Food and feeding conditions and prey selectivity of herring (*Clupea harengus*) through its feeding migrations from Coastal areas of Norway to the Atlantic and Arctic watermasses of the Nordic Seas

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Abstract

The feeding ecology of herring was studied using samples collected during cruises in 1994 , 1995 and 1996. Investigations were carried out in the Møre shelf region off western Norway where the major spawning of herring occurs, and in the off shelf area of the eastern Norwegian Sea, where herring migrate after spawning.

Our study shows low feeding activity of herring during their main spawning season with the peak feeding period occurring in May and June. After spawning in February - March herring fed upon euphausiids, mainly *Thysanoessa inermis* and *Meganyctiphanes norvegica* on the shelf and at the shelf edge. In late spring and summer herring that had migrated to the Norwegian Sea fed mainly on *Calanus finmarchicus*, copepodite stages IV and older. In colder waters e.g., waters influenced by East Icelandic Current, *C. hyperboreus* was important in the diet. By July and August when *Calanus* spp. (copepodite stages IV-V) migrate into deeper waters for overwintering, a wide variety of prey organisms were found in stomachs of herring caught in the central Norwegian Sea and on the Norwegian continental shelf. In the western part of the Norwegian Sea the zooplankton biomass was dominated by amphipods, *Themisto* spp., which is also a major prey of herring in that region. Herring were found to feed on fish at only a few stations.

The herring showed size selective feeding of copepodite stages of *C. finmarchicus* and *C. hyperboreous*. Larger prey such as krill and amphipods were preyed upon regardless of their size. The amount of food ingested by herring in the Mixed Atlantic/Arctic and Arctic water masses was comparatively higher than in the Atlantic water . The zooplankton biomass showed a similar distribution pattern.

Key words: herring, feeding ecology, zooplankton, prey selection, Nordic Seas

Introduction

The feeding and spawning migration patterns of the Norwegian spring spawning herring (*Clupea harengus*) has changed during and after the collapse of the stock around 1970 (Røttingen 1992). At present, herring spawn at several locations along the Norwegian coast with the main spawning occurring on the Møre coast, off western Norway and northwards. The spawning stock size in 1997 was estimated to be around 7 million tonnes (Anon. 1997). From the spawning areas along the coast of Norway, the offspring are brought with the north flowing currents into the southern Barents Sea (Gjøsæter, 1995). After two to four years, herring move out of the area, to join the adult stock living in the Norwegian Sea.

By April the adult herring start migrate from the spawning grounds to their early feeding grounds in the eastern and central parts of the Norwegian Sea (Dragesund, 1980). The main feeding grounds of herring before the collapse of the stock were located in the Norwegian Sea between Jan Mayen and Iceland, and in the late 1960 s, also in the area between Jan Mayen and the Bear Island (Dragesund 1980; Røttingen 1989). During a period when the stock size was very low, the feeding area of the herring was restricted to the coastal waters of northern Norway (Røttingen 1990, 1992). With the increase in the stock since the mid 1980 s, herring have migrated to their previous feeding grounds covering large areas of the Norwegian Sea. In late July and August the herring migrates eastwards and in September enters the wintering areas in northern Norway (Røttingen 1992).

Previous studies demonstrated that the copepod *Calanus* spp., especially *C. finmarchicus*, krill *Thysanoessa inermis*, *Meganyctiphanes norvegica* and amphipods *Themisto* spp. are the major prey of herring (Østvedt 1965; Harding and Nichols 1987; Last 1989; Dalpadado 1993; Melle *et al.* 1994, Holst *et al.* 1997). Pelagic fish such as herring are also important predators of fish eggs and larvae (Harding and Nichols 1987; Holst 1992). Holst (1992) reported cannibalism to occur in coastal waters of northern Norway where the distribution of 0-group and adult herring overlapped during the period when the stock was very low.

The dominant copepods *C. finmarchicus* and *C. hyperboreus* have wide distributions in the Norwegian, Icelandic and Greenland Seas, but the latter species tend to be most abundant in the colder water masses of the Greenland Sea (Wiborg 1955; Pavshtiks and Timokhina 1972; Melle *et al*, 1993; Hirche *et al.* 1994; Astthorsson and Gislason 1995). The dominant krill species *T. inermis*, *T. longicaudata* and *M. norvegica* also are widely distributed with high abundances of *M. norvegica* restricted to the warmer Atlantic waters (Einarsson 1945; Dalpadado *et al.* 1998). Hyperid amphipods, *Themisto* spp., are abundant and are available as prey for herring especially in the northwestern part of the Norwegian Sea (Dunbar 1957; Dalpadado *et al.* 1998).

The primary aims of the surveys carried out in the Norwegian Sea in 1994 to 1996 are to; 1) determine the major prey of herring in different regions/water masses e.g., Coastal, Atlantic, Arctic 2) examine the spatial distribution of herring in relation to its prey organisms, and 3) describe the stomach contents of herring in relation to prey availability.

Materials and Method

Herring stomachs were collected during several cruises undertaken in the Norwegian Sea in 1994 to 1996 (Table 1, Figs. 1-3).

The herring were located acoustically using a 38 KHz echosounder connected to the Bergen Echo Integrator (BEI). A pelagic trawl (Åkra trawl, see Valdermarsen and Misund 1995) with a 30 x 30 m mouth opening and a cod end with mesh size of approximately 16 mm (stretched) was used for sampling the herring. The trawl was fitted with a Scanmar depth sensor. The towing speed was 3 - 4 knots.

A random sample consisting of ca. 100 fish from the trawl catch were taken when possible. The length, weight, age and maturity of the herring were recorded according to the instructions given in Fotland *et al.* (1995). Twenty herring stomachs were preserved in formalin while 30 stomachs were frozen immediately.

In the current study only frozen stomachs were analyzed. Two fish in each one cm length group were used for stomach content analyses. We have weighted the stomach data by using number of fish in each cm length group in the randomly taken herring sample.

Herring stomachs were analyzed at the Institute of Marine Research (IMR), Norway. Stomach fullness and the state of digestion of the stomach contents were classified using the scales given by Fotland *et al.* (1995) for all specimens. The stomach content was carefully teased apart. All identifiable prey were identified to the lowest taxonomic group and enumerated. The length of prey organisms was measured to the nearest 0.1 mm using an ocular micrometer. For copepods the cephalothorax length or the developmental stages (copepodite I-VI) were determined. For all other organisms, the carapax or total length was recorded. Dry weights of all major prey categories were taken separately and the rest of the stomach contents were weighed together. Dry weight of the stomach content was obtained by keeping the samples in a drying oven at 80 °C for 24 hours or until a constant weight was obtained.

Plankton samples were obtained by using the MOCNESS (Multiple Opening Closing Net and Environmental Sensing System) plankton net (WIEBE et al. 1976, 1985). The MOCNESS was equipped with 8 nets of 180 µm mesh size. At most stations the nets were towed in oblique hauls from 700-500, 500-400, 400-300, 300-200, 200-100, 100-50, 50-25, and 25-0 meter depths close to the herring trawling location. At some stations, only the upper 200 meters were sampled with the MOCNESS. In addition to the combined trawl and MOCNESS sampling stations, the MOCNESS was regularly used separately.

The zooplankton samples were usually separated into two halves. One half was preserved in formaldehyde and the second half was size fractionated into three categories; 180 to 1000 µm, 1000 to 2000 µm and above 2000 µm. These categories were dried at 70°C for 24 hours before weighing. Large organisms e.g., euphausiids, shrimps and fish were treated separately. Lengths were measured on these specimens before taking the dry weight.

Analyses concerning prey size selectivity in the herring have been performed, based upon MOCNESS data and herring stomach contents.

On the basis of temperature and salinity data obtained at different depths (10, 100, 500 m) from 1994-96 and using the description of water masses given by JOHANNESSEN 1986 the Nordic Seas were divided into the following five hydrographic regions: 1) Norwegian Coastal water 2) Mixed Coastal/Atlantic water 3) Atlantic water, 4) Mixed Atlantic/Arctic water, and 5) Arctic water. Schematic presentation of water masses in the Nordic Seas is given in Fig. 4 (from Dalpadado *et al.* 1998)

Results

March 1995 and 1996

Stomach samples collected in March 1995 and 1996 from the Møre coast and shelf and shelf edge northwards had 32% and 43% empty stomachs respectively (Fig. 5).

In March 1995, however, majority of the herring (64% compared to 47% in 1996) had already spawned and these seem to have started to feed. Mean prey weight per fish in 1995 was comparatively higher than in 1996 (Fig. 6).

In the mixed Coastal/Atlantic and Atlantic waters, in March 1995, herring fed almost exclusively on krill comprising more than 90% of the total prey weight (Fig. 6a). The dominant krill species were *Thysanoessa inermis* and *Meganyctiphanes norvegica*.

In March 1996 krill constituted 95% of the prey weight in herring stomachs in the Coastal/Atlantic waters whereas in the Atlantic waters calanoid copepods dominated the diet 80% and 62% of the total prey weight in fish <30 cm and >30 respectively (Fig. 6b). In the Atlantic waters in addition to copepods, krill (26%) and chaetognaths (7%) were preyed especially by the larger herring.

Figure 7 shows the length distribution of *M. norvegica* and *T. inermis* consumed by herring during March 1995. The total krill lengths of *M. norvegica* varied from 9 - 43 mm with the length frequency distribution showing two peaks; one at 20 - 23 mm, the second at 34 - 37 mm. The length frequency distribution of *M. norvegica* from MOCNESS samples was similar showing a peak at 21 - 24 mm and another at 32 - 34 mm.

The length frequency distributions of *Thysanoessa inermis* from the stomach content and MOCNESS also revealed similar patterns, i.e. the two distributions are almost identical. Both distributions gave one peak at 20 - 24 mm length.

April 1995 and 1996

The cruises in April 1995 and 1996 were designed to cover the migration of the herring from the spawning grounds to their early feeding grounds in the eastern and central parts of the Norwegian Sea. Fifty percent of the herring examined for stomach contents were in spent and resting state. Percentage of empty stomachs decreased drastically from 32% and 43% in March 1995 and 1996 to 1% and 3.8 % respectively by April (Fig. 5). The average prey weight of herring which had migrated to mixed Atlantic/Arctic and Arctic was 306 mg in 1995 and 241 mg in 1996. (Fig. 8).

