

FEEDING RHYTHMS AND VERTICAL DISTRIBUTION OF MARINE COPEPODS

M. H. Daro

ABSTRACT

Three marine ecosystems are compared: the English Channel, the Southern Bight of the North Sea and the northern North Sea. Shipboard grazing experiments and countings of zooplankton were carried out at different depths of the water column during 24- to 48-h measurements of intervals of 4 or 6 h. In the English Channel, in late April, a shallow homogeneous water column (50 m), higher feeding rates in the deeper layers were observed due to the larger abundance of *Pseudocalanus elongatus*, during the 24-h period, resulting in an absence of upwards swarming at night, but an evident higher feeding at night. At the same station, the other dominant copepod *Oithona* showed higher feeding rate in the daytime. Secondly, in the Southern Bight, another shallow homogeneous system (25 m), vertical migration together with increasing feeding at night could be observed for *Temora longicornis* and *Pseudocalanus elongatus* in the month of May. Thirdly, in the northern North Sea, phytoplankton and zooplankton vertical distribution are strongly correlated but limited in the first 30 m above the thermocline. No vertical movements in this narrow space were observed, but there was a preference for a definite depth for each of the copepod species.

It is a known fact that zooplankton, particularly copepods, are able to vertically migrate 10 to 100 m every night (Cushing, 1951). It has been observed that copepod grazing is much more important at night (Fuller, 1937; Gauld, 1951). The link between active swarming behavior at night and increasing feeding activity was emphasized in different cases, particularly for *Calanus finmarchicus* (Daro, 1980). Many authors hypothesized that food distribution and vertical distribution of zooplankton are associated (Mullin and Brooks, 1972). The time spent at night in the upper layers is inversely proportional to the abundance of food (Pearre, 1973; Mackas and Bohrer, 1976; Arashkevich, 1977). Recently, suggestions that vertical migration behavior and feeding activity in many cases are not so linked: for krill (Morris and Ricketts, 1984), for the copepods, *Calanus* and *Pseudocalanus* (Bohrer, 1980). Rather, other environmental factors, such as species diversity and competition or seasonal factors (Williams and Conway, 1984), are playing an important role in modifying the migratory and feeding behavior.

My work for the past few years has been on zooplankton grazing in the Southern Bight of the North Sea, a very shallow ecosystem (25 m), with very strong tidal and residual currents, where mixing plays an important role. On several occasions, I observed migratory patterns and feeding rhythms in zooplankton. The results presented here are part of a more general research frame, where I have studied the grazing pressure on phytoplankton in different marine ecosystems. A few years ago, I came to the conclusion that in shallow and coastal ecosystems zooplankton grazing does play only a minor role in recycling organic matter provided from phytoplankton (Joiris et al., 1982). This observation contrasts with results obtained in the open ocean where almost 100% of primary production is grazed away by zooplankton. I compared the food chain structure of different ecosystems and the results presented here are from cruises in the English Channel, in the Southern Bight of the North Sea and in the northern North Sea.

METHODS

Measurements were made from an anchored ship at a fixed station every 4 or 6 h during 24 or 48 h. The English Channel station, on 28–30 April 1983, was located at 49°54'N, 03°52'E, the Southern Bight station, on 27–30 May 1981, at 51°23'N, 02°26'E, and the northern North Sea station, on 14–16 September 1983, at 57°34'N, 00°39'E (Fig. 1). Zooplankton was collected with Nansen bottles at 5-m intervals to the bottom at the Southern Bight station, and at 10-m intervals to the bottom at the two other stations; 30–40 liters were collected and preserved in 4% Formalin for enumeration; 2 × 5 liters were used for the feeding experiments. The method used in the feeding experiments was described by me (Daro, 1978). It consists of adding C¹⁴-bicarbonate to the natural sample of 5 liters at the time of the experiment, incubated under natural light of day; at night, phytoplankton alone is prelabelled for 1 or 2 h under artificial light, after which zooplankton is added to the radioactive phytoplankton, the grazing experiment occurring then in the dark. All grazing experiments have a maximal time of 1 h.

RESULTS

English Channel April 1983.—Two species dominate the species composition of the 48-h experiment on 28–30 April 1983: for *Pseudocalanus elongatus* (4,000 to 6,000 copepodites per m³ and 2–3,000 adults per m³) and for *Oithona similis*, 2–5,000 adults and 2–5,000 copepodites per m³ concerning *Pseudocalanus*. *Acartia clausi* were present in much smaller numbers (1,000 copepodites and 200–400 adults per m³). The figures for nauplii, which are always numerous in spring, vary between 10,000 and 40,000 per m³. No clear vertical movement of each of the different species could be detected, but there was a constant heterogenous distribution of the two dominant species, with a clear preference for the depths near the bottom (40–50 m), with the exception that *Oithona* copepodites dominated at the 10-m depth at 1300 h. Table 1 summarizes the data.

