

MIGRATORY AND GRAZING BEHAVIOR OF COPEPODS AND
VERTICAL DISTRIBUTION OF PHYTOPLANKTON

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ABSTRACT

The vertical distribution and grazing activity of copepods was studied during the summer of 1985 throughout the North Sea. In most areas, copepods did not vertically migrate and their vertical distribution followed that of the phytoplankton which was restricted to the upper 20-30 m. This behavior may be a consequence of barely sufficient or limiting food concentrations (about 200 mg·m⁻³). The diel grazing patterns as a function of variations in phytoplankton are described for the dominant zooplankton species: *Calanus finmarchicus*, *Oithona similis*, *Temora longicornis*, *Pseudocalanus elongatus*, *Acartia* spp., *Centropages hamatus*, *Microsetella* spp.

The nocturnal behavior of zooplankton is one of the most fascinating subjects of plankton literature. The most abundant near-surface zooplankton catches occur at night and in general the gut content of most of the species is also higher at night (Stearns, 1986). It has been often suggested that these two features are linked (Gauld, 1951; Sushkina, 1962; Daro, 1980). However, recent papers demonstrate that nocturnal vertical migration is not a fixed behavioral attribute, but can be related to season (Sameoto, 1984; Townsend et al., 1984; Landry and Hassett, 1985; Vidal and Smith, 1986), location (Williams and Lindley, 1980; Williams and Conway, 1984), and physiological events such as breeding or mating (Endo, 1984; Williams and Fragopoulou, 1985). In different areas with similar climatic and environmental conditions, the same species can simultaneously show different patterns of vertical distribution (Sameoto, 1984; Vidal and Smith, 1986). Sometimes the vertical migration behavior is clearly related to the presence of a thermocline (Sameoto, 1984) and at other times not at all (Williams and Fragopoulou, 1985; Wishner and Allison, 1986).

Most zooplankton groups are nocturnal feeders, such as calanoids, cladocerans and cyclopoids (Petipa, 1964; Daro, 1980; Tande and Slagstad, 1982; Baars and Oosterhuis, 1984; Simard et al., 1985). Nocturnal grazing is not necessarily linked to nocturnal vertical upward movements or swarming (Mackas and Bohrer, 1976; Nicolajsen et al., 1983; Head et al., 1985). Food availability can affect the vertical distribution of zooplankton in different ways. When food is abundant in the upper layer, vertical migrations can be of high amplitude with significant nocturnal feeding (Daro, 1980; 1985), but may cease entirely when food is scarce (Huntley and Brooks, 1982) even when nocturnal feeding still exists (Daro, 1985). In other cases, the disappearance of nocturnal migration is associated with a disappearance of diel differences in grazing rates (Lampert and Taylor, 1985). The different hypotheses proposing to explain the benefits of vertical migration such as the metabolic model (Enright, 1977), the predator avoidance mechanism and the feeding-growth model (McLaren, 1963; Zaret and Suffern, 1976) seem to apply separately or in combination depending on the biological or ecological situation. Williams and Conway (1984) clearly summarized the problem: "The copepod (*Calanus helgolandicus*) responds to its changing environment by exhibiting different patterns of behavior, i.e., feeding migrations, egg laying migrations, migrations which presumably give a net gain in energy, and non-migrating patterns which potentially conserve energy."



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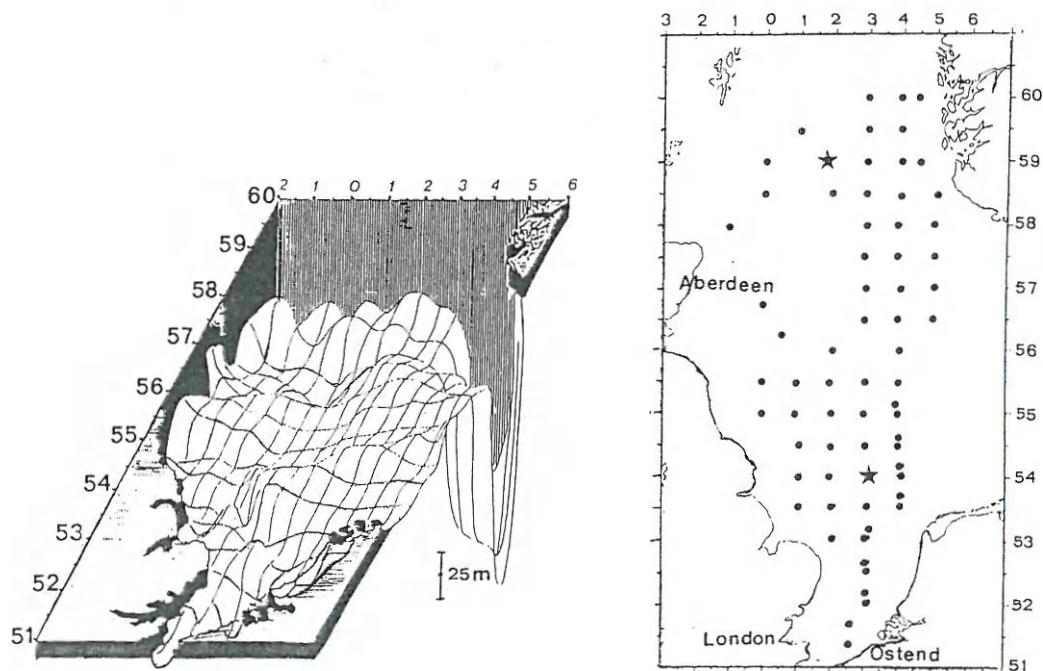


Figure 1. The study area: (Left) Depth distribution; (Right) Sampling stations are indicated by numbered crosses. Stars show the 48-h anchored stations.

We present here the results of a study performed in the North Sea in June and July 1986. The aim of the study was to look at the vertical distributions of the zooplankton together with their grazing activity in different areas.

METHODS

The sampling area, depth distribution and the station locations are shown in Figure 1. Sixty-eight stations were sampled from 11 June to 14 July 1985. The navigation time between two stations was about 3–4 h, the sampling time 1–2 h, so measurements were obtained every 5 to 7 h. In addition, we performed two 48-h stations at anchor, with sampling every 3 to 6 h: a southern station at 54°N, 3°E and a northern at 59°N, 1°E (Fig. 1, Right).

At each station temperature, salinity, chlorophyll, particulate organic carbon (POC), zooplankton abundance and zooplankton grazing were measured. Temperature and salinity data were obtained from an STD probe. All samples were taken with a 30-liter Niskin bottle at 10-m depth intervals from 3 m to the bottom. Chlorophyll data were obtained using the spectrophotometric method of Parsons and Strickland (1969) and the POC data using a coulomat method. To determine zooplankton abundance, the 30-liter sample from each depth was filtered through 25- μ m mesh and preserved in 4% formalin.

Zooplankton for the grazing experiments were collected in the same way, but only at 3-, 10-, 20- and 30-m depths. We observed in previous studies that horizontal or vertical hauls with a plankton net damaged the animals too much. Ten liters from each depth were put in a 40-liter tank, so that we obtained a combined sample of different depths. This is advantageous in that all different developmental stages and species are obtained. Daro (1985) observed that in some seasons some species or developmental stages remain at discrete depths; sampling only from the 3-m depth for grazing experiments will not provide adequate results because some stages or species are infrequent or absent. The phytoplankton used for the grazing experiments was from the 3-m depths, following the method developed by Daro (1978) with the slight modifications of Baars and Oosterhuis (1984). One liter of phytoplankton from the natural sample was labelled 1 to 4 h before the start of the experiment by adding 100 to 200 μ Ci $\text{NaH}^{14}\text{CO}_3$. Five to 10 liters of zooplankton from the combined depths sample were then concentrated on a 50- μ m mesh and added to the labelled water.

The 1-liter grazing bottles were kept up to 1 h in a deck incubator under natural light with filters to simulate light at the 3-m depth. After incubation phytoplankton in 100 ml from each grazing bottle was filtered onto a 0.8- μ m filter. The zooplankton were filtered through a 25- μ m mesh and both sets

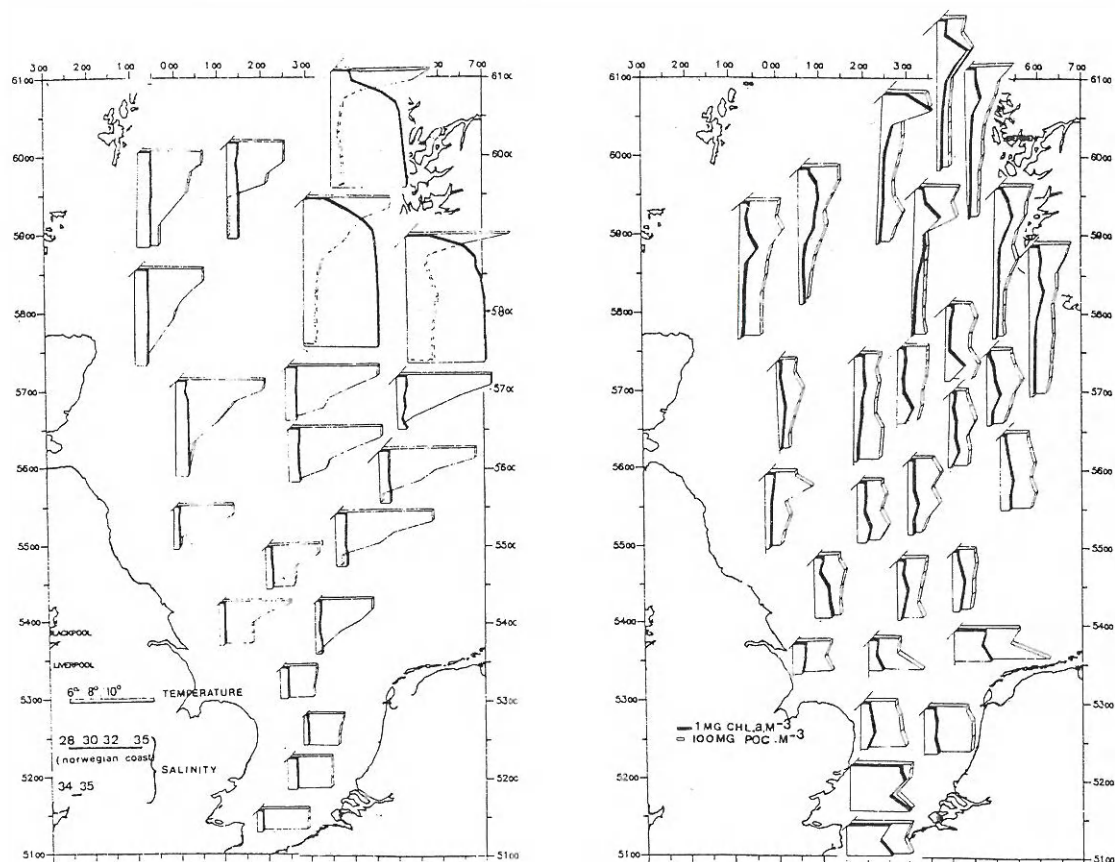


Figure 2. (Left) Horizontal and vertical distributions of salinity (‰) and temperature (°C); (Right) Horizontal and vertical distributions of particulate organic carbon (POC, $\text{mg} \cdot \text{m}^{-3}$) and chlorophyll *a* ($\text{g} \cdot \text{m}^{-3}$).

