PREDATION BY JUVENILE HERRING (*Clupea harengus* L.) ON BARENTS SEA CAPELIN (*Mallotus villosus* Müller) LARVAE

by

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ABSTRACT

In years with high abundance of juvenile Norwegian spring spawning herring in the Barents sea, the year-class strength of capelin has frequently been observed to be poor. It has therefore been suggested that predation by herring is an important determinant of year-class strength for capelin. In order to study predation by herring on capelin larvae, stomachs of herring were collected in areas of spatial overlap between herring and capelin larvae in 1992 and 1993. Based on the results of the investigations in these two years, a simple model was used to estimate the impact of predation by herring on capelin larvae through the years 1983-1992. It is concluded that it is likely that predation by herring is the explanation for the poor recruitment of capelin observed in years when rich year-classes of juvenile herring are distributed in the southern Barents Sea.

INTRODUCTION

Two abundant pelagic species of fish occur in the Barents Sea: juvenile Norwegian spring-spawning herring and capelin. The herring spawn in February-April along the west coast of Norway (Dragesund *et al.* 1980). The larvae drift with the Norwegian coastal current and when strong year-classes are produced, large amounts of herring larvae are distributed in the southern part of the Barents Sea during July. The adolescent herring stay there for 2-4 years before they migrate out of the Barents Sea and join the adult stock. The capelin spawn along the coast of northern Norway in March-June (Dragesund *et al.* 1973). Usually during May-July large amounts of capelin larvae are distributed in the southern Barents Sea (Alvheim 1985). As the herring larvae do not enter the Barents Sea until July (Dragesund 1970), there is usually not extensive spatial overlap between the 0-group herring and capelin. However, the youngest herring is distributed in the south and eastern parts of the Barents Sea and the older fish is distributed further to the west. Spatial overlap is therefore most likely to occur between the 1-3 year old herring and capelin larvae. In years when adolescent herring is distributed in the Barents Sea there is a spatial overlap between herring and capelin larvae during summer (Dragesund 1970, Alvheim 1985).

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In the period 1950 to 1980, three strong year-classes of herring were produced (Dragesund *et al.* 1980), in 1950, 1959, and 1960. Following these year-classes, major declines in the abundance of capelin were observed. This apparent inverse relationship between the recruitment of the two species has been pointed out by several authors (Olsen 1968, Hamre 1985, 1988, 1994). In 1983 a very strong year-class of herring was produced, and herring were distributed in the Barents Sea for the first time since the 1960s. The presence of herring seemed to have a dramatic effect on the recruitment of capelin in 1983-86 when very poor year-classes of capelin were produced (Fossum 1992). In early summer of 1986, the herring left the Barents Sea, and the 1986 year-class of capelin had very good survival and it became the basis of the rebuilding of the stock after the collapse in the capelin biomass in 1986-87 (Fossum 1992).

In 1991 and 1992, strong year-classes of herring were produced (Anon. 1992a), and this attracted new attention to the predation theory. Despite the strong indications of predation from the apparent negative influence of abundant herring year-classes on subsequent capelin recruitment, few observations of capelin larvae in the stomachs of herring existed. As a part of the multispecies-model for the Barents Sea, stomachs of herring were sampled in the period 1983-85 (Mehl and Yaragina 1991). From a total of 1505 herring stomachs, only two observations of capelin (1-group) were made (Bjarte Bogstad pers. comm., IMR, Bergen).

Predation by herring (*Clupea harengus* L.) on capelin larvae has been reported from Icelandic waters (Magnusson 1968) and from the Grand Banks (Templeman 1948).

Moksness and Øiestad (1987) studied the interaction between herring- and capelin larvae in a mesocosm experiment. Despite excellent growth, the capelin larvae disappeared in the experiment, and this was suggested to be caused by predation from herring. The capelin larvae disappeared, when the herring had just started schooling.

On the basis of this background knowledge the working hypothesis was made that predation by juvenile herring on capelin larvae has significant impact on capelin recruitment in years with herring in the Barents Sea. To test this hypothesis, stomachs of herring were sampled in the area of spatial overlap of the two species in May-July. This is the period in which predation is most likely to occur as the abundance of capelin larvae has been shown to be dramatically reduced by late August in years with herring present (Fossum 1992).

Hypothesis: Predation by juvenile herring on capelin larvae has significant impact on the recruitment of capelin.

