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DISTRIBUTION AND LIFE CYCLE OF KRILL NORTH OF 73° N IN THE BARENTS SEA, 1984 - 1992

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Sammendrag:

Thysanoessa inermis og *T. longicaudata* var de dominerende artene av krill , mens *T. raschii* og *Meganyctiphanes norvegica* sjelden ble observert i vestlige og sentrale deler av Barentshavet i perioden 1984 til 1992. Ingen av krillartene som finnes i Barentshavet er virkelig arktiske arter og de trenger i liten grad inn i de arktiske vannmassene i den nordlige del av Barentshavet. Store konsentrasjoner (opp til 100 - 200 individer m-2) av *T. inermis* og *T. longicaudata* ble funnet langs skråningen og i de dypere vannmassene langs sør og sør-øst siden av Svalbardbanken. Disse to artene gyter vanligvis i mai og juni, samtidig som planktonoppblomstringen er på det høyeste. *T. inermis* har en livssyklus på 3 til 4 år, mens *T. longicaudata* lever opp til 2 år. Undersøkelsene indikerer et predator - bytteforhold mellom lodde og krill i Barentshavet, og tyder på at mengden av krill for en stor del styres av beiting fra lodda.

Emneord - norsk:
1. Krill
2. Fordeling
3. Livssyklus

Emneord - engelsk:
1. Krill
2. Distribution
3. Life cycle

Prosjektleder

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ABSTRACT

Thysanoessa inermis and *T. longicaudata* were the dominant krill species whereas *T. raschii* and *Meganyctiphanes norvegica* were seldom observed in the western and central Barents Sea during 1984 to 1992. None of the krill species found in the Barents Sea are real Arctic species and penetrate very little into the Arctic water masses in the northern Barents Sea. . High abundances (up to 100-200 individuals m^{-2}) of *T. inermis* and *T. longicaudata* were found in the slope and adjoining deep waters south and south east of the Svalbard Bank. Main spawning of *T. inermis* and *T. longicaudata* is in May - June, coinciding with the spring phytoplankton bloom. *T. inermis* has a life span of 3 to 4 years while *T. longicaudata* can live up to 2 years. Growth took place from late winter to autumn with a marked negative growth during the late autumn and winter period. The seasonally oscillating von Bertalanffy growth function gave a reasonably good fit to the growth curves.

Coinciding with a strong reduction in the older capelin stock from 1984 to 1987, there was a subsequent increase in the abundance and biomass of *T. inermis* and *T. longicaudata.* A decrease in krill abundance and biomass was observed corresponding to the rapid recovery and growth of capelin stock up to 1991. This indicates clear predator-prey interrelationship between planktivorous capelin and krill in the Barents Sea, and suggests that the krill populations to a large extent are controlled by predation.

SAMMENDRAG

Thysanoessa inermis og *T. longicaudata* var de dominerende artene av krill , mens *T. raschii* og *Meganyctiphanes norvegica* sjelden ble observert i vestlige og sentrale deler av Barentshavet i perioden 1984 til 1992. Ingen av krillartene som finnes i Barentshavet er virkelig arktiske arter og de trenger i liten grad inn i de arktiske vannmassene i den nordlige del av Barentshavet. Store konsentrasjoner (opp til 100 - 200 individer m^{-2}) av *T. inermis* og *T. longicaudata* ble funnet langs skråningen og i de dypere vannmassene langs sør og sør-øst siden av Svalbardbanken. Disse to artene gyter valigvis i mai og juni, samtidig som planktonoppblomstringen er på det høyeste. *T. inermis* har en livssyklus på 3 til 4 år, mens *T. longicaudata* lever opp til 2 år. Krillen vokser fra sen vinter til høst, og har en markert negativ vekst om høsten og vinteren. Von Bertalanffys vekstkurve med sesongmessige svingninger viste rimelig god tilpasning til vekstdataene.

Samtidig som bestanden av eldre lodde gikk sterkt tilbake fra 1984 til 1987 var det en økning i tetthet og biomasse av *T. inermis* og *T. longicaudata.* Samtidig med den sterke veksten i loddebestanden fram til 1991, ble biomassen av krill lavere igjen. Dette indikerer et predator - bytteforhold mellom lodde og krill i Barentshavet, og tyder på at mengden av krill for en stor del styres av beiting fra lodda.

INTRODUCTION

The Barents Sea is a shallow continental shelf area with an average depth of 230 m (Zenkevitch, 1963). The waters in the northern Barents Sea are mainly of Arctic origin. The climatic conditions in the Arctic and especially in the Polar Front region are largely determined by the physical properties of the inflowing Atlantic water (Midttun and Loeng, 1987). The general ecology and the production of the Barents Sea has been reviewed by many authors (Dragesund and Gjøsæter, 1987; Loeng,1989a, 1989b; Skjoldal and Rey, 1989).

The physical properties of Arctic and Atlantic water masses most likely influence the distribution and abundance of krill in the northern Barents sea. Arctic water is generally characterised by a temperature below 0 °C and salinity varying between 34.4-34.8, whereas the Atlantic water is defined by a salinity higher than 35 and by temperatures above 2 °C. Between the Arctic and the Atlantic water masses, there is an area called the Polar front, where the two water masses mix. Special hydrographic conditions in the Polar front area can occasionally cause upwelling of nutrient rich waters to the euphotic zone, which can enhance the primary production in the area (Loeng, 1989a, 1989b).

Previous investigations have shown that a single genus of krill, *Thysanoessa* dominates in the Barents Sea. The two dominant species in the western Barents Sea are *T. inermis* (Krøyer) and *T. longicaudata* (Krøyer), which are mainly found in the Atlantic water. They penetrate only to a very limited extent into the Arctic water masses in the northern Barents Sea (Dalpadado and Skjoldal, 1991). *T. raschii* (M. Sars) is more common in the shallow waters of the eastern Barents Sea (Drobysheva, 1987; Timofeev, 1988). The larger krill species, *Meganyctiphanes norvegica* (M. Sars) is less common in the Barents Sea and is restricted to the warmer Atlantic water in the western part (Einarsson, 1945; Lindley, 1977; Drobysheva, 1979; Dalpadado and Skjoldal, 1991).

Krill form an important part of the diet of many commercially and ecologically important fish species in the Barents Sea such as capelin, herring, cod, haddock, red fish and polar cod (Lund, 1981; Panasenko, 1984; Mehl, 1989; Ajiad and Pushchaeva, 1991; Skjoldal and Hassel, 1991; Dalpadado, 1993). Krill are major prey of planktivorous capelin and can constitute most of the diet of 13-16 cm size group (Lund, 1981, Hassel *et al.*, 1991). The biomass of the 2 year and older capelin stock decreased drastically from about 2.6 million tons in 1983 to 0.7 million tons in 1985, and 0.02 million tons in 1987 (Gjøsæter, 1992). Skjoldal *et al.* (1992) indicate that after the sharp decline of the capelin stock from 1984 to 1986 there was an increase in large forms of zooplankton such as krill and amphipods and this again led to high individual growth rate and rapid recovery of the capelin stock up to 1990.

This study is an extension of the work of Dalpadado and Skjoldal (1991) on the distribution and life history of krill from the Barents Sea. In addition to studying the distribution, growth and life cycles of the two dominant krill species *T. inermis* and *T. longicaudata*, we have examined the predator-prey interactions between capelin and krill during the study period.

MATERIALS AND METHODS

The present study is based on samples of krill collected during several cruises to the Barents Sea from 1984 to 1992 (Fig. 1). The sampling area ranged from 73 ⁰N to 78 ⁰N and from 10 ⁰E to 45 ⁰E. Material from 18 cruises are included in the current investigation. Some of the data on krill from 1984-1989 (from 6 cruises) are extracted from Dalpadado and Skjoldal (1991).

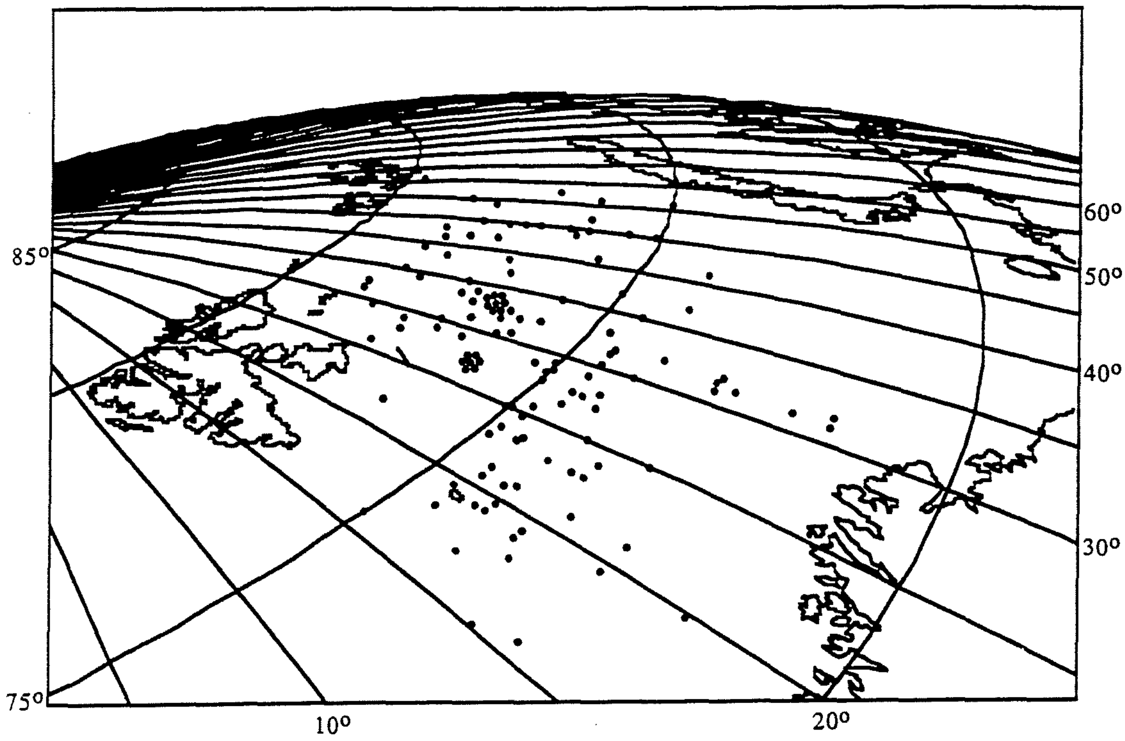


Figure 1. Locations of MOCNESS stations in the Barents Sea, from 1984 to 1992.

Figur 1. MOCNESS stasjoner i Barentshavet fra 1984 til 1992.

A MOCNESS sampler (Wiebe *et al.* 1985) with a 1m^2 mouth opening was used to collect the material for the present study. The towing speed of the boat was approximately 1.5 knots. The MOCNESS sampler was equipped with 9 nets made of 333 µm nylon mesh netting (dark blue). It was fished obliquely, allowing up to eight strata to be sampled. The volume of the water filtered in each stratum varied usually from 100 to 600 m^3.

The samples obtained from MOCNESS were used to determine the abundance and size distribution of krill. Samples were preserved in 4% formalin. Krill were identified to species and the number in each sample or sub-sample was recorded. Sub-samples were obtained by using a Motoda plankton splitter. The carapace length of krill (from the base of the eye-stalk to the posterior lateral edge of the carapace) was measured to the nearest mm below (Mauchline, 1980). For *T. raschii* and *M. norvegica* total length (from the tip of the rostrum to tip of telson) was recorded in addition to carapace length because the catch of these two species were too low to obtain any reliable relationship between the carapace and the total length. For *T. inermis* and *T. longicaudata* the carapace length (CL) was converted to total length (TL) by using the following regression equations:

For *T. inermis*
CL = 0.352 TL -1.092 (n=166,TL range = 9-29 mm, r^2=0.92) (from Dalpadado and Skjoldal, 1991)

For *T. longicaudata*
CL = 0.261TL - 0.198 (n= 303, TL range =6-15 mm, r^2 = 0.856)

The regressions given below describe the relationships between total length (TL) and dry body weight (DW). These regressions and information on mean lengths were used to convert data on numerical abundance to biomass.

For *T. inermis*
log WW= 3.33 log TL-2.58
DW =0.335 WW-1.256 (n=19, r^2=0.994.)

For *T. longicaudata*
DW=0.7 TL-5.8 (n=18, TL range = 10-21 mm, r^2=0.96)

The data on abundance (individuals m^{-2}), biomass (mg m^{-2}) and density (individuals m^{-3}) of krill estimated in a MOCNESS profile were classified into data from Arctic, Atlantic and Polar Front regions by using the description of water masses given by Loeng (1989, 1991).

Length frequency histograms for pooled data from each cruise were resolved into normally distributed components (Cohorts) using Bhattacharya´s 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 over the life span of the krill. The allocation of cohorts (year classes) was according to the description given by Dalpadado and Skjoldal (1991). Growth equations were fitted using the von Bertalanffy growth function (VBGF) modified for seasonal oscillations (Somers, 1988) using the Macintosh version of the SYSTAT module NONLIN.

RESULTS

Geographical distribution and abundance

The horizontal distribution of the two dominant krill species *T. inermis* and *T. longicaudata* are shown in Figs. 2 and 3 as the average abundance during the study period, from 1984 to 1992. The abundance and geographical distribution from individual cruises during the study period are given in Appendix figs. 1a-p and 2a-p respectively and mean abundance and biomass in Table 1 for the two species.

Of the 18 cruises investigated, only five (September/October 1992, September 1988, September/October 1990, August 1985 and 1984) covered the Arctic waters of the Barents Sea. The rest of the cruises were limited to the Atlantic and Polar Front regions. Very few krill were observed in the Arctic waters (Figs. 2, 3 and Table 1) indicating that none of the krill species found in the Barents Sea are real Arctic

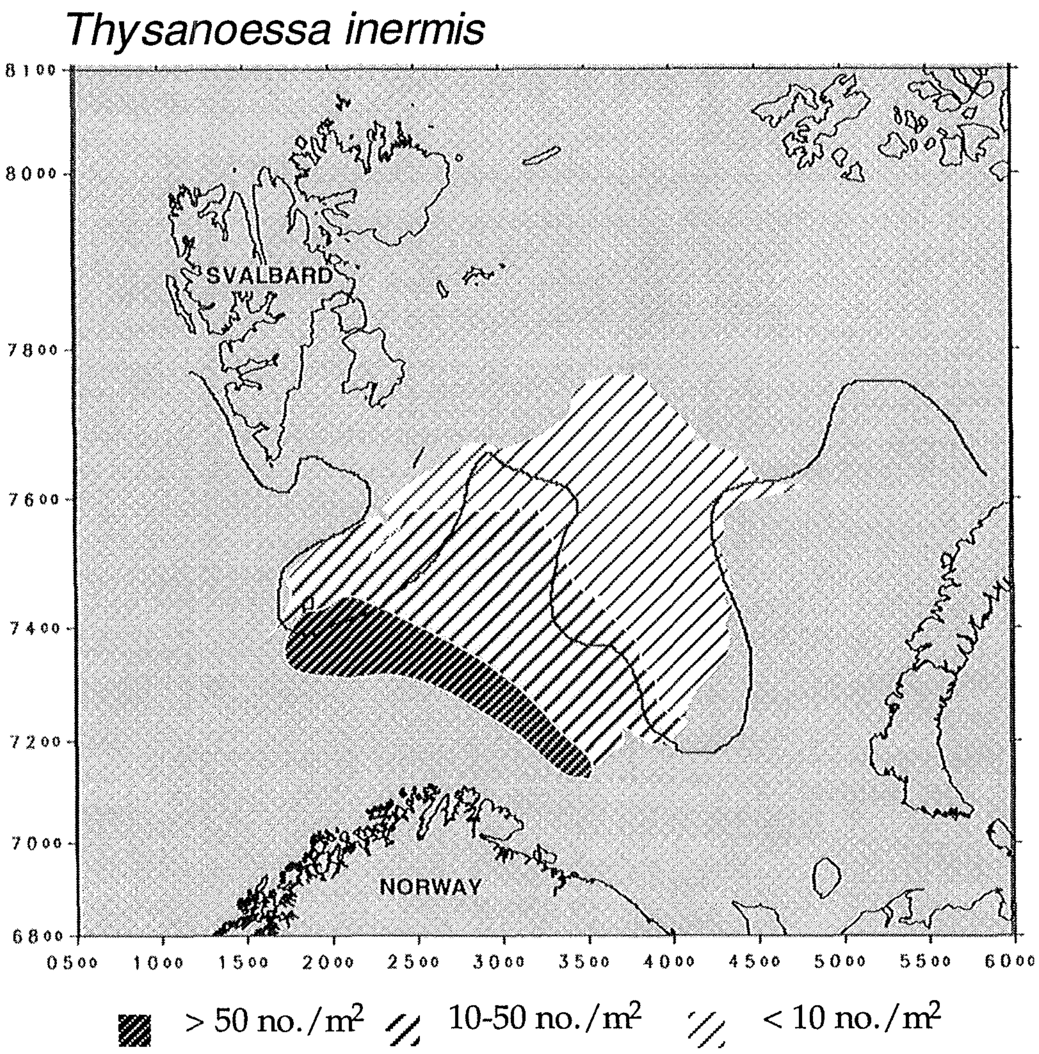


Figure 2. *Thysanoessa inermis*. Horizontal distribution in the Barents Sea, based on average numerical abundance (no. m^{-2}) from all cruises, 1984 -1992. The solid line indicates the Polar Front. Note that samples were not obtained outside the hatched areas, and the figure therefore does not show the total distribution area in the Barents Sea.

Figur 2. *Thysanoessa inermis*. Horisontalfordeling i Barentshavet. Gjennomsnittlig antall m^{-2} for alle tokt, 1984 - 1992. Heltrukket linje viser polarfronten. Merk at prøvene ikke ble tatt utenfor de skraverte områdene. Figuren viser således ikke den totale utbredelsen i Barentshavet.

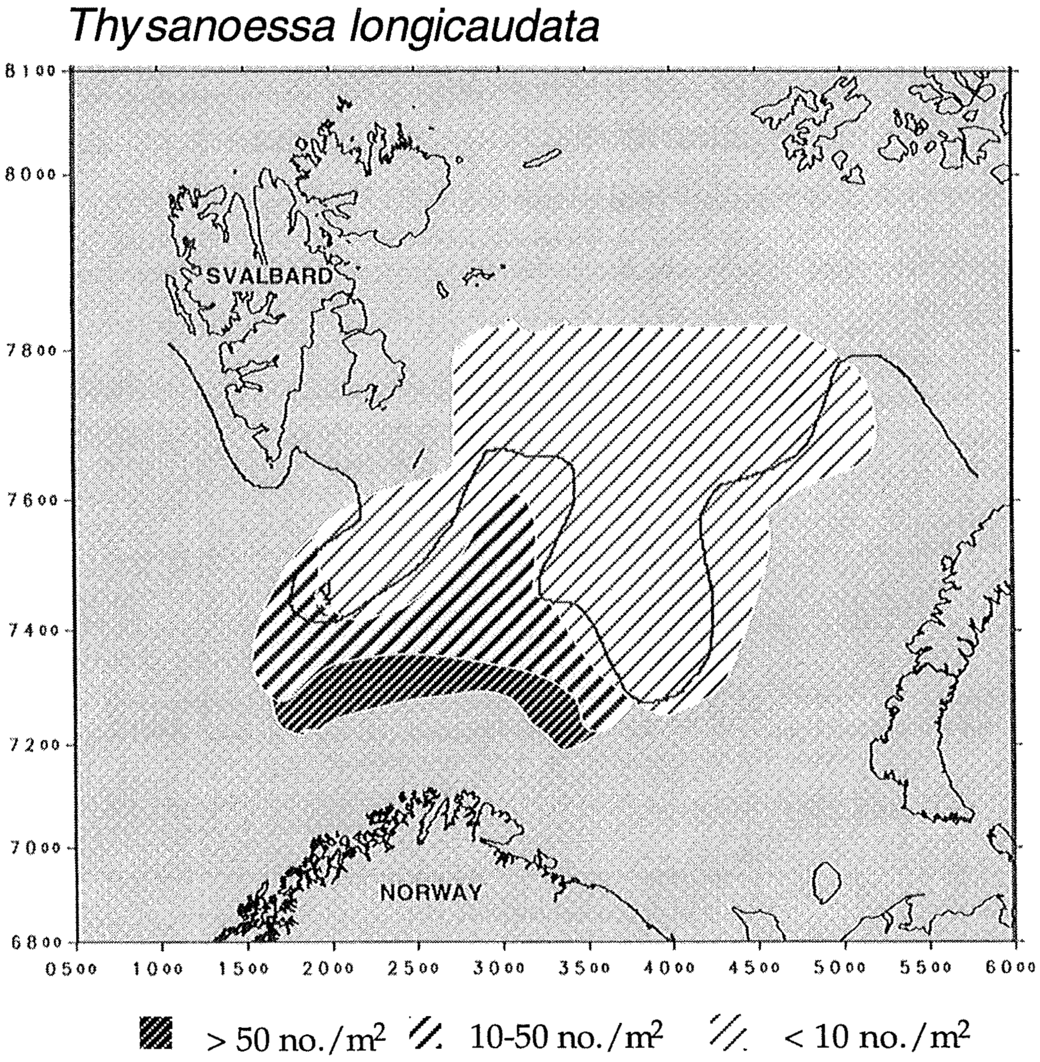


Figure 3. *Thysanoessa longicaudata*. Horizontal distribution in the Barents Sea, based on average numerical abundance (no. m^{-2}) from all cruises, 1984 -1992. The solid line indicates the Polar Front. Note that samples were not obtained outside the hatched areas, and the figure therefore does not show the total distribution area in the Barents Sea.

Figur 3. *Thysanoessa longicaudata*. Horisontalfordeling i Barentshavet. Gjennomsnittlig antall m^{-2} for alle tokt, 1984 - 1992. Heltrukket linje viser polarfronten. Merk at prøvene ikke ble tatt utenfor de skraverte områdene. Figuren viser således ikke den totale utbredelsen i Barentshavet.

Table 1. *Thysanoessa inermis* and *T. longicaudata*. Means and ranges of numerical abundance (number of individuals m-2), length (mm) and biomass (mg m-2) observed during different cruises from 1984 - 1992 in Atlantic/Polar Front and Arctic water masses.

Tabell 1. *Thysanoessa inermis* and *T. longicaudata*. Middelverdier og variasjonsbredde for antall individer m-2 og lengde (mm) observert under ulike tokt fra 1984 - 1992 i atlantiske/polarfront og arktiske vannmasser.