of filters were frozen at -18°C . At the beginning of the experiment, just before adding the concentrated zooplankton sample, 100 ml of the labelled phytoplankton mixture was filtered on a $0.8\text{-}\mu\text{m}$ filter and frozen. In the laboratory, the different zooplankton species and their developmental stages were sorted under a binocular microscope and put into scintillation vials. A scintillation mixture was then added and the samples counted in a liquid scintillation counter. Calculations of filtering rates at different light intensities were made according to the method in Daro and Baars (1986). They demonstrated that dividing the radioactivity/animal by the mean radioactivity/ml of phytoplankton between the initial and final time gives the best estimation of filtering rate in all different light conditions. This was true even in full daylight with further uptake of ^{14}C bicarbonate during the grazing experiments. All feeding data obtained from the same area were combined to obtain ingestion rates as a function of time and concentration of phytoplankton.

RESULTS

Salinity and Temperature. — Figure 2, Left shows the vertical and horizontal distribution of temperature and salinity. Four different areas can be distinguished, from south to north. (1) The triangle between the narrows of Calais, the east side of the Netherlands and the coast of England, with the northern boundary at about $53^{\circ}30'\text{N}$, is characterized by shallow depth (25 m on average) and is very turbulent due to strong south–north residual currents. As a consequence, temperature and salinity are vertically homogeneous (11°C and about 34.6‰ , respectively). (2) A central part extending from $53^{\circ}30'\text{N}$ to 57°N is deeper (about 40 m) and currents are slower due to enlargement of the basin. A large sand bank, the Dogger Bank, extends east–west in this area. Here the salinity is vertically homogeneous (34.5‰)

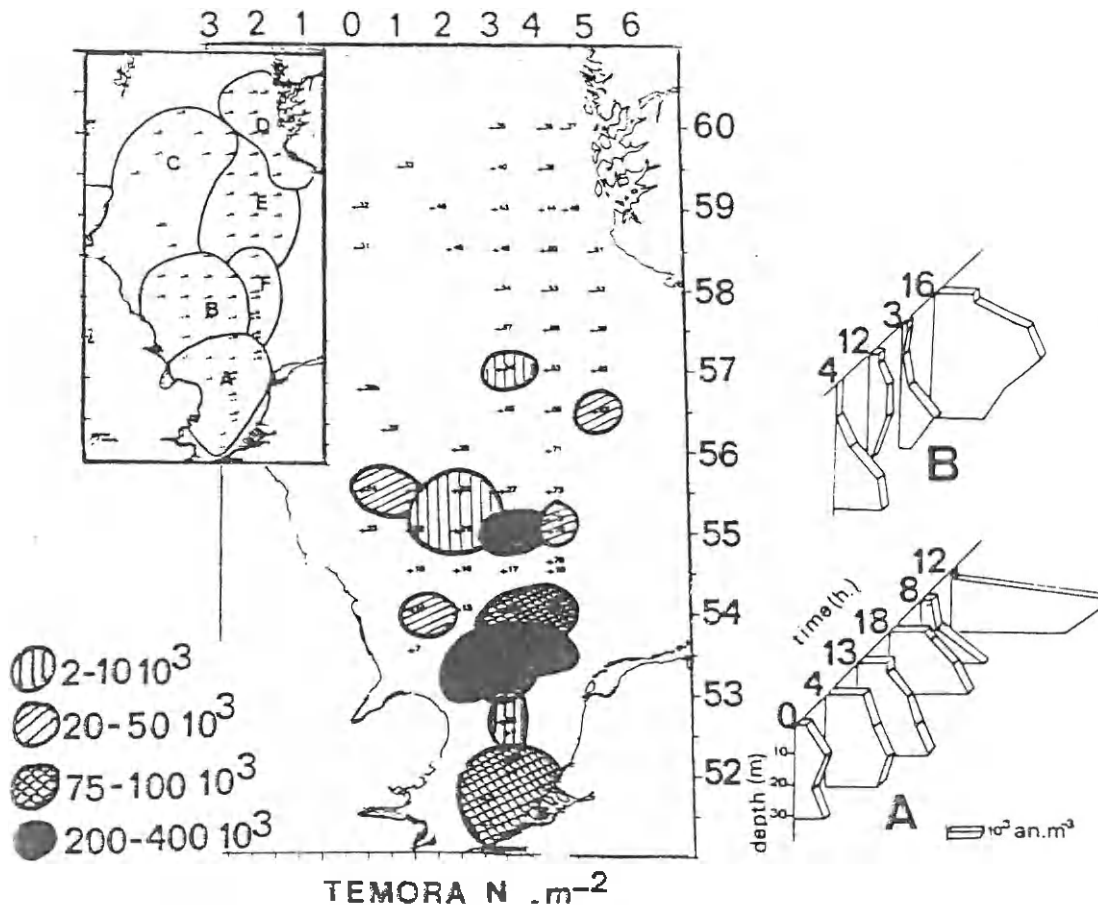


Figure 3. Distribution of *Temora longicornis*: (Left) Horizontal distribution in $n \cdot m^{-2}$ (total of adults + copepodites); (Right) Vertical distribution in $n \cdot m^{-3}$ over time in zones A and B.

but the temperature shows a sharp decrease at 15- or 20-m depth. (3) A northern region, from about 57°N extending to 60°W and from 1°W to 2°E , is deep (100- to 150-m depth) and under the influence of Atlantic water (a branch of the Gulf Stream flowing around the British Isles into the North Sea). Salinity is homogeneously distributed vertically (more than 35‰) and the temperature exhibits a rather slight decrease of 2.5°C between the surface and 20 m. (4) A north-east area along the Norwegian coast is under strong influence of Baltic water (Richardson, 1985). A layer 15–20 m thick shows a strong increase of salinity from less than 30‰ at the surface to 35‰ at 15–20 m and a decrease of temperature from 14°C to 5°C .

Chlorophyll a and POC.—In the shallow southern part of the North Sea, chlorophyll *a* and POC are rather homogeneously distributed vertically, with a slight tendency towards higher concentrations close to the bottom (Fig. 2, Right). The highest concentrations were found in this region: up to $4 \text{ mg chlorophyll } a \cdot m^{-3}$ and $0.8 \text{ g C} \cdot m^{-3}$. In the deeper central part of the North Sea, where different water masses are encountered, there is vertical stratification with a subsurface maximum of chlorophyll *a* and POC between 10- and 30-m depth. In the northern regions, two kinds of phytoplankton distributions can be observed. In the “Atlantic” North Sea, chlorophyll is distributed in a rather broad layer between 10- and 40-m depth, but the concentrations are very low. In the Norwegian part, chlorophyll *a* shows a sharp peak at the depth of the strong gradient of salinity and temperature.

