

Food and feeding conditions of Norwegian spring-spawning herring (*Clupea harengus*) through its feeding migrations

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

After spawning in February and 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 primarily on *Calanus finmarchicus*, copepodid stage IV and older. In colder waters e.g., those influenced by the East Icelandic Current, *C. hyperboreus* was important in the diet. By July and August, a wide variety of prey organisms was found in the stomachs of herring caught in the central Norwegian Sea and on the Norwegian continental shelf. In the western part of the Norwegian Sea, amphipods, *Themisto* spp., were important prey.

The herring showed size-selective feeding on copepodid stages of *C. finmarchicus* and *C. hyperboreus*. Larger prey, such as krill and amphipods, were preyed upon regardless of their size. The average weight of food in the stomach was generally higher in the mixed Atlantic/Arctic and Arctic waters, which were also characterized by higher zooplankton biomass.

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Introduction

The feeding migration pattern of the Norwegian spring spawning herring (*Clupea harengus*) changed during and after the collapse of the stock at the end of the 1960s (Røttingen, 1992; Dragesund *et al.*, 1997). In April, the adult herring start to migrate from the spawning grounds along the coast of Norway to their early feeding grounds, in the eastern and central parts of the Norwegian Sea (Dragesund *et al.*, 1980). Before the collapse of the stock, the main feeding grounds were located in the Norwegian Sea between Jan Mayen and Iceland and, in the late 1960s, also between Jan Mayen and Bear Island (Dragesund *et al.*, 1980; Røttingen, 1989). During a period when the stock size was very low, the feeding area was restricted to the coastal waters of northern Norway (Røttingen, 1992;

Dragesund *et al.*, 1997). With the increase in the stock since the mid 1980s, herring have returned to their previous feeding grounds, which cover large areas of the Norwegian Sea. The herring migrate eastward in late July and August, and enter the wintering areas in northern Norway in September (Misund *et al.*, 1998; ICES, 1999).

Previous studies demonstrated that the copepod *Calanus* spp., especially *C. finmarchicus*, krill *Thysanoessa inermis*, *Meganyctiphanes norvegica* and amphipods *Themisto* spp. comprise 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 in coastal waters of northern Norway where

Table 1. Surveys in the Nordic Seas and herring catch data from March to August 1994–1996. (l=mean length (cm); a=mean age (y); m=mean maturity stage).

Year	Vessel	Period	No. stations	No. stomachs	Depths (m)	l (range)	a (range)	m (range)
1994	G. O. Sars	3–18 June	9	125	30–0	31.2 (22.5–39.0)	6.6 (2.0–11.0)	3.3 (1.0–8.0)
1995	G. O. Sars	5–16 March	8	112	30–0	31.9 (22.5–39.5)	6.3 (4.0–12.0)	6.0 (2.0–8.0)
	G. O. Sars	21–25 April	8	111	400–0	30.6 (24.0–38.0)	5.8 (3.0–12.0)	5.8 (2.0–8.0)
1996	G. O. Sars	1–19 June	11	130	30–0	29.3 (20.0–38.0)	5.0 (3.0–12.0)	3.0 (1.0–8.0)
	G. O. Sars	8–31 July	23	332	30–0	30.7 (21.5–39.5)	5.2 (2.0–12.0)	3.7 (1.0–8.0)
	J. Hjort	2–14 August	16	177	30–0	31.3 (21.5–40.0)	5.5 (3.0–12.0)	2.7 (2.0–4.0)
	G. O. Sars	22–30 March	11	180	350–0	28.2 (19.0–37.5)	5.1 (3.0–13.0)	5.0 (1.0–8.0)
1996	G. O. Sars	6–14 April	17	260	400–0	29.4 (22.5–39.5)	5.4 (2.0–13.0)	4.9 (2.0–8.0)
	G. O. Sars	1–25 May	20	260	30–0	28.6 (20.0–38.0)	4.6 (2.0–13.0)	5.0 (1.0–8.0)
	G. O. Sars	30 July–13 August	18	171	30–0	31.5 (22.0–39.5)	6.0 (2.0–13.0)	4.1 (1.0–8.0)

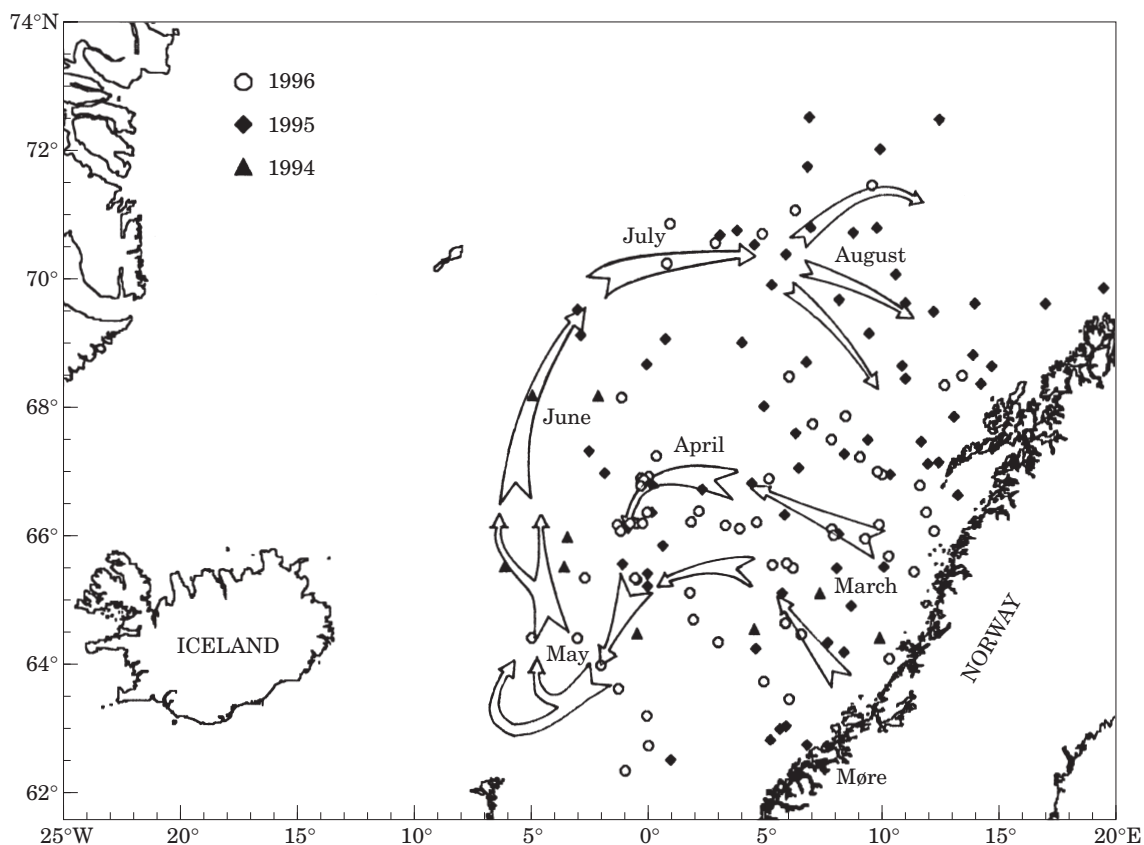


Figure 1. Locations of pelagic trawl stations where herring stomachs were analysed, from 1994, 1995 and 1996. The arrows show schematic presentation of migration pattern of herring at different time periods (Misund *et al.*, 1998.)

the distribution of 0-group and adult herring overlapped during the period of low stock.