Feeding experiments carried out every 6 h at two different depths (3 and 30 m) show clear differences in feeding behavior of the dominant species. Figure 2a and b shows the results for the adult females of *Oithona* and *Pseudocalanus*, expressed in $\mu\text{g chlorophyll} \times 10^{-3}/\text{animal/h}$. At 3 m *Oithona* and *Pseudocalanus* show inverse feeding rhythms. *Oithona* fed at a maximum rate at 1300 h and *Pseudocalanus* fed at night. At 30-m depth *Pseudocalanus* has a much higher feeding rate (the minimum at 30 m being equal to its maximum at 3 m), with the same feeding rhythm. *Oithona* feeding rhythm and rate remain almost the same at 3-m and 30-m depths.

Figure 3a and b shows the vertical distribution of POC and chlorophyll, the vertical distribution of zooplankton carbon (all species together) and the total grazing expressed in carbon. Two remarks can be made: (1) the phytoplankton (chlorophyll) as well as the POC are more or less homogeneously distributed throughout the water column, but there is no correlation between these two parameters; (2) the vertical distribution of zooplankton is strongly heterogenous, its biomass being 2 to 5 times higher near the bottom than at the surface and the grazing being more important near the bottom than at the surface (up to 10 times more); this phenomenon is more pronounced because of the higher ingestations by *Pseudocalanus* in the deeper layers.

We have here an ecosystem where, during the phytoplankton bloom in late April, the zooplankton do not make diel vertical migrations, but clearly show a feeding rhythm. *Oithona* has higher feeding rates during the day at 1300–1900 h while *Pseudocalanus*, which occurs in deeper layers, considerably increases its grazing at night 2100–0200 h. As it is homogeneously distributed throughout the water column, phytoplankton in this case does not seem to stimulate the feeding behavior.

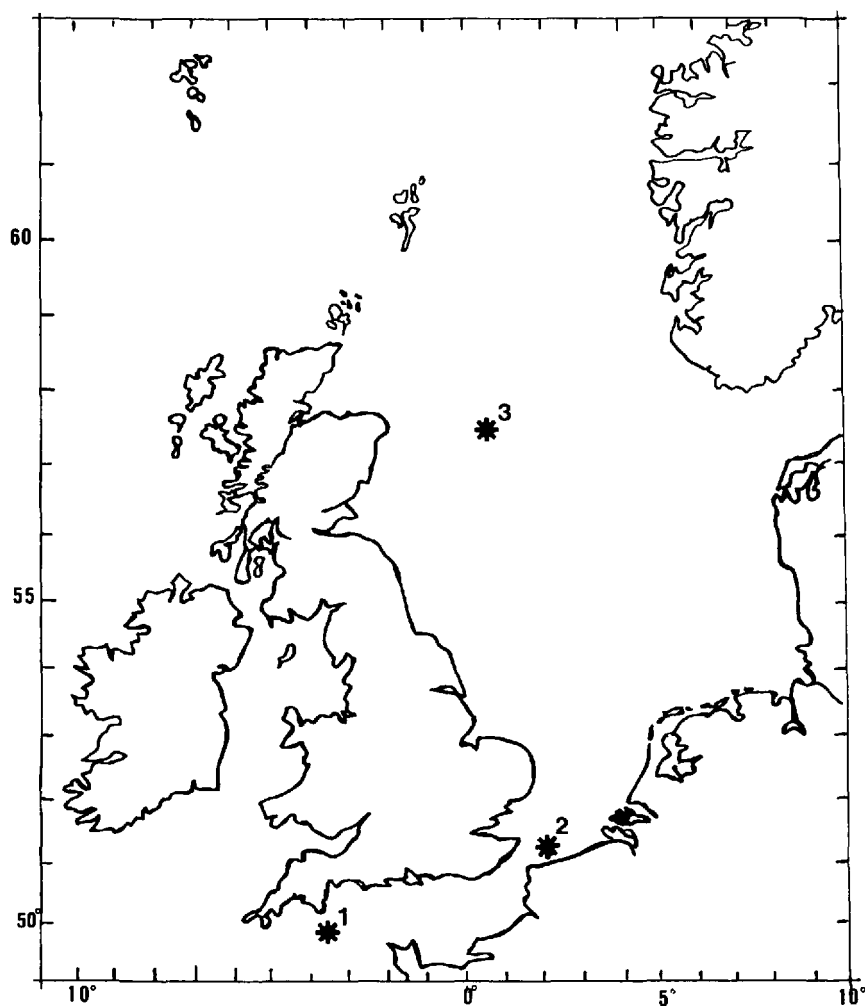


Figure 1. Position of different sampling stations: Station 1, English Channel 28 April 1983; Station 2, Southern Bight May 1981; Station 3, northern North Sea September 1983.