Cruise	No. of	Abundance		Length		Biomass	
	stations	(No m-2)		(mm)		(Mg m-2)	
Atlantic /P. F.							
T.inermis		mean	range	mean	range	mean	range
June 84	6	2,8	0,0-9,2	ca, 18		33,7	0,0-111,5
Jan.85	7	23,1	0,9-62,5	12,9	8,0-25,0	71,6	3,9-231,3
Aug. 85	8	1,9	0,0-7,5	15,9	8,0-27,0	26,6	0,0-124,8
Apr. 86	4	10,8	2,8-25,1	13,1	8,0-25,0	37,0	7,7-76,8
May 86	2	7,7	1,5-13,9	14,6	10,0-22,0	46,8	6,8-86,7
Jan.-Mar. 87	6	36,1	6,8-114,5	12,0	8,0-25,0	168,1	6,9-819,9
May-June 87	9	16,6	1,5-60,3	16,8	8,5-27,0	152,2	12,8-432,3
March 88	6	59,1	3,4-207,2	14,9	8,0-25,8	620,2	9,1-2769,6
Oct. 88	5	32,8	0,0-152,3	14,0	8,0-29,0	569,9	0,0-2812,1
Jan.89	6	60,8	33,5-130,0	16,7	7,0-30,0	583,0	266,1-1279,0
May 89	3	45,8	8,0-117,8	17,5	11,0-27,0	1088,0	33,5-3134,2
Sep.-Oct. 90	3	10,5	5,4-13,1	12,2	8,2-22,7	42,7	0,6-105,9
Jan.-Feb. 91	3	37,7	14,3-72,4	12,6	7,9-29,2	114,2	33,4-228,7
May-Jun. 91	6	2,4	0,0-3,89	19,3	13,9-27,0	38,2	0,0-60,3
Sep. - Oct. 92	6	34,9	3,8-80,8	11,9	7,1-29,5	84,4	1,2-182,6
Sep. - Oct. 92	5	8,6	1,0-35,9	13,5	9,1-21,6	33,2	0,6-132,6
T. longicaudata							
June 84	6	1,9	0,0-4,5	ca, 10		2,2	0,0-5,4
Jan.85	7	4,1	0,0-14,4	11,4	6,5-15,0	8,9	0,0-29,4
Aug. 85	8	2,5	0,0-8,5	9,9	6,0-16,0	1,2	0,0-3,1
Apr. 86	4	1,6	0,6-3,4	11,8	8,0-16,0	3,8	1,8-8,8
May 86	2	2,6	0,7-4,4	11,4	9,0-14,0	5,6	1,6-9,6
Jan.-Mar. 87	6	18,9	3,7-56,1	9,4	6,0-14,0	12,7	2,4-35,8
May-June 87	9	27,4	3,2-13,1	10,6	7,3-16,2	51,2	3,4-170,3
March 88	6	42,3	3,5-100,2	9,2	4,0-15,0	44,2	0,06-113,3
Oct. 88	5	26,9	6,6-61,6	9,7	5,0-16,0	38,2	2,8-168,7
Jan.89	6	45,0	9,4-63,6	10,0	5,5-17,0	51,3	16,5-77,4
May 89	3	36,4	12,6-79,9	10,7	8,0-15,5	59,5	19,5-123,8
Sep.-Oct. 90	3	9,4	0,6-15,7	13,3	8,8-18,0	33,2	1,9-56,4
Jan.-Feb. 91	3	12,8	7,7-17,2	9,9	6,1-15,3	14,1	7,1-22,9
May-Jun. 91	6	3,9	1,0-7,08	12,4	9,5-16,5	11,8	2,9-21,4
Sep. - Oct. 92	6	11,4	0,0-33,7	11,3	5,3-18,8	11,5	0,1-26,7
Sep. - Oct. 92	5	12,6	0,0-61,0	11,9	6,1-18,0	22,1	0,0-88,1
Arctic							
T.inermis							
Aug. 84	21	0,3	0,0-3,7	18,7	13,0-22,8	3,6	0,0-26,8
Aug. 85	11	0,5	0,1-1,5	20,0	13,0-26,0	8,0	0,0-19,4
Sep. 88	3	0,3	0,0-0,9	21,0	17,0-25,0	6,2	0,0-18,6
Sep.- Oct. 90	3	0,7	0,0-2,0	14,8	13,0-17,0	3,8	0,0-11,4
Sep. - Oct. 92	5	2,0	0,0-6,7	17,7	6,2-28,4	17,8	0,8-49,2
Sep. - Oct. 92	5	0,7	0,0-2,5	12,7	10,5-14,9	1,7	0,0-5,8
T. longicaudata							
Aug. 84	21	0,4	0,0-2,6	13,6	5,5-16,2	1,7	0,0-10,9
Aug. 85	11	1,1	0,0-5,3	12,6	6,5-17,0	2,8	0,0-20,4
Sep. 88	3	1,5	0,6-2,4	14,5	11,0-17,0	6,2	3,4-10,9
Sep.- Oct. 90	3	1,5	0,0-4,1	13,7	12,0-19,9	8,1	0,0-23,6
Sep. - Oct. 92	5	1,9	0,0-5,0	14,8	8,8-19,9	7,3	0,0-19,8
Sep. - Oct. 92	5	0,5	0,0-1,3	14,2	8,0-15,0	37,8	0,0-114,7

species. Low abundances of *T. inermis* (mean 0.75, range 0.30-2.04 no m^{-2}) and *T. longicaudata* (mean 1.13, range 0.38-1.90 no m^{-2}) were found in the Arctic waters. *T. raschii* were very seldom encountered (mean 0.03, range 0.00-0.06 no m^{-2}) while *M. norvegica* were absent in these waters.

In contrast to Arctic waters the abundances in the Atlantic and Polar Front regions were quite high (Figs. 2, 3, Appendix figs. 1, 2 and Table 1). Based on all the 18 cruises in the area *T. inermis* was the most abundant krill species with an overall mean abundance of 24.5 no m^{-2}. *T. longicaudata* was the second most abundant, with a mean of 16 no m^{-2}. High abundances, up to 207 no m^{-2} for *T. inermis* and 100 no m^{-2} for *T. longicaudata* were found in cruises in March 1988, January and May 1989, May 1991 and in Sep/Oct. 1992 in the slope and adjoining deep waters (300-400m) south and south east of Bear Island (Bjørnøya) -Svalbard Bank (Svalbardbanken) and west of Central Bank (Sentralbanken). Abundances of krill in the Atlantic waters were usually higher than in Polar Front regions. *T. longicaudata* was most abundant in the western Barents Sea (Appendix figs 2j, k) indicating that it is more closely related to the Atlantic waters than *T. inermis*, though we found some few larger individuals (up to 20mm) in the colder Arctic waters (Fig.3). The abundance of both species were usually higher in winter than in other seasons.

M. norvegica is clearly not a cold water form and was represented only in south western Barents Sea. The highest abundances of *M. norvegica* recorded were in two stations taken in March and October 1988 at 73° 30´N, 19° 20´E, and at 73° 30´N 19° 50´ E (47.5 and 11.6 no m^{-2} respectively)). The abundance of *M. norvegica* otherwise was quite low (0.37 no m^{-2}). *T. raschii* was present in most cruises, but with low abundance (mean 1.08, range 0.012-3.80 no m^{-2}).

Density

Very low densities of krill, usually below 0.1 individuals m^{-3}, were observed in the Arctic waters. In the Atlantic and Polar Front regions, densities varied from 0- 0.62 individuals m^{-3} for *T. inermis* and 0-0.41 individuals m^{-3} for *T. longicaudata* (Table 2). Densities of *M. norvegica* and *T. raschii* were very low in the area investigated.

Figure 4 shows the numerical density of *T. inermis* and *T. longicaudata* plotted against depth in vertical profiles at the sampling stations. The highest densities of *T. inermis* were found in deeper areas at depths between 400 and 500 m, in the Atlantic/Polar Front regions. In the Arctic waters no clear trend was seen . A similar trend in depth distribution was also observed for *T. longicaudata.*

Vertical density distribution of *T. inermis* and *T. longicaudata* from individual stations from a selected cruise in March 1988 are given in Appendix figs. 3 and 4 respectively. The data from individual stations seem to indicate that, in general high densities and the largest krill during this cruise were taken at depths between 200 to 400 m. These stations were taken south and south east of Svalbard Bank in deep waters .

Table 2. Means and ranges of numerical density (No m-3) of krill observed during different cruises from 1984-1992 in Atlantic/Polar Front and Arctic water masses.

Tabell 2. Middelverdier og variasjons-bredde for tetthet (No. m-3) av krill observert under ulike tokt fra 1984 - 1992 i atlantiske/polarfront og arktiske vannmasser.

		T.inermis		*T. longicaudata*		*T. raschii*		*M. norvegica*	
Cruise	No. of stations	density (No m-3)		density (No m-3)		density (No m-3)		density (No m-3)	
Atlantic/P.F.		mean	range	mean	range	mean	range	mean	range
June 84	6	0.014	0,000-0,048	0.010	0,000-0,023	0.006	0,000-0,021	0	0
Jan. 85	7	0.117	0,003-0,289	0.027	0,00-0,061	0.013	0,00-0,040	0	0
Aug. 85	8	0.012	0,000-0,045	0.013	0,000-0,042	<0,001	0,000-0,003	0	0
April. 86	4	0.097	0,032-0,209	0.014	0,008-0,026	0.015	0,002-0,039	0	0
May 86	2	0.090	0,005-0,176	0.012	0,009-0,015	0.019	0,000-0,039	<0,001	0,000-0,001
Jan.-Mar. 87	6	0.121	0,017-0,388	0.066	0,010-0,190	0.005	0,000-0,020	0.001	0,000-0,005
May-June 87	9	0.082	0,016-0,264	0.113	0,025-0,322	0.005	0,000-0,016	0	0
March 88	6	0.165	0,014-0,512	0.121	0,015-0,255	0.002	0,000-0,006	0.024	0,000-0,118
Oct. 88	5	0.110	0,000-0,506	0.111	0,059-0,205	0.002	0,000-0,005	0.009	0,000-0,039
Jan. 89	6	0.191	0,030-0,404	0.177	0,030-0,259	0.002	0,000-0,007	0.036	0,001-0,125
May 89	3	0.224	0,029-0,614	0.169	0,032-0,416	0.019	0,000-0,054	0	0
Sep.- Oct. 90	3	0.039	0,022-0,056	0.033	0,002-0,051	0.002	0,000-0,006	0.002	0,000-0,005
Jan. - Feb. 91	3	0.142	0,076-0,264	0.050	0,041-0,063	0.007	0,001-0,019	0	0
May -Jun. 91	6	0.007	0,000-0,012	0.012	0,006-0,017	<0,001	0,000-0,005	0.001	0,000-0,005
Sep. - Oct. 92	6	0.113	0,023-0,195	0.041	0,004-0,092	0.002	0,000-0,006	0.01	0,000-0,031
Sep. - Oct. 92	5	0.026	0,008-0,080	0.031	0,000-0,150	0.002	0,000-0,008	0.001	0,000-0,004
Arctic									
Aug. 84	21	0.001	0,000-0,004	0.002	0,000-0,015	<0,001	0,00-0,002	0	0
Aug. 85	11	0.003	0,000-0,014	0.013	0,000-0,095	<0,001		0	0
Sep. 88	3	0.001	0,000-0,004	0.006	0,003-0,010	0	0	0	0
Sep. - Oct. 90	3	0.005	0,000-0,014	0.007	0,000-0,021	0	0	0	0
Sep. - Oct. 92	5	0.014	0,000-0,044	0.014	0,000-0,045	<0,001		0	0
Sep. - Oct. 92	5	0.002	0,000-0,007	0.003	0,000-0,008	0	0	0	0

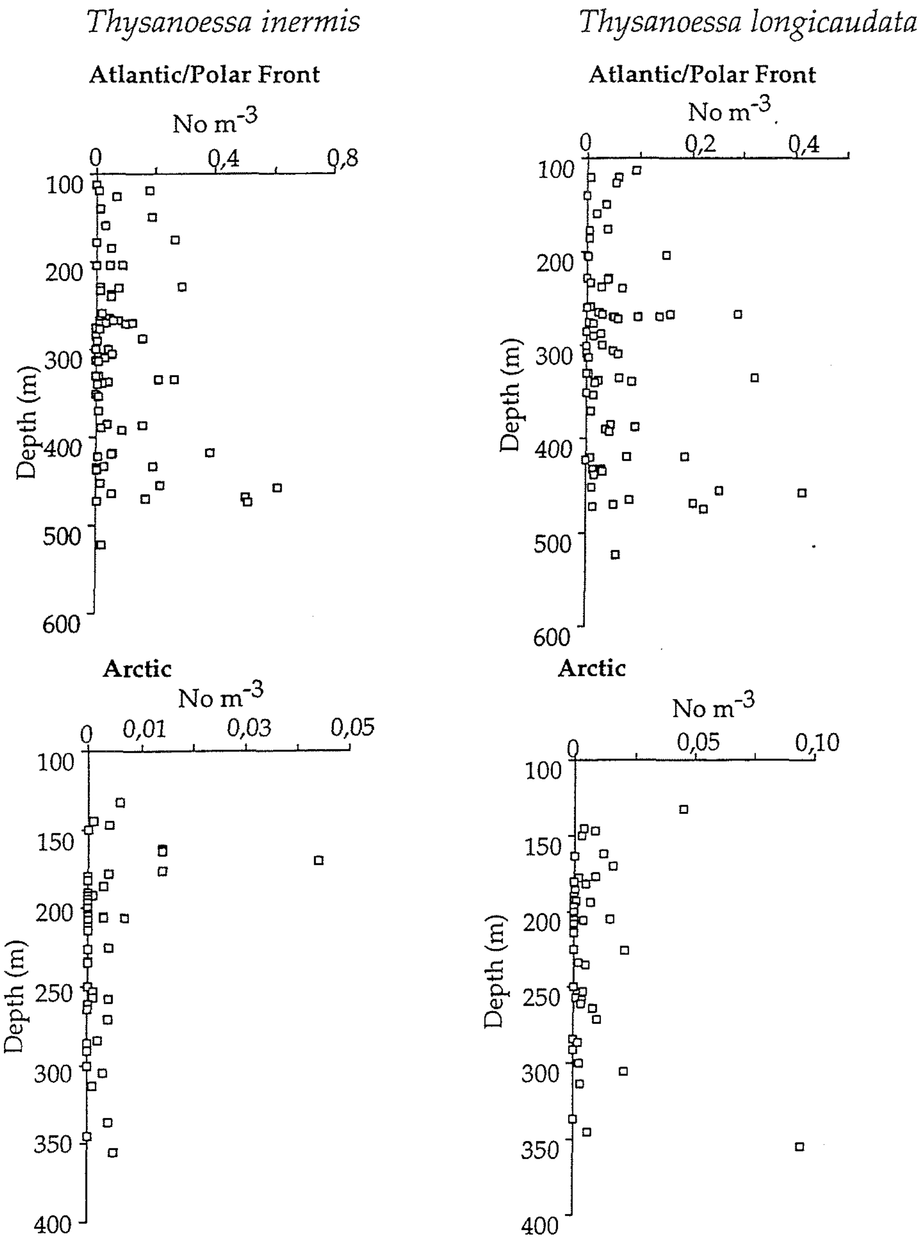


Figure 4. *Thysanoessa inermis* and *T. longicaudata*. Numerical density (individuals m^{-3}) in relation to depth in verticle profiles at sampling stations in Atlantic /Polar Front and Arctic water masses.

Figur 4. *Thysanoessa inermis* og *T. longicaudata*. Tetthet (antall m^{-3}) i relasjon til dyp på stasjonene i atlantiske/polarfront og Arktiske vannmasser.

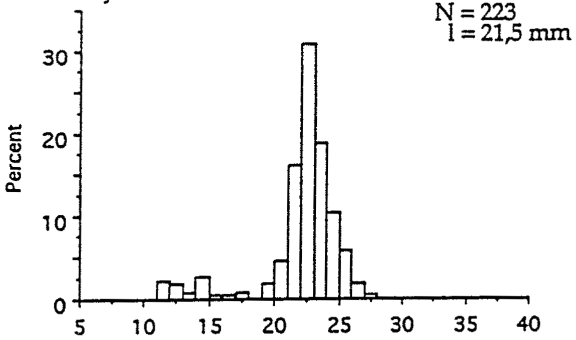
Growth and life span

Length frequency histograms for *T. inermis*, *T. longicaudata*, *T. raschii* and *M. norvegica* are given in Figs. 5-8. Total length of the most abundant species *T. inermis* varied from 5-35 mm, with few individuals above 30 mm. *T. longicaudata*, the smallest of all krill species in the Barents Sea ranged from 4 to 20 mm. Large individuals of this species (15- 20mm) was found mostly in the Arctic water masses. Size range of *T. raschii* varied from 7 to 26 mm and of *M. norvegica* from 9 to 41 mm, in the present study.

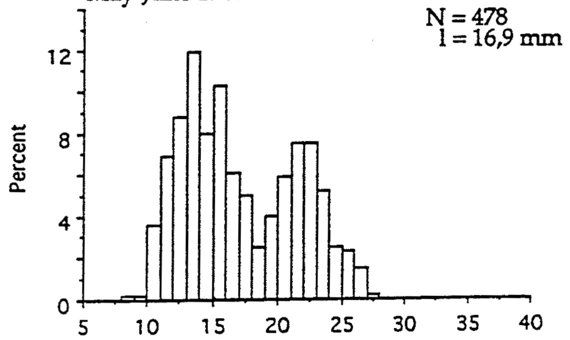
Thysanoessa inermis

Atlantic/Polar Front

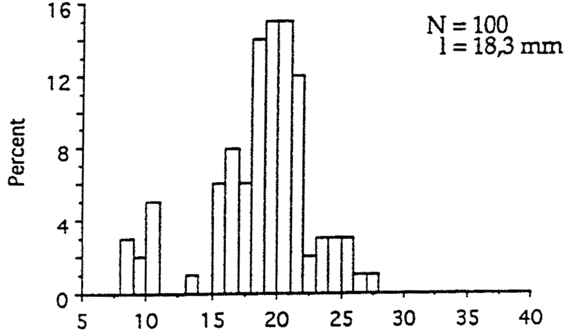
May 1989



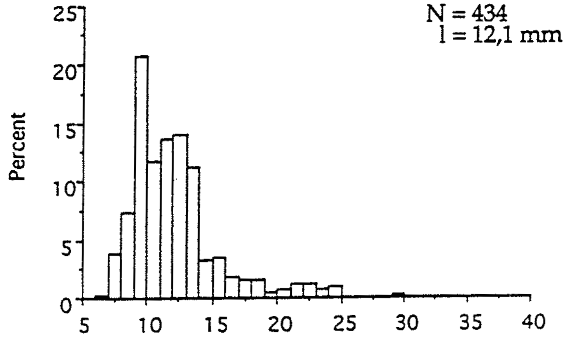
May-June 1987



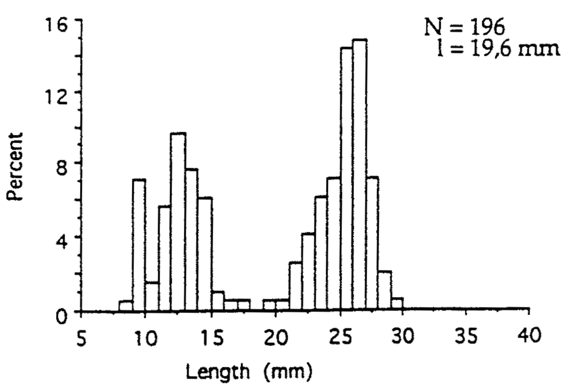
August 1985



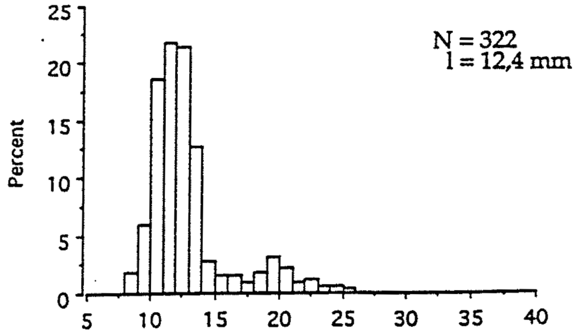
September/October 1992



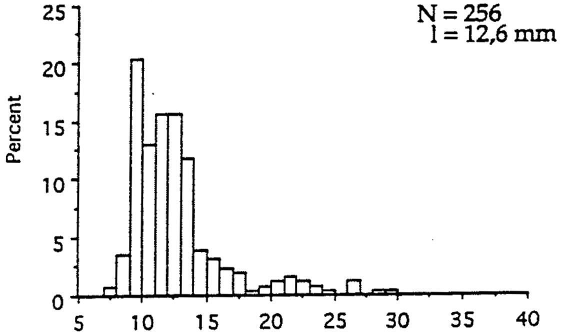
October 1988



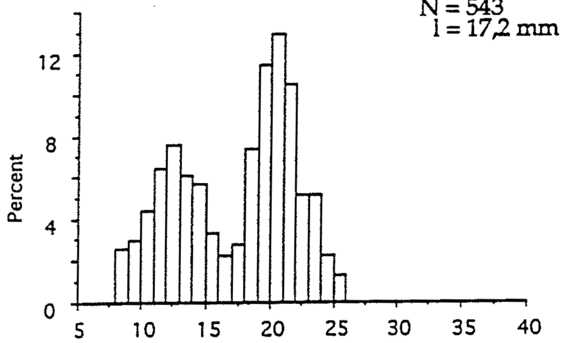
January 1985



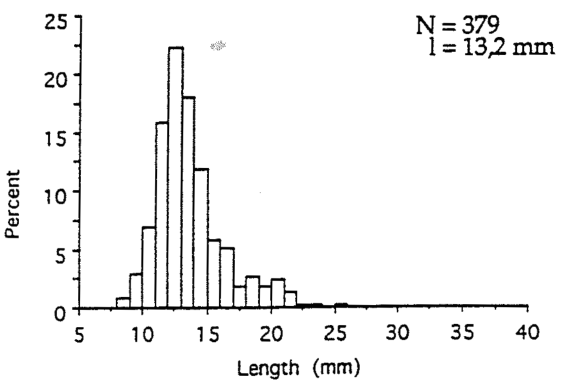
January/February 1991

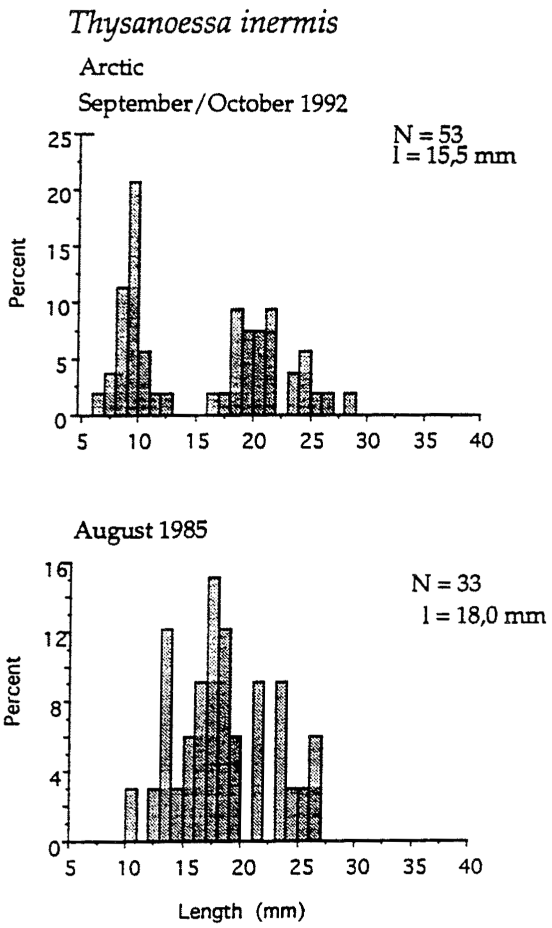


March 1988



April 1986





Thysanoessa inermis

Arctic

September/October 1992

August 1985

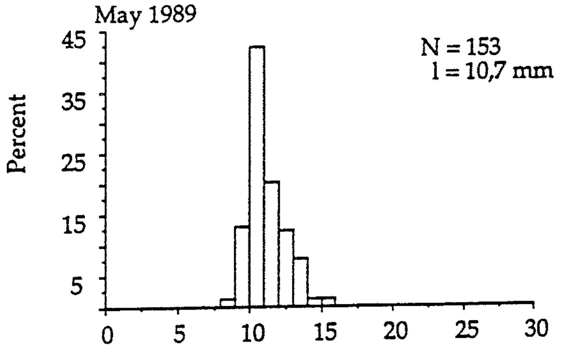
Figure 5. *Thysanoessa inermis*. Length frequency histograms from different cruises from 1984-1992. Open bars, Atlantic and Polar Front region; filled bars, Arctic waters. N = number of individuals, l = mean length.