The abundance and migration of the Norwegian spring spawning herring are monitored in annual ICES co-ordinated surveys. Several studies in recent years (Røttingen, 1992; Dragesund *et al.*, 1997; Misund *et al.*,

1998) have shown that Norwegian spring-spawning herring has undergone great fluctuations in abundance and migration. Misund *et al.* (1998) suggest that herring search and feed over a large area to accumulate energy reserves for spawning and over-wintering activity. These authors also indicate that the extended feeding

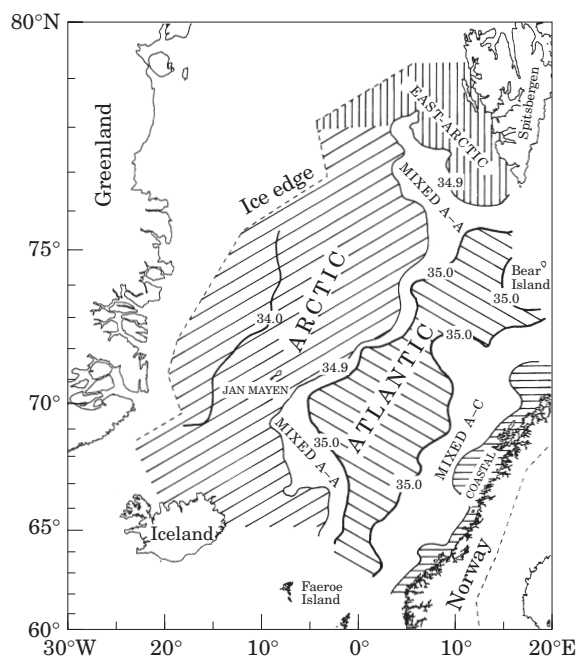


Figure 2. Schematic presentation of water masses in the Nordic Seas. A-C=Atlantic/Coastal; A-A=Atlantic/Arctic. (From Dalpadado *et al.*, 1998).

migration of older herring in 1996 reflected increased feeding pressure consequent on increased stock size in recent years. This study was aimed at gaining more knowledge on current feeding patterns, e.g. the type and size of prey, main feeding period, feeding grounds etc. This information is significant in evaluating the factors governing the migration and distribution pattern of herring. During surveys in the Norwegian Sea in 1994–1996, we focused on: (a) determining the major prey of herring in different regions/water masses e.g., Coastal, Atlantic, Arctic and (b) examining the spatial distribution of herring in relation to its prey organisms.

Materials and method

Herring stomachs were collected during cruises undertaken in the Norwegian Sea in 1994 to 1996 (Table 1; Fig. 1). Herring were sampled with a pelagic trawl (Åkra trawl, see Valdemarsen and Misund, 1995) with a 30 m × 30 m mouth opening and a codend with a mesh size of approximately 16 mm (stretched), towed at 3–4 knots.

A random sample of ca. 100 fish was taken from the trawl catch when possible. The length, weight, age, and maturity of the herring were recorded according to the

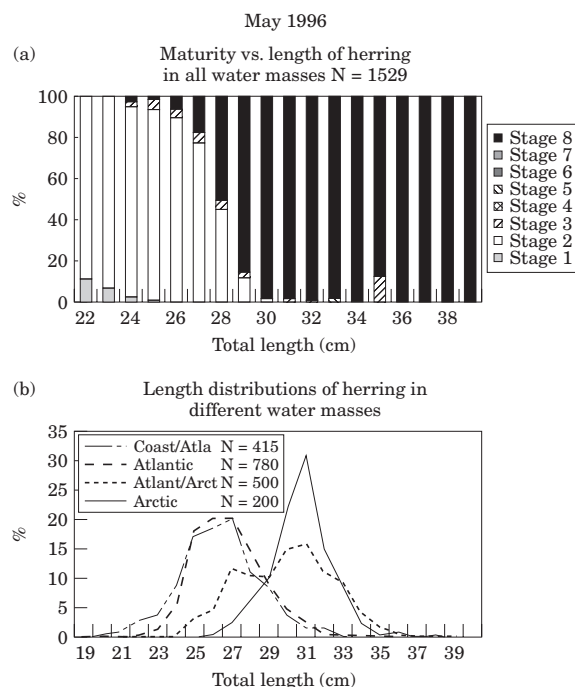


Figure 3. Percentage frequency distribution of (a) maturity stages and (b) length of herring from May 1996.

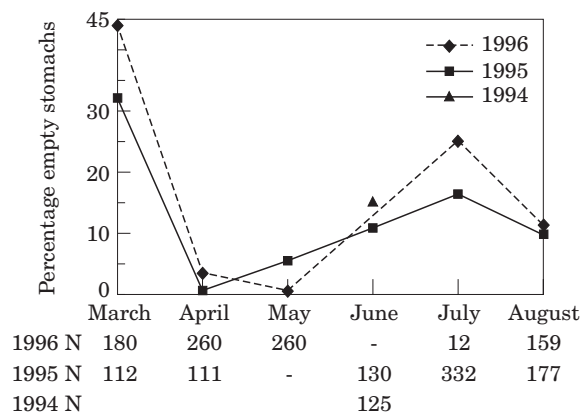


Figure 4. Percentage of empty stomachs from March to August 1994–1996. N=number of herring.

instructions given in Fotland *et al.* (1995). A total of 30 herring stomachs were frozen immediately. Two fish in each 1 cm-length group were used for stomach content analyses. The stomach data were weighted by the number of fish in each cm-length group in the random sample.

Herring stomachs were analysed 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). The stomach contents were carefully teased apart and all

Table 2. Average weight (mg) of stomach contents of small (<30 cm) and large herring (>30 cm) in different water masses and time periods. N=number of herring; E=empty stomachs; W=average weight of stomach contents; s.d.=standard deviation.

Size classes	Coastal		Coastal/Atlantic		Atlantic		Atlantic/Arctic		Arctic	
	<30	≥30	<30	≥30	<30	≥30	<30	≥30	<30	≥30
1994										
June	N	34	1		40		19	31		
	E	11			4		1	3		
	W	32.6	200		157.6		192.4	188.5		
	s.d.	46.6			142.5		200.3	181		
1995										
March	N		6	69	21	16				
	E		2	20	5	8				
	W		379.8	588.5	59.2	154				
	s.d.		813.8	1057	71	353.4				
April	N				28	7			23	53
	E				1	0			0	0
	W				166.1	65.7			312.1	300.5
	s.d.				182.6	42			304.5	376.6
June	N		34	8	34	54				
	E		7	0	6	1				
	W		105.7	73.4	61.3	506.5				
	s.d.		150.9	77.5	63.9	772.1				
July	N		81	15	56	180				
	E		9	5	12	28				
	W		122.9	38	46.9	119.5				
	s.d.		239.8	35.6	71	229.1				
August	N	24	12	40	28	73				
	E	6	5	1	2	3				
	W	14.1	7.4	28.7	53	164.7				
	s.d.	18.4	9.4	32	49.3	139.5				
1996										
March	N		33	14	77	49				
	E		28	14	13	17				
	W		1.6		44.4	51.6				
	s.d.		6.5		50	99.9				
April	N				19	17	133	91		
	E				2	7	0	1		
	W				84.6	30.8	235.2	247.1		
	s.d.				97.8	37.8	225.8	322.7		
May	N		51	8	88	25	24	39	8	17
	E		0	0	1	2	0	0	0	0
	W		173.4	202.6	80.6	82.7	316.3	563.9	1196	1326
	s.d.		226	297.3	56.2	87.6	147.6	412.1	444.1	683
August	N		50	31	15	75				
	E		16	2	1	2				
	W		92.5	189.9	77.4	304.3				
	s.d.		146.1	186.1	61.1	392.7				

identifiable prey 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 (copepodid I–VI) were determined. For all other organisms, the carapace or total length was recorded. Prey were weighed to the nearest mg after oven-drying at 70°C until a constant weight was obtained. Dry weights of all major prey categories were determined separately, and the rest of the stomach contents were weighed together.

