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Tittel:
DISTRIBUTION AND LIFE HISTORY OF *THEMISTO* (AMPHIPODA) spp., NORTH OF 73°N IN THE BARENTS SEA

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ABSTRACT

Two dominant hyperiid amphipod species were found in the western and central Barents Sea, *Themisto abyssorum* and *T. libellula*. *T. abyssorum* was predominant in the boreal and subarctic waters, *T. libellula* in the Arctic waters. *T. compressa* was rare and was restricted to the Atlantic waters. The subarctic species *T. abyssorum* has a one year life cycle, with the release of young (2-3 mm) in the May-June period. The Arctic species *T. libellula* seems to release their young earlier and have a prolonged breeding period. Both species release their young during the period of spring phytoplankton bloom in the Barents Sea. Our study shows peak aboundances of *T. abyssorum* and *T. libellula* in summer and in early autumn. High abundances, up to 122 individuals per m^2 of *T. abyssorum* were observed south and south east of Svalbard Bank in July and October 1988. Very high abundances, up to 430 individuals per m^2 of *T. libellula* were recorded in May-June 1987 and July 1988 close to the Polar Front region (at approx. 76^0N, 30-32^0E). Followed by a decrease in the capelin stock from 1986 to 1987, there was an increase in the abundance of *T. abyssorum* and *T. libellula*, probably owing to the reduced grazing pressure from capelin. With an increase in the capelin stock from 1987 up to 1991, a decrease in abundance of *T. abyssorum* and *T. libellula* was observed, indicating predator-prey interactions between capelin and their prey-amphipods.

SAMMENDRAG

To arter av hyperide amfipoder er dominerende i Barentshavet; *Themisto abyssorum* og *T. libellula. T. abyssorum* dominerte i subarktisk vann og *T. libellula* i arktisk vann. *T. compressa* var sjelden og ble kun funnet i atlantiske vannmasser. Den subarktiske arten *T. abyssorum* har en ettårig livssyklus og yngelen (2-3 mm) frigjøres i mai-juni. Den arktiske arten *T. libellula* synes å frigjøre yngelen noe tidligere, og har en lengre gyteperiode. Begge artene friggjør yngelen under våroppblomstringen i Barentshavet. Våre undersøkelser viser størst tetthet av *T. abyssorum* og *T. libellula* om sommeren og tidlig på høsten. Høye tettheter, opp til 122 individer m^{-2} av *T. abyssorum* ble observert sør og sørøst av Svalbardbanken i juli og oktober 1988. Svært høye konsentrasjoner, opp til 430 individer m^{-2} ,av *T. libellula* ble observert i mai-juni 1987 og i juli 1988 nær polarfronten (omkring 76^0N, 30-32^0E). Etter en reduksjon i loddebestanden fra 1986 til 1987 økte mengden av *T. abyssorum* og *T. libellula*, trolig på grunn av lavere beitetrykk fra lodde. Da loddebestanden økte fra 1987 til 1991, avtok mengden av *T. abyssorum* og *T. libellula*. Dette tyder på at det er et predator-bytteforhold mellom lodde og amfipoder.

INTRODUCTION

In general, amphipods are ranked third in numerical abundance, far exceeded by copepods and krill (Bowman, 1960). Members of the hyperid amphipod genus *Themisto* (a senior synonym of *Parathemisto* is the valid name of the amphipod genus (Bowman, 1982)), overwhelmingly dominate the cooler epipelagic amphipod fauna, and their importance in the north Atlantic has been documented by Dunbar (1957, 1964). Of the three commonly found amphipods, *T. compressa* (Goes) and *T. abyssorum* (Boeck) are regarded as subarctic species, whereas *T. libellula* (Mandt) is described as both arctic and subarctic (Dunbar, 1964). *T. libellua* can be regarded as a good indicator of the presence of Arctic water (Dunbar, 1964). Other amphipods, as *Hyperia* and *Gammarus,* are ocassionally found in the Barents Sea (Dunbar 1964, unpublished data). Amphipods, *G. wilkitzkii*, *Onisimus* spp. and *Apherusa glacialis* of the family Gammaridae, dominate the invertebrate ice fauna in the Barents Sea (Syvertsen *et al.*, 1990).

Amphipods are important food of many fishes, sea birds and mammals in the Barents Sea. Studies by Lund (1981) and Ajiad and Pushchaeva (1991) show *T. abyssorum* and *T. libellula* to be important food in the diet of Barents Sea capelin. Bowman, (1960); Lønne and Gulliksen, (1989), Lydersen *et al.* (1989), Nilssen *et al.*, (1991, 1992), and others have shown Polar cod, Arctic charr, ringed seal, harp seal and many sea birds to feed heavily on *T. libellula*. This species is mostly abundant in the Arctic waters and serves as an important link in the food chain between the copepods and other smaller planktonic forms and many vertebrates (Dunbar, 1957).

The information on life cycle of amphipods is scarse. Bogorov (1940) reports a two year life cycle for *T. abyssorum* in the Barents Sea. *T. libellula* can live up to two years in Hudson Bay, and in the waters of southeast Baffin Island (Dunbar, 1957). *T. compressa* has a one year life cycle in the 0-20^0 E sector of the southern ocean (Kane, 1966). Laboratory studies based on intermoult period and moult increment of *Themisto japonica* (10-17mm) from the Japan Sea indicate a life cycle of 333-593 days at 1^0 C and 195-347 days at 5^0 C (Ikeda, 1990).

The current study was conducted to gain more knowledge on the geographical and seasonal variation in abundance and distribution of amphipods in the northern Barents Sea. Longevity of the dominant amphipods, *T. abyssorum* and *T. libellula* is also investigated.

MATERIALS AND METHODS

Our study is based on the samples of amphipods collected during several cruises to the Barents Sea from 1984-1992 (Fig. 1). The sampling area covered 73 ^{0}N to 80 ^{0}N and from 9 ^{0}E to 50 ^{0}E. Material from 19 cruises are included in the current investigation; amphipod data from 12 cruises from Borkner (M. Sc. thesis, in prep.) are used to supplement the material we have examined from 7 cruises.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 333µm nylon mesh netting (dark blue). It was fished obliquely, allowing up to eight depth strata to be sampled. The volume of the water filtered in each stratum varied from 100 to 600 m^3.

Amphipods collected from MOCNESS sampler were preserved in 4% formalin. Samples were brought to the laboratory at the Institute of Marine Research, Bergen and were later analysed. Only the most commonly found hyperiid amphipod genus *Themisto* was taken into consideration in our study. Amphipods 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 total length of amphipods (from the front of the head to the tip of the longest uropod (Dunbar, 1957)) was measured to the nearest mm below. Sexes and maturity stages were separated by the characteristics of antennae, ovary and oostegite development given by Dunbar (1957) and Kane (1963) (Appendix table 1 and Appendix figures 1 and 2).

Length frequency histograms for each cruise were resolved into normally distributed components (Cohorts) using Bahttacharya´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.

The abundance (individuals m^{-2}) and density (individuals m^{-3}) estimated in a MOCNESS profile were classified with reference to Arctic, Atlantic and Polar Front regions by using the description of water masses given by Loeng (1989, 1991).

RESULTS

Distribution and abundance

Horizontal distributions of *T. abyssorum* and *T. libellula* based on average numerical abundance (individuals m^{-2}) from all cruises are given in Figures 2 and 3 respectively. Distributions based on individual stations for each year are given in Appendix figures 3a-i for *T. abyssorum* and 4a-j for *T.libellula*.

T. abyssorum and *T. libellula* were the dominant amphipod species found in the northern Barents Sea (Table 1, Appendix figs. 3 and 4).

T. abyssorum is wide spread and was found in both subarctic and Arctic waters, though mostly predominant in subarctic waters (Fig. 2). In the Arctic waters, the abundance of *T. abyssorum* was quite low (mean of all cruises, 1.8 individuals m^{-2}). In the Atlantic and Polar Front regions the abundance of this species varied from 0.16 to 52.6 individuals m^{-2} with an average of 8.9 individuals m^{-2} (Table 1). High abundances, up to 122 individuals m^{-2} of this species was found in deep waters (300-400m) south and south east of Svalbard Bank (Svalbardbanken) (Appendix fig. 3e-g and i).

The distribution of *T. libellula* seems to be closely related to the different water masses in the Barents Sea (Fig. 3). *T. libellua* was absent in about 80% of the stations taken between 73 and 75^0 N (Atlantic waters). In the area of the Polar Front, close to 76^0 N and between 30 -32^0 E, high abundances up to 430 individuals m^{-2} were recorded. The highest abundances of *T. libellula* were taken in May-June 1987 and July 1988 cruises (Appendix fig. 4e and f). More than 40% of the individuals taken in these two cruises were small (4-8 mm). *T. libellula* were recorded from all stations in the Arctic waters. The average abundance for all cruises from Arctic waters was 15.9 individuals m^{-2} (range 4.5-30.7 individuals m^{-2}).

T. compressa was very seldomly observed and was restricted to Atlantic waters. The abundances of this species were rather low, with an average of all cruises being 1.04 individuals m^{-2}. No *T. compressa* was recorded from the Arctic waters (Table 1).

Density

The numerical densities of *T. abyssorum*, *T. libellula* and *T. compressa* are summarised in Table 2. Density of *T. abyssorum* in the Arctic water masses was much lower than in Atlantic and Polar Front regions. The mean density of all cruises was 0.007 and 0.042 individuals m^{-3}, respectively in these two regions (Table 2). The highest densities for this species were observed in March, July and October 1988 and in January 1989 cruises from the Atlantic waters.

T. libellula from Arctic waters had a mean density of 0.182 individuals m^{-3}. In the Atlantic and Polar Front region the average density was 0.046 individuals m^{-3} (Table 2). Maximum density for this species was observed in August 1985 with 0.28 individuals m^{-3}. We observed very low densities of *T. compressa*, usually below 0.015 individuals m^{-3} in the area investigated.

Vertical distribution

Figure 4 shows the numerical density of *T. abyssorum* and *T. libellula* plotted against the water depth at sampling stations.

In the Atlantic and Polar Front region, the highest densities of *T. abyssorum* were taken in deeper areas at depths of 250 to 500m. This trend was not so clear in the Arctic waters. A single station with very high concentrations (0.8 individuals m^{-3}) of *T. libellula* was recorded in shallow waters (90m) of the Arctic region. In the Atlantic and Polar Front region the highest densities of this species were usually found at water depths of 250 to 325m.

Plots of densities of *T. abyssorum* and *T. libellula* vs mean sampling depths for individual stations from a selected cruise (July 1988, due to adequate depth coverage), are given in Figs. 5 and 6 respectively. The highest densities of *T. abyssorum* were taken at depths of 100-200m (Fig. 5). The maximum densities of *T. libellula* were recorded from the upper 50 m. Data from May-June 1987 cruise also show that very high densities, up to 1.4 individuals m^{-3} of *T. libellula* were taken in the upper 40 m. Most of the individuals taken in the upper 50 m were below 8 mm. Adults were usually found at depths between 100 to 250m.

Life cycle

Length frequency distributions of *T. abyssorum* and *T. libellula* are given in Figs. 7 and 8. The length of *T. abyssorum* varied from 2-16 mm, whereas for *T. libellula*, from 2-40 mm (Figs. 7 and 8). The length range recorded for *T. compressa* was 4-25 mm (Fig. 9).

Bahttacharya´s analysis of length frequency histograms of *T. abyssorum* gave one mode except in May-June samples (Table 3). In *T. libellula*, up to 5 modes were recorded (Table 4). Number of *T. compressa* in this study were too few to run Bahttacharya´s analysis.

Mature individuals of *T. abyssorum* (9-12 mm) were found from March-June whereas females bearing young were observed only in May and June. *T. abyssorum* seems to release their young during this period at a size of ca. 2-3 mm. This was the only time period we observed two cohorts in the Bahttacharya´s analysis. We define the first cohort with mean length of 2-3.5 mm to consist of newly released individuals (0-group) and 2nd with a mean of 9-10.3 mm to be 1 group (Fig. 10 and Table 3). By August/September the 0- group individuals had a mean length of 5-6mm. Individuals below average of 7.5 mm were not recorded from mid September onwards to April. No marked growth was observed during January to May. The maximum mean length of a cohort recorded in our study was 10.7 mm, in March. We did not observe spent females, with ruptured brood pouches in our study except in May. Our data suggest a one year life cycle for *T. abyssorum*. This species seem to spawn once and die.

For *T. libellula*, the interpretation of growth pattern is somewhat difficult. This species lives in colder waters than *T. abyssorum* and seems to have an earlier and prolonged breeding period. Mature females with brood pouches were observed in January while females bearing young were found only in March. In our study individuals of ca. 2.5 mm were observed in March and ca. 5mm from May to October. If we assume that an individual of 2 mm takes ca. 3 months to grow to a size of about 5 mm (as reported for *T. abyssorum*), this will imply that new broods are still being shed in July-August, indicating a considerable extended breeding period for *T. libellula*. We lack data from November-December.

Mature females of *T. compressa* were not recorded in our material. Mature males with long antennae were observed in May-June 1987 and May 1989.

DISCUSSION

Geographical distribution and life cycle

Three species of the genus *Themisto* (*T. abyssorum, T. libellula* and *T. compressa*) were recorded in our study. Of these *T. abyssorum* predominated in the sub Arctic waters, whereas *T. libellula* in the Arctic waters. *T. compressa was* rare and restricted to the warmer Atlantic waters. The distribution patterns of *Themisto* spp. from the North Atlantic, given by Bogorov (1940), Bowman, (1960) and Dunbar (1957, 1964), are similar to our observations. According to Schneppenheim, R and R. Weigmann-Haass (1986)*Themisto Compressa* (Goes) (until recently referred as *Parathemisto gaudichaudii* or*Themisto gaudichaudii)* and the Antarctic *T. gaudichaudii* (Guérin) are distinct and valid species.

In our study the highest abundances of *T. abyssorum* and *T. libellula* were recorded in the summer and early autumn. Bogorov (1940) found the highest abundances of *T. abyssorum* in the Barents Sea in late summer whereas studies by Wing (1976) in Alaskan waters showed peak abundances of *T. libellula* in late spring and early summer.

T. abyssorum seem to release their young at a size of ca. 2 mm in May-June. Our observations are similar to those of Bogorov´s (1940) from the Barents Sea. Females were mature around 9-12 mm. Our data suggests a one year life cycle for *T. abyssorum* . They seem to spawn once and die. Bogorov (1940) indicates a two year life cycle for *T. abyssorum*. His interpretaion is not clear and seems unreasonable.

We found the highest concentrations of *T. libellula* close to the Polar Front region in May-June 1987 and July 1988. Most of the individuals taken in these two cruises (93 and 42% respectively) were between 2 to 8mm. In the Arctic waters very few individuals below 8 mm were present. Our observations seem to indicate that breeding of this species occurs close to the productive Polar Front Region. Dunbar (1964) reports that since the food supply is rather poor in the Arctic Ocean, *T. libellula* may not breed in the main body of the Arctic zone. He suggests the center of production of this species to lie in the peripheral waters of the Arctic zone.

T. libellula seem to have a breeding period extending from March to July. As new brood are being shed over a long time, these individuals will be of different sizes, it is therefore difficult to interpret the growth pattern of this species using modes observed from Bahttacharya´s analysis. However, length frequency data from the Atlantic/Polar Front regions arranged disregarding the year as in Fig. 8 indicate a life span of up to two years for *T. libellula.* Our observations are in comparison with Dunbar´s (1957) studies from the Hudson Bay, Hudson Strait, and the waters of southeast Baffin Island and with Wing´s (1976) from Alaskan waters.

Both species seem to have a breeding period, generally coinciding with the spring phytoplankton bloom in the Barents Sea. Dissolved organic matter may play an important part in the direct diet of the small amphipods released from the parental brood pouches in the winter period (Dunbar, 1957).