In the Arctic as well as in the Atlantic waters, in 1995, copepods dominated the diet comprising 43% and 59% by weight, respectively (Fig. 8a). However, dietary differences were observed in these waters. In the Arctic waters *C. hyperboreous* was the most abundant copepod in the stomach content whereas in the Atlantic waters only *C. finmarchicus* was present. In addition to copepods, the fish *Maurolicus muelleri* was abundant prey of herring in the Arctic waters, and in the largest size classes (>30 cm) krill *M. norvegica* and arrow worms *Sagitta* spp. were also important constituents.

In 1996 in the Atlantic waters calanoid copepods (88%) were major prey of herring below 30 cm whereas chaetoganths (36%) and calanoid copepods (24%) dominated the diet of lager herring (Fig. 8b). In the mixed Atlantic/Arctic waters also calanoid copepods predominated the diet. In these waters chaetognaths were preyed up to 7%

and 22% by herring <30 and >30 cm, respectively. In the Atlantic waters *C. finmarchicus* was the dominant species whereas in the mixed Atlantic/Arctic waters both *C. finmarchicus* and *C. hyperboreus* were present (Fig. 8b).

May - June 1994, 1995 and 1996

By May and June herring occupied large feeding areas of the Nordic Seas. The percentage of empty stomachs in all 3 years in May and June were below 15%. Herring caught in May and June had in general higher average prey weight than other times of the year indicating high feeding activity during this period by herring. The highest average prey weight of 1200 mg was recorded in May 1996, in the Arctic waters (9c).

A total of 125 herring stomachs from 9 stations were analyzed from a cruise with "G. O. Sars" in June 1994 (Table 1). In the Coastal waters calanoid copepods dominated the diet of herring constituting up to 64% of the total dry prey weight (Fig. 9a). In addition, in Coastal waters, krill comprised 35 % of herring stomachs by weight. *M. norvegica* (20-45 mm) were the dominant krill species present in herring stomachs in the Coastal waters. In the Atlantic waters 96% of the total dry weight of prey in the larger herring (>30 cm) were calanoid copepods. In the mixed Atlantic/Arctic waters calanoid copepods constituted 74% and 83% of the diet of <30cm and 30>cm herring respectively. At most stations *Calanus* spp. consisted of overwintering stages (IV-VI). Only a small portion of the stomach contents was in an identifiable state. *C. finmarchicus* and *C. hyperboreus* constituted 10% and 6% of the total prey weight respectively of the identifiable portion.

Analysis of stomach contents in June 1995 in the coastal waters off Lofoten/Vesterålen showed that 45% of the prey weight in herring stomachs consisted of larvaceans (Fig. 9b). In the Atlantic waters herring fed almost exclusively on *C. finmarchicus.*

In May 1996 a total of 260 stomachs from 20 stations were analyzed. Calanoid copepods were the major prey of herring in mixed Coastal/Atlantic, Atlantic, mixed Atlantic/Arctic and Arctic waters varying 50-99% of the total prey weight (Fig. 9c). In the mixed Coastal/Atlantic and Atlantic waters krill were important in the diet especially in larger herring constituting 42% and 20% of the total prey weight. Also amphipods were preyed up to 11% of the total prey weight of herring in the mixed Coastal/Atlantic, Atlantic and mixed Atlantic/Arctic waters.

July - August 1995 and 1996

Figures 2 and 3 shows the location of the pelagic trawl stations from cruises in July - August 1995 and 1996. All stations were taken in the Coastal, mixed Coastal/Atlantic and Atlantic waters in the central Norwegian Sea and on the Norwegian continental shelf. The percentage of empty stomachs observed in our study in July increased up to 25% from May and decreased again to 10% by August (Fig. 5). Majority of the largest herring (above 35 cm) were found in the north western part of the study region.

In late July and August herring start migrating eastwards towards Coastal areas of Norway had generally lower average prey weight in stomachs than in May and

June. The maximum average prey weight of 304 mg was recorded in the Atlantic waters (Fig. 10).

Herring caught in July and August had a wide variety of prey organisms in their diet than other times of the year. In July and August 1995 in the Coastal and Mixed Coastal/Atlantic waters calanoid copepods, *Limacina* spp., and cladocera dominated the diet (Fig. 10a). In the Atlantic waters in July 1995 herring fed almost exclusively on amphipods whereas in August copepods (53%) and larvaceans (30%) predominated the diet. *Themisto abyssorum* (3-7 mm) were the dominant amphipod species (Figs. 10a and 11) while *C. finmarchicus* were the dominant copepod species recorded in herring stomachs in July and August.

In August 1996 in the Mixed Coastal/Atlantic waters krill were the major prey constituting 38% of the total prey weight (Fig. 10b). In addition, calanoid copepods and fish also were important prey in both size classes of herring. In the Atlantic waters herring below 30 cm had calanoid copepods (44%), amphipods (34%), krill (2.4%), and chaetognaths (4.4%) in their diet. The larger herring fed on calanoid copepods (37%), *Limacina* spp. (31.6%), krill (9%), and chaetognaths (4%).

<u>Size selectivity of copepods</u>
Figure 12 shows the frequencies of various developmental stages of *C. finmarchicus* in MOCNESS samples and in herring stomach contents from Coastal and Atlantic water masses. In Fig. 12a data from end of March to end of April from 1995 and 1996 were combined. The largest individuals were very frequent both in stomach content and in MOCNESS samples (*in situ*). Copepodite stage IV which constituted ca. 18% of the *in situ C.finmarchicus* stock made up only 1.8% in the herring stomachs. Developmental stages CI-CIII of *C.finmarchicus* made up ca. 42% *in situ*, only 1.5% of those eaten by herring.

In May to June the various ontogenetical stages were numerically relatively evenly distributed *in situ* except for adult males which were rather scarce. (Fig. 12b). The percentage frequencies varied from 10.4- 28.5. However, in the stomach contents the smallest stages were not observed, while the largest individuals- the adult females dominated (69%).

In August the smallest copepodite stages CI-CIV dominated (23-25%) *in situ* (Fig. 12c). In the stomach contents however, CI was totally absent and CI and CII were found in very small numbers. Adult females which made up only 2% of the *in situ C.finmarchicus* stock dominated (53%) in the herring stomachs.

In the Atlantic/Arctic water masses the cold water species *C.hyperboreus* is quite abundant. In late March to early April 1996 CV and CVIf (adult females) were observed both *in situ* and in herring stomachs (Fig. 13a). In Fig. 13b data from late April 1995 and May 1996 are combined. Stage CIV dominated in MOCNESS samples (76%) where as in the stomach contents only 3% were observed. In the stomach contents the larger developmental stages CV and CVIf dominated, constituting 51% and 45% respectively. The younger stages which occurred in small numbers were completely absent in the stomach contents.

***In situ* Zooplankton biomass based on MOCNESS profiles**

Fig. 14a and b show the zooplankton biomass in the upper 200 meters in the Norwegian Sea in May and June 1995 and May 1996, respectively, based upon sampling with the MOCNESS plankton net. Macroplankton organisms like euphausiids and shrimps were not included. The zooplankton biomass mainly consisted of copepods, with *Calanus finmarchicus* far exceeding other copepod species. In the western part there was an increasing frequency of the larger *C. hyperboreus*, though *C. finmarchicus* was still most numerous.

As seen from both figures there was an increasing biomass westwards from the Norwegian coast. In the eastern part of the Norwegian Sea the production of the first generation of *C. finmarchicus* usually starts in April. The presence of nauplii and the youngest copepodite stages (CI-CIII) in late May/June 1995 probably indicate the second generation of the year. These small individuals, though being present in large numbers, give rise to a relatively small biomass, less than 10 g/m^2. The production of *Calanus* moves westward with time. In the western area of the ocean it had just started. Some of the young developmental stages CI-CIII were observed at the Polar front area to the west, though the larger CIV-adults dominated. Together with the larger *C.hyperboreus* these formed the high biomasses observed, at some locations close to 40 g/m^2. The amphipod *Themisto abyssorum* was also present in the samples and added to the high biomass, though this amphipod is not representatively caught in the MOCNESS. The average biomass in the upper 200 m in May/June 1995 was 17.6 g/m^2.

In May 1996 young stages of *C. finmarchicus* were observed throughout the investigated area. In the eastern part the numbers were rather small, few copepod nauplii were present, and the production of the first *Calanus* generation of the year seemed to be declining. Towards west the frequency of young stages, and the total number of *Calanus finmarchicus*, increased. The presence of *C. hyperboreus* and *Themisto abyssorum* added to an increased biomass in the central and western area. The biomasses varied from below 5 g/m^2 in the eastern part to more than 30 g/m^2 in the eastern and northern part of the area investigated. An average biomass of 12.3 g/m^2 in the upper 200 m was somewhat lower than the one observed the previous year.

Zooplankton sampling in the same area in July - August both in 1995 and 1996 revealed a reduction in biomass compared to the situation in May. Still the highest concentrations were observed in the western part due to the higher frequency of large organisms like hyperiid amphipods, euphausiids, and *C. hyperboreus*, and an ongoing production of *C. finmarchicus*. The average biomasses in July-August 1995 and 1996 were 10.0 and 7.7 g/m^2, respectively. The average biomasses in July-August 1995 and 1996 were 10.0 and 7.7 g/m^2, respectively.

Discussion

The present analysis of stomach contents of adult herring (2-12 years) showed that copepods, krill, amphipods, chaetognaths, larvaceans and *Limacina* spp. were the most important prey in the diet. Rudakova (1966), Pavshtiks and Timokhina (1972), Harding and Nichols (1987), Last (1989) and other researchers made similar observations on herring from the North Atlantic. However, dietary differences were observed in herring caught from different regions and seasons. In the main spawning period, in February and March, when herring are mainly confined to the coastal and shelf areas of Norway they feed exclusively on krill, *M. norvegica* and *T. inermis*, often comprising more than 95% of their total prey weight.

Since euphausiids are fast swimmers and may to some extent avoid the MOCNESS sampler, the MOCNESS data used in Fig. 7 are based on night samples from March 1995 only. Krill were far too digested to be length measured in March 1996. In March there is a pronounced change in light between day and night, and the avoidance at night time is supposed to be minor. However, in the stomach content 12 % of the *M. norvegica* were equal to or larger than 37 mm, versus 2 % in the MOCNESS samples. This may be due to an avoidance of the plankton sampler by the largest specimens, even at night. The data from this study indicate that herring fed on krill regardless of their size.