Figur 5. *Thysanoessa inermis*. Lengde-frekvens histogrammer for ulike tokter fra 1984 - 1992. Åpne søyler, Atlantisk vann og polarfront , fylte søyler, Arktisk vann. N=antall individer. l=middel-lengde.

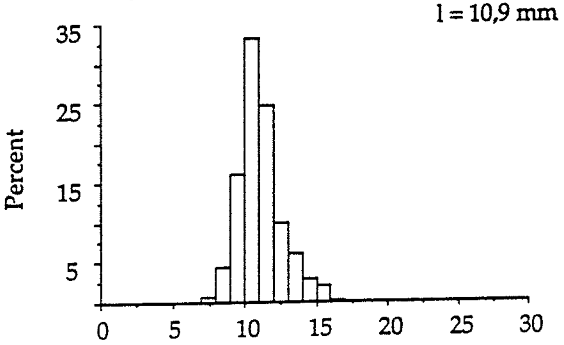
Thysanoessa longicaudata

Atlantic/Polar Front

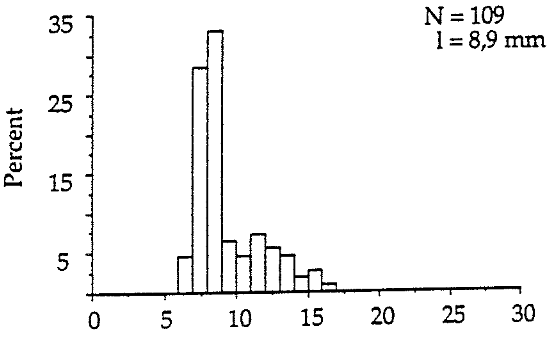
May 1989



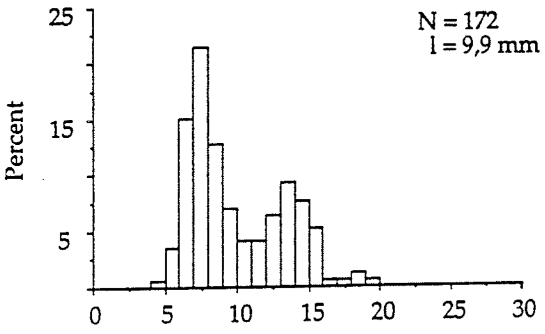
May/June 1987



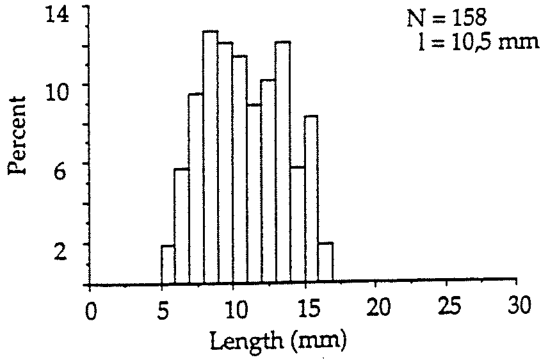
August 1985



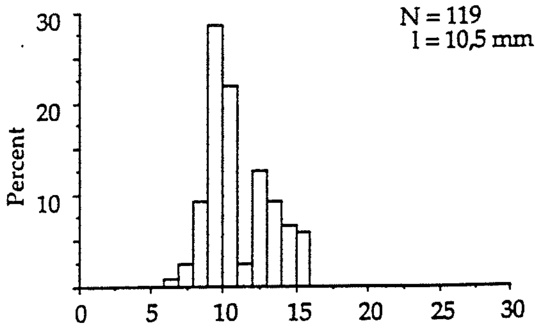
September/October 1992



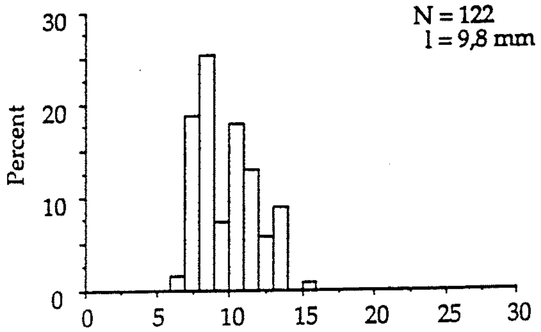
October 1988



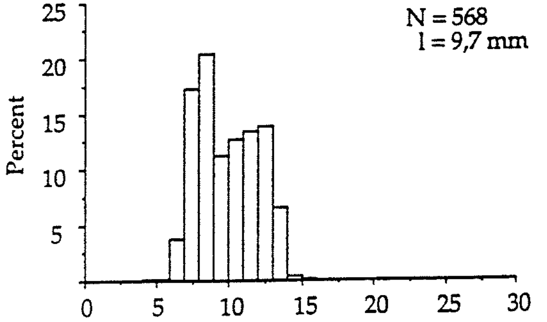
January 1985



January/February 1991



March 1988



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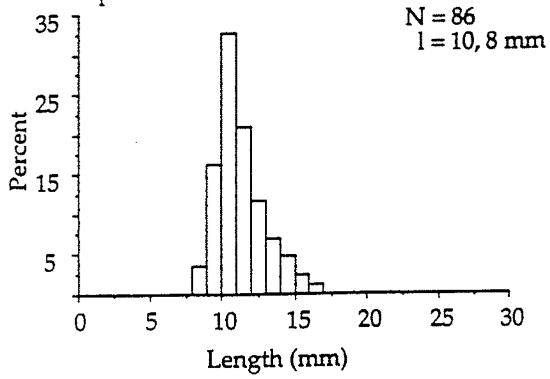


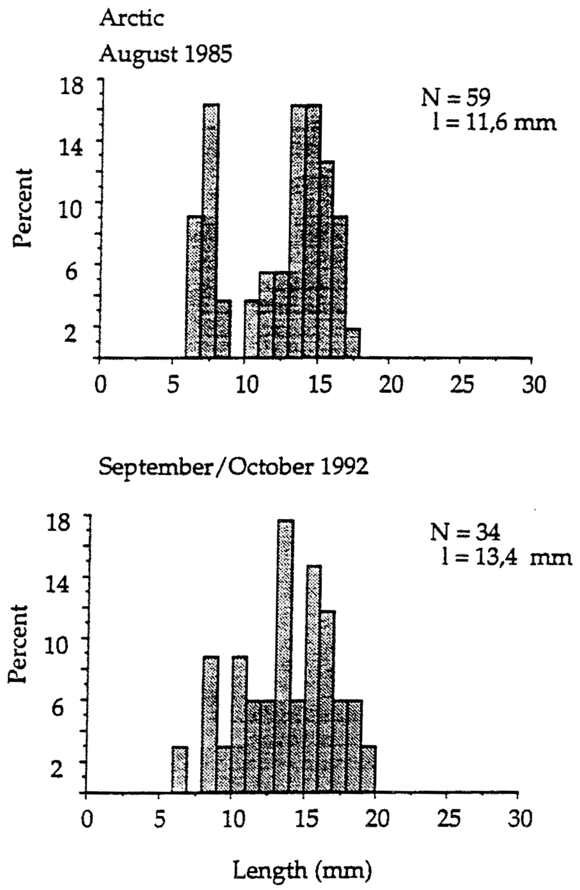


Figure 6. *Thysanoessa longicaudata.* Length frequency histograms from different cruises from 1984-1992. Open bars, Atlantic and Polar Front region; filled bars, Arctic waters. N = number of individuals, l = mean length.

Figur 6. *Thysanoessa longicaudata.* Lengde-frekvens histogrammer for ulike tokter fra 1984 - 1992. Åpne søyler, Atlantisk vann og polarfront , fylte søyler, Arktisk vann. N=antall individer. l=middel-lengde.

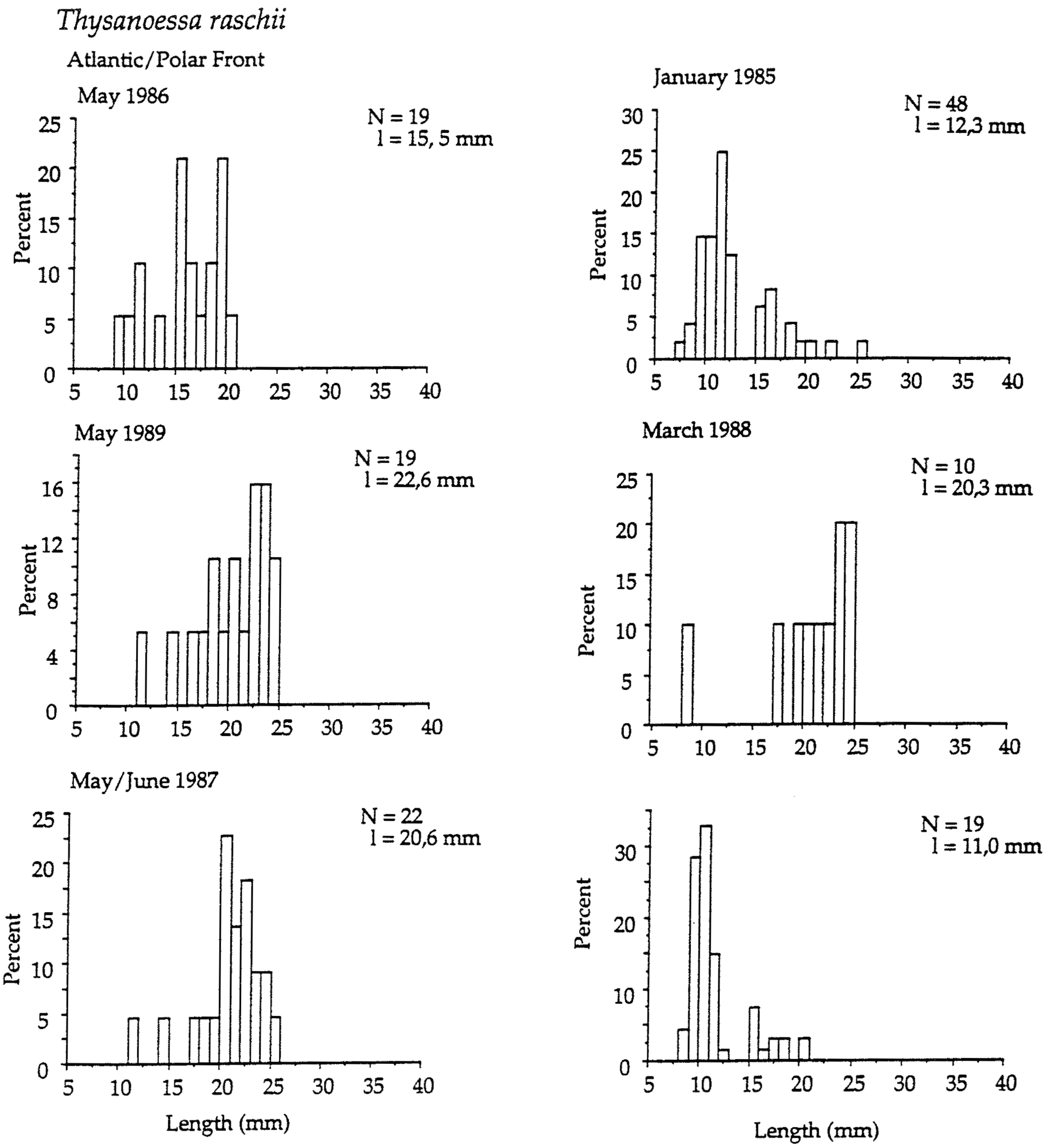


Figure 7. *Thysanoessa raschii.* Length frequency histograms from different cruises from 1984-1992. N = number of individuals, l = mean length.

Figur 7. *Thysanoessa raschii.* Lengde-frekvens histogrammer for ulike tokter fra 1984 - 1992. N=antall individer. l=middel-lengde.

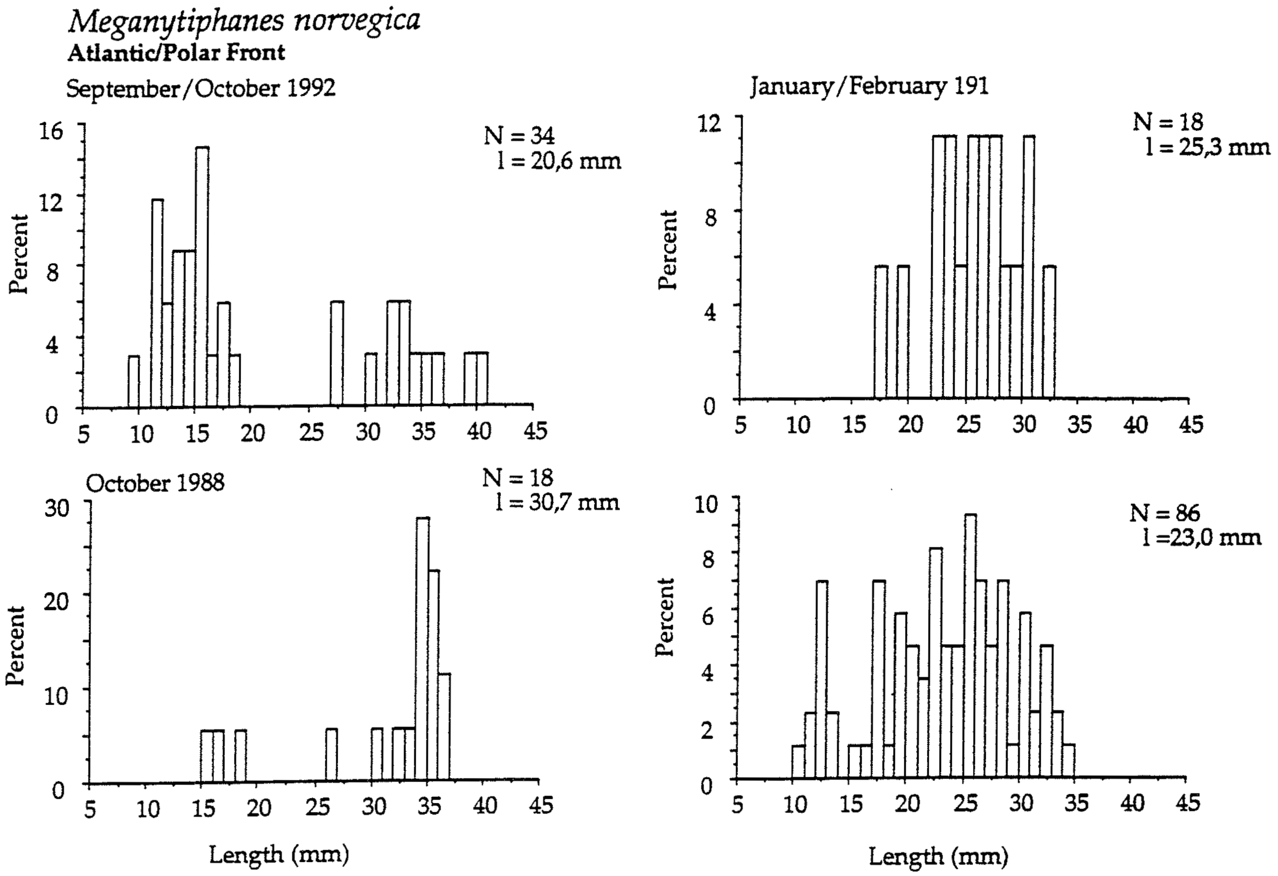


Figure 8. *Meganyctiphanes norvegica.* Length frequency histograms from different cruises from 1984-1992. N = number of individuals, l = mean length.

Figur 8. *Meganyctiphanes norvegica.* Lengde-frekvens histogrammer for ulike tokter fra 1984 - 1992. N=antall individer. l=middel-lengde.

Length frequency distributions for *T. inermis* and *T. longicaudata* from Atlantic and Polar Front regions were resolved into normal distribution components using Bhattacharya´s analysis. Statistical splitting of length frequency distributions usually gave 3 or 4 cohorts for *T. inermis* and 1 or 2 for *T. longicaudata* (Appendix tables 1 and 2). The 0-group of *T. inermis* had a mean length of 10.45 mm (range 8.2-12.8), 1 group 13.9 mm (range 11.6-18.7) , 2 group 18.5 mm (range 15.6 to 21) and 3 group 22.7 mm (19.7- 25.6 mm). For *T. longicaudata* the mean length was 9.3 mm (range 8.0-11.1) for the first mode and 12.8 mm (range 10.7-15.1) for the second mode. On two occasions (cruises in Sep./Oct. 92, and August 1985) a third cohort (mean 17.2 mm, range 15.8-18.5 mm) with few individuals were observed.

The seasonal variation in mean length of cohorts of *T. inermis* and *T. longicaudata* are shown in Fig. 9. The main growth of *T. inermis* seem to occur from about February to August, whereas for *T. longicaudata* the growth period extended until

October. A marked negative growth was apparent in *T. inermis* from August to February. A clear negative growth was seen also for *T. longicaudata,* in the mid-winter period.

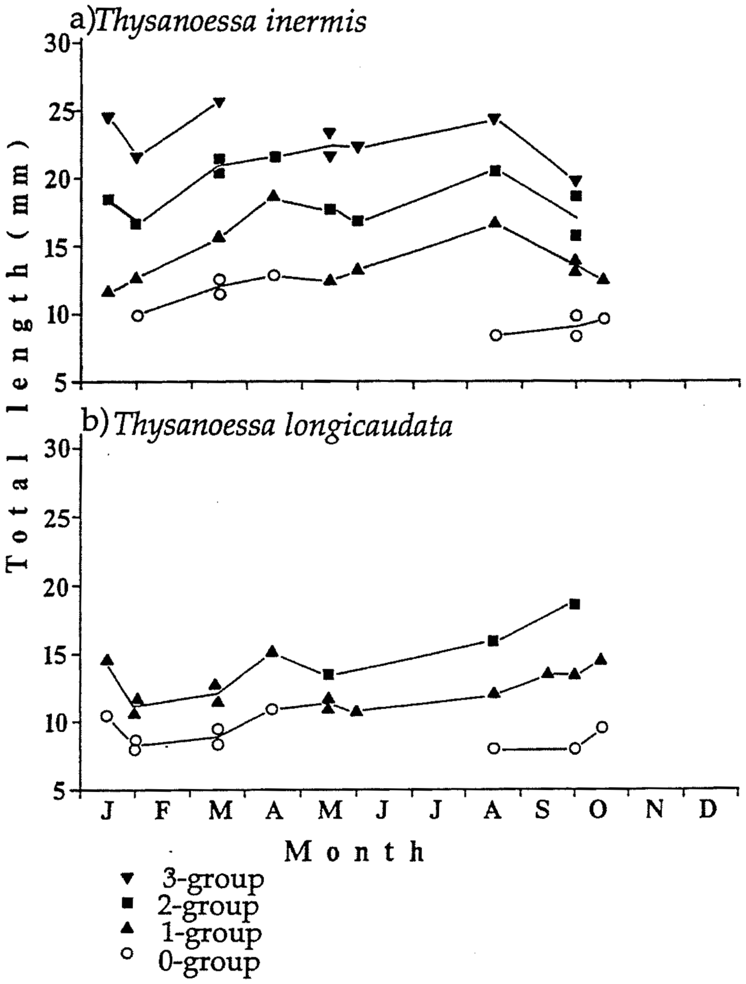
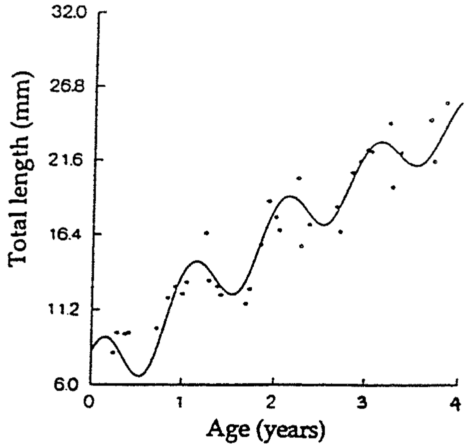


Figure 9. *Thysanoessa inermis* and *T. longicaudata*. Seasonal variation in mean length of individual cohorts separated in length frequency analysis. The identified cohorts have been ascribed as age groups.

Figur 9. *Thysanoessa inermis* og *T. longicaudata*. Sesongvariasjoner i middellengde av de enkelte kohorter separert i lengdefrekvens-analyser. De identifiserte kohortene er allokert til aldersgrupper.

The seasonalized version of VBGF was fitted to the growth data. The resulting growth curves are shown in Fig. 10 and the parameter values are given in Table 3. The seasonalized version gave reasonably good fit (corrected $r^2 = 0.92$ for *T. inermis* and 0.85 for *T. longicaudata*). The t_s values are quite similar for the two species whereas the amplitude of the growth oscillations was much higher for *T. inermis* ($C = 2.8$) than for*T. longicaudata* ($C = 1.5$).

a) *Thysanoessa inermis*



b) *Thysanoessa longicaudata*

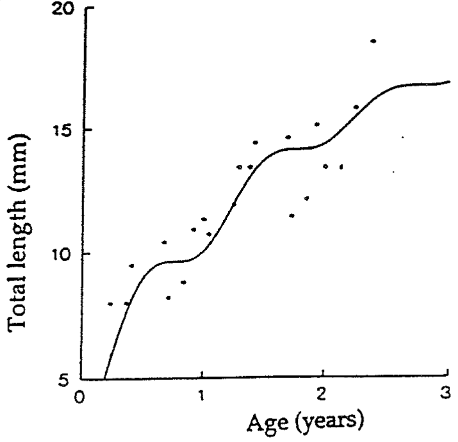


Figure 10. *Thysanoessa inermis* and *T. longicaudata*. Growth data fitted with seasonalized version of von Bertalanffy growth curve.

