THE MACROZOOPLANKTON COMMUNITY OF KOSTERFJORDEN, WESTERN SWEDEN. ABUNDANCE, BIOMASS, AND PRELIMINARY DATA ON THE LIFE CYCLES OF DOMINANT SPECIES

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The macrozooplankton abundance and biomass in Kosterfjorden (58°52′ N, 11°06′ E) were heavily dominated by the copepod *Calanus finmarchicus/helgolandicus*, euphausiid species being only temporarily important during summer. Carnivorous species contributed significantly, mainly in winter and spring. A comparison of zooplankton biomasses from coastal areas in Sweden and Norway indicates a direct relationship between water-column depth and community biomass. The macrozooplankton fauna in Kosterfjorden resembles that of Korsfjorden, western Norway by a similarity in the ranking of the quantitatively most important species. The siphonophore *Dimophyes arctica*, the polychaete *Tomopteris helgolandica*, and the crustaceans *Chiridius armatus*, *Thysanoessa raschii*, and *Parathemisto abyssorum* are more important in the former area, the crustaceans *Calanus hyperboreus* and *Boreomysis arctica*, and the chaetognath *Eukrohnia hamata* in the latter area. Analyses of the seasonal succession in the size structure and state of maturity within the populations of some species have been used to elucidate their life cycles in Kosterfjorden. They usually correspond well with those reported for these species from other areas at similar latitudes. The copepod *Calanus hyperboreus* and the euphausiids *Thysanoessa inermis* and *T. raschii* occur as expatriate species in Kosterfjorden.

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INTRODUCTION

Zooplankters are the main consumers in the pelagic, forming intermediate links in the biotransformation of energy and material in the marine ecosystem (STEELE 1974). However, geographical variations in species composition, biomasses, and production, both on small and large scales, are considerable, as pointed out by MATTHEWS & HEIMDAL (1980), and any generalization of the species composition and trophic structure for a given latitude cannot be given. MATTHEWS & BAKKE (1977) emphasized that many planktonic communities have a considerable carnivorous component which will cause significant reduction of the energy available to higher trophic levels (i.e. pelagic fish). These authors showed that up to 50 % of the standing stock of macrozooplankton in a Norwegian fjord at certain times of year consisted of carnivorous species.

Preliminary observations indicate that the plankton fauna of Kosterfjorden differs from that found further south on the Swedish west coast (compare BÅMSTEDT 1981a with ERIKSSON 1973). The standing stock of macrozooplankton in Kosterfjorden is heavily dominated by *Calanus finmarchicus* with a significant carnivorous component (BÅMSTEDT 1981a), thus resembling that of Korsfjorden, western Norway (cf. MATTHEWS & BAKKE 1977). In this paper the abundance and biomass of macrozooplankton in Kosterfjorden are quantitatively described and aspects of the population dynamics of the dominant species are discussed. The seasonal variation in proportion of organic matter is calculated for the whole community and for separate species, in order to define nutritionally superior (= high organic proportion) periods in the seasonal cycles.

Kosterfjorden has a north-south direction and a depth of 180–250 m. It is not a true fjord since it opens both in the northern and southern parts. The temperature of the surface water shows an annual range from below zero in February to c. 20° C in summer, whereas the temperature below 60 m varies with depth and season from c. 5 to c. 10° C (B. Rex pers. commn). Surface salinity is strongly influenced by the Baltic Current from the south and the freshwater supply from the Norwegian river Glomma, north of the area, the degree of influence mainly determined by the wind situation. Surface salinities below 20 ‰ occur occasionally, especially during spring/summer and autumn, when snow-melting and high precipitation, respectively, increase the runoff from the rivers. The salinity below 30 m is usually within the range 32.5–34.5 ‰ the year around (B. Rex pers. commn).

MATERIAL AND METHODS

Mid-day (1000–1300 h) zooplankton samples were taken by vertical net hauls, 200 to 0 m, on 32 occasions at 58°52′ N, 11°06′ E between July 1976 and July 1977, using a conical net with 1 m diameter and 0.4 mm mesh size. The net hauls were taken in an area with a depth varying between 210 and 240 m, and the sampled material thus represented almost the whole water column in the Kosterfjord trench, which has a maximum depth of 250 m. Due to bad weather and ice conditions samples were not taken during late winter. Three replicate towings were made each time. These samples were combined and immediately preserved in 4 % borax-buffered formaldehyde in seawater and stored until autumn 1977 before analysis of the material started.

All large-sized animals (e.g. hydrozoans, cnidarians, tomopterid polychaetes, euphausiids, amphipods, mysids, shrimps, and chaetognaths) were sorted out by eye from the samples, taxonomically classified, counted, and prepared for biomass determination. For some of the species the wet weight of each individual was determined in order to get a picture of the population structure, and for a few species additional records of sex, maturity, occurrence of eggs, embryos or parasites were also taken.

From the remaining part of the samples, containing only animals < c. 5 mm, three subsamples (each 1/25 of the whole sample) were taken for biomass determinations and three (each 1/100) for data on abundance and weight of each species. Small-sized species, mainly copepods of the genera *Acartia, Pseudocalanus, Paracalanus, Centropages, Temora,* and *Oithona* were included in the biomass determinations but were not separately studied, since they were not quantitatively sampled by the plankton net. Separate data on these species are therefore not provided in this paper.

The zooplankton biomass was determined as dry weight/m^2 for a 200 m deep water column. Since the material was preserved in formalin, a reduction of the organic weight of c. 20 % probably occurred during storage (see OMORI 1978). The calculations assumed 100 % filtering efficiency of the net, but tests on a few occasions, using a flow meter, indicated an efficiency closer to 90 %. The figures of abundance, individual weight, and biomass are not corrected for these biases and are thus somewhat underestimated.

The material used for weight determinations was briefly rinsed with distilled water, blotted on a paper towel for elimination of excess water, and weighed to the nearest 0.1 mg on a Mettler microbalance. It was then placed in tared aluminium boats, dried to constant weight at 60° C, and weighed to the nearest 0.1 mg. The content of organic matter was defined as the weight loss of the dried material after incineration in a muffle furnace at 500° C for 24 hours (cf. BÅMSTEDT 1974).

A list of the regularly occurring species considered in the paper, with their taxonomic and trophic positions is given in Table 1. The copepods *Calanus finmarchicus* GUNNERUS and *C. helgolandicus* (CLAUS) *(s.s.)* were grouped together and are referred to as *C. finmarchicus (s.l.)*, since juvenile stages could not be separately distinguished and *C. finmarchicus* always was the numerically dominant one among the adults.

Table 1. Taxonomic state and trophic position (as defined by MATTHEWS & BAKKE (1977)) of macrozooplankton species occurring regularly in Kosterfjorden. C = Carnivore. H = Herbivore. O = Omnivore.

Species	Taxonomic position	Trophic position
Aglantha digitale (O.F. MÜLLER)	Hydrozoa, Trachylina	C
Dimophyes arctica (CHUN)	Hydrozoa, Siphonophora	C
Beroe cucumis FABRICIUS	Ctenophora	C
Tomopteris helgolandica GREEFF	Polychaeta, Errantia	C
Tomopteris planktonis APSTEIN	» »	C
Calanus finmarchicus (GUNNERUS)	Copepoda, Calanoida	H
Calanus hyperboreus KRÖYER	» »	O
Chiridius armatus (BOECK)	» »	C
Euchaeta norvegica BOECK	» »	C
Metridia longa (LUBBOCK)	» »	H
Meganyctiphanes norvegica (M. SARS)	Euphausiacea	O
Thysanoessa inermis (KRÖYER)	»	O
Thysanoessa raschii (M. SARS)	»	O
Boreomysis arctica (KRÖYER)	Mysidacea	O
Hemimysis abyssicola G.O. SARS	»	O
Parathemisto abyssorum BOECK	Amphipoda, Hyperiidea	C
Pasiphaea multidentata ESMARK	Decapoda, Natantia	C
Eukrohnia bathypelagica ALVARINO	Chaetognatha	C
Eukrohnia hamata (MÖBIUS)	»	C
Sagitta elegans VERRILL	»	C
Sagitta setosa J. MÜLLER	»	C

RESULTS

General considerations

Fifteen of the species constituting the macrozooplankton community in Kosterfjorden contributed a significant percentage to the community biomass. Among these the copepod *Calanus finmarchicus* always made up the main part of the total biomass.

The zooplankton biomass varied between 3 and 13 g dry weight/m^2 with the maximum occurring in the beginning of October, followed by a period of steadily decreasing biomass (Fig. 1). When the ice stopped the sampling in late January the zooplankton biomass was at its minimum, c. 3 g dry weight/m^2. It was still at this level when the sampling was resumed in April, thereafter it discontinuously increased to c. 7 g/m^2 when the investigation ended in July 1977. Larger forms usually contributed little to the total biomass; highest relative values were recorded in early autumn and mid-winter, when these forms made up c. 30 % of the community biomass (Fig. 1).

For the whole macrozooplankton community the average proportion of organic matter ranged between 79 and 94 % of the dry weight, whereas the range for the smaller forms alone was 84 to 95 % (Fig. 1). The organic proportion of the smaller forms was almost invariably higher than that for the total zooplankton. There was a trend toward an increasing proportion of organic matter from summer to autumn, a relatively stable yet high proportion in early winter, and a retardation thereafter. The organic proportion fluctuated in spring and tended to increase again in early summer (Fig. 1).

The relative proportions of herbivorous, omnivorous, and carnivorous species in the community changed considerably over the year. Herbivores dominated throughout the investigation, especially during autumn when they made up more than 90 % of the zooplankton biomass. Omnivores were proportionally important in summer and early autumn when they reached a maximum of 25 % of the total biomass, whereas carnivores reached almost the same biomass as herbivores during winter and spring (Fig. 2).

