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The food of Norwegian spring spawning herring in the western Norwegian Sea in relation to the annual cycle of zooplankton

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Abstract

The food of the Norwegian spring spawning herring (*Clupea harengus*) in the western part of the Norwegian Sea was studied. The material was collected on 3 cruises in 1995 (April, May, June) and 2 cruises in 1996 (May, June). A total of 653 stomachs of herring, ranging in length from 24.1 to 44.0 cm, were examined. Of these 622 or 95% were found to contain food. The feeding activity of the herring was higher in May and June than in April, as indicated by both the higher proportion of stomachs with food in May and June (>95%) than in April (~82%), and the higher average stomach content in May and June (~830 and ~760 mg dry weight, respectively) than in April (~40 mg dry weight). Copepods (mainly *Calanus finmarchicus*, *C. hyperboreus* and *Metridia longa*) were the most important prey of herring, both in terms of numbers (~25->98%) and biomass (~50-90%). In June, amphipods (mainly *Themisto abyssorum*) were also important in the diet both in numbers (~10-50%) and biomass (~10-30%). Euphausiids (mainly *Meganyctiphanes norvegica*) were most important as prey of herring in June (~0-25% and ~0-10% by numbers and dry weight, respectively). The relations between herring migrations and the seasonal development of zooplankton are discussed.

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Introduction

In the 1950s and the early 1960s the Norwegian spring spawning herring undertook extensive migrations across the Norwegian Sea to the waters north of Iceland to feed on the abundant stocks of *Calanus finmarchicus* in the area (Jespersen 1932; Jakobsson 1980; Astthorsson *et al.* 1983). In the mid 1960s the ocean climate north of Iceland deteriorated dramatically and the abundant stock of *C. finmarchicus* collapsed (Jakobsson 1980; Astthorsson *et al.* 1983). In addition, the recruitment to the adult herring stock failed completely, mainly due to overfishing (Dragesund *et al.* 1980). As a result of these events the feeding migrations of the herring into the Norwegian Sea changed, and after 1969 they stopped altogether (Dragesund *et al.* 1980, 1997, Jakobsson and Østvedt 1999, Vilhjálmsson 1997).

From 1986 onwards, as the abundance of the Norwegian spring spawning herring stock gradually increased, the herring to some extent resumed to its previous feeding migration pattern, and during the Icelandic annual spring survey in 1994 schools of feeding Norwegian spring spawning herring were detected as far west as 8°V (Anon. 1995a, 1996, Dragesund *et al.* 1997, Misund *et al.* 1998).

Studies carried out before the herring stock collapsed indicate that the feeding migrations were to a large extent influenced by the abundance and development of the zooplankton stocks along the migration route, mainly those of *C. finmarchicus*, the main prey of the herring (Jespersen 1932, Lie 1961, Østvedt 1965, Pavshtkis and

Timokhina 1972, Jakobsson 1980). To understand the migration pattern of the herring during the current recovery period it is therefore of interest to monitor the food and feeding conditions during its migration in the Norwegian Sea.

This study was carried out in 1995 and 1996, with the aim of determining the major prey of the Norwegian spring spawning herring in the western part of the Norwegian Sea. Further, an attempt will be made to relate the feeding migration of the herring to the production cycle of the zooplankton stocks in the area. The investigation forms a part of a coordinated research programme by fisheries research institutes in Iceland, the Faeroes, Norway and Russia, which started in 1995. More recently institutes from the EU countries have also taken part in this work. The main aim of the programme is to monitor the abundance and migrations of the herring in relation to the physical and biological environment in the Norwegian Sea.

Material and Methods

The herring was sampled with pelagic trawls in the western Norwegian Sea during 3 surveys in 1995 (April, May, June) and 2 surveys in 1996 (May and June). The trawl had a vertical opening of approximately 20-30 m. The trawling time and depth varied from several minutes to one hour and from the near surface to approximately 300 m depth.

From each station an attempt was made to collect a random subsample of 5 fish of 4 cm length classes ranging from 24.1-44.0 cm (24.1-28.0, 28.1-32.0, 32.1-36.0 etc.). However, due to the different geographical distribution of the different length/age classes, this was not always possible and sometimes only a limited part of the size range could be sampled at a given station. After sampling, the stomachs were dissected from the fish and preserved in 4% neutralized formaldehyde-seawater solution until later analysis.

The laboratory analysis of the stomachs was somewhat dissimilar for the material sampled in the two years. For the material from 1995 the content of individual stomachs was emptied into a petri dish for identification to the lowest taxonomic level possible and counting. Finally, the wet weight of the stomach content as belonging to the following five main food categories: copepods, euphausiids, amphipods, other food groups and unidentifiable remains, was also measured. On the other hand, for the material from 1996, only the total wet weight of the stomach content was measured. The weightings were converted to dry weights using information from Matthews and Heimdal (1980).

The seasonal abundance of zooplankton was examined during 10 cruises (March 1995-February 1996) at two stations located just east of the front between the cold Arctic water of the East Iceland Current and the warmer Atlantic water in the central Norwegian Sea (65°00’N-9°00W, 65°00’N-10°07’W, Fig. 1). The samples were collected with a 60 cm diameter Bongo net (200 µm mesh), which was towed obliquely from the surface to 100 m depth and back to the surface, while the ship cruised at 2.5 knots. The samples were preserved in a 4 % neutralized formaldehyde-seawater solution until analysed ashore. In the laboratory the displacement volume of total zooplankton was measured. The samples were then subsampled with a Motoda splitter (Motoda 1959) and an aliquot containing at least 500 individuals analysed for species composition. In the present paper, the displacement data have been converted to dry weight biomass using information from Matthews and Heimdal (1980). Data on biomass and abundance are standardized per 1 m^{-2} and presented as means from the 2 stations.

Results

Herring migrations

The clockwise feeding migrations of the herring from the spawning grounds off mid Norway into the Norwegian Sea and back again to Norwegian coastal waters were largely similar during 1995 and 1996 and are well documented (Anon. 1995a, 1996, Misund et al. 1998). A generalized map of the migration pattern of the adult herring stock during 1995 is shown in Fig. 1 (year classes 1983, 1988-1991, Anon. 1995a). Superimposed on Fig. 1 is the approximate boundary of the arctic water (Anon. 1995a).