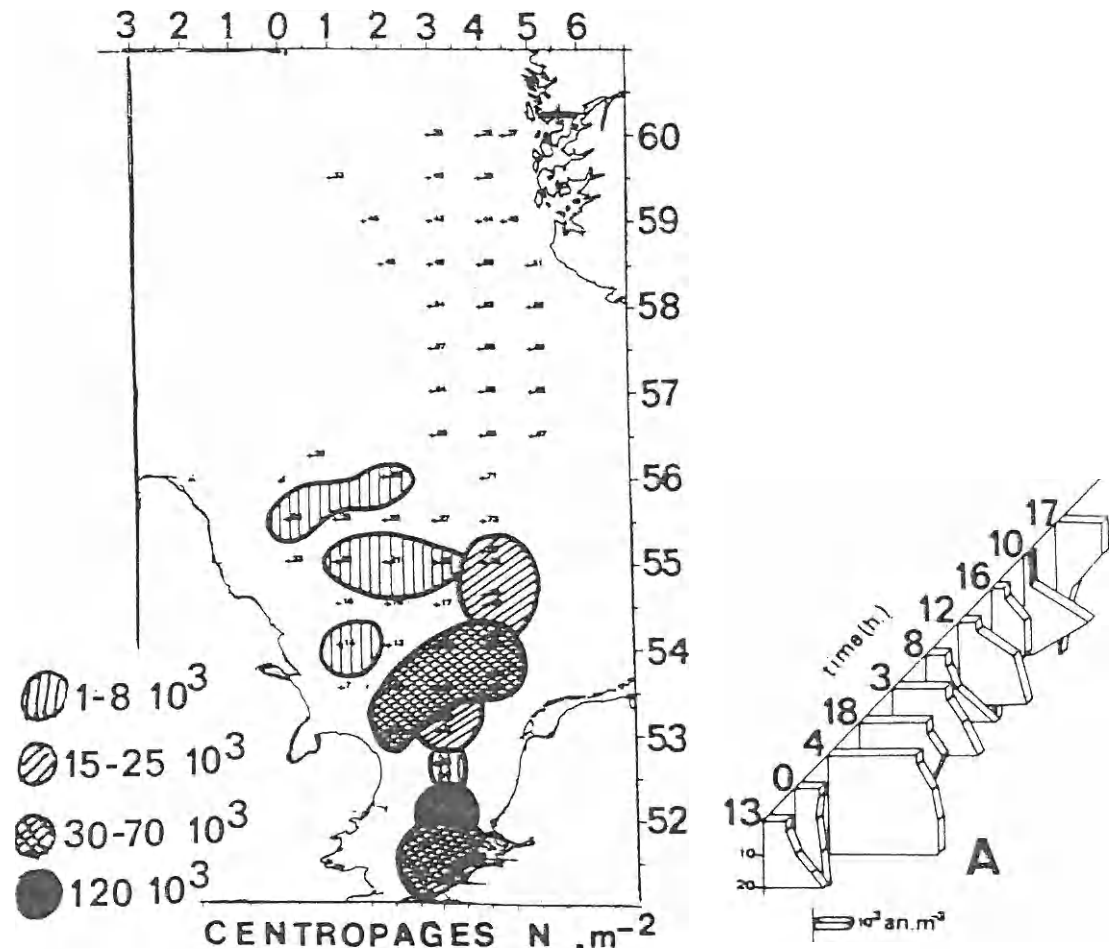


Figure 4. Distribution of *Centropages hamatus*: (Left) Horizontal distribution in $n \cdot m^{-2}$ (total of adults + copepodites); (Right) Vertical distribution in $n \cdot m^{-3}$ over time in the zone of dominance A.

For the North Sea as a whole minimal concentrations of chlorophyll and particulate matter generally occurred near the surface. Comparing the salinity-temperature distributions with those of chlorophyll and POC, the following generalizations arise: where physico-chemical conditions were rather homogeneous, so were phytoplankton and particulate matter, with slightly higher concentrations close to the bottom in shallow areas (30–40 m) or in a broad upper layer in deep areas such as the northern North Sea. Where the physico-chemical conditions of the water column were vertically heterogeneous, so was the phytoplankton, showing a sharp peak of development just above or just below the thermocline. We therefore divided the studied area into different regions called A, B, C, D, E, F as seen on Figures 3 to 9, on the basis of the physico-chemical structure of the water column.

Horizontal and Vertical Distributions of Zooplankton. — Figures 3 to 9 show the horizontal distribution of each species as the total number of copepods and copepodites per square meter, as well as their vertical distribution in various zones as a function of time of day. Figures 3 and 4 show that the neritic species *Temora longicornis* and *Centropages hamatus* were found in highest numbers in the southern portion of the North Sea (14 to $400 \cdot 10^3$ and $120 \cdot 10^3$ copepods $\cdot m^{-2}$, respectively, for a total depth of 30 m). The neritic species *Acartia clausi* and *longiremis*

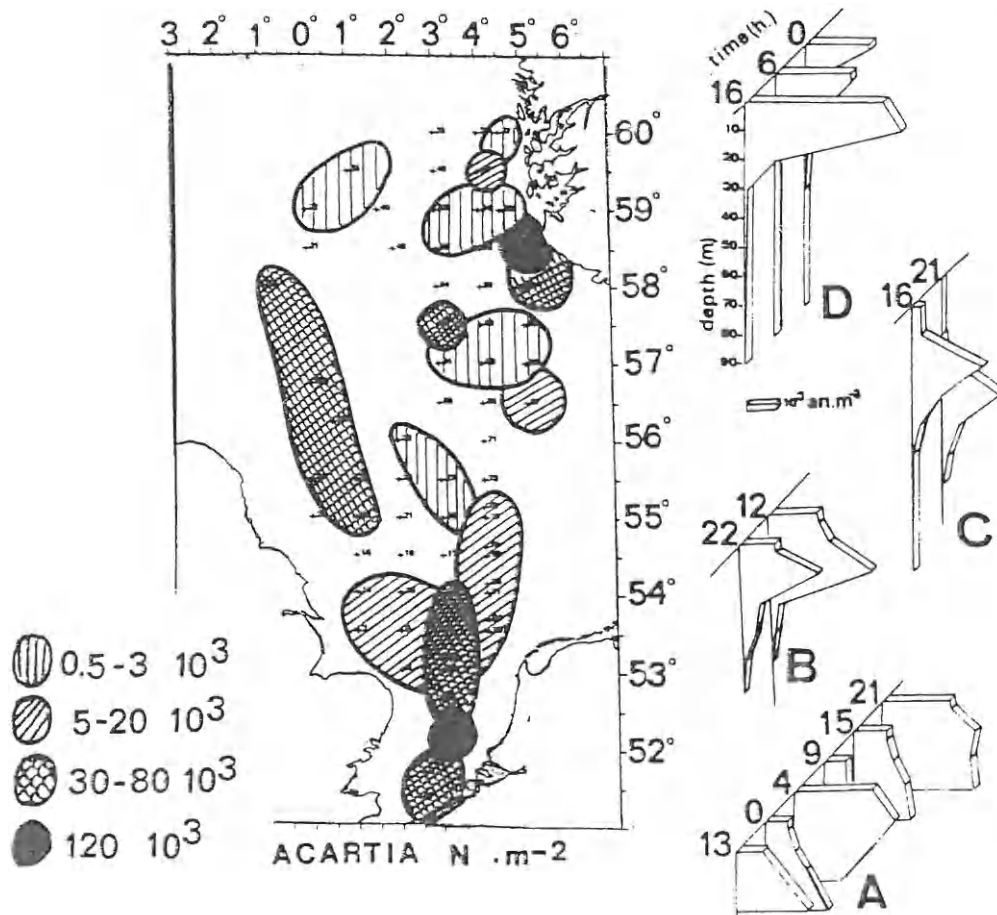


Figure 5. Distribution of *Acartia* spp.: (Left) Horizontal distribution in $n \cdot m^{-2}$ (total of adults + copepodites); (Right) Vertical distribution in $n \cdot m^{-3}$ over time in zones A, B, C and D.

often co-occurred; because the copepodites are difficult to distinguish from each other, we combined the results for the two species (Fig. 5). *Acartia* was most abundant in the south and along the coast of Norway (up to $120 \cdot 10^3$ copepods \cdot m^{-2} for total depth of 30 and 200 m, respectively). The vertical distribution of these species shows no significant difference at different times of the day in the areas considered. In zone A (south) the highest numbers are always observed close to the bottom. Peak concentrations are between 20 and 30 m in zone B (central North Sea) as well as in zone C (northern North Sea), although the latter zone is much deeper. This contrasts with the distribution in zone D, the area close to the Norwegian coast, where the highest numbers of *Acartia* occurred very close to the surface.

Pseudocalanus elongatus, while generally considered a neritic species, is not as restricted as the above species to shallow or coastal areas, and extends into the pelagic zone (Fig. 6). However, this species was most numerous in zone A (up to $500 \cdot 10^3$ copepods \cdot m^{-2}). Their vertical distribution follows the same pattern as the preceding species. In the southern zone (A) the animals remained for most of the day close to the bottom, except for a very short time at 2300 at 10-m depth. In the central North Sea (zone B), the animals remained at 20 m and along the Norwegian coast they were close to the surface at all times of day.

Calanus finmarchicus is more abundant in the northern North Sea (up to $220 \cdot$

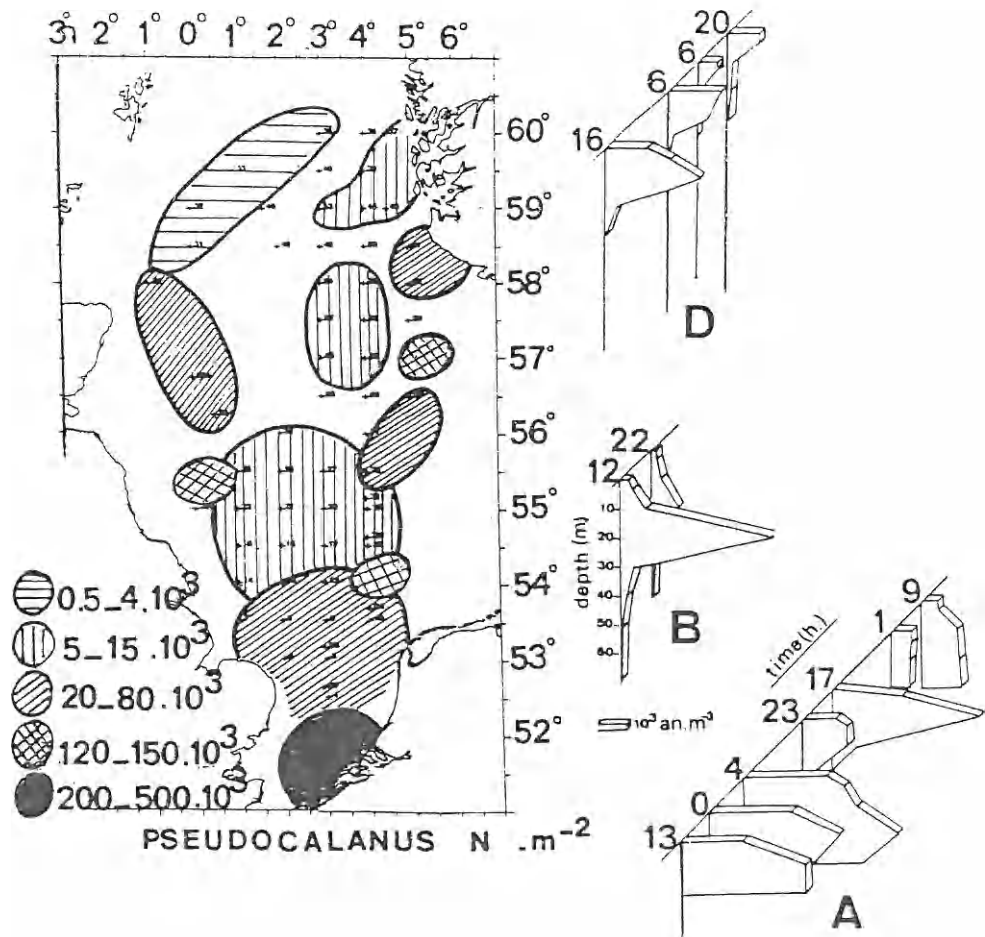


Figure 6. Distribution of *Pseudocalanus elongatus*: (Left) Horizontal distribution in $n \cdot m^{-2}$ (total of adults + copepodites); (Right) Vertical distribution in $n \cdot m^3$ over time in zones A, B, and D.

