Distribution and life history of krill from the Barents Sea

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Dalpadado, P. & Skjoldal, H. R. 1991: Distribution and life history of krill from the Barents Sea. Pp. 443–460 in Sakshaug, E., Hopkins, C. C. E. & Øritsland, N. A. (eds.): Proceedings of the Pro Mare Symposium on Polar Marine Ecology, Trondheim, 12–16 May 1990. *Polar Research 10(2).*

Krill from the Barents Sea were studied on six cruises from 1985 to 1989. *Thysanoessa inermis* and *T. longicaudata* were the dominant species, while *T. raschii* and *Meganyctiphanes norvegica* were rarer in the studied areas. The two dominant species *T. inermis* and *T. longicaudata* are mainly found in the Atlantic Water and they do not to a large extent penetrate into Arctic water masses in the northern Barents Sea. *M. norvegica* is a more strict boreal species that does not occur as extensively in the Barents Sea as do the *Thysanoessa* species. The mean population abundance ranged from 1 to 61 individuals m^{-2} for *T. inermis* and from 2 to 52 ind. m^{-2} for *T. longicaudata*. The mean dry weight biomass of these two species ranged from 14 to 616 and from 19 to 105 mg^{-2}. Length frequency distributions indicate a life span of just over two years for *T. inermis* and *T. longicaudata*. Growth took place from about April to autumn with no apparent growth during winter. Maturation and spawning seem to occur after two years for *T. inermis* and one year for *T. longicaudata*. Main spawning occurred from May to June coinciding with the spring phytoplankton bloom. Captive spawners of *T. inermis* (total length 17–22 mm) shed 30–110 eggs per female in a single batch.

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Introduction

Four species of krill are commonly found in the Barents Sea, *Thysanoessa inermis* (Krøyer), *T. raschii* (M. Sars), *T. longicaudata* (Krøyer) and *Meganyctiphanes norvegica* (M. Sars). Of these species, *T. inermis* and *T. raschii* are most dominant and widespread. *T. inermis* inhabits the western and southern areas of the Barents Sea, whereas *T. raschii* is more common in inshore waters in the eastern part (Drobysheva 1987).

The role of euphausiids in the marine food web has been well documented. Krill are an important link in transferring primary production to higher trophic levels. In the Barents Sea, krill serve as food for commercially important fish species such as cod, capelin, herring and redfish (Panasenko 1984; Mehl 1989; Skjoldal & Hassel 1991) and also for many sea birds and whales. Drobysheva & Panasenko (1984) calculated that fishes consumed about three quarters of the average yearly production of 50–70 million tonnes of krill in the Barents Sea.

Most studies on growth, maturation and longevity of krill have been based on samples of preserved specimens. Long-term laboratory experiments on the Antarctic krill, *Euphausia superba*, by Murano et al. (1979), Ikeda & Dixon (1982a, b), Buchholtz (1983, 1991) and Ikeda et al. (1985) have provided useful additional information on moulting, growth and other life history parameters. Laboratory studies on live *Thysanoessa* spp. are more limited. Jerde & Lasker (1966), Paranjape (1967) and Sameoto (1976) studied moulting cycles and respiration rates of *Thysanoessa* spp., while Dalpadado & Ikeda (1989) and Ikeda & Skjoldal (1989) studied moulting, growth, maturation, respiration and excretion of *T. inermis* from the Barents Sea.

A study on krill populations in the Barents Sea was begun in May 1987 as a part of the Pro Mare programme. This study was carried out to obtain information on distribution and life history parameters such as growth, maturity and spawning. Such information forms a basis for analyses of relationships between the krill species and the physical environmental conditions, seasonal development of phytoplankton, and distribution of capelin as a major krill predator.

Materials and methods

Samples of krill used for this study were collected in the Barents Sea during the following cruises with R/V G. O. SARS from the Institute of Marine Research, Bergen: 29 July–19 August 1985, 14 May–12 June 1987, 11 September–16 October 1988, 8–27 January 1989, and 9–22 May 1989. In addition, samples were collected during a cruise with M/S ENDRE DYRØY in the period 22–28 March 1988.

Samples were collected using a 1 m^2 MOCNESS sampler (Wiebe et al. 1985) and a Gulf III Plankton sampler, towed at speeds of about 1.5 and 5 knots, respectively. The MOCNESS was equipped with 9 nets of 333 μm nylon mesh netting (dark blue), and was fished obliquely so that up to 8 strata were sampled. The volume of water filtered in each stratum varied from 100 to 600 m^3. The MOCNESS was used to obtain samples for determination of population abundance and structure, maturation and growth. The Gulf III sampler (180 μm) was used in double oblique hauls down to 60–100 m. This sampler provided specimens of krill in better condition than the MOCNESS, and was used to obtain samples for determination of weight-length relationships. The Gulf III sampler was also used to catch live specimens for incubation experiments.

Samples were preserved in 4% formalin. Large samples were divided using a Folsom plankton splitter prior to analysis. Specimens were identified and the total length (TL; from tip of rostrum to tip of telson) was measured to the nearest 0.05 mm. In Gulf III samples from May–June 1987, carapace length (CL), uropod exopodite length (EL), and wet and dry weights (WW, DW) of *Thysanoessa inermis* were also recorded.

The MOCNESS samples were analysed in some detail. Gender was recorded by examining the secondary sexual characters, *petasma* of males and *thelycum* of females. Individuals with no visible secondary sexual characters were classified as juveniles. In females the gonads were examined and the maturity stage was determined using the scale given by Kulka & Corey (1978). Their division of oögenesis into five stages is based on the classifications of Ponomareva (1956), Zelikman (1958) and Mauchline (1968):

Stage I. Oocytes with a diameter of up to 0.1 mm, granular cytoplasm, and large nucleus.

Stage II. Oocytes 0.1–0.2 mm, very granular cytoplasm, and large nucleus.

Stage III. Oocytes 0.2–0.27 mm, distinct yolk globules, and nucleus rarely visible.

Stage IV. Oocytes 0.27–0.36 mm, transparent yolk globules, and nucleus rarely visible.

Stage V. After spawning. Remaining ova scattered, irregular in shape and of appearance similar to those of Stages I and II.

Males were graded according to their development of petasma, using a simplified version of the scale of Makarov & Denys (1980).

Stage I. Sub-adult; petasma wing-like.

Stage II. Sub-adult; developing petasma.

Stage III. Adult; fully developed petasma.

The presence of spermatophores both in males and in females was noted.

Length frequency histograms of samples from individual stations and sample size of more than 15 individuals were resolved into normally distributed components (cohorts) using Bhattacharya's (1967) analysis as implemented in the LFSA (Length Frequency Sample Analysis) by Sparre (1988). The mean lengths of the separated year classes have been used to obtain the seasonal growth pattern. This has been analysed using a modification of von Bertalanffy's growth function with seasonally oscillating growth (Somers 1988).

In the May 1989 cruise, some mature female krill (stage 4) were captured alive. These krill were kept separately in 2-liter bottles containing filtered seawater for about a week, and later transferred to a cold room at 1.5 (±0.5)°C at the Institute of Marine Research, Bergen. The krill were fed regularly with a mixture of cultured algae. The incubation flasks were inspected every day and moults and spawned eggs were removed and preserved in 4% formalin. The eggs were counted and their diameter measured. Some eggs were also measured in fresh condition prior to preservation. The size of the moults were determined by measuring the length of the exopodite of the uropod (EL). This was converted to total body length (TL) by using an established relationship between EL and TL.

Correlation analysis and fitting of growth curves were carried out on a Macintosh computer using the Systat programme (Systat Inc.).

Results

Abundance and distribution

Geographical distributions of *Thysanoessa inermis*, *T. longicaudata* and *Meganyctiphanes* *norvegica* are given in Fig. 1–3 for four different time periods: January–March (14 stations), May–June (15 stations), August (19 stations), and October (8 stations). The January–March, May–June and October samples were mainly restricted to Atlantic Water and the Polar Front region, whereas most of the August samples were from Arctic Water. The density estimate (number of individuals m^{-3}) at a station is an average of 4–8 depth intervals in a MOCNESS profile.

T. inermis and *T. longicaudata* were the dominant species in the area investigated. The highest densities of *T. inermis* ranged from 0.26 to 0.6 individuals m^{-3} (ca. 4–10 mg dry weight m^{-3}) for the January–March, May–June and October samples (Fig. 1). The maximum densities were found in the slope area south of Bjørnøya (Bear Island) at depths of 200–400 m. Very low densities of *T. inermis* (0.001–0.01 individuals m^{-3}) were found in the August samples. At that time, however, large numbers of larvae (stage 5 furcilia) of *T. inermis* were found in the area east of Hopen, with densities up to 50 individuals m^{-3}.