In 1995, after spawning off the west coast of Norway in February-March, the main part of the stock had reached the central parts of the Norwegian Sea in April (Anon. 1995a, Fig. 1). In May, the herring had migrated southwestwards and large and dense concentrations were found between 63°30'N and 65°45'N and 3°and 5°W. In early June, large shools were found near the eastern boundary of the frontal zone between the cold water of the East Icelandic Current (<2°C) and the warmer Atlantic water farther east (2-3.5 °C) (Anon. 1995a). The herring did not cross this boundary - although the feeding conditions as judged by the zooplankton biomass seemed far better in the cold waters of the East Icelandic Current than in the warmer Atlantic water (Anon. 1995b) - but migrated northwards and eastwards generally following the front (Anon. 1995a, Fig. 1). By late June the larger and older herring had migrated northwards into the Jan Mayen zone, and in July and August they were found in deep waters northwest of Lofoten. The younger adult herring did not migrate as far north as the older herring did, they remained in the southern and central Norwegian Sea during June, and had migrated back to the area off Vesterålen, northern Norway, in July (Anon. 1995a).

Annual cycle of zooplankton

Fig. 2 shows the seasonal development of zooplankton in the western part of the Norwegian Sea. The values shown are means from two stations located on the Atlantic side of the front between the cold Arctic water of the East Icelandic Current and the warmer Atlantic water in the western Norwegian Sea (Fig. 1). Thus the stations are located somewhat westward of the area from where the stomach sampling took place. However, since they are located off the shelf in the Atlantic domain of the Norwegian Sea, they may nevertheless indicate the main trends in the seasonal development of zooplankton in the area where the stomach sampling took place.

The seasonal variation in total zooplankton biomass was characterized by low winter values, a minor peak in May-June and a major peak in August (Fig. 2A). In March and early April the biomass remained low (<0.5 g m^{-2}). A spring increase began in late April and a small peak occurred in May-June (~3 g m^{-2}). In June-July a summer minimum was observed (~1 g m^{-2}). Thereafter the biomass increased again and a major peak was observed in August (~13 g m^{-2}). After that the biomass decreased to a low in October (~3 g m^{-2}). This autumn value was of a similar magnitude as the spring peak in May-June (Fig. 2A). During the winter the biomass of total zooplankton showed a trend to increase.

The seasonal cycle of zooplankton abundance was generally similar to that of the biomass (Fig. 2A, B). Thus, as with the biomass, the zooplankton numbers peaked twice during the summer. As with the biomass, the first peak in numbers in April-May (~13 000 individuals m^{-2}) was much lower than the second one in late July and August (~30 000-35 000 individuals m^{-2}).

The seasonal changes in the relative abundance of the major taxonomic groups are shown in Fig. 2C. Copepods dominated the zooplankton, except in July when ‘other groups’ (mainly cladocerans and cirripeds) made up a significant fraction of the catch. *Calanus finmarchicus* was the most abundant copepod species in terms of numbers (30% of all the copepods), followed by *Oithona similis* (26%) and *Metridia longa* (19%).

Fig. 3 illustrates the seasonal abundance of different developmental stages of *C. finmarchicus*. The seasonal succession of different developmental stages suggests a one year life cycle for this copepod in the open ocean of the western part of the Norwegian Sea, with the spring spawning probably taking place mainly in June and July. During April, May and June the stock was dominated by animals of the overwintered generation (G0), while individuals of the new G1 generation were mainly recruited to the older copepodite stages during July and August (Fig. 3).

Stomach content

The material sampled in each of the length classes during the different cruises is summarized in Table 1. In all, 653 stomachs were examined and of those 622 or 95% were found to contain food. The proportion of stomachs with food was lowest in April (82%) and highest during May and June (98 and 94%, respectively), indicating that these were the months when the feeding activity was highest.

The average total dry weight of food in the herring stomachs, as observed in the different cruises, averaged for all length classes and both years is shown in Fig. 4. The dry weight per stomach in April was on average only ~40 mg while in May and June it was ~830 and ~760 mg, respectively. Thus, the food in the stomachs was about 20 times greater in May and June than in April. Although we are not comparing stomachs from exactly the same length classes (Table 1), this clearly demonstrates that the feeding intensity was much higher during May and June than in April.

The percentage composition of the food of herring in terms of numbers in April, May and June 1995, when grouped into four major food categories: copepods, euphausiids, amphipods and ‘other groups’, is shown in Fig. 5. In April and May the copepods were the dominant prey of all length classes (>98%). In June, the food was also dominated by copepods (~25-85%), but amphipods and euphausiids were also abundant in the stomachs. The amphipods constituted ~50% of the diet from the smallest length class in June, while they were less abundant in the larger and older herring (~10-35%). Similarly, the euphausiids were most abundant in the smallest herring (~25%). However, as the number of stomachs with identifiable food was small in the smallest herring in June (Table 1), and further as only a few food items were found in each stomach, the result should be interpreted with care.

Due to the different sizes of the different prey groups their numbers in the stomachs may give a somewhat misleading picture of their actual importance as food for herring. In order to get a further idea of the relative importance of the different planktonic groups as food, Fig. 6 shows the constitution of the food for the same categories as Fig. 5 in terms of dry weight. The composition of the food of herring in terms of dry weight (Fig. 6) was very similar to its composition in terms of numbers (Fig. 5). In terms of weight the copepods were also the most important constituent of the food during both April and May (>90%), and June (~50-80%) (Fig. 6). In June the dry weight of amphipods (~10-50%) and euphausiids (~0-10%) was relatively greatest.

The composition in terms of numbers of the identifiable copepods found in the stomachs is shown in Fig. 7. In April the copepods *Calanus finmarchicus* and *Metridia longa* were the most numerous copepods found in the stomachs. *C. finmarchicus* was the only copepod identified from the smallest length class, while it constituted ~20-40% of all identifiable copepods from the other length classes (Fig. 7A). *M. longa* comprised ~60-80 % of all identified copepods in the stomachs of 28.1-39.0 cm herring in April. In May *C. finmarchicus* constituted >80% of the identified copepods, similar for all length classes, while *C. hyperboreus* was the second most numerous copepod in the stomachs (~5-10%, Fig. 7B). In June the abundance of *C. finmarchicus* decreased with the increasing length of the herring, from 100% in the smallest length class to ~15% in the largest one (Fig. 7C). *M. longa* was the second most numerous copepod found in the stomachs in June (~0-70%).