Position in the food web.
Amphipods are very important food of sea birds, harp seals and ringed seals (Lydersen *et al.* 1989; Dunbar, 1964; Bradstreet and Cross, 1982; Nilssen *et al.*, 1991,1992). Harp seal is the most abundant seal species in the Barents Sea. The diet of harp seal from northern packed-ice areas to the south of Kvitøya and Viktoria Island during September 1991, consisted 79.7% *T. libellula* in numbers and 28.7% in biomass (Nilssen *et al.* 1991, 1992). Bradstreet and Cross (1982) in describing the trophic relationships at ice edges in the Canadian High Arctic, showed *Themisto* spp. to be an important component of the zooplankton fauna. Our study also show that amphipods are dominant in the Arctic water masses of the Barents Sea. This is in contrast to the Barents Sea krill, *Thysanoessa spp.*, which are mainly restricted to the Atlantic waters (Dalpadado and Skjoldal, 1991, 1994). *Themisto* spp. are mainly carnivorous and feed on copepods, fish larvae, euphausiids etc. (Bigelow 1926; Dunbar, 1964, Sheader and Evans, 1975). They can also feed on microalgae (Wing, 1976; Bradstreet and Cross, 1982).

These studies clearly show that *Themisto* spp., especially pelagic *T. libellula* plays a key role in the Arctic ice edge food web, in serving as a link between the copepods and other smaller planktonic forms and many vertebrates. Studies by Percy and Fife (1981) from southern Baffin Island showed *T. libellula* to reserve high amounts of lipid (18.2-34.6 % of dry weight) over the course of the summer. The values are comparable to the ones given by Lee (1975) for *T. abyssorum* from Arctic waters. These studies, as well as Bradstreet and Cross´s (1982) show that Arctic zooplankton like *T. abyssorum* and *T. libellula* store energy as lipids during summer when primary and secondary production is high. These reserves are used through fall and winter, resulting in minimum values in spring.

Themisto spp. are important food also of many commercial fish species in the Barents Sea as capelin, polar cod and halibut (Lund 1981; Haug *et al.* 1989; Lønne and Gulliksen 1989; Ajiad and Pushchaeva, 1991). Haug *et al.* (1989) report that one group halibut of 9.5-13.2 cm, fed up to 55% on *T. libellula*. Studies by Lund (1981) show that the caloric importance of *T. abyssorum* and *T. libellula* in the diet of Barents Sea capelin (13-16 cm) can vary from 0.8 to 41.8%. The highest values were observed in autumn and the lowest in spring. Ajiad and Pushchaeva (1991) also showed the importance of *T. abyssorum* and *T. libellula* (14.5% by weight) in the diet of 9-12 cm capelin.

In the Barents Sea, the feeding areas of capelin overlaps with the distribution areas of amphipods. Figure 11 show the variation in abundance (individuals m^{-2}) of *T. abyssorum* and *T. libellula* plotted against the stock size of capelin (million tons). Strong reduction in the capelin stock occured from 1984 to 1986. Followed by this decrease there was an increase in the abundance of *T. abyssorum* and *T. libellula* . The highest abundance estimated in our study for *T. libellula* was in 1987 and for *T. abyssorum* in 1988. This could be as Skjoldal *et al.* (1992) point out due to the reduced grazing pressure from capelin. The very low abundance of *T. libellula* (0.4 individuals m^{-2}) in 1986 is due to that samples were only available from Atlantic waters.

With the increase in the capelin stock from 1989 upto 1991 a decrease in amphipod abundance was seen. This is probably due to the increased grazing pressure from capelin. Dalpadado and Skjoldal (1994) found similar trend in variation of capelin stock size with krill biomass during 1984-1992. Their´s and our results indicate clear predator-prey interactions between capelin and their major prey as krill and amphipods.

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Table 1. *T. abyssorum, T. libellula* and *T. compressa*. Means and ranges of numerical abundance (number of individuals m-2) and length (mm) observed during different cruises from 1984 - 1992.

Tabell 1. *T. abyssorum , T. libellula* og *T. compressa*. Middelverdier og variasjonsbredde for antall individer m-2 og lengde (mm) observert under ulike tokt fra 1984 - 1992.

Atlantic /P.F	Cruise	No.of	Abundance		Length	
T. libellula		stations	No/m2		(mm)	
			mean	range	mean	range
	Jun.84	6	4,79	0,00-21,12	12,44	5-32
	Aug.84	1	0	0	0	0
	Jan.85	7	0,65	0,00-1,98	26,9	15-38
	Aug.85	6	7,01	0,00-14,11	15,11	4-27
	May.86	2	0,035	0,00-0,07	7	7
	Feb/Mar.87	6	0,39	0,00-0,39	26,8	15-28
	Mai/Jun87	8	103,15	0,00-432,94	7,61	2-32
	Sep.87	6	7,52	0,26-15,57	21,36	5-37
	Mar.88	6	9,52	0,00-54,20	2,6	2-30
	Jul.88	7	33,27	2,3-50,33	11,31	4-38
	Oct.88	3	1,38	0,00-4,16	21,2	19-24
	Jan.89	6	2,23	0,00-11,32	26,25	21-31
	May.89	5	0,632	0,00-2,43	8,15	4-11
	Jan.91	3	0,55	0,00-1,66	12,56	10-16
	May/Jun.91	6	0,265	0,00-1,59	5,5	5-6
	Sep.92	7	1,75	0,00-0,73	23,85	20-28
	Sept/Oct92	6	0	0	0	0
T. abyssorum	Jun.84	6	3,47	0,00-14,74	6	3-14
	Aug.84	1	0,978	0,978	4,33	4-5
	Jan.85	7	4,36	0,15-13,12	9,64	4-14
	Aug.85	6	6,79	0,00-24,65	5,37	3-13
	Apr.86	4	0,79	0,14-1,98	10,2	5-15
	May.86	2	0,16	0,16	8	8
	Feb/Mar.87	6	7,42	0,00-15,38	10,7	7-14
	May/Jun.87	8	3,02	0,00-12,97	8,25	2-13
	Sep.87	6	9,13	0,00-24,2	4,97	3-12
	Mar.88	6	9,72	0,00-33,29	10,7	8-14
	Jul.88	7	52,58	0,77-122,10	5,72	3-12
	Oct.88	3	43,05	1,21-98,64	7,96	4-14
	Jan.89	6	17	2,64-28,73	10,4	5-16
	May.89	5	13,55	0,5-35,53	10,3	3-15
	Jan.91	3	1,09	0,82-1,39	12,56	10-16
	May/Jun.91	6	16,8	16,8	5,9	5-8
	Sep.92	7	0,67	0,67-3,05	9,81	3-15
	Sept/Oct92	6	8,83	0,68-31,46	7,11	3-14
Arctic						
T. libellula	Aug.84	5	13,08	6,44-18,05	16,69	6-36
	Aug.85	4	30,69	16,26-71,92	15,11	5-35
	Sep.87	3	10,28	1,27-21,90	23,96	5-41
	Sep.88	5	23,05	2,92-39,28	18,3	6-27
	Sep.92	4	4,53	0,71-11,16	19,32	7-28
	Sept/Oct.92	4	13,6	2,6-27,73	22,55	9-32
T. abyssorum	Aug.84	5	2,72	0,00-8,66	5,55	4-12
	Aug.85	3	0,75	0,38-1,44	5,85	4-10
	Sep.88	5	0,42	0,00-1,67	7,25	5-11
	Sep.92	4	2,72	0,69-4,78	7,45	5-11
	Sept/Oct92	4	2,56	1,14-6,73	8,32	3-11
Atlantic						
T. compressa	Jan.85	5	1,96	0,21-2,67	15,19	7-17
	Apr.86	4	0,012	0,00-0,05	17	17
	May/Jun.87	8	1,84	0,00-14,76	6,6	4-17
	Mar.88	6	1,51	0,00-6,45	11,25	10-16
	Oct.88	3	1,76	0,00-2,93	12,7	10-14
	Jan.89	6	0,21	0,00-1,3	12,5	12-13
	May.89	5	1,09	0,00-3,26	12,03	5-16
	Sep.92	7	0,67	0,00-3,05	11	7-15
	Sept/Oct92	6	0,34	0,00-2,06	12	8-15

Table 2. *T. abyssorum* ,*T. libellula* and *T. compressa*. Means and ranges of numerical density (number of individuals m^{-3}) observed during different cruises from 1984-1992.

Tabell 2. *T. abyssorum, T. libellula* og *T. compressa*. Middelverdier og variasjonsbredde for tetthet (antall individer m^{-3}) observert under ulike tokt fra 1984 - 1992.

Cruise	No.of	***T. abyssorum***		***T. libellula***		***T. compressa***	
	stations	Density		Density		Density	
		No/m3		No/m3		No/m3	
Atlantic/P.F		mean	range	mean	range	mean	range
Jun.84	6	0,018	0,00-0,076	0,024	0,00-0,108	0	0
Aug.84	1	0,005	0,005	0	0	0	0
Jan.85	7	0,019	0,007-0,050	0,003	0,00-0,007	0,007	0,00-0,016
Aug.85	6	0,038	0,00-0,156	0,036	0,00-0,080	0	0
Apr.86	4	0,006	0,001-0,015	0	0	0,0001	,0001-0,0004
May.86	2	0,001	0,00-0,002	0,0004	0,00-0,0009	0	0
Feb/Mar.87	6	0,024	0,00-0,052	0,001	0,00-0,008	0	0
May/Jun.87	8	0,015	0,00-0,053	0,418	0,00-1,424	0,006	0,00-0,050
Sep.87	6	0,034	0,00-0,088	0,024	0,00-0,128	0	0
Mar.88	6	0,042	0,00-0,087	0,041	0,00-0,220	0,0038	0,00-0,016
Jul.88	7	0,201	0,011-0,397	0,189	0,007-0,537	0	0
Oct.88	3	0,145	0,011-0,327	0,0046	0,00-0,013	0,006	0,00-0,009
Jan.89	6	0,067	0,011-0,129	0,008	0,00-0,040	0,0008	0,00-0,005
May.89	5	0,044	0,002-0,093	0,09	0,00-0,450	0,0036	0,00-0,012
Jan.91	3	0,004	0,003-0,005	0,002	0,00-0,008	0,001	0,00-0,003
May/Jun.91	6	0,006	0,00-0,041	0,001	0,00-0,006	0	0
Sep.92	7	0,052	0,003-0,119	0,0009	0,00-0,004	0,001	0,00-0,007
Sep/Oct.92	6	0,034	0,004-0,077	0	0	0,0008	0,00-0,0051
Arctic							
Aug.84	5	0,011	0,00-0,036	0,077	0,025-0,139	0	0
Aug.85	4	0,0026		0,28	0,068-0,84	0	0
Sep.87	3	0	0	0,053	0,005-0,128	0	0
Sep.88	5	0,001	0,00-0,005	0,094	0,023-0,137	0	0
Sep.92	4	0,017	0,004-0,029	0,031	0,004-0,073	0	0
Sep/Oct.92	4	0,011	0,006-0,019	0,084	0,023-0,196	0	0

Table 3. *T. abyssorum* . 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 and 1 with a change in age spring.

Tabell 3. *T. abyssorum*. Antall og middellengde av cohorter adskilt i lengde- frekvens analyse. Cohortene antas å representere aldersgruppene 0 og I med skifte om våren.

Time period	No.st	No.ind.	Cohort	No. of ind. in cohort	Mean No/m3	Mean leng.	Maturity observations
Jun.84	6	233	0	207	0,032	2,6	Female with young.
			1	22	0,003	9,4	Male with long antennae.
Aug.84	6	50	0	50	0,011	5	No adults.
Jan.85	8	209	0	209	0,019	8,23	
Aug.85	10	265	0	263	0,028	5,72	
Apr.86	4	54	0	54	0,006	9	
May.86	1	1*		1	0,001	8	
Feb/Mar.87	6	67	0	67	0,024	10,7	
May/Jun.87	8	59	0	32	0,007	3 to4	Female with young.
			1	27	0,006	9	Male with long antennae.
Sep.87	9	168	0	168	0,023	4,77	
Mar.88	6	138	0	139	0,042	9,6	Female with eggs.
Jul.88	7	411	0	409	0,201	5,7	4 mature individuals.
Sep.88	5	6*	0	6	0,001	6,5	
Oct.88	3	148	0	148	0,145	7,52	
Jan.89	7	182	0	182	0,067	9,54	
May.89	5	106	0	106	0,006	2	
			1		0,029	10	
Jan.91	3	12*		12	0,004	12,56	
Jun.91	6	51	0	50	0,006	5,69	
Sep.92	21	386	0	383	0,029	9,2	

*Too few individuals, not used in the analysis.

Table 4. *T. libellula*. Number of individuals and mean total lengths of cohorts separated in the length frequency analysis.

Tabell 4. *T. libellula*. Antall individer og middellengde av cohorter adskilt i lengde-frekvens analyse.

Time period	No.st	No of ind. in cohort	Cohort	Mean len.	Maturity observations
Jun.84	6	449	1	4,79	
Aug.84	6	516	4	5	
				10,93	
				15,86	Female with small oostegites.
				22,32	Male with small antennae.
Jan.85	8	24	2	24,73	
				33,74	Female with brood pouches
Aug.85	10	1075	2	8,48	Female with small oostegites.
				14,67	Male with small antennae.
May.86	2	1		7	
Feb/Mar.87	6	4		26,8	
May/Jun.87	8	1812	2	5,93	
				10,85	
Sep.87	9	306	5	9,58	
				15,5	
				19,55	
				27,25	
				34,66	
Mar.88	6	157	2	2,5	Female with young in the brood pouches
				24,67	
Jul.88	7	573	3	7,93	
				17,71	
				Ca 34	
Sep.88	5	184	2	10,71	
				20,57	
Oct.88	3	10			
Jan.89	7	23	2	24,77	Female with brood pouches.
				29,91	Male with long antennae.
May.89	5	169	1	4,79	
Jan.91	3	7		27,9	
Jun.91	6	9		5,5	
Sep.92	21	149	2	12	
				26,24	

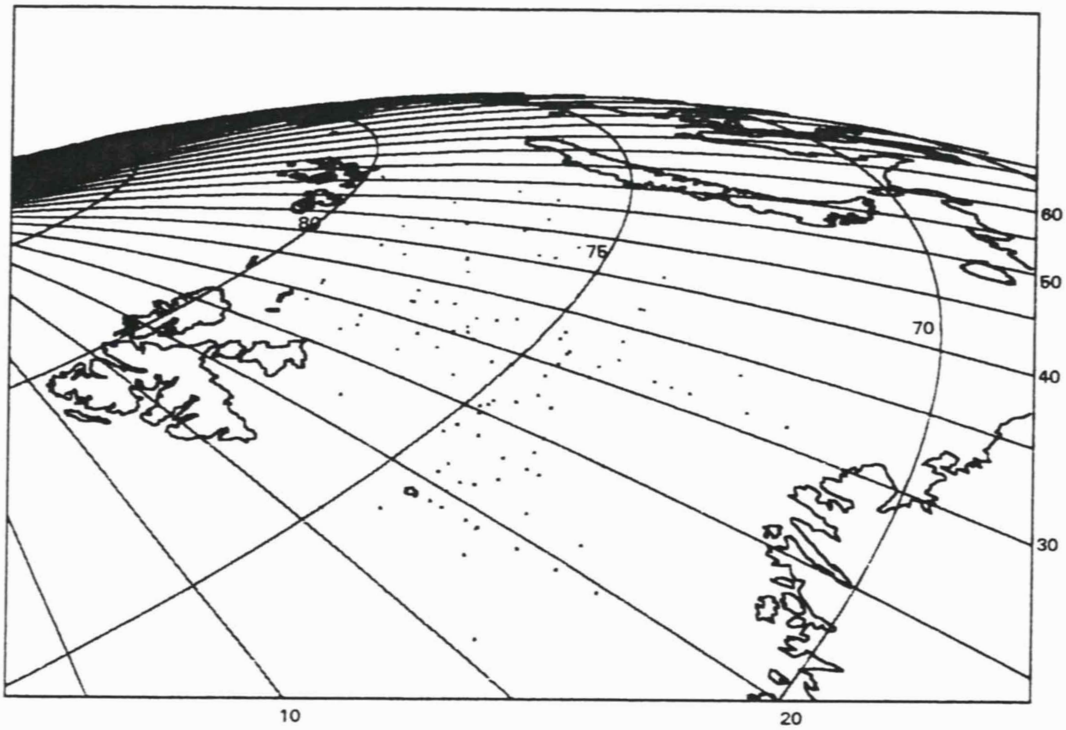


Figure 1. Locations of MOCNESS stations in the Barents Sea, from 1984 to 1992.