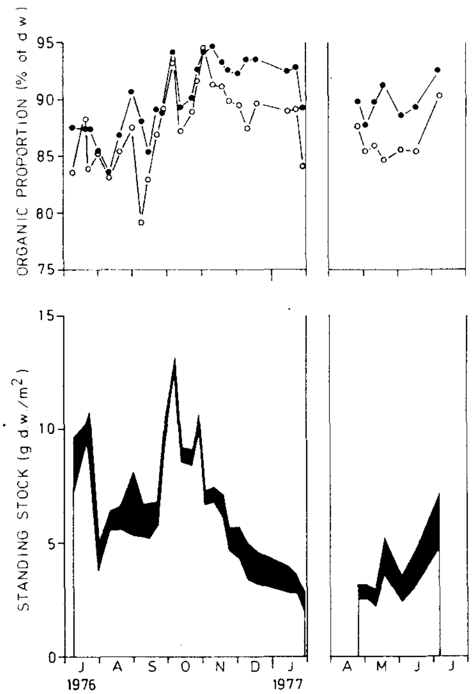

Fig. 1. Seasonal variation in standing stock (lower) and organic proportion (upper) of macrozooplankton in Kosterfjorden. Dark area represents large-sized animals. Organic proportion of total macrozooplankton is given by closed symbol, that of small-sized animals by open symbol.

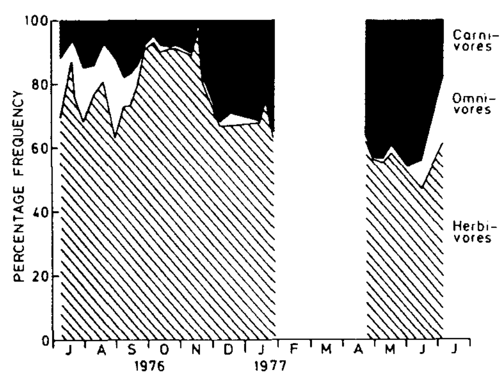

Fig. 2. Relative proportion of herbivores, omnivores, and carnivores over the investigation period.

Common species

Aglantha digitale (Fig. 3)

The results shown in Fig. 3 only include animals with bell height > 3 mm. This species increased from very low numbers in summer to a maximum of c. 130 individuals/m^2 in October. The biomass of the population increased throughout the year and reached a maximum of c. 400 mg dry weight/m^2 in December. Abundance and biomass remained both low from April to July 1977. The average individual dry weight fluctuated heavily during most of the year, but a clear tendency to increasing weight from November to January was found.

The organic content of *A. digitale* varied between 43.1 and 86.3 % of the dry weight during the year ($\bar{X}$ = 65.1, S.D. = 13.3, n = 24). There was a clear seasonal trend with highest values occurring in early winter and lowest values in spring or summer.

Dimophyes arctica (Fig. 3)

This siphonophore also showed an increasing abundance and biomass from summer towards winter, with a seasonal maximum in mid-winter of c. 150 specimens and 75 mg dry weight/m^2, respectively. The dry weight per specimen fluctuated between 0.5 and 3.0 mg in summer/early autumn, thereafter stabilizing around 0.5 mg, and remained there during spring and early summer. Eudoxids domina-

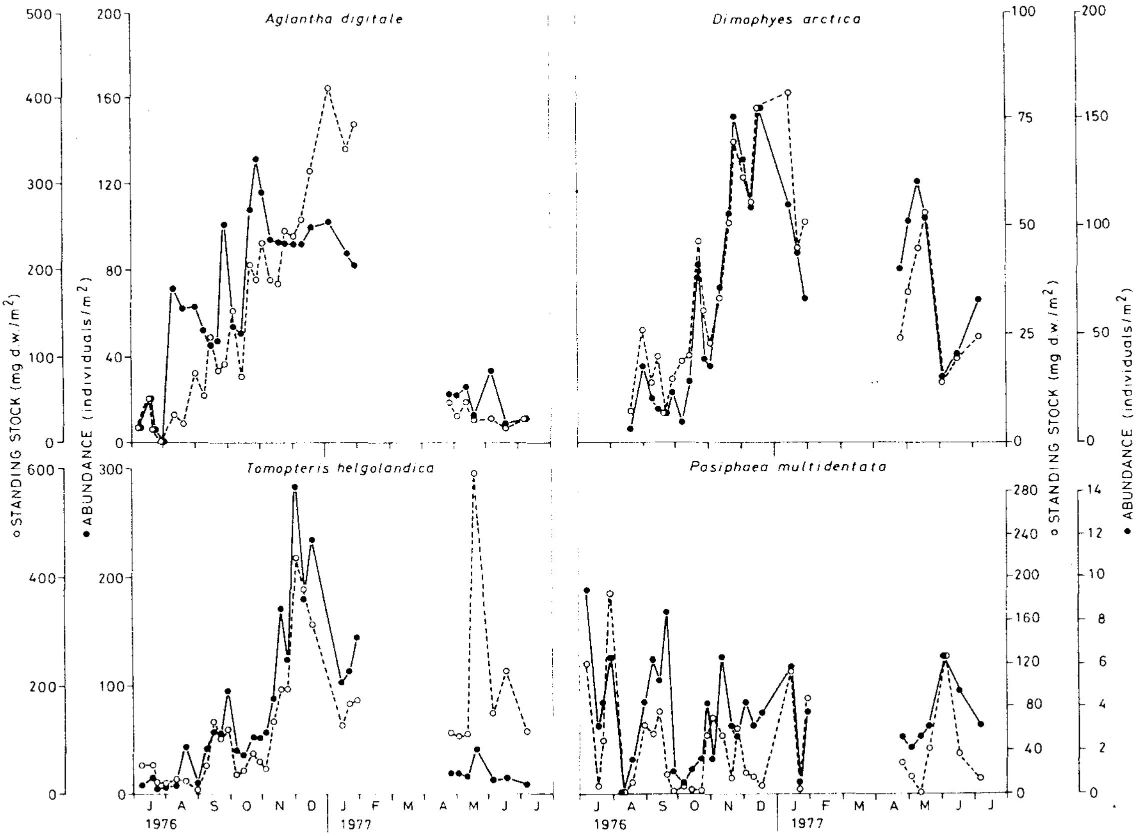

Fig. 3. Abundance and biomass of *Aglantha digitale, Dimophyes arctica, Tomopteris helgolandica,* and *Pasiphaea multidentata* during the investigation period.

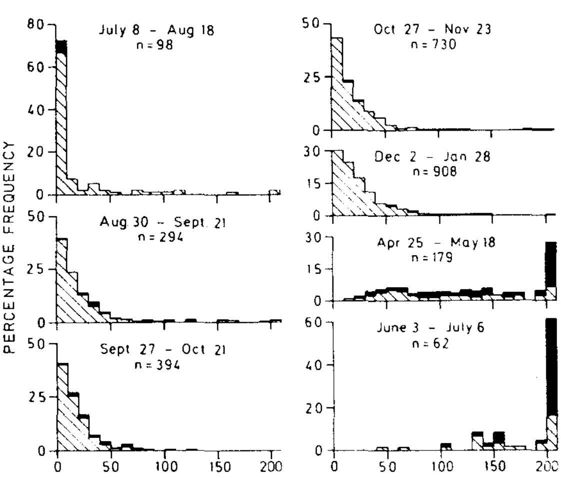

Fig. 4. *Tomopteris helgolandica.* Frequency distribution of individual wet weights during seven periods. Dark area represents females containing eggs.

ted in the population, except in late spring and early summer.

The average proportion of organic matter varied seasonally between 36.3 and 90.0 % of the dry weight ($\bar{X}$ = 70.3, S.D. = 14.1, n = 27). Highest values occurred from late autumn to early winter.

Tomopteris helgolandica (Fig. 3)

This polychaete species increased from c. 10 individuals/m^2 in summer to a maximum of c. 300 individuals/m^2 in early winter. From spring on the abundance was low at c. 10 individuals/m^2. The biomass showed two pronounced peaks over the year; one corresponding with the maximum abundance in early winter.

The individual dry weight showed a decreasing trend during late summer, stabilizing at c. 1.5 mg during autumn and winter, and increasing greatly during spring and early summer.

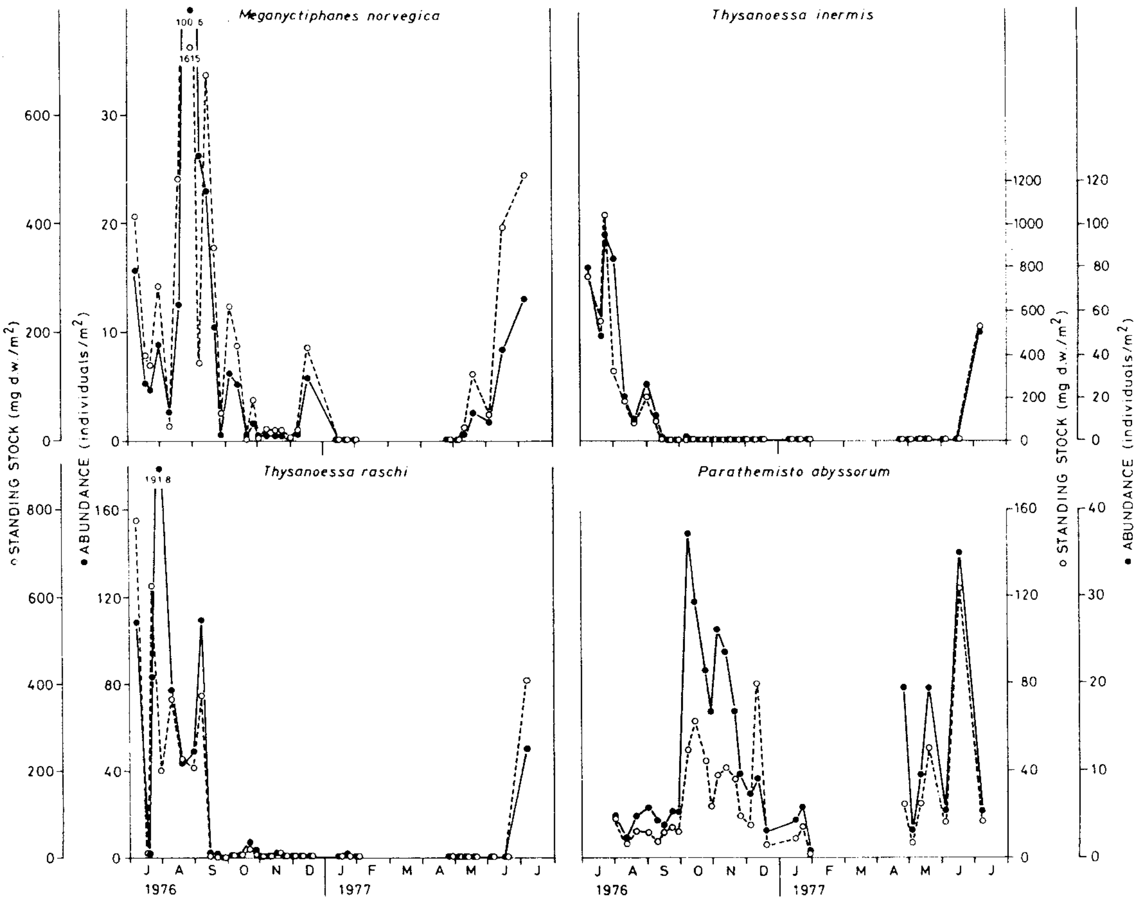

Fig. 5. Abundance and biomass of *Meganyctiphanes norvegica, Thysanoessa inermis, Thysanoessa raschii,* and *Parathemisto abyssorum* during the investigation period.