10^3 copepods $\cdot m^{-2}$) (Fig. 7). There seem to be two populations, one originating in the Atlantic and developing in very saline waters, and the other along the Norwegian coast. Fransz and Diel (1985) pointed out that the biomass of *Calanus finmarchicus* observed in the Fladen Ground is not locally produced but possibly derived from east of the Orkneys. The population along the Norwegian coast is derived from individuals overwintering in the Norwegian fjords, whose offspring are flushed out by freshwater outflow and accumulate at the offshore thermohaline front in April–May (Roed, 1986). The majority of animals in zones B and C was found at 20–30-m depth at all times of day. Along the Norwegian coast (zone D), the animals remained always close to the surface, and in zone E, central east North Sea, the depth of maximum occurrence was variable (20- to 50-m depth), but no clear vertical movement could be distinguished.

The cyclopoid *Oithona* spp. and the harpacticoid *Microsetella* were the most abundant copepods at this time of the year, both up to $1.5 \cdot 10^6$ animals $\cdot m^{-2}$. *Oithona* abundance was the highest in the central North Sea (Fig. 8) and *Microsetella* in the central eastern position and along the Norwegian coast (Fig. 9). Both were absent in the Southern Bight of the North Sea. Vertical distribution indicates that *Oithona* occurred in the central North Sea predominantly in deeper layers during the entire day. However, a part of the population seems to migrate to the surface at 2200, 2300 and 0000 in the zones B and E. In the northern zone (C),

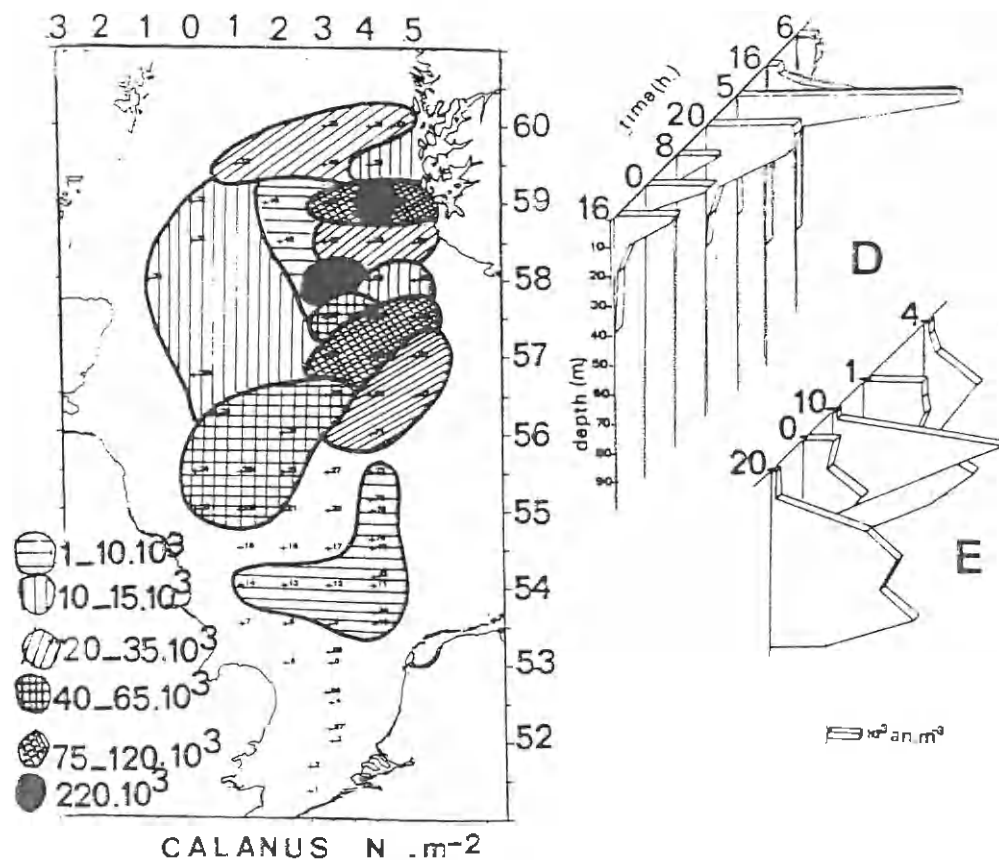


Figure 7. Distribution of *Calanus finmarchicus*: (Left) Horizontal distribution in $n \cdot m^{-2}$ (total of adults + copepodites); (Right) Vertical distribution in $n \cdot m^{-3}$ over time in zones B, C, D and E.

a peak of abundance occurred at 30–40 m and along the Norwegian coast (D) at 3 and 10 m at all times of day. In the shallow area (zone E) *Oithona* remained close to the bottom. *Microsetella* occurred in the central eastern North Sea in enormous numbers (up to 100,000 copepods $\cdot m^{-3}$) at 20-m depth, and along the Norwegian coast remained close to the surface at all times (Fig. 9). The only zone where this species seems to perform true vertical movements is the central North Sea (zone B), from 20–30-m depth to the surface at 0000 and 0300.

Figure 10 shows the vertical distributions expressed as the percentage of each species' population found at different depths in each zone. In the southern zone A, all species were found with the highest abundance close to the bottom. In the central North Sea, zone B, the calanoids avoided the surface at all times; the only clear vertical movements were observed for *Oithona* 1200 to 2200 and for *Microsetella* from 0000 to 0300, between 20-m depth and the surface. In the northern North Sea (zone C) minimal abundances occurred in the upper 20 m. No clear vertical movements could be observed. Along the Norwegian coast (zone D) 90% of the animals occurred in the upper 10 m at all times of the day. In the central eastern zone (E), the vertical distribution was variable and no clear vertical movement could be observed except for *Microsetella*.

Forty eight one-hour samples were taken in zones A and C. Results are presented in total numbers and in percentages for each species as a function of depth (Fig. 11). For the southern station (Fig. 11, Upper), relatively clear movements can be observed for *Pseudocalanus* and *Centropages* between 10-m depth and the surface.

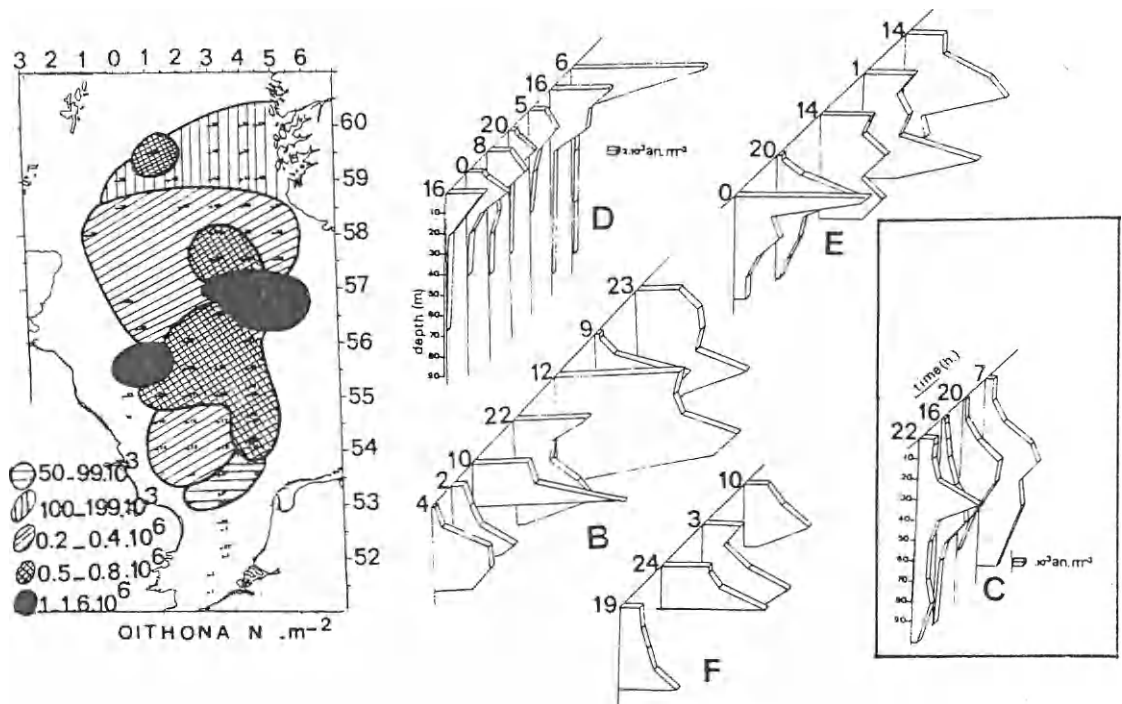


Figure 8. Distribution of *Oithona*: (Left) Horizontal distribution in $n \cdot m^{-2}$ (total of adults + copepodites); (Right) Vertical distribution in $n \cdot m^{-3}$ over time in zones B, C, D, E and F.