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

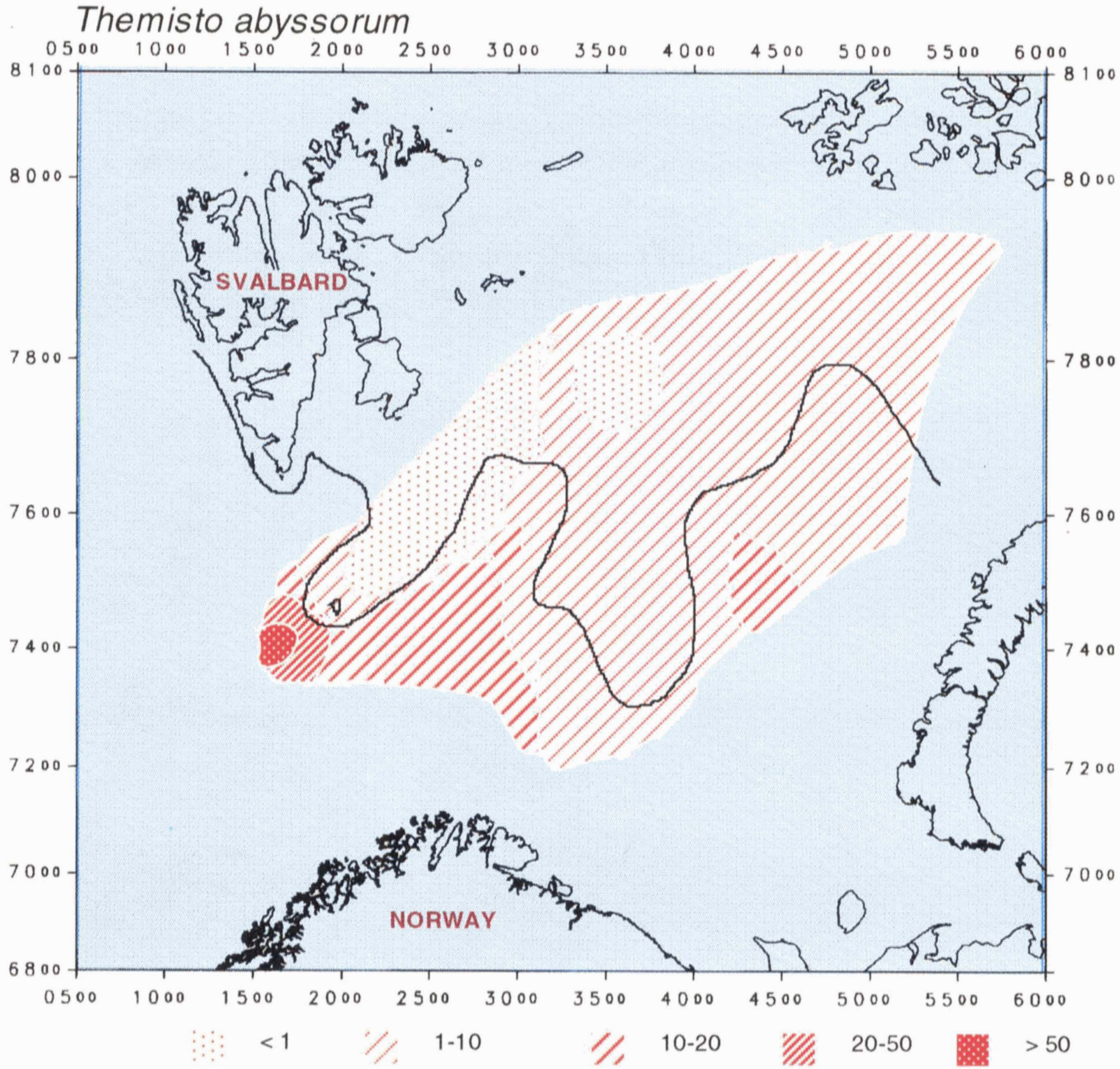


Figure 2. Horizontal distributions in the Barents Sea, based on average numerical abundance (no. m^{-2}) from all cruises, 1984 -1992. The black solid line indicates the Polar Front.

Figur 2. Horisontalfordeling i Barentshavet. Middelantall m^{-2} for alle tokt, 1984 - 1992. Heltrukket linje viser polarfronten.

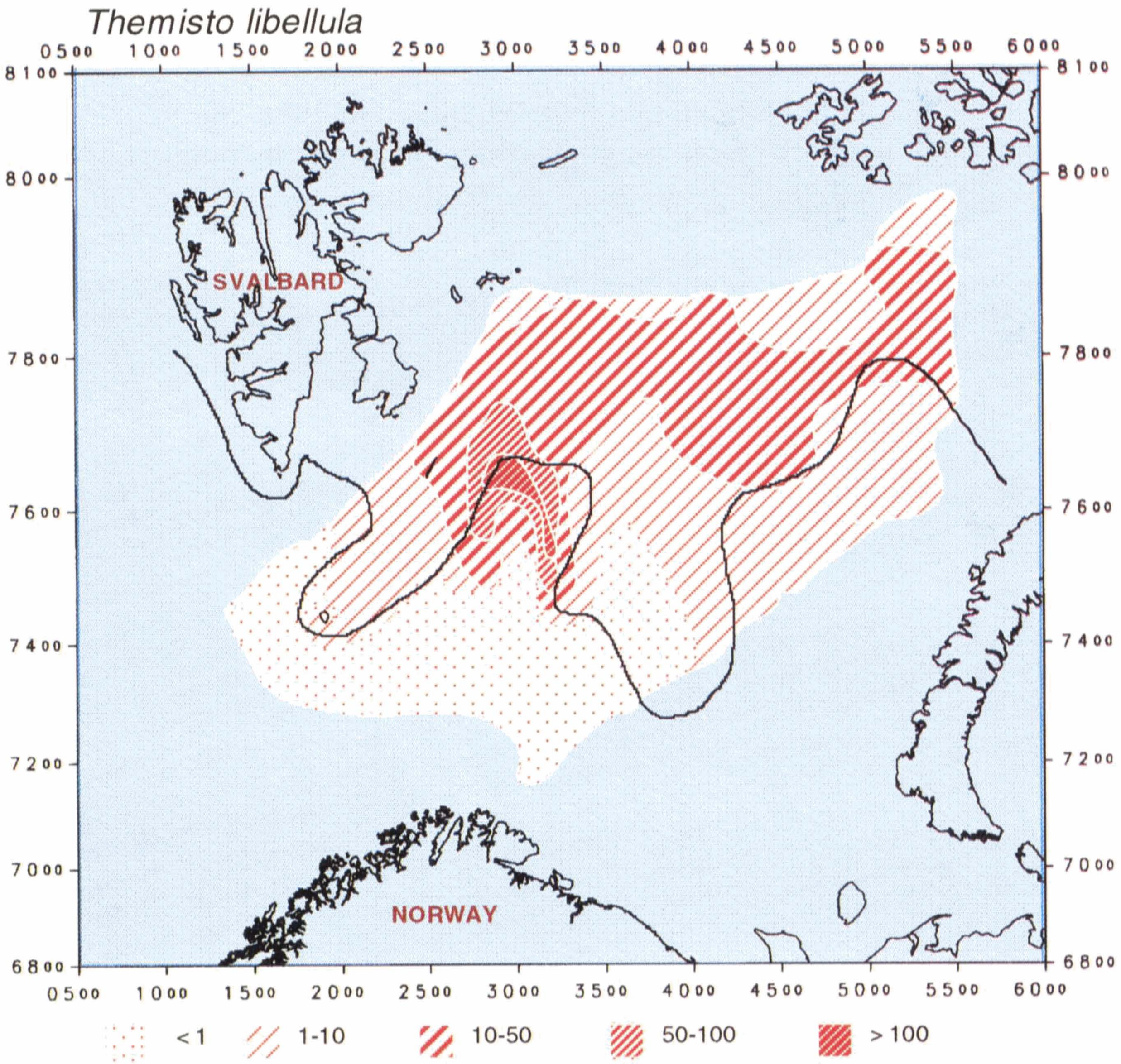


Figure 3. Horizontal distributions in the Barents Sea, based on average numerical abundance (individuals m^{-2}) from all cruises, 1984-1992. The black solid line indicates the Polar Front.

Figur 3. Horisontalfordeling i Barentshavet. Middelantall m^{-2} for alle tokt, 1984 - 1992. Heltrukket linje viser polarfronten.

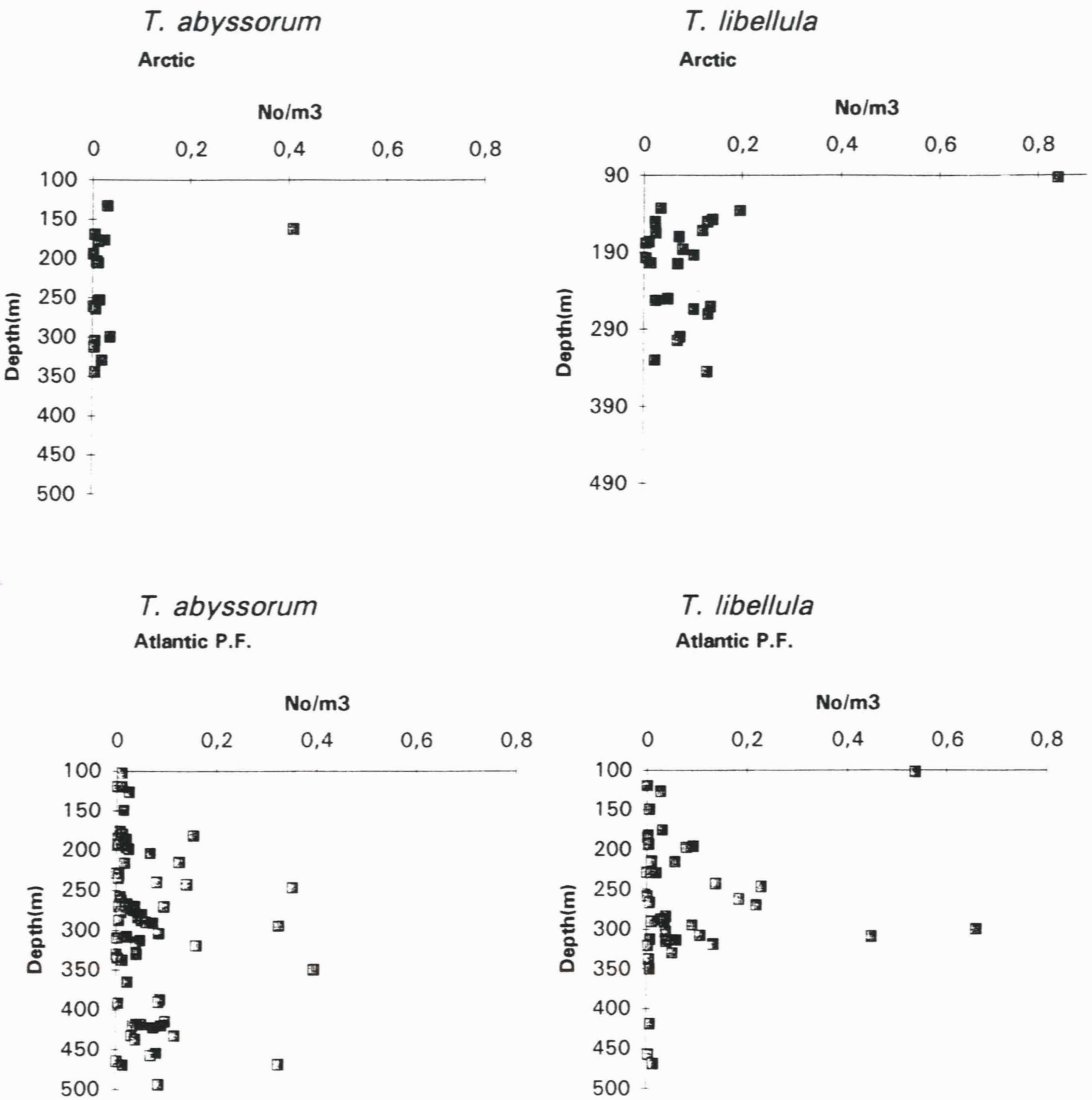


Figure 4. *T. abyssorum* and *T. libellula*.. Numerical density (individuals m^{-3}) in relation to water depth at sampling stations.

Figur 4. *T. abyssorum* og *T. libellula*. Tetthet (antall m^{-3}) i relasjon til dyp på stasjonene.

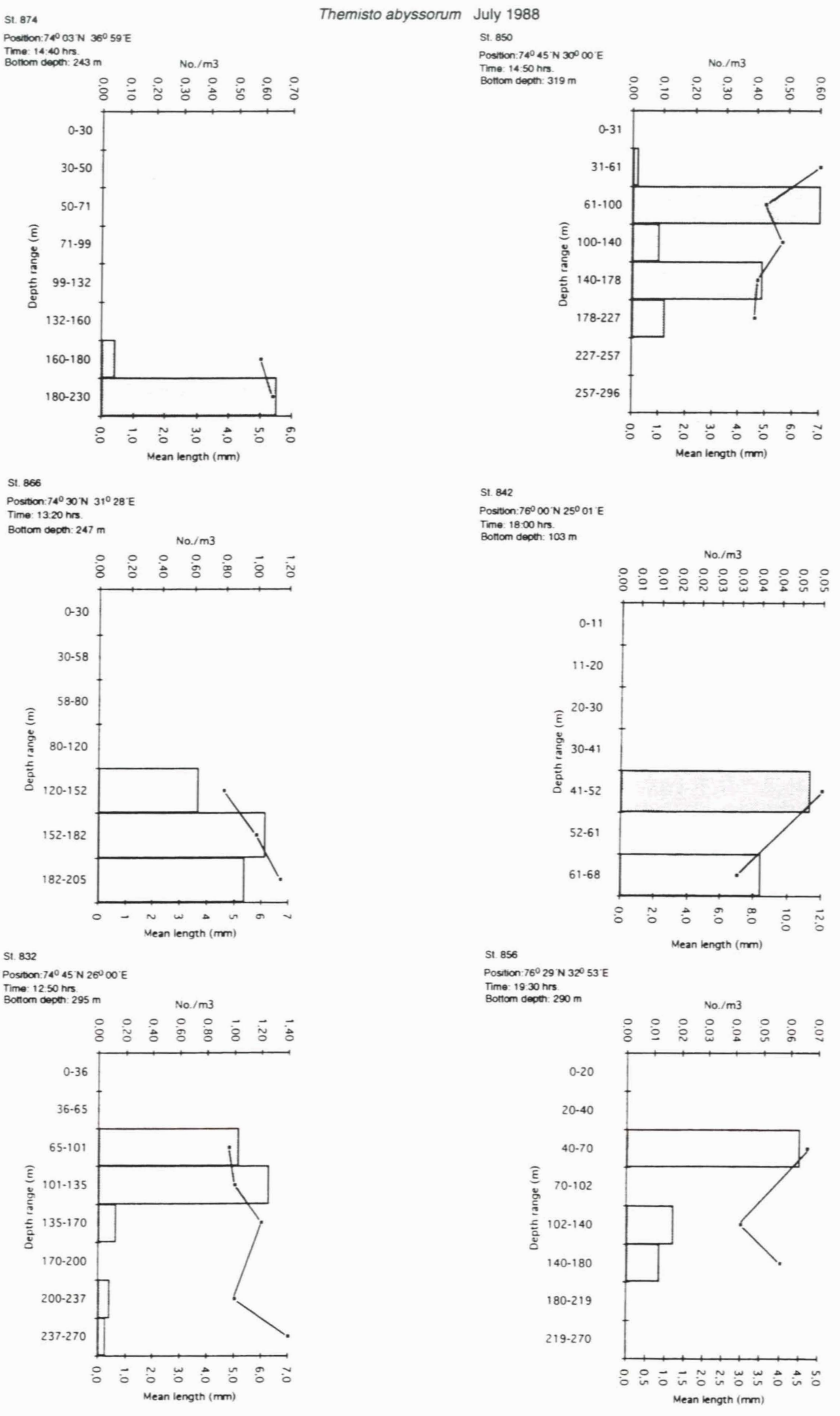


Figure 5. *T. abyssorum*. Numerical density (individuals m^{-3}) in relation to mean sampling depths, from July 1988.