Mean weight of the stomach contents were based on all stomachs in the sample, i.e. including empty stomachs.

To determine the potentially available herring prey, 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 eight 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 m depth strata

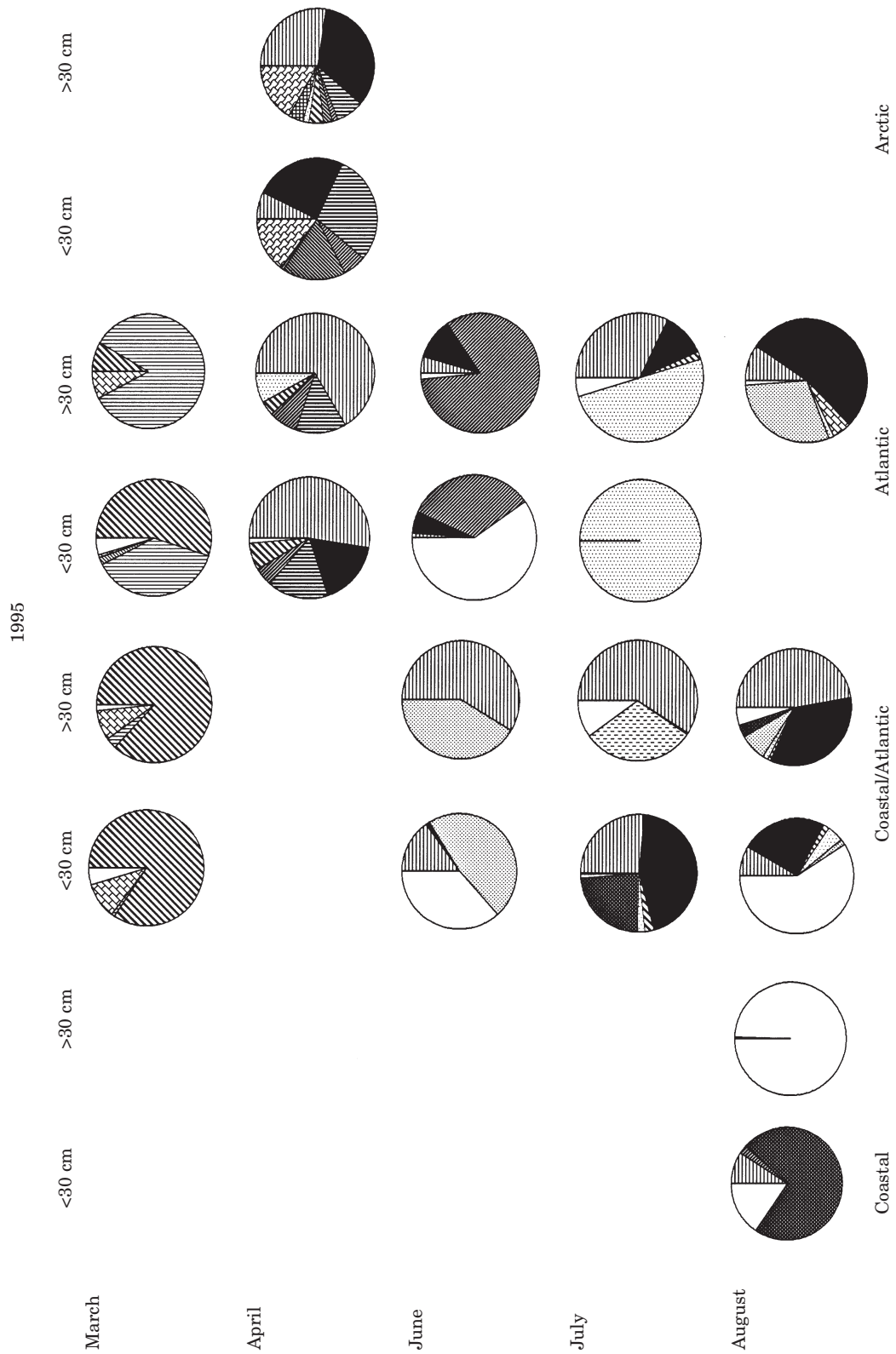


Figure 5. Major prey of herring as percentage of the total dry weight in different water masses and time periods in 1995. Hatching code as in Figure 7.

