i>	6 (0.8) 374	76 (8.1) 426	9 (2.0) 219	78 (13.4) 251	13 (5.0) 123	104 (15.8) 278	0 (0.0) 26	3 (6.3) 22	28 (1.9) 742	261 (11.8) 977	**
<i>Campylaspis costata</i>	2 (1.1) 93	30 (8.9) 154	2 (1.2) 84	21 (10.6) 89	4 (9.5) 19	20 (28.6) 25	0 (0.0) 47	3 (4.2) 34	8 (1.6) 243	74 (10.9) 302	**
<i>Diastylodes</i> spp.	0 (0.0) 80	0 (0.0) 118	9 (1.6) 272	42 (6.5) 296	2 (3.7) 26	23 (36.5) 20	0 (0.0) 2	4 (20.0) 8	11 (1.8) 308	69 (7.2) 442	Ns (* when April excluded)

Table 3. Catches of amphipods in day and night samples from Fanafjorden (N = number of samples). Numbers of individuals (n) summed for the 2 upper nets are represented by upper figures and numbers in the lower net by lower figures. Fraction (%) of total catch in the upper nets (based on mean from the 2 nets) is given in parentheses. Level of significance for differences between day and night catches in the upper nets: ** p < 0.01; * p < 0.05; Ns = not significant

Species	Apr		Jun		Sep		Dec		Total		Significance
	Day N = 3	Night N = 3	Day N = 3	Night N = 3	Day N = 2	Night N = 2	Day N = 3	Night N = 3	Day N = 11	Night N = 11	
<i>Monoculodes packardii</i>	36 (5.5) 307	275 (19.1) 583	2 (0.8) 36	19 (5.0) 194	8 (1.3) 294	363 (34.8) 340	2 (0.2) 496	18 (2.2) 399	48 (1.9) 1226	675 (18.2) 1516	*
<i>Bathymedon longimanus</i>	11 (4.8) 109	37 (12.5) 129	10 (14.3) 30	12 (13.0) 40	2 (3.1) 31	10 (33.3) 10	0 (0.0) 70	22 (15.7) 59	23 (4.6) 240	82 (14.7) 238	Ns
<i>Westwoodilla caecula</i>	2 (2.2) 44	51 (27.9) 66	4 (6.5) 29	30 (34.9) 38	2 (10.0) 9	13 (52.0) 6	0 (0.0) 18	11 (33.3) 11	8 (3.8) 100	105 (30.3) 121	**
<i>Bruzelia typica</i>	7 (10.8) 29	31 (20.3) 61	10 (6.2) 75	33 (11.1) 132	2 (4.0) 24	12 (15.0) 34	1 (1.1) 43	15 (14.9) 43	20 (5.5) 171	91 (14.4) 270	**
<i>Pardalisca tenuipes</i>	0 (0.0) 22	25 (18.0) 57	1 (4.8) 10	39 (28.9) 48	0 (0.0) 8	20 (34.5) 19	0 (0.0) 15	8 (19.0) 17	1 (0.9) 55	92 (24.6) 141	**

hauls from sunset until sunrise (Fig. 1 & 2) were considered as night hauls, while the 3 (2) others were considered as day hauls. Testing for differences was done by means of 2-way ANOVA (Sokal & Rohlf 1981) applied on log-transformed data from the upper net catches.

RESULTS

Cumacea

The daytime catches were characterized by low numbers of specimens in the upper compared to the lower net (Table 2).

Catches in the upper nets were significantly higher in darkness than during daylight, but still the main fraction was taken in the lower net (Table 2). An exception to the general increase in nocturnal catches above the sediment appeared in *Diastylodes* spp. in April. On this occasion, the population consisted of very small individuals. The apparent lack of vertical migration for this species in April leads to an insignificant result when testing for diel variations on the total material. When excluding the April samples from the analysis, significant diel cycles were revealed (Table 2).