Figur 5. *T. abyssorum*. Middeltetthet (antall m^{-3}) i relasjon til middel prøvetakings dyp, fra juli 1988.

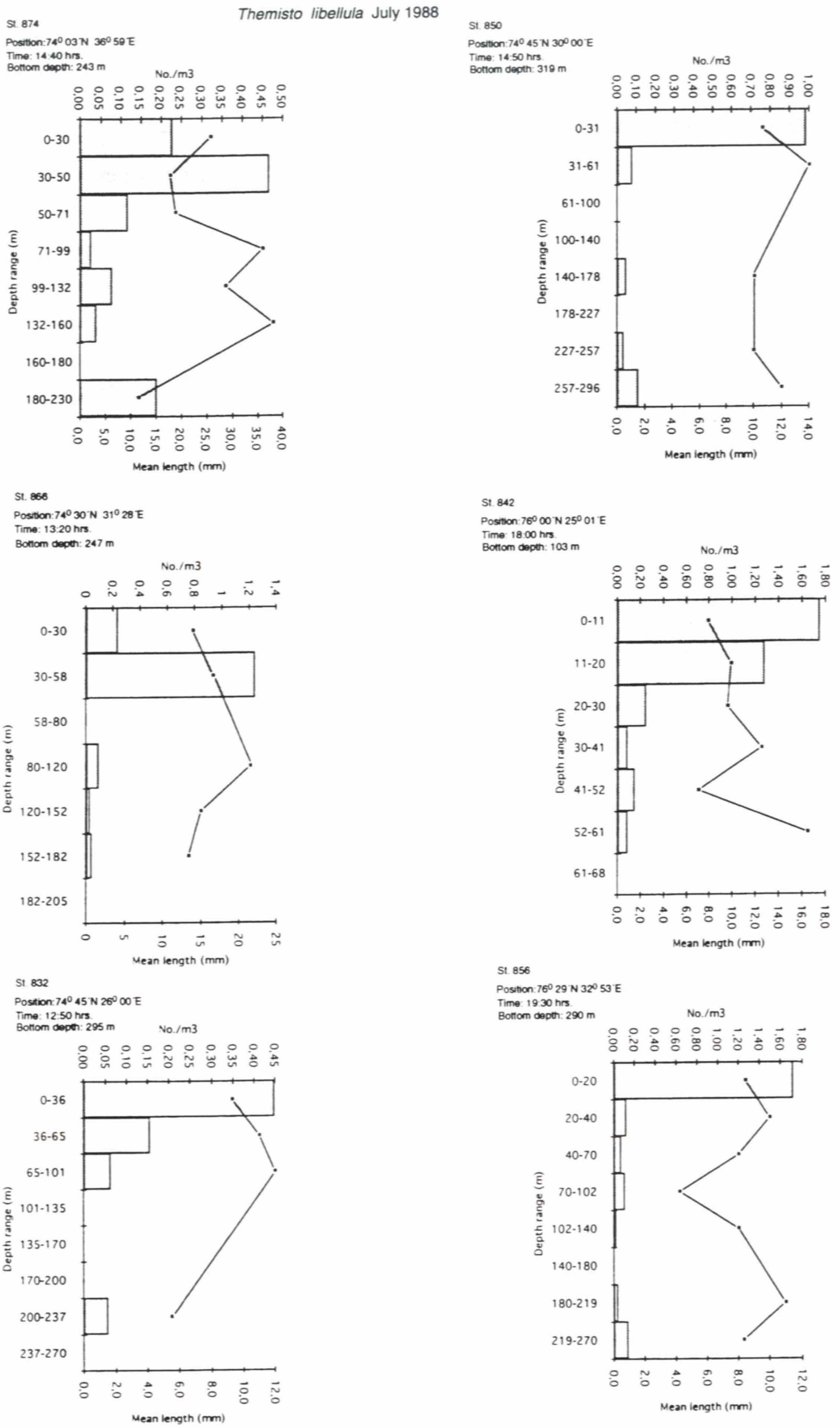
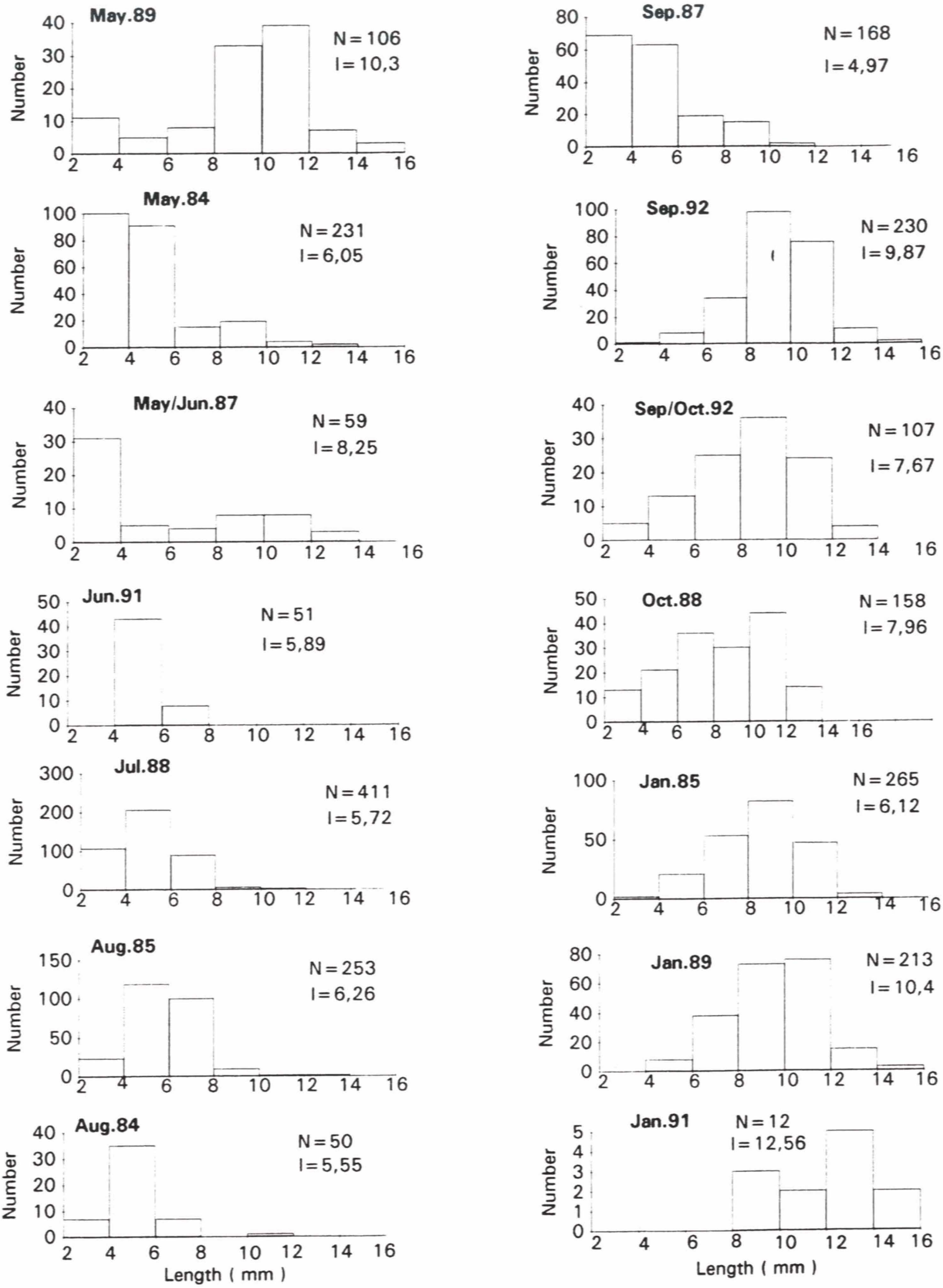


Figure 6. *T. libellula*. Numerical density (individuals m^{-3}) in relation to mean sampling depths, from July 1988.

Figur 6. *T. libellula*. Middelteltthet (antall m^{-3}) i relasjon til middel prøvetakings dyp , fra juli 1988

T. abyssorum **Atlantic / Polar Front.**



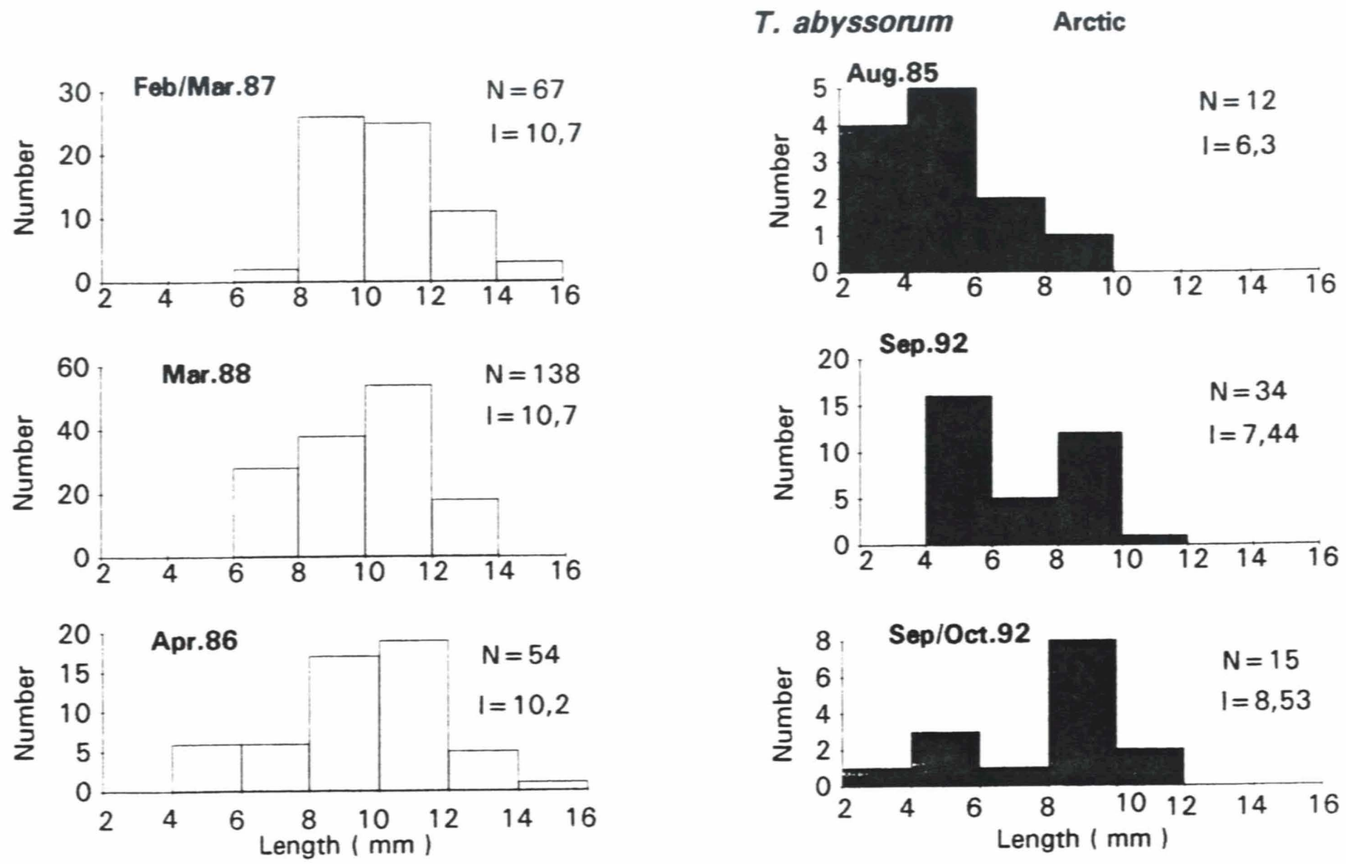


Figure 7. *T. abyssorum.* Length frequency histograms from different cruises from 1984-1992. Open bars, Atlantic and Polar Front region; filled bars, Arctic waters. N = number of individuals, l = mean length.

Figur 7. *T. abyssorum.* Lengde-frekvens histogrammer for ulike tokter fra 1984 - 1992. Åpne søyler, Atlantisk og polarfront område, fylte søyler, arktisk vann. N=antall individer. l=middel lengde.

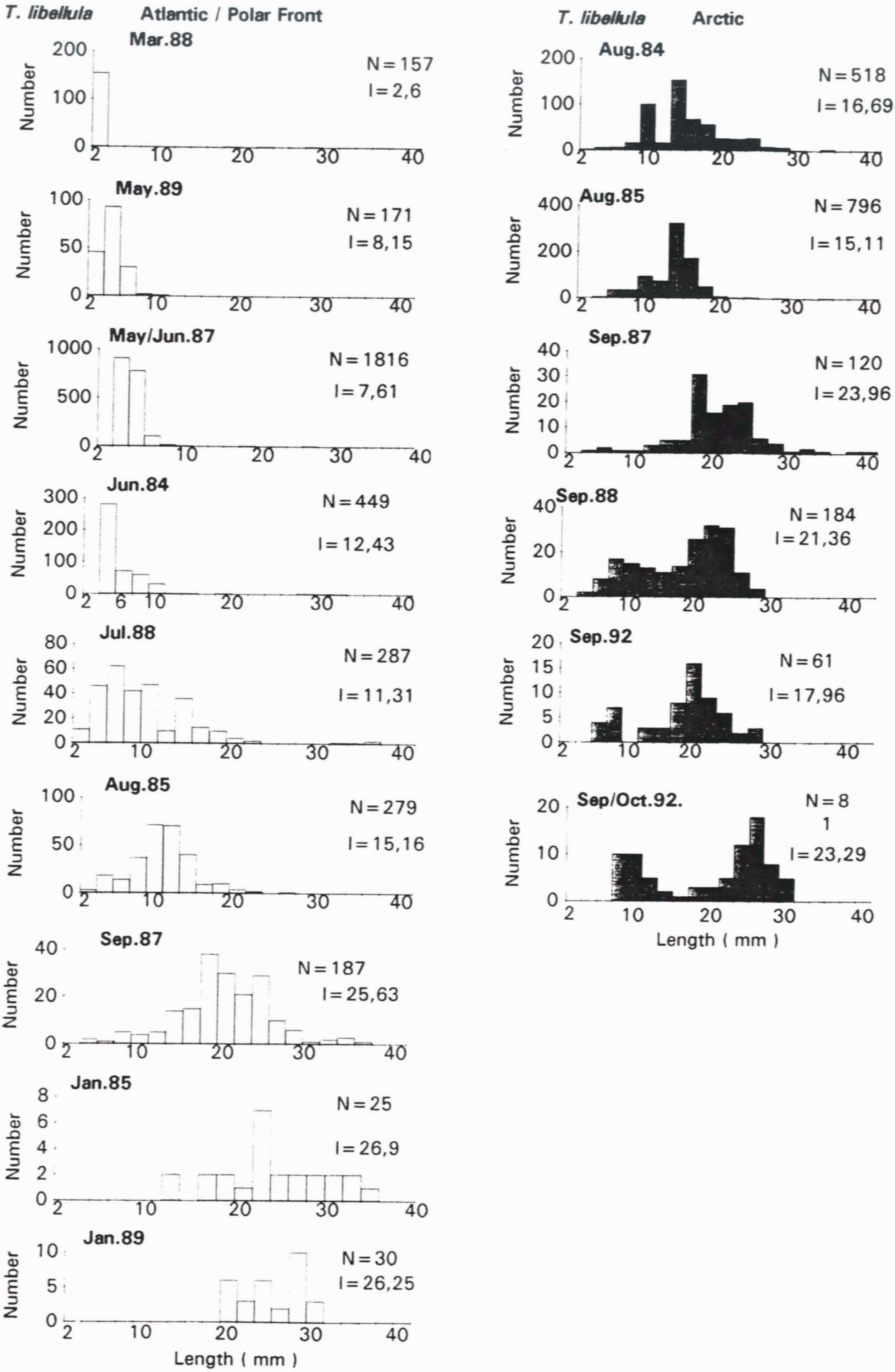


Figure 8. *T. libellula.* Length frequency histograms from different cruises from 1984-1992. Open bars, Atlantic and Polar Front region; filled bars, Arctic waters. N = number of individuals, l = mean length

Figur 8. *T. libellula.* Lengde-frekvens histogrammer for ulike tokter fra 1984 - 1992. Åpne søyler, Atlantisk og polarfront område, fylte søyler, arktisk vann. N=antall individer. l=middel lengde.