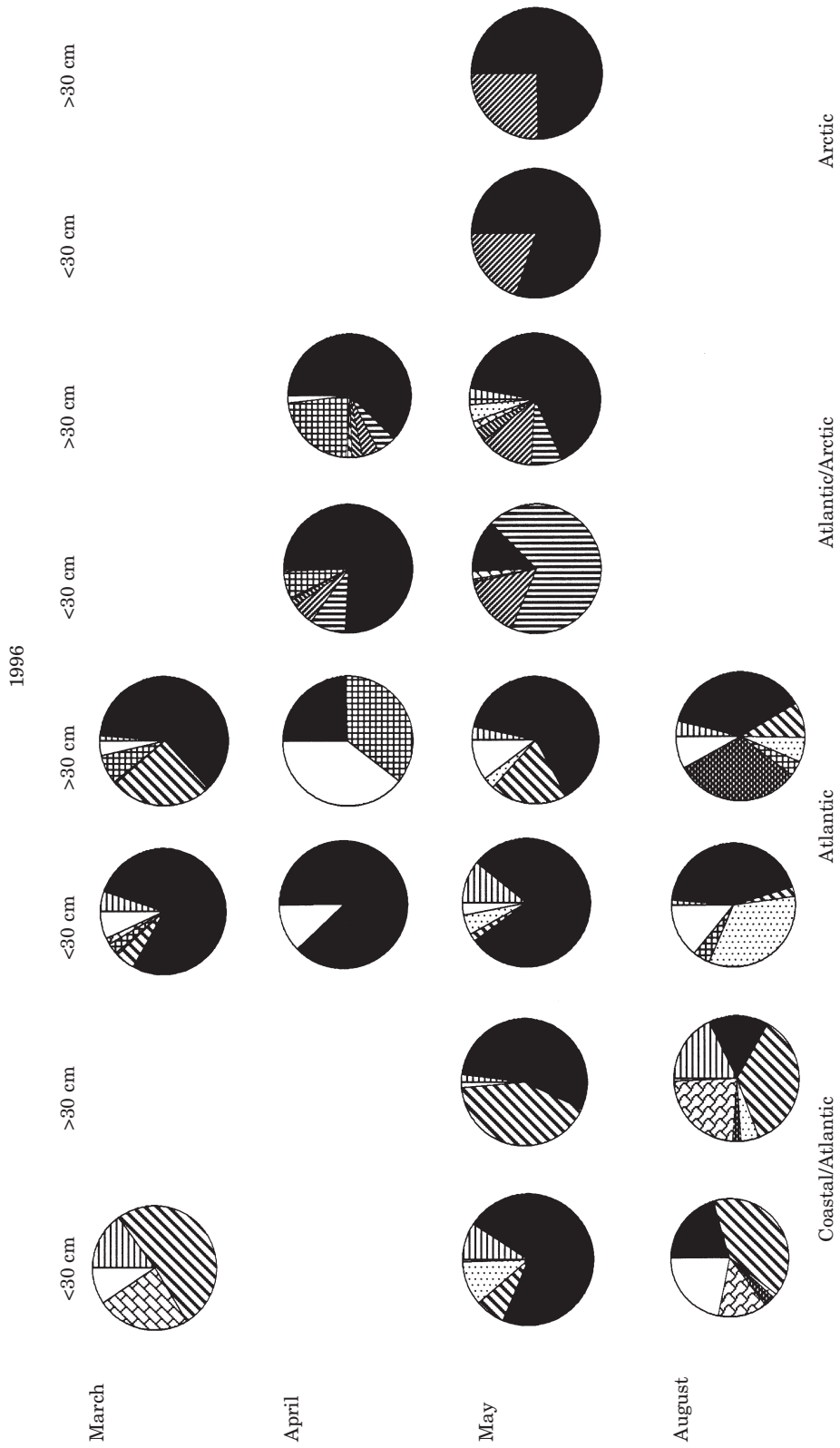


Figure 6. Major prey of herring as percentage of the total dry weight in different water masses and time periods in 1996. Hatching code as in Figure 7.

(Fig. 3(a)). Length frequency distributions of herring from different water masses show that in Coastal Atlantic and Atlantic waters, the majority of herring had a modal length of 26 cm, whereas in Atlantic/Arctic and Arctic waters, the modal length was higher, 31 cm (Fig. 3(b)).

Results

Major prey of herring in different water masses/regions

March 1995 and 1996

Herring collected in March 1995 and 1996 from the Møre coast and shelf and shelf edge northwards had 32% and 43% empty stomachs, respectively (Fig. 4). In March 1995, however, the majority of herring (64%, compared to 47% in 1996) had already spawned, and these seem to have started to feed. The mean stomach content weight in 1995 was higher than in 1996 (Table 2).

In the mixed Coastal/Atlantic and Atlantic waters, in March 1995, herring fed almost exclusively on krill, which comprised more than 90% of the total prey weight (Fig. 5). The dominant krill species were *Thysanoessa inermis* and *Meganycitiphanes norvegica*.

In March 1996, krill constituted 75% of the prey weight in herring stomachs in the Coastal/Atlantic waters, whereas in the Atlantic waters, calanoid copepods dominated the diet, comprising 80% and 62% of the total prey weight in fish <30 cm and >30 cm respectively (Fig. 6). In the Atlantic waters, krill (26%) and chaetognaths (arrow worms) (7%) were also consumed, particularly by the larger herring.

April 1995 and 1996

The percentage of empty stomachs decreased by nearly 40% from March to April in 1995 and 1996. The average weight of food in the stomachs of herring which had migrated offshore to mixed Arctic and Atlantic/Arctic waters was 306 mg and 241 mg in 1995 and 1996, respectively (Table 2).

In 1995, copepods dominated the diet in the Arctic and in the Atlantic waters, comprising 43% and 59% by weight, respectively (Fig. 5). However, in the Arctic waters *C. hyperboreus* was the most abundant copepod in the stomachs, whereas in the Atlantic waters, only *C. finmarchicus* was present. In addition to copepods, the fish *Maurolicus muelleri* was an important prey of herring in the Arctic waters, as were krill, *M. norvegica* and arrow worms, *Sagitta* spp. in the largest size classes (>30 cm).

In 1996 in the Atlantic waters calanoid copepods (88%) were the major prey of herring below 30 cm, whereas chaetognaths (36%) and calanoid copepods (24%) dominated the diet of larger herring (Fig. 6). In the mixed Atlantic/Arctic waters, calanoid copepods

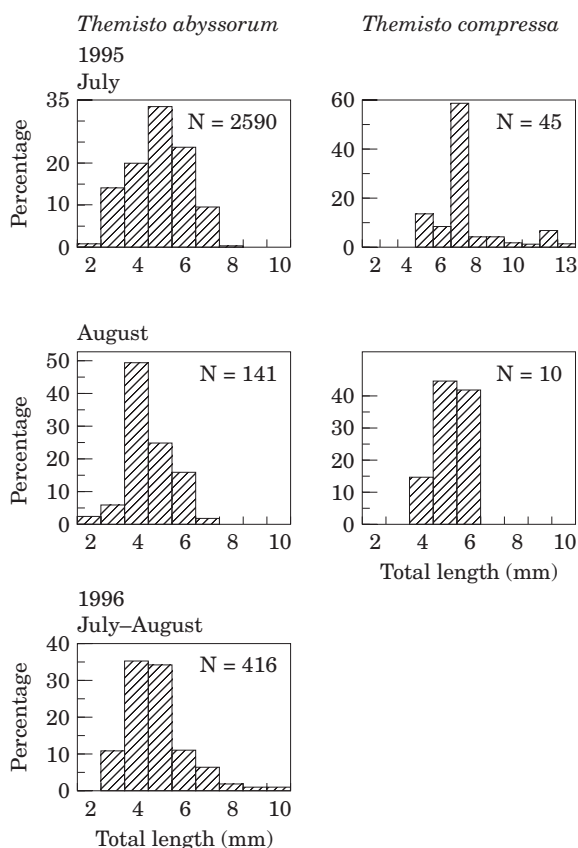


Figure 8. Length distribution of *Themisto abyssorum* and *T. compressa* in herring stomachs in July and August 1995 and 1996.

comprised the major part of the diet, and chaetognaths ranked second in importance (Fig. 6). In the Atlantic waters, *C. finmarchicus* was dominant among the identified calanoid copepods, whereas in the mixed Atlantic/Arctic waters, both *C. finmarchicus* and *C. hyperboreus* were present (Fig. 6).

May–June 1994, 1995, and 1996

By May and June, feeding herring occupied large areas of the Nordic Seas. The percentages of empty stomachs in all three years in May and June were below 15%. During this time the average weight of food in the stomach was generally greater than other times of the year, indicating high feeding activity. Greatest average weights were recorded in Arctic waters in May 1996 (Table 2).