The highest density of *T. longicaudata* was ca. 0.4 individuals m^{-3} in May 1989. As for *T. inermis*, the highest densities were found south of Bjørnøya (Fig. 2). *M. norvegica* was mostly found in warmer Atlantic Water. The highest density observed in our study was ca. 0.15 individuals m^{-3} in October (Fig. 3). No *M. norvegica* were recorded in the August samples. We observed very low densities of *T. raschii*, usually below 0.01 individuals m^{-3}. The highest density observed was 0.054 individuals m^{-3} at one station in May 1989.

The distributions of the two dominant krill

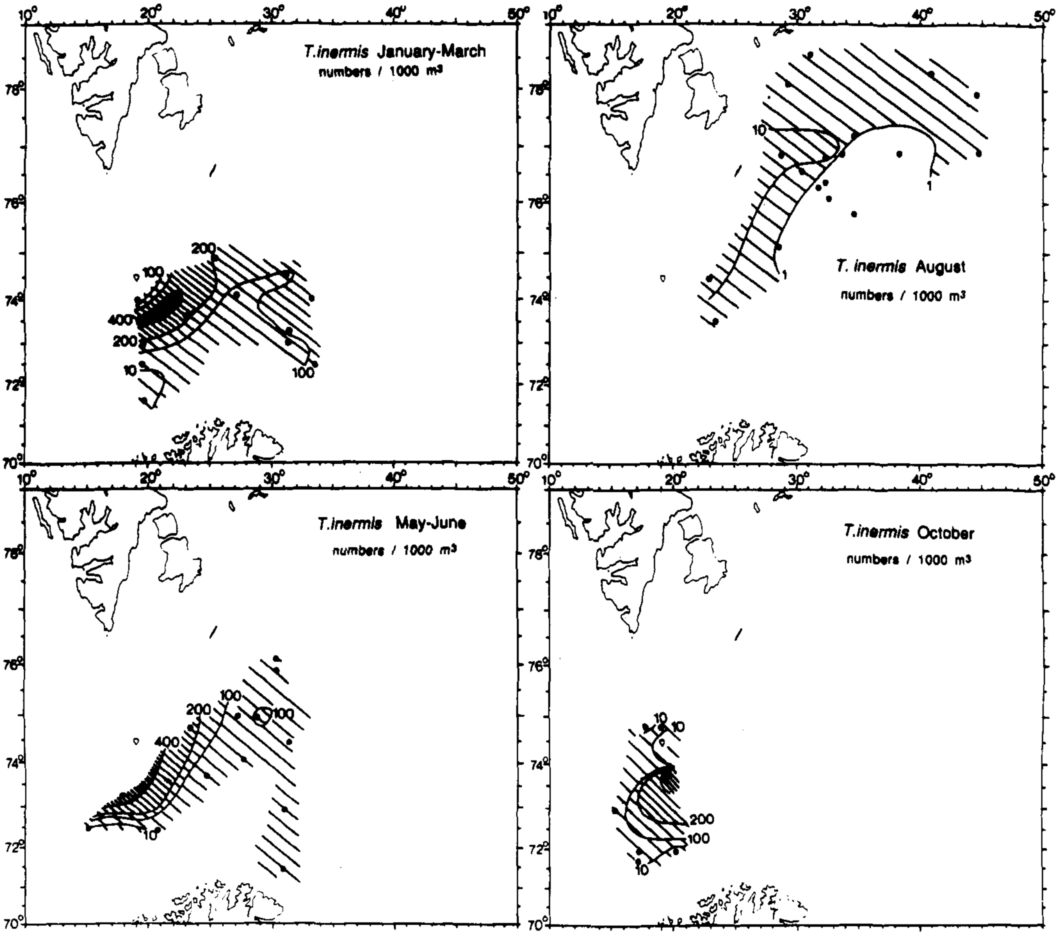

Fig. 1. Thysanoessa inermis. Horizontal distributions in the Barents Sea in January–March, May–June, August, and October.

species, *T. inermis* and *T. longicaudata*, were generally similar (Figs. 1 and 2). This was reflected in significant correlations between males and females, respectively, of the two species ($r = 0.66$ and 0.38; $n = 56$, $p < 0.01$, Table 1). The correlation between juveniles of the two species were lower and not significant ($r = 0.25$, $p > 0.05$).

The abundance of adults of *T. inermis* and *T. longicaudata* were positively and significantly correlated with the depth of the stations ($r = 0.35$–0.43, $p < 0.05$; Table 2, Fig. 4A and D). The highest abundances were found at salinities close to 35, which is characteristic of Atlantic Water (Fig. 4B, E). Both species occurred in the region of the Polar Front, characterised by low salinity and low temperature, but typically with low abundances (Fig. 4B, C, E and F). The abundance of *T. longicaudata* was more strongly positively correlated with salinity and temperature than that of *T. inermis* (Table 2). The correlations between the abundance of *T. inermis* and salinity and temperature of the deeper water (50–200 m) were particularly low. This suggests a closer connection with Atlantic Water for *T. longicaudata* than for *T. inermis*.

Biomass

The numerical abundances m^{-2} of *Thysanoessa inermis* and *T. longicaudata* are summarised in Table 3 as the means and ranges of values observed at each cruise. The mean abundance ranged from 1 to 61 individuals m^{-2} for *T. inermis*

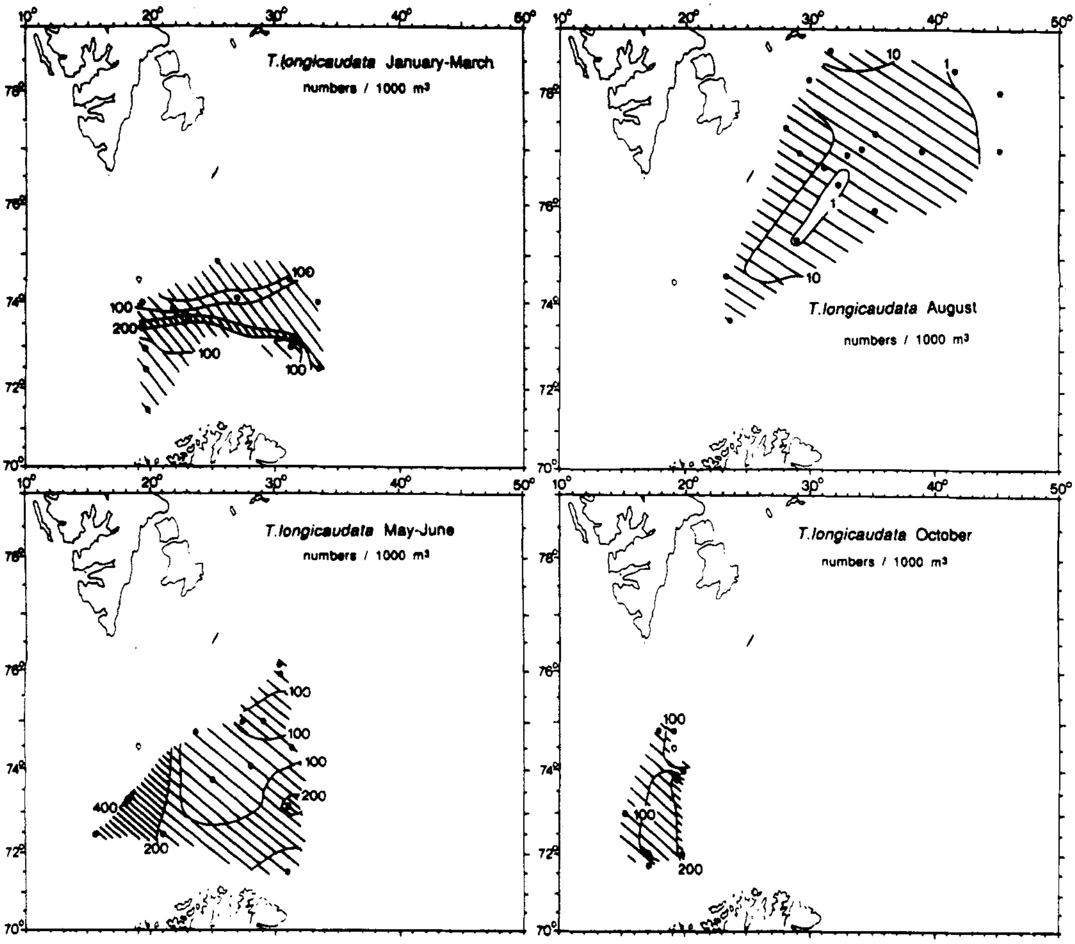

Fig. 2. Thysanoessa longicaudata. Horizontal distributions in the Barents Sea in January–March, May–June, August, and October.

and from 2 to 52 individuals per m^{-2} for *T. longicaudata*.

