HELGOLÄNDER MEERESUNTERSUCHUNGEN
Helgoländer Meeresunters. 34, 313–327 (1981)

Vertical distribution of faecal pellets during FLEX '76*

M. Krause

Universität Hamburg, Sonderforschungsbereich 94 – Meeresforschung;
Bundesstraße 55, D-2000 Hamburg 13, Federal Republic of Germany

ABSTRACT: During FLEX '76 (Fladen Ground Experiment), the vertical distribution of faecal pellets was studied at a time station on the Fladen Ground (North Sea). Generally, the faecal pellets showed a clearly-defined maximum above the main thermocline within a depth of 0–30 m. Only in a period of storms was the faeces-maximum lowered to the main thermocline, which occurred at 50–60 m depth. The maximum numbers of the copepod *Calanus finmarchicus*, the most important producer of faecal pellets, initially occupied the same level as the faeces maximum. However, from the middle of May, the *C. finmarchicus* population started a diel vertical migration, during which, as a rule, the copepods migrated away from the surface region into deeper waters. On this occasion, the faecal pellet maximum did not break up but remained in the uppermost layer of the water column. The high concentrations of faecal pellets found within the uppermost 30 m of the water column contradict the extremely high sinking rates of faeces reported by various authors. The quotients of the depth-integrated counts of faecal pellets and *C. finmarchicus* individuals were calculated. The main maximum of faeces per individual occurred in the period between 28 April and 6 May 1976. A second, smaller maximum was documented between 23–28 May 1976. These two maxima coincided with the development of phytoplankton blooms observed at this particular time station.

INTRODUCTION

During the International Fladen Ground Experiment in early 1976 (FLEX '76), continuous measurements of a large number of various parameters were undertaken at a time station (58 ° 55′ N, O ° 32′ E) between 26 March and 6 June. The objective of these measurements was to carry out a quantitative study of the planktonic spring bloom on the Fladen Ground, and to use the data obtained to test a mathematical model of its growth and to examine the influence of various biotic and abiotic factors on the algal developmental process. A first approach to study the dynamics by use of a two-component model was made by Radach (1980).

This presentation is concerned with the vertical distribution of faecal pellets, which arose as part of the results from the evaluation of zooplankton material from the time station. In a previous paper (Krause & Radach, 1980), the chronological development of both the counts of individuals and the biomass of some major groups of zooplankton was reported. A further paper (Krause & Radach, in preparation) is concerned with the development of the vertical distribution of some important zooplankton groups during the time station as well as with the occurrence of diel vertical migrations.

---

* JONSDAP '76 Contribution No. 68.

0174-3597/81/0034/0313/$ 02.00

MATERIAL AND METHODS

197 sample series were collected with a rosette sampler at the FLEX time station. The water samples were taken at the following standard depths: 3 m, 10 m, 20 m, 30 m, 40 m, 50 m, 60 m, 75 or 80 m, 100 m, and, during the second half of the time station also from near the bottom (ca. 150 m depth). Four series of samples should have been taken each day. However, for technical reasons this was not always possible.

5 or 10 l water samples were taken from the rosette sampler and filtered through a 30 μm gauze. The residue was preserved in 4 % formalin (buffered) to be taxonomically evaluated in the laboratory.

Various samples taken at noon and at midnight were counted for numbers of faecal pellets. During the second section of the cruise of R. V. "Meteor" (24 April to 16 May 1976), the counts only took place randomly. On the third section of the cruise of R. V. "Meteor" (22 May to 5 June 1976), where distinct diel vertical migrations of *C. finmarchicus* occurred, all available noon and midnight series of samples were counted for faecal pellets.

The faecal pellets were not catalogued by type. Nevertheless, the possibility can be excluded that the faeces were produced by organisms which were not caught by the rosette sampler used. Shape and size are comparable with those calanoid faeces described by Martens (1978). During the time station, *C. finmarchicus* represented by far the most numerous calanoid copepod. *Pseudocalanus elongatus* and *Paracalanus parvus* also occurred to a lesser extent in the upper 60 m of the water column. In the last third of the time station a massive population of *Microcalanus pusillus* developed at depths below the main thermocline and therefore took part to a certain extent in the faeces production. However, it is assumed that by far the most faeces were produced by *C. finmarchicus*.

The number of faecal pellets and the individual counts of *C. finmarchicus*, the main producer of the faeces, have been portrayed together in depth profiles. In this case, the curves have been reduced in proportion to $\sqrt{x}$. Further, the upper and lower limits and the centre of the main thermocline during the sampling period have been drawn in the diagrams as lines (Soetje & Huber, 1980). Isolines of the number of faecal pellets and the counts of *C. finmarchicus* over the period of the third part of the cruise of R. V. "Meteor" were also depicted, in order to show possible connections between diel vertical migrations of *Calanus* and the vertical distribution of the faeces.

RESULTS

The following is inferred from the depth profiles (Figs 1–5): as a rule, the faecal pellets showed a clearly-defined maximum above the main thermocline, often close under the surface in 0–30 m depth. The faeces maximum occurred directly in the main thermocline in 50–60 m depth only in depth profiles from 11, 12 and 16 May (Fig. 1). At this time, a number of other small organisms such as copepod eggs, nauplii and the copepodite stages of *Oithona similis* showed the tendency to become more abundant at greater depths (Krause & Radach, in preparation). The reason for this may be a series of storms which occurred at this time in the Fladen Ground area. On the 12–13 May, the strongest storms at the time station were registered. Evidently the vertical turbulance