Fig. 8 shows the stage composition of *C. finmarchicus* occurring in the stomachs. The juvenile stages (C1-C5) were grouped together in the analysis. However, most of them were relatively advanced stages (C4 and C5). In April these stages (C4 and C5) were most abundant, while in May, females were most numerous. This reflects the development of the *C. finmarchicus* population in the western part of the Norwegian Sea, i.e. most of the overwintering animals (G0) had developed to the adult stage in May (Fig. 3). In June the stage composition of *C. finmarchicus* occurring in the stomachs was very similar as observed in May.

Three species of euphausiids (*Meganyctiphanes norvegica*, *Thysanoessa inermis* and *T. longicaudata*) were found in the stomachs. *M. norvegica* was the most numerous one (69%), with *T. inermis* (26%) and *T. longicaudata* (5%) ranking second and third. Two species of amphipods (*Themisto libellula* and *T. compressa*) were found in the samples, the former being much more abundant (87%) than the latter.

Discussion

The present data demonstrate that in the western part of the Norwegian Sea both the biomass and numbers of total zooplankton began to increase in late April and reached an annual maximum in July-August (Fig. 2). The data further show that *Calanus finmarchicus* was the most abundant zooplankter in the area with main spawning in June-July (Fig. 3). The available information on the seasonal cycle of zooplankton in the western Norwegian Sea from other studies is very limited. However, our results seem to conform with the findings of Gaard (1996, 1999) from an area somewhat farther south, in the open waters north of the Faroe shelf. He also observed the zooplankton biomass to begin to increase in late April and to reach a maximum in June-July, and peak spawning of *C. finmarchicus* to occur during the second half of June. Thus our time series stations seem to reflect fairly well the seasonal changes in the zooplankton community in a wider region of the western part of the Norwegian Sea. At Weathership M, which is located in the eastern part of the Norwegian Sea, the spring increase of zooplankton begins on average about one month earlier (March, Lie 1968) than we observed in the western part (April, Fig. 2), while the annual maximum occurs at similar time in both areas (July). Similarily, the main spawning of *C. finamrchcius* occurrs earlier at weathership M (April and May, Niehoff *et al.* 1999) than in the western Norwegian Sea (June-July, Fig. 3).

In the western Norwegian Sea the feeding activity of herring was much greater in May and June than in April (Fig. 4). Similarly Dalpadado *et al.* (1996) reported higher feeding intensity (mean prey weight per stomach) of herring in the Atlantic waters of the Norwegian Sea in May and June than in April. The minimum in zooplankton biomass and abundance in May-June (Fig. 2A, B) may to some extent have been caused by the grazing pressure from the herring.

Copepods were the dominant prey category of the different length classes of herring, both in numbers and biomass (Figs 5, 6), *Calanus finmarchicus* and *Metridia longa* being the principal species consumed (Fig. 7). Information on the stage distribution of *C. finmarchicus* in the stomachs (Fig. 8) and in the sea (Fig. 3) during April, May and June suggests that the overwintering generation of *C. finmarchicus* was an important part of the diet. Melle *et al.* (1994) similarly suggested that the overwintered population of *C. finmarchicus* was important as food for herring in the central Norwegian Sea in April, May and early June, and Dalpadado *et al.* (1996) reported that the herring seemed to omit feeding on small copepodite stages of *C. finmarchicus* when larger ones were available. From the waters north and northeast of Iceland in the sixties, Østvedt (1965) similarly reported that the herring were confined to waters where old stages of the overwintered population of *C. finmarchicus* predominated, and that new areas were not invaded by the herring until the new spring generation of *C. finmarchicus* in these areas had developed into late copepodite stages. As discussed by Østvedt (1965), this suggests that the migration of the herring depends on the timing of the production cycle of *C. finmarchicus* in different water masses, as well as its density. In June-July, when the stocks of *C. finmarchicus* in the western part of the Norwegian Sea were dominated by young copepodites of the new spring generation (Fig. 3) - which as discussed above may not be the food preferred by the herring - the herring had shifted its migration from a westward to a northward heading and were found within the Jan Mayen zone (Fig. 1), where the spawning of *C. finmarchicus* may be expected to occur later than farther south (Pavshtiks and Timokhina 1972), possibly offering a better food environment for the herring. Thus, it is possible that the generation shift of the C. *finmarchicus* population in the western part of the Norwegian Sea in June-July from one dominated by overwintered animals to one dominated by young stages of the new spring generation was influencing the migration behavior of the herring. It has been suggested that the low sea temperatures in the frontal area between the cold waters of the East Icelandic current and the warm Atlantic water farther east, act as a barrier against a further westward migration of the herring across the cold front east of Iceland (Misund *et al.* 1998, Jakobsson and Østvedt 1999). However, as discussed by Misund *et al.* (1997), the migration behavior of the herring may be influenced by other factors as well, such as food availability and currents. In this context it should be noted that in the sixties, when crossing the cold front east of Iceland, the herring was observed at ambient sea temperatures as low as 0°C (Østvedt 1965), which is lower than the lowest temperatures experienced by the herring in the frontal areas during 1995 and 1996 (~1°C, Anon. 1995a, 1996, Misund *et al.* 1997).

Our findings on the food composition of herring in the western part of the Norwegian Sea agree largely with those reported by other workers. Jespersen (1932) reported copepods (mainly *C. finmarchicus*) to be numerically the main prey of herring from the area north of Iceland, whereas euphausiids were important in terms of biomass. Similarly, Melle *et al.* (1994) and Dalpadado *et al.* (1996) reported *C. finmarchicus* to be the main prey of herring from the central Norwegian Sea. In the North Sea copepods also dominate the diet (Last 1989).

In conclusion, the feeding activity of the herring in the western part of the Norwegian Sea was much higher during May and June than in April. The food mainly constituted of copepods, *C. finmarchicus* and *M. longa* being the principal species consumed. In June, amphipods and euphausiids also occurred in the stomachs together with the copepods. The generation shift of the C. *finmarchicus* population in the western part of the Norwegian Sea in June-July from one dominated by overwintered animals to one dominated by young stages of the new spring generation may have influenced the migration behavior of the herring.

