

A COMPARATIVE STUDY OF THE FEEDING HABITS OF HERRING (*CLUPEA HARENGUS*, CLUPEIDAE, L.) AND CAPELIN (*MALLOTUS VILLOSUS*, OSMERIDAE, MÜLLER) IN THE BARENTS SEA

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Capelin (*Mallotus villosus*) and adolescent Norwegian spring spawning herring (*Clupea harengus*) co-occur in the southern Barents Sea during early summer. The diets of both species were dominated by calanoid copepods, and the overlap in diet was large. Both for herring and capelin the proportion of copepods in the diet decreased with increasing fish size, while euphausiids and appendicularians increased in importance. The ontogenetic shift in diet was thus similar for the two species. Herring showed an increasingly deeper distribution with increasing body size. Capelin were found deeper than herring in areas of spatial overlap. Based on the similarities in diet it is concluded that the two species are potential competitors for food in times of high abundance of planktivores or of low food availability in the Barents Sea.

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KEYWORDS: herring; capelin; feeding; competition; distribution.

INTRODUCTION

The Barents Sea is an arctic-boreal sea with few, but abundant species of fish. The most abundant planktivores in the southern part are Norwegian spring-spawning herring (*Clupea harengus* L.) and capelin (*Mallotus villosus* MÜLLER). Herring drift into the Barents Sea as larvae during late summer and stay there for 2-4 years before they migrate into the Norwegian Sea to join the adult stock (DRAGESUND 1970; TORESEN & BARROS 1995). Capelin is a boreo-arctic salmonid fish (PROKHOROV 1968), which stays in the Barents Sea throughout its life span. The capelin spawn in spring along the coast of northern Norway and Murman (Russia), and feed along the Polar front during summer and autumn (PROKHOROV 1965; HASSEL & al. 1991; FIKSEN & al. 1995). In May-June the one year and older capelin are distributed in the central part of the Barents Sea along the southern edge of the Polar front (DALEN & DOMMASNES 1974; HAUG & MONSTAD 1974; BUZETA & al. 1976). The distributional area of the adolescent herring off northern Norway (DRAGESUND 1970) may be partly overlapping with that of capelin in early summer.

Few studies have been made on the feeding habits of herring from the northern part of the Atlantic and the Barents Sea. As part of the multispecies model program for the Barents Sea (BOGSTAD & al. 1992) at the Institute of

Marine Research (IMR) in Bergen, 1 505 stomachs of herring were investigated in 1984-1986 (MEHL & YARAGINA 1991), but the results of this study have not been published. Except for this we have not found any studies of the diet of herring in the Barents Sea and adjacent areas.

However, the feeding habits of capelin in the Barents Sea have been given several accounts (BOLDOVSKY 1936; PROKHOROV 1965; LUND 1981; PANASENKO 1981, 1984; AJIAD & PUSHCHAEVA 1991; HASSEL & al. 1991). Studies of the food of herring around the British Isles (HARDY 1924; DE SILVA 1973; LAST 1987, 1989) and in a Norwegian fjord (PEARCY & al. 1979), and capelin in the Barents Sea have shown that the diets of the two species are similar with copepods, euphausiids, and appendicularians as the most important prey. In times of co-occurring high abundance of herring and capelin or low zooplankton abundance (SKJOLDAL & al. 1992) in the Barents Sea, competition for food between the two species may thus occur. RASS (1933) stated that in spite of the resemblance in diet there is no marked competition for food between herring and capelin because they occupy different feeding grounds during summer. This is true for the mature part of the stocks, but during the adolescent stage the herring is usually distributed in the Barents Sea (DRAGESUND 1970), and may interact with capelin during this phase.

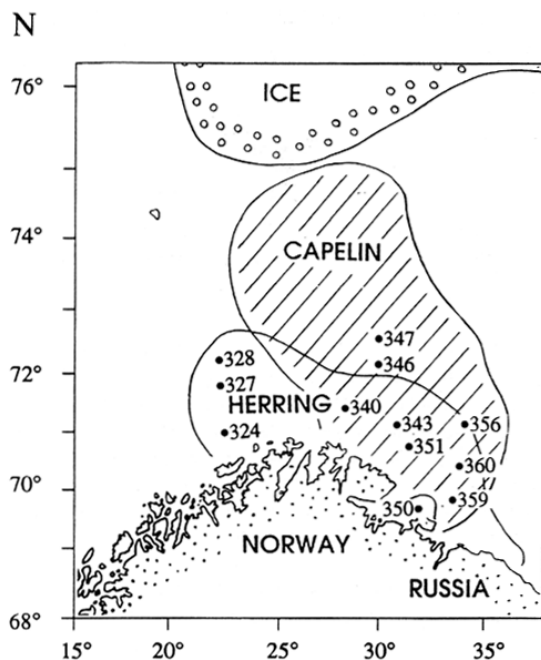


Fig. 1. The distribution of herring and capelin in the Barents Sea during summer. The distributions are typical and representative for the two years studied. The location of stations in 1992 is indicated.