A total of 125 herring stomachs were analysed from nine stations sampled in June 1994 (Fig. 1, Table 1). Calanoid copepods were the dominant component of the diet by weight in the Coastal, Atlantic, and mixed Atlantic/Arctic waters, although proportionately fewer copepods were consumed in Coastal Waters relative to

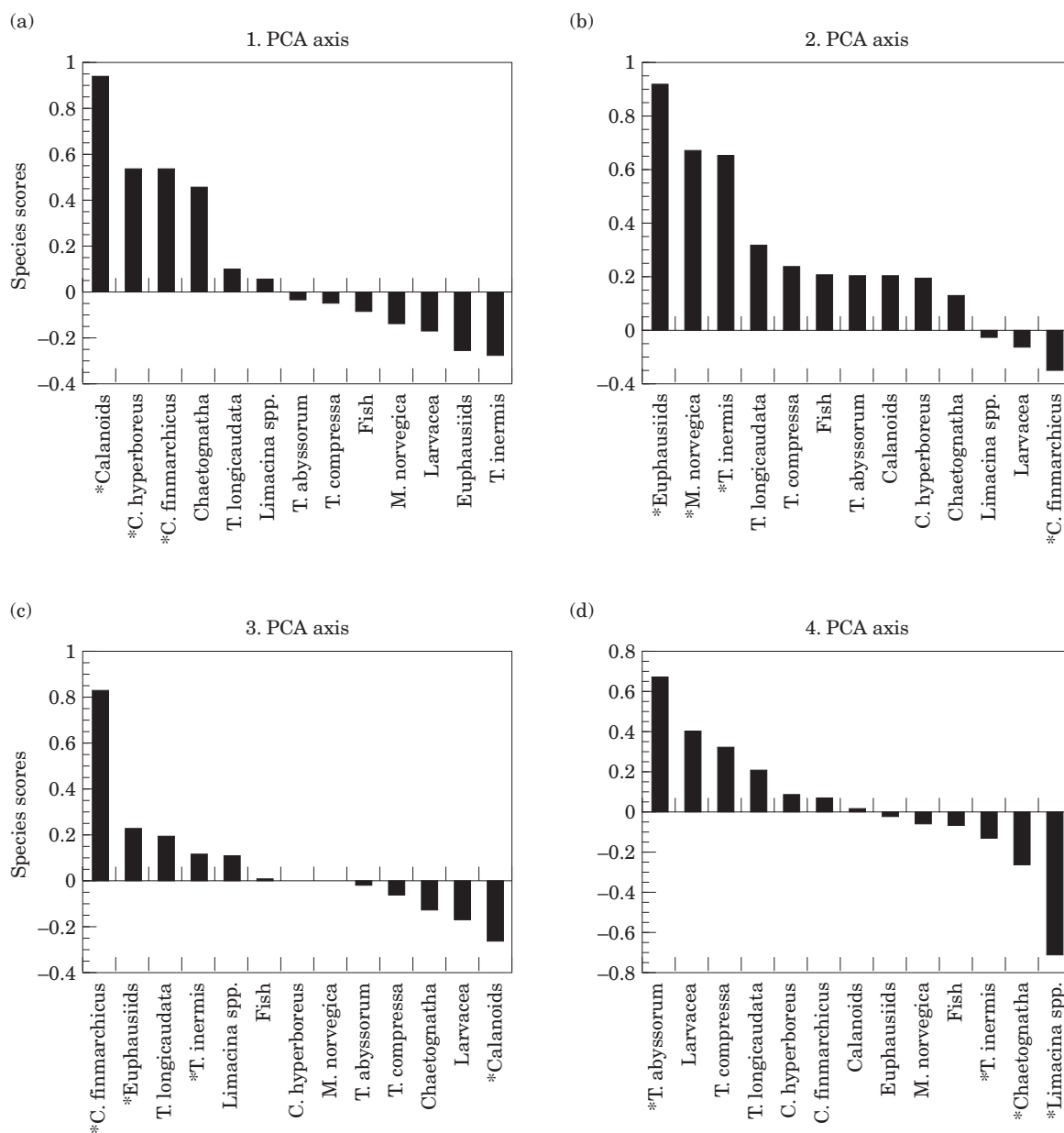


Figure 9. Species scores (Jongmann *et al.*, 1988) along PCA axes 1–4 (a–d). *Denotes species being significantly related to the axes as indicated by Cumulative fit per species (ter Braak and Prentice, 1988).

the offshore waters (Fig. 7). At most stations *Calanus* spp. consisted of overwintering stages (IV–VI). Analysis of stomach contents collected in June 1995 in the coastal waters off Lofoten/Vesterålen showed that about half of the weight of food consisted of larvaceans (Fig. 5). In the Atlantic waters, herring fed almost exclusively on *C. finmarchicus*.

A total of 260 stomachs were analysed from 20 stations sampled in May 1996. Calanoid copepods were

the major prey of herring in mixed Coastal/Atlantic, Atlantic, mixed Atlantic/Arctic, and Arctic waters varying between 50–99% of the total prey weight (Fig. 6). In the mixed Coastal/Atlantic and Atlantic waters, krill were important in the diet, especially in larger herring, and constituted 42% and 20% of the total prey weight, respectively. Amphipods accounted for up to 11% of the total prey weight of herring in the mixed Coastal/Atlantic, Atlantic, and mixed Atlantic/Arctic waters.