Using information on mean lengths of juveniles and adults and regressions describing relationships between body weight and length, the data on numerical abundance have been converted into biomass (Table 3). The mean biomass of *T. inermis* ranged from 14 to 616 mg dry weight m^{-2}, with an overall mean of 277 mg m^{-2}. The mean biomass of *T. longicaudata* tended to be lower, ranging from 19 to 111 mg m^{-2}, with an overall mean of 80 mg m^{-2}.

Table 1. Product moment correlation coefficients (r) between numerical abundances (number of individuals m^{-3}) of juveniles (juv), females (fem) and males (mal) of *Thysanoessa inermis* (Ti) and *T. longicaudata* (Tl)

	Ti-juv	Ti-mal	Ti-fem	Tl-juv	Tl-mal
Ti-mal	0.23				
Ti-fem	0.59	0.74			
Tl-juv	0.25	0.17	0.10		
Tl-mal	0.28	0.66	0.45	0.18	
Tl-fem	0.41	0.40	0.38	0.01	0.80

Population structure and size distribution

The abundances of males and females were significantly positively correlated for both *Thysanoessa inermis* and *T. longicaudata* (r = 0.74 and 0.80, respectively; Table 1). The sex ratio tended in general to be close to 1:1 for both species. A notable exception was the virtual

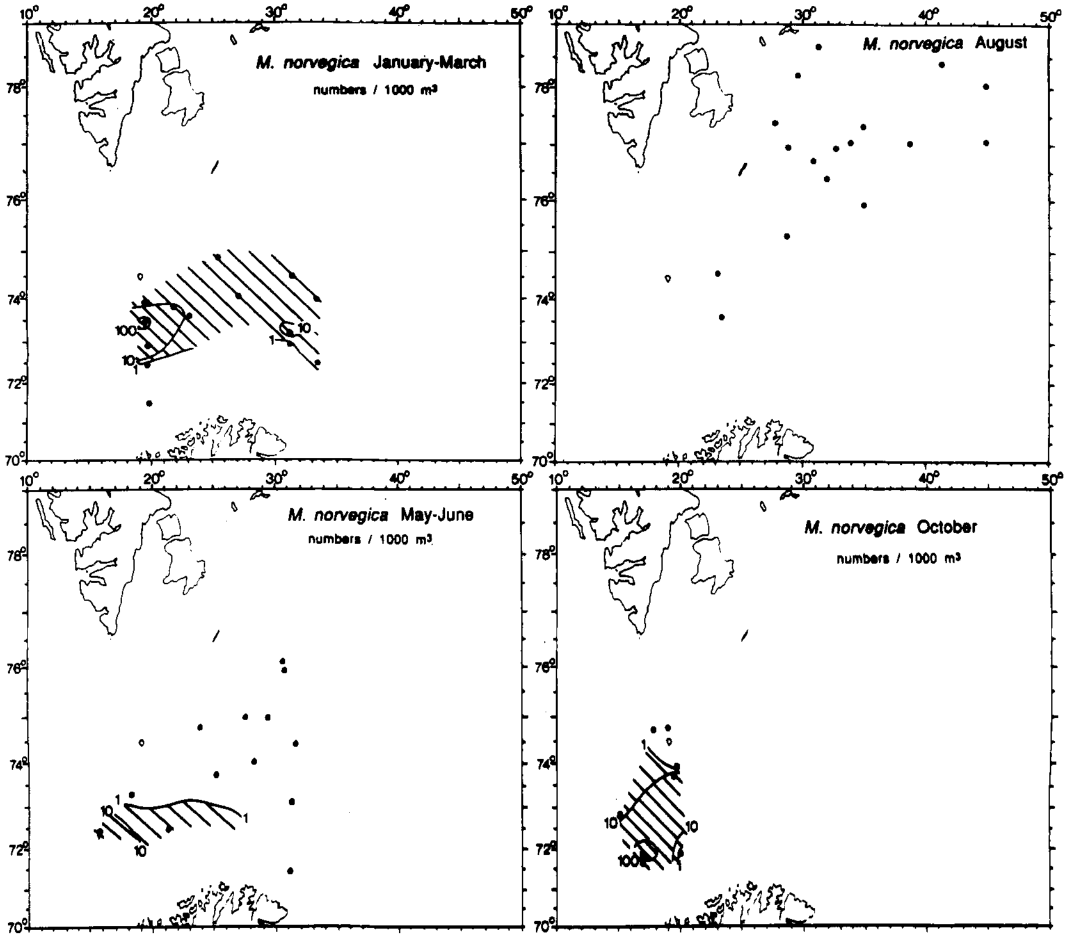

Fig. 3. Meganyctiphanes norvegica. Horizontal distributions in the Barents Sea in January–March, May–June, August, and October.

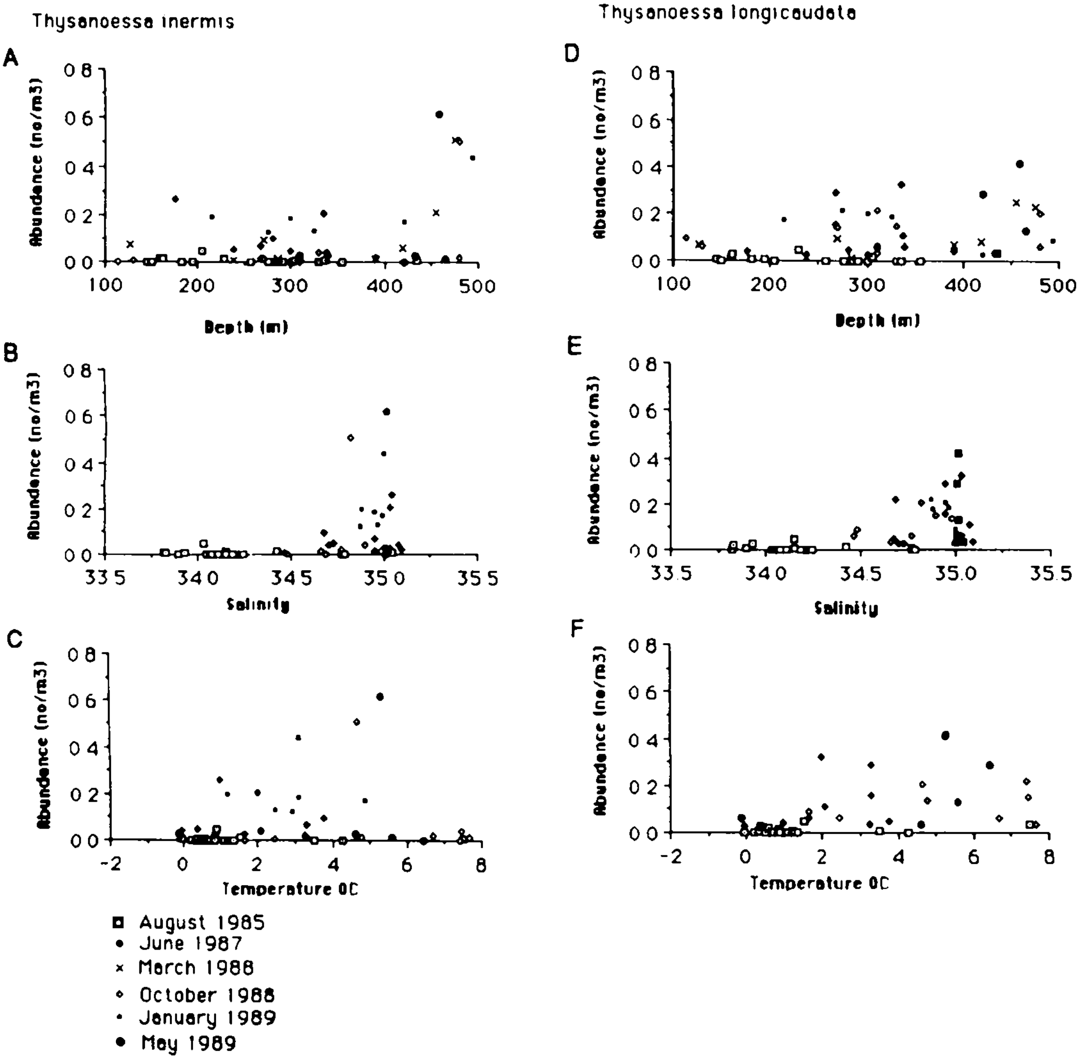

Fig. 4. Thysanoessa inermis (A–C) and *T. longicaudata* (D–F). Numerical abundance (number of individuals (adults + juveniles) m^{-3}) in relation to water depth at sampling stations (A, D) and average salinity (B, E) and temperature (C, F) in the upper 50 m. Data from the different cruises are plotted with different symbols as identified by the key.