In late spring and early summer herring which had migrated to the Norwegian Sea fed mainly on *Calanus finmarchicus*, copepodite stages IV and older. In colder waters, e.g. waters influenced by East Icelandic Current, *C. hyperboreus* was important in the diet. The average prey weight was generally higher in the mixed Atlantic/Arctic and Arctic waters, which is also reflected in the higher *in situ* zooplankton biomasses in this area. The higher average biomasses observed in May/June 1995 (17.6 g/m^2) compared to May 1996 (12.3 g/m^2) may be due to varying hydrographical features between years. It is most probably due to the different time of sampling in relation to the production cycle of the dominating *C. finmarchicus*, and the fact that a larger part of the rich Polar front area in the western part was sampled in 1995.

In the peak feeding period in May-June 1994-96, principal prey of herring is *C. finmarchicus* which is the most abundant zooplankton by weight in the warmer Atlantic waters of the Norwegian Sea (Wiborg, 1955; Pavshtiks and Timokhina 1972; Melle *et al.*, 1993). *C. finmarchicus* consisted mainly of overwintering stages (IV-VI).

Data from the present study indicate herring to select the larger individuals *of C. finamcrchicus* and *C. hyperboreus* despite the presence of smaller copepodite stages in large numbers *in situ*. This type of feeding behavior may be energetically beneficial for the herring, which may spend the same energy feeding upon a small or large copepod, provided the concentration of the larger specimens is above a certain threshold. Flinkman *et al.* (1992) compared the Baltic herring stomachs with plankton samples and concluded that females copepods were chosen due to their larger body size than males of the same species. Arrhenius (1995) stated that herring switched between particulate-feeding at low prey densities to filter-feeding at higher prey densities. Our data indicate that the herring in question perform particulate-feeding, since the smallest copepodites were not observed in the herring stomach contents even in areas where they occurred *in situ*.

The lack of young copepodite stages in the stomach contents could indicate a fast digestion due to their small size, thereby being underestimated. However, since they were not observed at all, even in stomachs showing minor digestion, they are probably not eaten by the herring.

C. hyperboreus is regularly observed in the cold water masses in the western part of the Nordic Seas though their concentrations are almost always far exceeded by *C. finmarchicus* (Wiborg 1955; Hirche *et al.* 1994). The fact that a proportionally higher number of *C. hyperboreus* is found in the stomach content, may be due to the selection towards larger organisms.

In July-August, herring migrating towards coastal areas for overwintering had lesser average prey weight than in May and June and had a wide variety of prey in their diet. The in situ zooplankton biomasses were also lower in July-August than two months earlier. By July copepods (CIV and CV) vertically migrate into deeper waters for overwintering (Østvedt 1955) and herring feed on other available prey organisms. In the Atlantic waters in 1995 and 1996 krill (*Thysanoessa* spp. and *M. norvegica*), amphipods, mainly *T. abyssorum* were major prey of herring in the western part of the Norwegian Sea where these species are commonly present (Dunbar 1964; Dalpadado 1998). The size distribution of *Themisto* species in herring stomachs in this study are comparable to those recorded in Barents Sea (Dalpadado *et al.* 1994). Investigations carried out in 1993 to 1995 by Dalpadado *et al.* (1998) showed large biomass of *Themisto libellula* in the subarctic and Arctic waters of the Nordic Seas. These organisms are not a major prey of herring as it seldom cross the Arctic Front into deep Arctic waters presumably due to preference by herring for water warmer than 2 C°(Misund *et al.* 1997).

Last (1989) did not find any marked differences in the diet between the smaller and larger herring (10-34 cm). The size of herring used in the present study ranged from 19 to 40 cm. As in Last's study no clear ontogenetical variations in the diet of herring with size were observed. Diurnal variation in diet could not be examined in the present study as most catches were taken in the upper layers at night time.

Stomach data from 1994 - 1996 show that the feeding pattern in the Nordic Seas has not changed much from early 1950 s and 1960s described by Russian workers (Rudakova 1966; Rudakova and Kaverina 1969; Pavshtiks and Timokhina 1972).

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Figure Text

1) Locations of pelagic trawl stations where herring stomachs were analyzed, from 3-18 June 1994.

2) Locations of pelagic trawl stations where herring stomachs were analyzed, from 5-16 March, and 21-25 April, 1-19 June, 8-13 July and 2-14 August 1995. The arrows show schematic presentation of migation pattern of herring in 1995.

3) Locations of pelagic trawl stations where herring stomachs were analyzed, from 22-30 March, 6-14 April, 1-25 May, and 30 July-13 August 1996. The arrows show schematic presentation of migation pattern of herring in 1996.

4) Schematic presentation of water masses in the Nordic Seas. A-C = Atlantic/ Coastal; A-A = Atlantic/Arctic. (from Dalpadado et al. 1998)

5) Percentage of empty stomachs from March to August 1994-1996.

6) Major prey of herring as percentage of the total dry weight in March a) 1995 and b) 1996. N= no. of fish; E = no. of empty stomachs; W = mean prey weight, and SD = standard deviation.

7) Length distribution of *Meganyctiphanes norvegica* and *Thysanoessa inermis* in herring stomachs (a), and in MOCNESS samples (b), in March 1995.

8) Major prey of herring as percentage of the total dry weight in April a) 1995 and b) 1996. N= no. of fish; E = no. of empty stomachs; W = mean prey weight, and SD = standard deviation.

9) Major prey of herring as percentage of the total dry weight in May and June a) 1994, b) 1995 and c) 1996. N= no. of fish; E = no. of empty stomachs; W = mean prey weight, and SD = standard deviation.

10) Major prey of herring as percentage of the total dry weight in July and August a) 1995 and b) 1996. N= no. of fish; E = no. of empty stomachs; W = mean prey weight, and SD = standard deviation.

11) Length distribution of *Themisto abyssorum* and *T. compressa* in herring stomachs in July and August 1995 and 1996.

12) Frequency distribution of developmental stages of *Calanus finmarchicus* in MOCNESS samples and herring stomachs a) 22 March-25 April, b) 1 May- 19 June, c) 1-14 August. CI-CV =copepodite stages one to five, CVIf= adult females, CVIm=adult males.

13) Frequency distribution of developmental stages of *Calanus hyperboreus* in MOCNESS samples and herring stomachs.

14) Zooplankton biomass based on MOCNESS profiles a) 26 May -22 June 1995, b) 29 April -28 May 1996.