Southern Bight of the North Sea May 1981.—As I stated earlier, vertical mixing is an important factor in this shallow sea. These conditions are encountered by the phytoplankton during the May bloom (Fig. 4a). Nevertheless, calm weather induces heterogeneity of the zooplankton vertical distribution (Fig. 4b). Vertical movements at night to the surface are clear for *Temora longicornis* and *Pseudocalanus elongatus*; these movements occur with increasing feeding rates (Fig. 4a) at the surface, by a factor of 10 between 1500 and 2300 h. Considering this second ecosystem, phytoplankton is homogeneous throughout the water column, but zooplankton performs diel vertical migrations followed by increasing its feeding rhythm at night, at least at this period of the phytoplankton bloom. Indeed, in other periods, in summer particularly, *Temora* loses its feeding rhythm (Daro, 1985).

Northern North Sea September 1983.—This part of the North Sea, which is much

Table 1. Dominant species (Nb/m³) at the English Channel Station on 28–30 April 1983 vertical distribution (Maximum is underlined; most animals found at 40–50 m depth all the time, with a few exceptions for *Oithona*)

Depth (m)	1 h					7 h				
	<i>Oithona</i> ad.	<i>Oithona</i> copites	<i>Pseudo-calanus</i> ad.	<i>Pseudo-calanus</i> copites	Nauplii	<i>Oithona</i> ad.	<i>Oithona</i> copites	<i>Pseudo-calanus</i> ad.	<i>Pseudo-calanus</i> copites	Nauplii
3	2,200	3,000	1,800	1,600	<u>22,400</u>	1,200	2,400	200	1,000	18,200
10	<u>4,200</u>	3,400	2,200	1,000	<u>19,600</u>	1,500	1,500	250	500	17,750
20	<u>2,400</u>	2,400	3,000	1,800	<u>14,200</u>	1,600	1,800	50	1,400	11,200
30	2,000	2,100	3,100	2,200	17,200	1,000	1,700	700	600	7,000
40	1,800	<u>5,200</u>	3,400	2,000	18,000	<u>3,400</u>	3,800	800	<u>3,600</u>	<u>21,400</u>
50	<u>4,200</u>	3,800	<u>4,000</u>	2,600	21,600	2,500	<u>7,100</u>	<u>1,800</u>	3,200	18,400
	13 h					19 h				
3	100	200	100	200	3,400	600	1,000	100	600	<u>36,000</u>
10	1,600	<u>6,800</u>	100	2,600	14,200	1,000	2,800	100	1,000	23,400
20	600	2,400	200	1,000	8,200	1,600	3,600	200	1,400	13,400
30	700	1,900	400	1,400	7,400	600	1,200	300	1,000	11,400
40	2,200	5,200	1,600	3,600	<u>18,400</u>	1,400	2,400	1,600	4,200	13,000
50	<u>3,400</u>	4,000	<u>1,800</u>	<u>4,400</u>	17,200	<u>5,200</u>	<u>6,000</u>	<u>2,800</u>	<u>5,800</u>	21,200

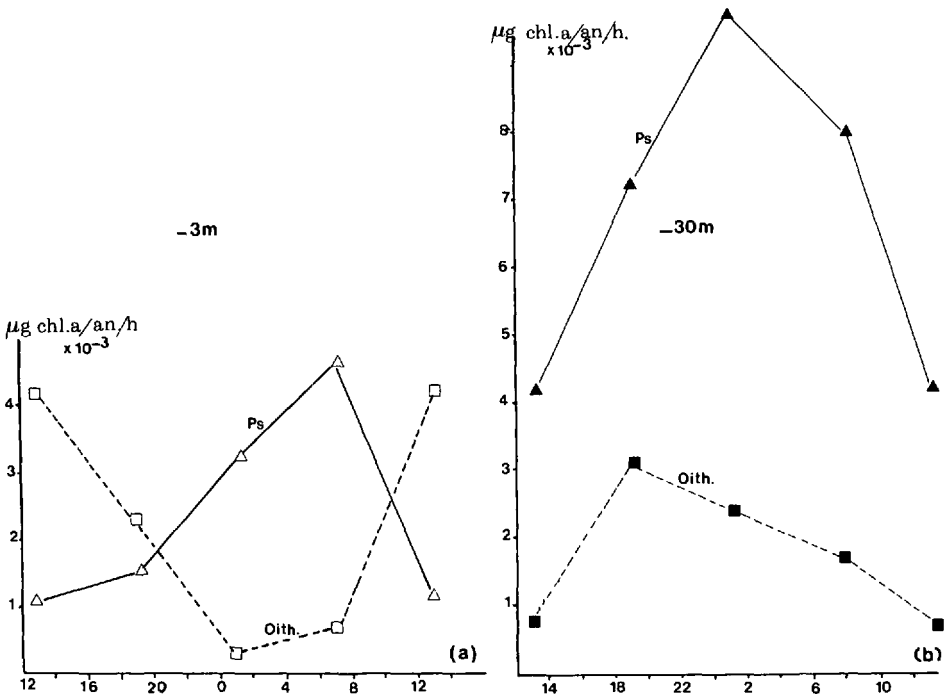


Figure 2. Individual hourly ingestion rates during 24 h for the two dominant species at the English Channel Station: Oith = *Oithona*; Ps = *Pseudocalanus*; (a) at 3 m depth; (b) at 30 m depth.