Figur 10. *Thysanoessa inermis* og *T. longicaudata*. Vekstdata tilpasset von Bertalanffys vekstkurve med sesongmessige svingninger.

Table 3. Parameters of von Bertalanffy growth function (VBGF) with seasonal oscillations. L_∞ = asymptotic length, K = growth constant, t_s = starting point of oscillation with respect to time t, t_0 = origin of the growth curve, C = amplitude of growth oscillation

Tabell 3. Parametre fra von Bertalanffy vekstfunksjon (VBGF) med sesongmessige svingninger. L_∞ = asymptotisk lengde, K = vekstkonstant, t_s = startpunkt for svingninger med hensyn på tid t, t_0 = utgangspunkt for vekstkurven, C = amplitude for vekstsvingninger.

Parameter	*T. inermis*	*T. longicaudata*
r2	0.93	0.85
L_∞	45.00	20.11
K	0.16	0.56
t_s	0.88	1.09
t_0	- 0.41	-0.27
C	2.80	1.47

Krill abundance, biomass and growth in relation to capelin stock size

The mean biomass of *T. inermis* and *T. longicaudata* observed in each year from 1984 to 1992 are shown in Fig. 11 together with the stock size of capelin, 2 years and older. The capelin stock collapsed from 1984 to very low levels in 1986. There was a subsequent strong increase in the abundance and biomass of both krill species (Table 1 and Fig. 11) with an earlier increase for *T. longicaudata* with the shortest life span. The capelin stock recovered rapidly after 1989 to a very high stock level in 1991. At the same time there was a marked decrease in abundance and biomass, most pronounced for *T. inermis* .

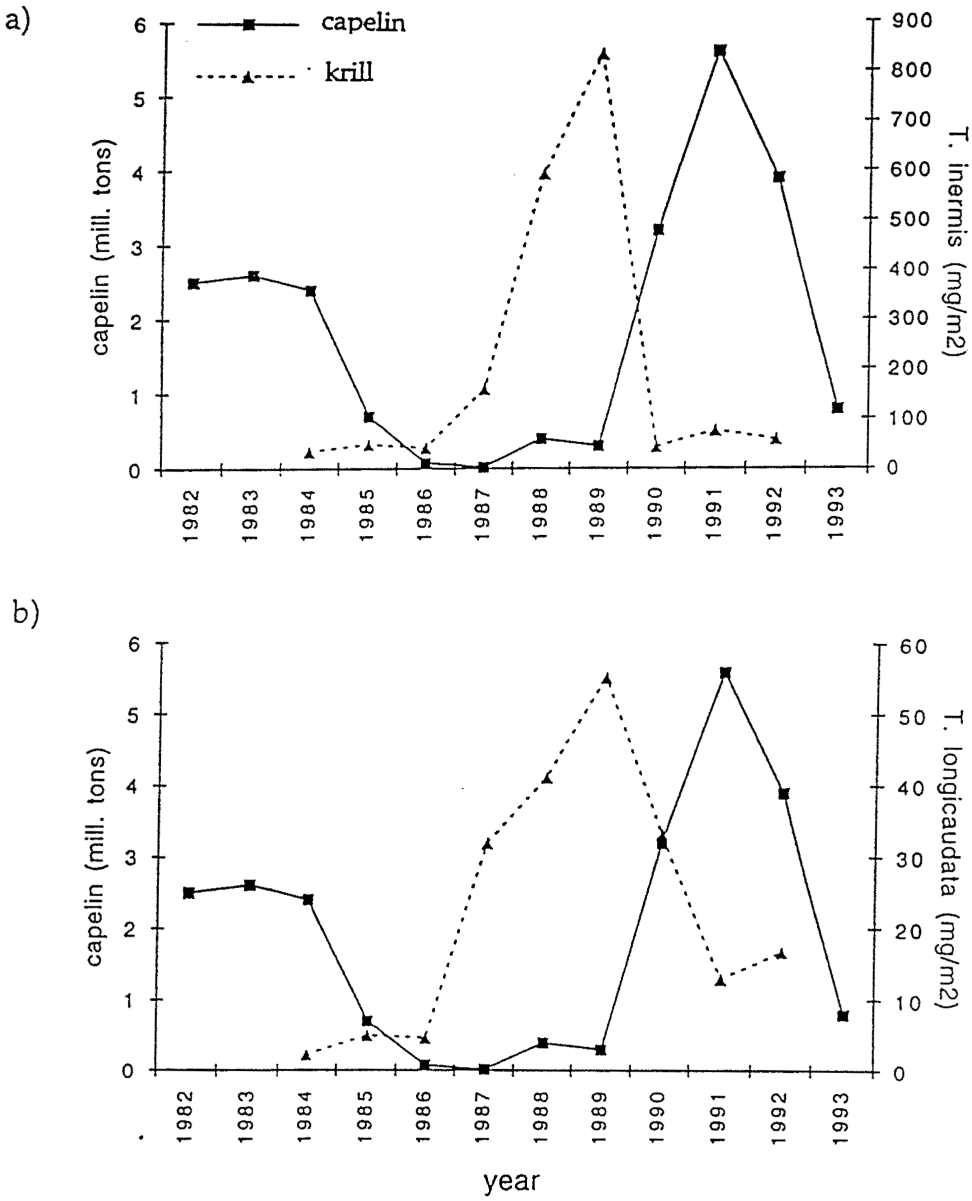


Figure 11. *Thysanoessa inermis* a) and *T. longicaudata b)*. Variation in biomass (mg dry weight m^{-2}) of krill and the stock size of two year and older capelin (million tons) from 1982-1992

Figur 11. *Thysanoessa inermis* a) og *T. longicaudata b)*. Variasjon i biomasse (mg tørrvekt m^{-2}) av krill og bestandstørrelse (millioner tonn) av lodde (to- åringer og eldre) fra 1982-1992.

Length frequency distributions for *T. inermis* and *T. longicaudata* are presented in Fig. 12 for three time periods; 1984-1986 when capelin stock size was decreasing, 1987- 1989 when the stock was at lowest levels and during 1990-1992 when the stock was very high. During 1987-89, when capelin stock was very low, larger (> 20mm) and old age groups (3 and 4 years) of *T. inermis* were present, probably due to reduced grazing pressure from capelin (Fig. 12). During periods with heavy predation a higher proportion of smaller individuals was observed. The mean length of *T. longicaudata* did not vary much during the different periods.

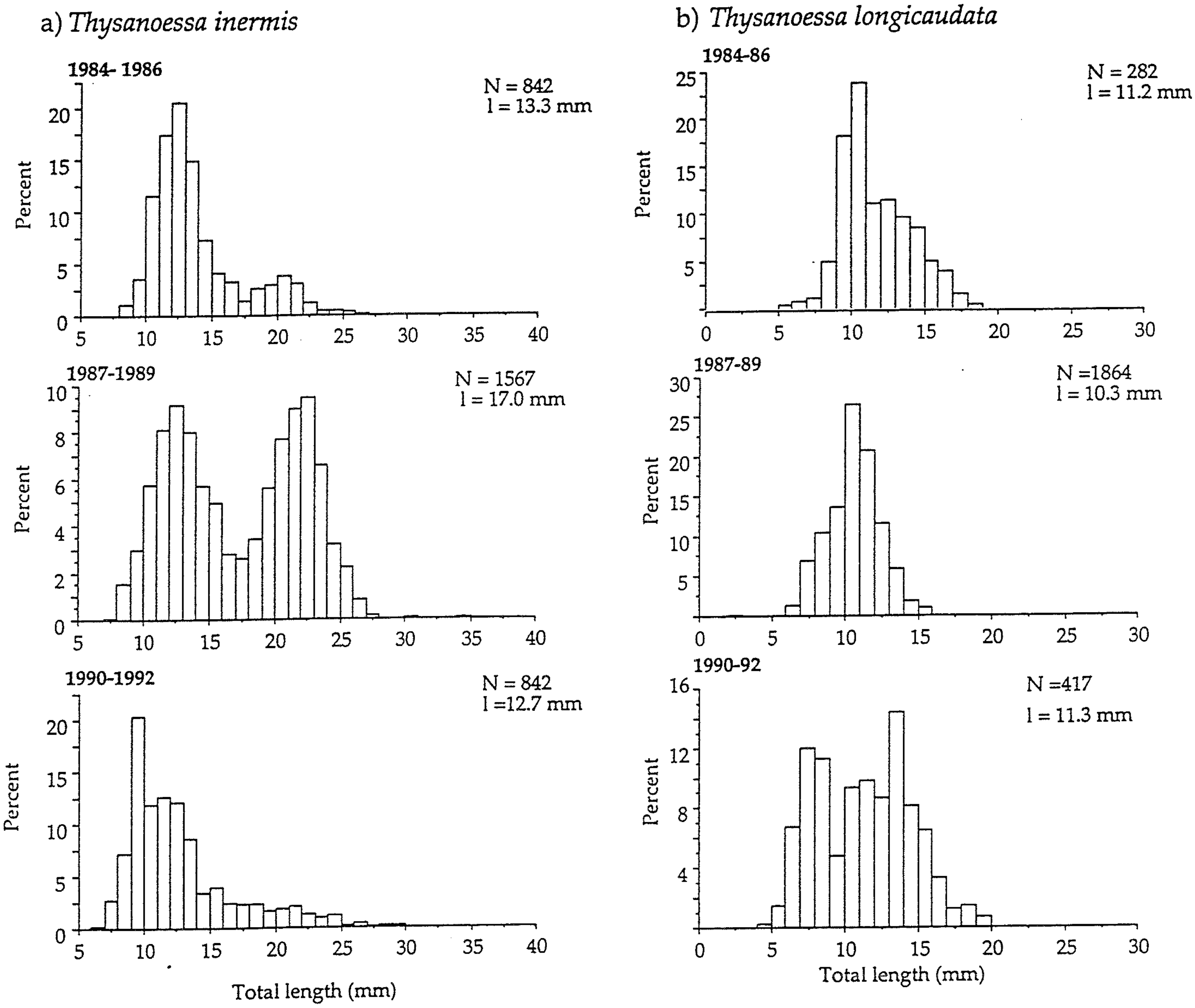


Figure 12. *Thysanoessa inermis* a) and *T.longicaudata b).* Length-frequency histograms for different time periods.

Figur 12. *Thysanoessa inermis* a) og *T.longicaudata b).* Lengde - frekvens histogrammer for forskjellige tidsperioder.

DISCUSSION

In the current study, the amount of krill caught at night was usually higher than at daytime, especially in autumn (September-October) and in spring (March-April) cruises. Our investigations also show that the krill catches in summer were somewhat lower than in winter. The krill abundance might have been underestimated in the current study, though the extent of this is not clear. In our previous paper (Dalpadado and Skjoldal, 1991) we discuss some possible factors (visual avoidance of nets, towing speed and sampling range of MOCNESS) that could lead to underestimate the krill abundance.

Our observations on the geographical distribution of krill confirm earlier studies (Einarsson, 1945; Dunbar, 1964; Mauchline, 1980; Dalpadado and Skjoldal, 1991) that none of the krill species found in the Barents Sea are real Arctic species.

T. inermis and *T. longicaudata* were the most abundant krill species found in the investigated area (73-78 ^{0}N and 10-45 ^{0}E) covering Atlantic, Polar Front (region of mixed Arctic and Atlantic water), and Arctic waters. The largest of these two species, *T. inermis* (up to 35 mm), was the most abundant. The highest abundances (115-207 individuals m^{-2}) and densities (0.25-0.60 individuals m^{-3}) of this species were found in the slope and deep waters (300-500 m) south and south east of the Svalbard Bank. High concentrations, up to 2 individuals m^{-3}, of *T. inermis* have also been reported from the shallower areas around the Svalbard Bank (Drobysheva 1979; Drobysheva and Panasenko 1984; Timofeev 1988).

T. longicaudata was found at most stations where *T. inermis* was present, though with lower abundance. For *T. longicaudata* the highest abundances were recorded from the southwestern part of the Barents Sea (72-74 ^{0}N, 15-20 ^{0}E) indicating that this species is more closely related to Atlantic water than *T. inermis*. Drobysheva (1979) made similar observations on this species from the Barents Sea. Abundances of *T. inermis* and *T. longicaudata* were generally higher in winter (January-March) than in other seasons.

T. raschii was found in most stations in the investigated area but with very low abundances (1 no m^{-2}). Stations with most *T. raschii* were found in the eastern part (72-75^{0}N, 30-40^0 E) of the study area. Very low abundances (0.02 no m^{-2}) and densities (<0.001 no/m^3) were observed in the Arctic region.

No *M. norvegica* was found in Arctic waters indicating this species to be clearly an Atlantic water form. Dunbar (1964) reports this species to be widely spread in the Atlantic extending from the Mediterranean.

The study of Lofnes (1993) on the distribution of krill eggs and larvae from the western and central Barents Sea supports our observations on the distribution of adult krill. He found the highest abundances of eggs and larvae of *T. inermis* (mean 12500 no/m^2) and *T. longicaudata* (mean 1050 individuals m^{-2}) in the Atlantic water in May 1989. In the Polar Front region, the mean abundances were lower than in the Atlantic waters (4702 and 188 individuals m^{-2} respectively). Only eggs and larvae of *T. inermis* (average 520 individuals m^{-2}) were found in Arctic waters. His observations showed very low abundances of eggs and larvae of *T. raschii* and *M. norvegica* in the studied area.

Dalpadado and Skjoldal (1991) showed that both *T. inermis* and *T. longicaudata* reproduce successfully in the Barents Sea and that the reproductive cycles of these two species were very similar. Their study and that of Zelikman (1958) show that the main spawning season of these two species in the Barents Sea is from May to June. Maturity observations from this study confirm these findings. *M. norvegica* probably do not breed in subarctic waters (Dunbar 1964) and the main spawning of this species seems to occur out side the Barents Sea (Jones, 1968; Mauchline, 1980; Dalpadado and Skjoldal, 1991). The reproductive cycle of *T. raschii* is similar to *T. inermis* (Zelikman, 1958).

As the main spawning season of *T. inermis* and *T. longicaudata* is restricted to May and June, we assume that each length cohort represents a year class with a denoted change of age in spring. Our results indicate a three to four year life span for *T. inermis* and a two year one for *T. longicaudata* with maturation and first spawning occurring at an age of 2 years and 1 year , respectively, for the two species (Dalpadado and Skjoldal, 1991). Einarsson (1945) reported that in western Greenland waters *T. inermis* could live for 3 years. In more southerly waters, *T. inermis* has a life cycle of 1 to 2 years (Einarsson, 1945; Jørgensen and Matthews, 1975; Kulka and Corey, 1978; Astthorsson, 1990).

The main growth of *T. inermis* in terms of length seems to occur from February to August. Falk-Petersen and Hopkins (1981) made similar observation on *T. inermis* from a fjord (Balsfjorden) in northern Norway. *T. longicaudata* seems to have a more extended growth period than *T. inermis*, from February to October. A marked negative growth was apparent for *T. inermis* already from August. During mid winter (January-February) a clear decrease in growth was seen for 2 and 3 group *T. inermis* as well as for 1 and 2 group *T. longicaudata.* Negative growth during winter when food supply is low is reported from other studies (Falk-Petersen and Hopkins, 1981; Hopkins *et al.* 1984, Astthorsson, 1990). Laboratory experiments on both Antarctic and Atlantic/Arctic krill have shown that negative growth is common, with positive growth being an exception under experimental conditions (Ikeda and Dixon, 1982; Polek and Denys, 1982; Dalpadado and Ikeda, 1989; Buchholz, 1991). As Dalpadado and Skjoldal (1991) pointed out, decrease in size might not pose much problems for population dynamic studies based on length frequency distributions for short lived species with well defined spawning season such as *T. inermis* and *T. longicaudata.*

For *T. inermis* a clear increase in size was seen during 1987 to 1989. When predation effect was minimum, reduced mortality allowed more individuals to grow into older age groups. The mean lengths of *T. longicaudata* were similar during periods with high and low predation activity by capelin. This could be due to that more cruises (e.g. August 1984, 1985 and September/ October 1992) covered the colder waters where larger individuals of *T. longicaudata* were recorded. *T. longicaudata* is apparently more dependent on the inflow from the Norwegian Sea than *T. inermis* which is more a shelf species. Major inflow events took place in 1982-83 and 1989 and reduced inflow in 1987-88 (Loeng, 1991, Ådlandsvik and Loeng, 1991).

It is possible that the inflow events transported a smaller proportion of *T. longicaudata* into the colder regions of the Barents Sea where they grow to a larger size and older age. *T. inermis* from different water masses did not show marked variation in size.

The krill distribution area overlaps with the feeding grounds of capelin, especially in the winter to early summer period. Krill are important food for capelin in the Barents Sea (Lund, 1981; Ajiad and Pushchaeva 1991; Skjoldal and Hassel, 1991; Hassel *et al.*, 1991). Lund (1981) showed that the amount of krill consumed by capelin (13-16 cm) in terms of calories could vary from 28 to 98% of the diet during different seasons. The highest values were observed in spring and the lowest in autumn.

The biomass of 2 year and older capelin decreased drastically from about 2.6 million tons in 1983 to 0.7 million tons by 1985 (Fig. 11). In 1984 there was low biomass of zooplankton in the Barents Sea and the individual growth of capelin was low (Skjoldal *et al.*, 1992). By 1987, the biomass of capelin was down to 0.02 million tons (Gjøsæter, 1992). The reduction in the capelin stock in the mid eighties most likely eased the grazing pressure on krill and this probably led to the increase in abundance of *T. inermis* and *T. longicaudata*. The strong decrease in krill abundance as the capelin stock size increased was most due to increased predation from capelin. The high abundance of large zooplankton prey such as krill contributed to high growth rate of capelin and to the rapid recovery of the capelin stock (Skjoldal *et al.*, 1992). They furthermore suggest that the abundance of krill to a large extent is regulated by predation. Dalpadado *et al.*, (1994) found similar trends in the variation of abundance of amphipods (*Themisto* spp.) during 1984 to 1992. These results therefore indicate clear predator-prey interactions between capelin and their major prey such as krill and amphipods, in the Barents Sea.

Acknowledgements
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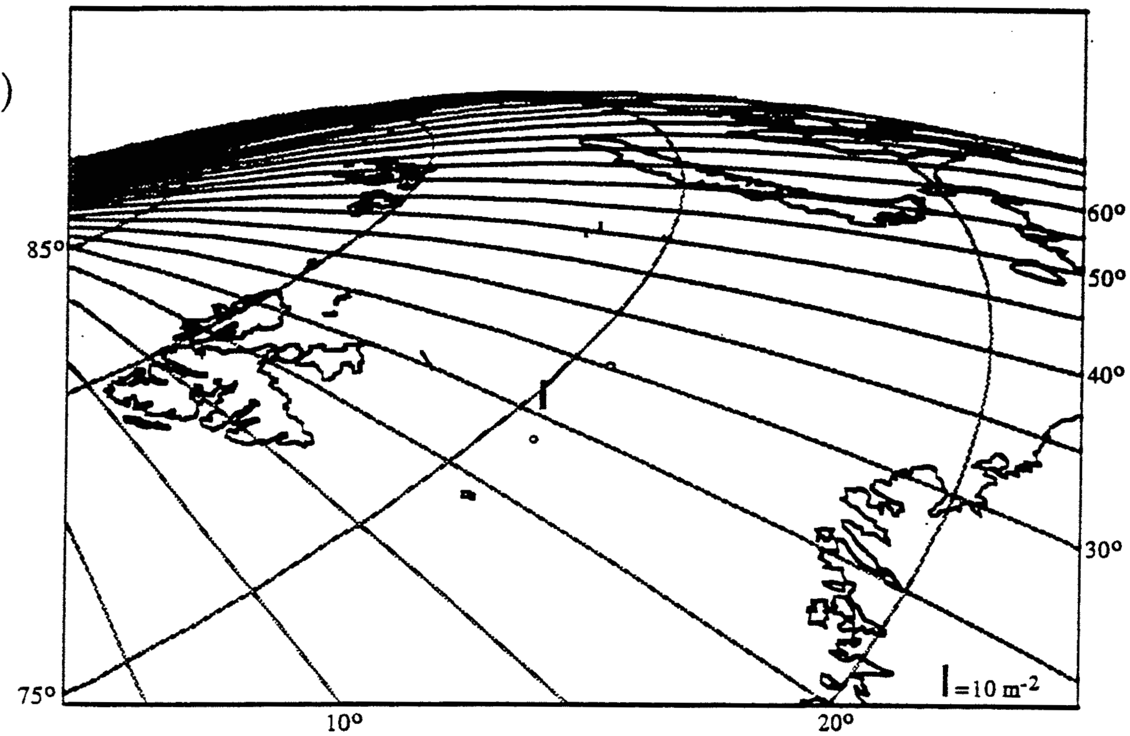
Appendix figure 1a-p. *Thysanoessa inermis*. Horizontal distributions (no. m^{-2}) in the Barents Sea from individual cruises, 1984 -1992.