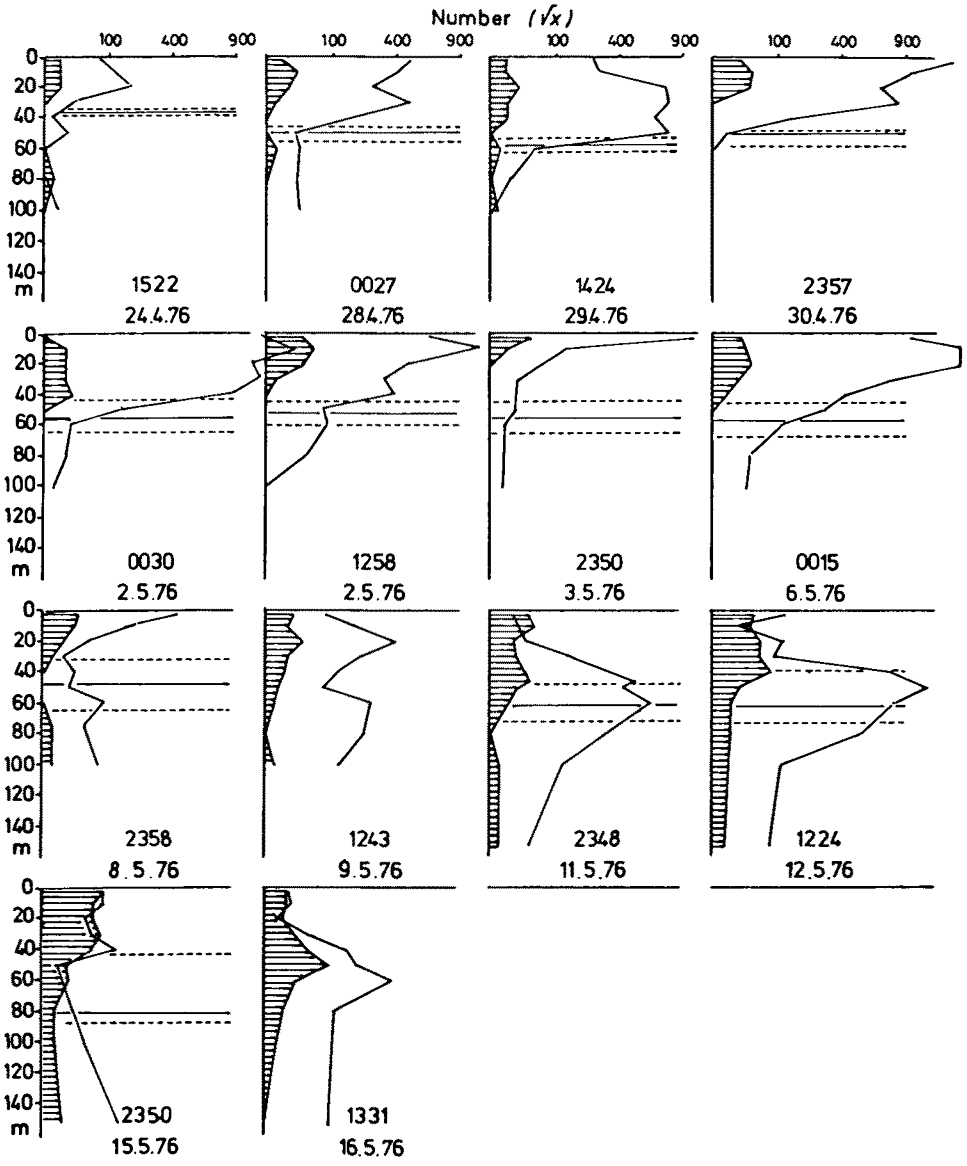

Fig. 1. Vertical profiles of *Calanus finmarchicus* (CI–CVI) (hatched curves) and faecal pellets of calanoid copepods (full lines) expressed in numbers per 10 l (24. 4.–16. 5. 1976). In Figs 1–5 the x-axis has been reduced in proportion to √x. The upper and lower limits (broken lines) and the centre (full line) of the main thermocline during the sampling period have been drawn in the diagrams as lines