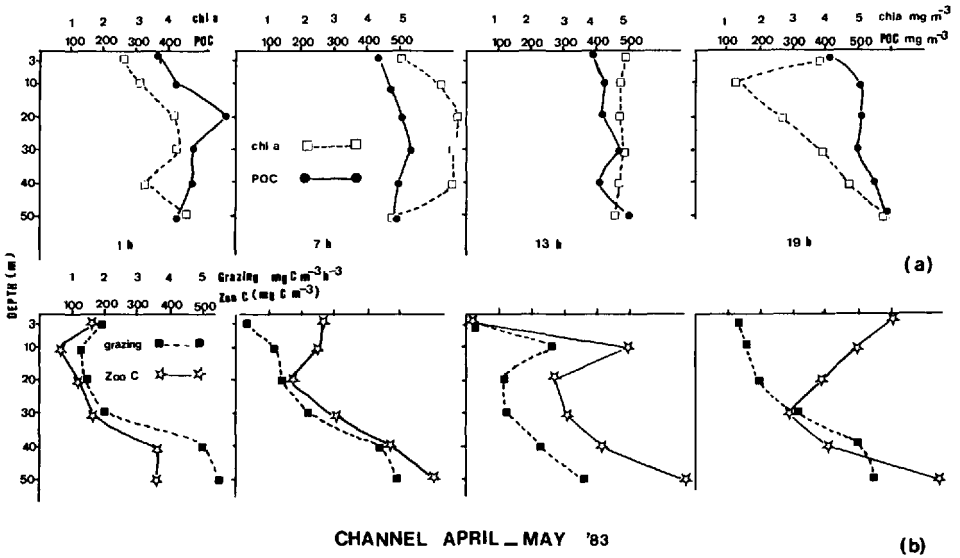


Figure 3. Vertical distribution of biological parameters at different times of the day at the English Channel Station: (a) chlorophyll and POC; (b) grazing and zooplankton C.

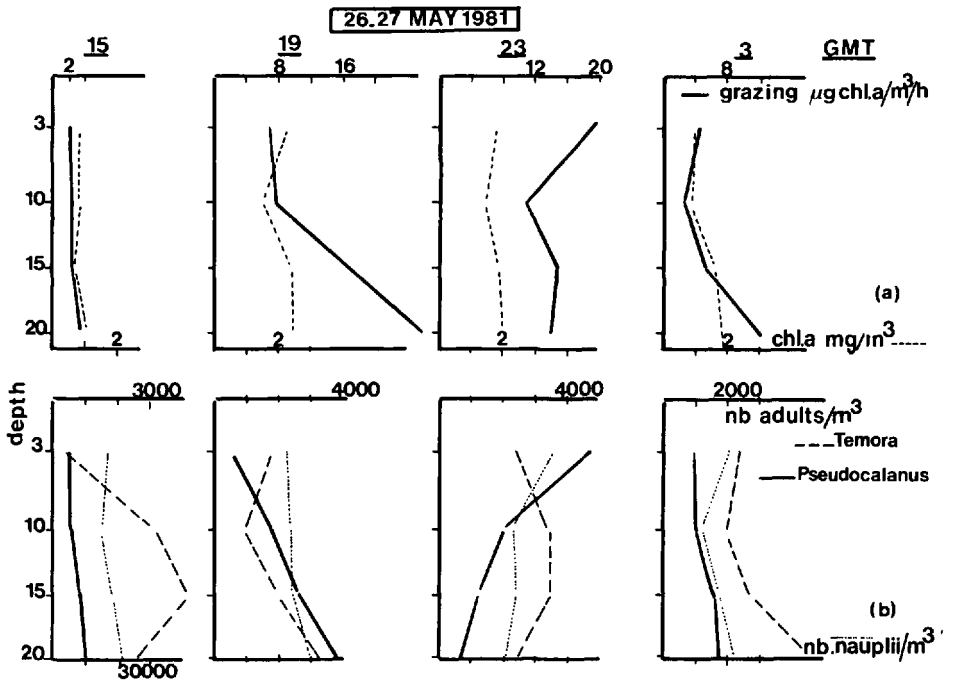


Figure 4. Vertical distribution of biological parameters at different times of the day at the Southern Bight Station: (a) chlorophyll and grazing; (b) numbers of copepods *Temora-Pseudocalanus* and nauplii.