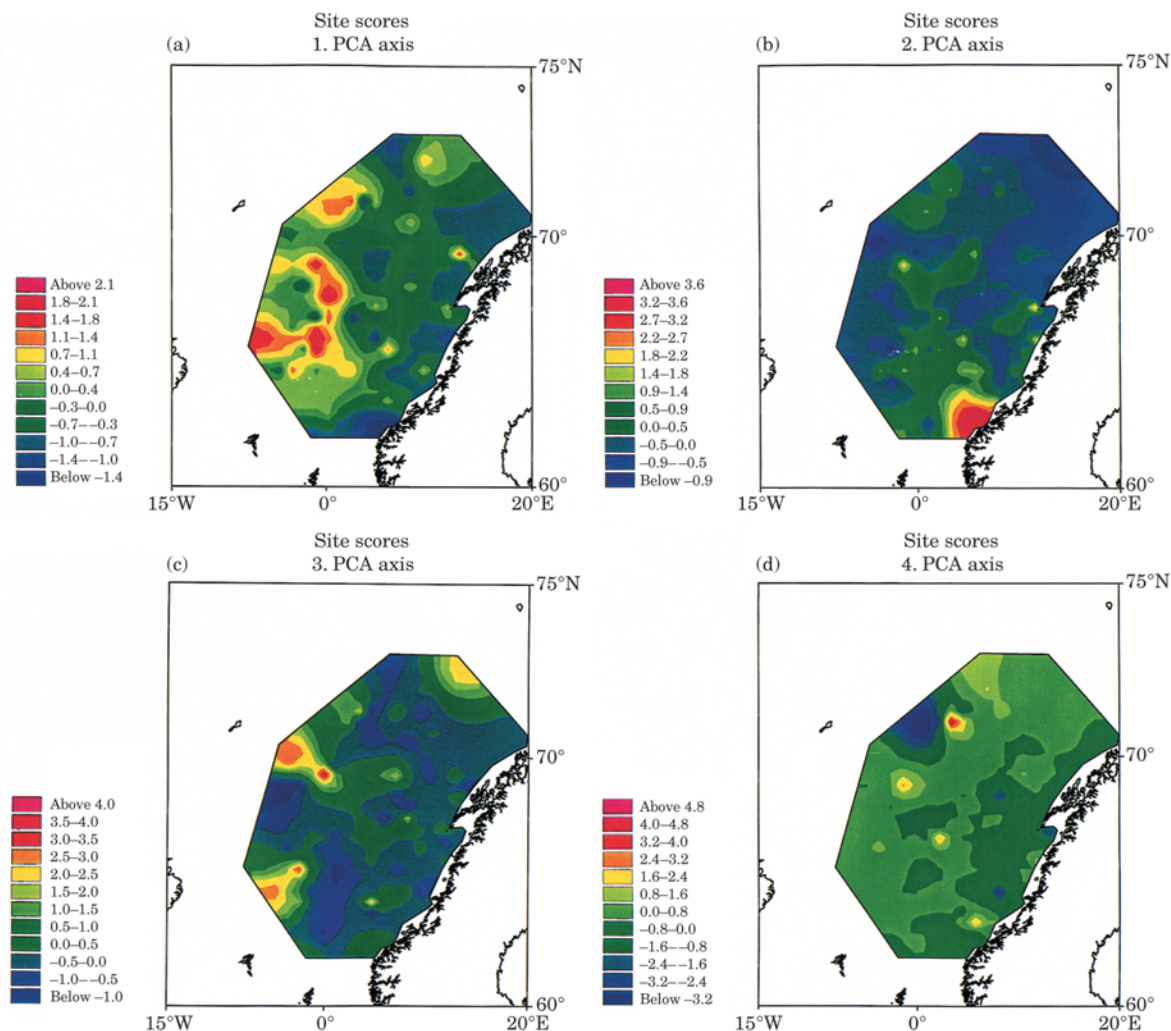


Figure 10. Site scores (Jongman *et al.*, 1988) along PCA axes 1–4 (a–d). High negative or positive scores along the PCA axes are sampling stations which are strongly correlated with the dominant species (food items) of these axes. E.g. at the stations with high positive site scores on the first axis, herring stomachs dominated of Calanoid copepods and *Calanus* spp.

July–August 1995 and 1996

In late July and August, herring start migrating eastwards towards coastal areas of Norway. The fish generally had lower average stomach content weights than in May and June (Table 2), but a wider variety of prey organisms in their diet than at 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. 5). In the Atlantic waters in July 1995, herring fed almost exclusively on amphipods, whereas August copepods (53%) and larvaceans (30%) predominated the diet. *T. abyssorum* (3–7 mm) was the dominant amphipod species (Fig. 8) *C. finmarchicus* was the dominant copepod species.

In August 1996 in the Mixed Coastal/Atlantic waters, krill were the major prey constituting 38% of the total stomach content weight (Fig. 6). 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%).

Statistical analysis of geographical, and temporal variations in feeding patterns

Four significant principal components (Fig. 9) were drawn from the data set by the PCA ($P=0.01$, Monte

Carlo test, 99 unrestricted permutations). The first PCA axis revealed a gradient (Jongman *et al.*, 1987; ter Braak and Prentice, 1988) ranging from herring which preyed heavily on the calanoid copepods and the two *Calanus* species (high scores) to herring which preyed mostly on euphausiids (low scores) (Fig. 9(a)). The scores of the stations on the first axis are plotted in Figure 10(a), which shows that calanoid copepods and *Calanus* were mainly consumed in the western and northern parts of the Norwegian Sea, regions with Arctic and mixed Arctic and Atlantic water. Euphausiids were mainly consumed along the Norwegian shelf break, in the Atlantic and to some extent in Coastal water. The fit, as a fraction of variance of the taxa (Table 3) at the negative end of the first PCA axis was not significant, and the distribution of krill as depicted in Figure 10(a) must therefore be interpreted with caution.

The second PCA axis (Figs 9(b), 10(b)) separates the prey taxa eaten by the herring in the Norwegian shelf area in March and April (euphausiids) from the taxa encountered further north and later in the feeding season in Atlantic water (mainly *C. finmarchicus*).

The third PCA axis (Figs 9(c), 10(c)) shows how *C. finmarchicus* is typically eaten in the mixed Arctic and Atlantic waters surrounding the Arctic waters of the East Icelandic current, as opposed to other calanoid copepods which are eaten in the cold water (see first PCA axis). At the negative end of the third axis, calanoid copepods and chaetognaths are found; these groups are deep dwelling and more Arctic in their distribution. The euphausiids that seem to occur with *C. finmarchicus* in the stomachs are mostly *T. inermis* and *T. longicaudata* which are both, especially the latter, Atlantic species.

The fourth PCA axis mostly describes late summer and early autumn feeding, when the major contributors to the spring and summer biomass, such as *Calanus*, have left the upper layers for their overwintering depths (Fig. 9(d)). During this time of the year the herring mainly feed on *Themisto* spp. and patches of *Limacina* spp. and larvaceans. The two areas in the northwest, where maxima of taxa from both the positive and negative end of the fourth axis occur, are related to a small number of stations where herring which had consumed considerable amounts of *Limacina* spp. and larvaceans were caught (Fig. 10(d)).

Size selectivity of krill and copepods

The length–frequency distributions of *M. norvegica* and *T. inermis* consumed by herring during March 1995 are shown in Figure 11. The mean size of krill in herring stomachs were similar to MOCNESS samples for both species, although neither the smaller krill of both species nor the largest *M. norvegica* (>38 mm) were represented in the MOCNESS. Only krill above

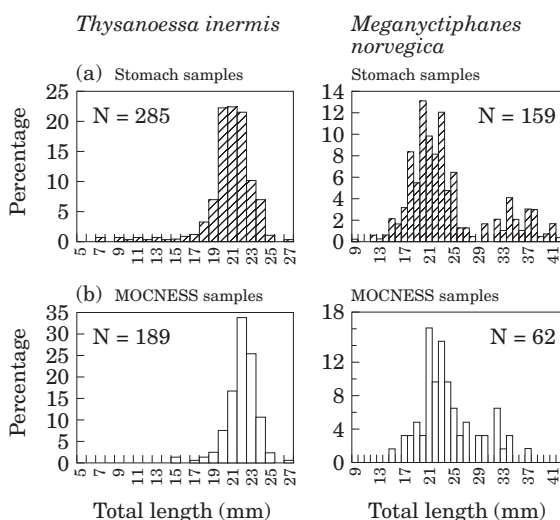


Figure 11. Length distribution of *Meganyctiphanes norvegica* and *Thysanoessa inermis* in herring stomachs (a), and in MOCNESS samples (b), in March 1995.

ca. 10 mm were usually identified to species in MOCNESS profiles.

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 Figure 12(a) 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. Copepodid stage IV, which constituted ca. 18% of the *C. finmarchicus* stock in MOCNESS samples, made up only 1.8% in the herring stomachs. Developmental stages CI–CIII of *C. finmarchicus* made up ca. 42% in MOCNESS hauls, but only 1.5% of those eaten by herring.

In May to June the stages CI–CIV, based on MOCNESS samples were more abundant as copepodid stages progressed (Fig. 12(b)). The frequencies varied from 10.4–28.5%. Adult *C. finmarchicus* females made up to ca. 10%, whereas males were rather scarce. However, in the stomach contents, the smallest stages were not observed, while the largest individuals, the adult females, dominated (69%).