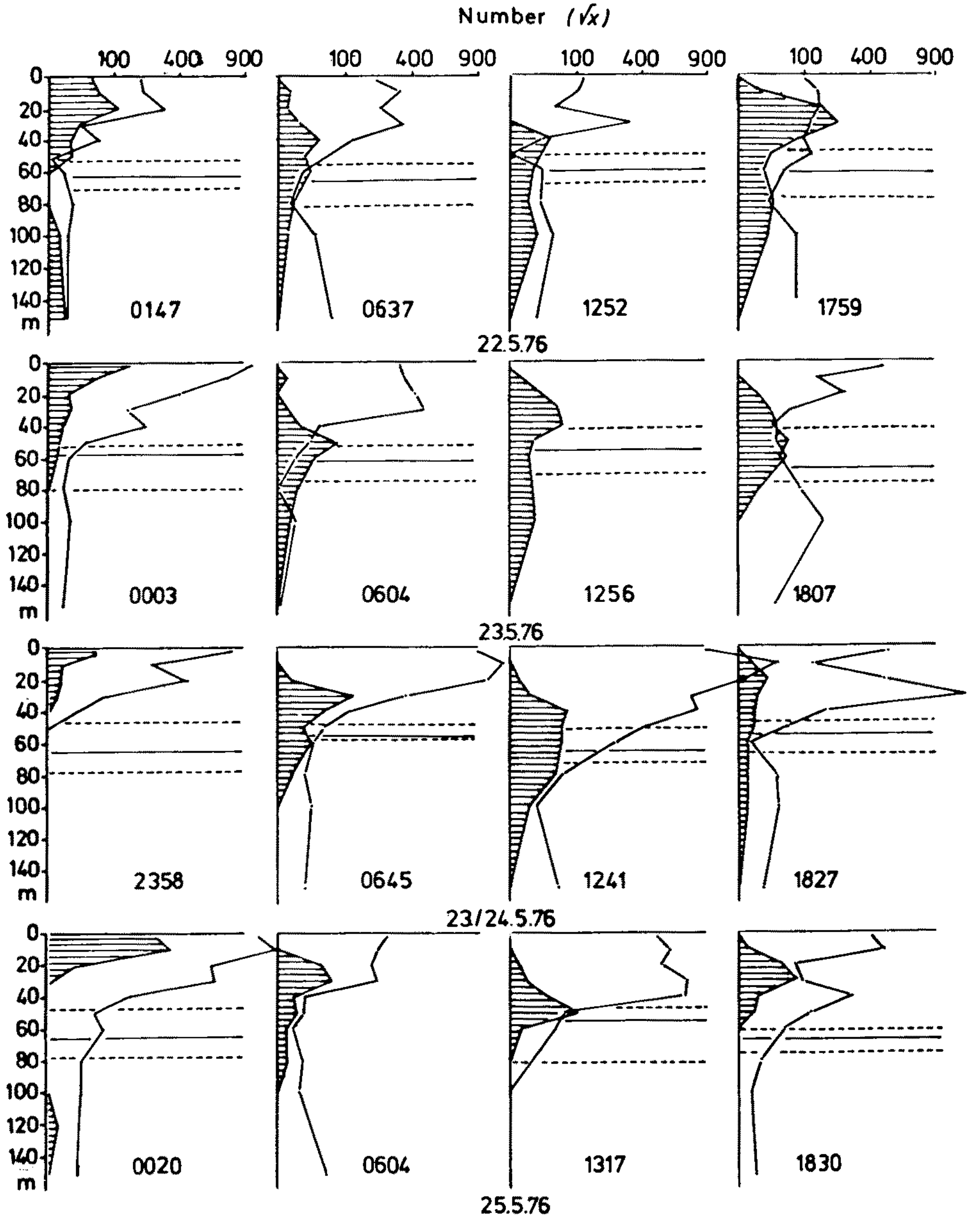

Fig. 2. Vertical profiles of *Calanus finmarchicus* (CI–CVI) (hatched curves) and faecal pellets of calanoid copepods (full lines) expressed in numbers per 10 l (22. 5.–25. 5. 1976)

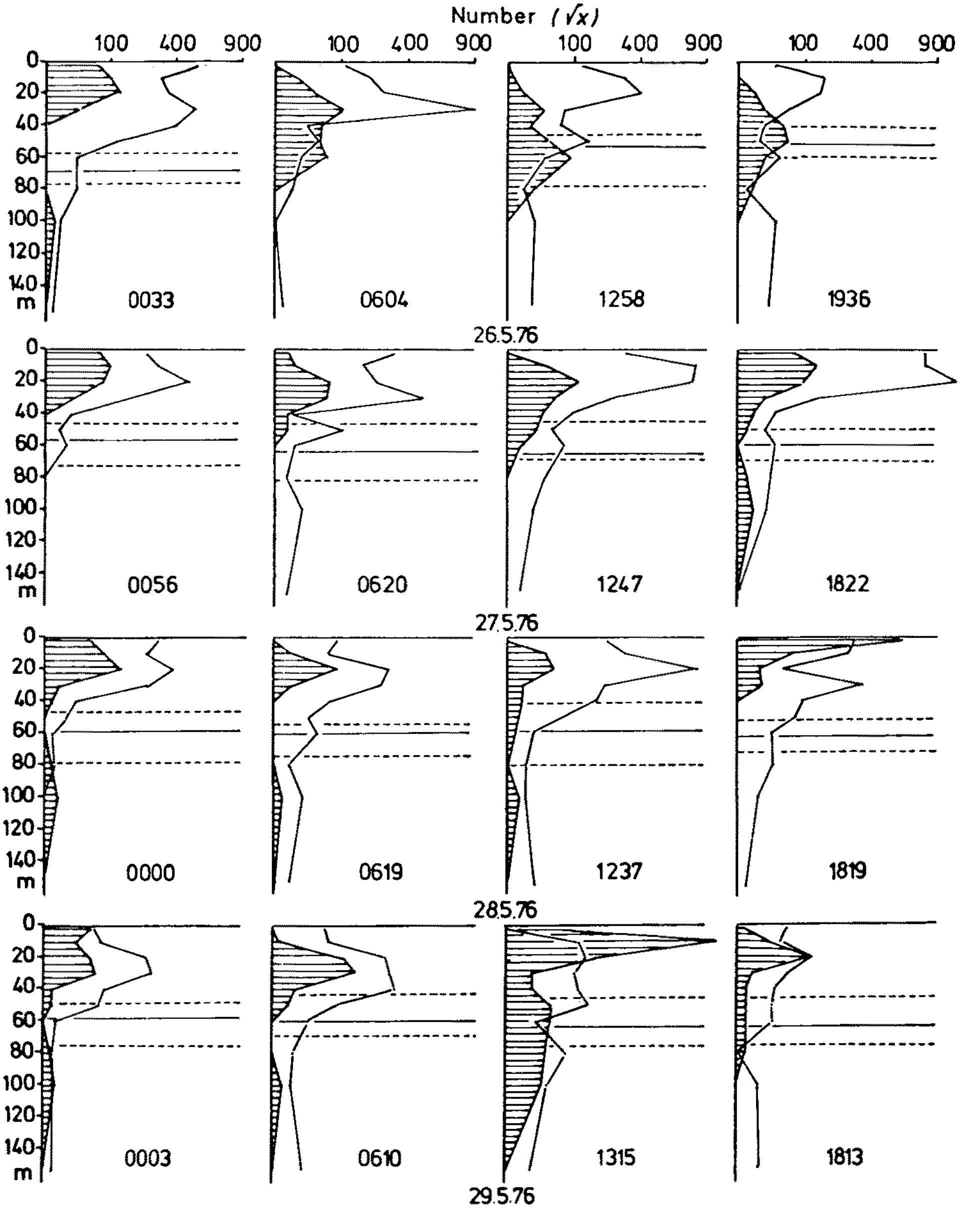

Fig. 3. Vertical profiles of *Calanus finmarchicus* (CI–CVI) (hatched curves) and faecal pellets of calanoid copepods (full lines) expressed in numbers per 10 l (26. 5.–29. 5. 1976)