**VERTICAL DISTRIBUTION CALANOIDEA
NORTHERN NORTH SEA SEPTEMBER '83**

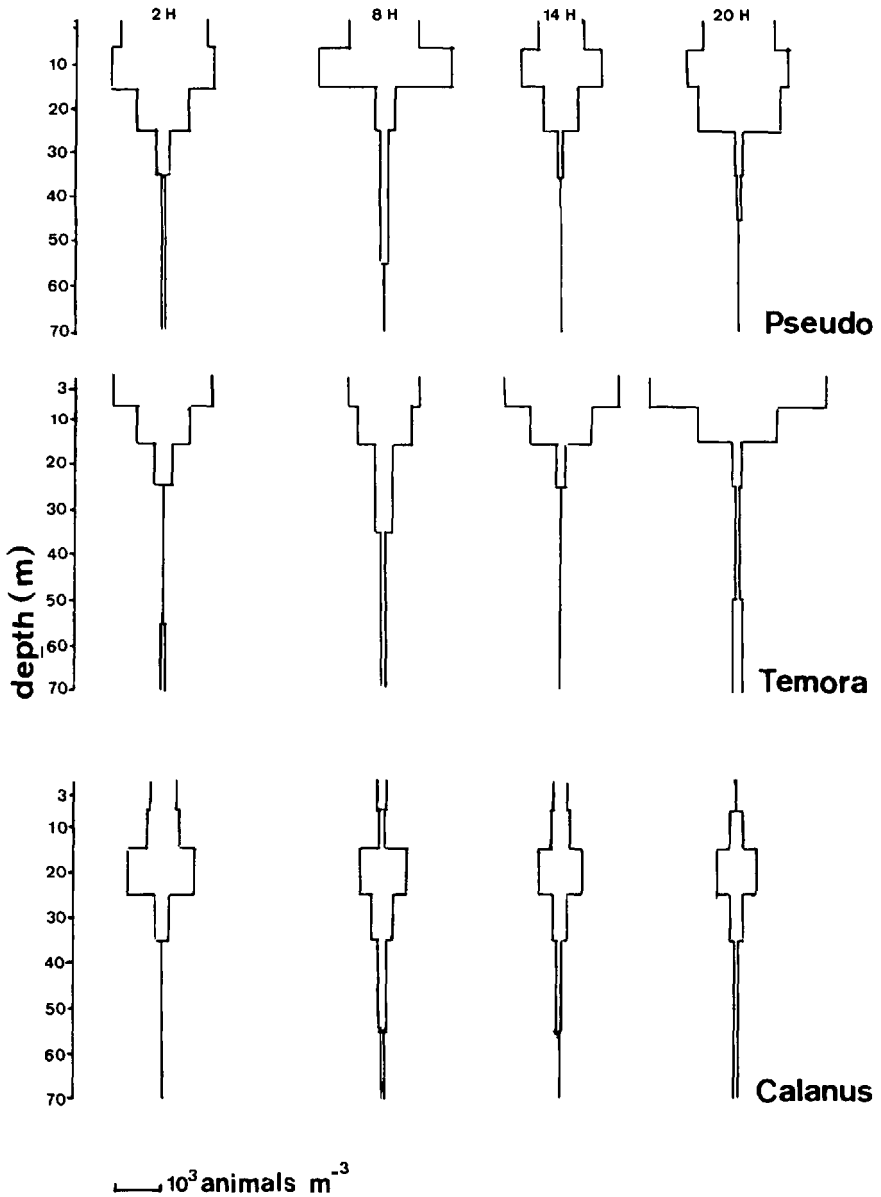
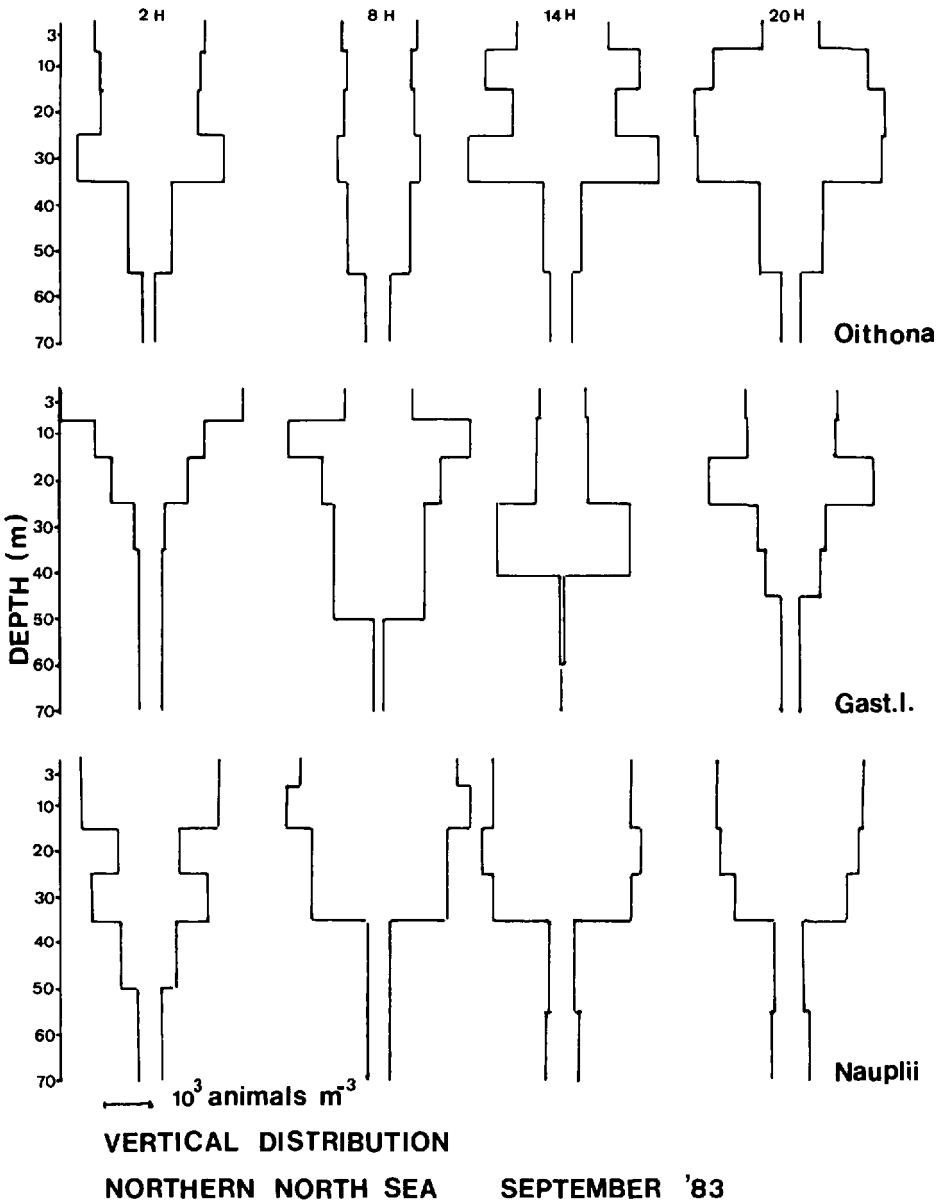