Fig. 1

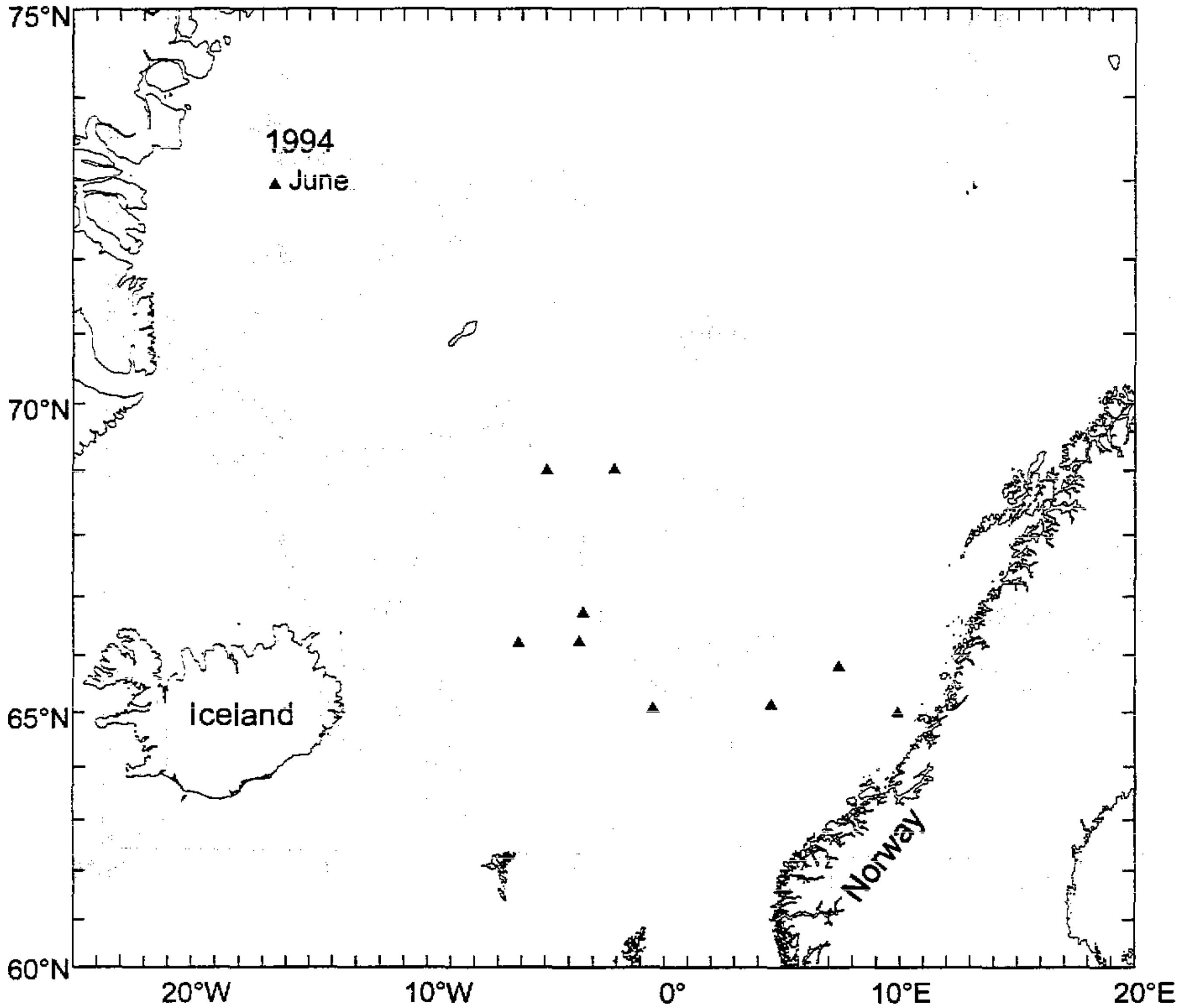
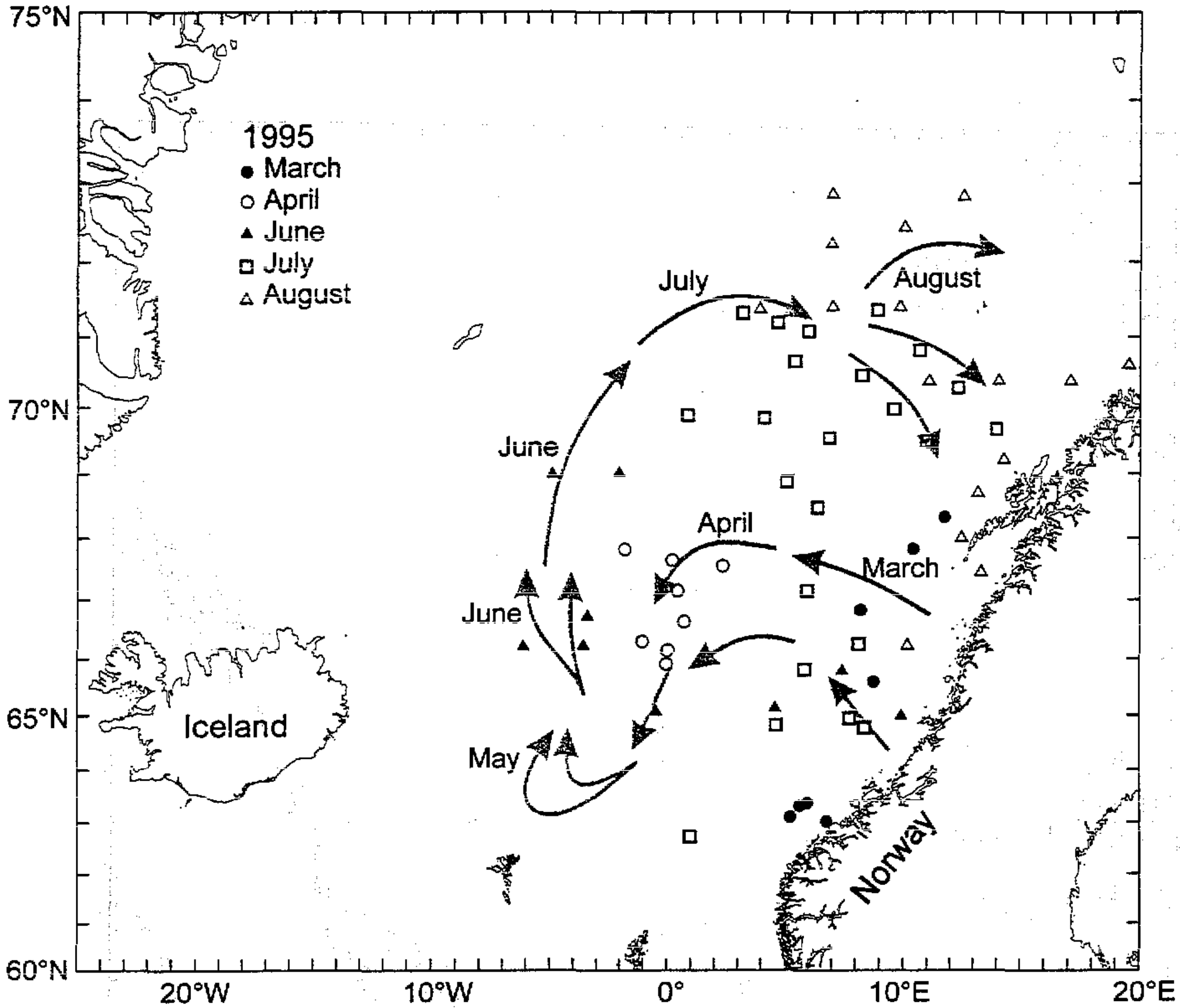
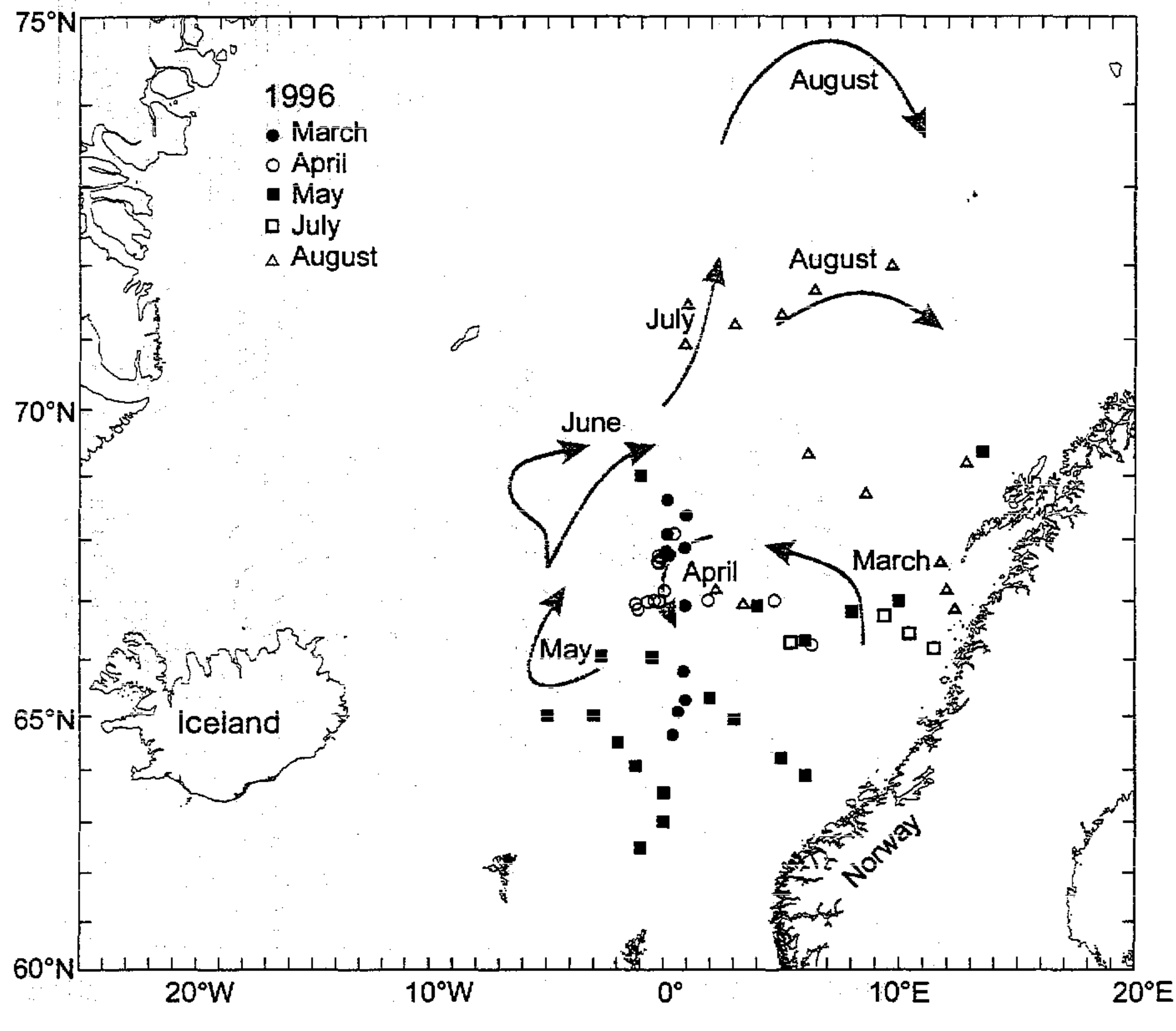


Fig. 2



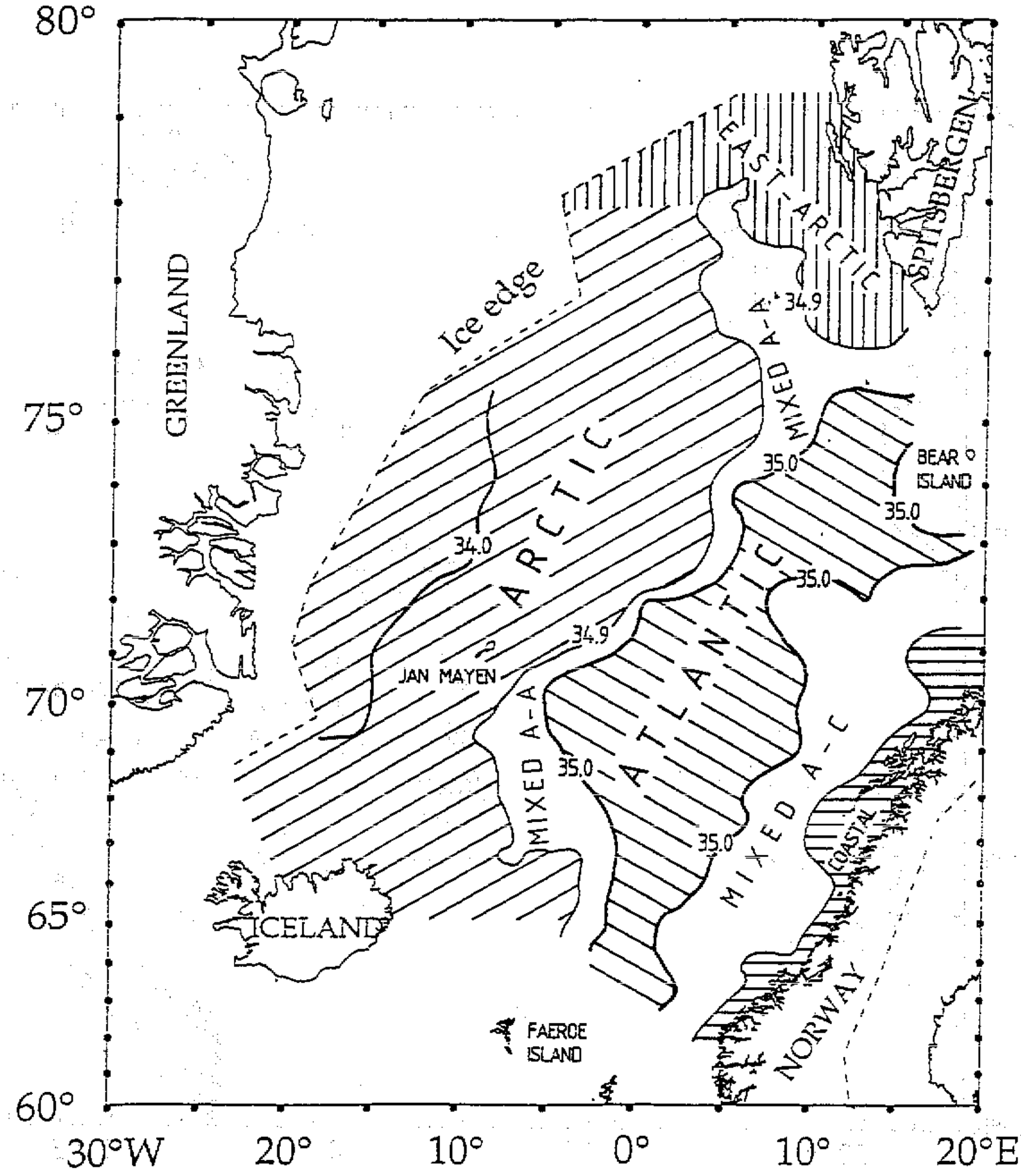
75°N
70°N
65°N
60°N
20°W
10°W
0°
10°E
20°E
1995
March
April
June
July
August
Iceland
Norway
July
August
June
April
March
June
May