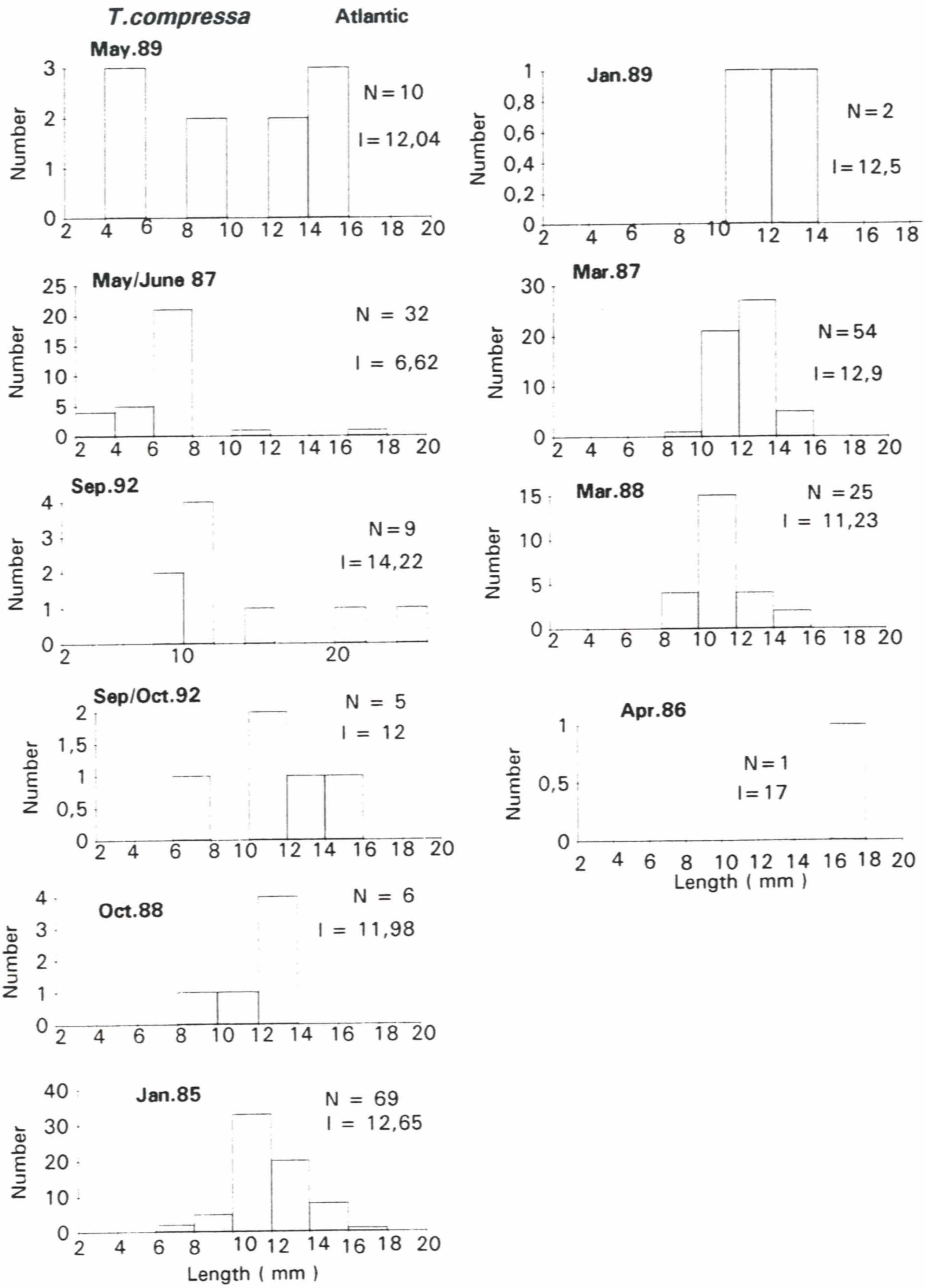


Figure 9. *T. compressa.* Length frequency histograms from different cruises from 1984-1992. Open bars, Atlantic region. N = number of individuals, l = mean length.

Figur 9. *T. compressa.* Lengde-frekvens histogrammer for ulike tokter fra 1984 - 1992. Åpne søyler, Atlantisk område. N=antall individer. l=middel lengde.

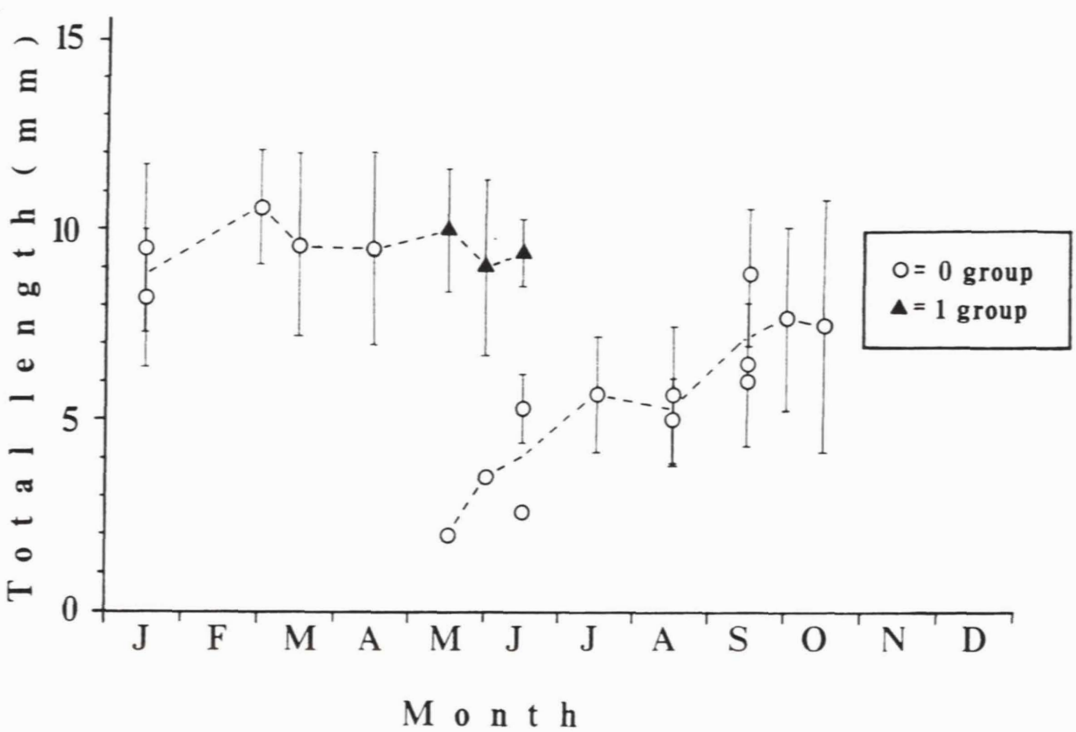


Figure 10. *T. abyssorum.* Seasonal variation in mean length of cohorts separated in length frequency analysis. Vertical bars represent two times standard deviation.

Figur 10. *T. abyssorum.* Sesongvariasjon i middel lengde av cohorter adskilt i lengde-frekvens analyse. Vertikale streker representerer to ganger standard avvik.

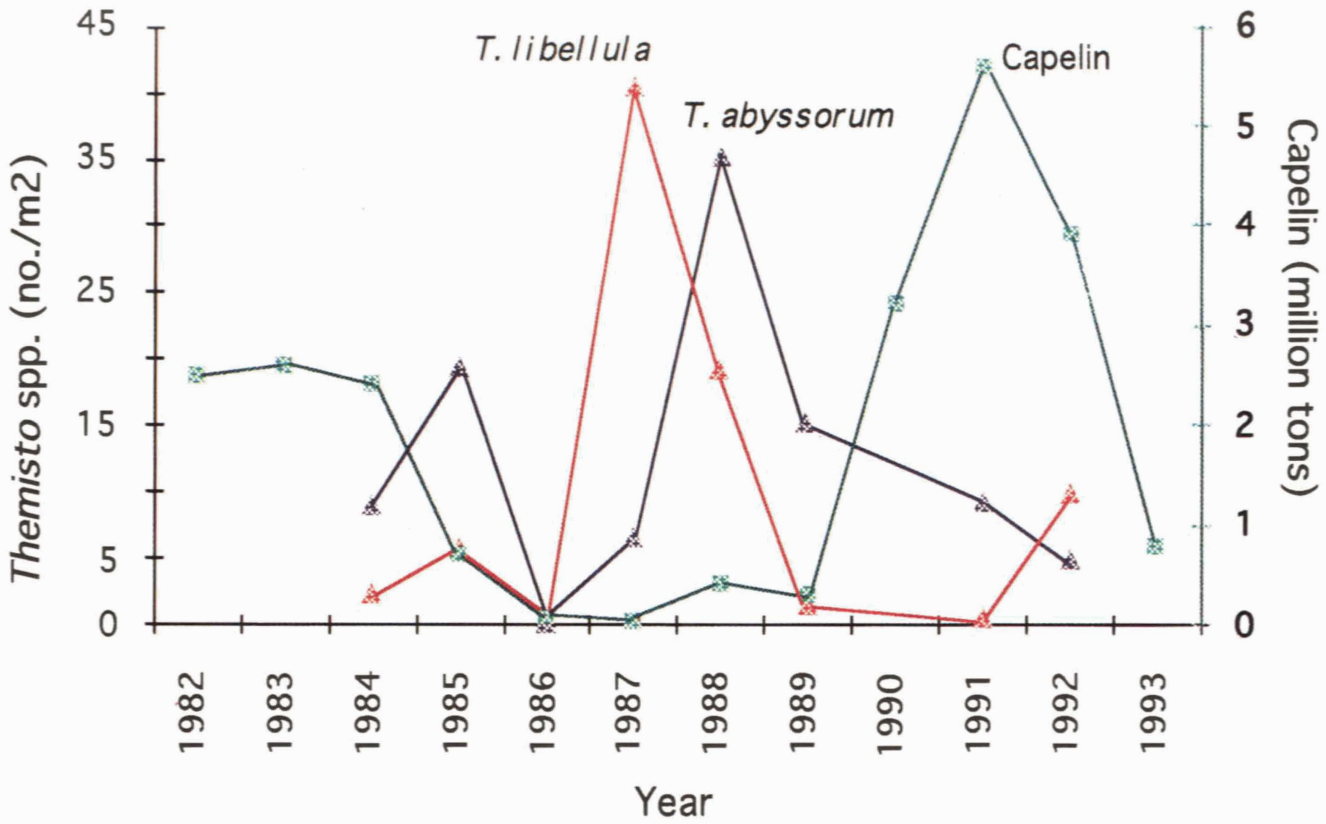


Figure 11. Variation in numerical abundance (individuals m-^{2}) of *T. abyssorum* and *T. libellula* and the biomass of two year and older capelin (million tons), from 1982-1992

Figur 11. . Variasjon i tetthet av *T. abyssorum* og *T. libellula* (individer m-^{2}) og biomasse av to år og eldre lodde (millioner tonn) fra 1982 - 1992.

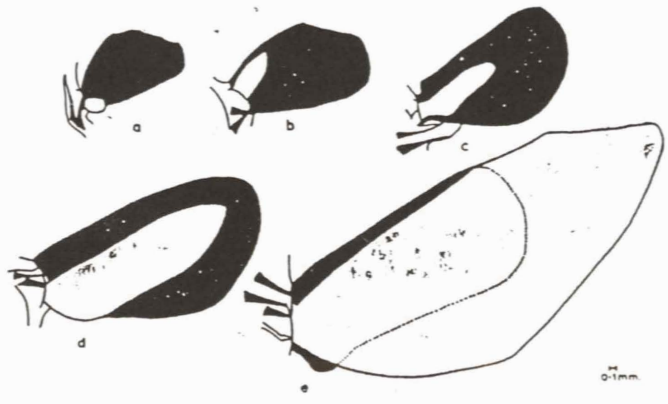
Appendix table 1. Description of maturity stages based on the development of the brood lamellae, or oostegites, in the female, and the growth of the antennae in the male (from Dunbar, 1957).

Appendiks tabell 1. Utvikling av modningsstadier basert på utviklingen av yngel lameller, eller oostegiter hos hunnen, og veksten av antennene hos hannen (basert på Dunbar (1957))

<u>Immature</u>: Antennae very short, no sign of the development of oostegites
<u>Females</u>
1. Maturing: Oostegites increasing in size from the adolescent condition. Ovaries larger, with cells about 0.2mm in diameter or larger. 2. Mature: Oostegites fully developed, almost twice the length of the gill plates. Specimens often with eggs or young in brood pouch ((Appendix figure 3).
<u>Males</u>
1. Adolescent male: Antennae increasing in length. 2. Mature male: Antennae fully developed, the first antennae reaching to the hind margin of the first pleonal segment, the second antennae reaching beyond the hind margin of the last pleonal segment (Appendix figure 4).

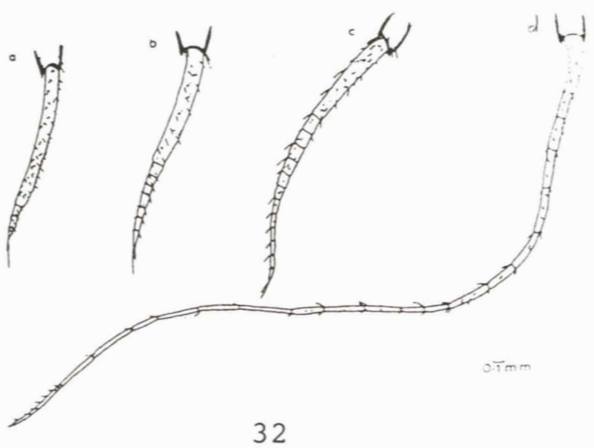
Appendix figure 1. Development of oostegites. a). Oostegite length = 0.25mm, b). Oostegite length = 0.5mm, c). Oostegite length = 1.0mm, d). Oostegite length = 2.5mm, e). Oostegite length = 4.0mm. (the gill is shown in black) (from Kane, 1961).

Appendiks figur 1. Utvikling av yngel lamelle (oostegiter) hos hunnen.



Appendix figure 2. Development of the second antennae in the male. a). Four segments formed; length of flagellum = 1.56mm, b). Eight segments formed; length of flagellum = 1.8mm, c). Thirteen segments formed; length of flagellum = 2.4mm, d). Twentyone segments formed; length of flagellum = 7.2mm (from Kane, 1961).