The population structure, as given by a frequency histogram of the individual wet-weights, showed a dominance of small individuals from summer throughout winter (Fig. 4). Large-sized animals were usually present during this period but made up only a small fraction of the population. Females containing eggs were present in low frequencies during this period, mainly as relatively small animals in summer and early autumn. The population structure was completely changed in spring and early summer, then being dominated by large-sized animals, and a greater part of the population was composed of egg-carrying females (Fig. 4).

The proportion of organic matter of *T. helgolandica* showed a seasonal range from 53.2 to 80.0 % of the dry weight ($\bar{X}$ = 66.0, S.D. = 6.8, n = 28). Highest values occurred mainly in late autumn and early winter, whereas lowest values were recorded in summer.

Pasiphaea multidentata (Fig. 3)

The abundance and biomass of this species was characterized by large fluctuations, independent of season. A median value of c. 4 individuals/m^2 seemed to hold for the whole investigation period, corresponding to a biomass of c. 50 mg dry weight/m^2.

The individual wet weight ranged from a few to c. 700 mg but small individuals weighing less than 20 mg dominated all the year round.

P. multidentata had an organic proportion varying between 83.0 % and 91.3 % ($\bar{X}$ = 84.8 %, S.D. = 2.4 %, n = 24) of the dry weight. There was no clear seasonal trend in organic proportion of this species.

Meganyctiphanes norvegica (Fig. 5)

This species was not caught from late winter to late spring. The abundance and biomass fluctuated con-

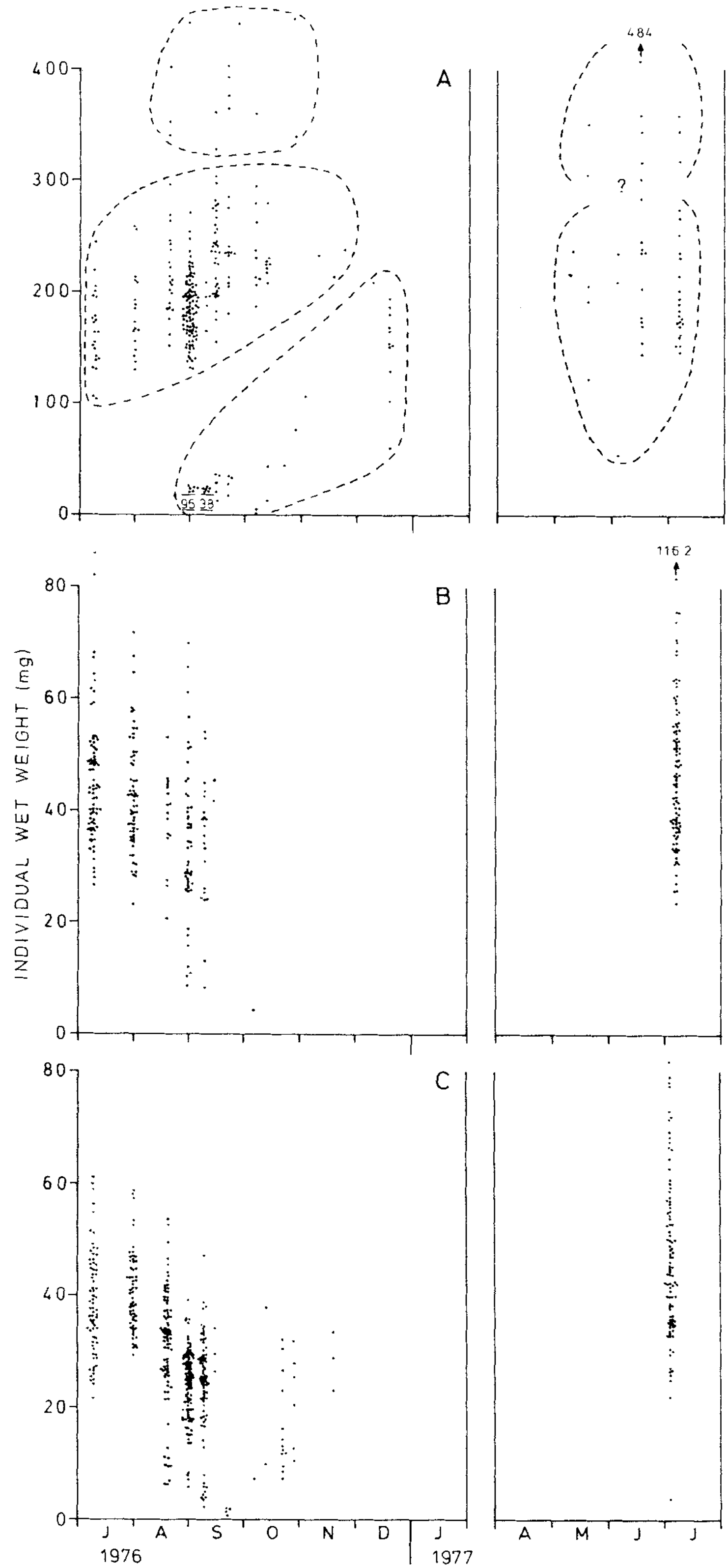

Fig. 6. Scatter diagram of individual wet weights of three euphausiid species over the investigation period. A. *Meganyctiphanes norvegica*, B. *Thysanoessa inermis*, C. *Thysanoessa raschii*. The numbers enclosed by horisontal lines in A indicate the number of data points within these limits.

siderably, with a main peak in September of 101 individuals/m^2 and 1615 mg dry weight/m^2. From autumn to winter the fluctuating values tended to decrease towards zero, but from May on both abundance and biomass increased steadily.

The size structure within the population has been visualized by plotting the wet weight of each individual in a scatter diagram (Fig. 6A). Significant year-class separations, using the method of CASSIE (1963), was given for September and October 1976. Although few significant separations were obtained year-class separations are indicated for the whole sampling period. It appears that the one-year old age group (I) dominated during most of 1976, recruitment of the new year-class (0) occurring at the end of August. The few large animals present in autumn 1976 probably represented the two-year old age group (II) which died out during this year. In 1977 *M. norvegica* occurred again at the beginning of May, probably represented by the former year-classes 0 and I. Furcilia (not included in Figs 5 and 6A) were recorded between 19 July and 10 August 1976, precursory to the occurrence of small euphausiids in the end of August. Average growth within the I group was estimated to c. 75 mg wet weight per individual between July and October 1976 (three months). A less reliable estimate for the 0 group indicated individual growth from c. 10 to c. 150 mg wet weight from beginning of September to mid-December 1976.

The organic proportion of this species was relatively stable, ranging from 82.7 to 91.7 % of the dry weight ($\bar{X}$ = 85.3, S.D. = 2.3, n = 23). Several of the highest values were recorded in late autumn.

Thysanoessa inermis (Fig. 5)

This species was not recorded from early October to mid-June. The highest abundance and biomass occurred in late summer, with 95 individuals/m^2 and 1 040 mg dry weight/m^2, a biomass only exceeded by *Calanus finmarchicus* and *Meganyctiphanes norvegica*. The disappearance occurred earlier and the spring increase occurred later than for *M. norvegica* (cf. Fig. 5).

The population structure of *T. inermis* is shown in a scatter diagram of individual wet weights (Fig. 6B). There was no period with recruitment of small individuals and the population, when present, could hardly be divided into separate year-classes. Statistical tests by the method of CASSIE (1963) confirmed this. The data indicate a decrease rather than an increasing average size during 1976, mainly as a result of relatively small individuals occurring in August/September. The absence of new recruits and the very wide range in individual weight indicate that the population structure is affected by immigration and emigration.

The proportion of organic matter of *T. inermis* ranged between 87.1 and 91.5 % of the dry weight ($\bar{X}$ = 89.2, S.D. = 1.9, n = 10). No seasonal trend was shown.

Thysanoessa raschii (Fig. 5)

The abundance and biomass fluctuated greatly and the same seasonal trend seen for the other two euphausiids was also true for this species, with occurrence mainly restricted to summer and autumn. The high abundance (maximum of 192 individuals/m^2) and biomass (maximum of 780 mg dry weight/m^2) during summer/autumn emphasize the seasonal importance of this species.

The population structure, illustrated by a scatter diagram of individual weights (Fig. 6C), indicates the presence of more than one year-class. It was not possible, however, to make a consistent separation by using the statistical method of CASSIE (1963). Recruitment seems to have been haphazard; the single small individual from July 1977 and the few small ones from September 1976 certainly represented the new year-class, but the very wide range and decreasing trend in individual weight during summer and autumn indicate that immigration and emigration were important factors.