MATERIALS AND METHODS

The surveys

The material was collected during two surveys on the research vessel "G.O.Sars" in the Barents Sea in the period 26 May to 14 June 1992 and in the period 1 June to 24 July 1993. The objectives of these surveys in addition to the present study, were to estimate the abundance of juvenile herring by acoustic methods, and to estimate the abundance of capelin larvae. Sampling of herring and capelin larvae was carried out off the coast of northern Norway between latitude 70°30'N and 72°30'N, and longitude 23°00'E and 33°00'E and in 1993 also off the Murman coast eastwards to 36°00' E and southwards to 69°00'N.

The surveys were carried out by running north-south grid lines one degree longitude apart (about 20 nautical miles (NM)). The abundance of herring was estimated by standard acoustic methods (MacLennan and Simmonds 1992). Fish were recorded using the Simrad EK 500 scientific echo sounder (Bodholt *et al.* 1989) connected to the Bergen Echo Integrator (Knudsen 1990). The estimated capelin larvae abundance was based on Gulf III stations performed every 20 NM within the distribution area of the capelin larvae. The total abundance was calculated based on these samples using the method of calculation outlined by Alvheim (1985).

Sampling equipment

Capelin larvae were collected using Gulf III 375 µm mesh and MIK 2000 µm nets (500 µm in hindmost 1.5 m). The Gulf III was hauled double obliquely to 60 m at a speed of 0.5 m/s with a vessel speed of 5 knots. A flow meter in the opening (19 cm diameter) of the sampler measures the water flow through the sampler (Zijlstra 1971). In July 1993, a circular MIK net (opening 2 m diameter) was applied instead of the Gulf III in order to catch the large capelin larvae (>20 mm) more representatively (Methot 1986; Munk 1988). The MIK was towed in the same way as described for the Gulf III, but with a vessel speed of 3 knots.

Trawling

Pelagic trawling using a midwater trawl ("Fotø" herring trawl in 1992, "Åkra" trawl in 1993) was carried out when echo recordings of fish were done. In areas of high capelin larvae abundance, "blind hauls" were sometimes carried out in order to try to catch herring not observed on the echo sounder or sonar. Trawling depth varied from the surface to 310 m. Trawling time was approximately 30 minutes. The opening height of the trawl was observed by a wireless hydroacoustic sensor attached to the headline of the trawl.

When herring were caught, Gulf III or MIK samples were taken in the same position to obtain an estimate of the local capelin larvae abundance.

Preservation

In 1992 a total of 799 stomachs of herring were collected (18 stations) of which 534 stomachs were preserved, either in formalin or frozen, and 265 were examined fresh. Formalin was injected into the abdominal cavity of the fish to ensure rapid preservation, and the whole fish was thereafter stored in formalin. The herring were frozen whole. The preserved material was examined in a laboratory and the results are presented by Huse and Toresen (1995).

In 1993 a total of 2560 stomachs were collected (48 stations) of which 2140 were examined fresh, and 450 were preserved. At each station, up to 60 herring were collected for stomach content analysis of which 50 stomachs of herring were investigated fresh, and 10 were preserved. The stomachs were preserved individually in 20 ml vials in 96% ethanol. If fewer than 50 herring were caught, all stomachs were investigated fresh.

Stomach content analysis

The stomachs that were investigated fresh, were analysed within one hour after being captured, and the stomachs were kept cool (<8°C) prior to the investigation in order to slow down the digestive process. The sea temperature in the study area was stable and usually below 6°C (Midttun and Loeng 1987). Digestion rate is positively correlated with temperature (Elliott and Persson 1978; Flowerdew and Grove 1979).

For each herring stomach, dominating prey groups and the number of capelin larvae were recorded.

The predation model

The impact of predation on the mortality of capelin larvae was estimated by using a model. The model was based on the method for estimation of predation outlined by Bailey and Houde (1989). The daily amount of capelin larvae consumed by herring was determined by using Bajkov's method (1935) somewhat modified. The following simple multiplicative model was used to estimate the total number of capelin larvae eaten by herring (TP) in each year:

$$TP = X \cdot C \cdot N \cdot D \cdot M \quad (1)$$

where
X=average number of capelin larvae in herring stomachs
C=proportion of herring containing capelin larvae
N=estimated number of 1-3 year old herring in the Barents Sea
D=number of days that capelin larvae are confined to the predatory field of herring
M=number of meals of herring/day

The distribution area of capelin larvae encompassed the herring distribution in both years studied. All the herring in the Barents Sea were therefore potential predators of capelin larvae, and used in the model.