Table 2. Product moment correlation coefficients (r) between numerical abundances of juveniles and adult males and females of *Thysanoessa inermis* and *T. longicaudata* and environmental variables (depth, temperature (Temp) and salinity (Sal) in the 0–50 m and 50–200 m depth intervals, and chlorophyll *a* (Chl *a*) in the 0–50 m layer).

	Depth (m)	Temp 0–50 m	Temp 50–200 m	Sal 0–50 m	Sal 50–200 m	Chl *a* 0–50 m
T. inermis						
Juveniles	0.30	0.04	0.08	0.41	0.22	0.04
Males	0.37	0.19	0.13	0.25	0.10	−0.06
Females	0.43	0.13	0.08	0.31	0.12	−0.17
T. longicaudata						
Juveniles	0.05	0.45	0.52	0.32	0.18	0.32
Males	0.41	0.37	0.35	0.49	0.36	0.19
Females	0.35	0.13	0.21	0.48	0.34	0.30

Table 3. Thysanoessa inermis and *T. longicaudata*. Means and ranges of numerical abundance (number of individuals m^{-2}) and dry weight biomass (mg m^{-2}) observed during the different cruises from August 1985 to May 1989.

	Abundance (No. m^{-2})			Biomass (mg m^{-2})	
Cruise No. of	stations	Mean	Range	Mean	Range
T. inermis					
August 1985	19	1.1	0.0–7.4	14.2	0.0–47.1
June 1987	10	17.3	1.5–60.3	191.3	42.2–668.8
March 1988	8	44.8	0.6–207.2	296.7	3.8–1372.6
October 1988	8	22.5	0.0–152.3	101.6	0.0–688.2
January 1989	6	60.8	33.5–130.0	616.1	338.8–1317.0
May 1989	5	28.2	0.0–117.8	443.4	0.0–1853.5
T. longicaudata					
August 1985	19	1.7	0.0–7.2	18.5	0.0–93.4
June 1987	10	27.5	5.7–93.5	111.2	102.9–116.6
March 1988	8	36.5	2.7–100.2	63.8	57.8–69.3
October 1988	8	30.6	6.6–61.6	82.8	70.5–97.3
January 1989	6	45.0	9.4–63.3	100.3	98.5–102.5
May 1989	5	52.4	12.6–109.3	104.9	94.8–108.2

absence of males of *T. inermis* in the August samples when females occurred frequently although with low abundance.

The abundance of juveniles showed no correlation with the abundances of adult males or females for *T. longicaudata* ($r = 0.18$ and 0.01, $n = 33, p > 0.05$). The juveniles of *T. inermis*, on the other hand, were significantly correlated with the abundance of females ($r = 0.59$, $n = 56$, $p < 0.01$; Table 1).

Length frequency distributions of *T. inermis* were clearly bimodal throughout most of the year (Fig. 5). Bhattacharya's method usually gave two and in a few cases three modes in the length frequency distributions (Table 4). We assume that these modes are year classes, with a denoted change in age in spring when reproduction occurs (see below). We interpret the first mode to represent individuals of year class 0 for the October to March period and year class 1 for the May and June period. The first mode consisted mostly of juveniles and had an overall mean length of 12.5 mm (range 10.7 to 15.5 mm). The second mode represents individuals of year class 1 (October–March) or 2 (May–June) (mean length 20.4 mm, range 18.5 to 22.1 mm). The third mode represents individuals of year class 2 or 3 (mean length 24.3 mm, range 22.5 to 25.8 mm).

T. longicaudata showed a less clear separation of modes in the length frequency distributions than did *T. inermis*, particularly for the samples from May and June (Fig. 6). However, the statistical splitting of the length frequency histograms gave in most cases two modes. The mean length of year class 0 was 8.2 mm in October. The length of year class 1 individuals ranged from 8.9 to 14.5 mm, whereas the length of year class 2 individuals ranged from 11.7 to 14.9 mm (Table 4).

There was in general good agreement between the statistically separated size modes and separation of juveniles and adults based on examination of secondary sexual characters (see Figs. 5 and 6). The size of the smallest mode was significantly correlated with the size of juveniles for both *T. inermis* ($r = 0.96$, $n = 26$, $p < 0.01$) and *T. longicaudata* ($r = 0.78$, $n = 22$, $p < 0.01$).

The number of individuals of *Meganyctiphanes norvegica* and *Thysanoessa raschii* were too few to be analysed by Bhattacharya's method. The largest size of *M. norvegica* was 37 mm (Fig. 7). All individuals above 27 mm were adults. The size distribution of *T. raschii* was generally similar to that of *T. inermis*.

Weight and length relationships

The relationship between wet weight (WW, mg) and total length (TL, mm) of *Thysanoessa inermis* from the Barents Sea in May–June 1987 was described by the regression equation:

$$\log \mathrm{WW} = 3.33 \log \mathrm{TL} - 2.58 \quad (n = 168, r^2 = 0.94).$$

The relationship between total length and length of the exopodite of the uropod (EL) of moults of

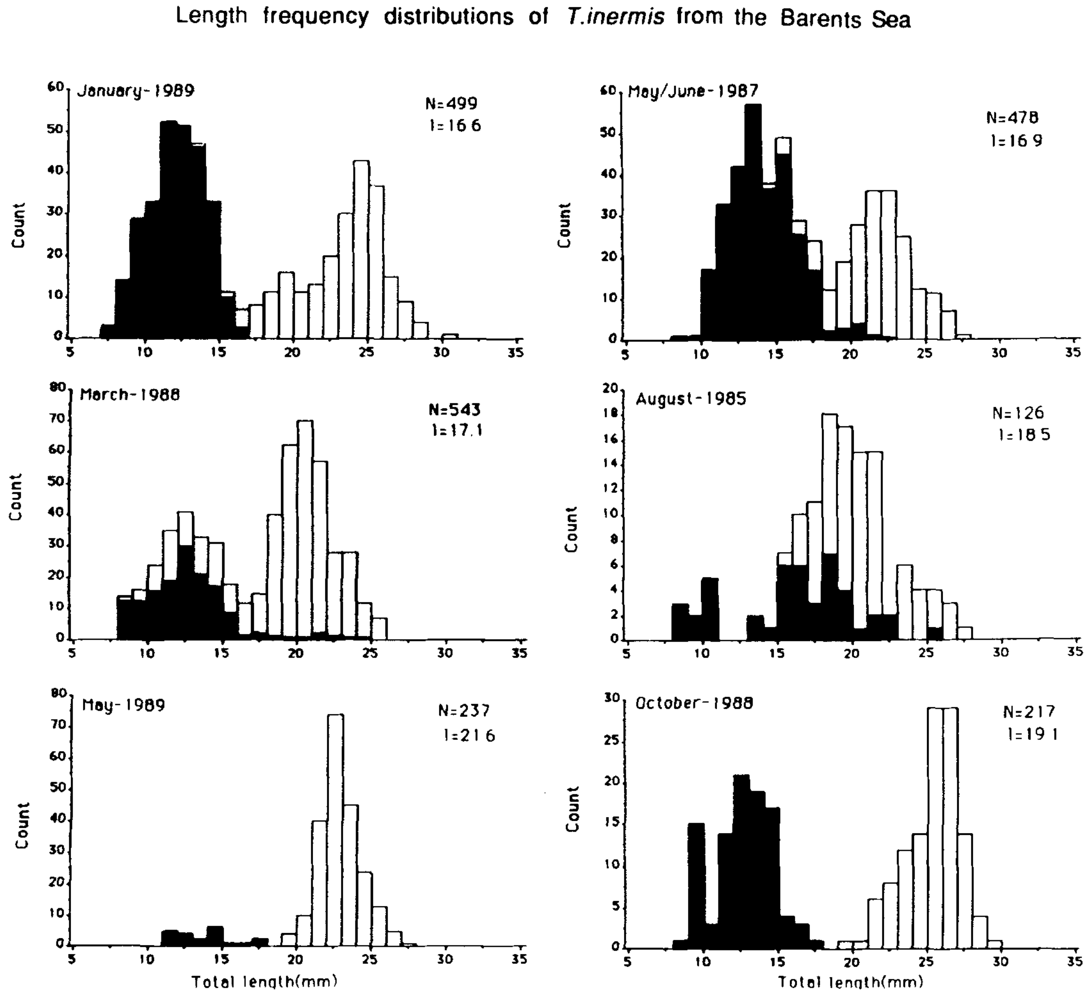

Fig. 5. Thysanoessa inermis. Length-frequency histograms for the different cruises. Filled bars represent juveniles.