Fig. 3



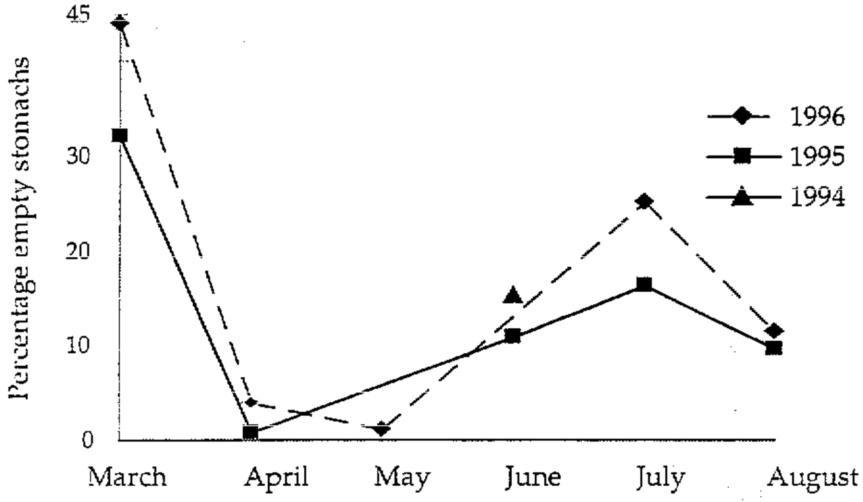
75°N
70°N
65°N
60°N
20°W
10°W
0°
10°E
20°E
1996
March
April
May
July
August
August
August
July
June
April
March
May
Iceland
Norway

Fig. 4



80°
75°
70°
65°
60°
30°W
20°
10°
0°
10°
20°E
GREENLAND
Ice edge
EAST-ARCTIC
SPITSBERGEN
34.9
MIXED A-A
35.0
BEAR ISLAND
35.0
ARCTIC
34.0
35.0
34.9
JAN MAYEN
ATLANTIC
MIXED A-A
35.0
35.0
MIXED A-C
COASTAL
ICELAND
FAEROE ISLAND
NORWAY

Fig. 5



1996	N	180	260	260	-	12	159
1995	N	112	111	-	130	332	177
1994	N				125		

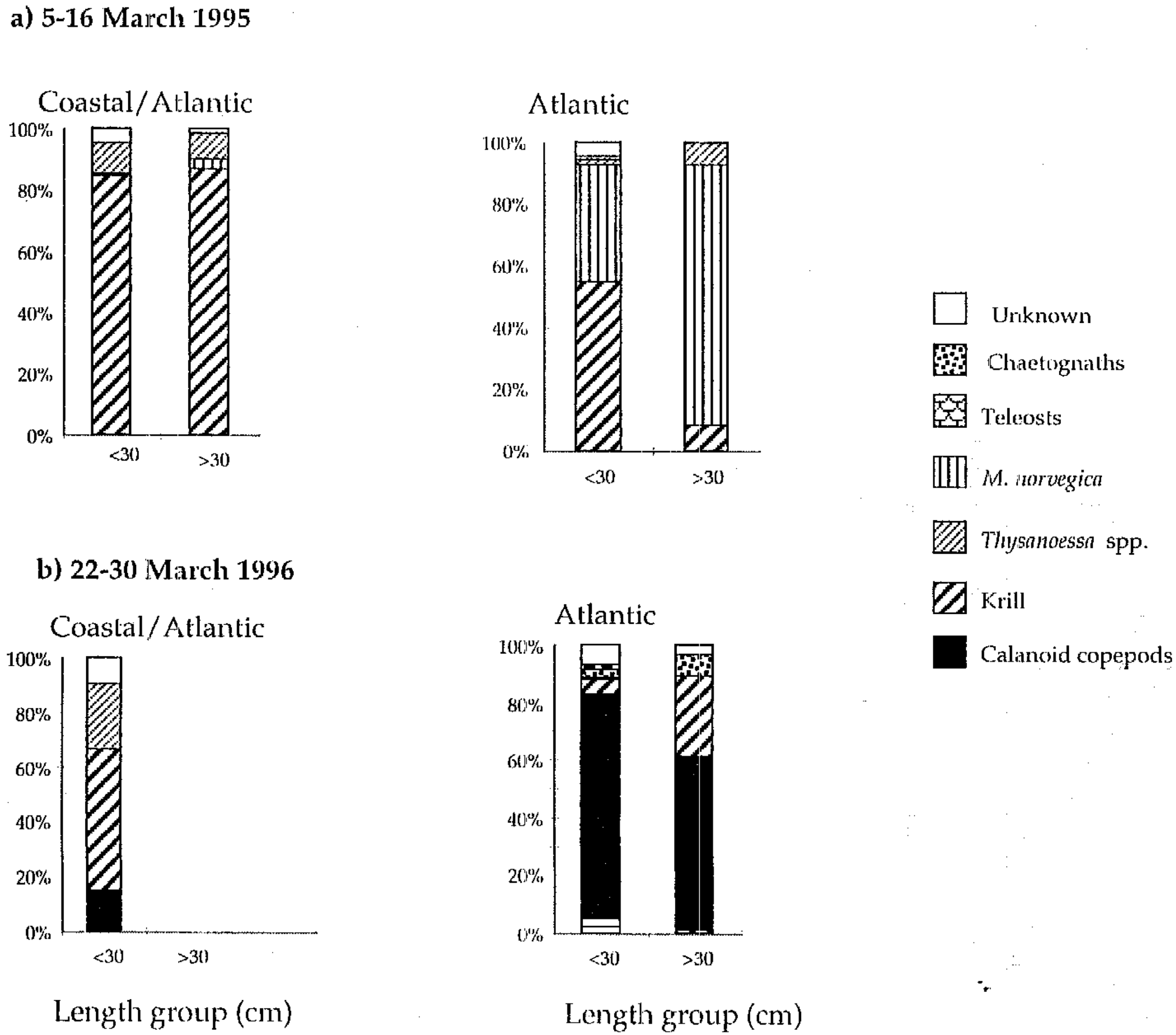

a) 5-16 March 1995
Coastal/Atlantic
Atlantic
100%
80%
60%
40%
20%
0%
<30
>30
b) 22-30 March 1996
Coastal/Atlantic
Atlantic
Length group (cm)
Length group (cm)
Unknown
Chaetognaths
Teleosts
M. norvegica
Thysanoessa spp.
Krill
Calanoid copepods

Fig. 6

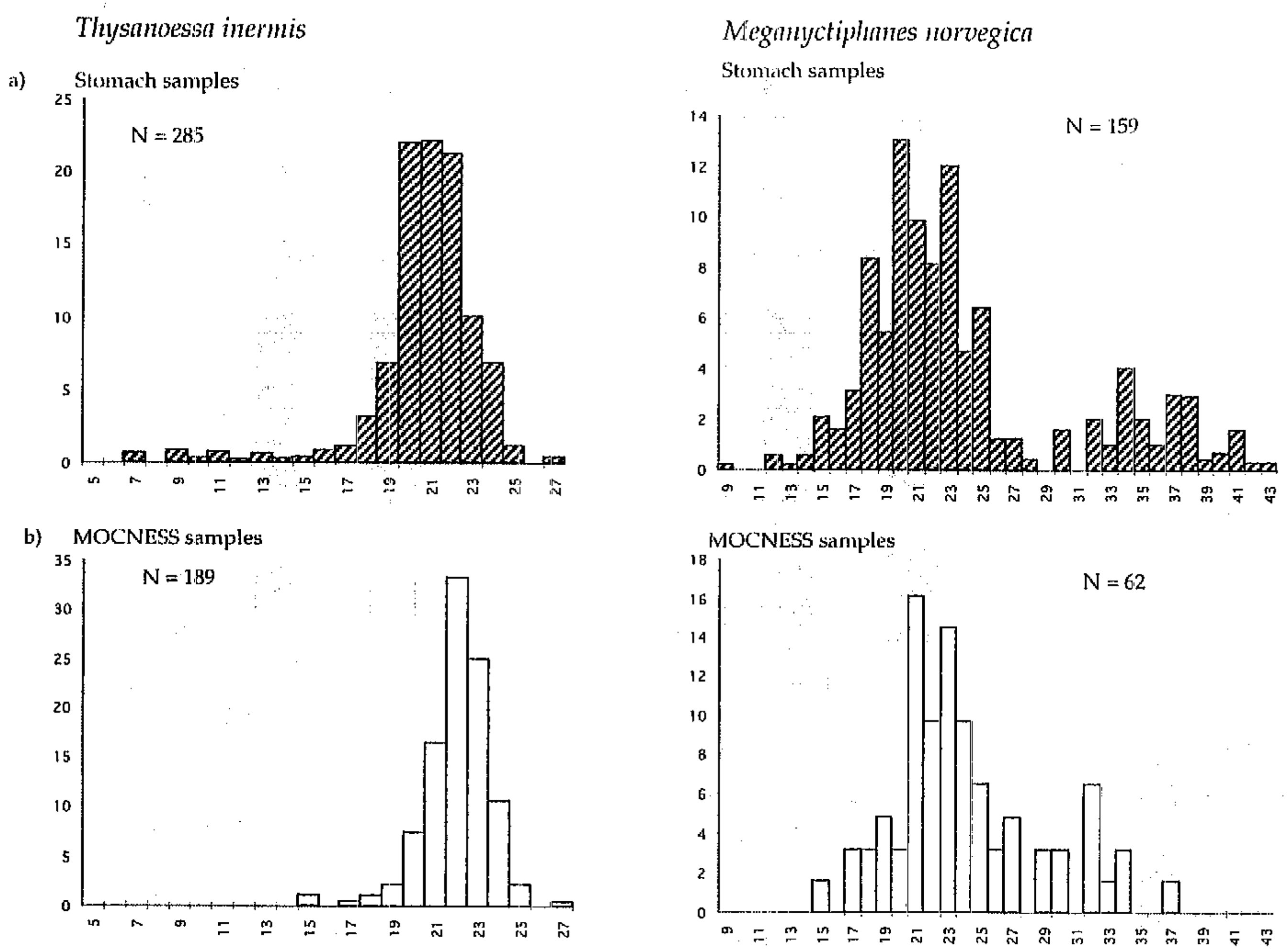

Thysanoessa inermis
a) Stomach samples
N = 285
b) MOCNESS samples
N = 189
Meganyctiphanes norvegica
Stomach samples
N = 159
MOCNESS samples
N = 62