Statistical analysis

As the assumptions of homogeneity of variance and normality of the data were violated, nonparametric statistics were applied. One way ANOVA was carried out using Kruskal-Wallis (Kruskal and Wallis 1954) or Kolmogorov-Smirnov test (Zar 1984). Correlations were carried out using Spearman rank correlation (Zar 1984). The significance level was set at p=0.05.

RESULTS

Horizontal distribution

Herring

In 1992, the herring were distributed between longitudes 21°00'E and 36°00'E, and latitudes 69°20'N and 73°00'N (Figure1). The highest concentrations of herring were detected north-east of the Nordkyn peninsula, east of Vardø, and close to the Murman coast. The herring in the western part of the distribution area were predominantly three year olds, while one and two year old fish dominated in the eastern parts.

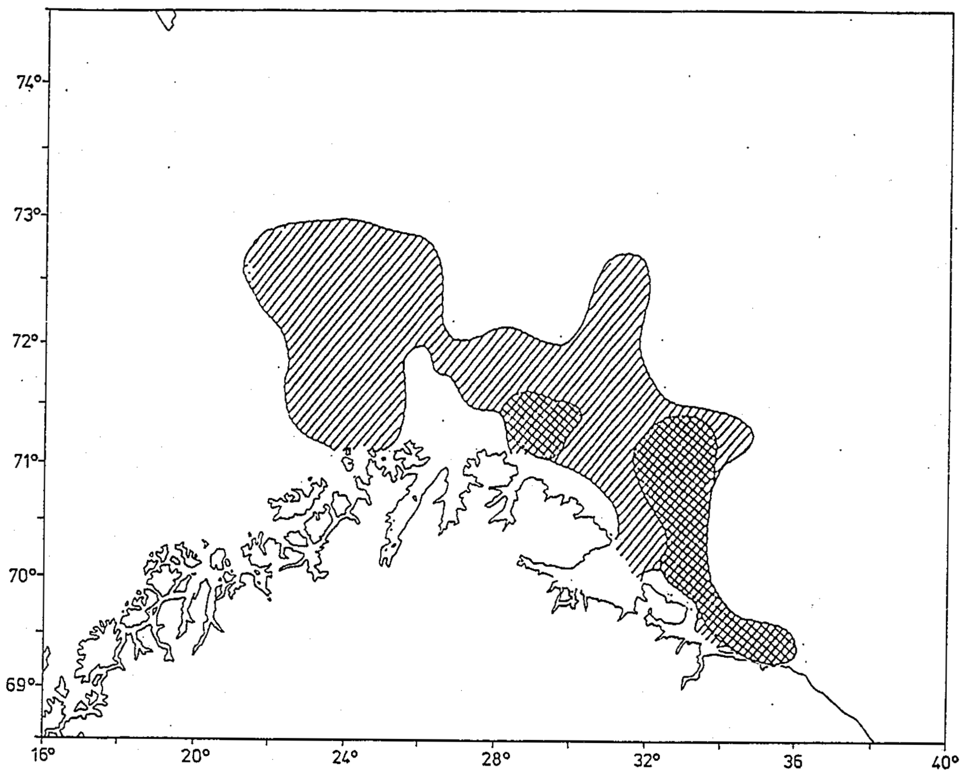

Figure 1. Distribution of adolescent herring June 1992. Double hatched areas indicate highest density. Anon 1992a.