T. inermis was:

$$TL = 8.39\ EL - 1.772\ (n = 173,\ r^2 = 0.995).$$

The relationship between carapace length (CL) and total length was:

$$CL = 0.352\ TL - 1.092\ (n = 166,\ r^2 = 0.92).$$

Maturity and spawning

There was a clear seasonality in the maturity of adult females and males of both *Thysanoessa inermis* and *T. longicaudata*. Mature and spawning females were found only in the late spring period. In the samples from May and June, about 60–80% of the female krill were in a state ready to spawn (Stages III and IV), while 3–10% had already spawned (Stage V) (Figs. 8 and 9). Mature males (Stage III) were found in samples from March to June. About 80% of the mature males carried spermatophores. The number of males bearing spermatophores decreased in August. The presence of spermatophores in females was observed only in the samples from May and June, indicating that spermatophore transfer occurred in April and May. By August all females were in

Table 4. Thysanoessa inermis and *T. longicaudata*. Means and ranges of numerical abundance (number of individuals m^{-3}) and total length (mm) of cohorts separated in length frequency analysis. The cohorts are assumed to represent year classes and ascribed to age groups 0, 1, 2 and 3, with a change in age in spring.

Cruise	No. of stat.	No. of ind.	Cohort	Abundance (No. m^{-3}) Mean	Range	Total length (mm) Mean	Range
T. inermis							
June-87	10	908	1-gr.	0.058	0.000–0.185	13.4	11.6–15.5
			2-gr.	0.042	0.000–0.160	20.8	19.5–21.4
			3-gr.	0	–	–	–
Mar-88	8	2101	0-gr.	0.084	0.046–0.133	12.1	10.9–13.1
			1-gr.	0.101	0.016–0.358	19.8	19.1–20.9
			2-gr	0.003	0.000–0.017	22.5	–
Oct-88	8	438	0-gr.	0.053	0.000–0.169	12.5	11.5–13.5
			1-gr.	0.010	0.000–0.040	18.5	–
			2-gr.	0.074	0.000–0.298	24.4	–
Jan-89	6	1225	0-gr.	0.107	0.047–0.193	11.7	10.7–12.3
			1-gr.	0.042	0.010–0.072	20.3	19.1–21.6
			2-gr.	0.057	0.000–0.167	24.5	24.2–25.8
May-89	5	517	1-gr.	0.010	0.000–0.029	13.1	–
			2-gr.	0.174	0.000–0.523	22.1	–
			3-gr.	0.030	0.000–0.091	24.2	–
T. longicaudata							
June-87	10	1402	1-gr.	0.123	0.030–0.289	10.1	8.9–10.9
			2-gr.	0.009	0.000–0.044	13.7	12.7–14.9
Mar-88	8	1479	0-gr.	0.067	0.032–0.120	7.3	6.5–7.8
			1-gr.	0.064	0.030–0.140	11.1	10.0–12.0
Oct-88	8	592	0-gr.	0.110	0.050–0.210	8.2	7.7–9.2
			1-gr.	0.026	0.009–0.130	13.4	12.0–14.5
Jan-89	6	930	0-gr.	0.130	0.047–0.160	8.7	7.8–9.6
			1-gr.	0.044	0.029–0.066	12.1	10.5–13.4
May-89	5	1078	1-gr.	0.247	0.127–0.342	10.6	10.0–10.9
			2-gr.	0.031	0.004–0.074	12.6	11.7–13.5

Stage I and most males were in Stages II or I (Figs. 8 and 9).

The seasonal reproductive cycle was quite similar for *T. inermis* and *T. longicaudata* (Figs. 8 and 9). The weighted mean maturity stage was calculated as maturity indices for females and males at each sampling station. The maturity indices of females and males were significantly correlated between the two species ($r = 0.68$ and 0.88 for females and males, respectively; $n = 33$ and 26; $p < 0.01$). The reproductive cycle of *T. inermis* was somewhat more advanced in time, however, compared to that of *T. longicaudata*, as judged from the development of the maturity stages (Figs 8 and 9).

The observations on gonad development of *Meganyctiphanes norvegica* and *T. raschii* are too few to draw firm conclusions. Compared to *T. inermis* and *T. longicaudata*, fewer Stage III males and females of *M. norvegica* were found in the March samples (Fig. 10). Few individuals of *M. norvegica* were found in May and none of these were spawning (Stage IV) or had spawned (Stage V). The few observations on *T. raschii* indicate that spawning took place in May and June.

Spawning krill of *T. inermis* belonged to the second peak in the size distributions (Fig. 5). They were therefore 2 or 3 years old. The abundance of the 3-group individuals of *T. inermis* was less than 20% of that of the 2-group individuals in May and June (Table 4). Thus the majority of spawning krill was two years old. The scarce data for *T. raschii* indicate a similar situation for this species. For *T. longicaudata* the juveniles apparently changed into adults during spring and virtually no juveniles were found in May–June (Fig. 6). This indicates that *T. longicaudata* matures and spawns as one year old individuals. The mean size at spawning (Stage IV) for *T. inermis* was 22.6 mm

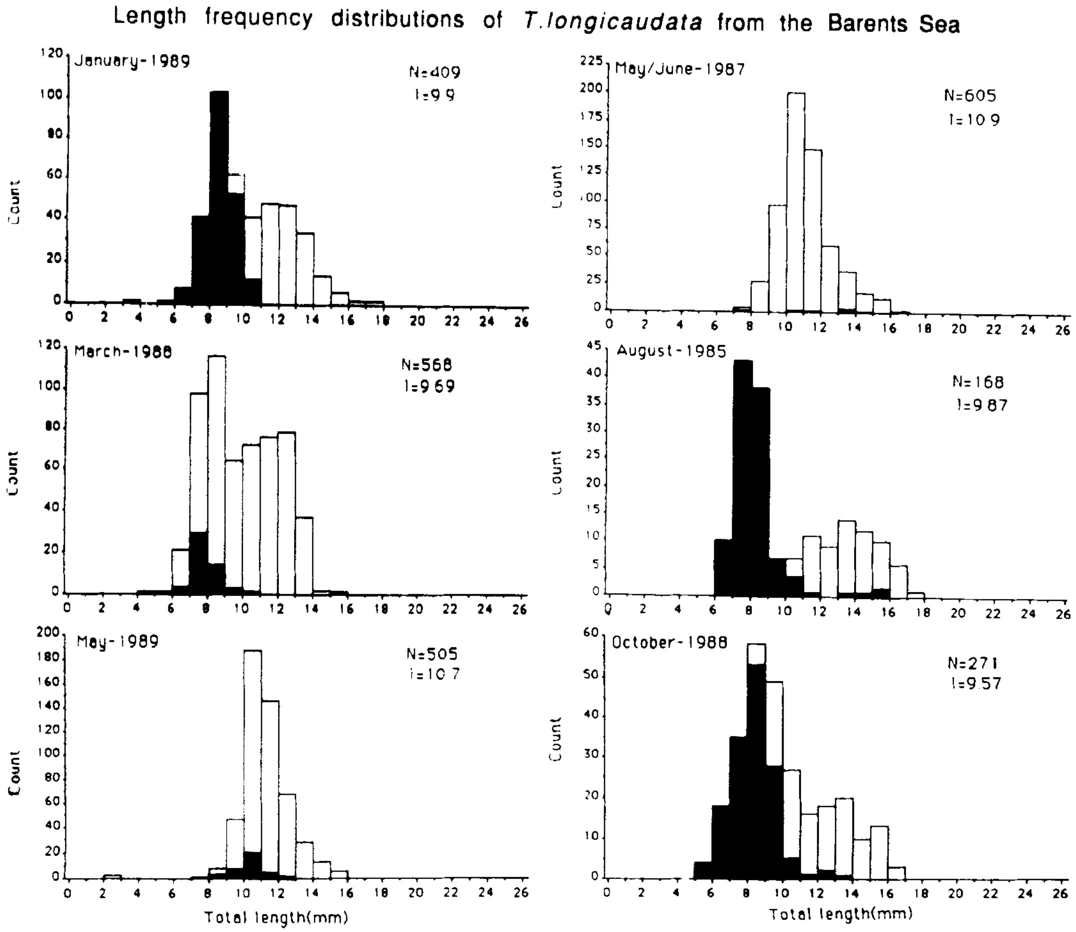

Fig. 6. Thysanoessa longicaudata. Length-frequency histograms for the different cruises. Filled bars represent juveniles.

in May–June 1987 and 24.0 mm in May 1989. For *T. longicaudata* the mean size at spawning was 11.6 mm for both cruises. Spawning females of *T. raschii* were only found during the May–June 1987 cruise and their mean size was 21.9 mm. No spawning females of *M. norvegica* were found in the present study.

Spawning females of *T. inermis* and *T. longicaudata* were characterised by a light blue gonad colour, and they were therefore easily recognisable. Shipboard experiments with eight spawning females of *T. inermis* (17–22 mm in length) in May 1989 showed that they released from 32 to 110 eggs in a single batch. Of the eight krill, three died within a few days after spawning. The remaining five were kept alive for about three months in a cold room (1.5 ± 0.5°C). No eggs were released during this period. The diameter of fresh eggs, including the perivitelline space, was from 0.8 to 1.0 mm, while the diameter excluding the perivitelline space was from 0.42 to 0.65 mm. The diameter of eggs in preserved condition ranged from 0.62 to 0.86 mm and from 0.38 to 0.40 mm with and without the perivitelline space, respectively.