Figure 5. Vertical distribution of numbers of animals at the northern North Sea Station: (a) copepods (*Pseudocalanus*, *Temora*, *Calanus*); (b) *Oithona*, gastropod larvae and nauplii.

deeper (100–200 m) than the Southern Bight, is marked by a physical heterogeneity of the water column. At this time of the year the thermocline is very persistent at about 30 m, where a change of 2°C is observed within. Biological heterogeneity is also observed: calanoid copepods (Fig. 5a) are all observed in the first 20 m, with only a few animals below the thermocline. I also detect, among the Calanoidea,



a preference for *Temora* at the surface, for *Pseudocalanus* at 10 m depth and for *Calanus* at 20 m depth. As to the other dominant species of zooplankton (Fig. 5b), substantial numbers of *Oithona*, nauplii and gastropod larvae are found below the thermocline, although the largest numbers are present above 30 m.

Very remarkable for the Calanoida is the total absence of vertical movements and a constant distribution pattern. The only species showing vertical displacement of the maximal numbers are gastropod larvae, a fact not very often observed in meroplankton. The phytoplankton vertical distribution (Fig. 6a) shows a strong

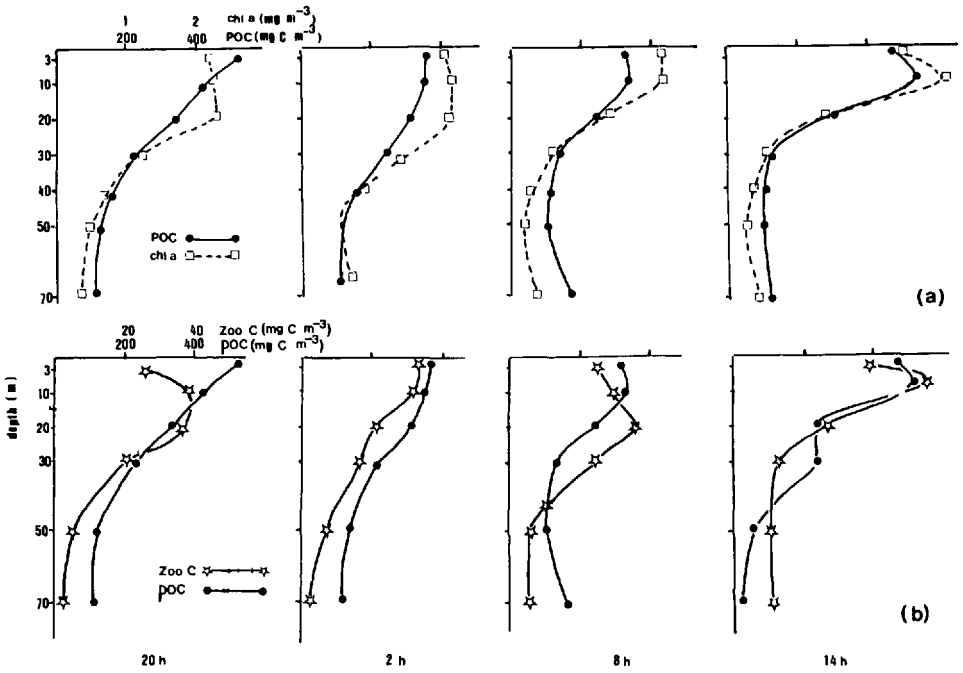


Figure 6. Vertical distribution of biological parameters at the northern North Sea Station: (a) chlorophyll and POC; (b) zooplankton C and POC.

heterogeneity as does chlorophyll and POC. These two parameters are very strongly correlated ($r = 0.91$). In Figure 6b the total zooplankton carbon (all species together) is shown. The vertical distribution follows the phytoplankton vertical distribution almost exactly.