Studies on feeding ecology of herring and on interspecific competition between the fish stocks in the Barents Sea are scarce (DRAGESUND & GJØSÆTER 1988). The aim of the present study was therefore to investigate the feeding ecology of herring and also to compare this with the feeding ecology of capelin on the basis of potential competition for food.

MATERIAL AND METHODS

The surveys

The material in the present study is for the most part from a survey in 1992 with R/V *G.O. Sars* (Institute of Marine Research, Bergen), but additional material on herring from a corresponding survey in 1993 is included. The survey in 1992 took place in the period 26 May to 14 June. Sampling was carried out off the coast of Finnmark (northern Norway), at latitudes 70-73° N and longitudes 22-36° E (Fig. 1). The sampling in 1993 was carried out in the same manner as in 1992 for an extended period of time.

Acoustics

The Bergen Echo Integrator system with a Simrad EK 500 (38 kHz) echo sounder (KNUDSEN 1990) was used for estimation of fish abundance during the survey. The echo integrator measures the intensity of returned echoes which are transformed to S_A (area backscattering coefficient) values by a specific target strength function (MACLENNAN & SIMMONDS 1992). S_A values which are given separately in depth intervals are allocated to different species of fish according to standard methods. The relative abundance (S_A values) of herring and capelin in the 10-50 m depth interval to the total abundance in all depth intervals were used to compare the vertical distributions. The S_A values that were tested statistically were average values per nautical mile over 5 nautical miles. The 5 nautical miles values of herring and capelin from the overlap area were tested as well as the 5 nautical miles values of herring in the western area.

Plankton sampling

Plankton was collected using a WP-2 net (180 μ m mesh, 56 cm diameter) which was hauled vertically from about 5 m above the bottom, or from 100 m to the surface with a wire speed of 0.5 ms^{-1} . At two stations where the WP-2 was not applied, the Gulf III (375 μ m, ZIJLSTRA 1970) and the MOCNESS (200 μ m, WIEBE & al. 1976, 1985) sampler were used (for the two hauls respectively). The Gulf III was hauled double obliquely at a speed of 0.5 ms^{-1} with a vessel speed of 5 knots. The MOCNESS was applied to sample plankton at seven different depth intervals. The relative composition of zooplankton in the water column was calculated by summing up the number of zooplankton in each depth interval, weighted by the volume sampled.

Fish sampling

Pelagic trawling was carried out on the scattering layer based on echo recordings using a midwater trawl ('Åkra' trawl, VALDEMARSSEN 1991). Trawling time was approximately 30 min and trawling depth varied from 5 to 310 m. The opening of the trawl was observed by a wireless hydroacoustic sensor attached to the headline of the trawl. Fish samples were preserved in 4 % buffered formaldehyde solution (formalin) immediately after capture. Formalin was injected into the abdominal cavity of the fish to ensure rapid preservation. Some additional herring were frozen whole (-25°C). At each station, 7-30 specimens of each species were sampled for stomach content analysis. In 1992, 542 stomachs from 12 stations were investigated (herring and capelin, Table 1). Regurgitation (as a result of preservation) did not seem to be a problem as indicated by the very low amount of prey items mixed with the preserved fish in the vials. In 1993 a total of 2 590 stomachs of herring were collected (48 stations) of which 2 140 were examined fresh, and 450 were preserved in formalin. Each fish was length measured to the nearest 0.5 cm below and weighed (0.1 g resolution). Age determination by otolith readings (GJØSÆTER 1985) was carried out on 30 fish of each species at most of the stations.

Stomach content analysis

In 1992 the stomach content was sorted, measured (prosome length of copepods, total length of euphausiids, and standard length of fish larvae), and dried (for 48 hours at 60° C). Each taxonomic group was then weighed (0.1 mg resolution). Samples of 20 or less were used to calculate mean lengths of taxonomic groups for each fish. There were problems in classifying some of the stomach content to species level due to advanced digestion. Some of the prey were therefore pooled into prey groups based on taxonomic relationships (Table 2). For every fish the weight of each prey group was expressed as a percentage of the total weight of the stomach content. The percentage of each prey group was then averaged over all fish in a sample (weight-%, JONES 1973; PEMBERTON 1976). The index of stomach fullness (ISF) scales the weight of the stomach content to the weight of the fish:

$$(1) \quad ISF = (SC \cdot 7 / W) \cdot 100$$

where SC is stomach content (dry weight in grams) and W is fish body weight (wet weight in grams). Stomach content was converted from dry to wet weight by a factor of 7 (PARSONS & al. 1977). By grouping the fish into weight groups, and assuming that within each group the individual with the highest SC was satiated, the stomach content relative to the highest SC values (in each weight group) was calculated as:

$$(2) \quad RSF_{in} = (SC_{in} / HSC_n) \cdot 100$$

where RSF_{in} is relative stomach fullness of fish i in weight group n , HSC_n is the highest weight of stomach content in weight group n . The weight groups had 5 g and 2 g intervals of herring and capelin respectively. If lighter weight groups had fish with more stomach content (higher HSC) the HSC of this group replaced the HSC_n value of the heavier group. The ISF and RSF measures were averaged over all stomachs in a sample, including empty stomachs.