The successive moults of the spawners of *T. inermis* showed that the female secondary sexual organ (thelycum) regressed with time following spawning. The uropod exopodite length of the moults was converted to body length by using the regression equation between these two parameters. During the three months of incubation, both increase and decrease in body length were observed. These phenomena have been

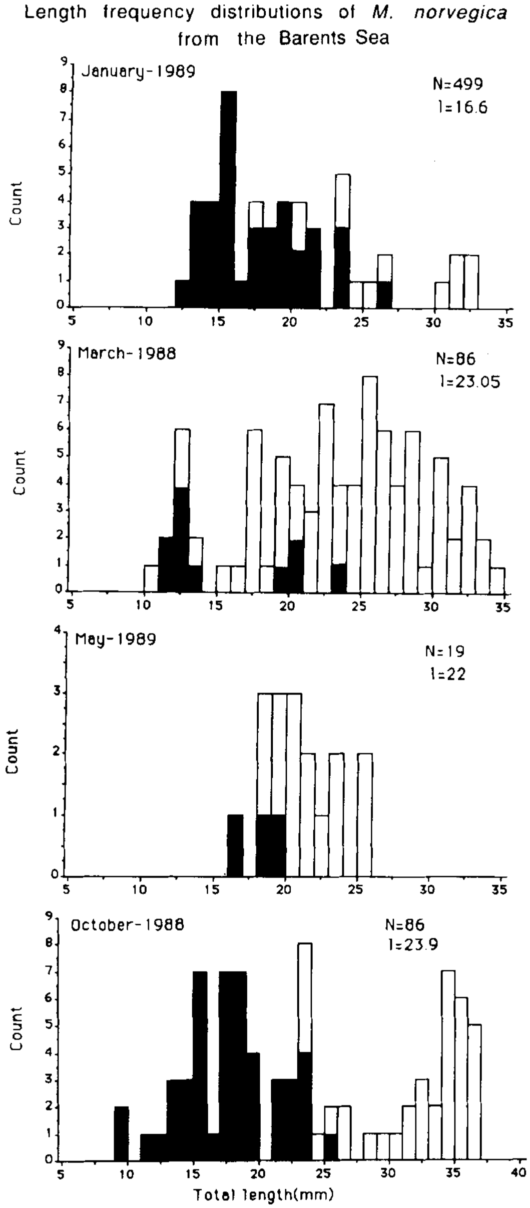

Fig. 7. Meganyctiphanes norvegica. Length-frequency histograms for the different cruises. Filled bars represent juveniles.

reported in more detail by Dalpadado & Ikeda (1989) for *T. inermis* from the Barents Sea.

Growth

The length frequency data are from different years and areas and this prevents an accurate assessment of growth. A rough picture of the seasonal pattern of growth has been obtained, however, by combining the data from the different cruises and years. The lengths of the separated modes in the size frequency distributions are summarised in Table 4 and plotted against time of the year in Fig. 11.

The 0-group individuals of *Thysanoessa inermis* had grown to a mean length of 12.5 mm in October. The main period of growth of one and two year old krill was apparently from about April until autumn (Fig. 11A). There was no apparent growth during winter. It was not possible to separate size modes at each station with the August data due to the low abundance. Instead the average sizes of juveniles and adults have been plotted in Fig. 11 for comparison. The size of the immature juveniles of *T. inermis* was in general agreement with the expected size of the 1-group individuals (Fig. 11A). The fact that they were still not mature indicates a delayed maturation in these northern waters covered during the August cruise. The size of the mature adults was smaller than expected for the 2-group individuals, which might reflect that some matured 1-group individuals were included among the adults.

A similar growth pattern seemed to exist for *Thysanoessa longicaudata*, although only 2 size groups were separated for this species. The mean length of the 0-group individuals was 8.2 mm in October and 8.7 mm in January, decreasing to 7.3 mm in March (Fig. 11B). The 1-group individuals grew to a mean size of 13.4 mm in October. The 2-group individuals were of a similar size in May–June, as were the mature adults in August. The juveniles in August belonged to two size groups. At three stations in the northeastern area the mean size corresponded well with the expected size for 1-group individuals. Juveniles at stations farther to the west had a mean size of 7.4 mm and belonged probably to the 0-group (Fig. 11B).

The von Bertalanffy's growth function with seasonal oscillation (Somers 1988) was fitted to the data on mean length in Table 4 and Fig. 11. The following parameter values were obtained for *Thysanoessa inermis* and *T. longicaudata*:

	T. inermis	*T. longicaudata*
L_∞	30.3	16.8
K	0.53	0.65
t_0	−0.29	−0.45
C	−1.55	−2.00
t_s	0.20	0.10

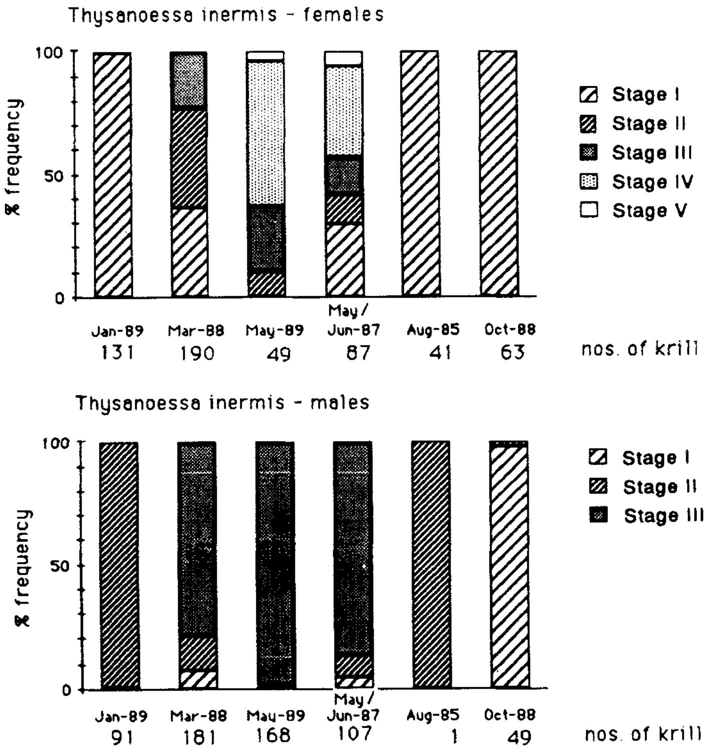

Fig. 8. Thysanoessa inermis. Frequency of maturity stages of adult females and males in different seasons.

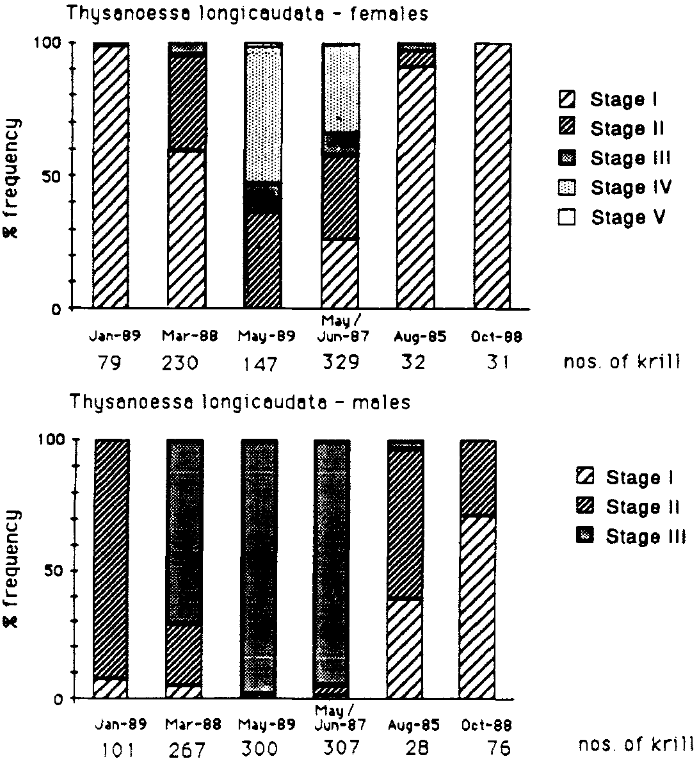

Fig. 9. Thysanoessa longicaudata. Frequency of maturity stages of adult females and males in different seasons.