The following table summarizes all results of grazing experiments. For *Calanus* ♀ and stage V much higher rates are measured at sunset and night. In the case of copepodites of *Pseudocalanus* and *Temora* the higher rates could be artefacts.

Table 2. Feeding in $\mu\text{g C}/\text{animal}/\text{h}$ in northern North Sea September 1983 at different times of the day (Significant differences are underlined)

20 h	2 h	8 h	14 h	
<u>3.01</u>	<u>4.08</u>	0.12	0.39	<i>Calanus</i> ♀ + V
0.42	0.8	0.33	—	Copepodites III-IV
0.37	0.55	0.48	0.28	<i>Pseudocalanus</i> ♀ V
0.25	<u>0.48</u>	0.07	0.06	III-IV Copepodites
0.16	0.07	0.06	0.09	I-II Copepodites
0.41	0.70	0.47	0.41	<i>Temora</i> ♀ ♂ V
0.24	—	0.38	0.12	III-IV Copepodites
0.15	<u>0.65</u>	—	0.01	I-II Copepodites
0.06	<u>0.32</u>	0.10	<u>0.25</u>	<i>Oithona</i> adults
0.05	0.01	0.05	<u>0.16</u>	<i>Oithona</i> copepodites
0.18	0.04	0.07	<u>0.07</u>	Gastropods
0.10	0.07	0.03	0.06	Nauplii

Table 3. Vertical distributions of some abiotic factors at the three studied stations

Depth	English Channel Station		Southern Bight Station				Northern North Sea Station (°C)
	Temperature (°C)	Salinity (g/liter)	Temperature (°C)	Salinity (g/liter)	pH	O ₂ (mg/liter)	
0	10°1	35.2	12°5	—	8.1	9.88	14°6
3	9°9	35.2	12°5	—	8.1	9.6	—
10	9°6	35.2	12°5	—	8.2	9.44	14°
15	9°6	35.2	12°	—	8.2	9.36	—
20	9°5	35.15	12°	—	8.3	9.36	13°6
30	9°5	35.15					13°4
40	9°4	35.2					11°2
50	9°4	35.2					11°
60	9°2	35.2					10°5
70	9°1	35.2					9°8
80	9°	35.2					—

Oithona seems to have a bimodal feeding rate. From these data grazing follows the zooplankton biomass almost exactly. I observed that the physical structure of the water column is conditioning the whole biological structure with all biological events occurring in the first 20 m (about 20% of the whole water column). This very narrow space where many species are present together forces them to revise their normal vertical migration behavior and to occupy, with a perfect constant pattern, a very definite depth. With the exception of *Calanus*, all species feed at a constant rate all day. Table 3 summarizes different abiotic factors for the 3 stations.

DISCUSSION

The results from this comparative study suggest that increasing feeding activity at night is not necessarily linked with swarming behavior. The very pronounced feeding rhythms of *Pseudocalanus* in late April at the English Channel station in the deeper layers, suggests that this rhythm is ontogenetic: considering that a constant temperature, almost constant phytoplankton biomass and total darkness at 50 m during 24 h, no environmental factor can serve as an explanation or a stimulation, as suggested by Ringelberg (1980).

In the Southern Bight, despite a homogeneous vertical distribution of phytoplankton, the two dominant species in May, *Temora* and *Pseudocalanus*, both show a vertical migration pattern and increasing feeding at night. Nevertheless, the variation based on the difference between day and night is by far lower than that observed in the English Channel, suggesting that food supply, when abundant, does modify by smoothing the rhythm and the feeding behavior, as also shown by Bohrer (1980).

In the northern North Sea, evidence is shown that a strong correlation exists, at least in September, between vertical distributions of phytoplankton and zooplankton; the presence of a pronounced stable thermocline at 30 m limits all biological events occurring in the first 20 m, where phytoplankton is already scarce, and where a high diversity of numerous animals are segregated in fixed depths, as also suggested by Lane (1975). In this case, only *Calanus* show a certain feeding rhythm, but by far lower than the rhythm observed in spring (Daro, 1980). Hayward (1980) also pointed out that guts of copepods in the Central Gyre of the North Pacific were fuller at night than during the day, even in non-migrating

species, and that when a night-time distribution was observed, no special depth was preferred for feeding.