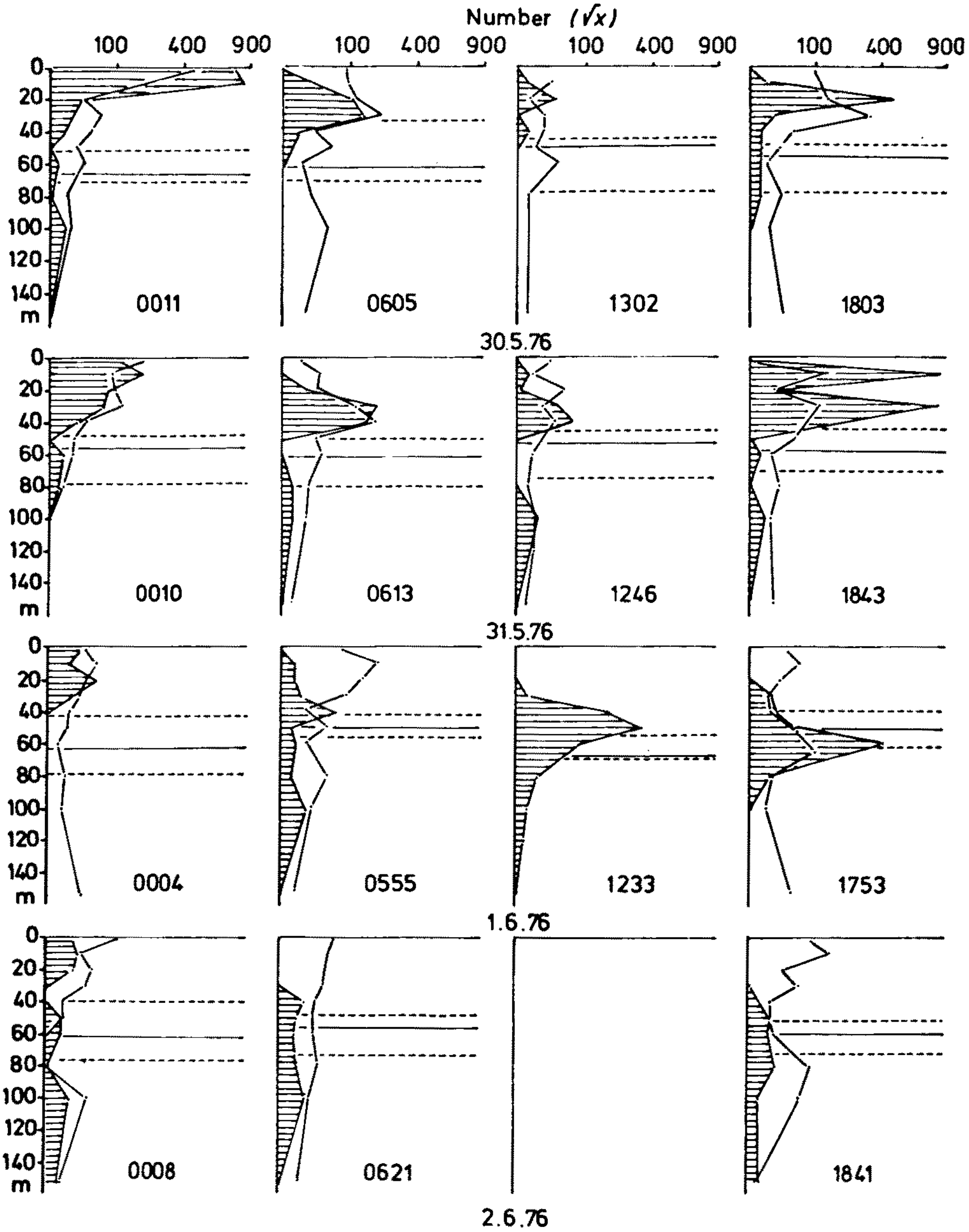

Fig. 4. Vertical profiles of *Calanus finmarchicus* (CI–CVI) (hatched curves) and faecal pellets of calanoid copepods (full lines) expressed in numbers per 10 l (30. 5.–2. 6. 1976)

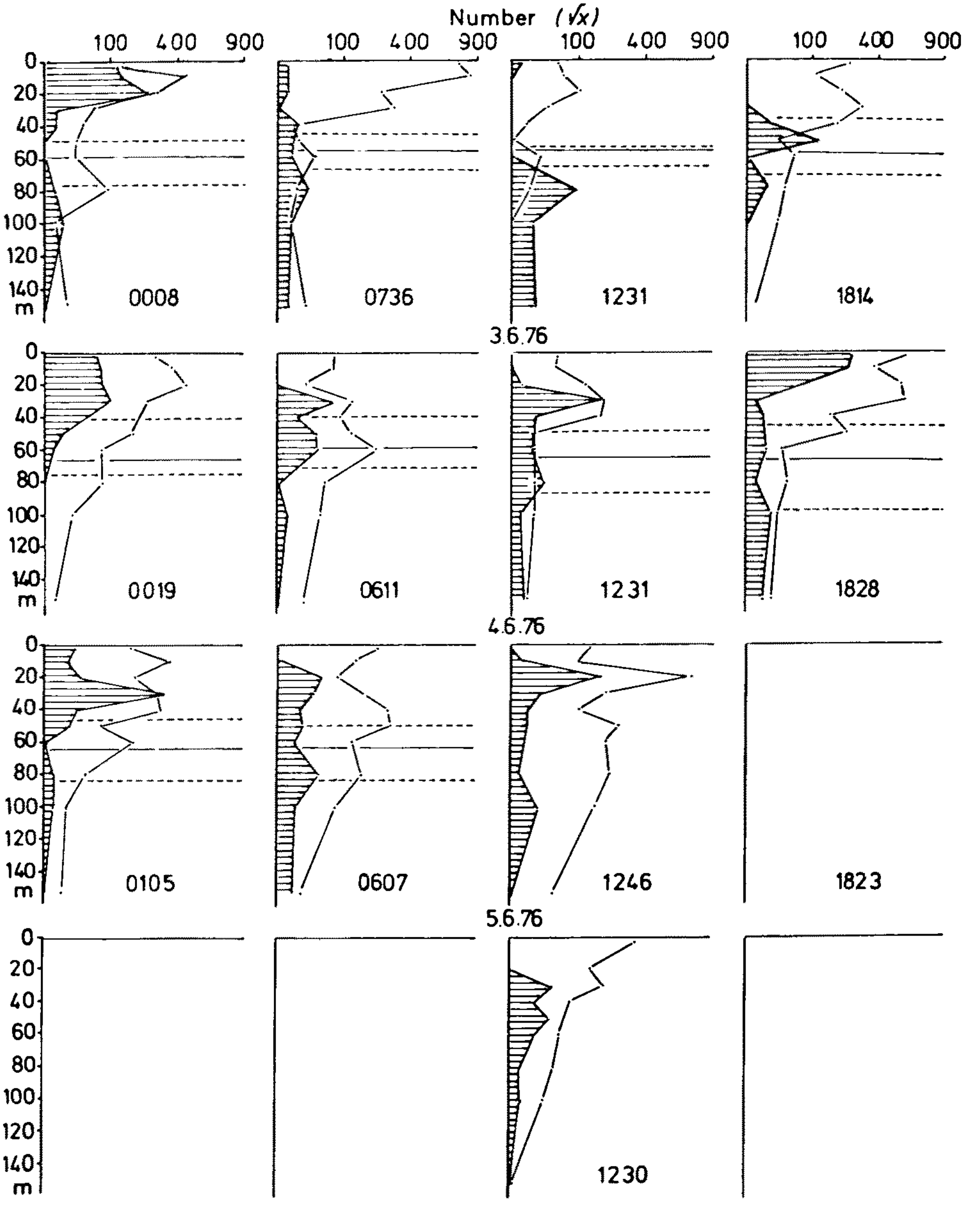

Fig. 5. Vertical profiles of *Calanus finmarchicus* (CI–CVI) (hatched curves) and faecal pellets of calanoid copepods (full lines) expressed in numbers per 10 l (3. 6.–12. 6. 1976)

which had been produced by the storm was strong enough to bring about a transport of particles into deeper water.