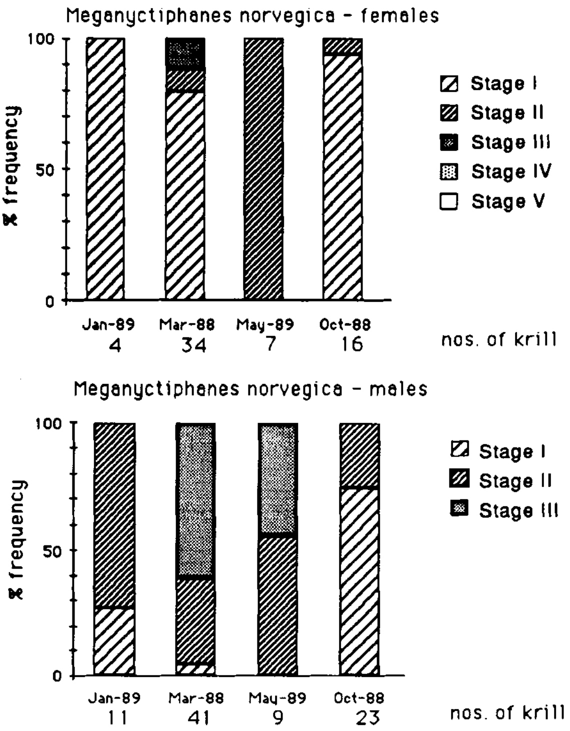

Fig. 10. Meganyctiphanes norvegica. Frequency of maturity stages of adult females and males in different seasons.

Discussion

Sampling

Quantitative sampling of large and mobile zooplankton such as krill is difficult due to their avoidance of zooplankton nets. Our estimates of population abundance are based on samples collected with a 1 m^2 MOCNESS net. Wiebe et al. (1982) compared the 1-m^2 and a 10-m^2 MOCNESS for sampling of the krill *Nematoscelis megalops* which were 15–25 mm in length. The number of krill caught was much lower in day-time than in night-time samples, particularly for the 1-m^2 net. This indicates visual avoidance of the net and undersampling of the krill during day-time. Wiebe et al. (1982) found, however, no marked effect of avoidance on the size frequency distribution of *N. megalops*.

Our MOCNESS samples are likely to have resulted in underestimates of the abundance of krill, but the extent of underestimation is not clear. Visual avoidance would be largest in daytime and in the summertime. In the winter darkness when the sun is below the horizon, one would expect visual avoidance to be very small. In agreement with this, the highest abundance and biomass of *Thysanoessa inermis* were found during the January 1989 cruise. However, the average biomass in January was only slightly higher than the biomass found during the May 1989 cruise (Table 3). For *T. longicaudata* the average abundance and biomass were approximately similar in January and May. This similarity between winter and summer data indicates that the effect of visual avoidance have been limited, particularly for *T. longicaudata*.

Further support for a limited effect of avoidance is found if one compares the krill biomass with maximum expected krill production. The annual primary production in this area of the Barents Sea is about 70 g C m^{-2} (Rey et al. 1987). Massive sedimentation of spring blooms has been observed (Rey & Skjoldal 1987; Wassmann 1989). If one assumes that half of the primary production is "lost" to sedimentation and the "microbial loop", about 35 g C m^{-2} is available to larger herbivores. Dividing this equally between copepods and krill, and assuming a growth efficiency

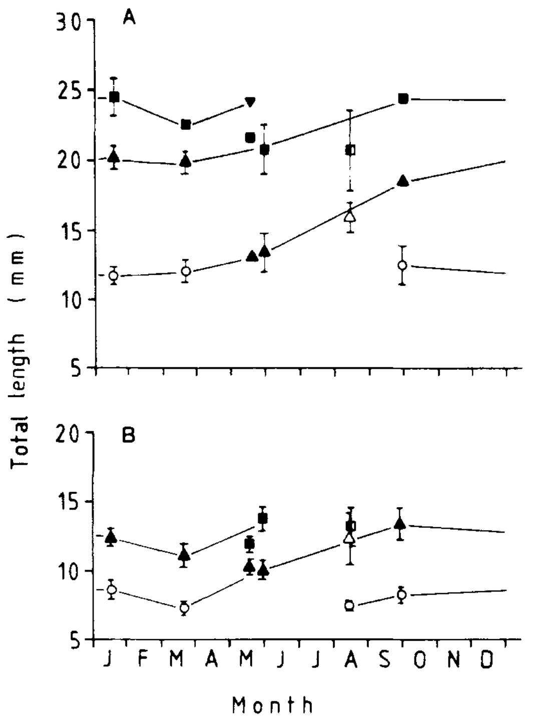

Fig. 11. Thysanoessa inermis (A) and *T. longicaudata* (B). Seasonal variation in mean length of cohorts separated in length frequency analysis. ○ = 0-group, ▲ = 1-group, ■ = 2-group, ▼ = 3-group. For the August samples, mean lengths of juveniles (○, △) and adults (◧) are plotted. Vertical bars represent two times standard deviation.

of 20%, this can support a krill production of about 4 g C or about 8 g dry weight $m^{-2} y^{-1}$. With an annual P/B ratio in the range 2–4 (Berkes 1977; Drobysheva & Panasenko 1984), this is equivalent to a krill biomass of 2–4 g dry weight m^{-2}. This is likely to be a maximum estimate for krill populations under low predation pressure. The observed mean biomass for *T. inermis* and *T. longicaudata* combined ranged from 0.2 to 0.7 g dry weight m^{-2} (Table 3).

Apart from avoidance, the vertical distribution can also determine the extent to which krill are being sampled. *T. inermis* and *T. raschi* can form dense concentrations near the bottom in summer following the spawning period (Drobysheva & Panasenko 1984). We have operated the MOCNESS to within 20–30 m from the bottom for safety reasons, and may therefore have missed such near-bottom concentrations. This would have led to underestimates of the krill abundance during the summer and perhaps autum. In midwinter, *T. inermis* has been found to be distributed in the upper water layer (Hassel et al. 1986) when they would be more amenable for sampling with the MOCNESS.

Distribution

Thysanoessa inermis and *T. longicaudata* were the predominant krill species in our study area, while *Meganyctiphanes norvegica* and *T. raschii* were found in smaller numbers. Zoogeographically, the three *Thysanoessa* species are classified as arcto-boreal species, while *M. norvegica* is a boreal species (Einarsson 1945; Mauchline & Fisher 1969). *T. inermis* and *T. raschii* are neritic species found both in the North Atlantic and in the North Pacific, whereas *T. longicaudata* and *M. norvegica* are more oceanic species found only in the North Atlantic.

Earlier studies of krill on the shelf at Møre in western Norway revealed a difference in the pattern of distribution of the krill species. *T. inermis* and *T. raschii* were found to occur primarily over the coastal banks on the shelf, while *T. longicaudata* and *M. norvegica* occurred most abundantly off the shelf break (Hjort & Ruud 1929). *T. inermis* and *T. raschii* occur commonly in the fjords of western Norway together with *M. norvegica* (Wiborg 1970; Jørgensen & Matthews 1975; Kaartvedt & Svendsen 1990). *T. inermis* and *T. raschii* are the dominant krill species in the fjords of northern Norway and in the Barents Sea (Drobysheva 1979; Falk-Petersen & Hopkins 1981; Hopkins et al. 1984).

The Barents Sea is a shelf sea with an average depth of 240 m. The water circulation is characterised by inflowing coastal and Atlantic waters from the southwest that are cooled and gradually transformed into Arctic Water in the Barents Sea (Loeng 1989; Midttun 1989). This makes the Barents Sea a zoogeographical transition zone between the boreal and the Arctic and an ecosystem strongly dependent on advective transport of zooplankton with the inflowing currents (Skjoldal & Rey 1989).

T. inermis is an important species in the southern and western Barents Sea. Sars (1874) described it as an offshore species that could be concentrated in fjords or bays such as the Varangerfjord. Here blue whales in former times aggregated during the summer to feed on dense concentrations of *T. inermis*. High concentrations of *T. inermis* have also been reported from the shallower areas around Spitsbergenbanken in the northwestern part of the Barents Sea with abundances up to 2 individuals m^{-3} (Drobysheva 1979; Drobysheva & Panasenko 1984; Timofeev 1988). Our results are in agreement with this pattern, showing the highest concentrations of *T. inermis* south and east of Bjørnøya (Fig. 1).

The maximum abundances of *T. inermis* were found over the deeper areas at depths between 400 and 500 m and with decreasing abundances towards the shallower parts of the Spitsbergenbanken (Fig. 4A). Although *T. inermis* is a neritic shelf species, our results indicate that its association with the bottom and bottom topography is not particularly strong. Instead, *T. inermis* has a widespread distribution in the Atlantic Water of the western and central Barents Sea, as suggested already by Sars (1874).