In 1993 the stomach content of herring was only defined by using a relative index of dominating prey groups, due to time limitations when investigating fresh material. The prey groups which appeared to be dominating in each stomach in terms of volume were recorded. Three prey groups at the most were classified as dominating in one stomach. All the investigations were carried out by the same person.

A comparison was made of the proportion by weight that each prey group made up in the diet of herring and capelin. The lower of the two values for each prey group was then considered to be the amount of overlap in that prey group. The sum of these

values for all prey groups (n) is the percentage overlap (PO, KREBS 1989) in the diet of herring and capelin:

$$(3) \quad PO = 100 \cdot \sum_i^n (\text{minimum } P_{ih}, P_{ic})$$

where P_{ih} and P_{ic} is the proportion that prey i constitutes of the total weight of prey eaten by herring and capelin, respectively. Food intake as a function of body weight usually decreases with increasing size of the fish (JOBLING 1992). Due to size differences between herring and capelin, the stomach fullness were compared only for fish smaller than 25 g (including all capelin (< 16.5 cm) and one year old herring (≤ 13.5 cm)).

RESULTS

Distribution of herring and capelin

Herring were distributed between longitudes 21° E and 36° E and were found northwards to about 73° N (Fig. 1). The western area (Stns 324, 327, 328) was dominated by the three year old fish. In the eastern area the one- and two years old fish were the most abundant, with the one year old fish furthest to the east. Capelin were found to the east of 28° E, and were distributed from the coast of northern Norway and throughout the northern extension of the study area. Spatial

Table 1. Stations in 1992 included in the study.

Station	Species	Numbers analysed
324	Herring	30
327	Herring	30
328	Herring	30
340	Herring/Capelin	30/30
343	Herring/Capelin	30/30
346	Capelin	30
347	Capelin	30
350	Capelin	21
351	Herring/Capelin	30/30
356	Herring/Capelin	7/7
359	Herring/Capelin	19/30
360	Herring/Capelin	30/30

Table 2. Pooled prey groups.

Prey group	
Calanoid copepods	<i>Calanus finmarchicus</i> , <i>Metridia</i> sp., <i>Pseudocalanus</i> sp.
Calyptopis larvae	Second larval stage of euphausiids, <i>Thysanoessa</i> sp.
Furcilia larvae	Third larval stage of euphausiids, <i>Thysanoessa</i> sp.
Krill	Adult stages of <i>Thysanoessa</i> sp. and <i>M. norvegica</i>
Appendicularia	<i>Oikopleura</i> sp. and <i>Fritillaria</i> sp.

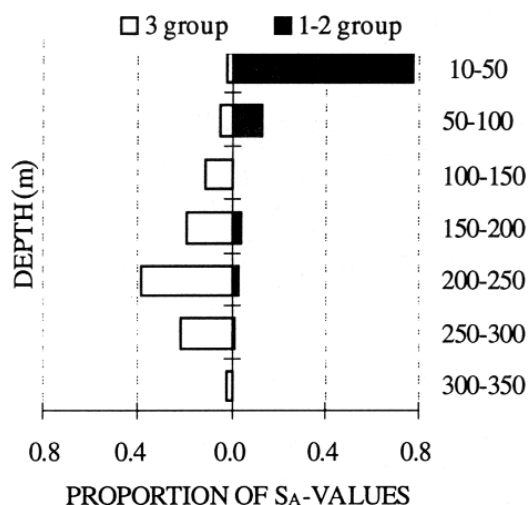


Fig. 2. Vertical distribution of herring in the eastern and western area dominated by 1-2 group and 3 group, respectively. The figure is based on 210 (5 nautical miles) readings of acoustic density (S_A).

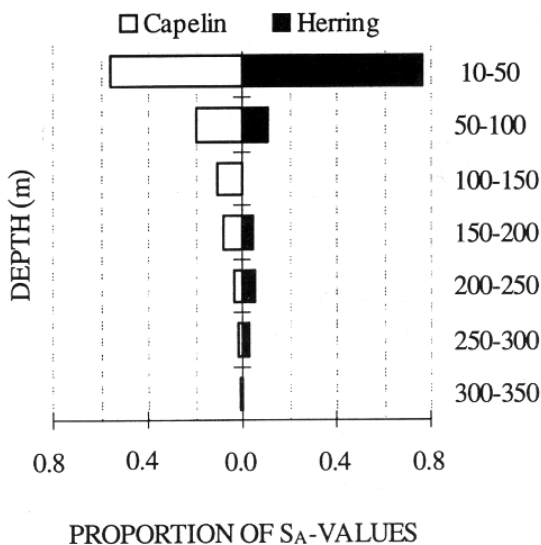


Fig. 3. Vertical distribution of herring and capelin in overlapping areas, based on 85 (5 nautical miles) readings of acoustic density (S_A).

overlap between herring and capelin was found between latitudes 69°00' N - 71°30' N, and longitudes 28° E - 36° E (Fig. 1). In the western area the herring were found mainly at 100-300 m depth, significantly deeper (Kruskal-Wallis nonparametric test, ZAR 1984, $N = 210$, $p < 0.001$) than in the eastern area where they were mostly found in the upper 50 m (Fig. 2). Capelin were distributed between 30-250 m, and were found deeper than herring in the area where the two species overlapped (Fig. 3, Kruskal-Wallis, $N = 85$, $p < 0.001$). Vertical overlap between herring and capelin in the area of spatial overlap occurred mainly in the 10-50 m depth interval, where 76 % ($SE = 3.1$ %) and 56 % ($SE = 1.9$ %) of the S_A values of herring and capelin were detected, respectively.