The proportion of organic matter of this species was always below that of *T. inermis*, ranging between 80.8 and 88.7 % of the dry weight ($\bar{X}$ = 84.7, S.D. = 2.3, n = 11).

Parathemisto abyssorum (Fig. 5)

This hyperiid amphipod was most abundant in autumn and early summer, with a maximum of c. 40 individuals/m^2 corresponding to c. 60 mg dry weight/m^2. Both abundance and biomass showed the same large fluctuations, annual minimum and maximum for the latter being 5 mg dry weight/m^2 (January) respectively 120 mg dry weight/m^2 (June).

Animals carrying eggs or embryos occurred all seasons but were never common. Animals hosting an unidentified parasite between their swimming legs occurred from the beginning of August to mid January, with highest frequency (up to 42 %) in early winter. Female *P. abyssorum* were infected more frequently than males.

A scatter diagram of individual wet weights of *P. abyssorum* is shown in Fig. 7. Small individuals occurred during most of the year but in 1976 with the greatest abundance in October. The size distribution

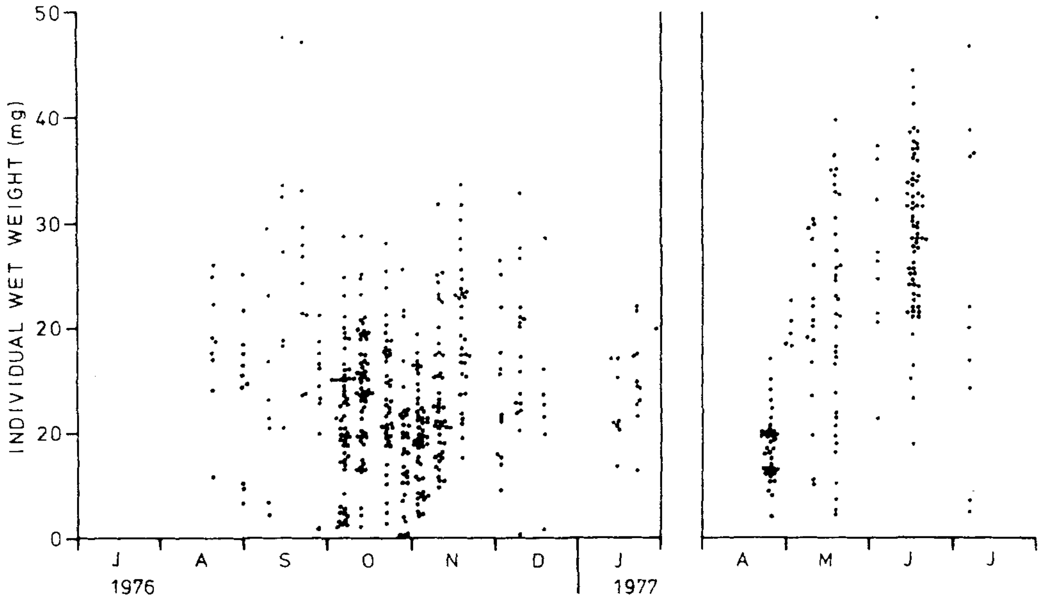

Fig. 7. *Parathemisto abyssorum*. Scatter diagram of individual wet weights over the investigation period.

was, however, always continuous and the statistical method of CASSIE (1963) gave no significant generation separation. In April 1977 the dominance of animals weighing 5–10 mg may indicate that recruitment of a new generation had occurred earlier in the year. The trend to increasing individual weight thereafter may then be seen as the growth of individuals from this cohort. However, the occurrence of egg-bearing females all year round and the weight scatter during 1976 suggest that reproduction was not restricted to a defined period.

The proportion of organic matter of this species ranged seasonally from 71.3 to 96.2 % of the dry weight ($\bar{X}$ = 81.7 %, S.D. = 5.5 %, n = 27), with highest values recorded for late autumn and early winter, and lowest values occurring mainly in summer.

Calanus finmarchicus (Fig. 8)

Although the plankton net did not capture the smaller developmental stages, this species was conspicuously the most common one in the samples, ranging in abundance from 5 000 to 81 000 individuals/m^2. This dominance was also reflected in the biomass, which ranged between 670 and 11 600 mg dry weight/m^2. Its contribution to the total biomass was most pronounced in autumn. The average individual dry weight fluctuated considerably during summer and early autumn, rose to a relatively stable level of c. 200 μg in November/December and began to decrease in December/January. The lowest values for the whole period were recorded when sampling was resumed in April (c. 40 μg/individual). The rest of the period was characterized by an increasing trend in individual dry weight, but with large fluctuations.

The proportion of organic matter varied between 84.5 and 97.8 % of the dry weight ($\bar{X}$ = 90.9, S.D. = 2.6, n = 32), with the highest level in the autumn, and lowest level in the spring. The seasonal variation was small, with only 7 out of totally 32 sampling occasions outside the range 90 ± 3 %.

Calanus hyperboreus (Fig. 8)

This species varied greatly in abundance throughout the investigation perdiod, as closely reflected in the population biomass. In autumn and mid-winter the abundance reached almost 300 individuals/m^2, corresponding to a biomass of 150–200 mg dry weight/m^2. The average individual dry weight of unsorted developmental stages fluctuated around 500 μg from summer to mid-winter 1976, from 700 to 1400 μg in April to July 1977.

The proportion of organic matter was significantly lower in this species than in the former, ranging between 74.2 and 94.5 % of the dry weight ($\bar{X}$ = 83.4, S.D. = 4.4, n = 28), and exceeding 90 % on only two occasions. Highest levels were noted during early summer, lowest ones in early autumn.

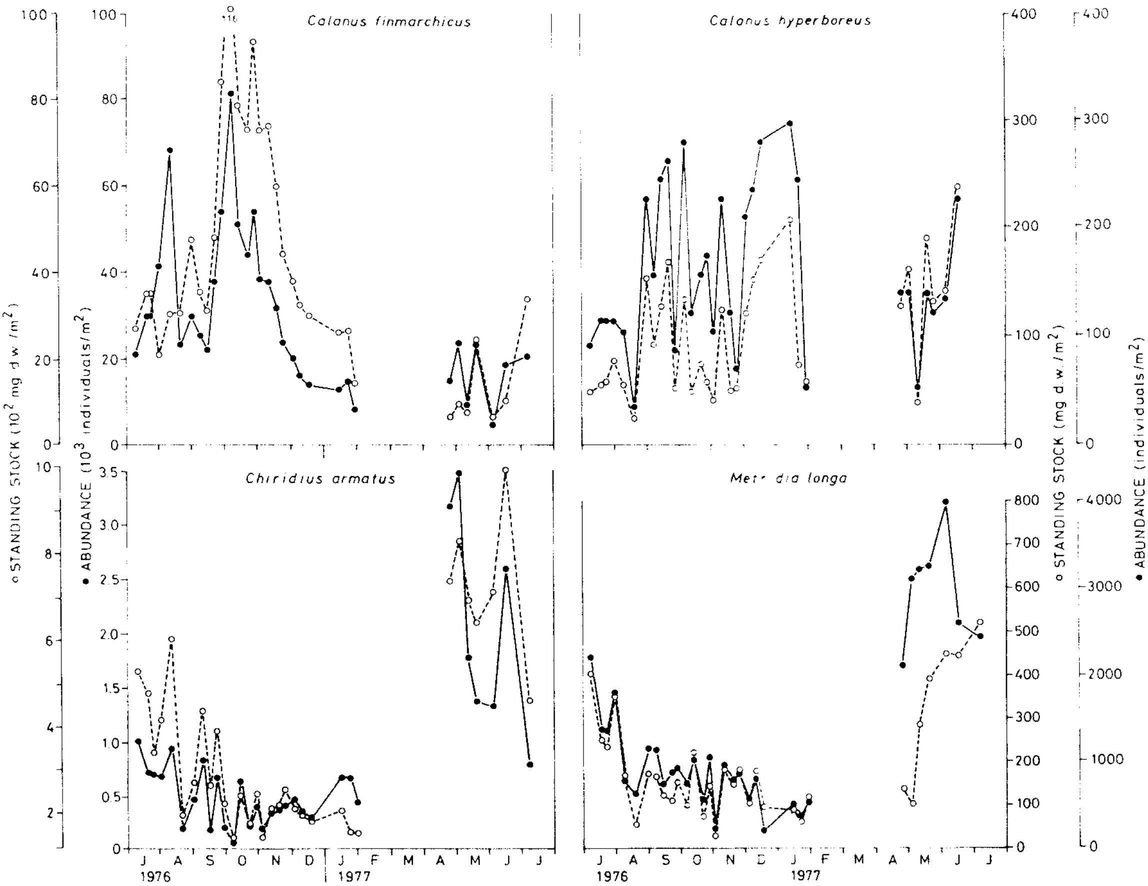

Fig. 8. Abundance and biomass of *Calanus finmarchicus*, *Calanus hyperboreus*, *Chiridius armatus*, and *Metridia longa*, during the investigation period.

Chiridius armatus (Fig. 8)

This carnivorous copepod reached an abundance and biomass similar to those of *Metridia longa*. Both the abundance and biomass tended to decrease from July 1976 to January 1977, the abundance from c. 1000 to c. 500 individuals/m^2, the biomass from c. 400 to c. 30 mg dry weight/m^2. Maximum abundance was recorded in the beginning of May (c. 3500 individuals/m^2), maximum biomass in June (c. 900 mg dry weight/m^2), both tending to decrease thereafter.

The average individual dry weight of unsorted copepodites fluctuated around 400 μg during summer and autumn, and decreased thereafter to a minimum value of 60 μg in late January. From April to July 1977, average individual dry weight increased from c. 200 to c. 450 μg.

The proportion of organic matter ranged from 73.6 to 88.4 % of the dry weight ($\bar{X}$ = 83.9, S.D. = 3.4, n = 30). Values below 80 % only occurred in September, whereas the animals collected between 21 October and 28 January showed an organic proportion of 83.8 to 88.4 %.