Nocturnal increases in upper net catches were generally feeble in December, possibly because of small population-sizes at this time of the year (Table 2).

Marked sex-specific patterns in swimming activity were found in *Leucon nasica* and *Campylaspis costata* in September. The dominance of mature males above the bottom during darkness (Fig. 1) was also reflected in the corresponding lower net catches. On the other hand, for both species lower net catches during day were clearly dominated by juvenile individuals. Mature males of *L. nasica* and *C. costata* were very scarce in the population at the other seasons sampled. Nevertheless, the same overall increase in swimming at night was found, then mainly carried out by juvenile specimens.

The first trace of nocturnal swimming was indicated in the afternoon (Fig. 1). This is best documented for *Leucon nasica* in September. On this occasion, both the number of individuals in the upper nets (13) as well as the fraction of males (10 individuals) suggest an initiation of nocturnal swimming 1 to 2 h prior to sunset.

Catches generally decreased towards the end of the night.

Amphipoda

As for the cumaceans, daytime samples were characterized by low numbers of specimens in the upper compared to the lower net (Table 3).

In 4 of the 5 species, there was a significant increase in upper net catches during darkness. Nevertheless, the main part of the catches still originated from the lower net (Table 3). Significant difference between day and night was not found for *Bathymedon longimanus* in the overall material, although there were indications of enhanced nocturnal activity some of the nights. Because of the separation in time between individual hauls, these cannot be considered as replicates. This is highlighted by the marked maximum in catches of *B. longimanus* in some of the tows (see below). Trends in single nights could thus not be tested statistically.

A seasonal variation in diel activity patterns coinciding with changes in the presence of mature males in the population was obvious in *Monoculodes packardii*. Mature males prevailed in the high nocturnal upper net catches in April and September (Fig. 2). Lower net catches, however, were in April dominated by mature females both day and night, except at sunset when the 2 sexes were equally represented. Females were caught in high numbers in the lower net in September also. In June and December the nocturnal increase in swimming activity was less conspicuous (Table 3). In these cases, the population was dominated by juvenile individuals.

In April, the first sign of emergence from the sediment was found already prior to sunset. The tow in the afternoon (finished about 1 h prior to sunset), gave 28 individuals (of which 23 were males) of *Monoculodes packardii* in the upper nets. Occasionally, conspicuous peak catches were obtained at sunset (e.g. *M. packardii* in April and September). In other cases (e.g. *Bathymedon longimanus* in April and December and *Pardaliscia tenuipes* in April and June) there was a marked maximum in catches after some hours of darkness (Fig. 2).

There was a recurrent decrease in catches towards the end of the night.

DISCUSSION

The difficulties in obtaining replicate quantitative samples of the hyperbenthic fauna have been focused on by a number of authors (e.g. Hesthagen 1973, Anger & Valentin 1976, Hesthagen & Gjermundsen 1978, Huberdeau & Brunel 1982). These difficulties seem to arise from the lack of a gear sampling the lowermost cm towards the sediment adequately, rather than from biological factors like patchiness. In my investigation, also, haul-to-haul variations in catches by the lower net were substantial. This was at least in part caused by methodological problems such as varying by-catch of animals in sediment collected by the sledge (Anger & Valentin 1976). A detailed analysis of the lower