Fig. 7

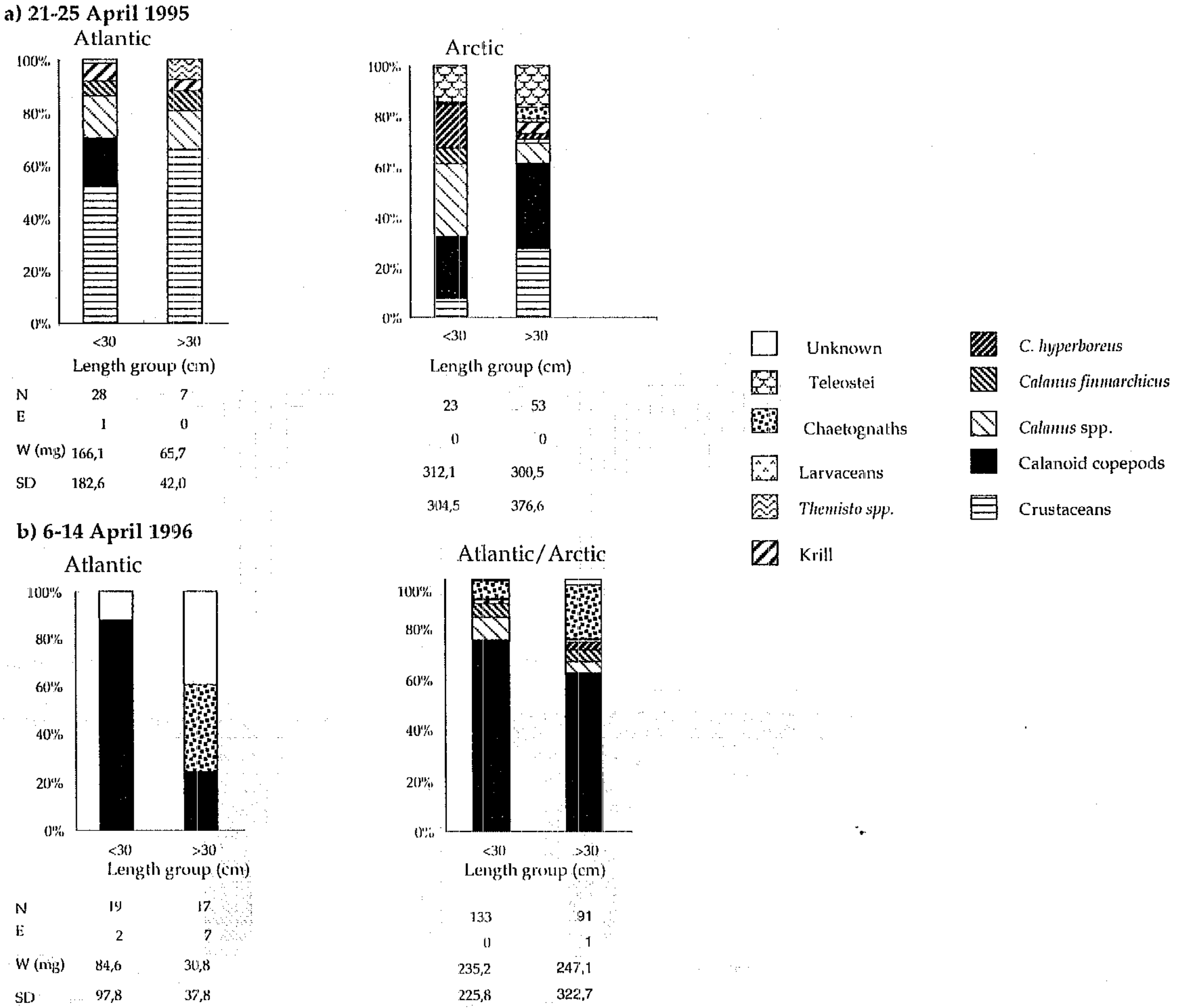
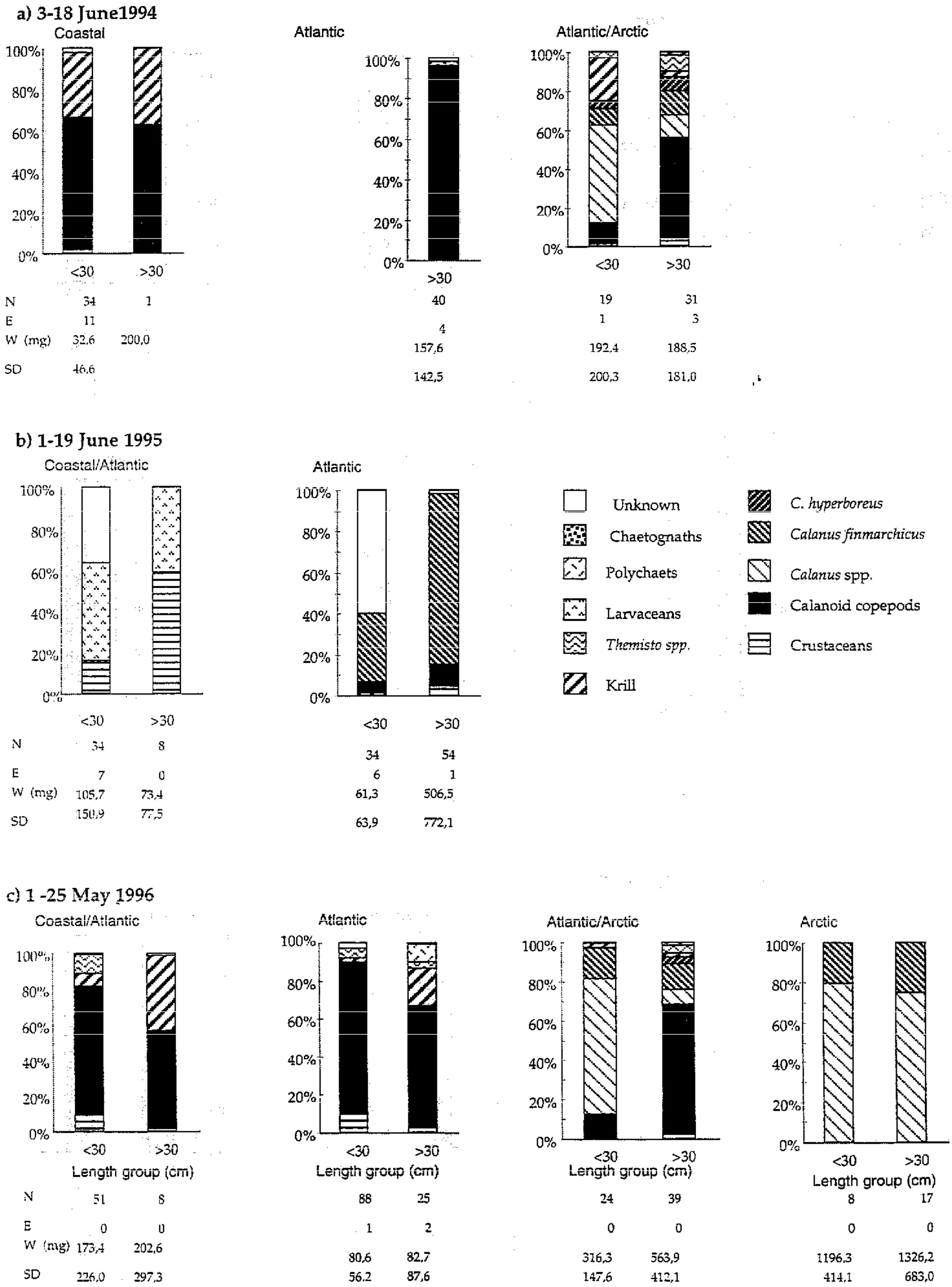

a) 21-25 April 1995
Atlantic
100%
80%
60%
40%
20%
0%
<30
>30
Length group (cm)
N 28 7
E 1 0
W (mg) 166,1 65,7
SD 182,6 42,0
Arctic
100%
80%
60%
40%
20%
0%
<30
>30
Length group (cm)
23 53
0 0
312,1 300,5
304,5 376,6
b) 6-14 April 1996
Atlantic
100%
80%
60%
40%
20%
0%
<30
>30
Length group (cm)
N 19 17
E 2 7
W (mg) 84,6 30,8
SD 97,8 37,8
Atlantic/Arctic
100%
80%
60%
40%
20%
0%
<30
>30
Length group (cm)
133 91
0 1
235,2 247,1
225,8 322,7
Unknown
Teleostei
Chaetognaths
Larvaceans
Themisto spp.
Krill
C. hyperboreus
Calanus finmarchicus
Calanus spp.
Calanoid copepods
Crustaceans