Metridia longa (Fig. 8)

This species usually ranked second in dominance after *Calanus finmarchicus* among herbivorous/omnivorous macrozooplankton in Kosterfjorden. The seasonal patterns of variation in abundance and biomass were similar from summer to late winter, showing a decreasing trend from more than 2000 to c. 500 individuals/m^2, and 400 to c. 100 mg/m^2, respectively. The abundance showed a pronounced peak of 4000 individuals/m^2 in early summer 1977. The biomass increased continuously from early May to July, reaching a maximum value of 523 mg dry weight/m^2.

The average individual dry weight of unsorted copepodites fluctuated between 80 and 220 μg from

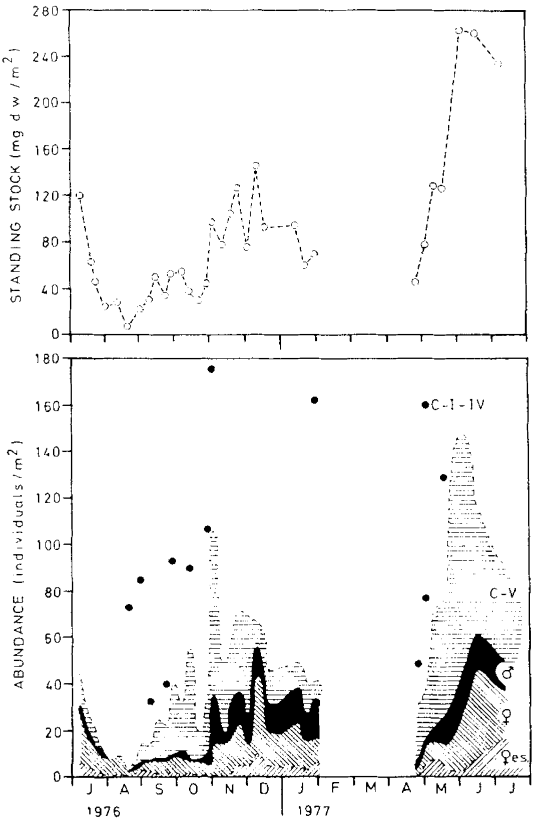

Fig. 9. *Euchaeta norvegica*. Abundance and biomass of adults and stage V copepodites over the investigation period. Stages I–IV are not included in the biomass figures and only occasionally included in the abundance figures. 'e.s.' denotes adult females with an egg sac.

July 1976 to January 1977. Minimum average dry weight of c. 35 μg was recorded in May 1977; in the following two months it continuously increased to c. 220 μg.

The organic content of this species varied between 74.9 and 92.6 % ($\bar{X}$ = 83.1, S.D. = 4.6, n = 29), with the last value being the only exceeding 90 %. Highest values occurred in early winter (86.0–92.6 %), while lowest values were recorded from summer to early autumn (74.9–83.0 %).

Euchaeta norvegica (Fig. 9)

This large, carnivorous copepod was sorted to developmental stages (copepodite stages I–IV, V and VI). Copepodite stages I–IV were counted from three subsamples, whereas the other stages were counted from the whole samples. Values for the former are therefore less reliable, and since the net did not capture the smaller stages quantitatively they are not included in the biomass figures.

There were two periods of high population abundance and biomass. In mid-winter adult females and males showed peaks of 43 and 21 individuals/m^2 respectively, and stage V copepodites occurred with up to 70 individuals/m^2. The second period of high abundance occurred in early summer, with maximum abundance of 46, 17, and 102 individuals/m^2 for respectively adult females, males, and stage V copepodites. The population biomass reached maxima of 145 mg dry weight/m^2 in early December, and 263 mg/m^2 in early June. Adult females carrying an egg sac occurred throughout the investigation period, but with highest frequency in mid-winter and mid-summer, indicating two main reproduction periods per year. This is also suggested by the seasonal variation in abundance of adult males and the sex ratio of stage V copepodites; from autumn to early December the sex ratio of stage V copepodites increased from c. 25 % males to over 80 % males, whereafter it decreased again.

The proportion of organic matter (average for females, males, and stage V copepodites) ranged between 77.1 and 92.1 % of the dry weight, with an average value for the whole period of 87.6 % (S.D. = 3.5, n = 32). Values above 90 % occurred mainly in November and December, whereas lowest values occurred in early autumn. Adult females, males, and stage V copepodites differed little from each other, resulting in average values over the investigation period of 88.3, 87,9 and 86,8 % of the dry weight, respectively.

Eukrohnia hamata (Fig. 10)

Results for animals > c. 15 mm total body length are presented in the figure. In addition individuals of *E. hamata* and *Sagitta elegans* < c. 15 mm were counted from the subsamples as one group. The abundance of these small animals ranged between 20 and 1400/m^2 and the biomass between 0.3 and 117 mg dry weight/m^2 with highest values occurring mainly in summer and autumn.

Animals > c. 15 mm were divided into stages of maturity according the the following criteria: 1, no sign of gonads; 2, small ovaries and testes; 3, well developed ovaries but no large ova; 4, large ovaries containing large ova. The abundance of these animals fluctuated considerably but tended to increase from summer towards winter, with a seasonal maximum in December of c. 170 individuals/m^2. The biomass fluctuated from almost zero to 470 mg dry weight/m^2 without any clear seasonal trend. Maturity stage 4 occurred with highest frequency in late

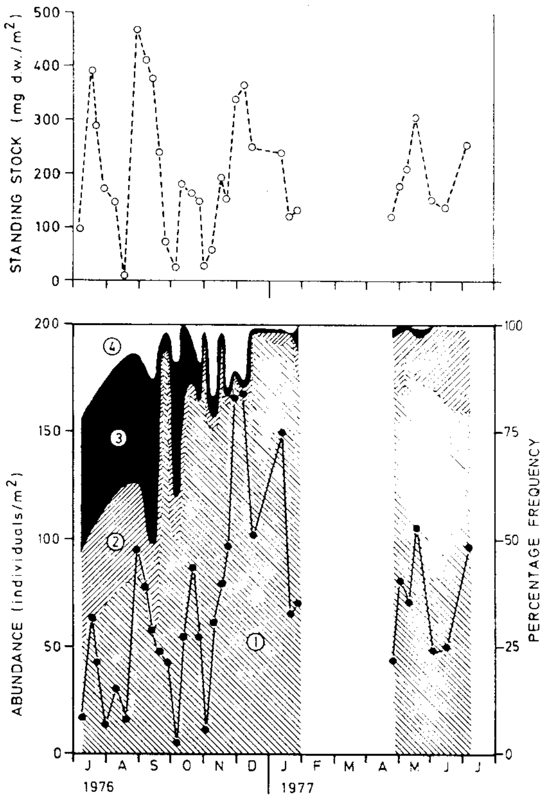

Fig. 10. *Eukrohnia hamata.* Abundance, biomass, and relative proportion of maturity stages of animals > 15 mm over the investigation period.

summer and autumn, indicating that breeding was most intense in this period, but stage 1 was always dominant in the population.

The individual dry weight and the proportion of organic matter usually decreased with increasing maturity. Stage 1 showed an average dry weight and organic proportion of 1.9 mg and 80.1 %, respectively, stage 2, 5.8 mg and 75.6 %, stage 3, 6.9 mg and 74.3 %, and stage 4, 7.0 mg and 70.4 %. Highest organic proportions tended to occur in late autumn or early winter.

Sagitta elegans (Fig. 11)

The results concern animals > c. 15 mm total body length. The abundance increased intermittently from c. 20 individuals/m^2 in summer to c. 120 individuals/m^2 in autumn, whereafter it steadily decreased to c. 10 individuals/m^2 in mid-winter. The abundance remained at that low level during spring and early summer. The seasonal maximum in biomass occurred in autumn, reaching 100 mg dry weight/m^2. Maximum average individual dry weight was recorded in May.

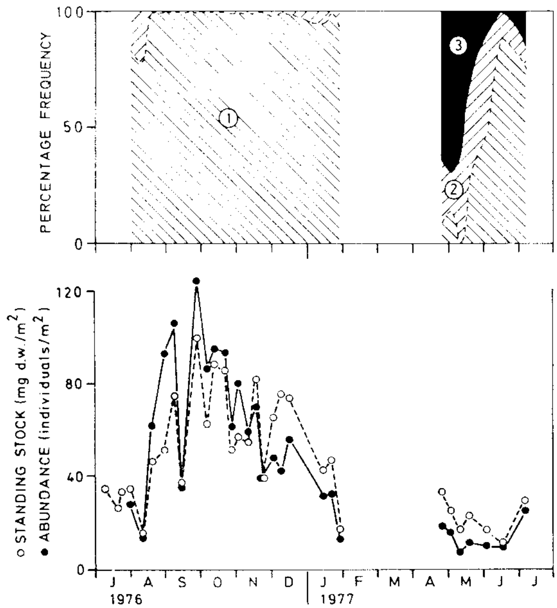

Fig. 11. *Sagitta elegans.* Abundance, biomass, and relative proportion of immature (1), slightly mature (2), and fully mature (3) individuals > 15 mm over the investigation period.

From late July 1976 to January 1977 usually 100 % of the individuals in the population were immature, a small percentage with small ovaries and small ova occasionally being present. From April to July 1977 fully mature animals comprised on average 36 % of the population, with the highest percentage in the beginning of the period. This indicates a single breeding period in spring.

The average organic proportion of the sampled animals varied between 65.5 and 86.0 % of the dry weight ($\bar{X}$ = 73.1, S.D. = 6.1, n = 29) with a significant tendency toward highest values in late autumn and early winter.

Less common, regularly occurring species

These species contributed relatively little to the total abundance and biomass of the macrozooplankton community, although their regular presence indicated that they were a stationary part of the Kosterfjord fauna.

Beroe cucumis

Three ctenophore species, *Pleurobrachia pileus* (O.F. MÜLLER), *Bolinopsis infundibulum* (O.F. MÜLLER) and *Beroe cucumis* were abundant seasonally, but the former two could not be accurately quantified since they generally disintegrated in the samples.