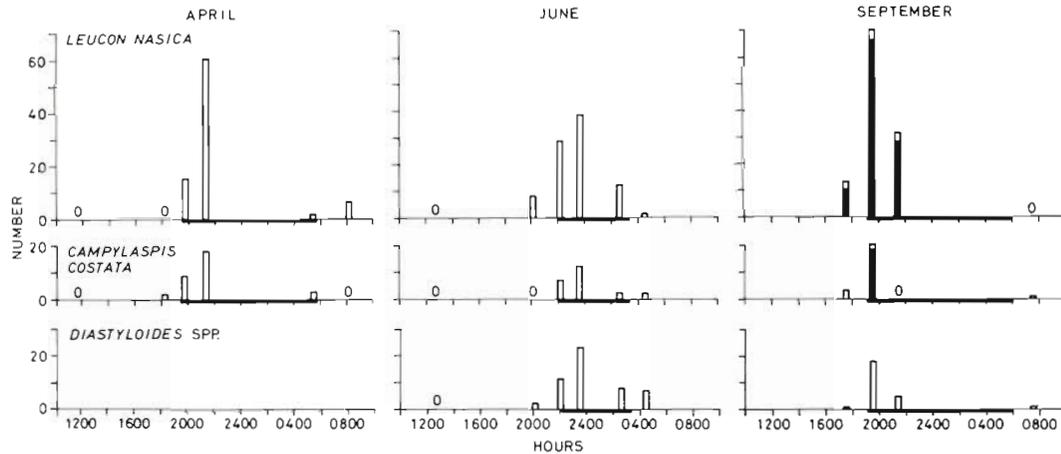


Fig. 1. Catches of cumaceans in the 2 upper nets (30 to 80 cm above the sediment) in Apr, Jun and Sep (there were no upper net catches of *Diastylodes* spp. in Apr and for all species only negligible catches in Dec). In Sep, mature males of *Leucon nasica* and *Campylaspis costata* are represented by filled part of histograms. Unfilled histograms otherwise represent all categories combined. Time interval between sunset and sunrise is indicated by a heavy line

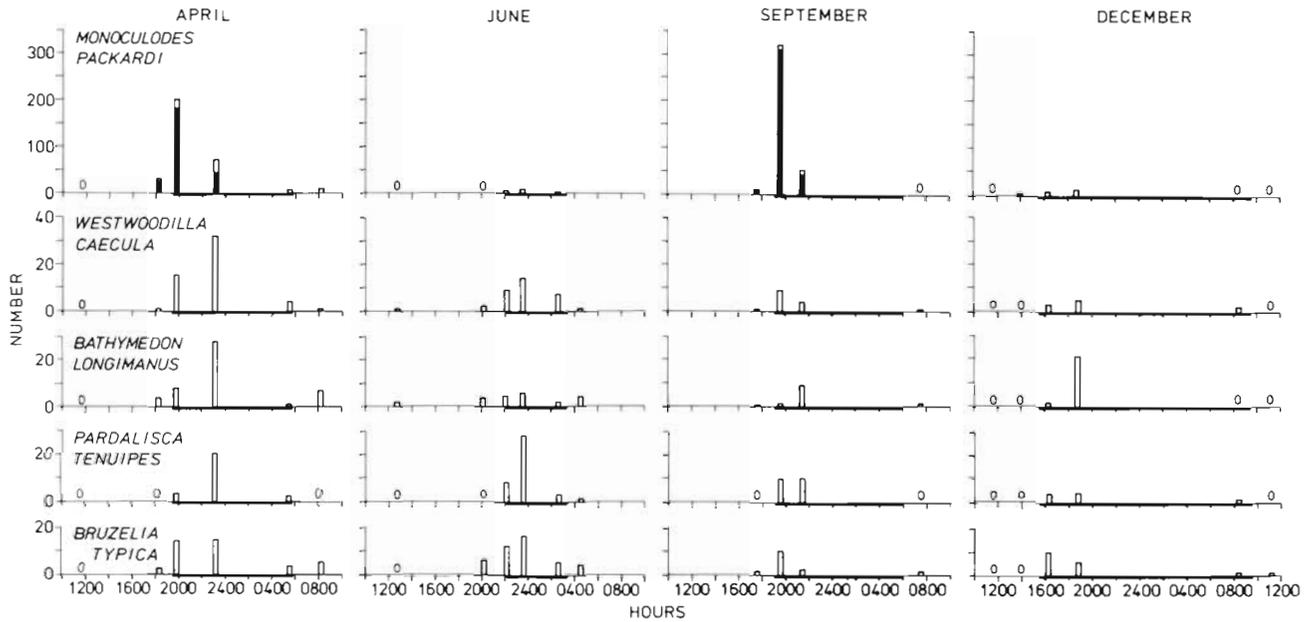


Fig. 2. Catches of amphipods in the 2 upper nets (30 to 80 cm above the sediment) in Apr, Jun, Sep and Dec. In Apr and Sep, mature males of *Monoculodes packardii* are represented by filled part of histograms. Unfilled histograms otherwise represent all categories combined. Time interval between sunset and sunrise is indicated by a heavy line