Distribution of zooplankton

The plankton samples were dominated by calanoid copepods of which *Calanus finmarchicus* was the most abundant species (Fig. 4). The calanoid copepods made up more than 50 % by numbers in the samples at all stations where plankton samples were taken except at Stn 351 (48.3 %). Other groups such as *Oithona* sp. and nauplius larvae were abundant at some stations while absent at others. At Stns 350 and 351, appendicularians made up 8.0 % and 18.5 % respectively, but were not found in such concentrations at other stations. The furcilia and adult stages of euphausiids were not captured representatively by the samplers, and no data are thus available on the distribution and abundance of these zooplankton.

Stomach content

In 1992, the proportion of empty stomachs was 7.9 % of 304 herring from nine stations and average stomach fullness (ISF) was 1.26 (highest value 13.44). The most abundant prey group was calanoid copepods (Fig. 5). Appendicularia were the second most abundant prey, and together these two prey made up 87 % of the diet by weight (Fig. 5). Furcilia- (third larval stage of euphausiids) and adult stages of *Thysanoessa* sp. and *Meganyctiphanes norvegica* made up most of the remaining diet. *Oithona* sp. and *Evadne nordmanni* were also frequently observed in the stomachs (Table 3), but did not contribute much to the diet in terms of weight. The herring data from 1993 (Fig. 5) confirmed the findings from the previous year of a high share of calanoid copepods in the diet. Furcilia larvae were found to be more abundant in the diet than in 1992, while the appendicularians were less abundant. The low share of adult krill and the high share of copepods reflected that the herring investigated in 1993 mainly consisted of one year olds while in 1992 more of two and

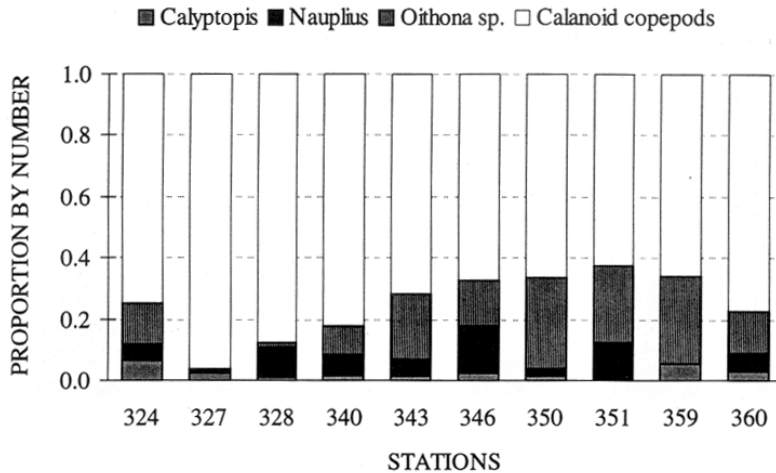


Fig. 4. Relative abundance of the main plankton groups at each sampling station. Furcilia larvae (euphausiids) and adult euphausiids were not sampled adequately by the applied gear, and abundance figures for these prey were thus not used. Nauplius and calyptopis are larval stages of euphausiids.

three year olds were captured (TORESEN & BARROS 1995). The diet was dependent on the size of the herring, and copepods were more important in the diet of herring smaller than 13.5 cm than in larger herring (Kruskal-Wallis $p < 0.001$, $N = 279$, Fig. 6), while euphausiids were more important for fish greater than 16.5 cm (Kruskal-Wallis $p < 0.01$, $N = 279$, Fig. 6). Appendicularians increased in importance with increasing size of the fish and were more abundant in the diet of the 3-4 group than for the younger fish (Kruskal-Wallis $p < 0.0001$, $N = 279$). The high share of appendicularians was not reflected in the plankton samples (Fig. 4). ISF decreased substantially with increasing size of the herring and was two times higher for the one year olds than for the two year olds (Fig. 7A). The one year olds had 50 % higher ISF than similar sized (by weight) capelin (Figs 7A and 9A). RSF also decreased with increasing size of the fish (Fig. 7B) which indicated a higher feeding rate for the smallest fish.