During the second section of the "Meteor" cruise (Fig. 1), the maximum count of individuals occurred in the same water layers, as did the faecal pellets which, however, were present in larger numbers. The maximum count of *C. finmarchicus* was higher in the uppermost layers only when storms caused the fecal pellets to sink into the thermocline (11–12 and 16 May).

During the third section of the "Meteor" cruise, *C. finmarchicus* displayed a diel vertical migration (Krause & Radach, in preparation). Here, the vertical profiles (Figs

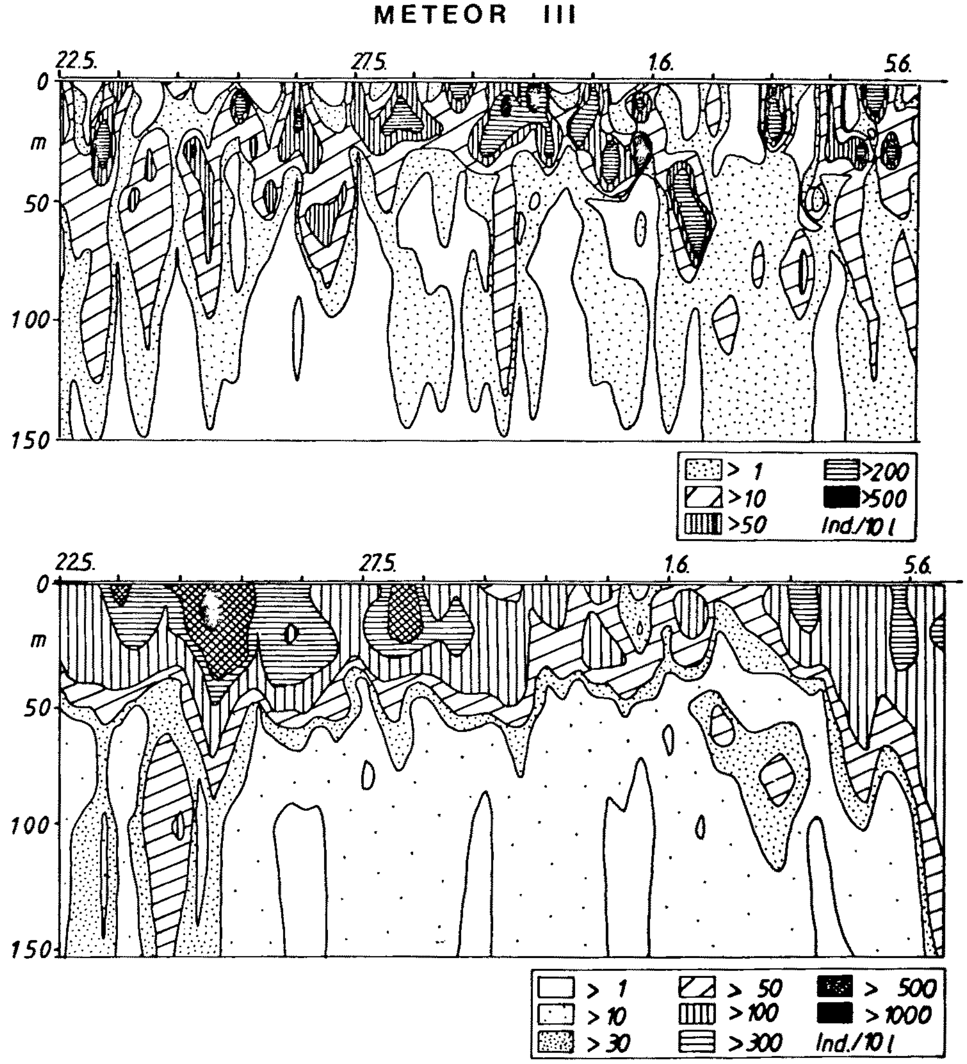

Fig. 6. Isolines of the individual numbers of *Calanus finmarchicus* (above) and the quantities of faecal pellets (below) over time and depth

2–5) showed that *C. finmarchicus* is able to migrate out of the zone of maximal concentration of faecal pellets, but re-assembled there again during the night (see 22–26 May, 3 June). Consequently, the faeces maximum in the surface layer did not break down when *C. finmarchicus* withdrew to deeper zones at noon. Comparison of the isolines of *C. finmarchicus* and faecal pellets during the third section of the "Meteor" cruise also showed that the depth distribution of the faeces does not follow the diel vertical migration of the copepods. Moreover, they remained en masse in the uppermost layers of the water column (Fig. 6).