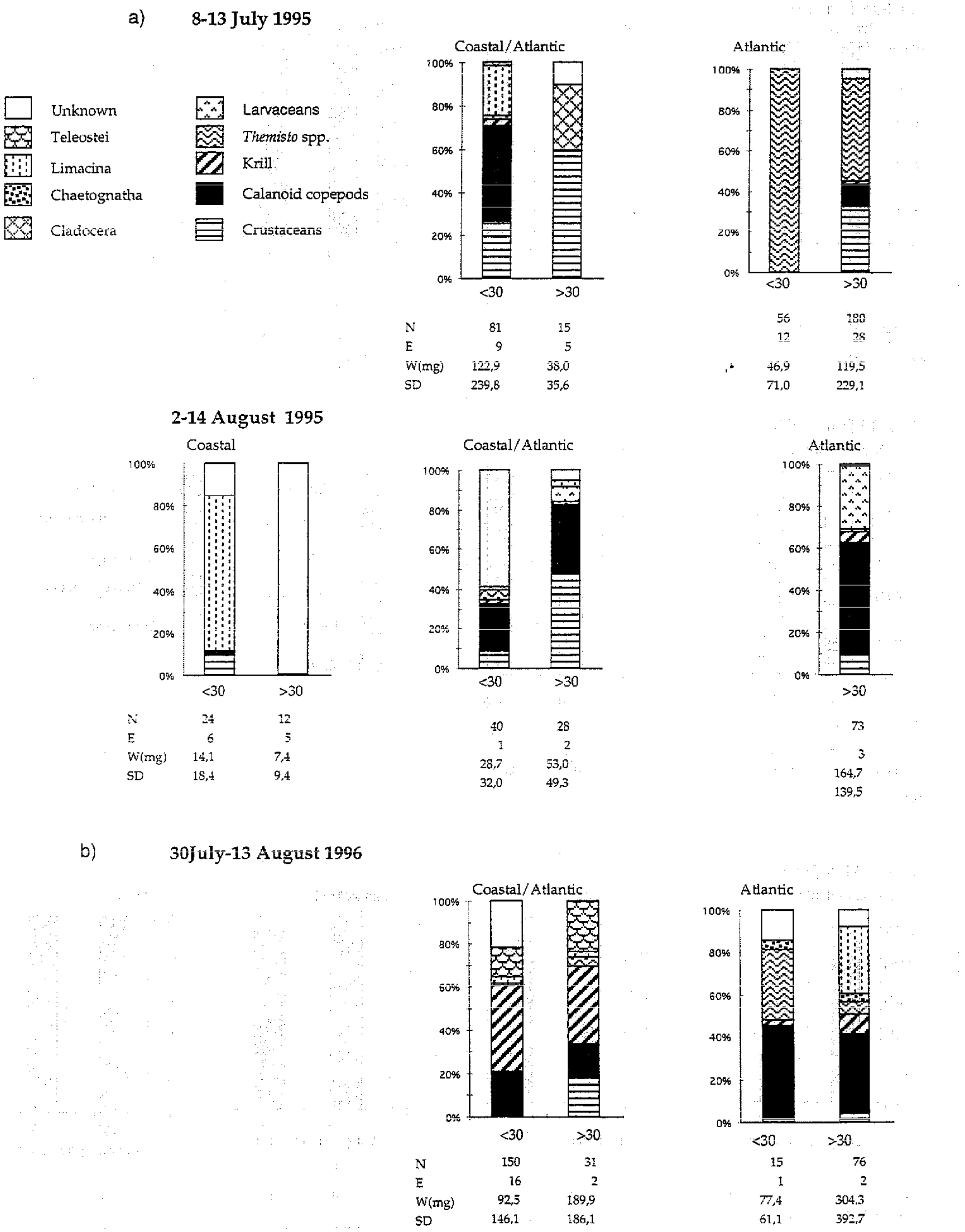
Fig. 8

Fig. 9



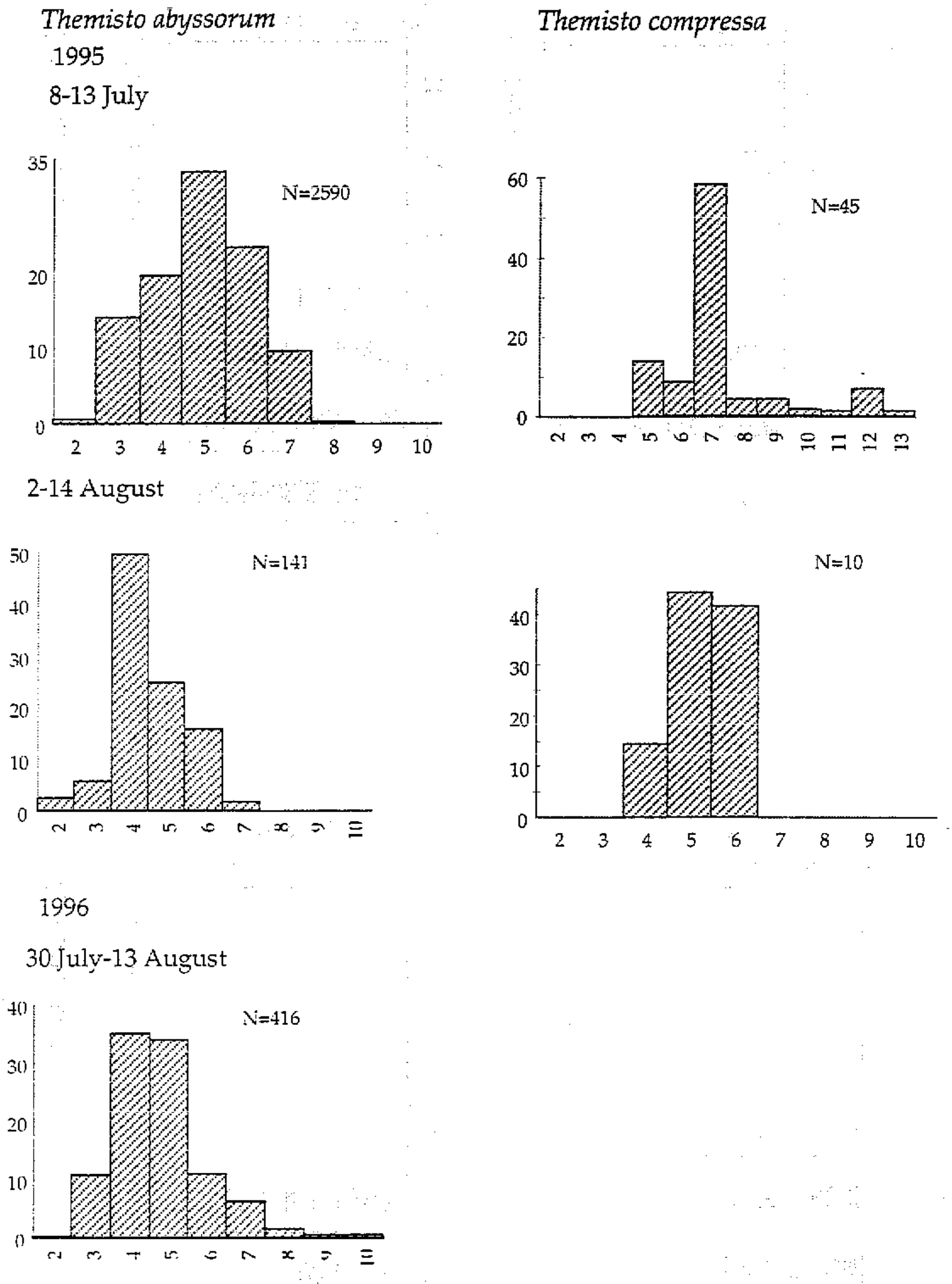
a) 3-18 June1994
Coastal
Atlantic
Atlantic/Arctic
100%
80%
60%
40%
20%
0%
<30
>30
N 34 1 40 19 31
E 11 4 1 3
W (mg) 32,6 200,0 157,6 192,4 188,5
SD 46,6 142,5 200,3 181,0
b) 1-19 June 1995
Coastal/Atlantic
Atlantic
N 34 8 34 54
E 7 0 6 1
W (mg) 105,7 73,4 61,3 506,5
SD 150,9 77,5 63,9 772,1
Unknown
Chaetognaths
Polychaets
Larvaceans
Themisto spp.
Krill
C. hyperboreus
Calanus finmarchicus
Calanus spp.
Calanoid copepods
Crustaceans
c) 1 -25 May 1996
Coastal/Atlantic
Atlantic
Atlantic/Arctic
Arctic
Length group (cm)
N 51 8 88 25 24 39 8 17
E 0 0 1 2 0 0 0 0
W (mg) 173,4 202,6 80,6 82,7 316,3 563,9 1196,3 1326,2
SD 226,0 297,3 56,2 87,6 147,6 412,1 414,1 683,0

Fig. 10



a) 8-13 July 1995
Unknown
Teleostei
Limacina
Chaetognatha
Cladocera
Larvaceans
Themisto spp.
Krill
Calanoid copepods
Crustaceans
Coastal/Atlantic
Atlantic
100%
80%
60%
40%
20%
0%
<30
>30
N 81 15 56 180
E 9 5 12 28
W(mg) 122,9 38,0 46,9 119,5
SD 239,8 35,6 71,0 229,1
2-14 August 1995
Coastal
Coastal/Atlantic
Atlantic
N 24 12 40 28 73
E 6 5 1 2 3
W(mg) 14,1 7,4 28,7 53,0 164,7
SD 18,4 9,4 32,0 49,3 139,5
b) 30July-13 August 1996
Coastal/Atlantic
Atlantic
N 150 31 15 76
E 16 2 1 2
W(mg) 92,5 189,9 77,4 304,3
SD 146,1 186,1 61,1 392,7

Fig 11



Themisto abyssorum
1995
8-13 July
N=2590
35
20
10
0
2 3 4 5 6 7 8 9 10
2-14 August
N=141
50
40
30
20
10
0
2 3 4 5 6 7 8 9 10
1996
30 July-13 August
N=416
40
30
20
10
0
2 3 4 5 6 7 8 9 10
Themisto compressa
N=45
60
40
20
0
2 3 4 5 6 7 8 9 10 11 12 13
N=10
40
30
20
10
0
2 3 4 5 6 7 8 9 10