A total of 238 stomachs of capelin from 9 stations were investigated. The share of empty stomachs was 17.6 %, and the average stomach fullness (ISF) was 1.78 (highest value 8.93). As for herring the most abundant prey groups were calanoid copepods and appendicularians which together made up 71.8 % of the diet by weight (Fig. 8). Euphausiids in different stages made up 23.8 %. The furcilia dominated, but the calyptopis (second larval stage of euphausiids) were much more frequently observed than in the herring. This was partly explained by high abundance

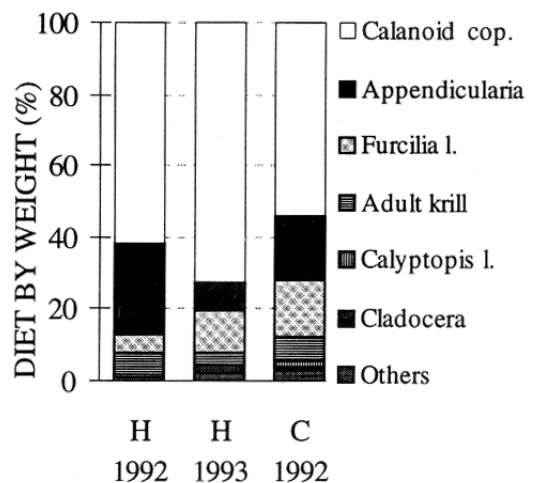


Fig. 5. Diet of all herring (H) and capelin (C) in the study.

of calyptopis larvae at the northern stations where herring were absent (346, 347, 350). *Oithona* sp. was found more often in the stomachs of capelin than in herring. At three stations (350, 359, and 360) capelin eggs were found in many of the capelin stomachs. Small stones were often detected in these stomachs, which

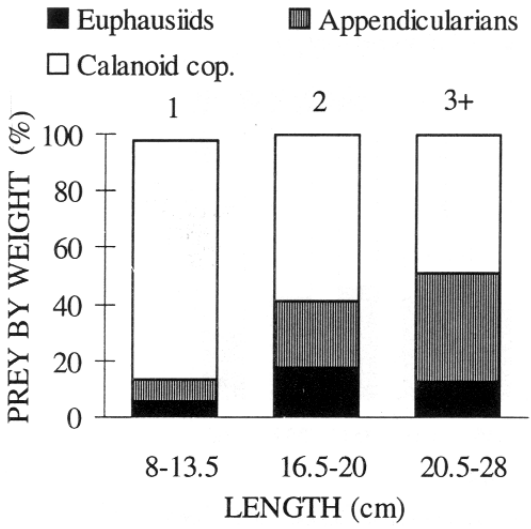


Fig. 6. Main prey of herring as a function of fish length. Number of fish in each length group is: 8-13.5: 75, 16.5-20: 84, 20.5-28: 145. Numbers in diagram indicate age.

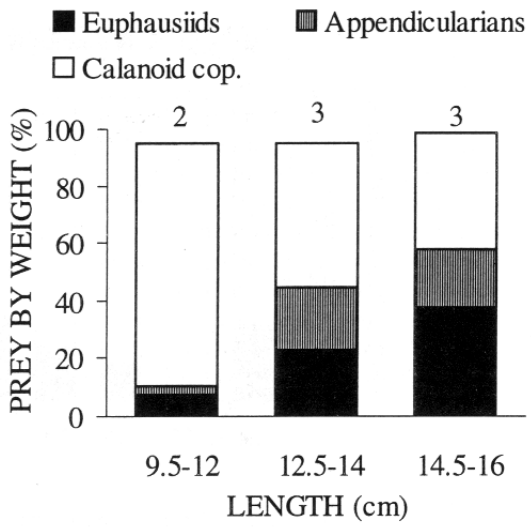


Fig. 8. Main prey of capelin as a function of fish length. Number of fish in each length group is: 9.5-12: 37, 12.5-14: 144, 14.5-16: 57. Numbers in diagram indicate age.

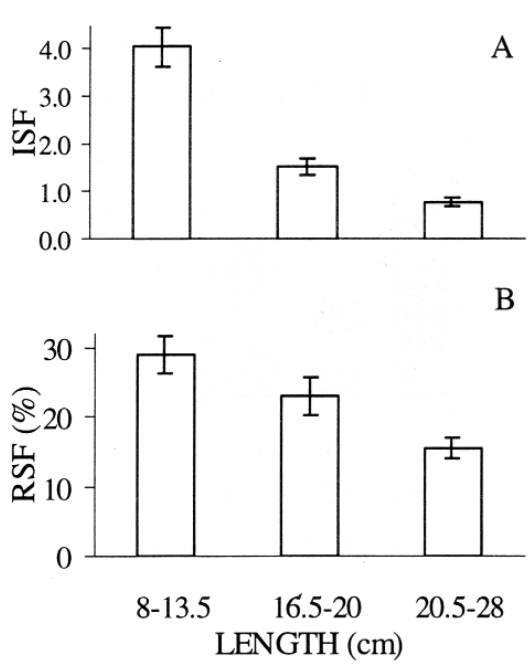


Fig. 7. Index of stomach fullness (ISF, A) and relative stomach fullness (RSF, B) of herring (high/low lines indicate S.E.).