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Table 1. Summary according to length classes (cm) of material used for analysis of the food of Norwegian spring spawning herring in April, May and June 1995, and June and July 1996. The number and percentage of stomachs with some kind of food is also shown.

		Length classes					
	Sampling time	24.1-28.0	28.1-32	32.1-36	36.1-40	40.1-44.0	Total
Number analysed	April 1995	4	10	10	10		34
Number with food		2	9	9	8		28
%		50	90	90	80		82.4
Number analysed	May 1995		36	35	34		105
Number with food			36	35	34		105
%			100	100	100		100
Number analysed	June 1995		5	10	10		25
Number with food			5	10	8		23
%			100	100	80		92
Number analysed	May 1996	22	133	129	119	1	404
Number with food		19	128	124	112	1	384
%		86.3	96.2	96.1	94.1	100	95
Number analysed	June 1996	15	27	26	17		85
Number with food		15	26	25	16		82
%		100	96.3	96.2	94.1		96.5

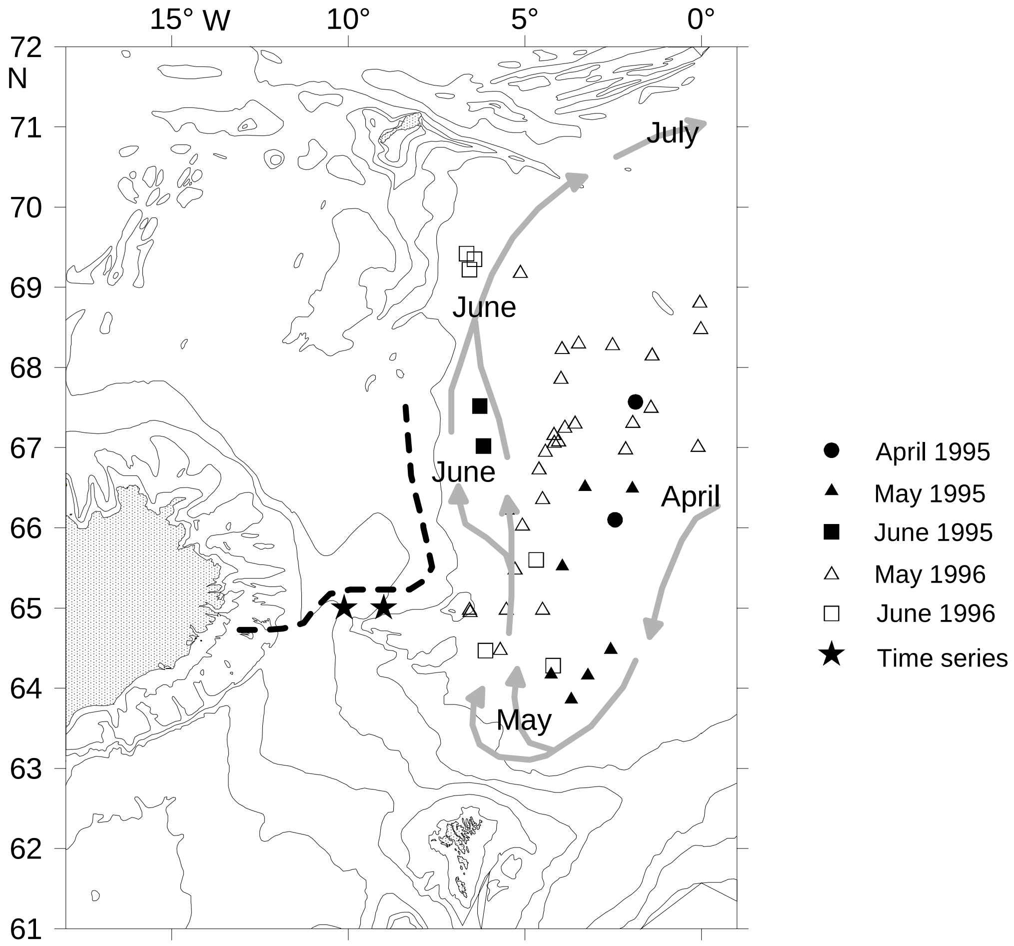

Figure 1. Location of trawling stations for stomach samples in the western part of the Norwegian Sea. Also shown is a schematic presentation of the general migration pattern of the adult Norwegian spring spawning herring (year classes 1983, 1988-1991) during spring and summer 1995 (adapted from Anon. 1995a). The stars denote the stations from which zooplankton was sampled from March 1995-February 1996 in order to study the annual cycle of zooplankton.