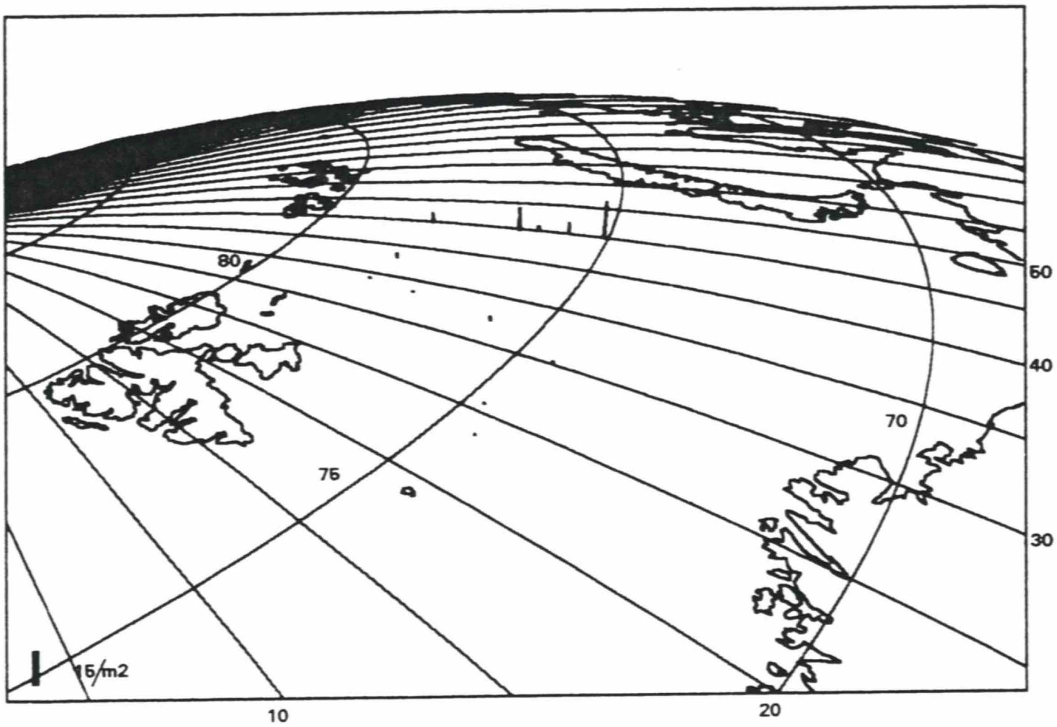
Appendiks figur 2. Utvikling av andre antenne hos hannen.



Appendix figure 3a-i. *T. abyssorum.* Horizontal distributions in the Barents Sea based on numerical abundance (individuals m-2) from individual stations, 1984-1992.

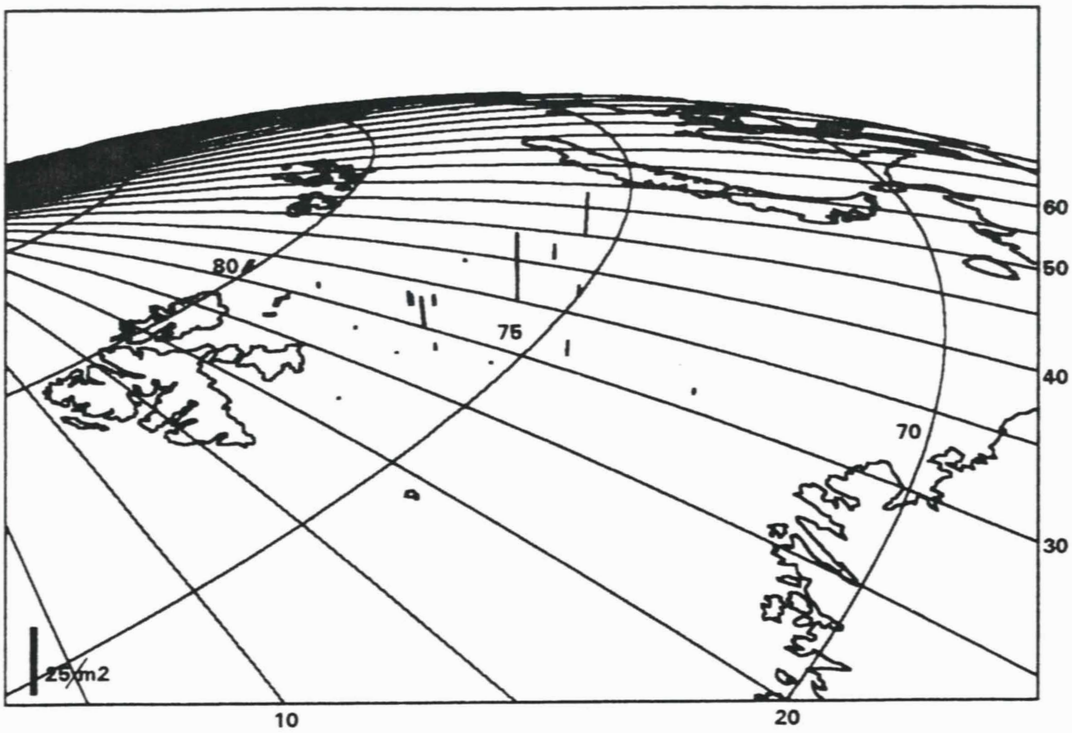
Appendix figur 3a-i. *T. abyssorum.* Horisontal fordeling i Barentshavet; Middelantall m-2 fra individuelle stasjoner, 1984 - 1992.

a ***T.abyssorum***



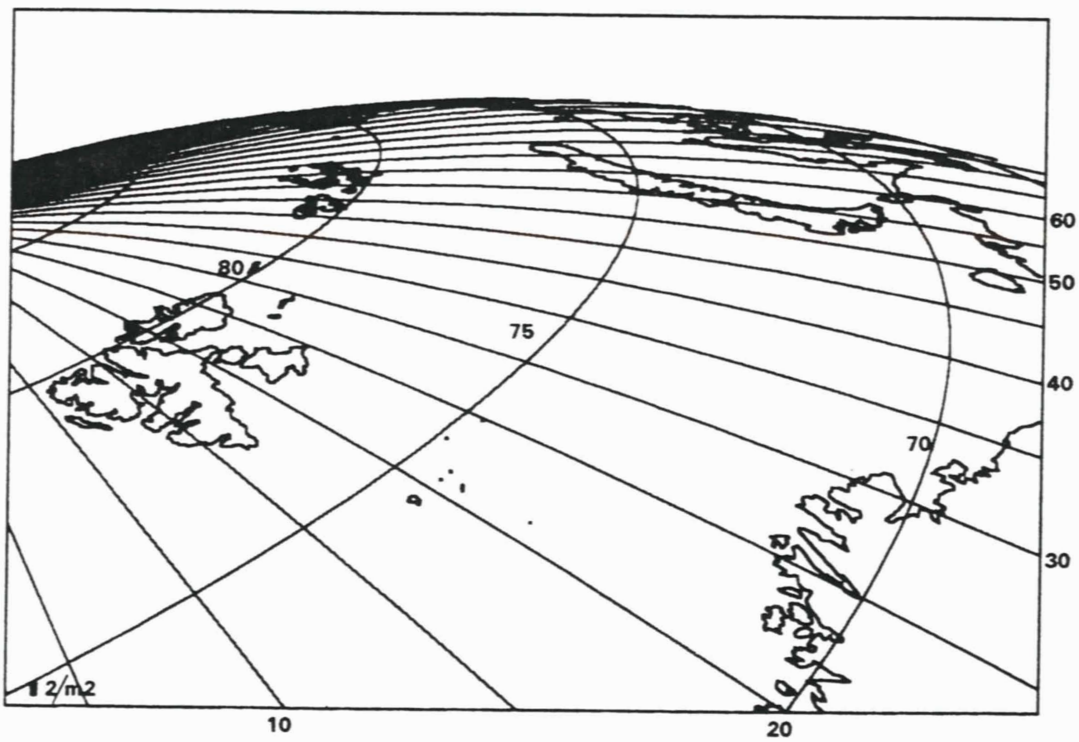
1984 June and August.

b.



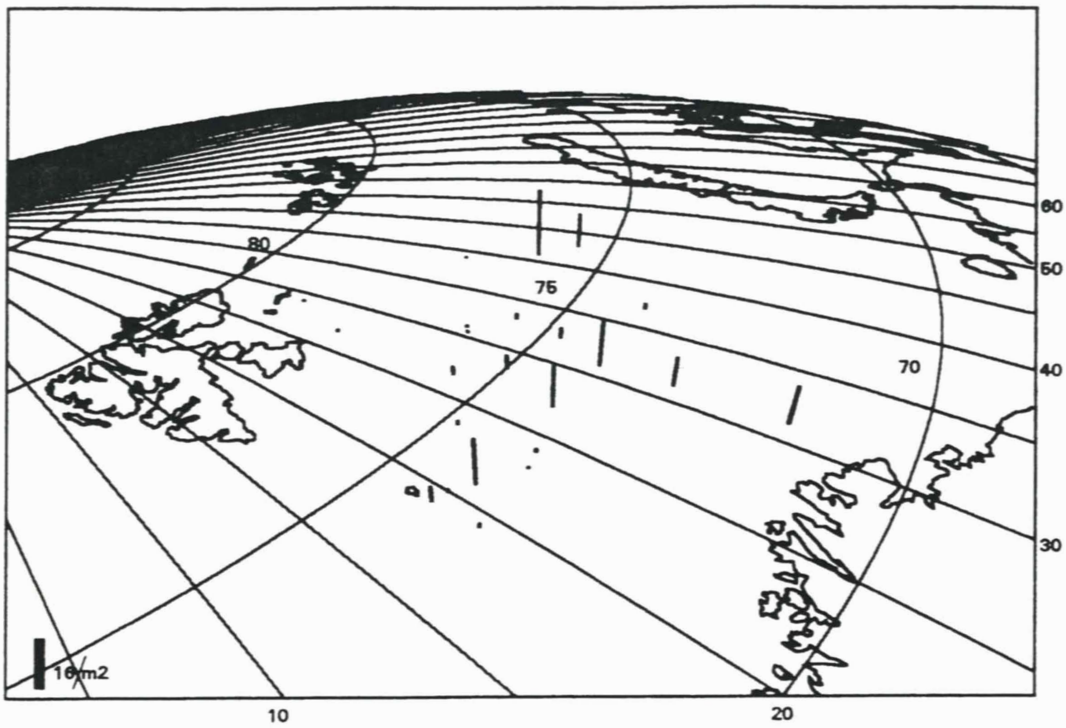
1985 January and August.

c.



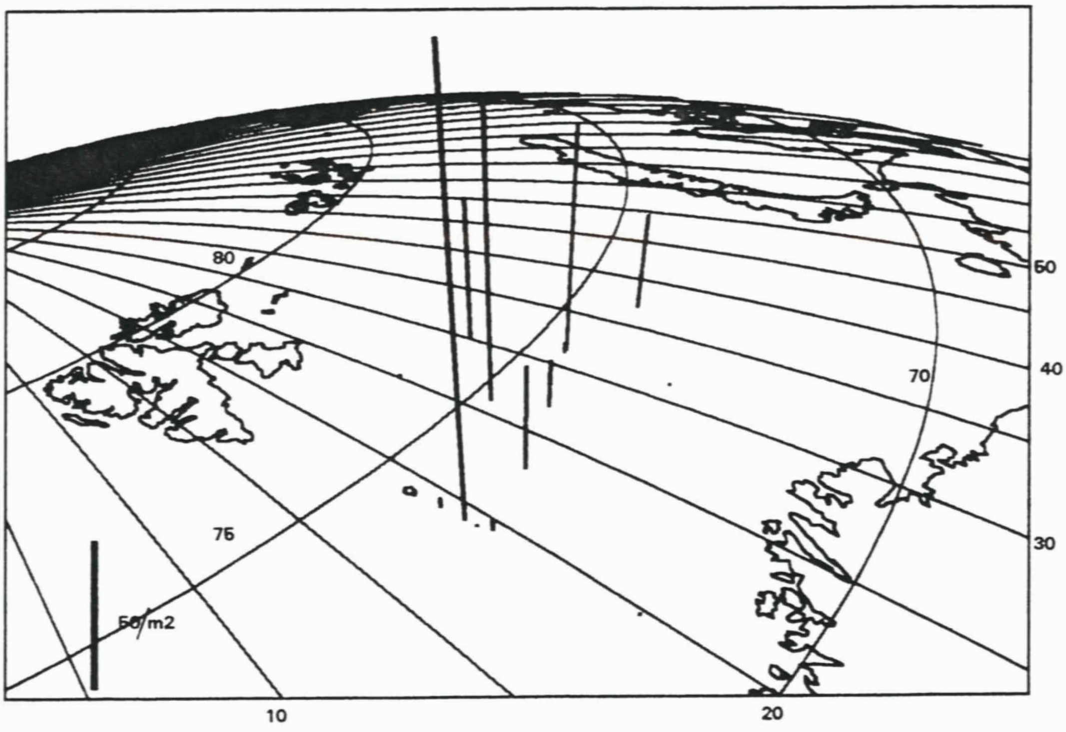
1986 April and May.

d.



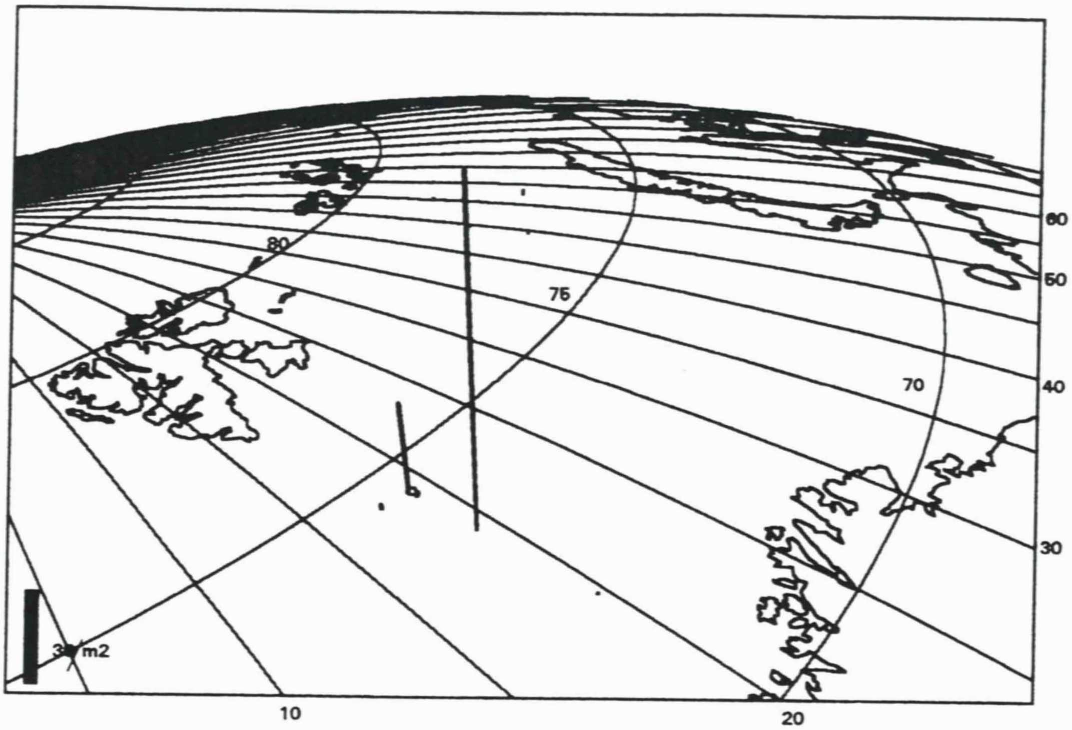
1987 February/March , May/June and September.

e.



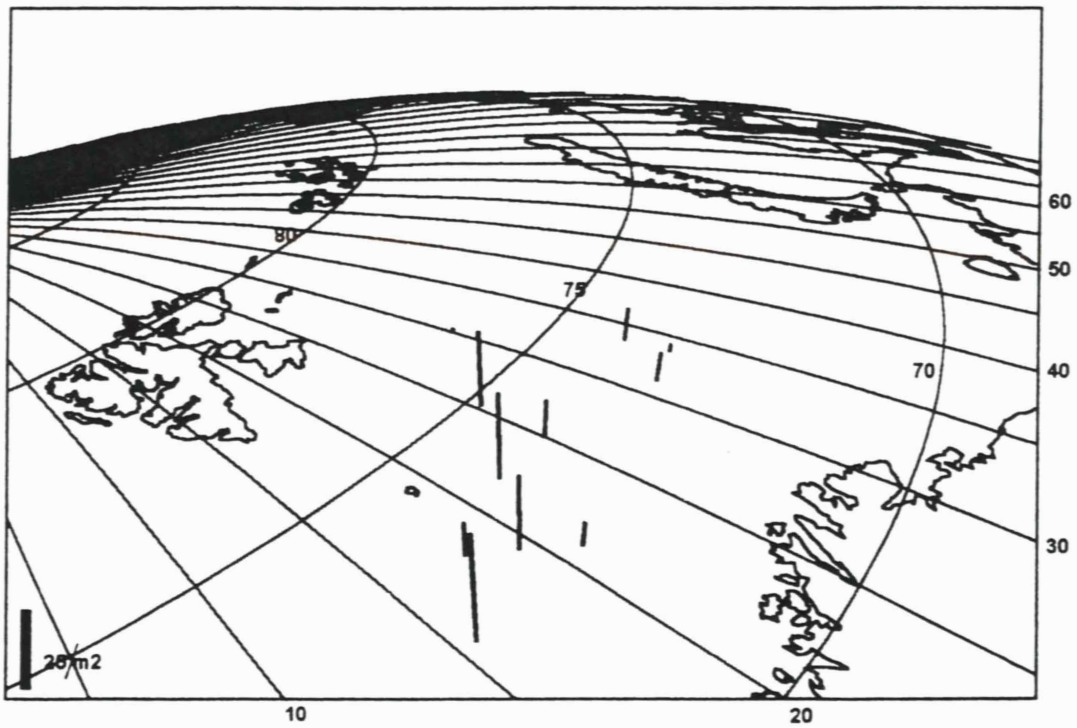
1988 March and July.

f.