The greatest differences were observed between the 0900 and 2100 distributions on both days. For *Microsetella*, most of the population was involved in vertical movements between the surface and 30 m, with the biggest contrasts in vertical distribution being observed between 0300 and 0900 or 1500. For northern stations, since only *Oithona* was present in the samples and was found in low numbers, the conclusions are limited. As in the whole of zone C, minimal numbers were always observed in the upper 10 m, and the highest concentrations were observed around 20 to 40 m.

The above figures indicate that the North Sea copepods in summer generally do not exhibit a pronounced vertical migration behavior. Many species remain all day and all night at approximately the same depth, although this depth varies among the zones. When migration occurs, it covers only 10 m and lasts a very short time. In the sections below I attempt to relate the vertical distribution of copepods to the phytoplankton concentration.

POC and Zooplankton Vertical Distributions.—Figure 12, Upper shows the vertical distribution of the concentration of both POC and all copepods combined in the different zones. Figure 12, Lower shows the same during the 48-h cycle. Zooplankton and POC both tend to be more concentrated close to the bottom in the southern zone (A). In the central North Sea (zone B), POC concentrations are low and more concentrated in the first 10–20 m, but the copepods remain in general at or deeper than 20 m. In the northern North Sea (zone C) POC development occurs in the first 20 m whereas the copepods are much deeper (30–40 m), while in the Norwegian zone (D) the development of both phyto- and zooplankton occurs in the upper 10 m. In the northeast zone (E + F) we again observe the phenomenon of different layers of concentration for phytoplankton (upper layer) and copepods (20–30, even 40 m). Both 48-h cycles confirm the results of

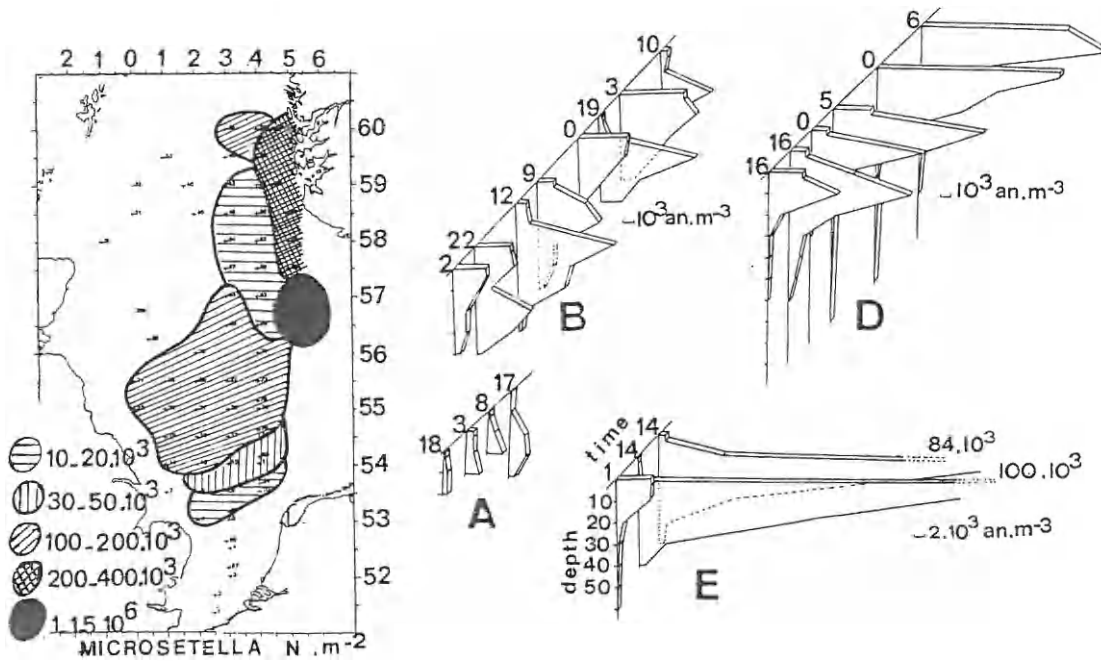


Figure 9. Distribution of *Microsetella* spp.: (Left) Horizontal distribution in $n \cdot m^{-2}$ (total of adults + copepodites); (Right) Vertical distribution in $n \cdot m^{-3}$ over time in zones A, B, D and E.

zone C for the northern station, but the 48-h measurement at the southern station is more representative of zone B than zone A (Fig. 12, Lower). Thus, in regions A and D maxima of total POC and zooplankton co-occur, and not in regions B, C, E and F.

Diel Variations in Copepod Grazing.—As indicated in the Methods section, all ingestion values from the same area were combined. Results are expressed in units of phytoplankton carbon using the correlations between chlorophyll *a* and POC shown in Table 1. Figure 13 shows all results obtained for the dominant species. Different curves are shown depending upon the concentration of phytoplankton carbon encountered. We could distinguish two kinds of diel patterns of feeding for some species and developmental stages.

Several species greatly reduced or lost their diel rhythms of grazing if concentrations dropped below $200 \text{ mg C} \cdot m^{-3}$, although this was not necessarily true for all developmental stages. Females and CV's of *Temora* showed feeding rhythms which were independent of phytoplankton concentrations, but males and younger copepodites drastically reduced their feeding rates and even lost their diel rhythm at low concentrations. Similarly, combined feeding rates for males, females and CV's of *Acartia* showed greatly depressed diel rhythms at concentrations less than $200 \text{ mg C} \cdot m^{-3}$, while *Pseudocalanus* lost its feeding rhythm entirely.

The copepodite stages of *Calanus* were not affected by decreasing concentrations. However, females showed depressed diel rhythms and shifted their peak feeding time to 1600 at low concentrations. *Oithona* also showed a depressed diel rhythm and a shift in peak feeding time towards midnight. For two species, *Centropages* and *Microsetella*, only minimal reductions in the diel grazing rhythm at low concentrations were observed.

These observations indicate that within a species, the day-night feeding patterns can be different according to the development stage. Some stages are sensitive to decreasing food concentrations, others not at all, and the feeding rate can some-

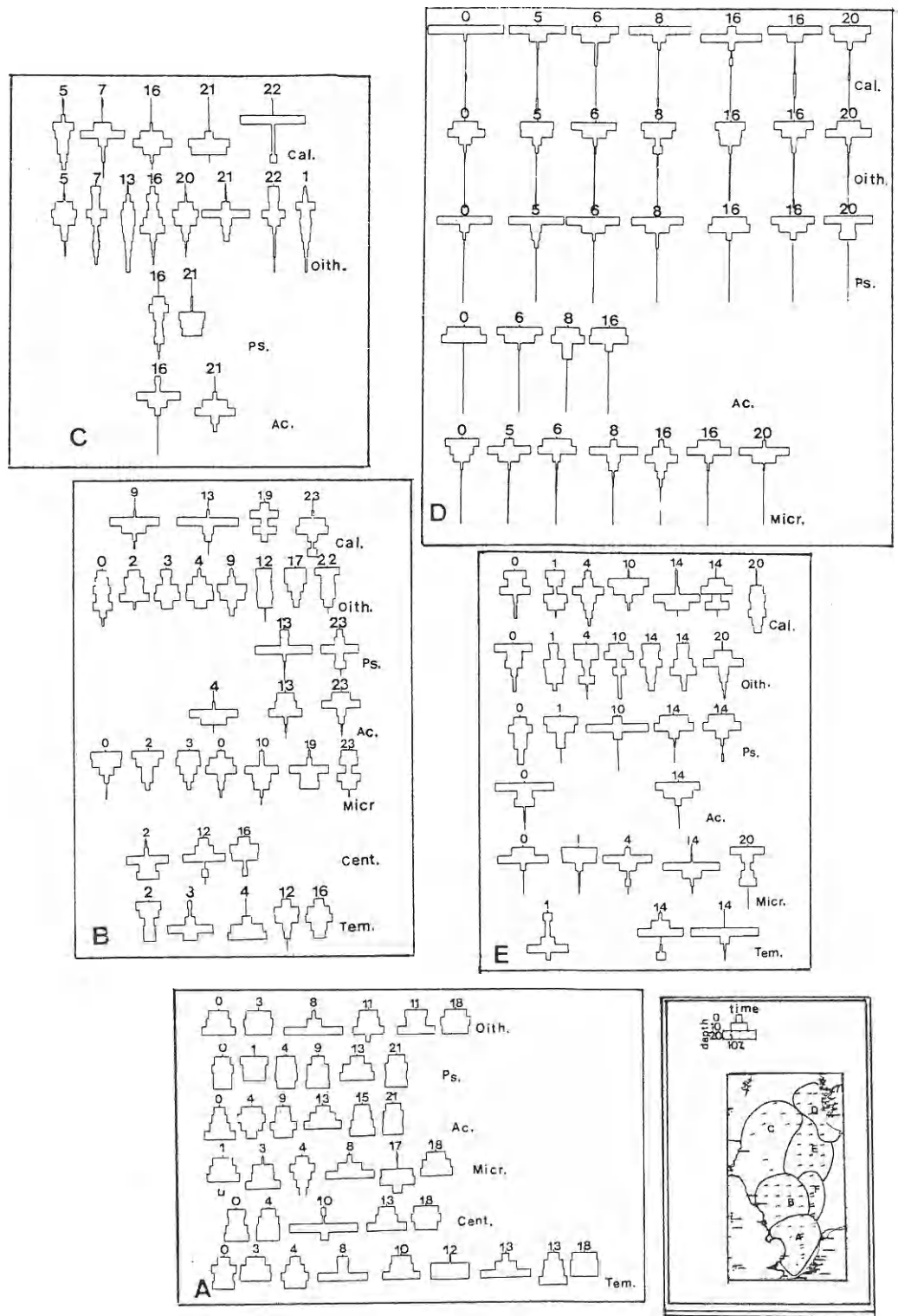


Figure 10. Vertical distribution of various copepod species in zones A to E, expressed as percentage of individuals of the specified species at different depths. Numbers above each diagram indicate the time in hours. Cal.: *Calanus*; Oith.: *Oithona*; Ac.: *Acartia*; Ps.: *Pseudocalanus*; Tem.: *Temora*; Micr.: *Microsetella*.