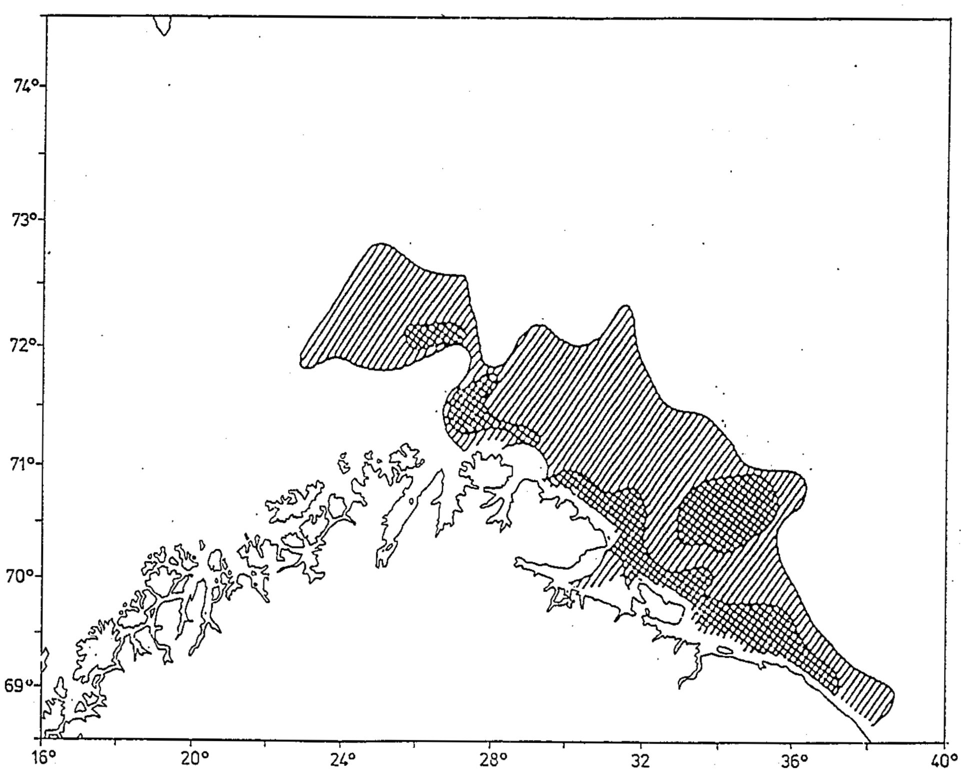

Figure 2. Distribution of adolescent herring June 1993. Double hatched areas indicate highest density. Anon. 1993a.

In 1993 the herring were distributed along the Norwegian and Russian coasts between longitudes 23°00'E and 39°00'E, and extending some 90 NM off the coast (Figure 2). The highest concentrations were recorded in a belt along the coast of Norway (30x180 NM) from about 29°30'E and eastwards along the Russian coast to about 38°30'E. Another high density area was recorded around 70°30'N and 34°00'E extending some 30 NM in each direction. Some very dense schools were also recorded to the east of Vardø and north of Murmansk. The herring in the western part of the survey area (north of Norway) consisted mainly of two year old fish, while the concentrations in the eastern part were dominated by one year old fish. The three year olds seemed to have migrated out of the Barents Sea prior to the survey.

Capelin larvae

Both in 1992 and 1993, the capelin larvae distribution encompassed the entire herring distribution. Some areas of high concentrations of capelin larvae were found, but most of the larvae were distributed evenly within the distribution area, decreasing in abundance towards the edges of the distribution. In 1992, the highest concentrations of capelin larvae were found in the area north-east of North Cape and east of Vardø (Figure 3), where concentrations of up to 1000 larvae per m^2 were found. The highest concentrations of herring and capelin larvae were thus found in the same areas.

In 1993, the highest concentrations of capelin larvae were found in June close to the shore in three separate areas (Figure 4): the area to the west of North Cape (500 larvae/m^2), the area north of the Nordkyn peninsula (100 larvae/m^2) and in the Varanger fjord (100 larvae/m^2). In July, the concentrations were highest in the inner shelf zone (100 m depth) off Syltefjord.

Vertical distribution

Herring

In both years, the herring aggregated in dense schools of varying size with a vertical extension of about 20 m. The schools were mostly recorded in the upper 80 m layer with a dominating distribution closer to surface than 40 m in both years.