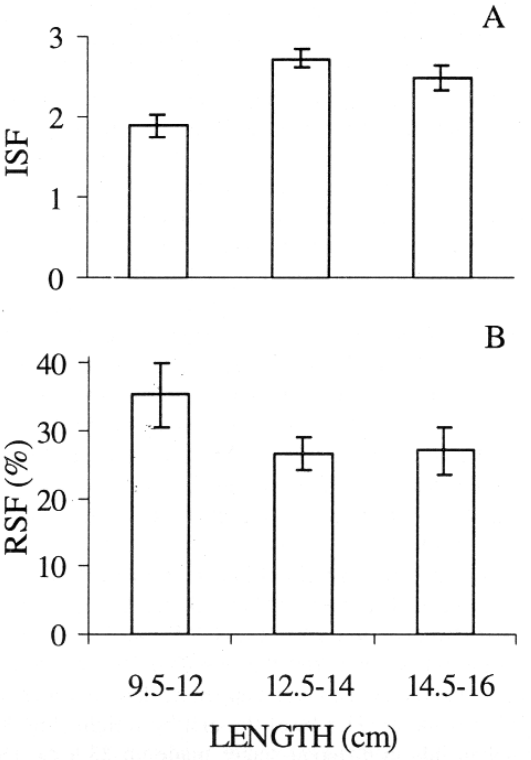


Fig. 9. Index of stomach fullness (ISF, A) and relative stomach fullness (RSF, B) of capelin (high/low lines indicate S.E.).

verified that bottom feeding on the demersal eggs had taken place. Copepods were more important in diet of fish 12 cm and smaller than for the larger capelin (Kruskal-Wallis, $p < 0.0001$, $N = 196$). The share of euphausiids generally increased with increasing length of the capelin and fish larger than 14 cm ingested more than the other size groups (Kruskal-Wallis, $p < 0.01$, $N = 196$). Appendicularians also became increasingly more important with increasing size of the fish (Kruskal-Wallis, $p < 0.0001$, $N = 196$). As opposed to herring ISF and RSF was not consistent with regard to size dependent trend (Fig. 9). While RSF was highest, the ISF was lowest for the smallest fish. In order to examine the ontogenetic development of competition potential, the diet overlap of the different size (age) groups of herring and capelin were compared. Percentage overlap (PO) in the diet of the two species was high, but decreased from 95 % for the smallest size groups to 65 for the largest individuals (Fig. 10).

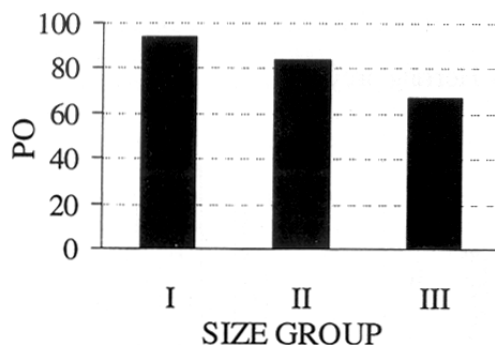


Fig. 10. Percentage overlap (%) in diet of the three size groups of herring and capelin. Herring: I = 8-13.5, II = 16.5-20, III = 20.5-28. Capelin: I = 9.5-12, II = 12.5-14, III = 14.5-16.

Prey size

Capelin ingested a wider range of prey sizes than herring (Fig. 11). At the stations where both herring and capelin were captured, capelin ingested on average larger copepods (herring 1.6 mm, capelin 1.8 mm, Kruskal-Wallis, $p < 0.001$, $N = 198$) and furcilia larvae (herring 3.6 mm, capelin 3.8 mm, Kruskal-Wallis, $p < 0.05$, $N = 143$) than herring. The lengths of calanoid copepods and furcilia larvae were correlated with body lengths of herring and capelin, based on the importance of these prey in the diets. There was a positive correlation between prey length and fish body length for herring vs. calanoid copepods ($R = 0.75$, $p < 0.001$, $N = 94$), for herring vs. furcilia larvae length ($R = 0.56$, $p < 0.001$, $N = 41$), for capelin vs. calanoid copepods ($R = 0.28$, $p < 0.01$, $N = 120$) and for capelin vs. furcilia larvae length ($R = 0.35$, $p < 0.001$, $N = 134$).

DISCUSSION

The percentage overlap in the diet of herring and capelin was large, and thus in accordance with the comprehension that the diet of the two species is quite similar. The similar ontogenetic shift in diet for herring and capelin underlines the close relationship in feeding habits. Capelin growth appears to be density dependent (HOPKINS & NILSSEN 1991; SKJOLDAL & al. 1992), and weight at age varies considerably between years with high and low biomass of capelin (ANON. 1995). Density dependent growth has been reported for herring as well (TORESEN 1990), and it therefore seems as if both capelin and herring growth may be limited

by zooplankton abundance. Due to the similarities in diet the species are potential competitors for food. It is thus plausible that interspecific competition may reduce herring and/or capelin growth in times of high abundance of planktivorous fish or of low food availability in the Barents Sea.