Fig. 12

C. finmarchicus

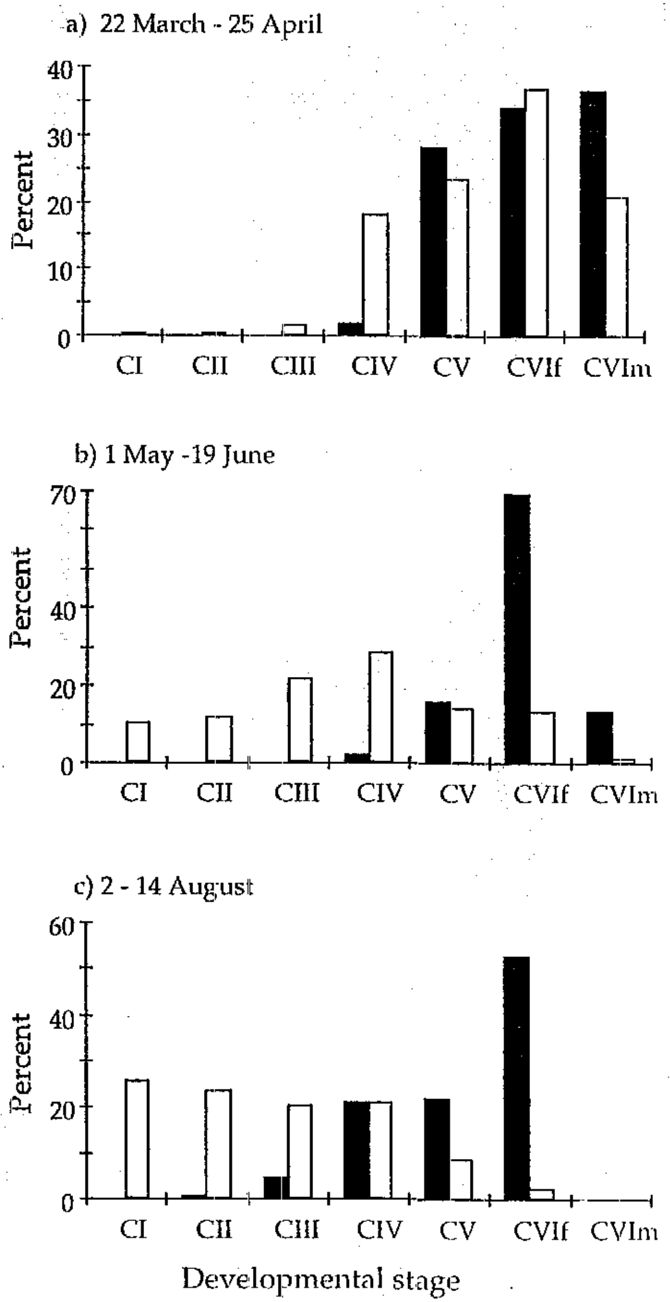


Fig. 13

C. hyperboreus

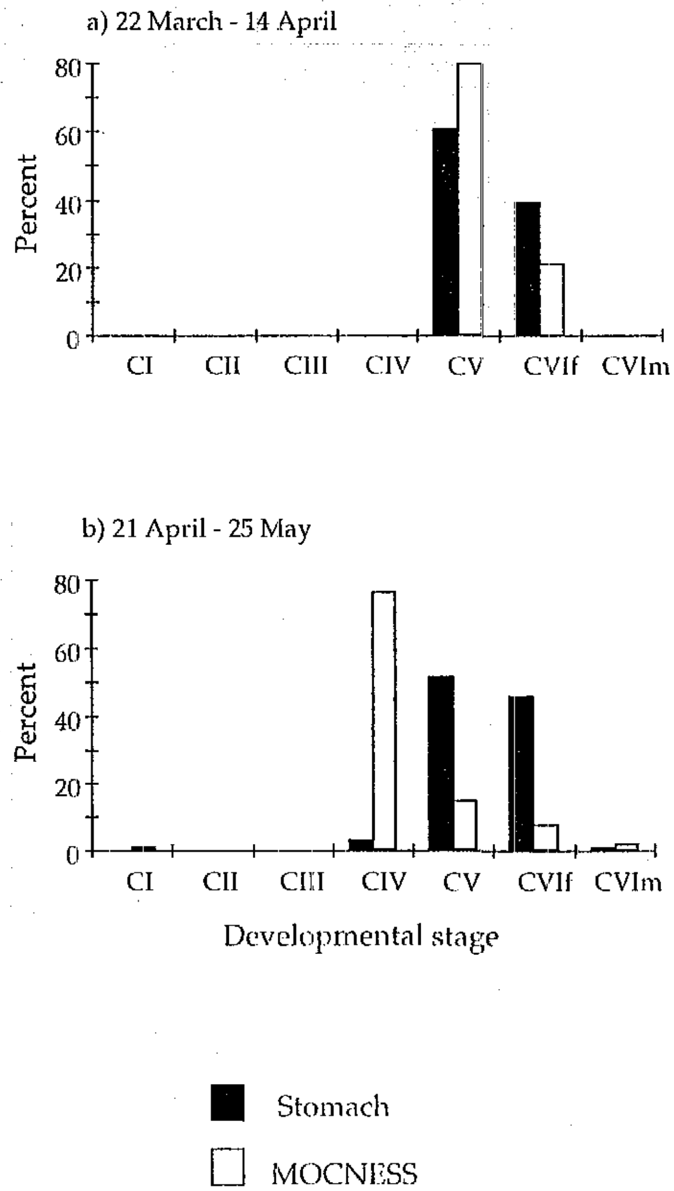


Fig. 14

a)

b)

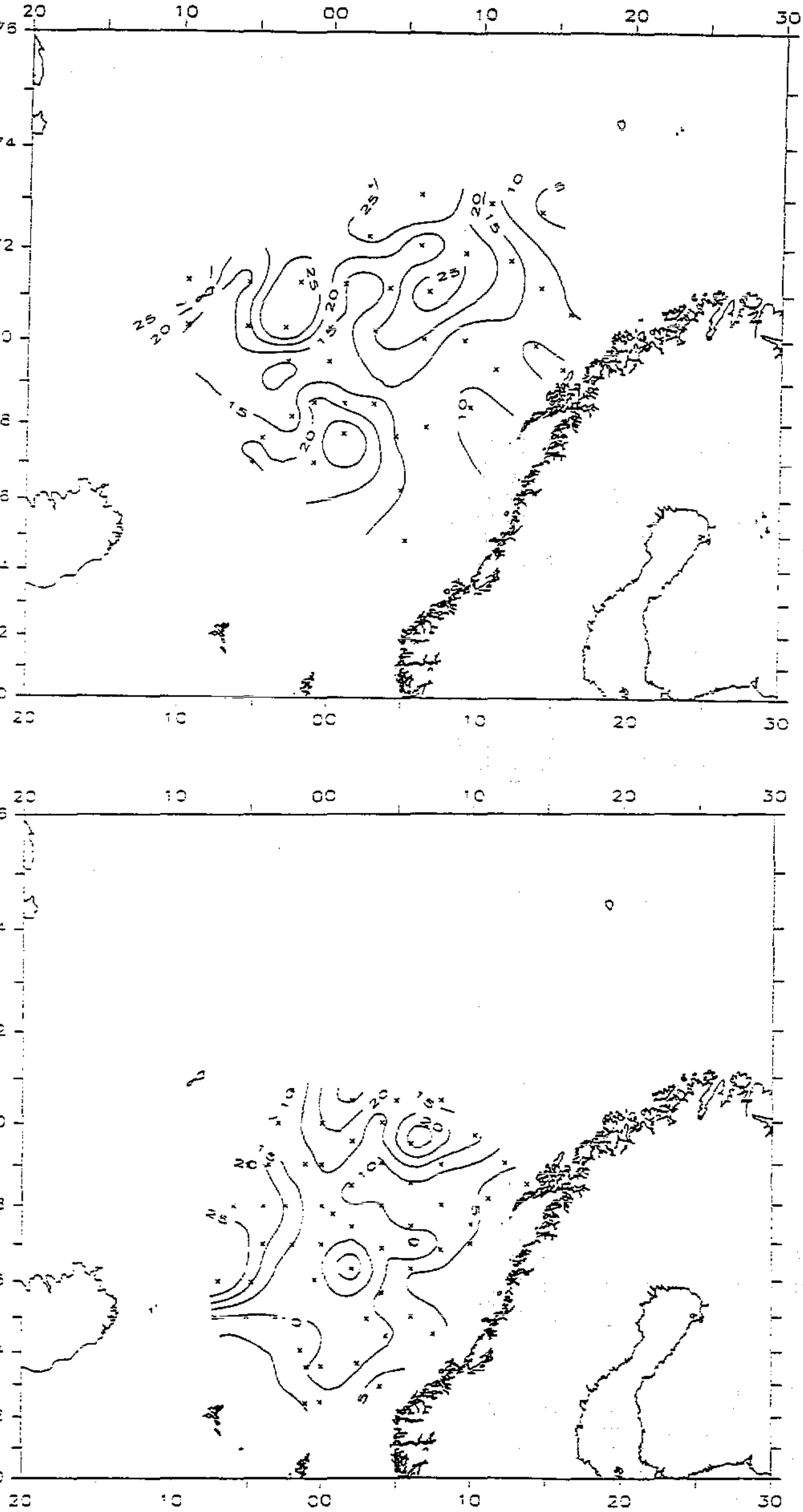


Table 1. Surveys in the Nordic Seas from March to August 1994-96.

Year	Vessel	Period	No. stations	No. stomachs	Depths (m)	Mean length (range) cm
1994	G.O. Sars	3-18June	9	125	30-0	31,2(22,5-39,0)
1995	G.O. Sars	5-16 March	8	112	30-0	31,9 (22,5-39,5)
	G.O. Sars	21-25April	8	111	400-0	30,6 (24,0-38,0)
	G.O. Sars	1-19June	11	130	30-0	29,3 (20,0-38,0)
	G.O. Sars	8-31July	23	177	30-0	30,7 (21,5-39,5)
	J. Hjort	2-14 August	16	332	30-0	31,3 (21.5-40.0)
1996	G.O. Sars	22-30 March	11	180	350-0	28,2 (19,0-37,5)
	G.O. Sars	6-14 April	17	260	400-0	29,4 (22,5-39,5)
	G.O. Sars	1-25 May	20	260	30-0	28,6 (20,0-38,0)
	G.O. Sars	30 Jul-13 Aug	18	171	30-0	31,5 (22,0-39,5)