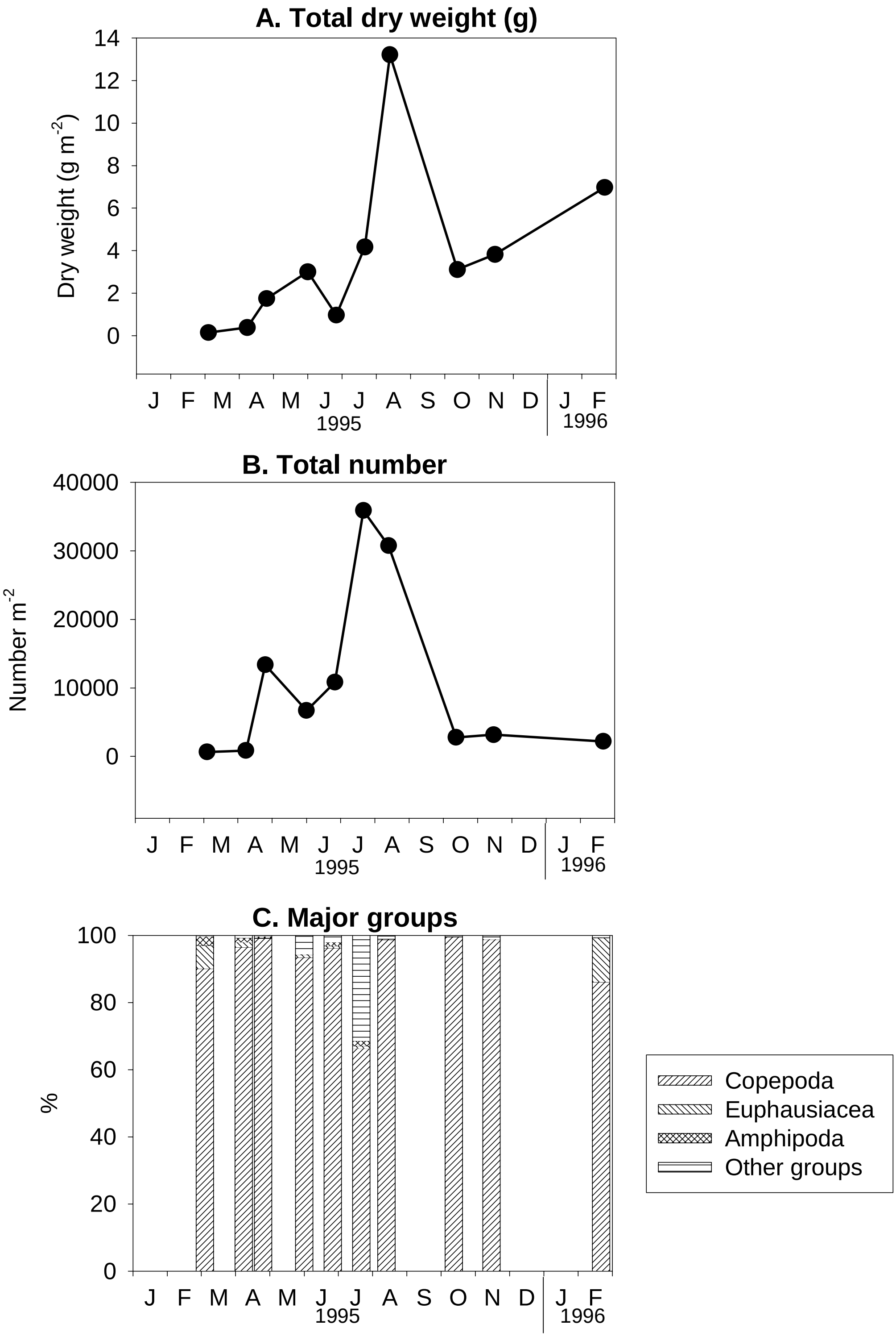

Figure 2. Dry weight of total zooplankton (A), number of total zooplankton (B), and relative frequency of most numerous zooplankton taxa (C) in the western Norwegian Sea from March 1995-February 1996. The values are means from 2 stations.

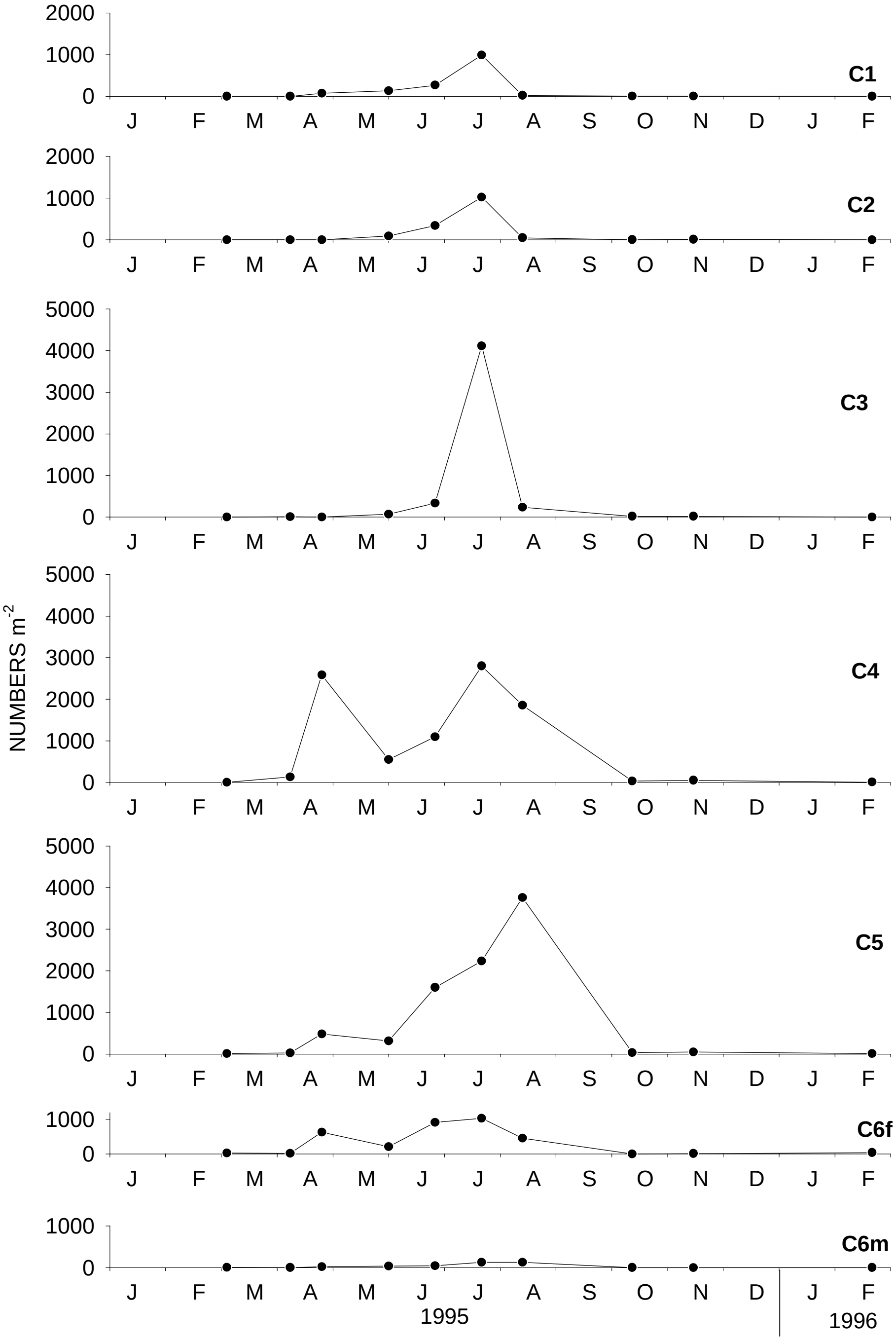

Figure 3. The abundance of different developmental stages of *Calanus finmarchicus* in the western Norwegian Sea from March 1995-February 1996. The values are means from 2 stations.