The abundance of *B. cucumis* varied from zero to 30 individuals/m^2 ($\bar{X}$ = 9.7, S.D. = 9.3, n = 28) with a seasonal trend of increased abundance from summer to early winter, and population decline in late winter. The biomass increased from zero in summer to almost 50 mg dry weight/m^2 in late November, but the highest value (270 mg dry weight/m^2) was recorded in mid-June 1977. The average biomass for the investigation period was 23.7 mg/m^2 (S.D. = 53.4, n = 32).

The organic proportion of *B. cucumis* varied from 59.4 to 87.9 % of the dry weight ($\bar{X}$ = 72.1, S.D. = 8.2, n = 20). The variation could not be related to any seasonal trend.

Tomopteris planktonis

This species was usually present from the end of August to the end of May and reached the highest abundance (c. 5 individuals/m^2) in early winter. The annual average abundance was 1.4 individuals/m^2 (S.D. = 1.5, n = 32) and the annual average biomass 1.0 mg/m^2 (S.D. = 1.0, n = 32). The average individual dry weight varied seasonally between 0.3 and 1.8 mg, except on 18 May when the single individual captured weighed 5.2 mg. Females containing eggs were recorded between 14 September and 21 January. The proportion of organic matter ranged between 34.7 and 96.2 % of the dry weight ($\bar{X}$ = 73.1, S.D. = 18.3, n = 16).

Boreomysis arctica

This was the most common mysid, and was found throughout the year with an abundance of up to 5 individuals/m^2 ($\bar{X}$ = 2.2, S.D. = 1.7, n = 32) and a corresponding biomass ranging between close to zero and 54 mg dry weight/m^2 ($\bar{X}$ = 17.9, S.D. = 15.4, n = 32). Females with eggs or embryos were recorded in late winter, spring, and summer.

The average individual dry weight ranged between 0.4 and 20.8 mg ($\bar{X}$ = 7.4, S.D. = 4.1, n = 26) without any clear trend of seasonal variation. The organic proportion of *B. arctica* varied between 68.5 and 88.9 % of the dry weight ($\bar{X}$ = 83.2, S.D. = 4.6, n = 24) with highest values occurring in late autumn and early winter.

Hemimysis abyssicola

This mysid was present from October to the end of the investigation. The abundance ranged between 0 and 1.6 individuals/m^2, but due to the low abundance no seasonal trend could be detected. Females carrying eggs or embryos were recorded from November to June. Maximum biomass of this species reached 7 mg dry weight/m^2 in spring, with an annual average of 0.8 mg (S.D. = 1.4, n = 32). The average individual dry weight varied between 0.8 and 4.3 mg ($\bar{X}$ = 2.1, S.D. = 1.1, n = 12).

The organic proportion of *H. abyssicola* showed a range from 60.0 to 93.1 % of the dry weight ($\bar{X}$ = 81.8, S.D. = 9.6, n = 10) with highest values recorded for late autumn and lowest for early summer.

Eukrohnia bathypelagica

This species was regularly found in Kosterfjorden from early autumn to early summer. A maximum of 29 individuals/m^2 was reached in mid-September, with a second peak in mid-December. The average abundance for the year was 4.6 individuals/m^2 (S.D. = 7.0, n = 32). The biomass reached 101 mg dry weight/m^2 in September and 81 mg/m^2 in December, with an annual mean of 16.2 mg (S.D. = 25.0, n = 32).

The average individual dry weight was relatively high, ranging between 1.7 and 6.3 mg ($\bar{X}$ = 3.6, S.D. = 1.2, n = 23). Animals in a late stage of maturity (stages 3 and 4, see earlier for *E. hamata*) always dominated in the population and animals in stage 1 were never found.

The organic proportion of *E. bathypelagica* varied seasonally between 46.0 and 84.0 % of the dry weight ($\bar{X}$ = 60.1, S.D. = 8.1, n = 22), only exceeding 70 % at two occasions, both occurring in autumn.

Sagitta setosa

This chaetognath occurred throughout the investigation but was quantified separately only during the periods from 19 July to 6 October 1976, and from 25 April to 6 July 1977. During these periods it ranged in abundance from almost zero up to 2300 individuals/m^2 $\bar{X}$ = 652, S.D. = 785, n = 17) with the biomass reaching a seasonal maximum of 125 mg dry weight/m^2 in the beginning of October and showing a seasonal mean of 35.6 mg/m^2 (S.D. = 38.7, n = 17).

The average individual dry weight of *S. setosa* caught in the net (small individuals were inefficiently caught) ranged from 7 to 114 μg ($\bar{X}$ = 60.4, S.D. =

30.0, n = 15) with highest values recorded in summer/autumn. Between 19 July and 6 October 1976, the proportion of individuals with well developed ovaries varied between 32 and 100 % ($\bar{X}$ = 58.3, S.D. = 19.7, n = 10). Fully mature animals were again recorded 18 May 1977 but represented a low proportion of the population throughout the investigation. These results thus indicate a main breeding period from mid-summer to autumn.

The organic proportion of this species was only analysed during the summer and autumn. During this period it ranged from 62.7 to 76.5 % of the dry weight ($\bar{X}$ = 69.8, S.D. = 4.2, n = 9).

Sporadically occurring species

Several species of hydrozoans were occasionaly found in the samples. The leptomedusa *Eutonina indicans* ROMANES was most common in April/May (maximum of 21.5 individuals/m^2) as was the anthomedusa *Euphysa aurata* FORBES (maximum of 11 individuals/m^2). The leptomedusa *Phialidium hemisphaericum* (L.) and the anthomedusa *Leucartiara octona* (FLEMING) both occurred most abundantly in autumn (maxima of 125 and 15 individuals/m^2 respectively). Other leptomedusae, recorded only occasionally and in low numbers, were *Melicertum octocostatum* (M. SARS), *Helgicirrha schulzei* HARTLAUB, *Cosmetira pilosella* FORBES, *Eutima gracilis* FORBES & GOODSIR, and *Obelia* sp. The anthomedusae *Sarsia tubulosa* (M. SARS), *S. eximia* (ALLMAN), and *Bougainvillia principis* (STEENSTRUP) were recorded a few times, and the siphonophore *Nanomia cara* AGASSIZ occurred with up to 14 individuals/m^2.

Large-sized crustaceans other than those mentioned previously were also recorded. The hyperiid amphipod *Scina borealis* G.O. SARS was captured irregularly (maximum abundance 3.1 individuals/m^2, 18 May 1976) and the related species *Parathemisto gauchicaudi* GUERIN and *Hyperia medusarum* O.F. MÜLLER were recorded on a few occasions. Larvae of *Calocaris macandreae* BELL (Decapoda, Anomura) began to occur in October and steadily increased in abundance to a maximum of 13.6 individuals/m^2 in the beginning of December. Several other large-sized crustacean larvae were recorded, but were quantitatively unimportant. The amphipod *Orchomenopsis obtusa* G.O. SARS, the isopod *Munnopsis typica* M. SARS, the two mysids *Leptomysis gracilis* G.O. SARS and *Schistomysis ornata* NORMAN, and the euphausiid *Thysanoessa longicaudata* KRÖYER were all caught on a few occasions during the investigation.

DISCUSSION

The macrozooplankton stock in Kosterfjorden shows a seasonal progression similar to that of zooplankton stocks from other northern areas. MATTHEWS & BAKKE (1977) recorded a macrozooplankton biomass in Korsfjorden (690 m depth), western Norway, which reached a maximum of 40 to 60 g dry weight/m^2 between May and October during three successive years. HOPKINS (1981) recorded very fluctuating quantities of zooplankton in Balsfjorden (190 m depth), northern Norway, but the annual maximum of 11.9 g dry weight/m^2 occurred in September. LINDAHL & HERNROTH (1983) found annual maxima of mesozooplankton biomass in Gullmarsfjorden (120 m depth), western Sweden, between September and November for three years, with up to c. 8 g dry weight/m^2. Although differences in these annual maxima may be partly due to the use of different sampling equipment, they indicate that water column depth partly determines the size of the zooplankton biomass. However, one must question the very high value of MATTHEWS & BAKKE (1977) since such high zooplankton biomass could hardly be sustained by the food supply in the same area; the annual primary production in various coastal areas of Scandinavia ranges from 90 to 230 g C/m^2 (cf. LÄNNERGREN 1976, 1978; OLSSON & ÖLUNDH 1974; LINDAHL & HERNROTH 1983; EILERTSEN & TAASEN 1984). J. Matthews (pers. commn) now considers the high zooplankton biomass of Korsfjorden as partly being an effect of advective processes.

With respect to its zooplankton community, Kosterfjorden is similar to larger fjords and open areas, which are characteristically dominated by *Calanus* spp. (MATTHEWS & HEIMDAL 1980). From their investigation in Korsfjorden MATTHEWS & BAKKE (1977) found large variations in species composition between three successive years but consistent seasonal changes in the unstructured stocks of herbivores, omnivores, and carnivores, and adopted the idea of ISAACS (1973) that an unstructured food web most realistically explains the trophic relationships in the sea. In Kosterfjorden the seasonal cycle of relative proportions of herbivore, omnivore, and carnivore biomass was strikingly similar to that found by MATTHEWS & BAKKE (1977) over a three-year period. A comparison of the zooplankton biomasses in the two fjords is presented in Table 2 and shows that the Norwegian fjord usually held much larger stocks. It also shows that the two carnivorous species *Chiridus armatus* and *Tomopteris helgolandica* are much more important in Kosterfjorden than in Korsfjorden, whereas the opposite is true for *Calanus hyperboreus*, *Eukrohnia hamata*, and *Boreo-*

Table 2. Ranking and extreme values of biomasses (B, in mg dry weight per m^2) of zooplankton species in Kosterfjorden (present study) and Korsfjorden, western Norway (from MATTHEWS & BAKKE 1977). Only species quantitatively analyzed in the present study are concerned.