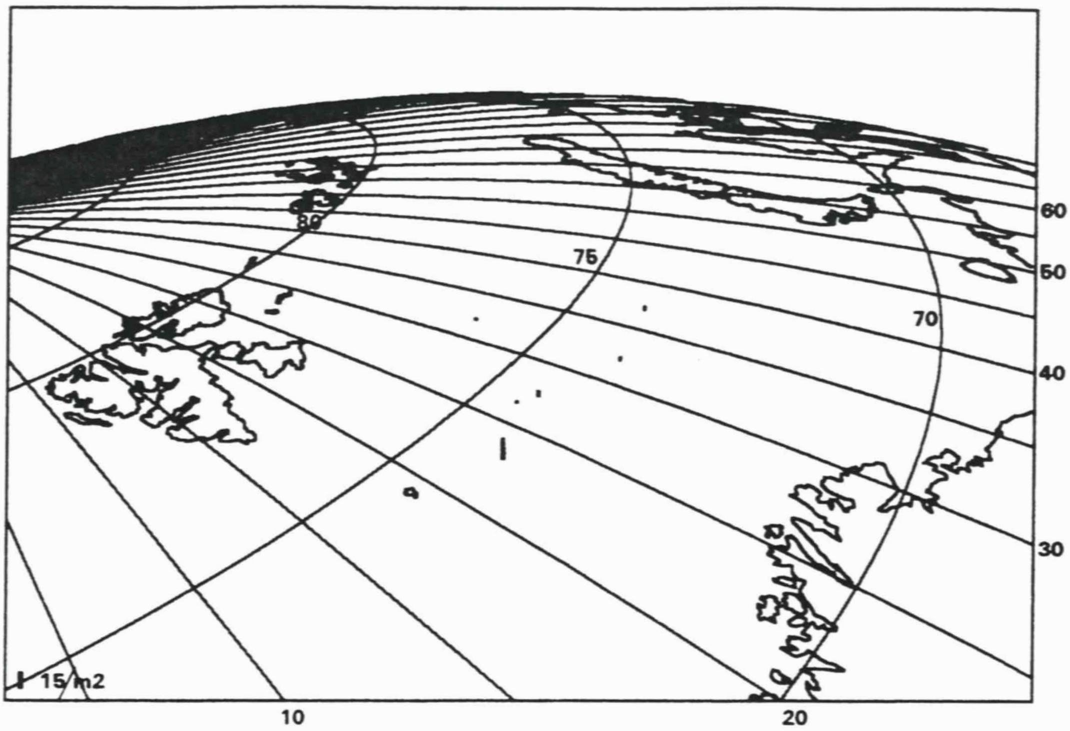
1988 September and October.

g.



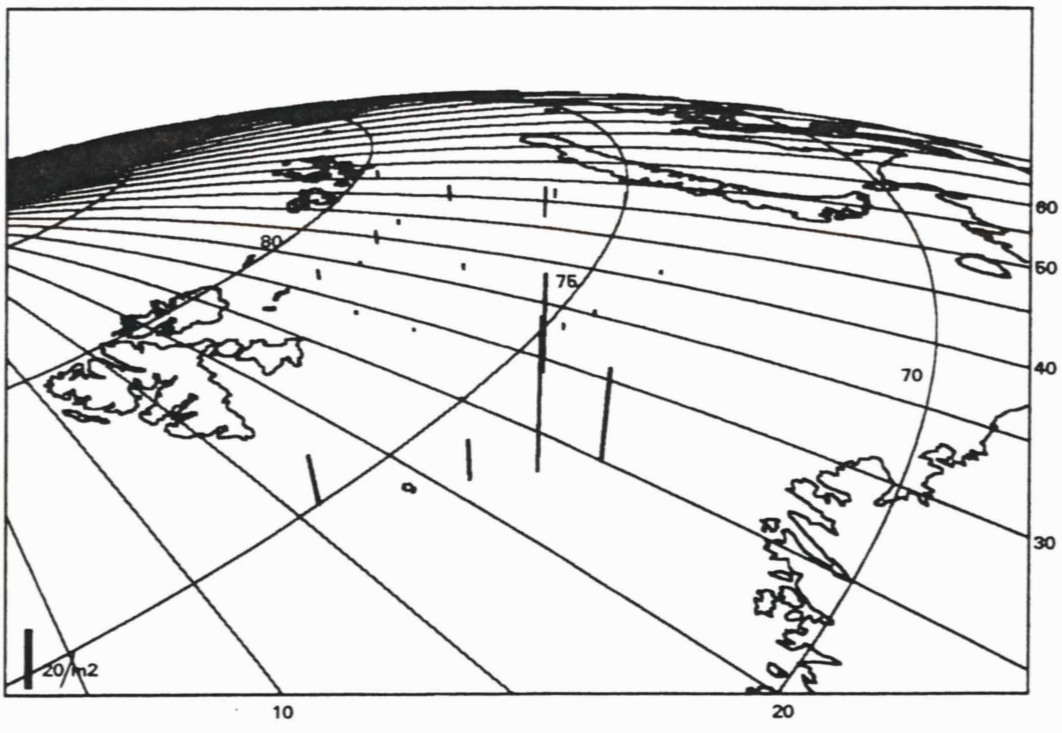
1989 January and May.

h.



1991 January and June.

i.

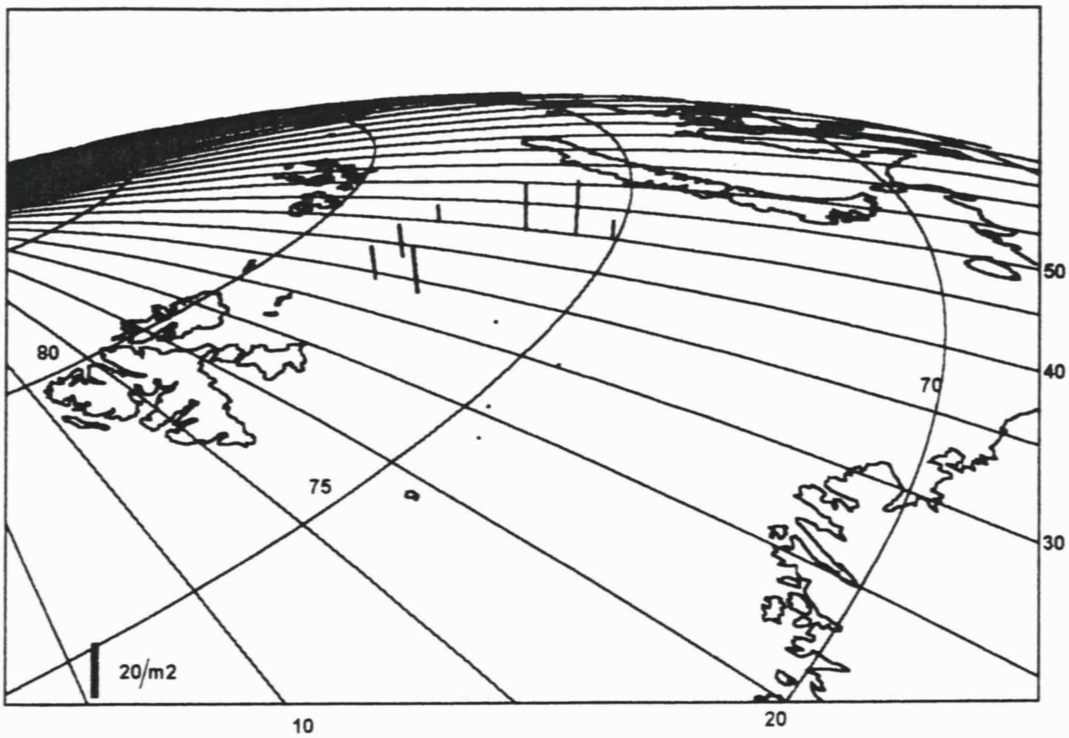


1992 September/October and September.

Appendix figure 4a-j. *T. libellula.* Horizontal distributions in the Barents Sea based on numerical abundance (individuals m^{-2}) from individual stations, 1984-1992.

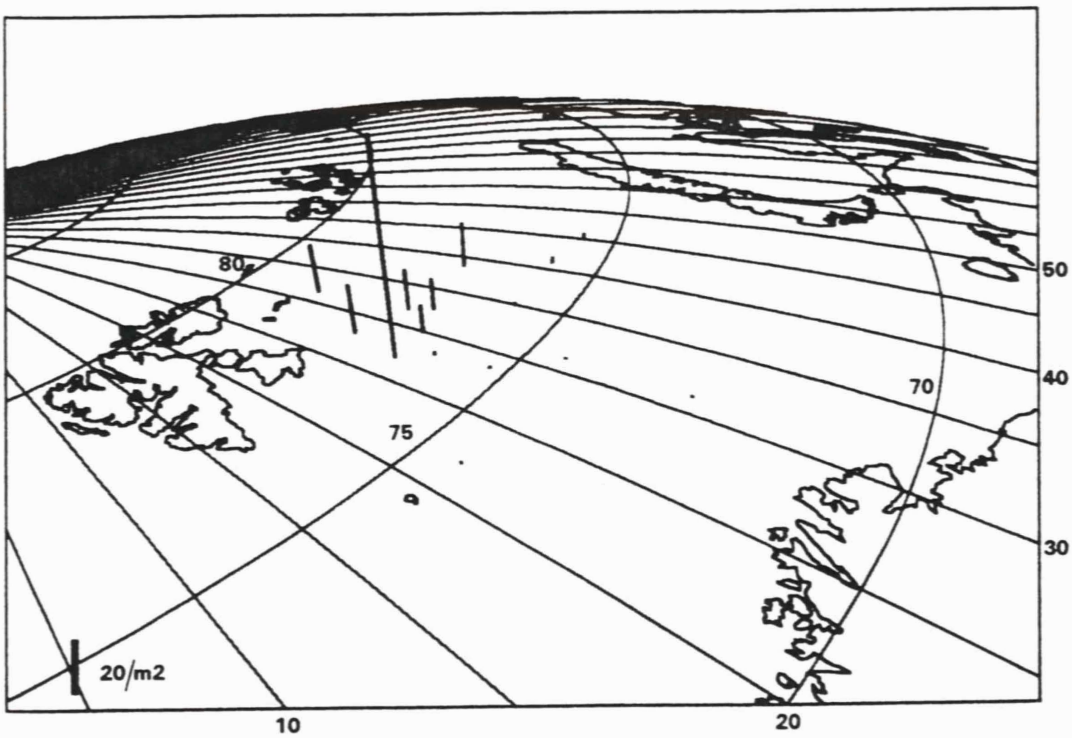
Appendix figur 4a-j. *T. libellula.* Horisontal fordeling i Barentshavet; Middelantall m^{-2} fra individuelle stasjoner, 1984 - 1992.

a **T.libellula**



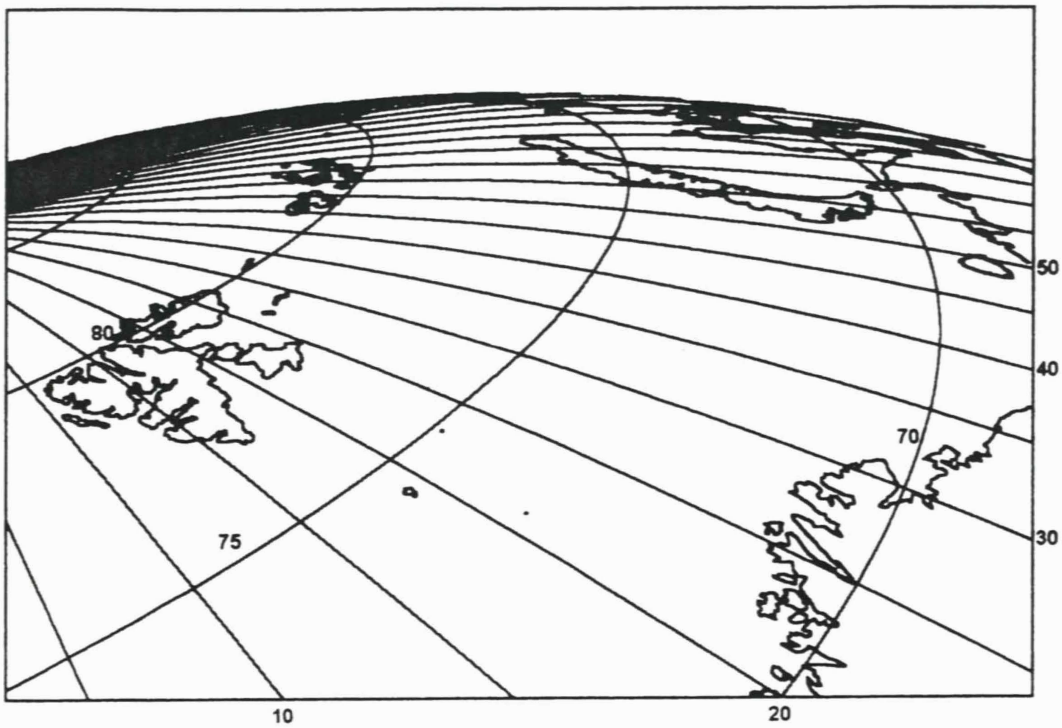
1984 June and August.

b.



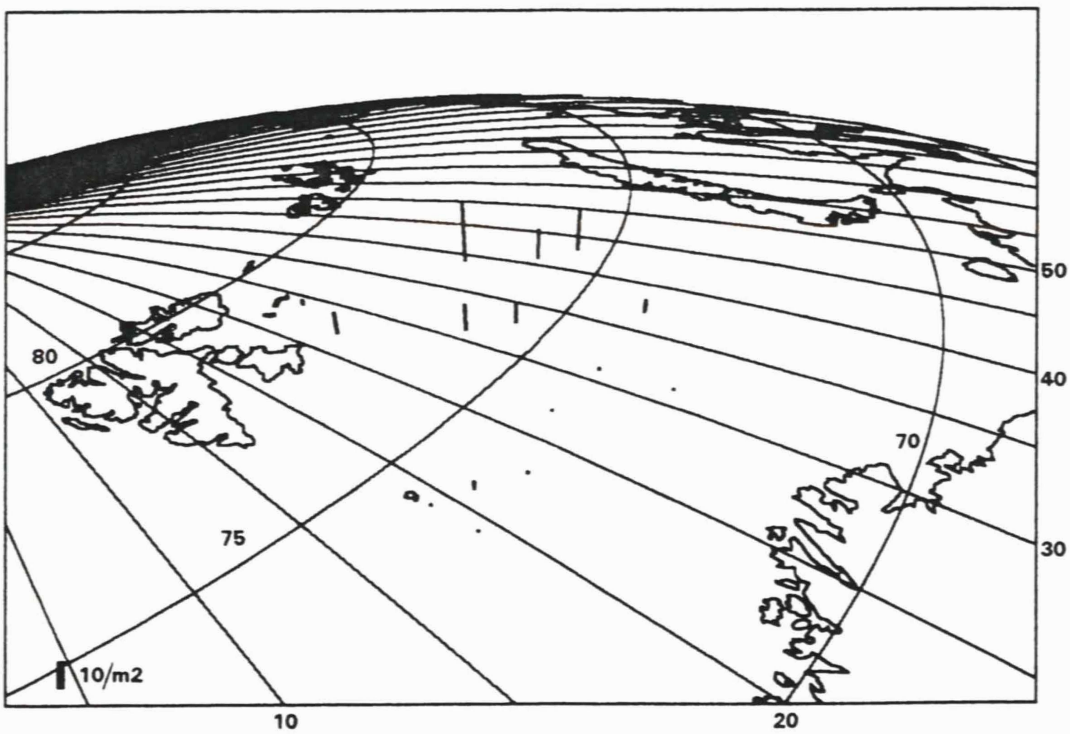
1985 January and August.

c.