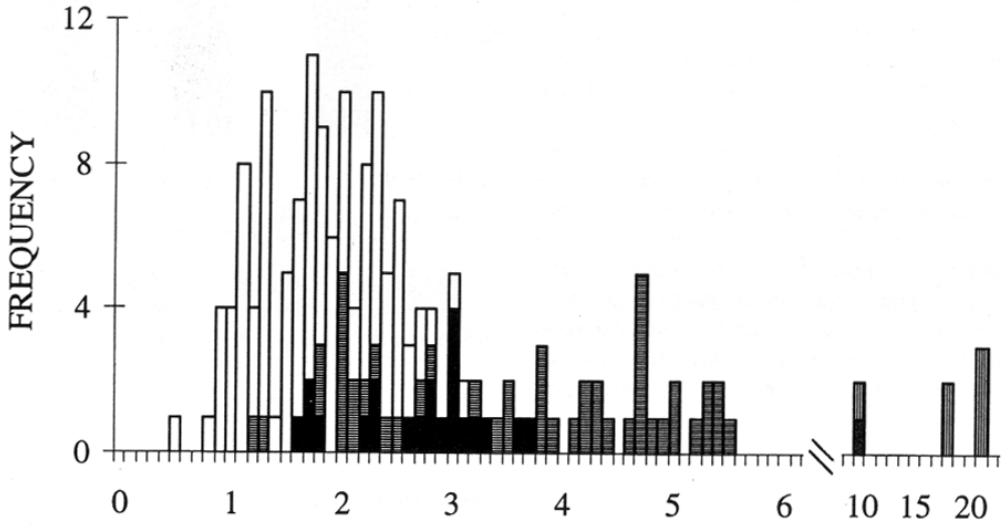
Distribution

The observed increasing age of herring from east to the west was in accordance with former studies (DRAGESUND

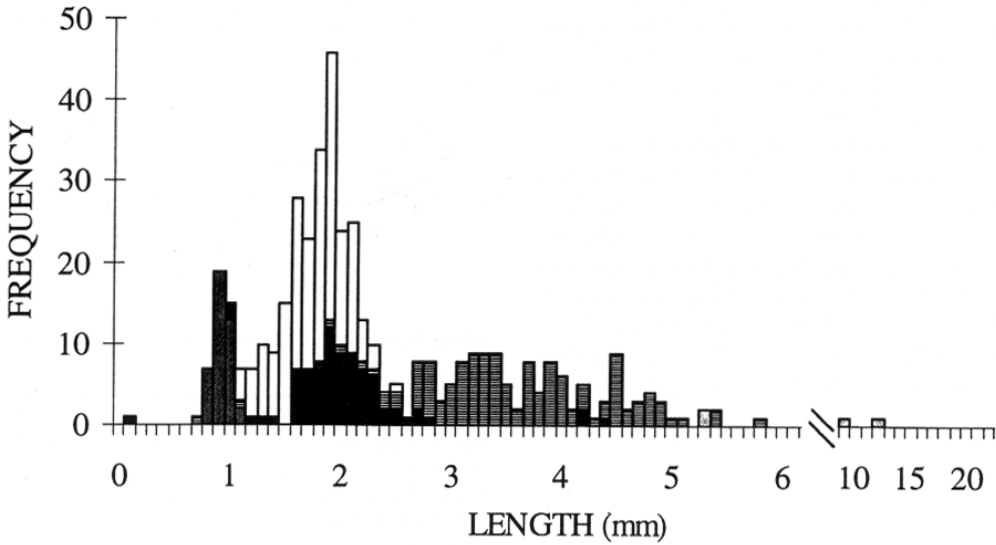
Table 3. Percentage of occurrence of prey in stomachs (ranked for herring).

Prey	Herring	Capelin
Calanoid copepods	76.3	80.5
<i>Oikopleura dioica</i>	59.8	48.6
<i>Thysanoessa furcilia</i>	51.6	72.7
<i>Evadne nordmanni</i>	18.7	36.4
<i>Oithona</i> sp.	12.4	27.0
<i>Meganyctiphanes norvegica</i>	9.9	4.6
<i>Verruca stroemia</i>	8.8	15.3
<i>Parathemisto abyssurum</i>	8.5	5.6
<i>T. inermis</i>	8.5	5.1
<i>T. calyptopsis</i>	7.4	47.1
Capelin larvae	5.6	0.5
<i>T. raschii</i>	1.8	0.0
<i>Euchaeta norvegica</i>	1.1	0.0
<i>Limacina</i> sp.	1.1	0.0
<i>Balanus balanoides</i>	0.7	6.4
Capelin eggs	0.4	6.5
Zoea larvae (crab)	0.4	0.0
<i>Podon polyphemoides</i>	0.0	1.9

A Herring prey



B Capelin prey



■ *E. nordmanni* ■ *Calyptopsis* l. ▨ Krill ▩ *Furcilia* l. □ Calanoid cop. ▤ Capelin l.

Fig. 11. Prey size of herring and capelin. *Calyptopsis* l. and *furcilia* l. are second and third larval stages of euphausiids, krill refers to adult euphausiids.

1970; TORESEN & BARROS 1995). During 1973–75, the abundance of capelin in the Barents Sea was estimated acoustically in May–June (DALEN & DOMMASNES 1974; HAUG & MONSTAD 1974; BUZETA & al. 1976), and the distribution of capelin in these years corresponded with the present findings. According to these studies and the present findings about 20 % of the capelin stock may be found in the ‘overlap area’ depending on the hydrographical conditions. In warm years the capelin are distributed further north than in cold years (OZHIGIN & USHAKOV 1985), and the degree of overlap between herring and capelin may thus be temperature dependent. The magnitude of interaction will also be determined by the abundance of herring and capelin (< 3 years old) which in turn is dependent on previous recruitment. The present data seem to be fairly representative for the described period of time which is somewhat limited. However, early summer is the time when the geographical overlap and hence the potential for interspecific competition between the two species is most prominent.