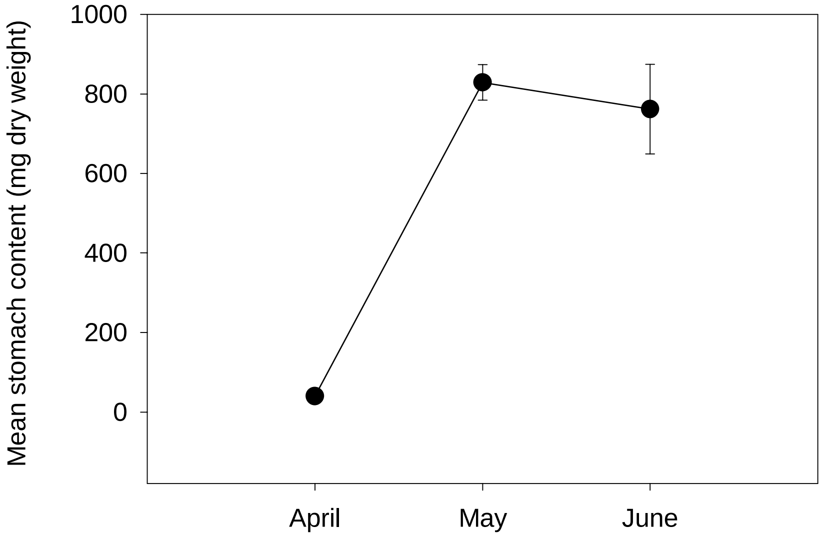

Figure 4. Mean stomach content (dry weight) of Norwegian spring spawning herring in April, May and June. The values are averaged for all length classes (length classes 24.1-28.0, 28.1-32.0, 32.1-36.0, 36.1-40.0, 40.1-44.0) and both years (1995 and 1996). Vertical lines denote standard error.

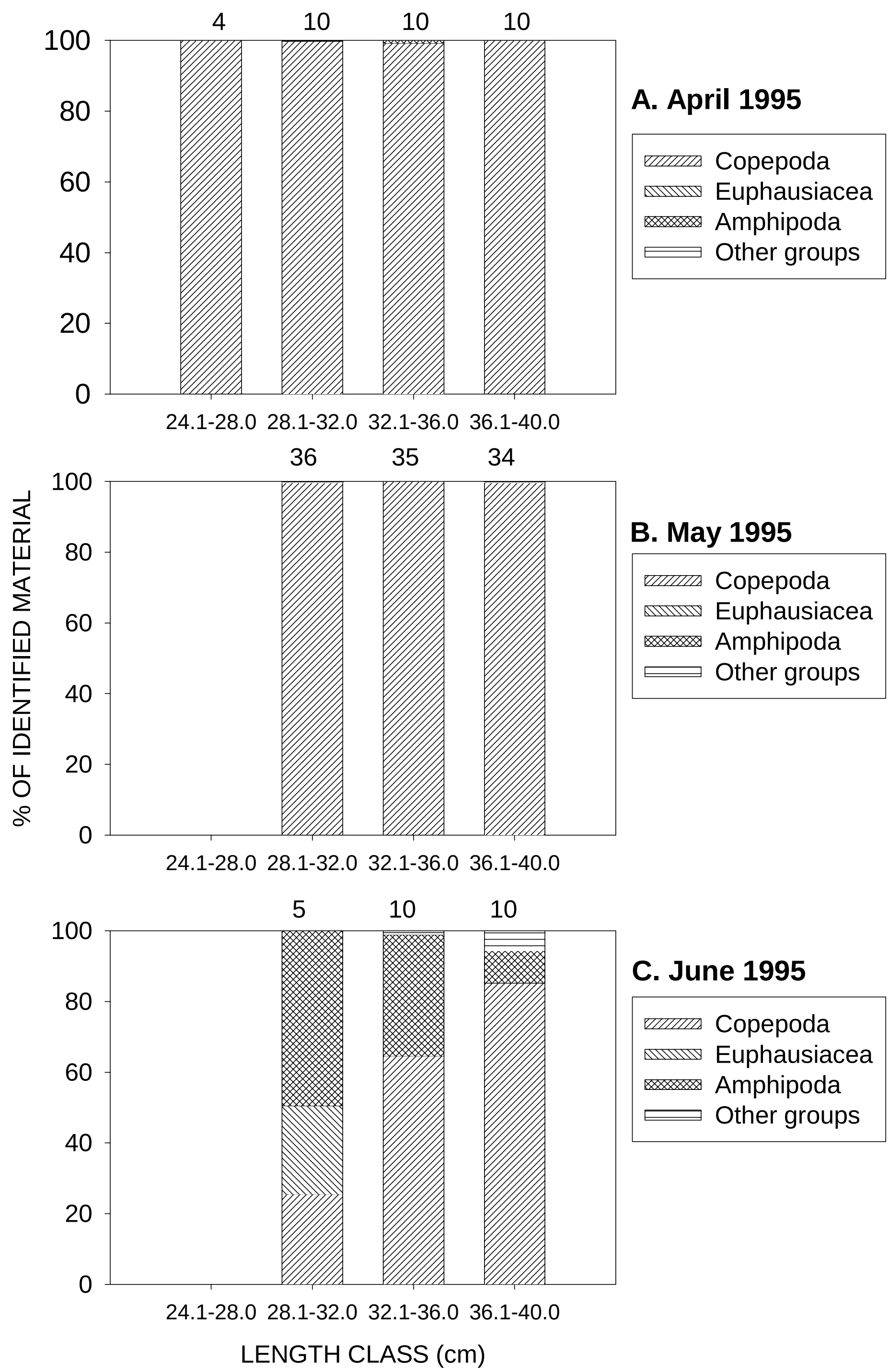

Figure 5. Food composition (percentage number) of Norwegian spring spawning herring in April (A), May (B), and June (C) 1995. The numbers at the top of the figures show the number of fish with identifiable food.