Appendix figur 1a-p. *Thysanoessa inermis*.. Horisontalfordeling i Barentshavet (no. m^{-2}) fra individuelle tokter, 1984 1992.

a)



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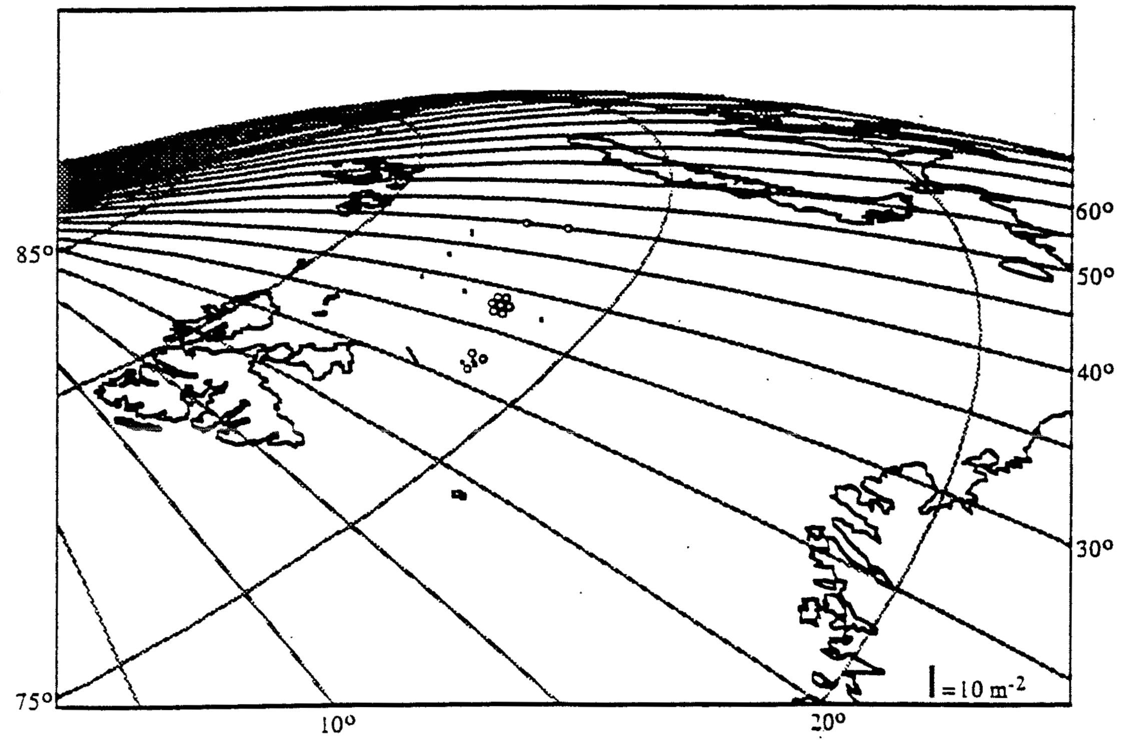

August 1984

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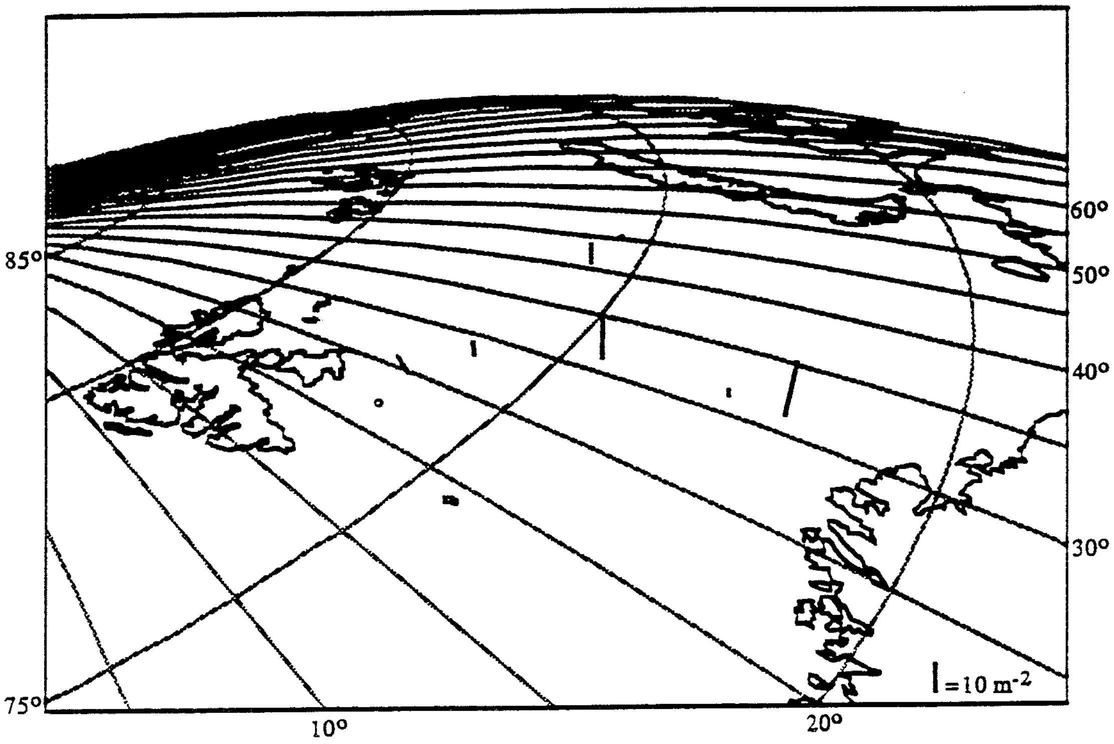

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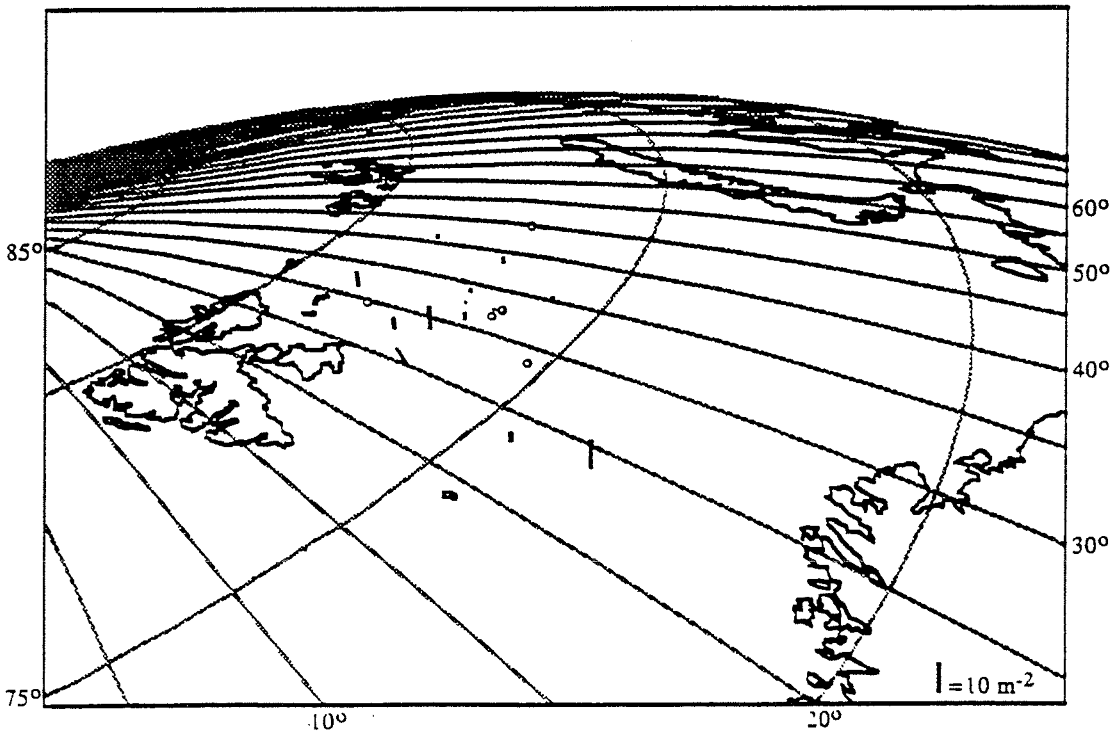

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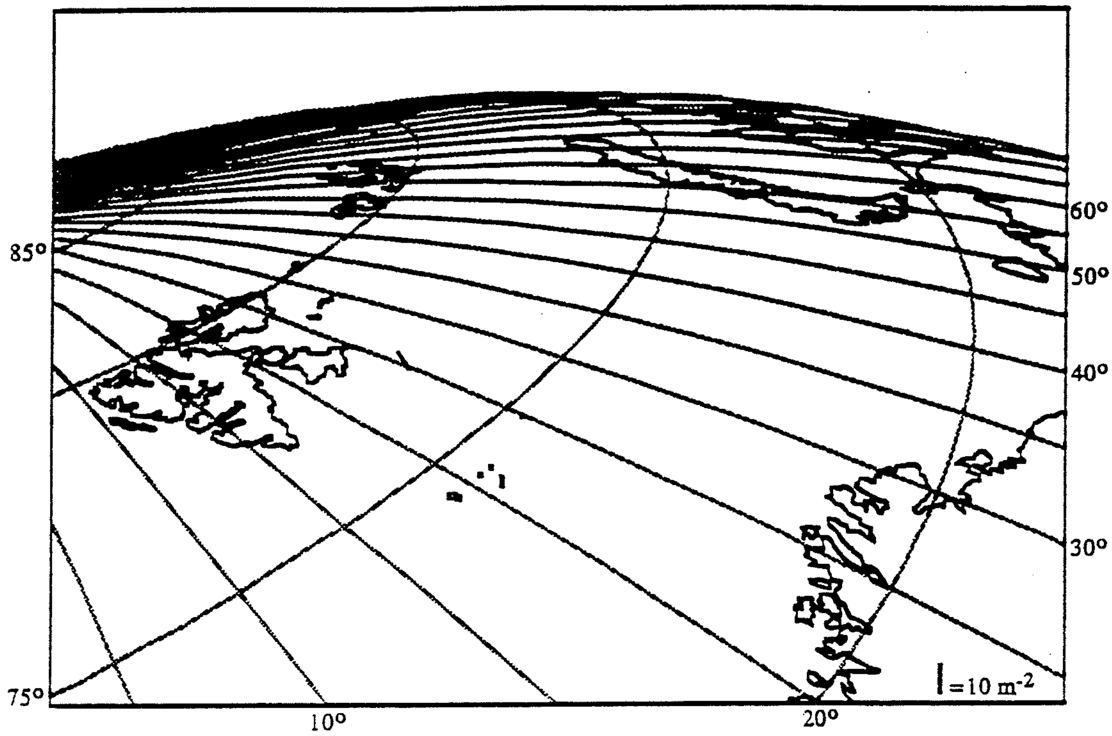

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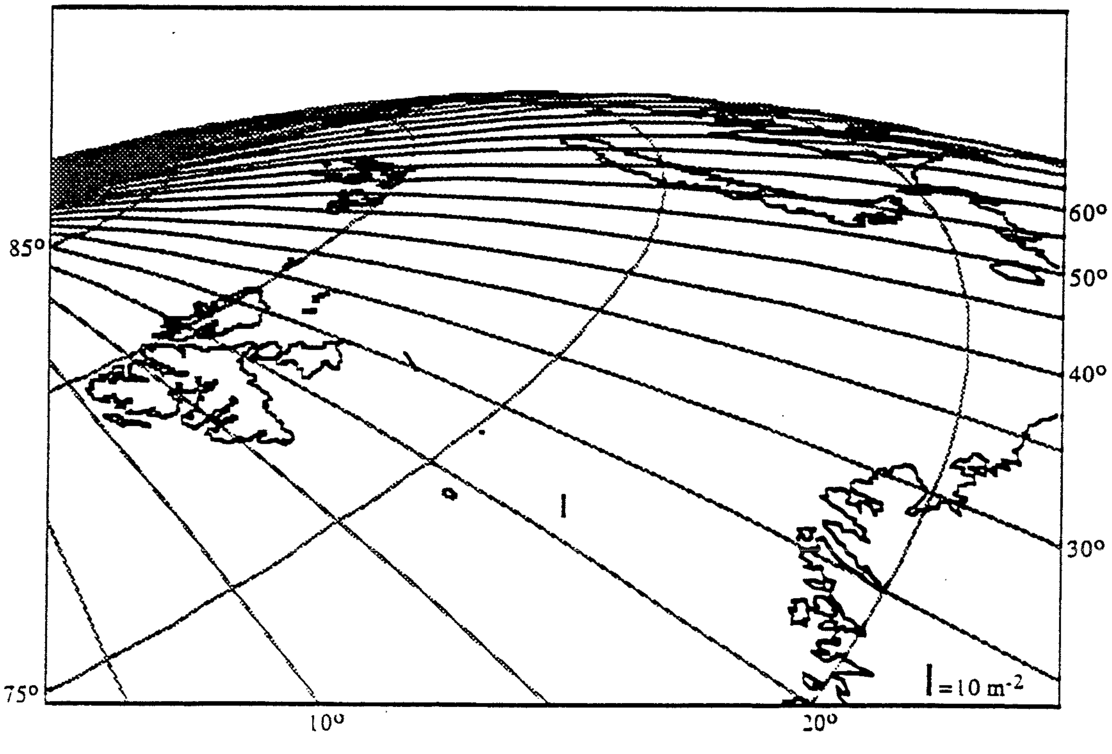

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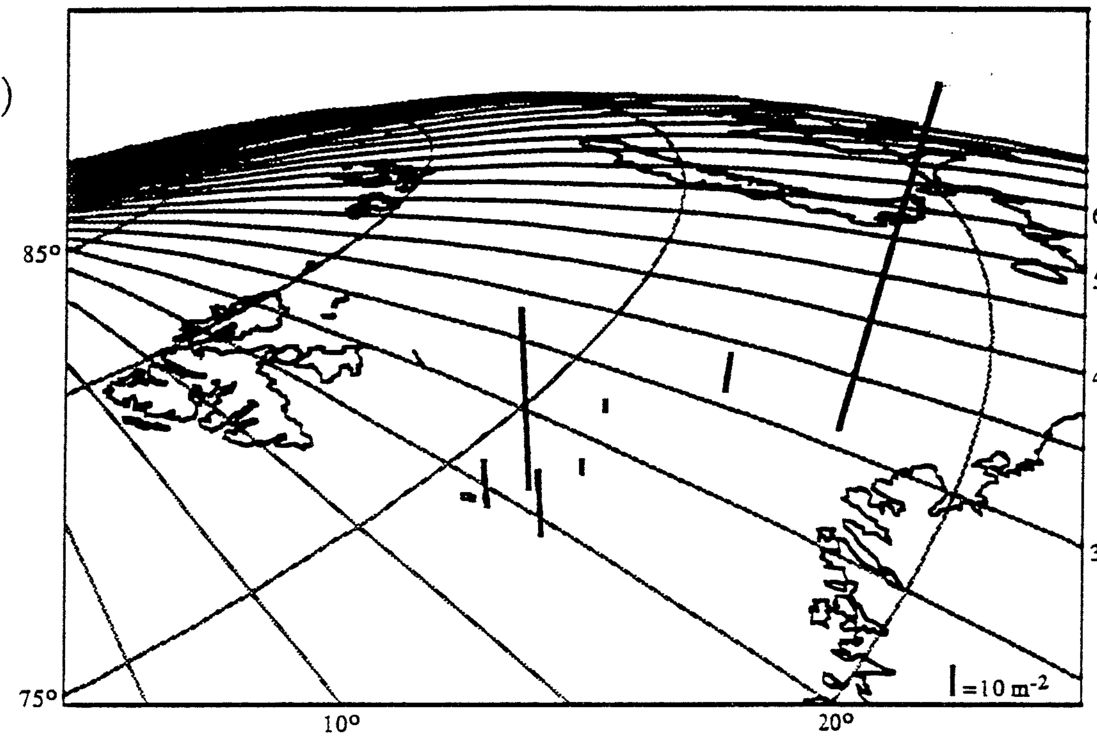

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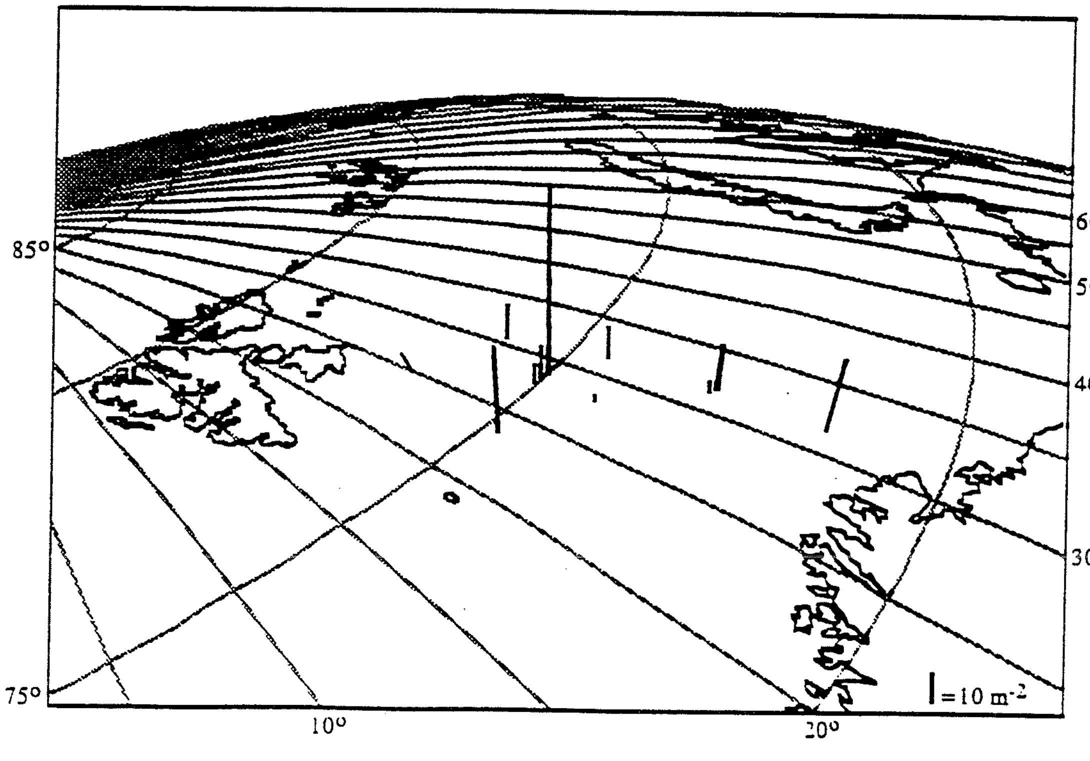

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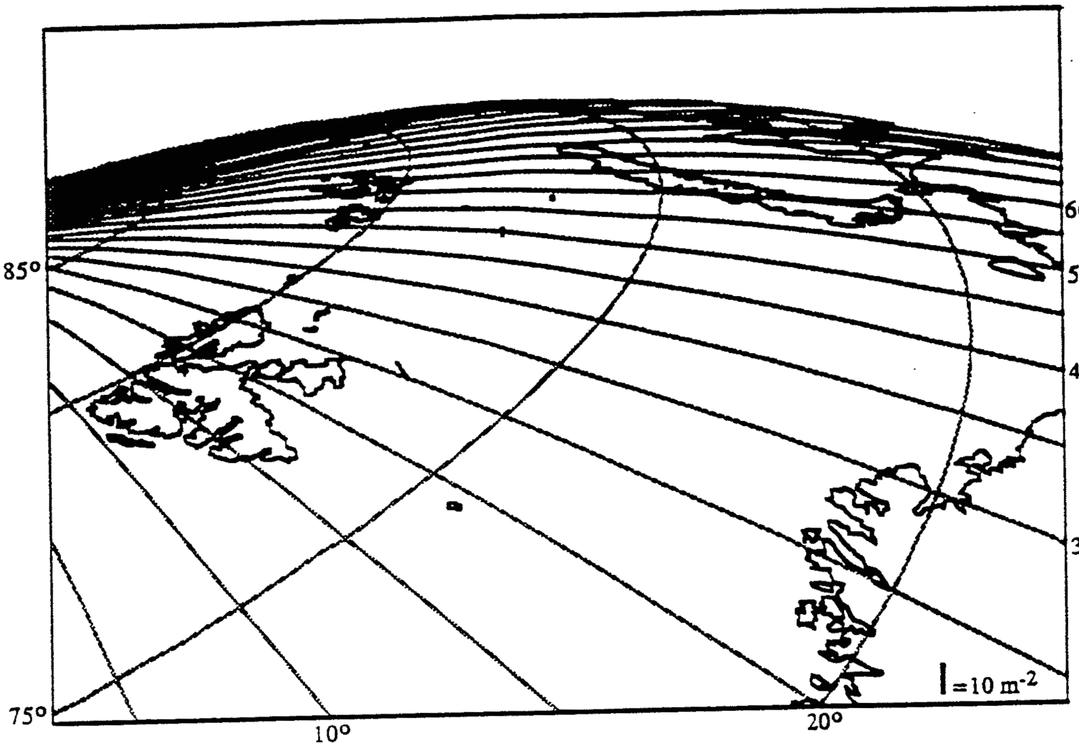
i)



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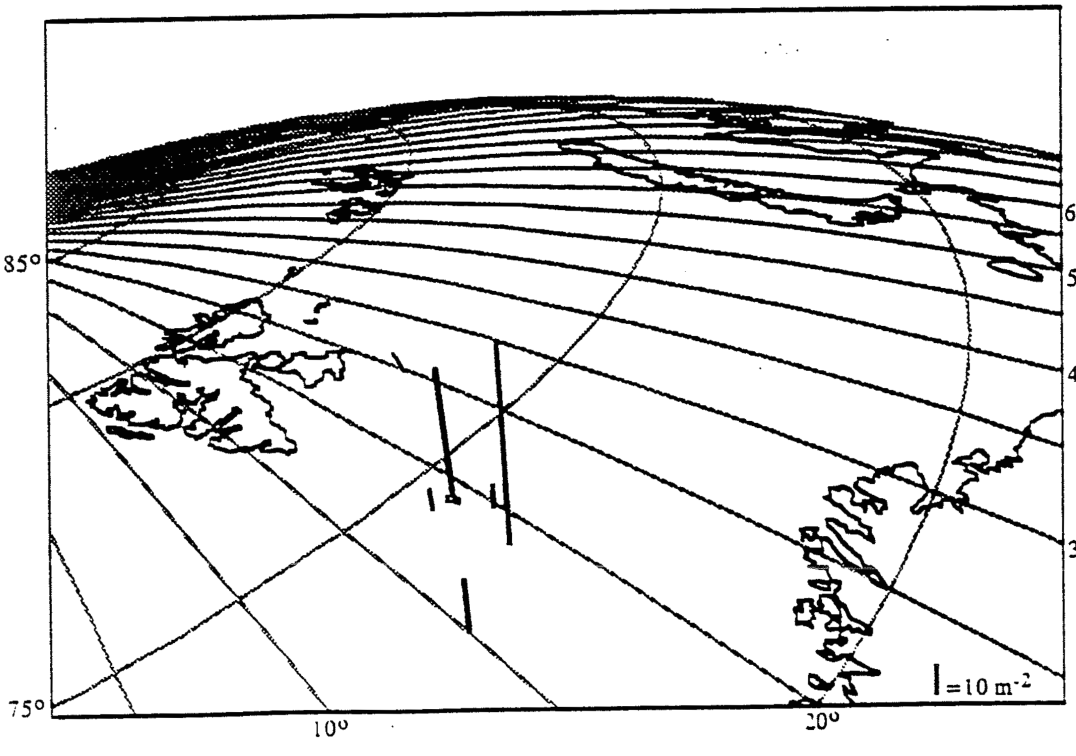