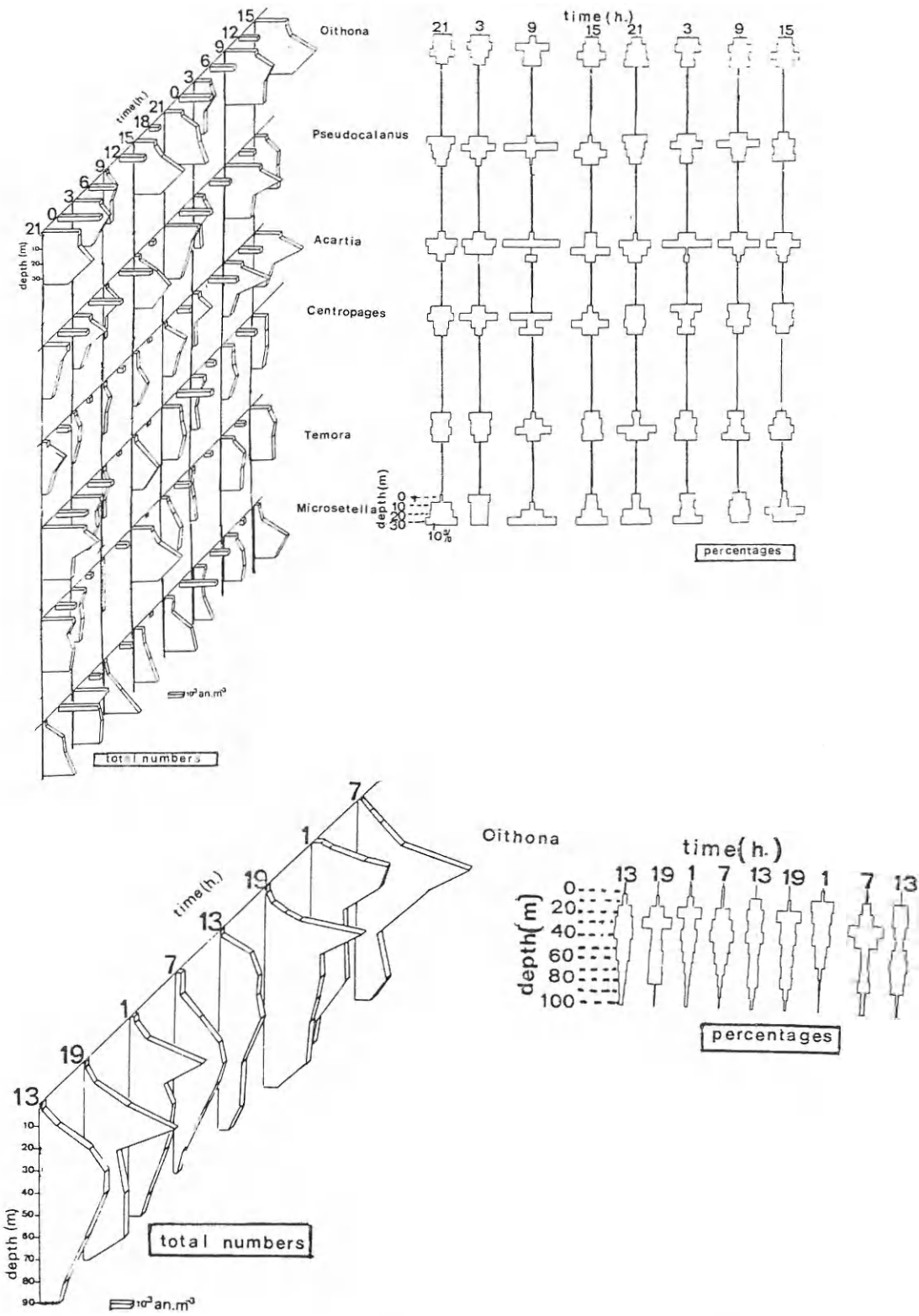


Figure 11. (Upper) 48-h measurements at the southern and (lower figure) northern stations (see stars on Fig. 1 left). The vertical distribution (in $\text{n} \cdot \text{m}^{-3}$) and percentages are shown together at the different sampling times.

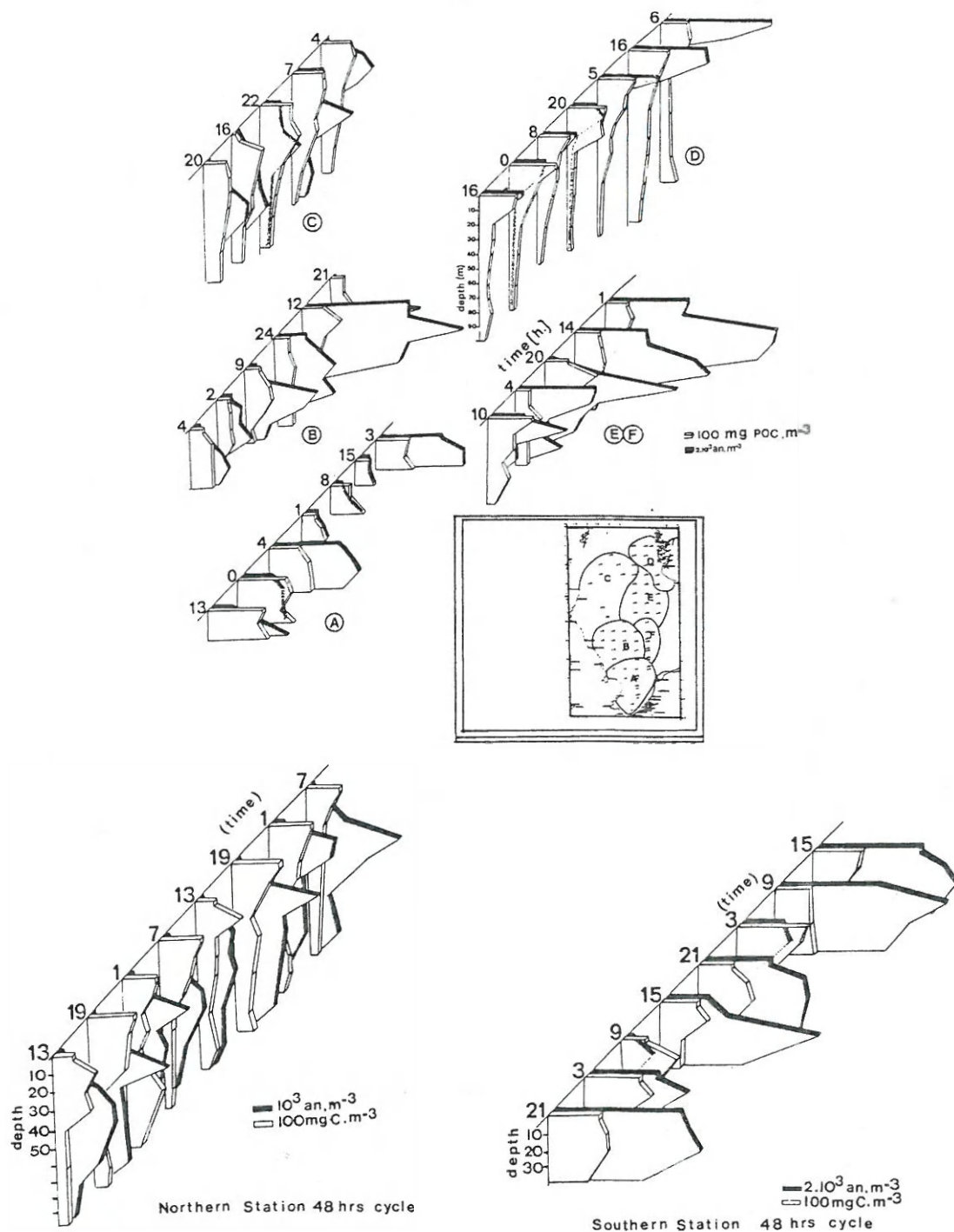


Figure 12. Vertical distributions of total numbers of copepods of all species (adults + copepodites) and total particulate organic matter in $n \cdot m^{-3}$ and $mg C \cdot m^{-3}$, respectively: (upper figure) in the different zones of the North Sea over time, and (lower figure) during the 48-h measurements at different times of the 2 succeeding days.

times be higher in younger than in older stages when the concentration of food decreases. A range of different feeding rates vs. time of day was observed: (1) no feeding (or extremely low) during the day and rapid increases at night, (2) regular increases from day to night or inversely, from night to day, (3) rather high feeding

Table 1. Correlation between chlorophyll *a* and POC in different zones

Area	Depth (m)	Observations (No.)	Correlation	Correlation coefficient
Southern Bight	3-10	26	mg C = 85 + 575 mg chl <i>a</i>	0.80
Southern Bight	20-40	17	mg C = 50 + 300 mg chl <i>a</i>	0.82
Central east	3-20	22	mg C = 220 + 300 mg chl <i>a</i>	0.72
Central east	30-40	12	mg C = 122 + 175 mg chl <i>a</i>	0.87
North	3-10	19	mg C = 1,350 mg chl <i>a</i>	0.78
North	20-30	14	mg C = 700 mg chl <i>a</i>	0.85
North	40	16	mg C = 300 mg chl <i>a</i>	0.70

rates during the day and moderate increases at night, or (4) disappearance of any rhythm.

Daily Grazing and Vertical Distribution of Phytoplankton.—The daily grazing values were calculated by integrating the 24 h of the different hourly values shown in Figure 13. Grazing calculations in the water column took into account the different concentrations of phytoplankton carbon at the different sampling depths, recalculated by the mean of the equations of Table 1.