net catches therefore seemed unwarranted. Such methodological problems, however, do not relate to the upper net catches, and by means of these, the present investigation has revealed significant diel cycles in vertical distribution above the sediment both in cumaceans and amphipods.

The observations demonstrate that both the cumaceans and amphipods lived in close vicinity to the bottom during the day. This is in accordance with the general knowledge of species in shallow water (Anger & Valentin 1976, Hobson & Chess 1976, Jones 1976, Alldredge & King 1980, 1985, Stretch 1985). The esti-

mates of transmission of light to 150 m are too unreliable for detailed analysis of the data. It can nevertheless be concluded that the substantial fluctuation in the extinction of the surface illumination (Table 1) must have caused marked seasonal variations in the light intensities near the bottom. Still there were no indications of seasonal differences in daytime distribution. Within the prevailing light intensities there is consequently no support for the view that the weak light in deep waters may invoke a noteworthy increase in swimming activity during daylight (Besner 1976, Fosså 1985).

There was, however, a tendency towards an earlier start of nocturnal swimming than has been reported for the shallow water populations. Considering the time for onset of nocturnal swimming, an hourly scale with sunset as the cue factor seems to be a more natural reference than the absolute light intensities. The shift towards an onset of nocturnal activity prior to sunset was less extensive than has been proposed for other benthic invertebrates (Chapman et al. 1975), but in accordance with what was found for mysids in the same locality (Kaartvedt 1985). Since the large-eyed mysids, and the cumaceans and amphipods which have more poorly developed eyes, responded to changes in light intensity in the same time interval (0 to 2 h prior to sunset), any differences in exact time for initiation of vertical migrations may rather be species-specific than governed by the accomplishment of visual organs. Visual power has been used as an important factor in classification of other aspects of nocturnal behaviour (Brunel 1979).

A decrease in catches in the course of the night may either be caused by the animals swimming higher up in the water column, above the region sampled by the sledge, or be a result of re-entry to the sediment (Hesthagen 1973). By the latter interpretation, the recurrent decrease in upper net catches towards the end of the night is in accordance with *in situ* observations by Anger & Valentin (1976) who found a return to the sediment after some hours of swimming in *Diastylis rathkei*. These results indicate a difference in the photokinetic control of activity between dawn and dusk (cf. Macquart-Moulin 1985).

The proportion in a population that performs vertical migrations cannot be established because reliable estimates of the total population as well as the number of specimens that have left the sediment are lacking. The extent of the vertical migrations also cannot be determined by the method used. Single specimens of cumaceans and amphipods can often be found well up in the water column. Kaartvedt (1982) reports on a male specimen of *Monoculodes packardii* caught at least 50 m above the bottom and both *M. packardii* and *Westwoodilla caecula* have earlier been reported from planktonic catches at night (Bossanyi 1957, Macquart-Moulin 1984, Sainte-Marie & Brunel 1985). However, the generally high numbers caught near the bottom at night (Tables 2 & 3) indicate that the main part of the population remained relatively close to the substrate during darkness. This picture differs from the results on the mysids in the same locality (Kaartvedt 1985). In general, mysids disappeared from the hyperbenthic region at night. The same tendency was found by Brunel (1979). In mysids with what Brunel called 'functional eyes', large proportions of the populations migrated far up into the water column, while most

amphipods and cumaceans performed nocturnal vertical migrations of limited extent.

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