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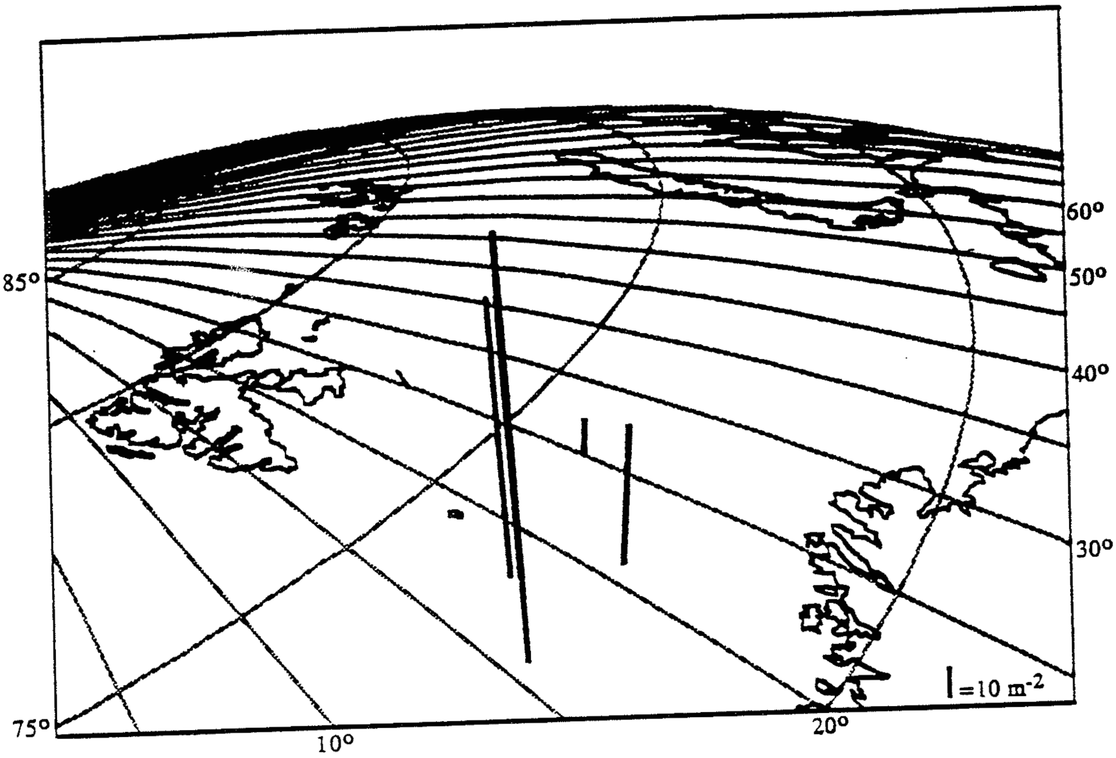

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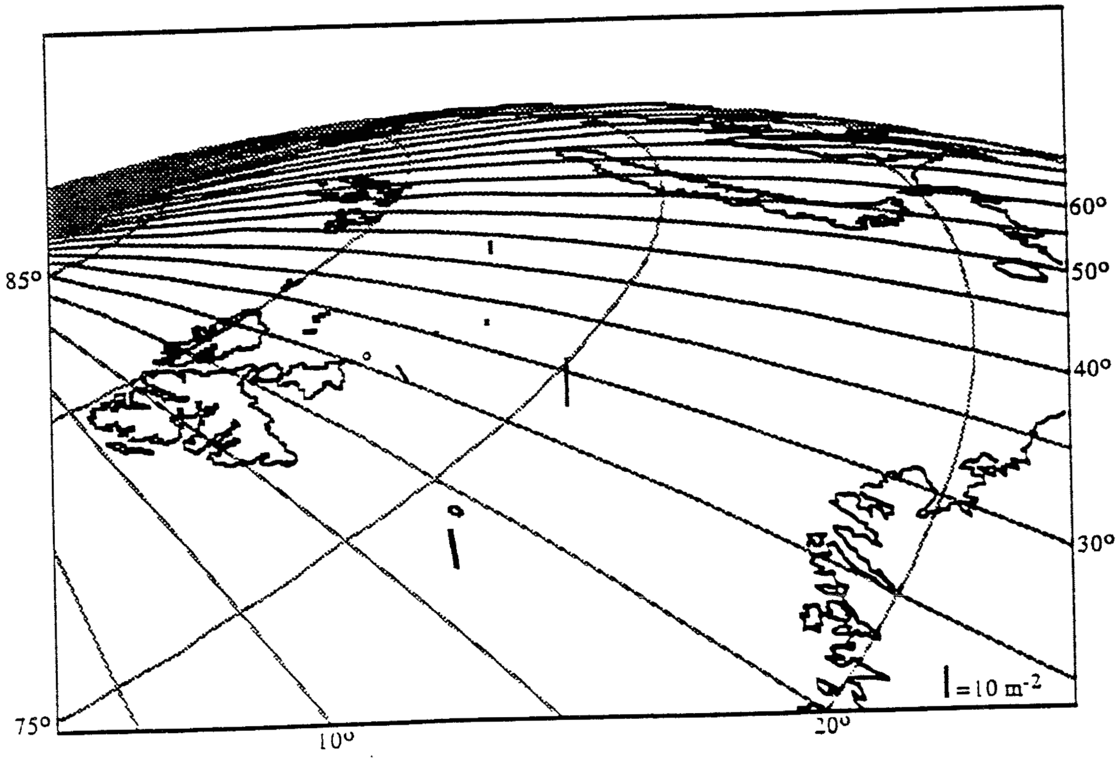

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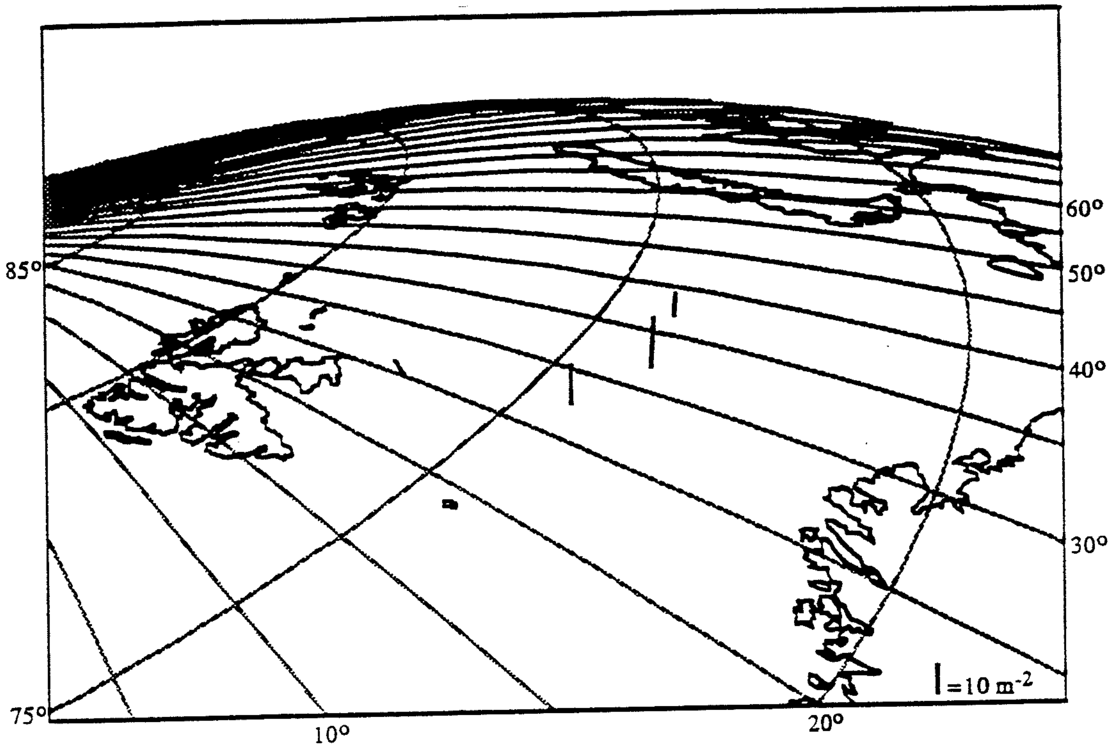

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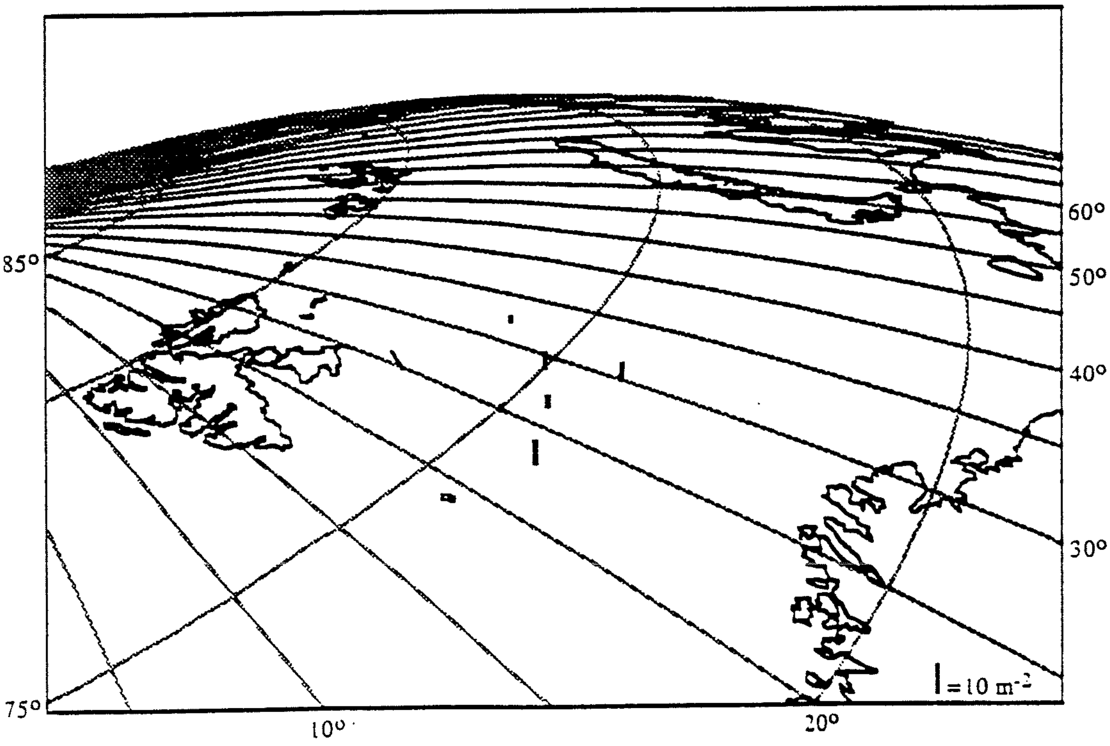

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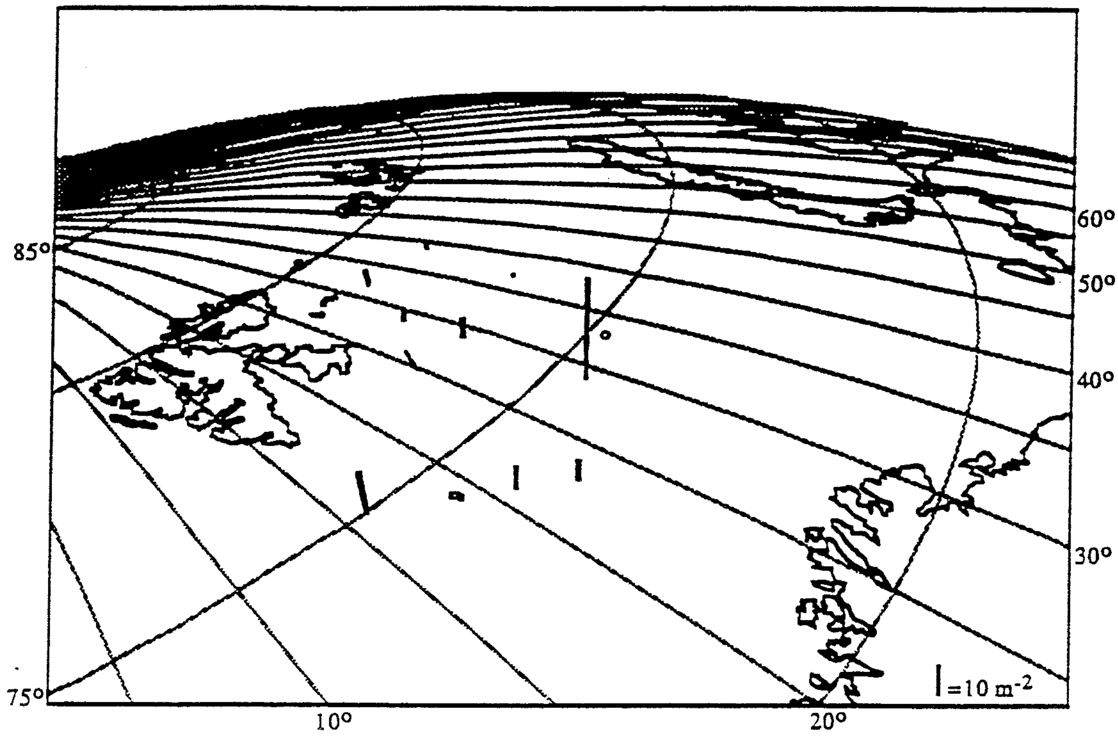
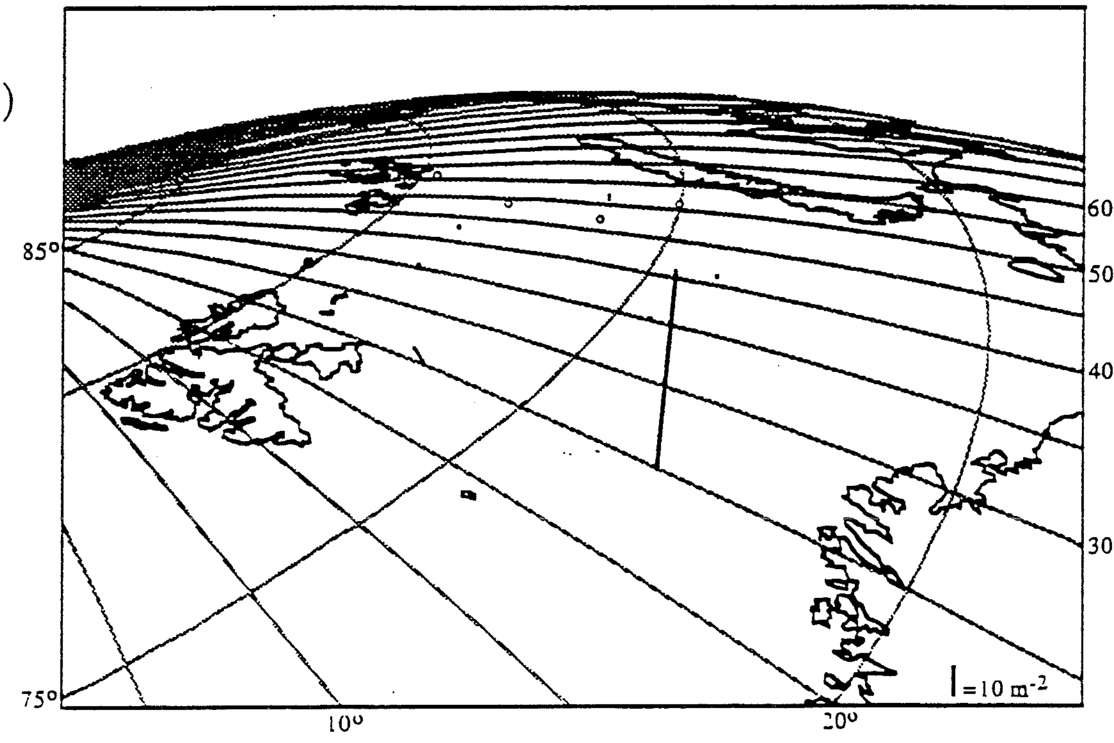


October 1992. R/V "G. O. Sars"

p)

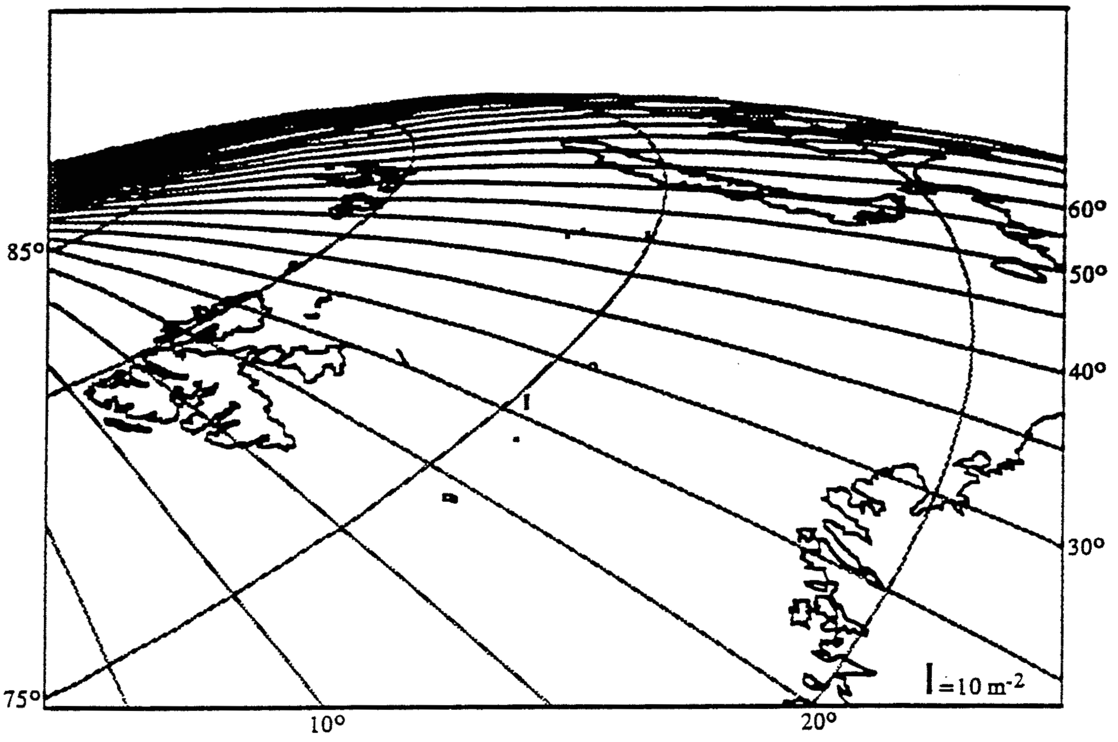


September/October 1992 R/V "Johan Hjort"

Appendix figure 2a-p. *Thysanoessa longicaudata*. Horizontal distributions (no. m^{-2}) in the Barents Sea from individual cruises, 1984 -1992.

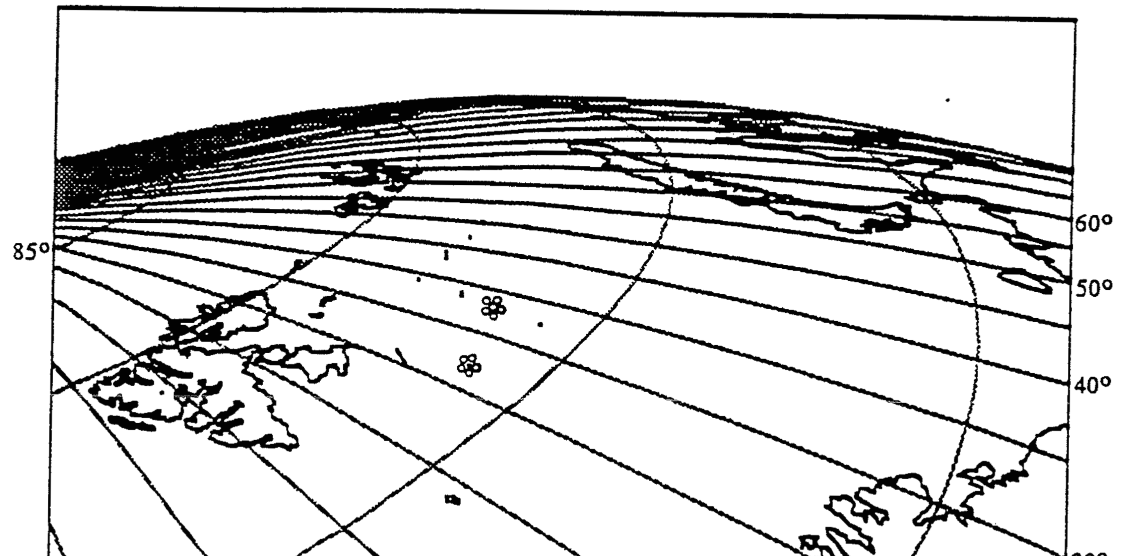
Appendix figur 2a-p. *Thysanoessa longicaudata.*. Horisontalfordeling i Barentshavet (no. m^{-2}) fra individuelle tokter, 1984 1992.

a)



June 1984

b)



August 1984

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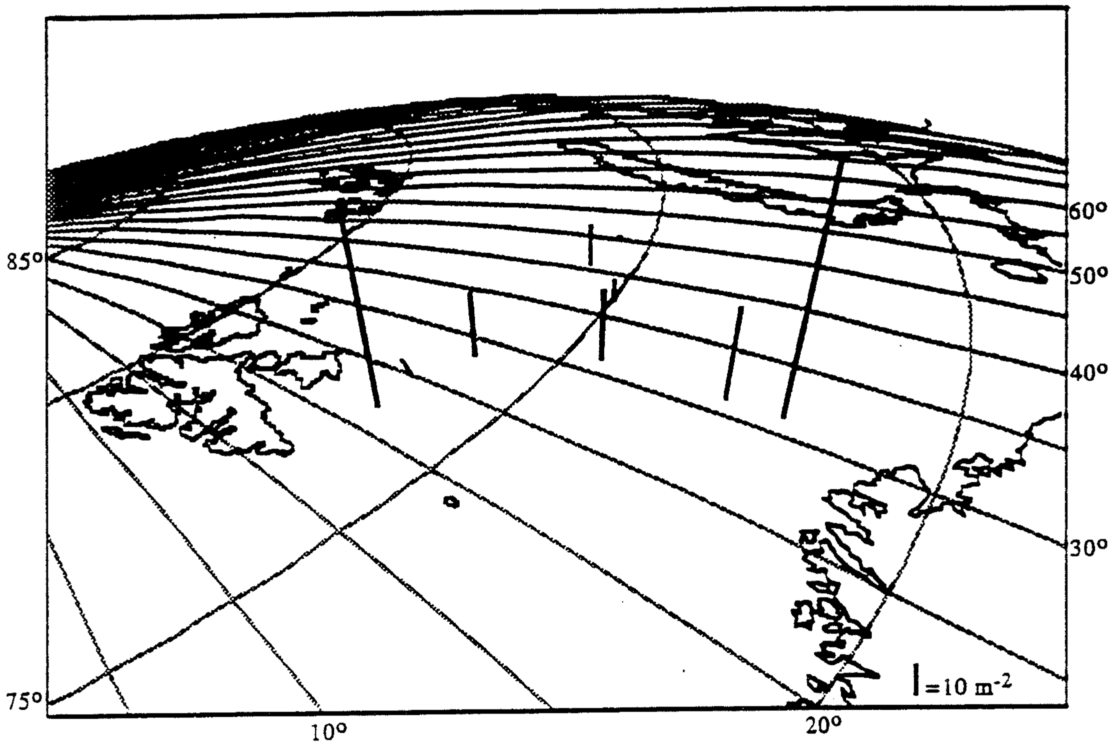