The onset of vertical migration behavior seems to occur in very young stages, such as Nauplius III of *Calanus pacificus* (Huntley and Brooks, 1982), so that it is difficult in some cases to decide if a diel rhythm is ontogenetic or stimulated by environmental factors in the very young life of an animal. These same authors also observed that when food availability declines, the migration amplitudes decreased and even ceased. I also observed this in the northern North Sea. Segregation by depths, when diversity is high, was evident in the northern North Sea, and also showed by Paffenhöfer (1983) in the northeastern Florida Shelf. But when diversity is low, such as in the English Channel, I also show a segregation by the time of the peak of the feeding, so that the animals show different strategies in occupying the different niches.

I conclude that all zooplankton species, particularly copepods, are able to modify their diel rhythm following the environmental factors present, so that for each species different patterns exist, making part of a global strategy of maximum harvesting of energy with minimal costs.

LITERATURE CITED

- Arashkevich, Ye C. 1977. Relationship between the feeding rhythm and the vertical migrations of *Cypridina sinuosa* (Ostracoda, Crustacea) in the western part of the equatorial Pacific. *Oceanology* 17: 466-469.
- Bohrer, R. N. 1980. Experimental studies on diel vertical migration in evolution and ecology of zooplankton communities. W. C. Kerfoot, ed. University Press, London 1980. 11: 111-121.
- Cushing, C. H. 1951. The vertical migration of planktonic organisms. *Biol. Rev.* 26: 158-192.
- Daro, M. H. 1978. A simplified ^{14}C method for grazing measurements on natural planktonic populations. *Helgoländer wiss. Meeresunters.* 31: 241-248.
- . 1980. Field study of the diel feeding of a population of *Calanus finmarchicus* at the end of a phytoplankton bloom. "Meteor" Forsch. Ergebn. A 22: 123-132.
- . 1985. Field study of the diel, selective and efficiency feeding of the marine copepod, *Temora longicornis* in the Southern Bight of the North Sea. *Bull. Mar. Sci.* 37: abstract.
- Fuller, J. L. 1937. Feeding rate of *Calanus finmarchicus* in relation to environmental conditions. *Biol. Mar. Biol. Lab. Woods Hole* 72: 233-246.
- Gauld, D. T. 1951. Diurnal variations in the grazing of planktonic copepods. *J. Mar. Biol. Assoc. U.K.* 31: 461-474.
- Hayward, T. L. 1980. Spatial and temporal feeding patterns of copepods from the North Pacific central gyre. *Mar. Biol.* 58: 295-309.
- Huntley, M. and E. R. Brooks. 1982. Effects of age and food availability on diel vertical migration of *Calanus pacificus*. *Mar. Biol.* 71: 23-31.
- Joiris, C., G. Billen, C. Lancelot, M. H. Daro, J. P. Mommaerts, A. Bertels, M. Bossicart, J. Nijs and J. H. Hecq. 1982. A budget of carbon cycling in the Belgian coastal zone: relative roles of zooplankton, bacterioplankton and benthos in the utilization of primary production. *Neth. J. Sea Res.* 16: 260-275.
- Lane, P. H. 1975. The dynamics of aquatic systems: a comparative study of the structure of four zooplankton communities. *Ecol. Monogr.* 45: 307-336.
- Mackas, D. L. and R. Bohrer. 1976. Fluorescence analysis of zooplankton gut contents and an investigation of diel feeding patterns. *J. Exp. Mar. Biol. Ecol.* 25: 77-85.
- Morris, D. J. and C. Ricketts. 1984. Feeding of krill around South Georgia. I. A model of feeding activity in relation to depth and time of day. *Mar. Ecol. Progr. Ser.* 16: 1-7.
- Mullin, M. H. and E. R. Brooks. 1972. The vertical distribution of juvenile *Calanus* (Copepoda) and phytoplankton within the upper 50 m of water at La Jolla, California. Pages 347-354 in A. Y. Takenouti, ed. *Biological oceanography of the northern North Pacific Ocean and Bering Sea*.
- Paffenhöfer, G. A. 1983. Vertical zooplankton distribution on the northeastern Florida Shelf and its relation to temperature and food abundance. *J. Plankton Res.* 5(1): 15-33.
- Pearre, S., Jr. 1973. Vertical migration and feeding in *Sagitta elegans*. *Ecology* 54: 300-314.
- Ringelberg, J. 1980. Causal and teleological aspects of diurnal vertical migration: introductory remarks in evolution and ecology of zooplankton communities. W. C. Kerfoot, ed. University Press London 1980. 6: 65-68.

Williams, R. and D. V. P. Conway. 1984. Vertical distribution, and seasonal diurnal migration of *Calanus helgolandicus* in the Celtic Sea. Mar. Biol. 79: 63-73.

DATE ACCEPTED: May 31, 1985.

ADDRESS: *Free University of Brussels, Labo Ecology, 2, Pleinlaan, B-1050 Brussels, Belgium.*