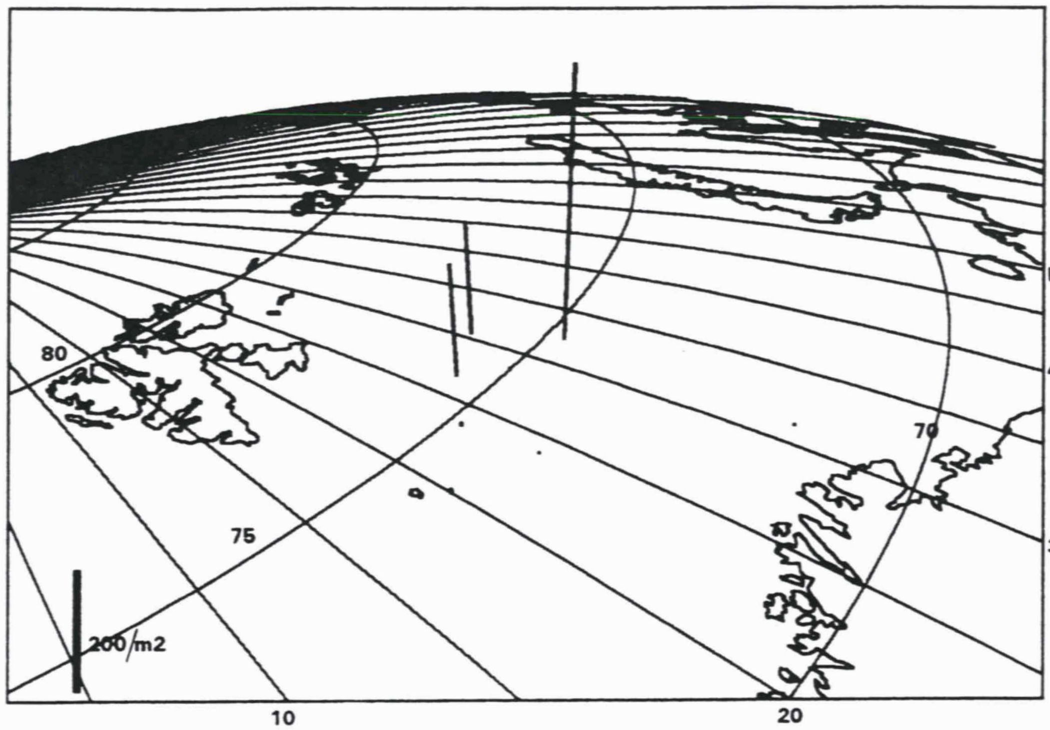
1986 May

d.



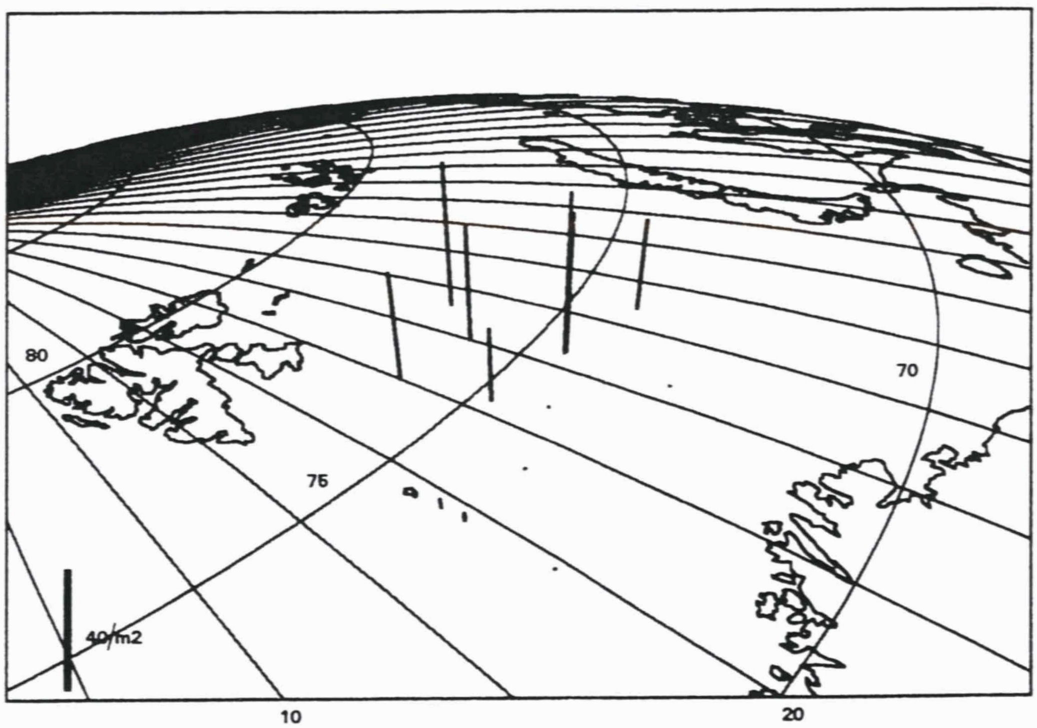
1987 February/March and September.

e.



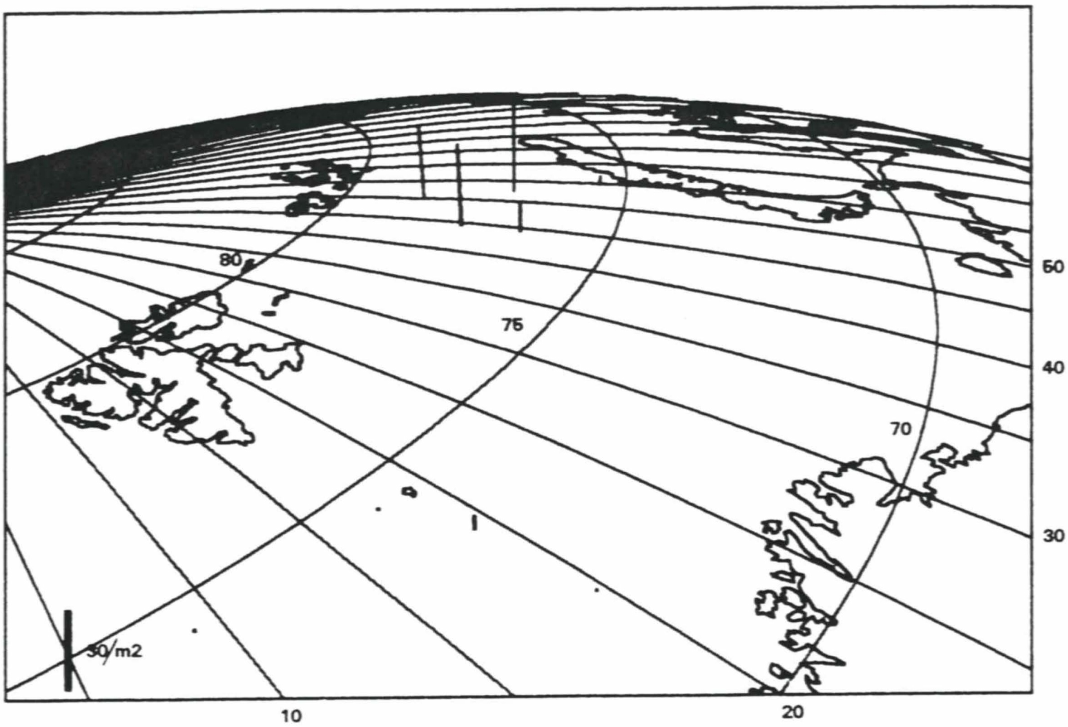
1987 May/June

f.



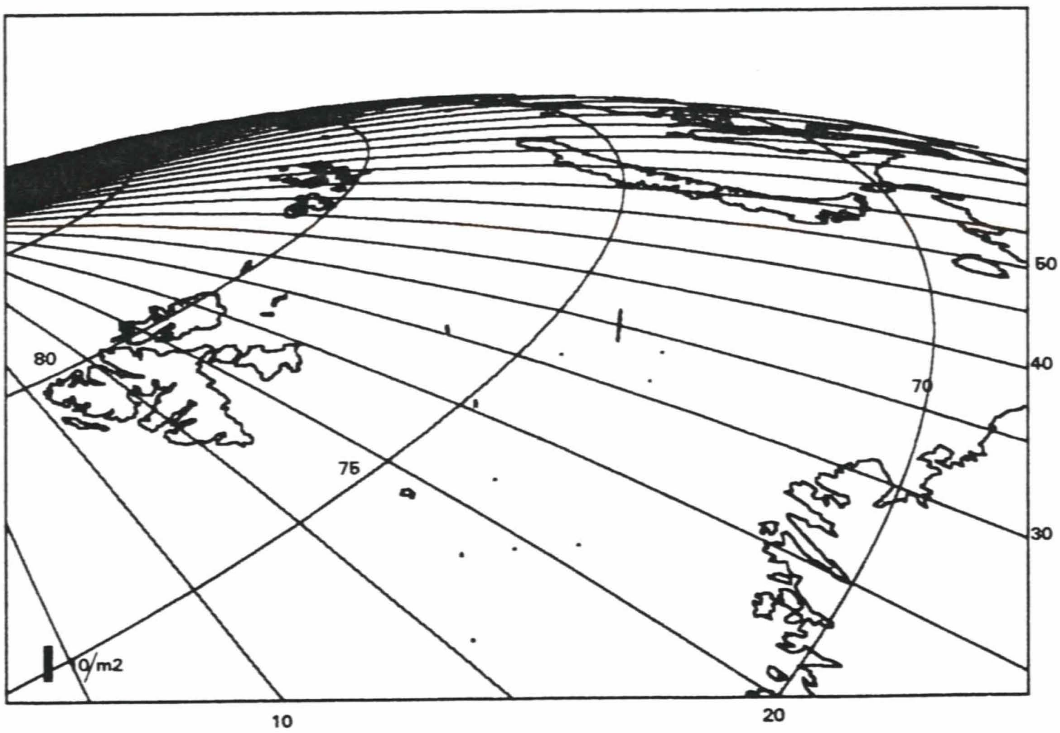
1988 March and July.

g.



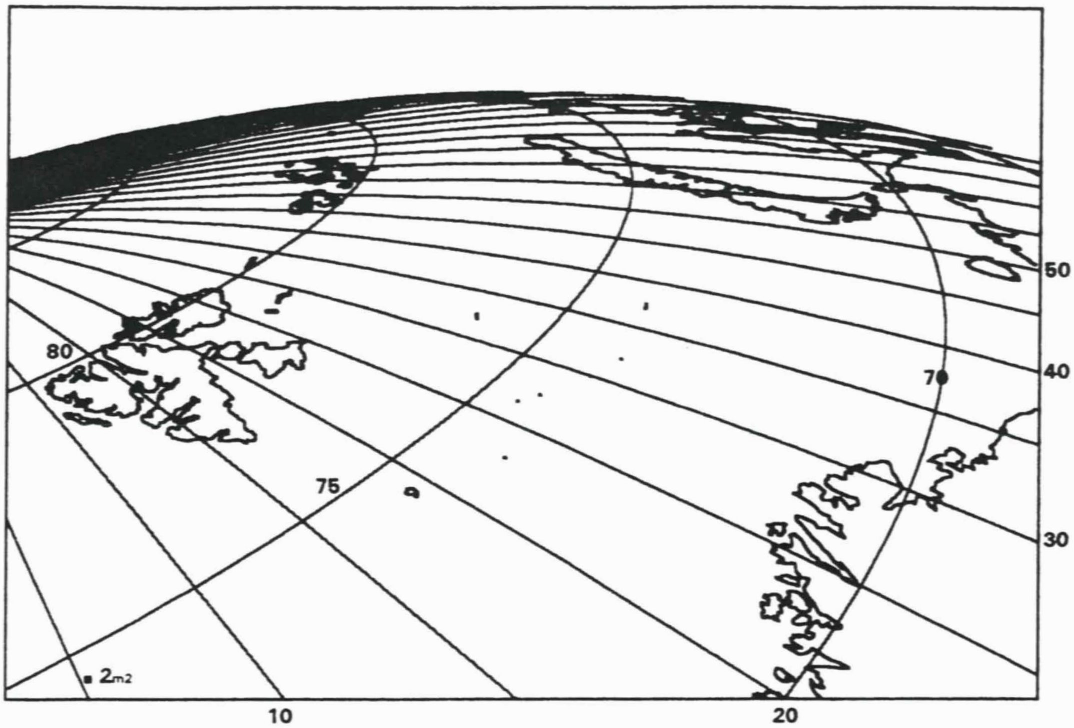
1988 September and October.

h.



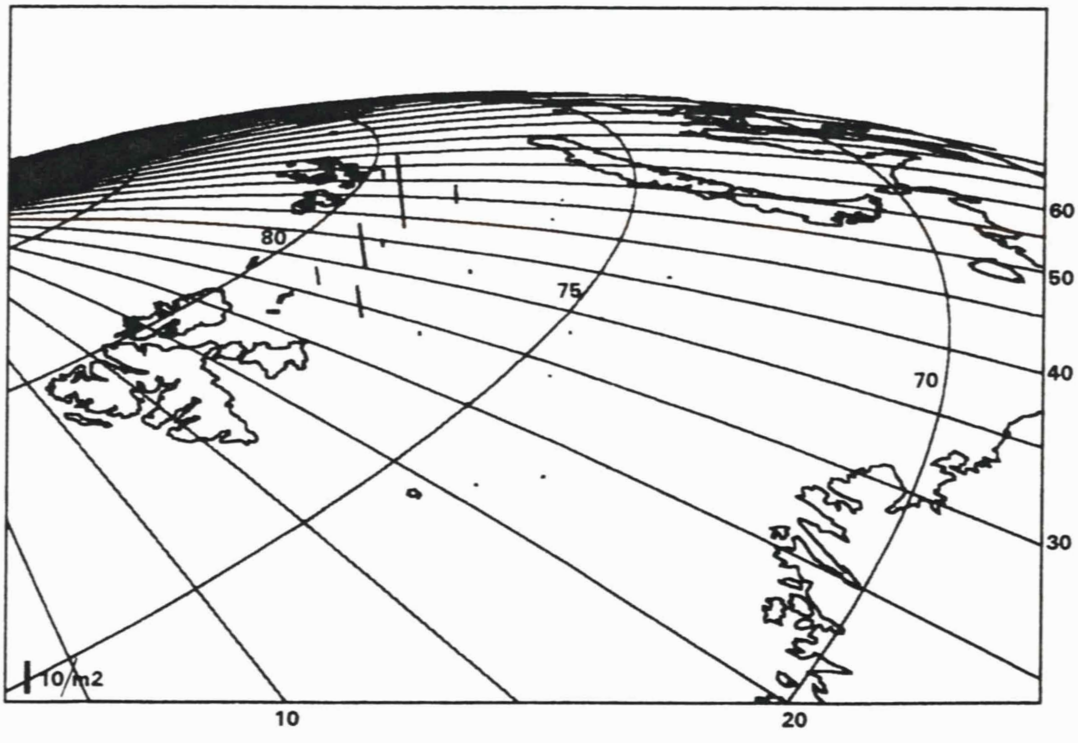
1989 January and May.

i.



1991 January and June.

j.



1992 September and September/October.