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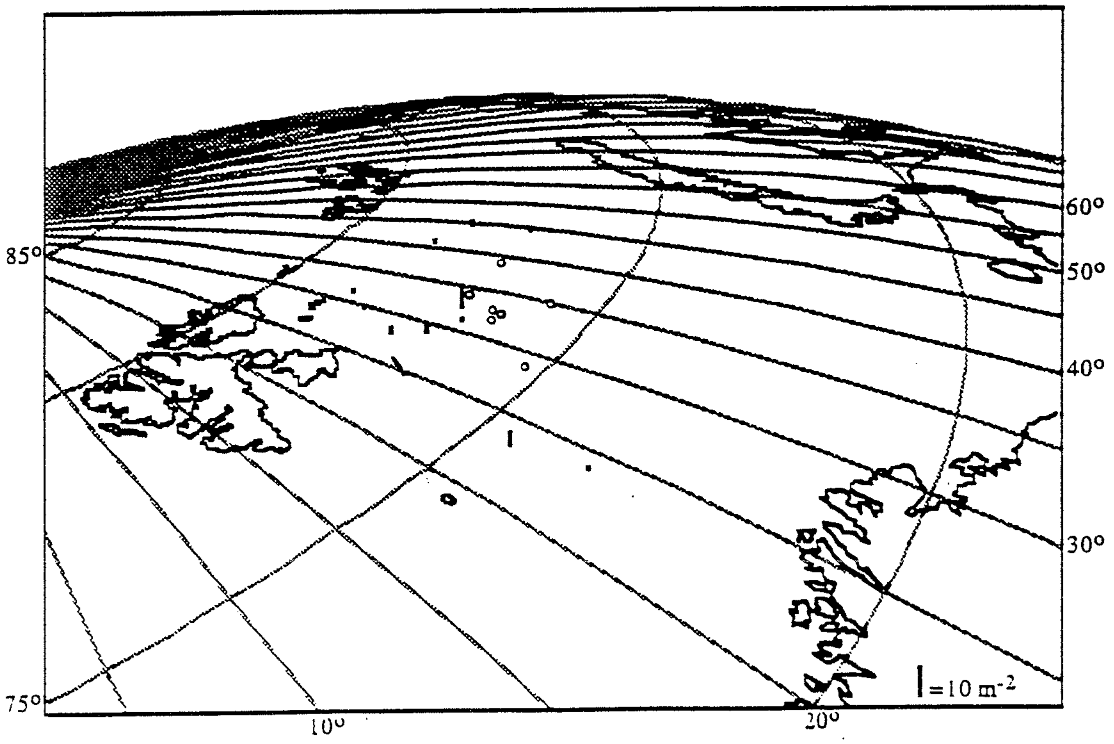

August 1985

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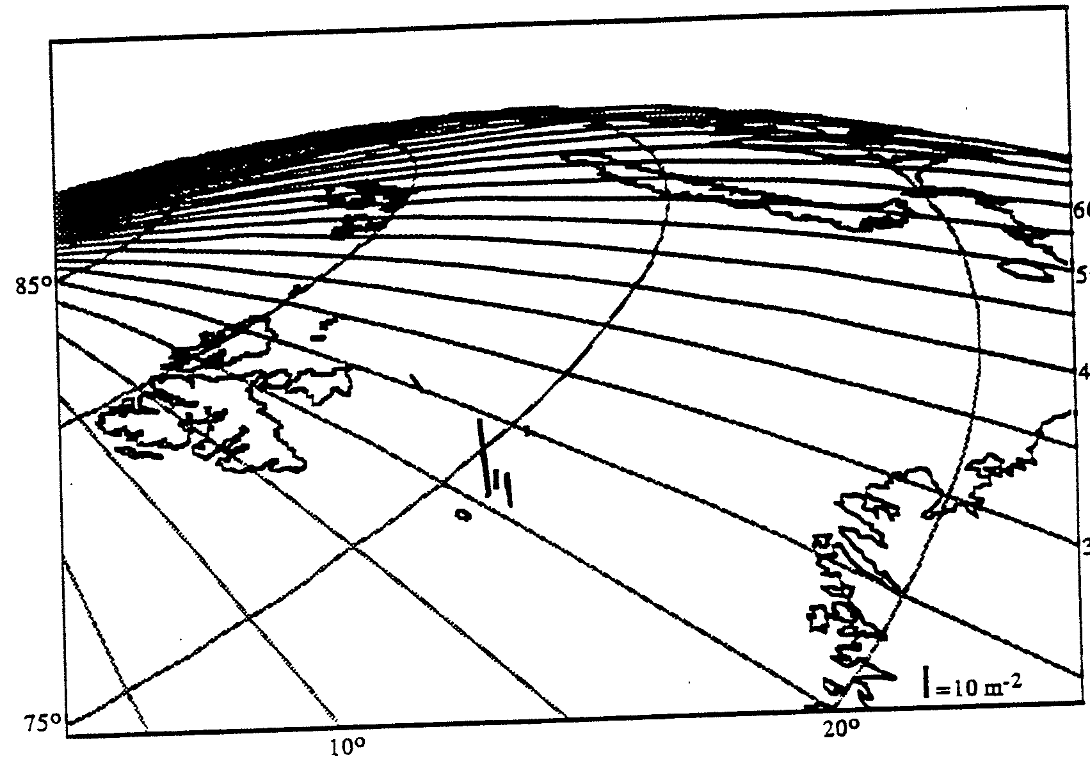

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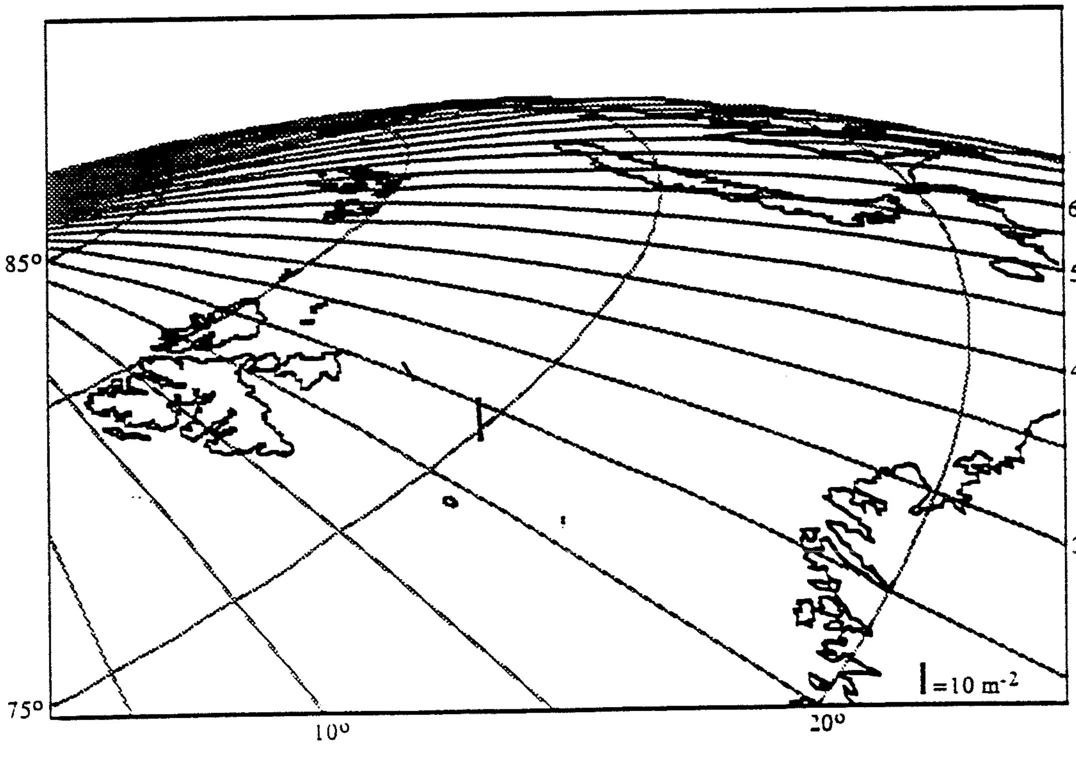

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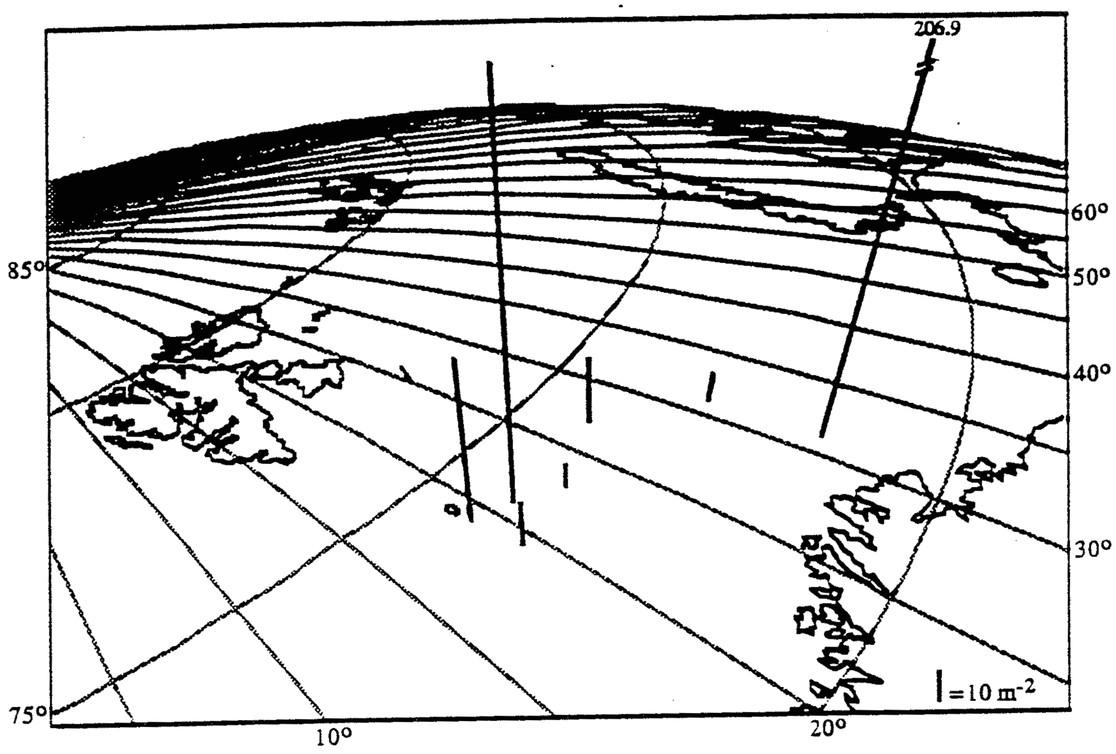

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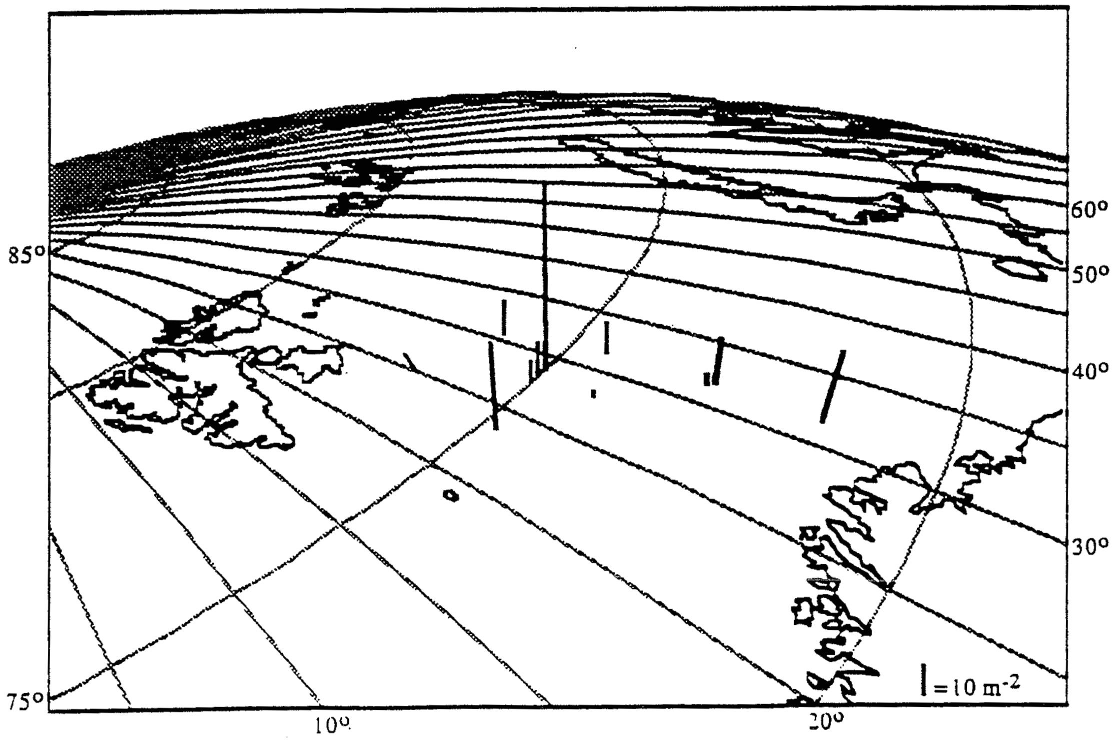

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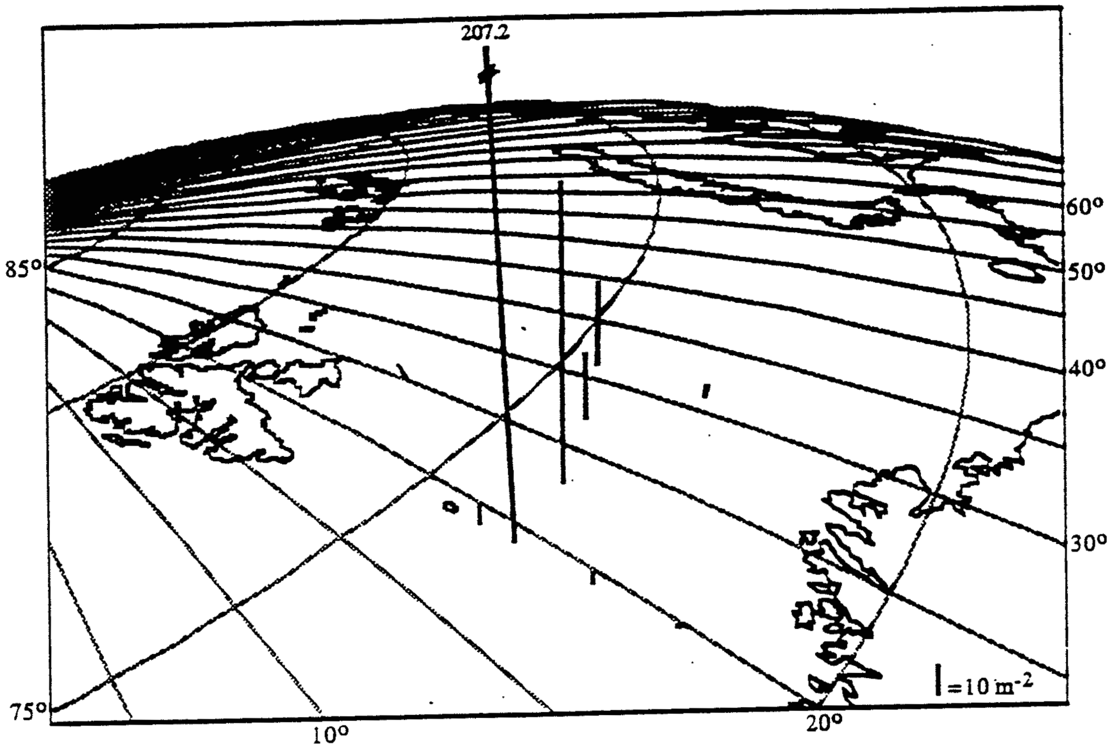

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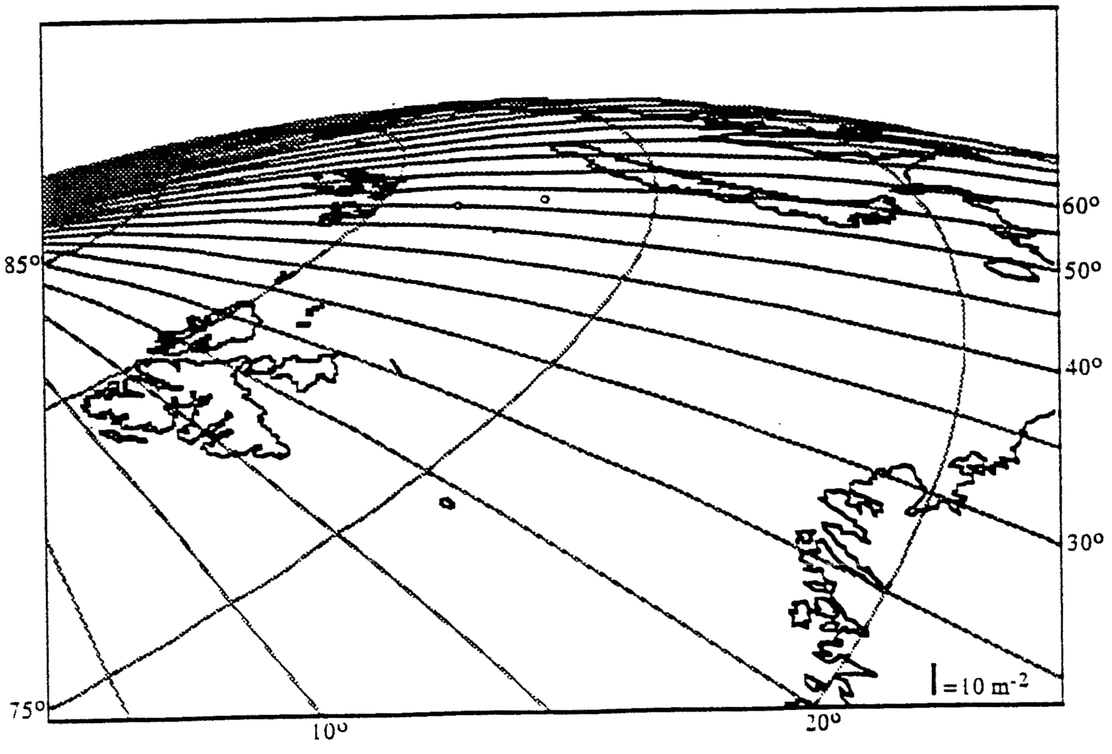

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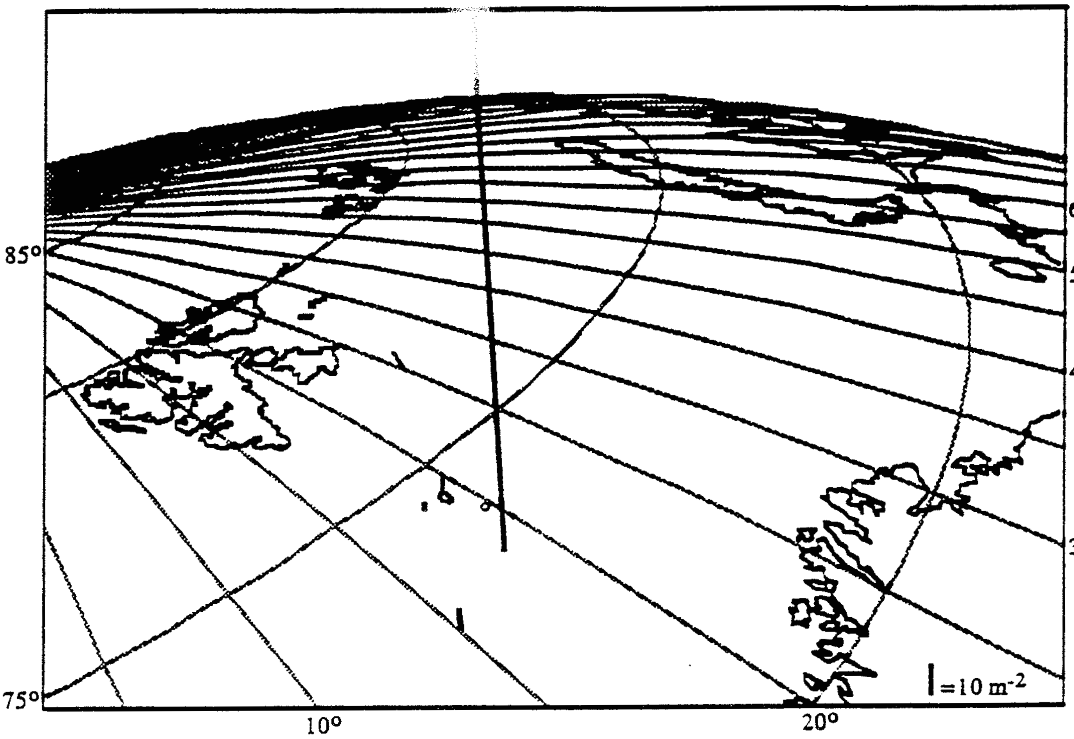

October 1988

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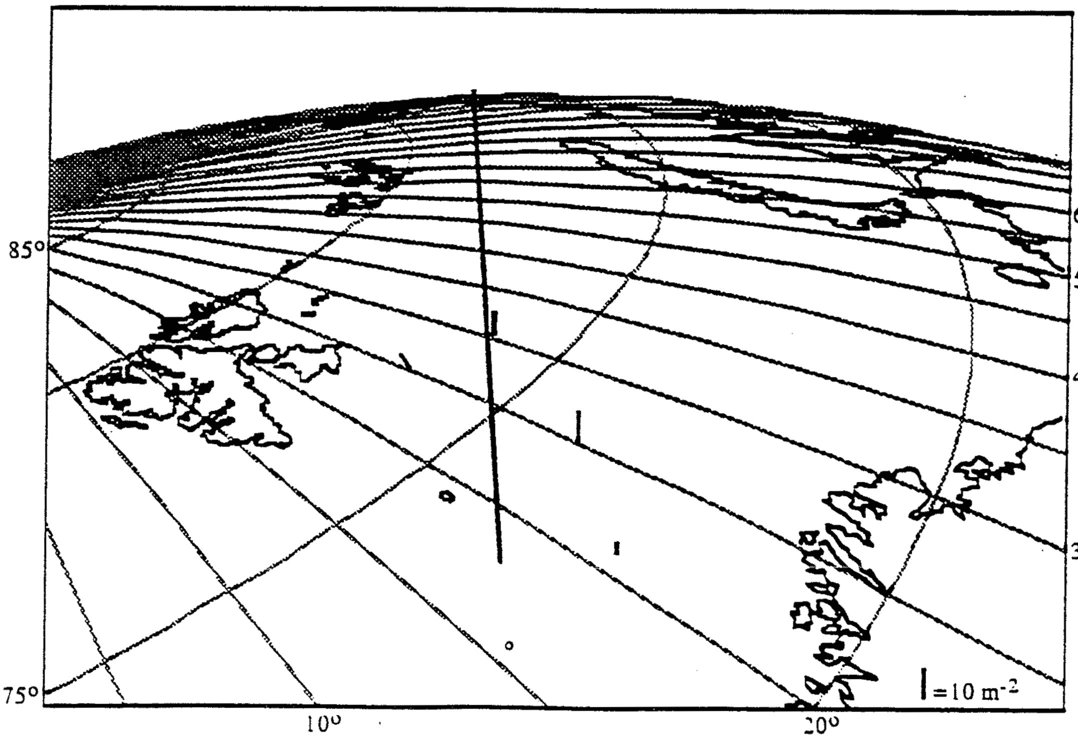