Species	Kosterfjorden					Korsfjorden				
		Maximum		Minimum			Maximum		Minimum	
	Rank	Month	B	Month	B	Rank	Month	B	Month	B
Calanus finmarchicus	1	Oct.	11 600	Mar.	600	1	May	50 000	Mar.	< 1000
Chiridius armatus	2	Jun.	870	Oct.	30	10	Oct.	250	Mar.	< 25
Metridia longa	3	Jul.	520	Nov.	30	3	Oct.	3 000	Mar.	< 100
Meganyctiphanes norvegica	4	Sept.	1 615	Jan.-May	0	6	Nov.	800	May/Jun.	0
Tomopteris helgolandica	5	May	590	Aug.	5	13	Oct.	30	Jan./May	0
Pasiphaea multidentata	6	Jul.	185	Aug.	0	8	Jun.	900	Feb.	0
Euchaeta norvegica	7	Jun.	260	Aug.	10	7	Dec.	650	Mar.	< 50
Calanus hyperboreus	8	Jun.	240	Aug.	25	2	May	4 000	Mar.	< 100
Aglantha digitale	9	Jan.	410	Jul.	2	11	Feb.	130	May	0
Thysanoessa inermis	10	Jul.	1 050	Oct.-Jun.	0	12	Nov.	40	Apr./May	0
Thysanoessa raschii	11	Jul.	780	Dec.-Jun.	0	–	–	–	–	–
Eukrohnia hamata	12	Sept.	470	Aug.	10	4	Sept.	2 000	Mar.	< 100
Parathemisto abyssorum	13	Jun.	125	Jan.	2	–	–	–	–	–
Sagitta elegans	14	Sept.	100	Jul.	10	10	Oct.	140	Jun.	< 5
Dimophyes arctica	15	Jan.	80	Aug.	7	–	–	–	–	–
Eukrohnia bathypelagica	16	Jul.	100	Jun.	0	9	Dec.	400	Apr.	0
Boreomysis arctica	17	Dec.	55	Aug.	2	5	Mar.	1 000	May	< 50
Tomopteris planktonis	18	Sept.	3	Jun.-Aug.	0	14	Aug.	10	Mar.	0

mysis arctica. The three species *Thysanoessa raschii*, *Parathemisto abyssorum*, and *Dimophyes arctica* contribute significantly to the total zooplankton stock in Kosterfjorden, whereas these species were not classified as important species in Korsfjorden (MATTHEWS & BAKKE 1977). These differences in details and the similarity in trophic structure over the year indicate that the seasonal pattern in trophic structure (Fig. 2; MATTHEWS & BAKKE, fig. 6) is generally applicable to boreal zooplankton communities.

Population dynamics of the species

Although the investigation was not specifically designed to detail the population dynamics of the species (inefficient sampling of the largest and smallest organisms, no separation of developmental stages), it provides some information in this respect. The average individual dry weight in the population is determined by the proportion of different size (age) classes, whereby a low average individual weight indicates the dominance of young individuals and a high weight the dominance of older stages.

There are differing interpretations of the generation cycle of the trachymedusa *Aglantha digitale* in northern latitudes. RUSSELL (1938) suggested three to four generations per year in coastal waters near Plymouth, while KRAMP (1927) and SMEDSTAD (1972) suggested one annual generation in the North Sea and Skagerrak, and Oslofjorden, respectively. Similarly, WILLIAMS & CONWAY (1981), and WILLIAMS & HOPKINS (1975) suggested, on the basis of data from Ocean Weather Station 'India' in the northeast Atlantic, that *A. digitale* has only one generation per year and that breeding occurs in spring. The last suggestion is also the most likely situation in Korsfjorden, western Norway (J. Matthews pers. commn). In the present investigation there was an abrupt drop in average individual dry weight between July and August indicating recruitment of small individuals from the new generation. A following continuous increase in body weight throughout autumn and winter must be interpreted as individual growth, undisturbed by recruitment of small individuals.

The dominance of large-sized, ovigerous females in the population of *Tomopteris helgolandica* in spring and early summer indicates that this species has an annual generation in Kosterfjorden, although the presence of mature animals all year round suggests that reproduction is not restricted to the spring–summer period. Since the abundance increased throughout autumn, at the same time that the average individual dry weight was relatively constant, continuous recruitment of small individuals from the new generation and individual growth probably occurred simultaneously.

The size-distribution of *Meganyctiphanes norvegica* shows that recruitmendt of young individuals occurs in late summer and autumn, and that the population at that time is composed of two or even three year-classes. MATTHEWS (1973) concluded that *M. norvegica* from Korsfjorden reproduces in spring and early summer and attains an age of two or occasionally three years. BÅMSTEDT (1976) calculated average individual dry weights of c. 6, 60, and 100 mg, respectively, for the three generations present in July in Korsfjorden. With a water content of 76 % (BÅMSTEDT 1981b) this corresponds to 25, 250, and 417 mg wet weight, respectively. Individuals representing these three size classes were found in Kosterfjorden so this species thus seems to have the same life cycle in Kosterfjorden as the population on the Norwegian west coast.

The size distribution of the two abundant *Thysanoessa* species, which were present in Kosterfjorden only in summer and autumn, indicates that the occurrence of these euphausiids was not an effect of recruitment through growth of small individuals in Kosterfjorden, but was more probably caused by immigration from outside. Data from Korsfjorden (JØRGENSEN & MATTHEWS 1975) indicate that both species have a generation cycle in these latitudes which is very similar to that of *M. norvegica* although *Thysanoessa* spp, do not appear to be as long-lived as *M. norvegica* (J. Matthews, pers. commn). It is highly probable, therefore, that these species are expatriates in Kosterfjorden.

The weight-frequency distribution of *Parathemisto abyssorum* does not give a simple description of the life cycle, since small animals never dominated in the population. This must be interpreted as a result of an extended reproduction period, which is also suggested by the presence of ovigerous females during the whole year. However, the annual minimum in average dry weight and maximum in abundance occurred simultaneously in October, and this period probably represents the time when the bulk of the new generation is recruited.

For *Calanus finmarchicus* the varying individual dry weight in summer indicates a sporadic recruitment of smaller stages, and the increased average weight thereafter indicates that the recruitment ceased during autumn and the population then consisted mainly of the overwintering stage V copepodites. The very low individual weight in April–May shows that the spring reproduction was synchronized, creating a population consisting for a short while solely of early developmental stages. MATTHEWS & al. (1978) could separate two generations per year in a population from Korsfjorden, but their results and others from western Norway (cf. WIBORG 1954; LIE 1965) indicate that reproduction is not restricted to well defined periods. Recent more detailed studies on the population dynamics of this species in Kosterfjorden indicate that its main breeding periods occur in March, June, and August (own observations).

The dominance of large-sized individuals of *C. hyperboreus* throughout the investigation period gave no evidence of reproduction occurring in Kosterfjorden. It is an arctic species with the main distribution confined to the Arctic seas and the North Atlantic (see RAYMONT 1983). It is found in relatively high abundance in Korsfjorden but its continued occurrence is highly dependent on transport from outside (MATTHEWS & al. 1978). In Korsfjorden as in Kosterfjorden, reproduction probably does not occur.

In northern Norway *Metridia longa* has a one-year life cycle (TANDE & GRØNVIK 1983). In Kosterfjorden the minimum in average individual dry weight of *M. longa* in the beginning of May indicates that reproduction and development of the first generation occurs synchronously in the population in spring. Recent more detailed studies from Kosterfjorden confirm this, but also suggest that a second generation may be produced in early summer (own observations). The increase in the average individual weight indicates that the growth to adult size occurs within two months in the Kosterfjord population. The present results indicate a stable average body weight during summer and autumn. Synchronous reproduction in the population therefore seems to be restricted to the first breeding in March.

The individual dry weight of *Chiridius armatus* was lowest in January, thus indicating that reproduction had occurred in mid-winter, and that the recruitment of young (small) individuals had started. A half-year life cycle for this species with intense reproduction in mid-winter and mid-summer has been suggested by BAKKE & VALDERHAUG (1978) from studies in Korsfjorden. MATTHEWS (1964) suggested that *C. armatus* from Raunefjorden at the Norwegian west coast had one main breeding period per year, which occurred in September–March. From the results of individual body weight of this species in Kosterfjorden there is no evidence of intensified reproduction in mid-summer. A separate counting of adult individuals displayed a more or less continuous decrease in abundance during summer, autumn, and winter, and recruitment of adults mainly occurring before late April. The population in Kosterfjorden thus seems to have a life cycle similar to that described by MATTHEWS (1964).

The occurrence of different developmental stages and eggs in the population of *Euchaeta norvegica* indicates that reproduction occurs throughout the year but is most intense around mid-winter and mid-summer. This is in accordance with data from Korsfjorden (see BAKKE 1977).

The maturity data on *Eukrohnia hamata* indicate that breeding takes place mainly in summer and autumn in Kosterfjorden. SANDS (1980) recorded breeding from spring to autumn in Korsfjorden, most intense in the beginning and end of the period, while GIDSKEØDEGÅRD (1975, cited in SANDS 1980) suggested a breeding period from January to April in Trondheimsfjorden. In the Barents Sea and the coastal waters off Greenland, *E. hamata* breeds mainly in summer-autumn (BOGOROV 1940; KRAMP 1917, 1939; both cited in SANDS 1980).

SANDS (1980) suggested that *E. hamata* has a two-year life cycle on the Norwegian west coast, which corresponded with data from other areas, referred to in her paper. Even if size frequencies are not available for the population in Kosterfjorden the dominance of immature individuals throughout the investigation indicates that either maturation is weakly synchronized in the population or that the animals have a several-year life cycle.

Previous investigations indicate that *Sagitta elegans* has an annual generation in coastal waters of Sweden and Norway (cf. JAKOBSEN 1971; SANDS 1980; TANDE 1983; ØRESLAND 1985). The data on the frequency of maturation in the Kosterfjord population are in accordance with this, and suggest that breeding mainly occurs in spring and early summer, as was found for the populations in the nearby Oslofjorden (JAKOBSEN 1971) and Gullmarsfjorden (ØRESLAND 1985).