The correlation between the vertical distribution of grazing values and phytoplankton concentration (expressed in carbon, using the regression equations of Table 1) is obvious in regions A and D (Fig. 14). The arrows on the figure indicate $200 \text{ mg C} \cdot \text{m}^{-3}$, the concentration at which many species or developmental stages decrease their ingestion. In zone A, grazing was the highest where the concentrations of phytoplankton were the highest, i.e., close to the bottom. In this zone the phytoplankton concentrations were almost always higher than $200 \text{ mg C} \cdot \text{m}^{-3}$. In zone D (Norwegian coast) the grazing was also highest where the phytoplankton concentrations were the highest, i.e., close to the surface. There, at most stations the phytoplankton concentrations were below $200 \text{ mg C} \cdot \text{m}^{-3}$ at 20–30 m depth.

In zones B, C and E the concentrations of phytoplankton are limiting (i.e., lower than 200 mg C) at many depths and at many stations. In zone B (central North Sea), the grazing pressure was also very low; the phytoplankton concentrations were often limiting at the surface, so that the highest grazing activity occurred around 20–30-m depth. In zone C (northern North Sea), the concentration of phytoplankton was highest in the upper 20 m, but the grazing pressure was very low and maximal around 20–30 m, where the phytoplankton concentration was slightly more than $200 \text{ mg C} \cdot \text{m}^{-3}$. In zone E the grazing pressure was much higher at some stations and the vertical distribution of the grazing followed the vertical distribution of phytoplankton, which was in limiting concentrations at the surface and close to the bottom.

Figure 14b (lower) shows the relationship between daily grazing by all the copepods combined and the phytoplankton concentration. The curve for each zone is slightly different, but all exhibit the same kind of relationship generally observed for single species, with low values at low concentrations, a region of increase and a plateau. In all zones the low values are observed at concentrations less than $200 \text{ mg C} \cdot \text{m}^{-3}$, the region of increasing rates is between 200 and 300–400 mg C and the plateau is at concentrations greater than 300 or 400 $\text{mg C} \cdot \text{m}^{-3}$. In general, at this time of the year, we observed a high sensitivity of copepod grazing to phytoplankton in often limiting concentrations; in most cases the animals did not perform vertical migrations or when they occurred they were very slight, because animals appeared to follow the best available food concentrations.

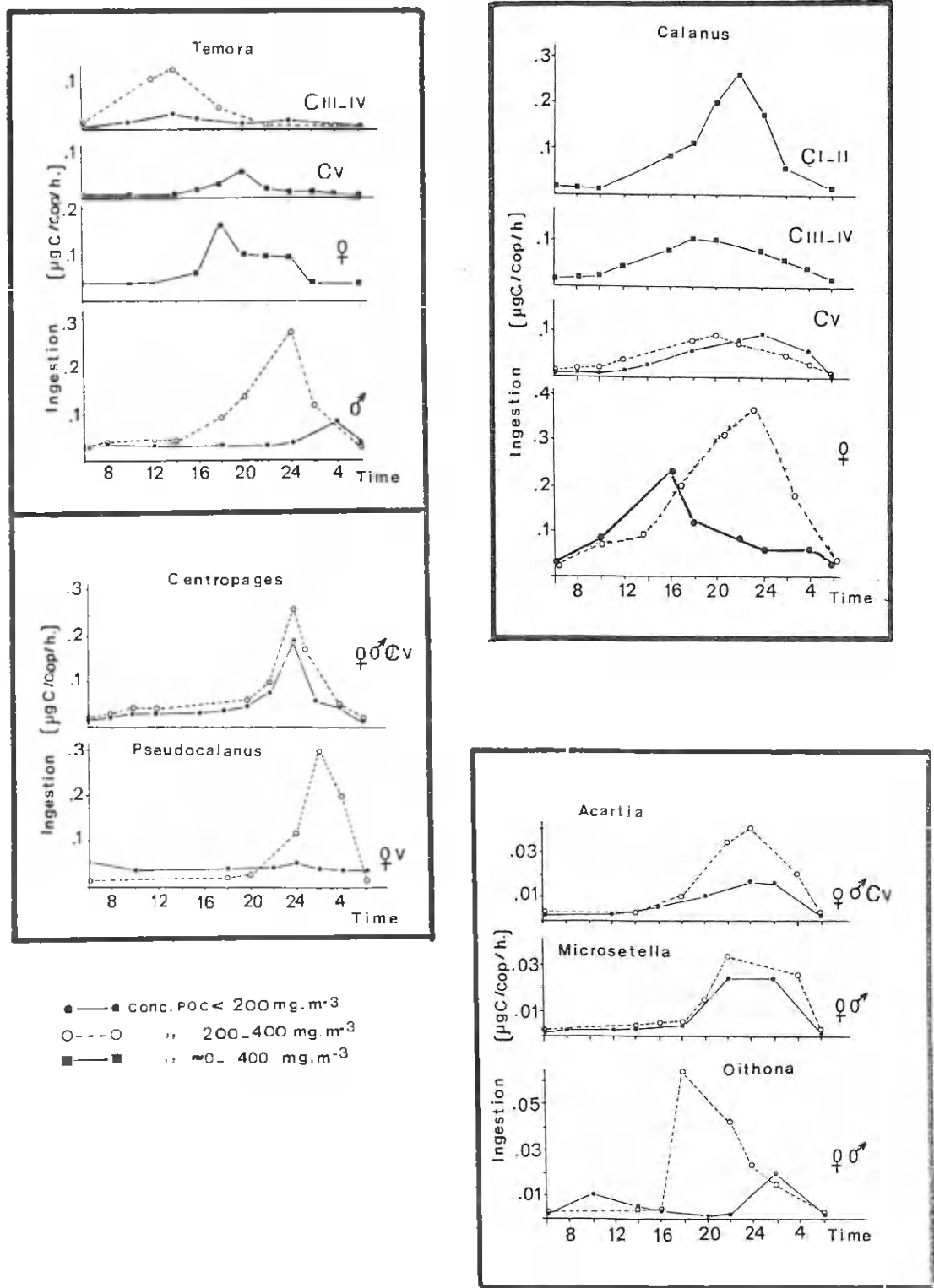


Figure 13. Feeding rates as a function of the time of the day. Different feeding rate curves are shown for different concentrations of phytoplankton (expressed in $\text{mg C}\cdot\text{m}^{-3}$).

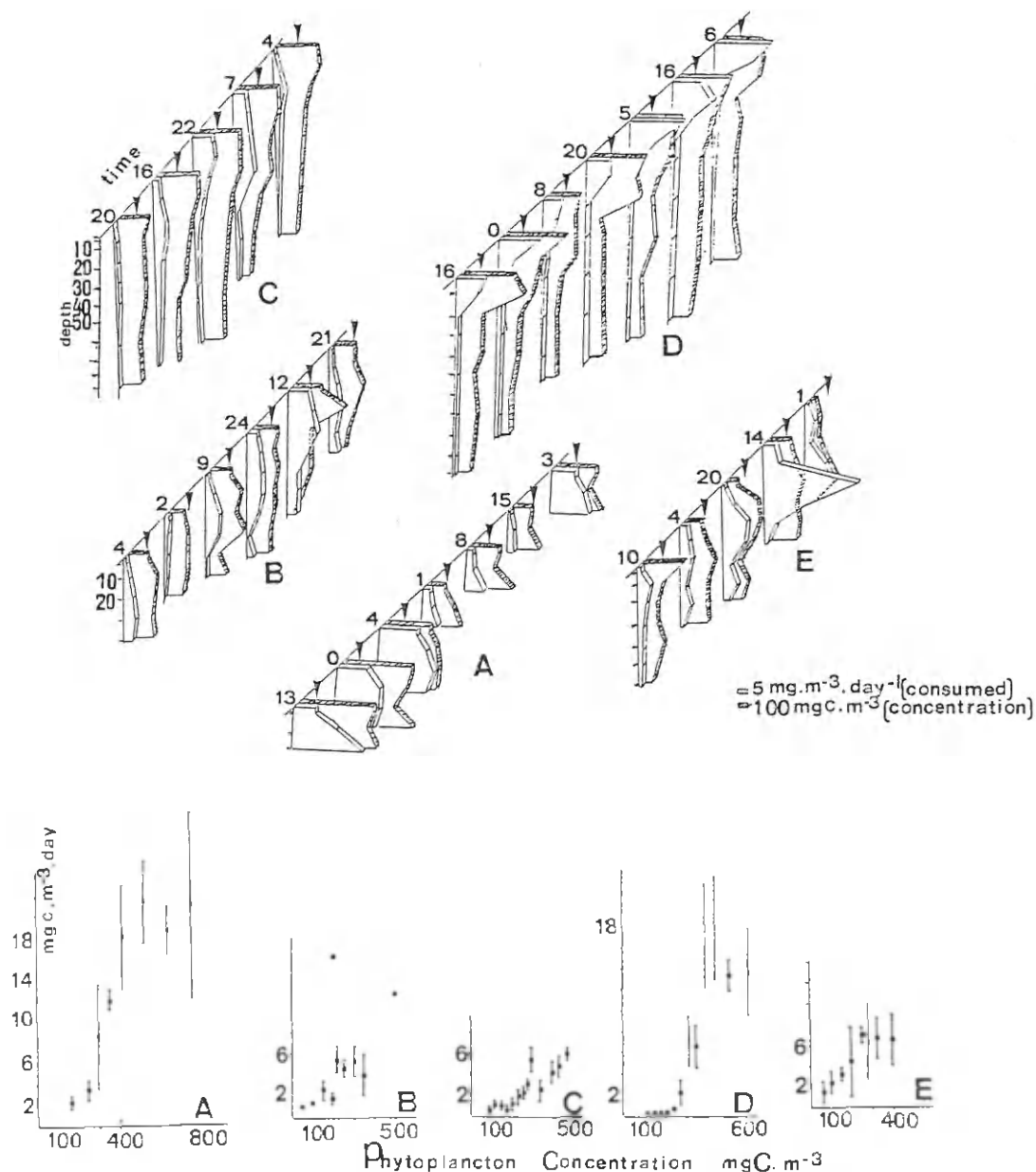


Figure 14. Total grazing and concentration of phytoplankton (expressed in carbon, using equations of Table 1). The concentration of $200 \text{ mg C} \cdot \text{m}^{-3}$ is shown with an arrow: (upper figure) vertical distribution in the different zones over time; (lower figure) relationships between daily grazing and phytoplankton concentration in the different zones.