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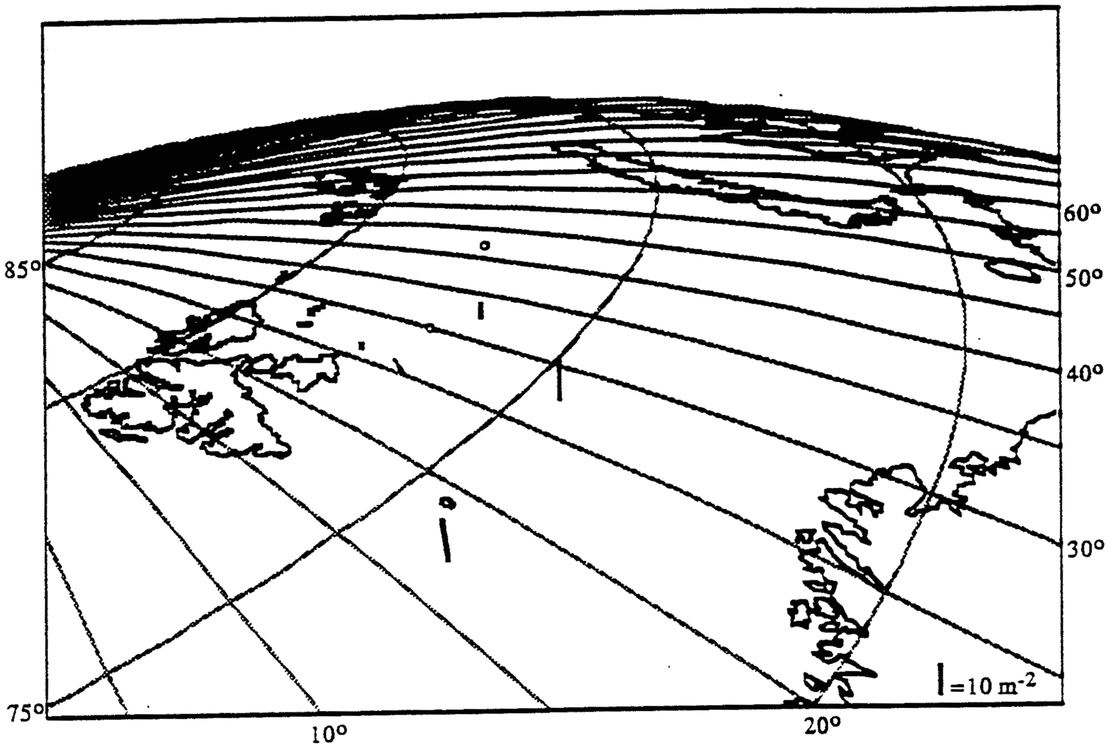

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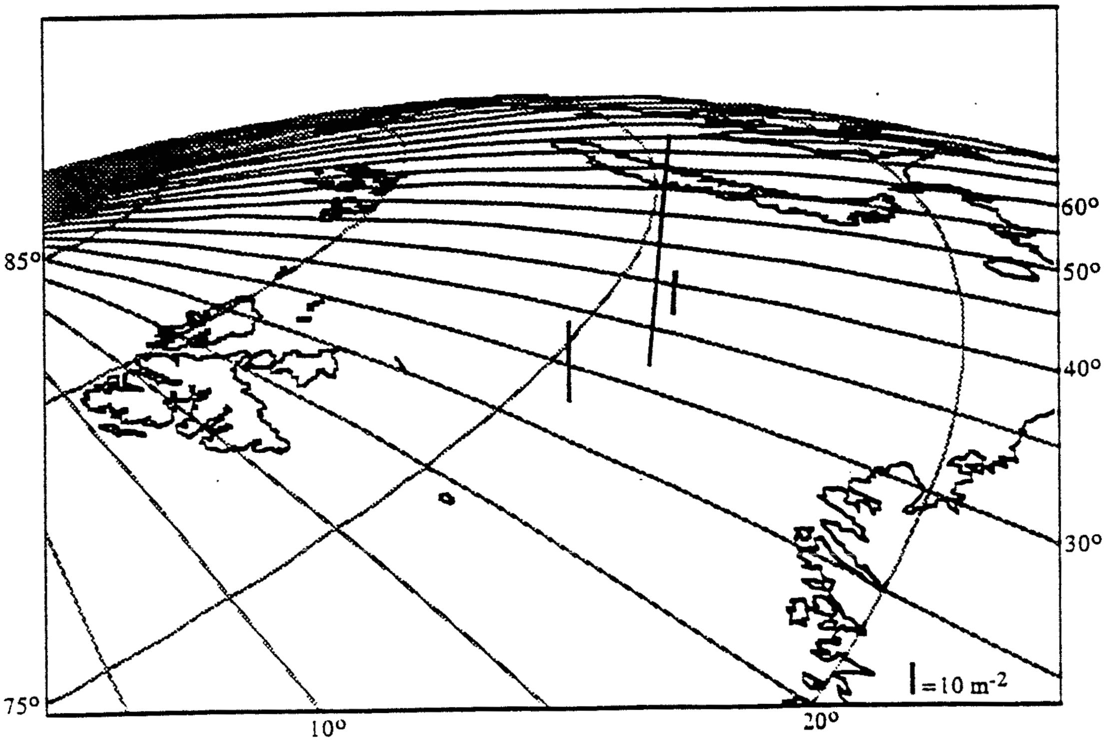

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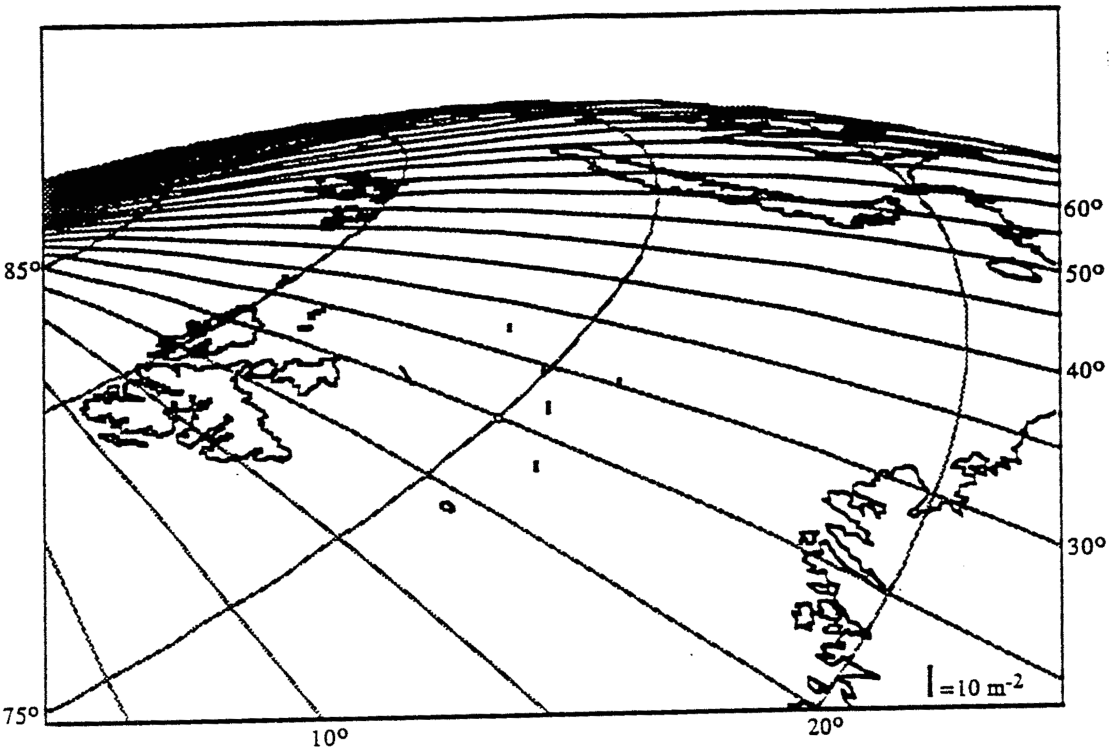

May 1991

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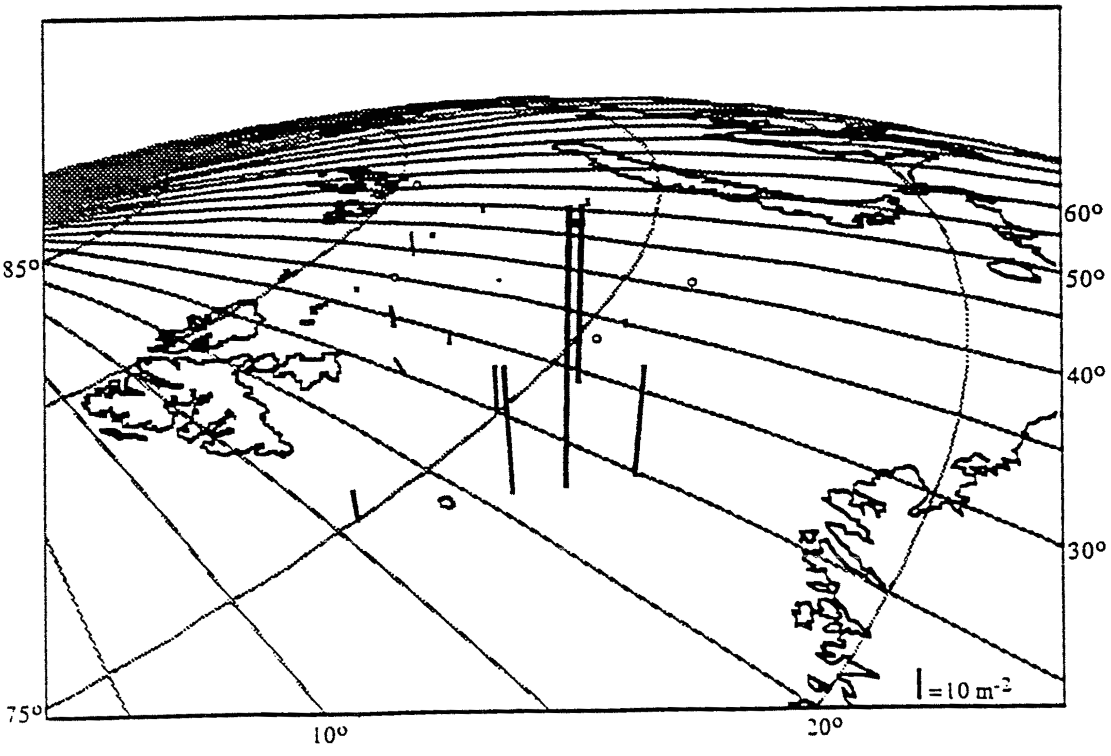
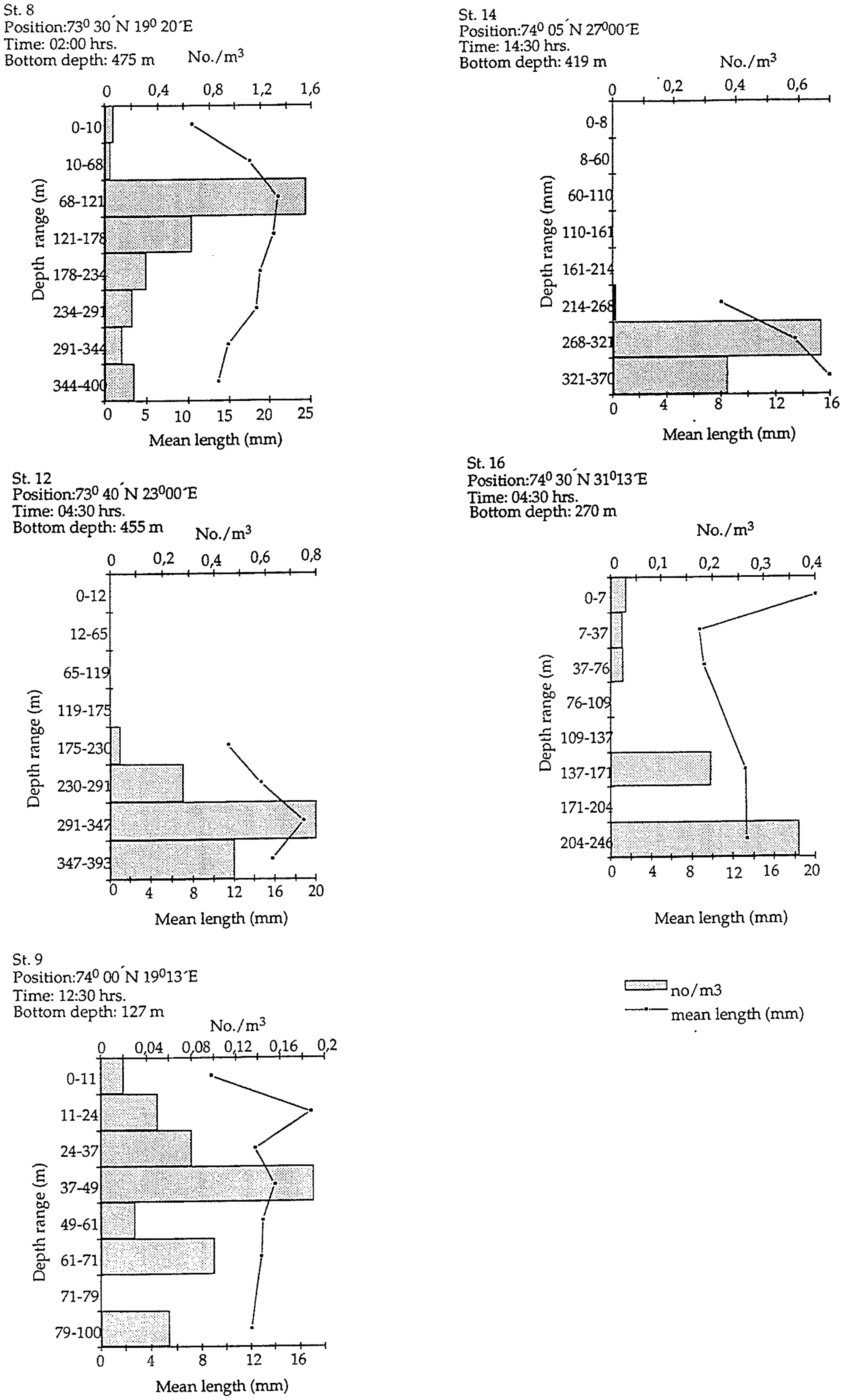


September/October 1992

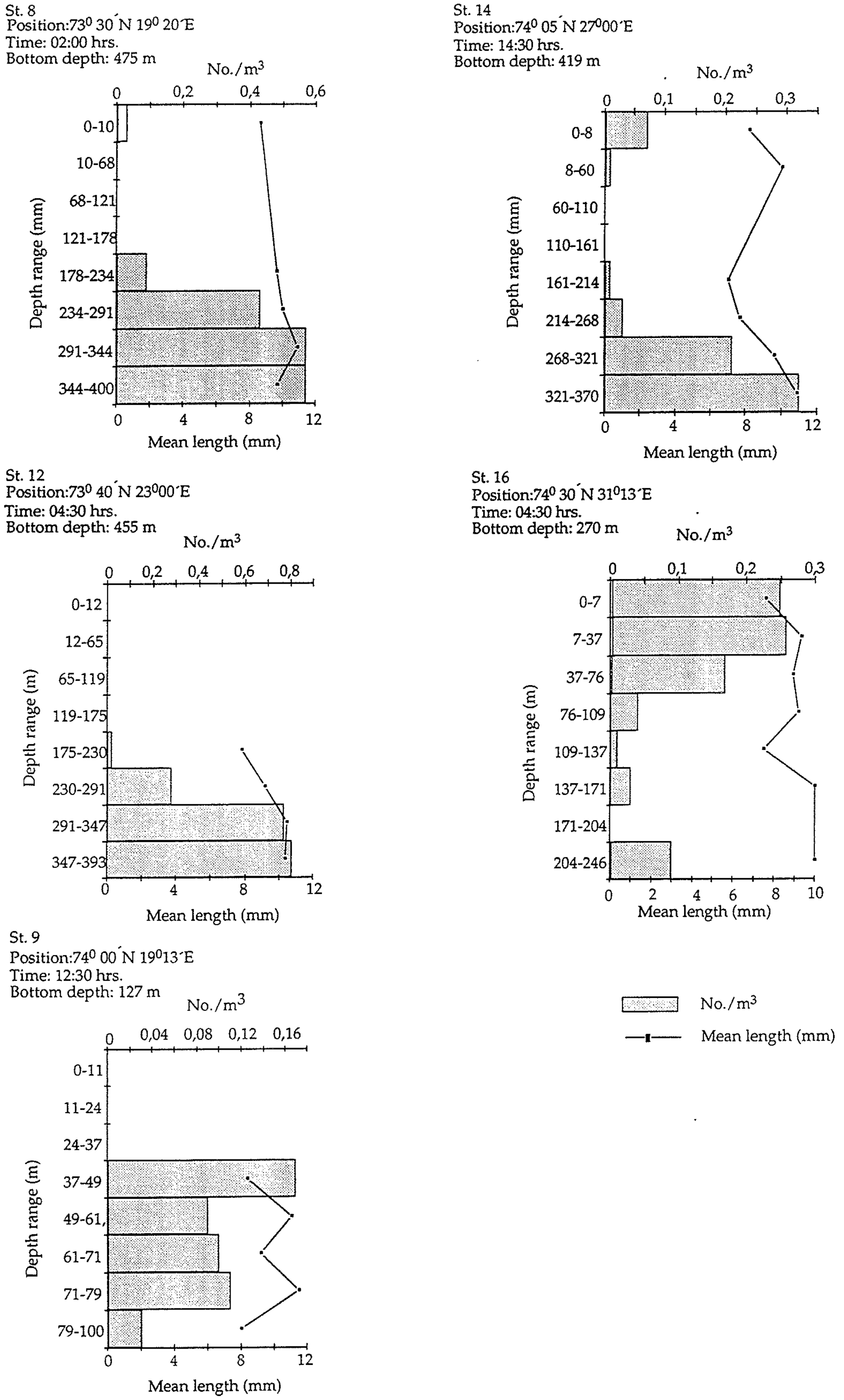
Thysanoessa inermis March 1988



Appendix figure 3.*Thysanoessa inermis*. Average numerical density (individuals m^{-3}) and length of krill in relation to sampling depths, from March 1988.

Appendix figur 3. *Thysanoessa inermis*. Gjennomsnittlig tetthet (antall m^{-3}) og lengde av krill i relasjon til prøvetakingsdyp, i mars 1988.

Thysanoessa longicaudata March 1988



Appendix figure 4. *Thysanoessa longicaudata*. Average numerical density (individuals m^{-3}) and length of krill in relation to sampling depths, from March 1988.

Appendix figur 4.*Thysanoessa longicaudata*. Gjennomsnittlig tetthet (antall m^{-3}) og lengde av krill i relasjon til prøvetakingsdyp, i mars 1988.

Appendix table 1. *T. inermis.* Number of individuals and mean total lengths of cohorts separated in the length frequency anal
The cohorts are assumed to represent year classes and ascribed to age groups 0,1, 2, 3 and 4 with a change in age spring.

Appendix tabell 1. *T. inermis*. Antall og middellengde av cohorter adskilt i lengde- frekvens analyse. Cohortene antas å representere aldersgruppene 0, I, 2, 3 og 4 med skifte om våren.

Cruise	No. of stations	Total no. of indivi.	Cohort	No. of indiv. in each cohort	Abundance mean (No/m2)	Length mean (mm)
Sep/Oct.1992	11	434	0	201	0,0131	9,5
			1	172	0,0112	12,8
			2	40	0,0026	17,1
			3	17	0,0011	22,1
Jan./Feb.1991	3	256	0	113	0,0197	9,9
			1	105	0,0183	12,6
			2	16	0,0028	16,6
			3	17	0,0030	21,5
Sep. 1990	3	113	0	66	0,0106	9,6
			1	18	0,0029	13,2
			2	11	0,0018	15,6
			3	17	0,0027	19,7
May 1989	3	223	0	few indi.		
			1	few indi.		
			2	few indi.		
			3	205	0,0611	23,2
March 1988	6	543	0	210	0,0197	12,4
			1	few indi.		
			2	310	0,0291	20,2
Oct. 1988	5	196	0	18	0,0063	9,6
			1	50	0,0176	12,2
			2	few indi.		
			3	few indi.		
			4?	119	0,0418	25,4
March 1987	6	295	0	160	0,0254	11,6
			1	8	0,0013	15,7
			2	37	0,0059	21,3
			3	9	0,0014	25,6
ay-June 1987	9	478	1	191	0,0176	13,1
			2	114	0,0105	16,7
			3	172	0,0159	22,2
April_1986	4	379	0	329	0,1754	12,8
			1	35	0,0187	18,7
			2	12	0,0064	21,5
May 1986	2	119	1	71	0,0105	12,3
			2	15	0,0022	17,6
			3	31	0,0046	21,5
January 1985	8	322	1	276	0,0130	11,6
			2	40	0,0019	18,3
			3	6	0,0003	24,4
August_1985	8	100	0	10	0,0005	8,2
			1	34	0,0018	16,5
			2	45	0,0024	20,3
			3	20	0,0011	24,2

* very few individuals present, allocation of cohorts visually, not by statistical splitting

Appendix table 2. *T. longicaudata.* Number of individuals and mean total lengths of cohorts separated in the length frequency analysis. The cohorts are assumed to represent year classes and ascribed to age groups 0, 1 and 2 with a change in age spring.

Appendix tabell 2. *T. longicaudata.* Antall og middellengde av cohorter adskilt i lengde- frekvens analyse. Cohortene antas å representere aldersgruppene 0, 1 og 2 med skifte om våren.

cruise	No. of stations	Total no. of indivi.	Cohort	No. of indiv. in each cohort	Abundance mean (No/m2)	Length mean (mm)
Sep/Oct. 1992	11	172	0	113	0,0074	8
			1	55	0,0036	13,4
			2	4	0,0003	18,5
Jan./Feb. 1991	3	122	0	65	0,0113	8,2
			1	44	0,0077	11,4
Sep. 1990	3	76	1	75	0,0120	13,4
May 1989	3	153	1	151	0,0450	11,5
March 1988	6	568	0	304	0,0286	8,3
			1	259	0,0243	11,6
Oct. 1988	5	158	0	109	0,0383	9,5
			1	49	0,0172	14,4
March 1987	6	119	0	95	0,0151	9,4
			1	24	0,0038	12,6
May-June 1987	9	605	1	552	0,0510	10,7
April_1986	4	86	0	75	0,0040	10,9
			1	10	0,0005	15,1
May 1986	2	40	1	30	0,0044	11,1
			2	10	0,0015	13,4
January 1985	8	119	0	96	0,0045	10,4
			1	23	0,0011	14,6
August_1985	8	109	0	79	0,0043	8
			1	26	0,0014	11,9
			2	3	0,0002	15,8