The depth distribution of herring seemed to be linked with age (or size) and the older herring were distributed deeper than the younger ones. The vertical distribution of *Calanus finmarchicus* is ontogenetically modulated (UNSTAD & TANDE 1991), where the larger stages occur progressively deeper (FIKSEN & GISKE 1995). In the area of overlap herring was found shallower than capelin. This may explain the smaller average copepod size in herring stomachs. The older herring in the western area were found much deeper, and correspondingly they contained larger copepodites and adult calanoids. The good correlation between fish body length and prey length for herring vs. calanoid copepod length can thus be explained in terms of analogous size dependant vertical distribution of herring and *C. finmarchicus*.

No diel vertical migration of herring and capelin was detected using echo sounder. This is probably due to the continuous light conditions throughout the Arctic day, and corresponds to former observations on capelin during May–June (LUKA & PONOMARENKO 1983).

Feeding

Few accounts have been given on the feeding habits of herring from higher latitudes. However, the dominance of copepods in the diet of herring in the present study corresponds well with studies from the North Sea and the areas around the British Isles (HARDY 1924; SAVAGE 1937; DE SILVA 1973; LAST 1989). The secondary importance of euphausiids and appendicularians is also in agreement with these studies. Capelin larvae were the only fish larvae consumed and were only observed in a modest amount of the herring stomachs analysed. The diet of herring was

consistent in the two years studied with a slightly higher share of copepods in 1993. This was probably due to the fact that the samples in 1993 were dominated by the abundant 1992 year class (TORESEN & BARROS 1995), which as one year olds would be expected to have a high share of copepods in their diet.

Copepods and euphausiids have been reported to be the most important food of the Barents Sea capelin (PROKHOROV 1965; LUND 1981; ELLERTSEN & al. 1982; HASSEL & al. 1991). In the present study copepods were the most important prey and euphausiids and appendicularians were ranked second, as equally important. The high share of copepods may be a result of the large share of rather small capelin with a diet shifted more towards copepods than euphausiids. Such a size-dependency in the diet has also been reported in former studies (LUND 1981; VESIN & al. 1981; PANASENKO 1984). Prey size was positively correlated with fish body size for capelin, but the correlation values were low. This may have been an artefact of small variation in the length of capelin. However, it may also be explained in terms of smaller variation in depth distribution of capelin in which case the supply of different sizes of copepods would be limited. Due to the size uniformity of herring and capelin within each catch it was difficult to test whether the apparent ontogenetic trend in diet was in fact a regional trend and not a function of size. The plankton samples were inadequate for such thorough preference determinations. There were large horizontal differences in the frequency of occurrence (FO) of some of the prey such as *Oithona* sp., *Evadne nordmanni* and calyptopis larvae of euphausiids. These differences were to a large extent attributed to regionality in the distribution of these prey, and were probably not a direct function of preference of herring and capelin.

Capelin has generally been considered to be primarily filter feeding using gill rakers (TEMPLEMAN 1948; PROKHOROV 1965). Adult krill must be ingested singly by biting due to their size. The observed cannibalistic ingestion of eggs must have been carried out by picking the eggs up from the substrate as small stones were observed in most of the stomachs containing capelin eggs. The variety of prey ingested thus indicates that the feeding repertoire of capelin includes biting and demersal pick-up behaviour in addition to filtering.

Life-history strategies

Herring and capelin have different life histories with respect to size at maturity among other things. Herring thus have to grow faster than capelin in order to fulfil their life history. The minimise mortality/growth rule (WERNER & GILLIAM 1984) shows that juvenile fish should stay where the ratio between mortality and growth is minimised. Both

predation risk and food abundance generally decrease with increasing depth (CLARK & LEVY 1988; AKSNES & GISKE 1990). The one year old herring were found high in the water column and had a 50 % higher ISF than similar sized capelin, which indicates that the herring had a higher feeding rate than capelin (other things being equal). In order to cope with the added mortality risk associated with staying higher in the water column, herring occurred in denser shoals. The capelin were found somewhat deeper than herring which is an alternative strategy of predator avoidance, similar to the strategy of mesopelagic fish (GISKE & AKSNES 1992; ROSLAND & GISKE 1994). Herring and capelin hence seem to have different ways to minimise mortality/growth. Despite a much lower ISF, capelin had a somewhat higher RSF than herring and thus did relatively well. Herring is still likely to be a more eager competitor for food and this may be an important factor in determining the outcome of competition between the two species.

Herring had a marked ontogenetic decrease in ISF not seen for capelin. However, while the herring were neatly divided into three age groups, the capelin material only consisted of two age groups. The span in age was thus more pronounced for herring and the ontogenetic trend should hence be expected to be stronger.

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