T. raschii is common in the fjords of northern Norway (Falk-Petersen & Hopkins 1981) and occurs abundantly in the shallower regions of the eastern Barents Sea (Drobysheva 1979). It seems therefore to be a more neritic species than *T. inermis*. *T. raschii* occurred in the western and central areas of the Barents Sea covered in our investigations, but its abundance was low.

T. longicaudata is a more oceanic species that has been found mainly in the southwestern part of the Barents Sea (Drobysheva 1979). We found its distribution to be quite similar to that of *T. inermis* (Figs. 1, 2 and 4), and the abundances of the adults of the two species were correlated (Table 1). Soviet investigations have indicated that *T. longicaudata* and *T. inermis* in the Barents Sea depend on resupply to the populations with the inflowing Atlantic Water from the west (Drobysheva 1979, 1980). Our results show that both species are found mainly in Atlantic Water and that they do not to a large extent penetrate into the Arctic water masses in the northern Barents Sea.

T. longicaudata and *T. inermis* were found in Arctic Water to north of 78°N during the August cruise, but they were rare with a mean abundance of only about 1 individual m^{-2} (Figs 1 and 2, Table 3). Their maturation seemed to be retarded in these Arctic waters. It is therefore likely that they were expatriated individuals transported with Atlantic Water flowing northwards as a deep current east of Hopen or southwards from north of Spitsbergen (Loeng 1989). *T. inermis* shows a similar distribution in the Bering Sea where it occurs most abundantly on the outer shelf in warmer water (Cooney 1978). The arcto-boreal *Thysanoessa* species are therefore primarily found in the warmer waters south of the Polar Front, and they occur only rarely in true Arctic waters. This is in contrast to the Antarctic krill *Euphausia superba* which is distributed south of the Antarctic Polar Front well into ice-covered waters (Miller & Hampton 1989; Sakshaug & Skjoldal 1989).

M. norvegica has been found mainly in the southwestern part of the Barents Sea where its occurrence depend on transport with inflowing water from west (Drobysheva 1979). This pattern was found also in our study, with appreciable numbers of *M. norvegica* being caught only at the westernmost stations at the entrance to the Barents Sea (Fig. 3). *M. norvegica* was not found at the central and northern part of the area investigated in May–June, nor at any stations during the August cruise to the northern Barents Sea. This underlines that *M. norvegica* is a more strict boreal species that does not occur as extensively in the Barents Sea as do the *Thysanoessa* species.

Reproduction and life cycle

Our observations show that the main spawning activity of *Thysanoessa inermis* and *T. longicaudata* occurs in May–June, as about 60–80% of the krill taken in these months were mature individuals in stages 3 and 4 (Figs. 8 and 9). Also *T. raschii* seemed to spawn mainly in this period. Males of *T. inermis* and *T. longicaudata* matured earlier than the females. This is in agreement with results from studies by Zelikman (1958) and Mauchline (1968) who found that males matured at least a month before the females. Plankton samples collected with 30-L Niskin water bottles or vertical Juday net hauls from the Barents Sea in January 1985, April 1986, May 1982, June 1982, 1984 and 1987, and August 1985 contained krill eggs only in samples from May and June (unpubl. data).

The main spawning period of the *Thysanoessa* species in May–June coincides with the spring phytoplankton bloom in the Barents Sea. The temporal development of the spring bloom is determined by stability formation in the water column (Skjoldal et al. 1987; Skjoldal & Rey 1989; Sakshaug & Skjoldal 1989). This occurs by warming of the upper layer of the Atlantic Water south of the Polar Front, which is a slow process. The spring bloom in open waters therefore develops slowly during spring and culminates typically in June (Skjoldal et al. 1987). Astthorsson (1990) also found spawning of krill in Isafjord-deep in northwest Iceland to be closely related to the spring phytoplankton bloom.

The reproductive cycles of *T. inermis* and *T. longicaudata* were remarkably similar (Figs. 8 and 9) and both species seem to reproduce successfully in the Barents Sea. The maturation of ovaries started in late winter and lasted about three months. This is similar to maturation times previously reported for *T. inermis*, *T. raschii* and *Meganyctiphanes norvegica* (Zelikman 1958; Ponomareva 1966; Mauchline 1968; Kulka & Corey 1978).

No mature females or males of *M. norvegica* were found in the present study. This supports earlier findings that *M. norvegica* spawns mainly outside the Barents Sea (Jones 1968; Mauchline & Fisher 1969). *M. norvegica* is known to spawn north to about 70°N in the Norwegian Sea, but in particularly warm years it may extend its breeding area into the Barents Sea and to the waters off western Greenland.

Our shipboard experiments show that *T. inermis* (17–22 mm in length) sheds 32–110 eggs in a single batch. Most eggs were spherical with a relatively large perivitelline space, and slightly heavier than seawater. The general morphology and size of the eggs are in agreement with other studies from the Barents Sea (Einarsson 1945; Zelikman 1958; Ponomareva 1966). Recent shipboard experiments by Nicol (1989) indicate that the Antarctic krill *Euphausia superba* sheds its eggs in a single batch. Whether krill species shed their eggs in a single batch under natural conditions or repeatedly in several batches during a spawning season is a question which is not yet resolved.

The life span of krill species seems to vary with latitude. In Korsfjorden, western Norway, *Thysanoessa* species live about one year (Jørgensen & Matthews 1975). In colder waters such as the Gulf of St. Lawrence (Berkes 1973, cited in Kulka & Corey 1978), the Bay of Fundy (Kulka & Corey 1978), and East Greenland and South Iceland (Einarsson 1945), *T. inermis* can live up to two years. Recent studies by Astthorsson (1990) show that *T. inermis* and *T. raschii* from the Isafjord-deep on the northwestern coast of Iceland have a life span of just over two years. In western Greenland waters, *T. inermis* can live for three years (Einarsson 1945). Our data on length frequency suggest a two years life cycle for *T. inermis* in the Barents Sea, while some individuals may live three years. *T. longicaudata* matures after one year, but part of the population lives for two years. Our data on *M. norvegica* and *T. raschii* are too few to draw any firm conclusions.

The juvenile recruits of *Thysanoessa inermis* and *T. longicaudata* had grown to a mean size of about 9.5 and 6.5 mm, respectively, in August. For *T. inermis*, this is a slower development than reported for juveniles from the Bay of Fundy (Kulka & Corey 1978) and from the south and west coasts of Iceland (Einarsson 1945; Astthorsson 1990), but a somewhat more advanced development than reported from the north and east coasts of Iceland (Einarsson 1945; Astthorsson 1990).

The main growth of *Thysanoessa inermis* and *T. longicaudata* occurred from about April to October (Fig. 11). This growth pattern is generally similar to that reported for *T. inermis* in Icelandic waters (Einarsson 1945; Astthorsson 1990), although Astthorsson (1990) found a somewhat shorter growth period for 1-group individuals. The growth period of *T. inermis* and *T. raschii* from Balsfjorden in northern Norway also appears to be somewhat shorter, with the main growth in terms of length from March to August and from April to June for 1- and 2-group individuals, respectively (Falk-Petersen & Hopkins 1981).

There was no apparent growth during winter, with a tendency of decreasing size for *Thysanoessa longicaudata* (Fig. 11B). Decreasing length of *Thysanoessa* spp. has previously been found for populations from Balsforden and Isafjord-deep (Falk-Petersen & Hopkins 1981; Hopkins et al. 1984; Astthorsson 1990). Krill growth occurs through moulting. Studies by Dalpadado & Ikeda (1989) on *T. inermis* showed that the intermoult period (IP) is linearly dependent upon temperature. They observed a marked negative growth during the course of the experiment for some of the individuals. Most laboratory experiments on Antarctic krill *Euphausia superba* (Murano et al. 1979; Ikeda & Dixon 1982a, b; Polek & Denys 1982) show no growth or body shrinkage, with positive growth as the exception. This is most probably due to the maintenance situation and may be caused by handling effects, insufficient size of the containers and deficiencies in food (Buchholtz 1983, 1991).

Decreasing size during winter may cause difficulties in population dynamical studies based on length frequency distributions. This has been the case in studies of Antarctic krill where it has been recognized that other methods, such as analysis of fluorescent age pigment, should be used in addition to length frequency distributions (Berman 1990; Berman et al. 1989). Degrowth poses little problems, however, for short-lived species such as *Thysanoessa inermis* and *T. longicaudata*, which have a well-defined spawning period and a synchronized seasonal growth in the population governed by the seasonal cycle of primary production.

Acknowledgements. – The present research was funded by the Norwegian Council of Fisheries Research (NFFR) as part of Pro Mare. We thank our colleagues and crew members who have helped in collecting the samples, often under harsh conditions. We thank A. Gundersen for assistance in analysing the krill samples, J. Gjøsæter and T. Mümtaz for help with the Bhattacharya's growth analyses, and F. Buchholz, J. A. Lindley and C. C. E. Hopkins for critical comments on the manuscript.

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