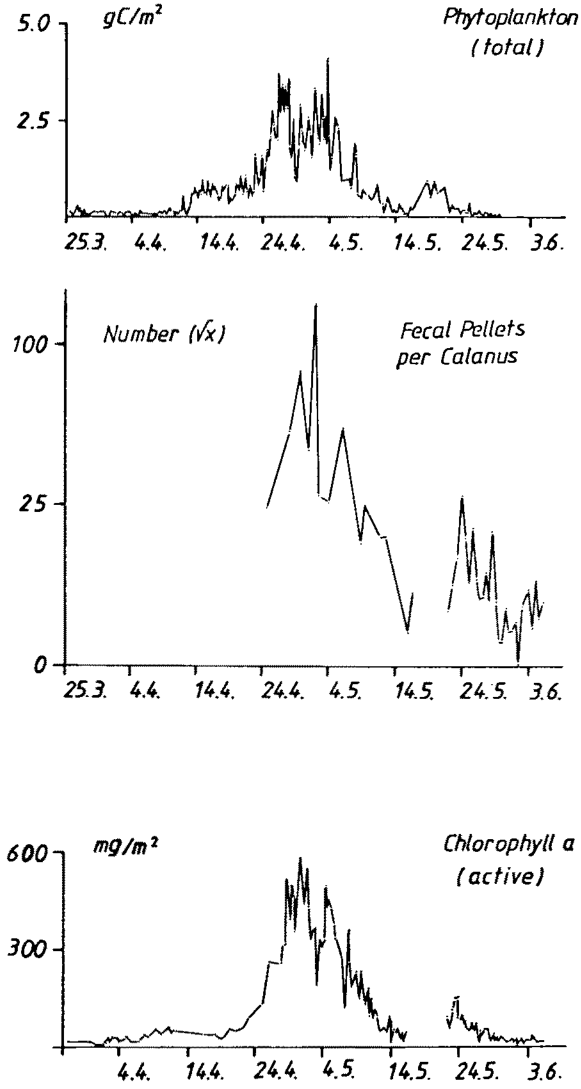

Fig. 7. Depth-integrated time series of the phytoplankton (according to M. Gillbricht), of the quotients from the counts of faecal pellets and *Calanus finmarchicus* (CI–CVI) and of the active chlorophyll *a* (according to A. Weber)

The quotients of the depth-integrated numbers of the faecal pellets and counts of *C. finmarchicus* were calculated and are presented for this period of time in Figure 7. The largest number of faeces per *Calanus* individual was noted within the period 28 April and 6 May 1976. Here, up to 127 faeces were calculated per *Calanus* individual. A second, small maximum occurred in the time between 23–28 May 1976. These two maxima coincided with the maxima of the phytoplankton cells counted by Gillbricht and the chlorophyll *a* measurements of Weber (Radach et al. 1980) during the time station (Fig. 7).

DISCUSSION

The observation that *Calanus finmarchicus* produces a larger number of faecal pellets with increased feeding (phytoplankton blooms) is in accordance with the opinion of several authors. Because of its automatic filtration behaviour (Marshall & Orr, 1955; Gauld, 1966), *C. finmarchicus* shows a larger intake rate with greater food availability, and this rate asymptotically approaches a maximum value (Mullin, 1963; Haq, 1967; Frost, 1972; Gamble, 1978). This leads to a higher production of faecal pellets by these copepods (Butler et al., 1970; Corner et al., 1972; Gaudy, 1974). By so doing, the nutritional efficiency is most probably reduced because of the faster passage through the alimentary canal. Those faeces, which were collected during the phytoplankton bloom, as a rule showed a deep green colouring which allows the conclusion that the food was insufficiently digested.

The clearly-defined and regularly-occurring maximum of the faecal pellets within the upper 0–30 m of the water column during FLEX '76 is difficult to explain. Laboratory experiments by various authors show constantly high rates of sinking for faecal pellets:

Smayda (1969) collected faecal pellets with nets to determine their speed of sinking. The different sized faecal pellets were isolated by means of Boleyns apparatus, placed in an ampoule with filtered seawater (32 ‰) and preserved for several days at 2 °C. The experiment was carried out in seawater (34.4 ‰) and at 15 °C, and the faecal pellets were kept for a few hours at the temperature of the experiment before measuring the rate of sinking. On the basis of these experiments, Smayda suggested sinking rates of between 36 and 376 m/day. He assumed that different diets influenced the density of the faeces and therefore its rate of sinking. Thus the larger faecal pellets of the Euphausiids showed a lower speed of sinking than those of the copepods.

Smayda (1971) began work with cultures of *Acartia clausi* which were fed with microflagellates. The rate of sinking of the faecal pellets (using the same measurement technique as in 1969) on this occasion lay between 74 and 210 m/day. The smaller faecal pellets, though, showed a tendency to sink the fastest.

Fowler & Small (1972) determined the rates of sinking of faecal pellets from different, freshly-caught euphausiids. The animals were placed in glass containers with filtered seawater. The resultant pellets were collected, measured under a microscope and subsequently used in the sinking-rate experiment. The rates of sinking amounted to 126–862 m/day. As a rule, the largest pellets sank quickest, and the smallest were the slowest. Those individuals which were fed in the aquarium with *Artemia*, produced faecal pellets which seemed to be less compact and showed a lower rate of sinking, between 53 and 411 m/day. Fowler & Small found higher rates of sinking for euphausiids than Smayda (1969).

Wiebe et al. (1976) obtained faecal pellets with sediment traps. The faeces were counted under a microscope, measured and subsequently frozen until the measurement of the rate of sinking. Wiebe established rates of sinking between 50 and 225 m/day. 10 % of the faecal pellets sank quicker, up to 941 m/day. The mean value at 5 °C was 159 m/ day; and the mean value at 21.7 °C was 171 m/day.

Turner (1977) used faecal pellets from the copepod *Pontella meadii* for his observations. The individuals were fed with *Skeletonema, Dunaliella* or *Gonyaulax*, or a mixture of *Skeletonema* and *Nitzchia*. After a feeding time of 16–24 hours, the faecal pellets were pipetted from the bottom of the containers, and measured under a microscope. The investigation was accomplished with unpreserved faeces. As a rule they remained stationary for a few seconds before they began to sink. The rate of sinking lay between 15 and 153 m/day, with an average of 66 m/day. The tendency for the largest pellets to sink quickest and the smallest, in contrast, correspondingly slower, could not be significantly demonstrated. Faeces which were produced as a result of feeding with *Skeletonema costatum* and *Nitzchia* sp. had the largest average volume and the fastest rate of sinking. Otherwise, no clear relationship could be observed between diet and the rate of sinking. Overall, a two-to three-times difference in the rate of sinking of faecal pellets of the same size and diet was observed. Turner (1977) attributed this to small-scale fluctuations in water density in the measurement vessels and suggested that to make a statement on the sinking behaviour in the strongly variable medium of the ocean is extremely difficult.

Honjo & Roman (1978) fed the copepods with bacteria-free cultures of coccolithophorids and diatoms as well as with inorganic calcite and aragonite microcrystals. Measurements were made on freshly-produced faeces. Those for *Acartia tonsa* showed an average sinking speed of 120 m/day (80–150 m/day) at 15 °C. The faeces of *C. finmarchicus* sank 180–220 m/day at 15 °C. At 5 °C, the average sinking rate was 35 % lower.