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

In the mixed Atlantic/Arctic water masses, the cold water species *C. hyperboreus* is quite abundant. In late March to early April 1996, relatively large numbers of CV and CVIf (adult females) were observed in

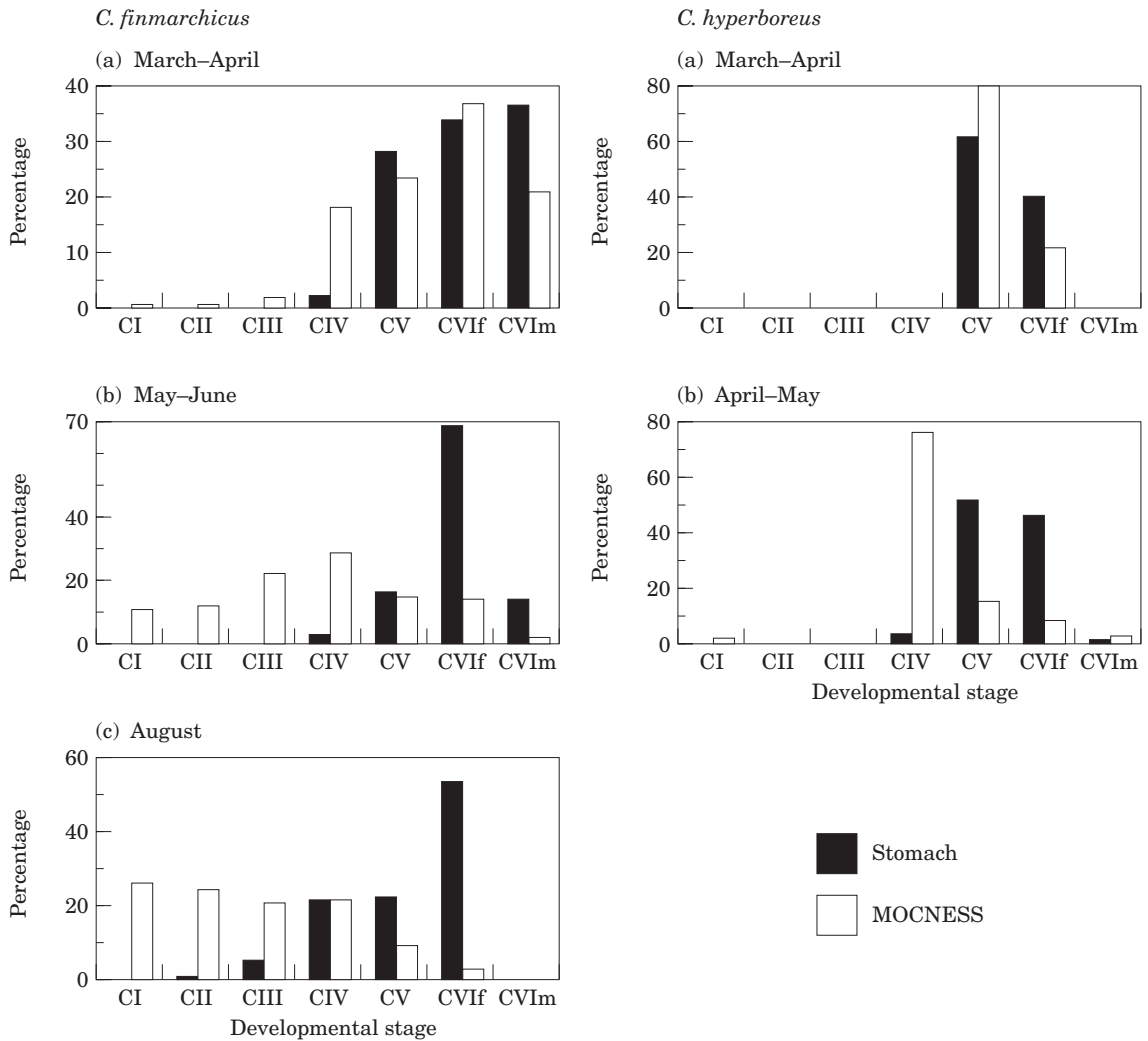


Figure 12. Frequency distribution of developmental stages of *Calanus finmarchicus* in MOCNESS samples and herring stomachs (a) 22 March–25 April, (b) 1 May–19 June, (c) 1–14 August. CI–CV=copepodid stages one to five, CVIf=adult females, CVIm=adult males.

Figure 13. Frequency distribution of developmental stages of *Calanus hyperboreus* in MOCNESS samples and herring stomachs. (a) 22 March–14 April, (b) 21–25 April–25 May.

MOCNESS hauls and in herring stomachs (Fig. 13(a)). In Figure 13(b) data from late April 1995 and May 1996 are combined. Stage CIV dominated in MOCNESS samples (76%) but represented only 3% of the stomach contents. The larger developmental stages, CV and CVIf, each contributed about half in the stomach contents. The younger stages, which occurred in small numbers in MOCNESS profiles, were completely absent in the stomachs.

Zooplankton biomass distribution based on MOCNESS profiles

Figure 14(a) and (b) show the zooplankton biomass in the upper 200 m in the Norwegian Sea in May and June

1995 and May 1996, respectively. Macrozooplankton organisms, such as euphausiids and shrimps were excluded from the analysis. The zooplankton biomass mainly consisted of copepods, with *C. finmarchicus* far exceeding other copepod species. In the western part there was an increasing frequency of the larger *C. hyperboreus*, although *C. finmarchicus* was still the most numerous.

As seen from both Figures, there was an increasing biomass westwards from the Norwegian coast. In the eastern part the biomass was low, 10 g m^{-2}. To the west, copepodid stages CIV, CV and adult *C. finmarchicus*, together with the larger *C. hyperboreus* accounted for most of the high biomass observed, which was

Table 3. Cumulative fit per species (taxon) as fraction of variance of the species (ter Braak and Prentice, 1988).

Axis 1		Axis 2		Axis 3		Axis 4	
Calanoid	0.9	Calanoid	0.9	<i>C. finmarchicus</i>	0.9	<i>C. finmarchicus</i>	0.9
<i>C. hyperboreus</i>	0.3	Euphausiids	0.9	Calanoid	0.9	Calanoid	0.9
<i>C. finmarchicus</i>	0.3	<i>T. inermis</i>	0.5	Euphausiids	0.9	Euphausiids	0.9
Chaetognatha	0.2	<i>M. norvegica</i>	0.5	<i>T. inermis</i>	0.5	Limacina	0.5
<i>T. inermis</i>	<0.1	<i>C. hyperboreus</i>	0.3	<i>M. norvegica</i>	0.5	<i>T. inermis</i>	0.5
Euphausiids	<0.1	<i>C. finmarchicus</i>	0.3	<i>C. hyperboreus</i>	0.3	<i>T. abyssorum</i>	0.5
Larvacea	<0.1	Chaetognatha	0.2	Chaetognatha	0.2	<i>M. norvegica</i>	0.5
<i>M. norvegica</i>	<0.1	<i>T. longicaudata</i>	0.1	<i>T. longicaudata</i>	0.2	<i>C. hyperboreus</i>	0.3
<i>T. longicaudata</i>	<0.1	<i>T. compressa</i>	<0.1	Larvacea	<0.1	Chaetognatha	0.3
Fish	<0.1	Fish	<0.1	<i>T. compressa</i>	<0.1	Larvacea	0.2
<i>T. compressa</i>	<0.1	<i>T. abyssorum</i>	<0.1	Fish	<0.1	<i>T. longicaudata</i>	0.2
<i>T. abyssorum</i>	<0.1	Larvacea	<0.1	<i>T. abyssorum</i>	<0.1	<i>T. compressa</i>	0.2
Limacina	<0.1	Limacina	<0.1	Limacina	<0.1	Fish	<0.1

close to 40 g m⁻², at some locations. The amphipod *T. abyssorum* (TL 15 mm) also contributed to the high biomass. The average biomass in the upper 200 m in May and June was 17.6 g m⁻².