48-Hour Measurements.—Figure 15 shows data analogous to the preceding section for the 48 h. Figure 15, Upper shows the vertical distribution of the hourly grazing by the total community of copepods and their total numbers, while Fig. 15, Lower shows the hourly grazing and concentrations of phytoplankton. The highest concentrations of copepods were found at all times of the day at about the same depth (20 m for the southern, 20 to 30 m for the northern station). The night grazing was maximal close to the surface or 10-m depth at 2100 and 0300 at the southern station, but was different during the 2 succeeding days at the northern station, showing maximal values at 20–30 m at 1900 and 0100 on the

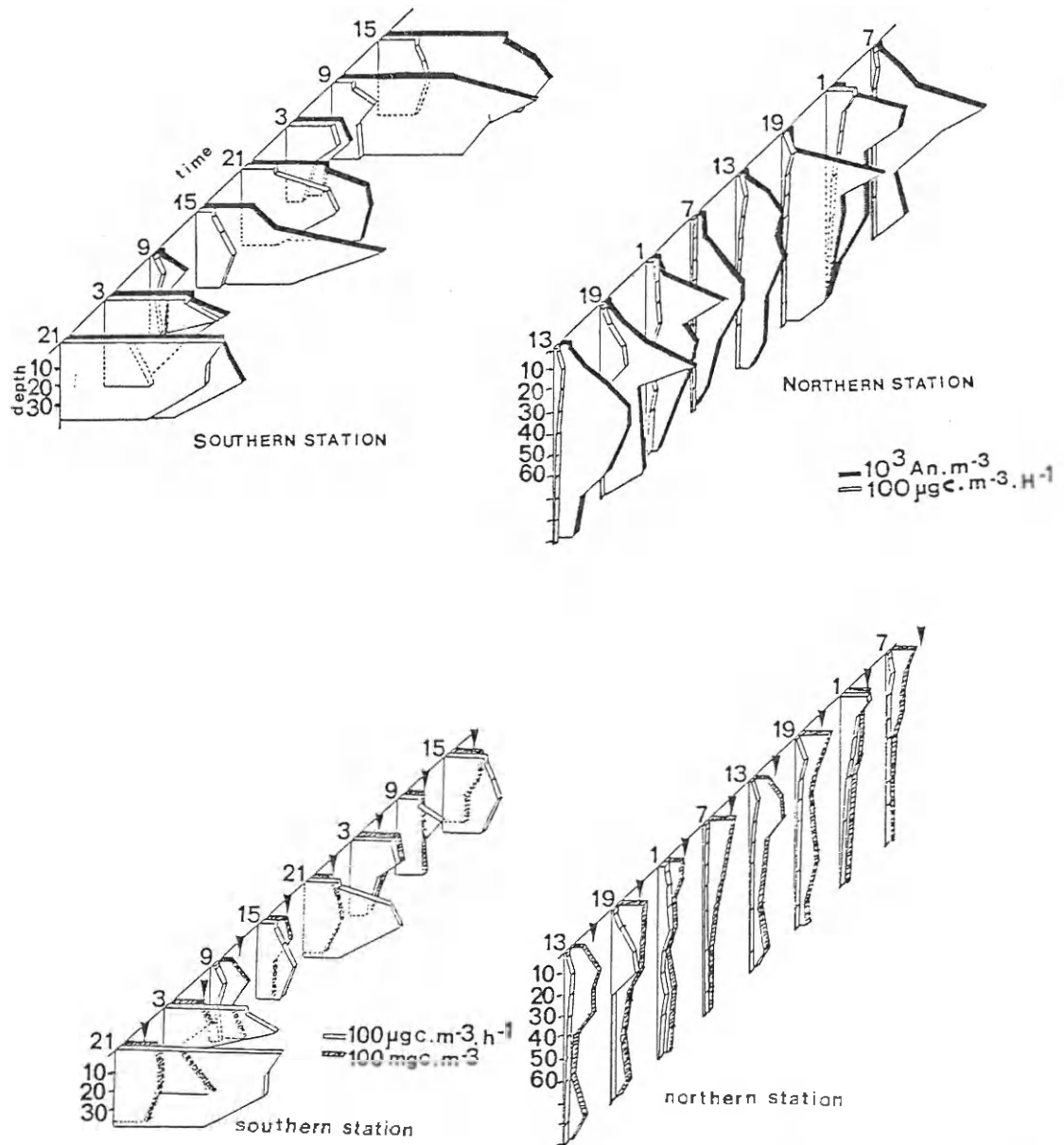


Figure 15. Total hourly grazing at the 48-h stations: (upper figure) vertical distribution of hourly grazing of the total community of copepods and total numbers of copepods at different sampling times and (lower figure) vertical distribution of hourly grazing and phytoplankton concentration. Arrows show the 200 mg C concentration.

first night and 0 and 3 m on the second night. Grazing values are not always linked with the total numbers of copepods. Figure 15, Lower shows that hourly grazing at 2100 and 0300 was maximal at the depths of maximal concentrations of phytoplankton, which were limiting (equal or lower than $200 \text{ mg C} \cdot \text{m}^{-3}$) at the other depths. At the northern station, the maximal nightly grazing occurs at the depths where the concentrations just reached $200 \text{ mg C} \cdot \text{m}^{-3}$. We can conclude from the results of the detailed observations of nightly grazing of the total community of copepods that it exhibits the same sensitivity to phytoplankton concentrations as observed for the 24-h grazing. This conclusion was expected since we calculated that the nightly grazing accounts for about 70% or more of the total 24-h grazing.

DISCUSSION

Copepods exhibited very different patterns of feeding behavior but most of the time had a higher nocturnal food intake. The same species were very sensitive to variations in phytoplankton biomass, some developmental stages much more than others. During summer the limiting concentrations of phytoplankton in the North Sea seemed to be around $200 \text{ mg C} \cdot \text{m}^{-3}$. In most of the areas, this concentration was only found in the upper 20–30 m of the water column. As a consequence, the copepods followed this concentration such that the vertical distribution of the grazing activity in the water column was concentrated in the upper 20–30 m.

The limiting concentration of 200 mg C phytoplankton could seem a high value. This is due to two facts. On one hand the ratios of phytoplankton C/chl *a* from Table 1 range from 175:1 up to 1,350:1, extremely high values. This is an observation I have been making during more than 10 years of work in the North Sea. These high carbon values are due, in the southern area, to the presence of *Phaeocystis pouchetti*, a species surrounded by a very large mucous envelope and, in other regions, the phytoplankton was dominated by the dinoflagellate *Ceratium*. On the other hand, the grazing values presented in this paper are field data, where probably part of the food in this kind of natural conditions is not consumed with high efficiency, and the radiocarbon method provides no evidence of any kind of food preference.

Another important observation was the absence of major vertical migrations. When they occurred, they involved movements of only 10–20 m. In the Southern Bight of the North Sea the phytoplankton concentration was not limiting the feeding rate of copepods; nevertheless, as the phytoplankton biomass was highest close to the bottom, so were the copepod numbers both day and night. This was a case when high nocturnal feeding rates were not linked with upward vertical movement.

One question is why both nocturnal behaviors, migration and feeding, do not always cease together, and why only one of the two ceases. Light seems to be a controlling factor in the timing of nocturnal grazing, and the onset appears related to a low light level (Head et al., 1985). Grazing may also be inversely related to light intensity, with the highest change in rates occurring at twilight (Stearns, 1986). In our case, just at the onset of the summer, the nights were very short, particularly in the northern area where the sunset occurred at 2300–2400 and sunrise at 0100 or 0200. However, the increase in feeding rate of most species began late in the afternoon (1800–2000), when the sun and consequently the light intensity were still very high.

The vertical distributions of phyto- and zooplankton are rather constant in the different areas. The POC concentration was highest close to the bottom in the shallow homogeneous southern seas and so was the zooplankton concentration. In the central and northern part the maximal values were found just above or under the thermocline. In general, highest concentrations were not at the surface, with the exception of the Norwegian region where there was a strong gradient of salinity and temperature. No clear association between the distribution of plankton and the distribution of temperature and salinity could be found on a statistic basis. The light penetration in the water column may play a more important role in this case. It may be too high at the surface, providing light inhibition of phytoplankton primary production, and leading to a subsurface maximum. We show a clear association between the phytoplankton distribution and the zooplankton grazing distribution, and reduced or absent vertical movements of copepods, the latter concentrating at the depths of the best available food concentrations.

Scrope-Howe and Jones (1986) showed that when discrete chlorophyll *a* maxima are observed, the zooplankton can concentrate within the maxima. Townsend et al. (1984) also pointed out that the vertical structure of phytoplankton is closely associated with post-naupliar stages in June, but not in September. So in some seasons in some environments copepods follow the distribution of phytoplankton. On the other hand, well-fed organisms migrate daily and hungry individuals widely vary their migration pattern (Dagg, 1985). In the case we are reporting here, the zooplankton seem to be just at the limit of sufficient food, so that the metabolic losses due to vertical movements would be too high compared to the gain of a few hours of high feeding rates. This behavior could be a transition between the large vertical migrations and high night food intake typical of spring, and the fall behavior where migrations and feeding rhythm cease (Daro, 1985; Lampert and Taylor, 1985).

This study contributes to our understanding of the plasticity of behaviors of marine copepods, who can exhibit different adaptations to environmental variations. There is never only one explanation or interpretation available. During spring, temperature and light can play the most important role; in summer light and phytoplankton; in fall competition for food. I suggest as a hypothesis that the species that can adapt their behavior to the different variations numerically dominate the zooplankton, such as *Calanus finmarchicus*. Others, which are less plastic in their behavior, decline after one season, such as *Temora*.

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