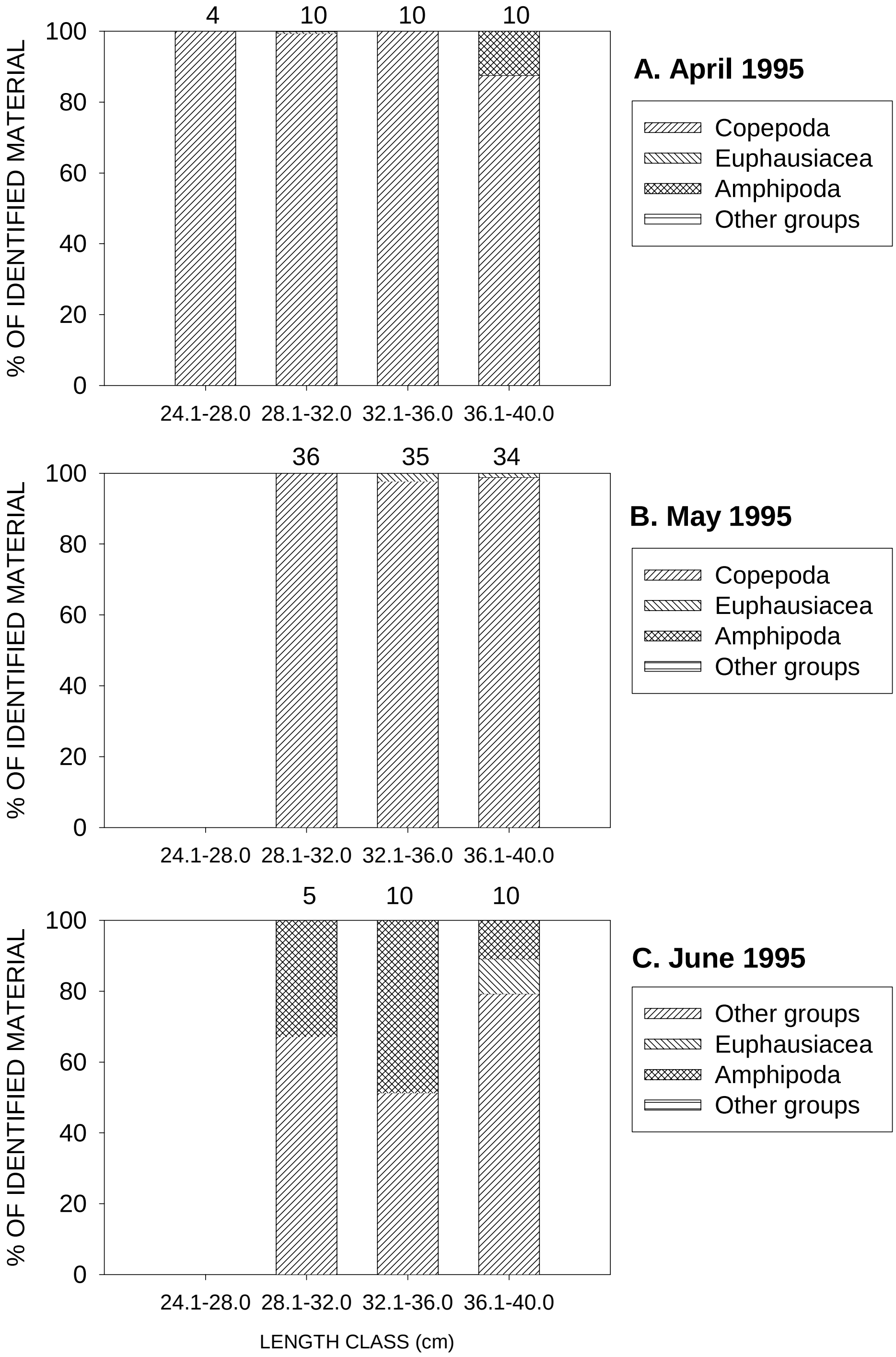

Figure 6. Food composition (percentage dry weight) of Norwegian spring spawning herring in April (A), May (B), and June (C) 1995. The numbers at the top of the figures show the number of fish with identifiable food.