Recent studies on the populations of *S. setosa* in the Kattegat and the English Channel indicate that this species has a one-year life cycle in both areas (ØRESLAND 1983, 1986). *S. setosa* from Kattegat bred between mid-July and December, most intensely in August and September (ØRESLAND 1983), and the data presented for Kosterfjorden thus suggest that the life cycle of *S. setosa* is the same along the Swedish west coast.

Organic proportion of zooplankton

In respect of the proportion of organic matter, the macrozooplankton in Kosterfjorden can be separated into two groups, the crustacean species which usually have more than 80 % of the dry weight bound as organic matter, and non-crustacean species, containing coelenterates, ctenophores, polychaetes, and chaetognaths with organic matter usually comprising less than 70 % of the dry weight. This division corresponds with a separation into 'normal' and 'watery' species and is confirmed by earlier published data from the same area, based on unpreserved material (see BÅMSTEDT 1981b). As earlier recorded by BÅMSTEDT (1981b) *Calanus finmarchicus* was found to have a higher proportion of organic matter than *C. hyperboreus*, and *Eukrohnia hamata* higher than *E. bathypelagica*. It is impossible to say whether this were due to differences in fitness of the species to this particulate habitat or to inherent differences not governed by environmental factors. The results do not give clear evidence of successful reproduction of either *C. hyperboreus* or *E. bathypelagica* in Kosterfjorden, so this area may represent the outer limit of their occurrence.

The proportion of organic matter for the whole zooplankton community as well as for most of the individual species showed a maximum in autumn and early winter. This is an indication of energy storage. The concomitant maximum in biomass of the whole community as well as for the most species populations seems to be of general significance for macrozooplankton communities in high latitudes. High population biomass and a surplus of stored body energy provide conditions for successful overwintering of the populations.

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REFERENCES

Bakke, J.L.W. 1977. Ecological studies on the deep-water pelagic community of Korsfjorden, western Norway. Population dynamics of *Euchaeta norvegica* (Crustacea, Copepoda) from 1971 to 1974. – *Sarsia* 63:49–55.

Bakke, J.L.W. & V. Alvarez Valderhaug 1978. Ecological studies on the deep-water pelagic community of Korsfjorden, western Norway. Population biology, biomass and caloric content of *Chiridius armatus* (Crustacea, Copepoda). – *Sarsia* 63:247–254.

Båmstedt, U. 1974. Biochemical studies on the deep-water pelagic community of Korsfjorden, western Norway. Methodology and sample design. – *Sarsia* 56:71–86.

— 1976. Studies on the deep-water pelagic community of Korsfjorden, western Norway. Changes in the size and biochemical composition of *Meganyctiphanes norvegica* (Euphausiacea) in relation to its life cycle. – *Sarsia* 61:15–30.

— 1981a. Seasonal energy requirements of macrozooplankton from Kosterfjorden, western Sweden. – *Kieler Meeresforschungen, Sonderheft* 5:140–152.

— 1981b. Water and organic content of boreal macrozooplankton and their significance for the energy content. – *Sarsia* 66:59–66.

Bogorov, B.G. 1940. On the biology of Euphausiidae and Chaetognatha in the Barents Sea. – *Byulleten Moskovskogo Obshchestra Ispÿtatelei Prirody* 49:3–18.
Cassie, R.M. 1963. Test of significance for probability paper analysis. – *New Zealand Journal of Science* 6:474–482.
Eilertsen, H.C. & J.P. Taasen 1984. Investigations on the plankton community of Balsfjorden, northern Norway. The phytoplankton 1976–1978. Environmental factors, dynamics of growth, and primary production. – *Sarsia* 69:1–15.
Eriksson, S. 1973. Abundance and composition of zooplankton on the west coast of Sweden. – *Zoon* 1:113–123.
Gidskeødegård, R. 1975. *Pilorm (Chaetognatha) fra tre lokaliteter i Trondheimsfjorden.* – Cand.real.thesis, Univ. Trondheim, Norway. 170 pp.
Hopkins, C.C.E. 1981. Ecological investigations on the zooplankton community of Balsfjorden, northern Norway: changes in zooplankton abundance and biomass in relation to phytoplankton and hydrography, March 1976–February 1977. – *Kieler Meeresforschungen, Sonderheft* 5:124–139.
Isaacs, J.D. 1973. Potential trophic biomasses and trace-substance concentrations in unstructured marine food webs. – *Marine Biology* 22:97–104.
Jakobsen, T. 1971. On the biology of *Sagitta elegans* Verrill and *Sagitta setosa* J. Müller in inner Oslofjord. – *Norwegian Journal of Zoology* 19:201–225.
Jørgensen, G. & J.B.L. Matthews 1975. Ecological studies on the deep-water pelagic community of Korsfjorden, western Norway. Population dynamics of six species of euphausiids in 1968 and 1969. – *Sarsia* 59:67–84.
Kramp, P.L. 1917. Chaetognatha collected by the 'Tjalfe' expedition to the west coast of Greenland in 1908 and 1909. – *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i Kjøbenhavn* 69:19–55.
— 1927. The hydromedusae of the Danish waters. – *Kongelige Danske Videnskabernes Selskabs Skrifter,* Afd. 8, Række XII (1):1–291.
— 1939. The Godthaab Expedition 1928: Chaetognatha. – *Meddelelser om Grønland* 80(5):1–40.
Lännergren, C. 1976. Primary production in Lindåspollene, a Norwegian land-locked fjord. – *Botanica Marina* 19:259–272.
— 1978. Phytoplankton production at two stations in Lindåspollene, a Norwegian land-locked fjord, and limiting nutrients studied by two kinds of bioessays. – *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 63:57–76.
Lie, U. 1965. Quantities of zooplankton and propagation of *Calanus finmarchicus* at permanent stations on the Norwegian coast and at Spitsbergen, 1959–1962. – *Fiskeridirektoratets Skrifter, Serie Havundersøkelser* 13:5–19.
Lindahl, O. & L. Hernroth 1983. Phyto-zooplankton community in coastal waters of Sweden – An ecosystem off balance? – *Marine Ecology Progress Series* 10:119–126.
Matthews, J.B.L. 1964. On the biology of some bottom-living copepods (Aetideidae and Phaennidae) from western Norway. – *Sarsia* 16:1–46.
— 1973. Ecological studies on the deep-water pelagic community of Korsfjorden, western Norway. Population dynamics of *Meganyctiphanes norvegica* (Crustacea, Euphausiacea) in 1968 and 1969. – *Sarsia* 54:75–90.
Matthews, J.B.L. & J.L.W. Bakke 1977. Ecological studies on the deep-water pelagic community of Korsfjorden (western Norway). The search for a trophic pattern. – *Helgoländer wissenschaftliche Meeresuntersuchungen* 30:47–61.
Matthews, J.B.L. & B.R. Heimdal 1980. Pelagic productivity and food chains in fjord systems. – Pp. 377–398 in: Freeland, H.J., D.M. Farmer & C.D. Levings (eds). *Fjord oceanography.* Plenum Press, N.Y.
Matthews, J.B.L., L. Hestad & J.L.W. Bakke 1978. Ecological studies in Korsfjorden, western Norway. The generations and stocks of *Calanus hyperboreus* and *C. finmarchicus* in 1971–1974. – *Oceanologica Acta* 1:277–284.
Øresland, V. 1983, Abundance, breeding and temporal size distribution of the chaetognath *Sagitta setosa* in the Kattegat. – *Journal of Plankton Research* 5:425–439.
— 1985. Temporal size and maturity-stage distribution of *Sagitta elegans* and occurrence of other chaetognath species in Gullmarsfjorden, Sweden. – *Sarsia* 70:95–101.
— 1986. Temporal distribution of size and maturity stages of the chaetognath *Sagitta setosa* in the western English Channel. – *Marine Ecology Progress Series* 29:55–60.
Olsson, I. & E. Ölundh 1974. On the plankton production in Kungsbacka Fjord, an estuary on the Swedish west coast. – *Marine Biology* 24:17–28.
Omori, M. 1978. Some factors affecting on dry weight, organic weight and concentration of carbon and nitrogen in freshly prepared and in preserved zooplankton. – *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 63:261–269.
Raymont, J.E.G. 1983. *Plankton and productivity in the oceans 2, Zooplankton,* Pergamon Press, Oxford, 2:nd edition. 824 pp.
Russell, F.S. 1938. The Plymouth offshore medusa fauna. – *Journal of the marine biological Association of the United Kingdom* 22:411–439.
Sands, N.J. 1980. Ecological studies on the deep-water community of Korsfjorden, western Norway. Population dynamics of the chaetognaths from 1971–1974. – *Sarsia* 65:1–12.
Smedstad. O.M. 1972. On the biology of *Aglantha digitale rosea* (Forbes) (Coelenterata: Trachymedusae) in the Oslofjord. – *Norwegian Journal of Zoology* 20:111–135.
Steele, J.H. 1974. *The structure of marine ecosystems.* – Harvard Univ. Press, Cambridge, Mass. 114 pp.
Tande, K.S. 1983. Ecological investigations on the zooplankton community of Balsfjorden, northern Norway: population structure and breeding biology of the chaetognath *Sagitta elegans* Verrill. – *Journal of Experimental Marine Biology and Ecology* 68:13–24.
Tande, K.S. & S. Grønvik 1983. Ecological investigations on the zooplankton community of Balsfjorden, northern Norway: sex ratio and gonad maturation cycle in the copepod *Metridia longa* (Lubbock). – *Journal of Experimental Marine Biology and Ecology* 71:43–54.
Wiborg, K.F. 1954. Investigations on zooplankton in coastal and offshore waters of western and northwestern Norway. – *Fiskeridirektoratets Skrifter, Serie Havundersøkelser* 11:1–246.

Williams, R. & D.V.P. Conway 1981. Vertical distribution and seasonal abundance of *Aglantha digitale* (O.F. Müller) (Coelenterata: Trachymedusae) and other planktonic coelenterates in the northeast Atlantic Ocean. – *Journal of Plankton Research* 3:633–643.
Williams, R. & C.C. Hopkins 1975. Biological sampling at OWS "India" in 1973. – *Annales Biologiques, Copenhague* 30:60–62.

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