In field studies, Schrader (1971) found the maximum numbers of faecal pellets in the uppermost 100 m of the water column. He suggested that, at approximately 300 m, most faeces have already broken down, in which case only a small percentage reach the sea bed. Faeces have been found in the Baltic Sea up to a depth of 459 m. Off Portugal, faeces containing diatoms were found in depths of 4000 m (2 pellets m^3). According to Schrader (1971) the faecal pellets rapidly leave the euphotic zone because of their high sinking rate (40–400 m/day) and, therefore, remove silicate and other nutrients from the upper water.

The work of Honjo & Roman (1978) contradicts Schrader's hypothesis that, in spite of such a fast rate of sinking, the faecal pellets are already broken down at a depth of 300 m. They even found intact faecal pellets after 20 days in water of 5 °C. At 20 °C, on the other hand, according to their observations the surface membranes of the faeces were even broken down within 3 hours by rapid bacterial activity. When the surface membranes are consumed, the microbiological breakdown shifts inside the faecal pellets. Finally they collapse into small particles. However, a water temperature of 20 ° would seem unlikely in the middle and deeper parts of the water column.

Martens (1975) has calculated the rate of secondary production of organic material

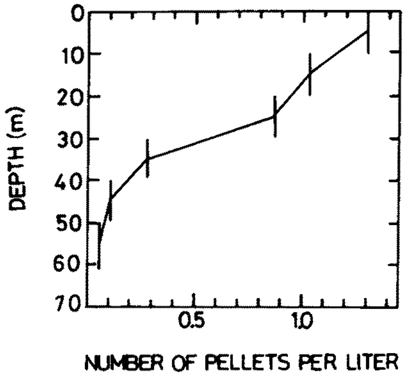

Fig. 8. Vertical distribution of calanoid copepod faecal pellets in the Lake Michigan during June 1975 (data from Ferrante & Parker)

in the plankton in a water column of approximately 20 m in the Eckernförder Bucht (Baltic Sea). Mainly, these calculations were concerned with copepods. The production amounted to between 23.7 g C/m^2/year and 56.7 g C/m^2/year (mean value 40.2 g C/m^2/year). On the other hand, the total amount of sedimented copepod faeces totalled only 1.25 g C/m^2/year. Martens uses these figures with caution since for this calculation only the complete faecal pellets were counted. Nevertheless, this value seems very low, for Marshall & Orr (1955) found a faecal pellet production rate for *C. finmarchicus* of 6–12/hour. Gaudy (1974) established a production rate for copepods of 200 faecal pellets/individual/day. According to Petipa et al. (1970) this led to a daily defaecation rate of 14.8 % of the body weight of *C. finmarchicus* or *Pseudocalanus elongatus*. However, Martens (1975) only found about 3 % of the total secondary production in the form of faecal pellets on the sediment. The suggestion could be made that a considerable proportion of the faecal pellets in the 20 m deep water column of Eckernförder Bucht became utilized before having settled down.

Ferrante & Parker (1977), working in fresh water, ascribe the breakdown of the faecal pellets in the first instance to the bacterial decomposition of the peritrophic membrane, which is composed of polysaccharides, for example, chitin. They showed that a 50 % breakdown of the membrane occurred within 6–7 days. A total breakdown of the faeces membrane occurred within 13–14 days. Ferrante & Parker calculated a sinking rate of 4.7 m/day for faecal pellets collected in sediment traps in Lake Michigan. From these values, they estimated the vertical distance which a faecal pellet can sink until it is broken up into pieces and dissolved. The vertical distance lies between 28 m (6 days x 4.7 m/d^{-1} for a 50 % decomposition of the membrane) and 66 m (14 days × 4.7 m/d^{-1} for a complete decomposition of the membrane). Ferrante and Parker believe that faecal pellets which have been produced near the surface do not reach the bottom in waters deeper than 70 m. In their opinion the vertical transport of substances is caused by the diel vertical migrations of copepods.

Figure 8 shows the vertical distribution of copepod faeces in Lake Michigan (according to Ferrante & Parker). Here, there are similarities to the vertical distribution of faecal pellets on the Fladen Ground (Figs 1–5). In each case the maximum lay near the surface. In general, a strong reduction of the numbers takes place at a depth of 40–60 m.

A review of the literature on the rates of sinking of faecal pellets shows considerable differences and vagueness. Especially when studying laboratory experiments, where very high rates of sinking have been established throughout, the question arises, amongst others, whether the extremely high values could not have been caused by the treatment of the faecal pellets (freezing, storage at 2 °C for weeks, counting and measuring under a warm light microscope).

The strong maxima of faecal pellets in the surface layer which was established in the Fladen Ground area, can possibly be explained in the following manner:

The faecal pellets, probably enriched with bacteria in the gut of the copepod, inevitably have an anaerobic metabolism. The gas bubbles which develop during the bacterial activity in the faeces, at first cause a floating or even a buoyancy of the faecal pellets. This causes them to remain in the euphotic zone, where they can be re-cycled. One can easily imagine that with faecal pellets such as those used in the sinking rate experiments, the activity of the alimentary canal bacteria has been stopped, and any gas bubbles present have been driven out by the various methods of handling. For example, through freezing, or through storage at 2 °C for many days or, not least, through counting and measuring the faeces under the light microscope, where the material is heated quite considerably. Honjo & Roman (1978), though, found no gut bacteria in the faeces of copepods fed on bacteria-free cultures of coccolithophorids and diatoms. However, Johannes & Satomi (1966) examined fresh faecal pellets of the prawn, *Palaemonetes pugio*, which were densely packed with bacteria. They belonged to the gut flora.

The retention of faeces in the surface layer, or, at least, a reduced release of faeces into the deeper water layers, is certainly of great importance to the ecosystem. According to Petipa et al. (1970), *C. finmarchicus* has a daily defaecation of 14.8 % of its body weight. Were the faecal pellets to sink into deep water at the experimentally-determined high rates, that would mean that an amount of organic material equivalent to about 15 % of the standing stock of copepods in the trophogenic layer is being lost every day. Such a rapid impoverishment of the trophogenic layer in summer seems unlikely. In contrast, the observed occurrance of faecal pellets in the mixed layer on the Fladen Ground means that they will be re-cycled and the nutrients will then be of benefit to algae growth. The role of faecal pellets in energy transport during the spring bloom could be considerable, and should be included in the mathematical model of processes on Fladen Ground.