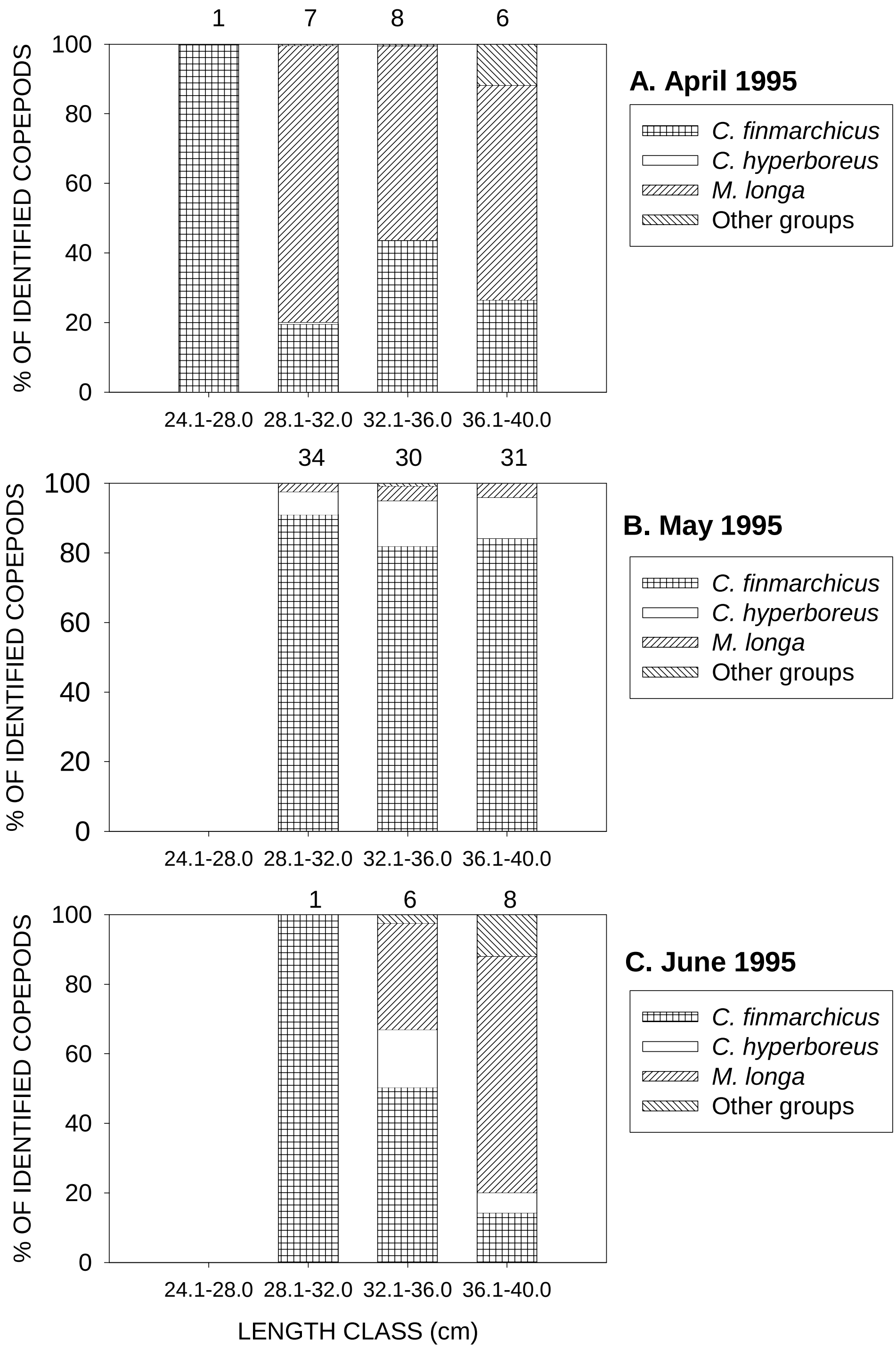

Figure 7. Copepods (percentage number) occurring in the stomachs of Norwegian spring spawning herring in April (A), May (B), and June (C) 1995. The numbers at the top of the figures show the number of fish with identifiable copepods.

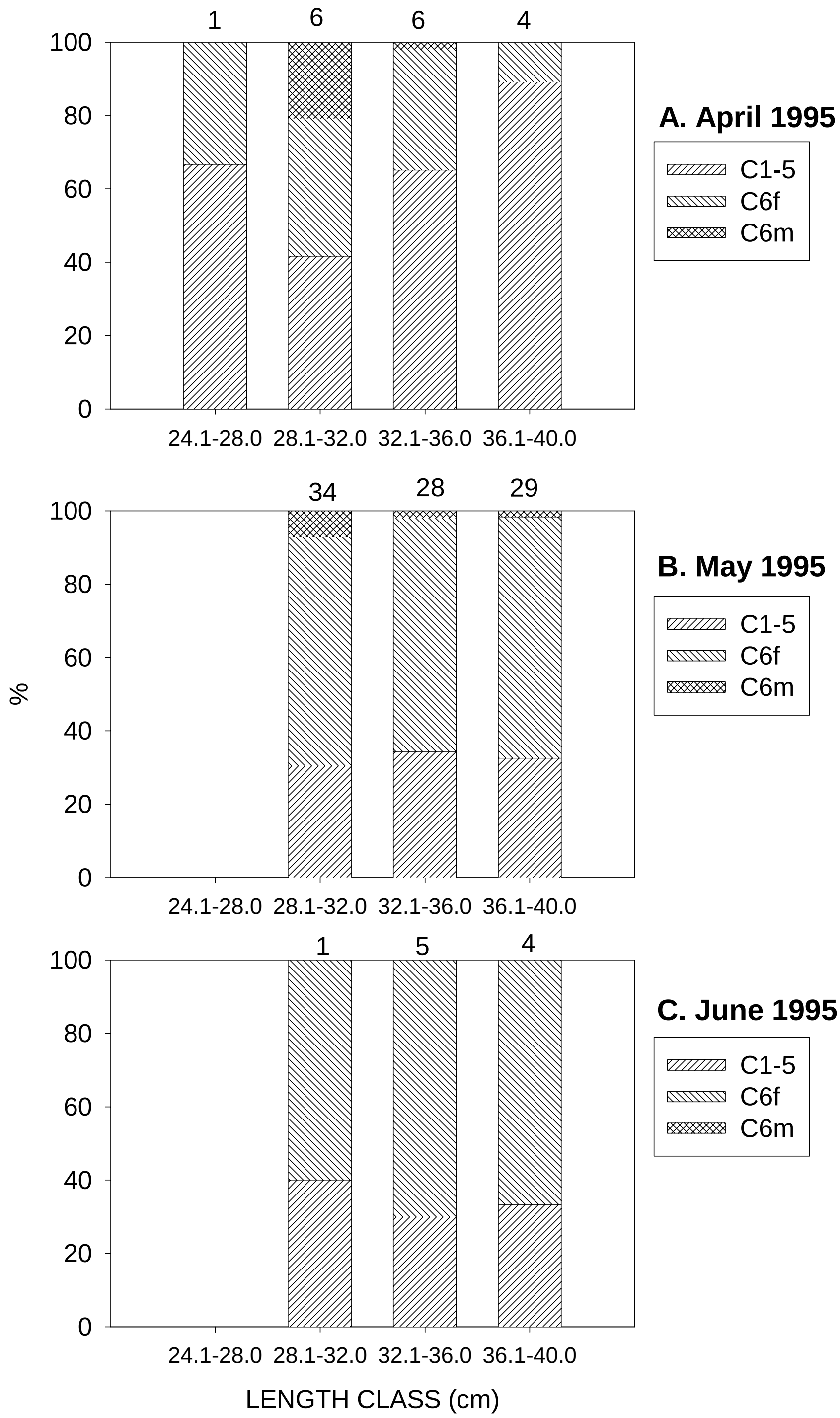

Figure 8. Stage distribution of *Calanus finmarchicus* (percentage number) occurring in the stomachs of Norwegian spring spawning herring in April (A), May (B), and June (C) 1995. The numbers at the top of the figures show the number of stomachs with *C. finmarchicus* that could be identified to stage.