In May 1996 young stages of *C. finmarchicus*, together with *C. hyperboreus* and *T. abyssorum* comprised a major fraction of the total zooplankton biomass in the central and western region. The biomass varied from <5 g m⁻² in the eastern part to >30 g m⁻² in the western and northern part of the area investigated. The average biomass of 12.3 g m⁻² in the upper 200 m was somewhat lower than in 1995. 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. The highest concentrations were still observed in the western part, due to the higher frequency of large organisms like hyperiid amphipods, and *C. hyperboreus*, and an ongoing production of *C. finmarchicus*. The average biomass in July–August 1995 and 1996 was 10.0 and 7.7 g m⁻², respectively.

Discussion

Inter and intra annual seasonal trends in food composition

Although the annual migration route of the herring changed between the 1960s until the time of our present investigations, the spawning area has been somewhat constant along the Norwegian coast, so has been the herring feeding during the spawning period. Investigations carried out by Melle *et al.* (1993) show that krill eggs and larvae (*M. norvegica* and *T. inermis*) are found in large concentrations (up to 6000 per 1000 m³) in April in the Møre shelf region, which is a major spawning site of the herring. Previous investigations (Rudakova, 1966; Pavshikovs and Timokhina, 1972) and results here show that herring fed primarily on *T. inermis* and *M. norvegica* during their spawning period.

By May, the beginning of the main feeding period, herring cover larger areas of the Norwegian Sea and are able to utilise the higher zooplankton biomass in the west. In the peak feeding period in May–June 1994–1996, the principal prey of herring is *C. finmarchicus*, which is the most abundant zooplankton by weight in the mixed Arctic and Atlantic waters of the Norwegian Sea (Wiborg, 1955; Pavshikovs and Timokhina, 1972; Melle *et al.*, 1993; Mauchline, 1998; this study). *C. finmarchicus* consisted mainly of over-wintering stages (IV–VI). In colder waters, e.g. the East Icelandic Current, *C. hyperboreus*, which dominated the copepod population, was important in the diet. This is in accordance with the results of Rudakova (1966), who found that in summer herring consumed mainly *C. finmarchicus*, and that *C. hyperboreus* was also an important food item in the mixed Atlantic/Arctic and Arctic water masses. These findings were also confirmed by PCA analyses.

By July copepods 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 the major prey of herring in the central and northern Norwegian Sea where these species are commonly present (Dunbar, 1964; Dalpadado *et al.*, 1998; this study). Investigations carried out in 1993 to 1995 by Dalpadado *et al.* (1998) showed a large biomass of *Themisto libellula* in the subarctic and Arctic waters of the Nordic Seas. These organisms are not a major prey of herring, since the fish seldom cross the Arctic Front into deep Arctic waters due to the preference of herring for water warmer than 2°C (Misund *et al.*, 1997).

In the 1950s and 1960s, herring partly fed in the cold waters between east Iceland and Jan Mayen during the summer (Rudakova, 1966), while in the 1990s they hardly entered these waters. The increased influence of the East Icelandic Current in the Norwegian Sea since

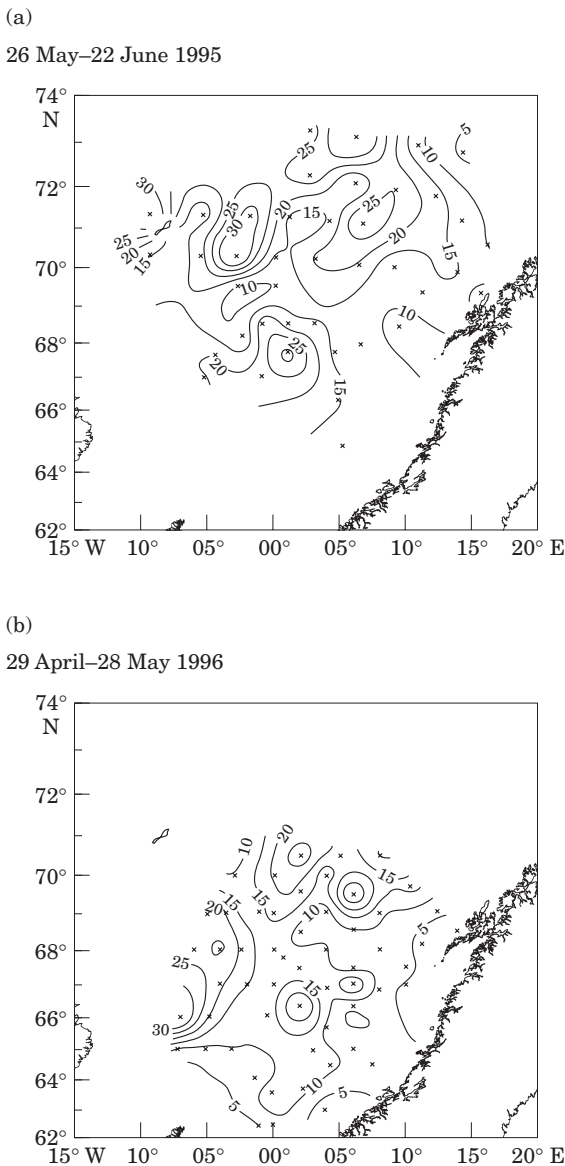


Figure 14. Zooplankton biomass based on MOCNESS profiles (a) 26 May–22 June 1995, (b) 29 April–28 May 1996. Contour units are g m^{-2} . Symbol "x" represents locations of MOCNESS stations.

the late 1960s has resulted in a cooling of surface waters in the western and central Norwegian Sea (Blindheim *et al.*, 1996). Therefore, the summer feeding of herring still takes place in relatively cold waters and the feeding pattern at present does not seem to have changed much from that of the early 1950s.

Prey size selectivity

The rather similar size distributions of euphausiids caught in the MOCNESS and those observed in herring

stomach indicate that the herring fed on euphausiids regardless of their size, at least up to about 37 mm. The fact that 12% of *M. norvegica* in the stomach content was equal or above 37 mm vs. 2% in MOCNESS samples, is probably due to an avoidance of the MOCNESS by the largest krill. Only night samples taken in March by the MOCNESS are included to minimize the effect of sampler avoidance in this comparison. The present study indicates that herring select larger individuals of *C. finmarchicus* and *C. hyperboreus*, despite the availability of smaller copepodid stages in the water. This type of feeding behaviour 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 female rather than male copepods of a given species were chosen due to their larger body size. 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 perform particulate-feeding, since the smallest copepodids were not observed in the stomachs, even in areas where they were available in relatively high numbers.

Although differential digestion rates could explain the lack of young copepodid stages in the stomach, the fact that they were not observed at all, even in stomachs showing minor digestion, indicate that they are probably not consumed by herring. *C. hyperboreus* is regularly observed in the cold water masses in the western part of the Nordic Seas although it is usually much less abundant than *C. finmarchicus* (Wiborg, 1955; Hirche *et al.*, 1994; this study). 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.

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

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