If the faecal pellets remain in the mixed layer, this certainly means that the faeces do not possess the property of cleaning the trophogenic layer as hoped by several authors (Beasley et al., 1978). Heavy metals and radionuclides are probably not transported by them into the depths, and sedimented, but are released again into the trophogenic layer. Consequently, these substances can be passed on and concentrated in the food chain.

Acknowledgements. I should like to thank Dr. J. Trahms for his participation in planning the zooplankton experiment, for his part in taking the samples at sea and for many helpful discussions. I am furthermore grateful to Prof. Dr. M. Gillbricht who kindly provided the cell counts of phytoplankton and with whom I had many effective discussions. Thanks are also due to Dr. G. Hentzschel and to Dr. G. Radach for their helpful comments upon this paper. Special thanks are due to G. Carretero Alcobendas and J. Beil for carefully sorting the zooplankton material and also to A. Sanchez and R. Kopp for their help in sampling. This research was sponsored by the Deutsche Forschungsgemeinschaft through the Sonderforschungsbereich 94 – Meeresforschung, Hamburg.

LITERATURE CITED

Beasley, T. M., Heyraud, M., Higgo, J. J. W., Cherry, R. D. & Fowler, S. W., 1978. Po-210 and Pb-210 in zooplankton fecal pellets. – Mar.Biol. *44*, 325–328.

Butler, E. I., Corner, E. D. S. & Marshall, S. M., 1970. On the nutrition and metabolism of zooplankton VII. Seasonal survey of nitrogen and phosphorus excretion by *Calanus* in Clyde Sea-area. – J. mar. biol. Ass. U. K. *50*, 525–560.

Corner, E. D. S., Head, R. M. & Kilvingten, C. C., 1972. On the nutrition and metabolism of zooplankton VIII. The grazing of *Bidulphia* cells by *Calanus helgolandicus*. – J. mar. biol. Ass. U. K. *52*, 847–861.

Ferrante, J. G. & Parker, J. I., 1977. Transport of diatom frustules by copepod fecal pellets to the sediments of Lake Michigan. – Limnol. Oceanogr. *22*, 92–98.

Fowler, S. W. & Small, L. F., 1972. Sinking rates of euphausid fecal pellets. – Limnol. Oceanogr. *17*, 273–296.

Frost, B. W., 1972. Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. – Limnol. Oceanogr. *17*, 805–815.

Gamble, J. C., 1978. Copepod grazing during a declining spring phytoplankton bloom in the northern North Sea. – Mar.Biol. *49*, 303–315.

Gaudy, R., 1974. Feeding four species of pelagic copepods under experimental conditions. – Mar.Biol. *25*, 125–141.

Gauld, D. T., 1966. The swimming and feeding of planktonic copepods. In: Some contemporary studies in marine science. Ed. by H. Barnes, Allen, London, 313–334.

Haq, S. M., 1967. Nutritional physiology of *Metridia lucens* and *M. longa* from the Gulf of Maine. – Limnol. Oceanogr. *12*, 40–51.

Honjo, S. & Roman, M. R., 1978. Marine copepod fecal pellets: production, preservation and sedimentation. – J. mar. Res. *36*, 45–57.

Johannes, R. E. & Satomi, M., 1966. Composition and nutritive value of fecal pellets of marine crustacean. – Limnol. Oceanogr. *11*, 191–197.

Krause, M. & Radach, G., 1980. On the succession of developmental stages of herbivorous zooplankton in the northern North Sea during FLEX '76. 1. First statements about the main groups of the zooplankton community. – Meteor Forsch. Ergebn. (A) *22*, 133–149.

Marshall, S. M. & Orr, M. A., 1955. The biology of a marine copepod *Calanus finmarchicus* (Gunnerus). Oliver & Boyd, London, 188 pp.

Martens, P., 1975. Über die Qualität und Quantität der Sekundär- und Tertiärproduzenten in einem marinen Flachwasserökosystem der westlichen Ostsee. Thesis, Universität Kiel, 111 pp.

Martens, P., 1978. Fecal pellets. – Fich. Ident. Zooplancton *162*, 1–4.

Mullin, M. M., 1963. Some factors affecting the feeding of marine copepods of the genus *Calanus*. – Limnol. Oceanogr. *8*, 239–250.

Petipa, T. S., Pavlova, E. V. & Mironov, G. N., 1970. The food web structure, utilization and transport of energy by trophic levels in the planktonic communities. In: Marine food chains. Ed. by J. H. Stelle, Univ. of California Press, Berkely, 142–167.

Radach, G., 1980. Preliminary simulations of the phytoplankton and phosphate dynamics during FLEX '76 with a simple two-component model. – Meteor Forsch. Ergebn. (A) *22*, 151–163.

Radach, G., Trahms, J. & Weber, A., 1980. The chlorophyll development at the Central Station during FLEX '76 – two data sets. – Proceedings of the final ICES/Jonsis workshop on JONSDAP '76 (Liège, Belgium, 29 April–2 May 1980). – C.M.–ICES/*C3*, 3–21.

Schrader, H.-J., 1971. Fecal pellets: Role on sedimentation of pelagic diatoms. – Science, N. Y. *174*, 55–57.

Smayda, T. J., 1969. Some measurements of the sinking rate of fecal pellets. – Limnol. Oceanogr. *14*, 621–625.

Smayda, T. J., 1971. Normal and accelerated sinking of phytoplankton in the sea. – Mar. Geol. *11*, 105–122.

Soetje, K. C. & Huber, K., 1980. A compilation of data on the thermal stratification of the Central Station in the northern North Sea during FLEX '76. – Meteor Forsch.Ergebn. (A) *22*, 69–77.

Turner, J. T., 1977. Sinking rates of fecal pellets from the marine copepod *Pontella meadii*. – Mar. Biol. *40*, 259–259.

Wiebe, P. H., Boyd, S. H. & Winget, C., 1976. Particulate matter sinking to the deep-sea floor at 2000 m in the Tongue of the Ocean Bahamas, with a description of a new sedimentation trap. – J. mar. Res. *34*, 341–354.