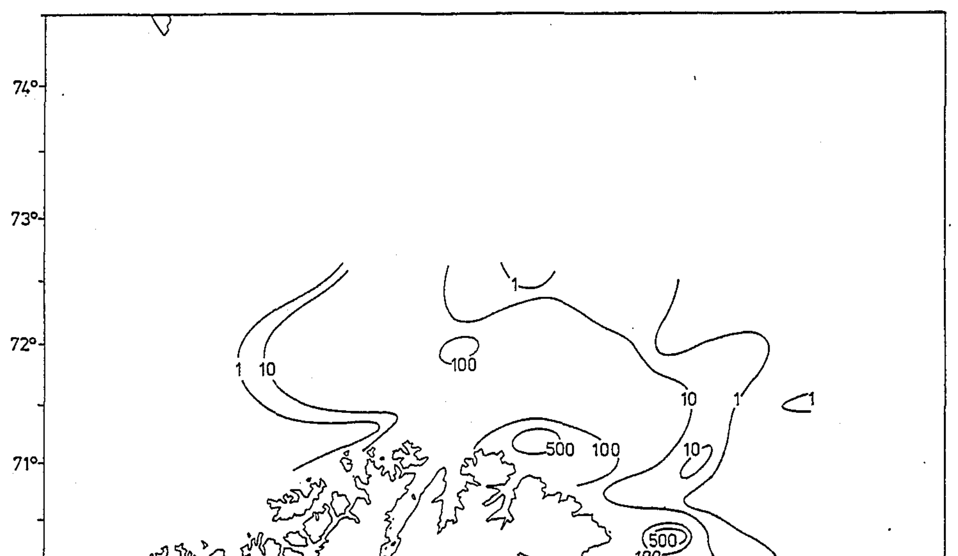

Figure 3. Distribution of capelin larvae in June 1992. Figures in chart indicate number of larvae per m^2. Anon. 1992b. Stippled line indicates 0-line of capelin larvae abundnce.

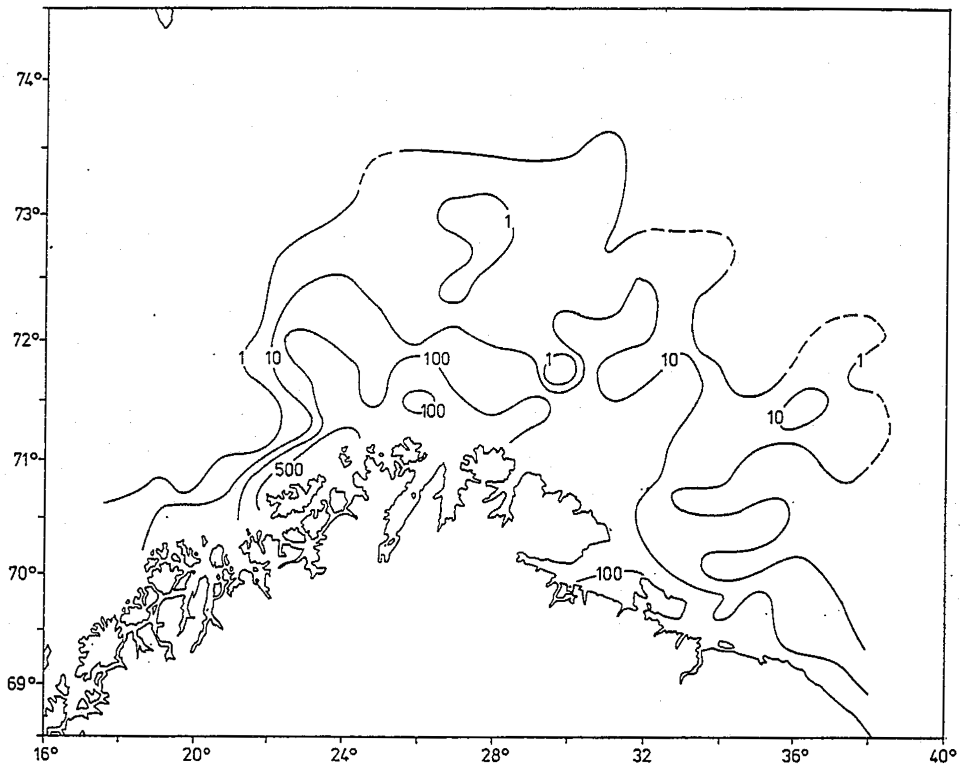

Figure 4. Distribution of capelin larvae in June 1993. Figures indicate number of larvae per m^2. Anon. 1993a.

Capelin larvae

Alvheim (1985) studied the vertical distribution of capelin larvae in three depth intervals 5-25, 30-50 and 55-75 m, and found a decrease in numbers with increasing depth, with only 9% of the total number of capelin larvae in the deepest interval.

Abundance

Herring

The abundance of herring in the Barents Sea in the years 1983 - 1993 is shown in Table 1.

Table 1. Abundance of herring in the Barents Sea. Numbers (N) in billions, (Toresen and Barros 1995).

	Age-groups				
Year	1	2	3	4	Total
1983	0	0	0	0	0
1984	21.4	0	0	0	21.4
1985	0.3	13.9	0	0	14.2
1986	0.5	0.2	3.2	0	3.9
1987	0	0	0	.0	0
1988	0	0	0	0	0
1989	2.2	0	0	0	2.2
1990	4.6	0	0	0	4.6
1991	24.3	5.2	0	0	29.5
1992	32.6	14.0	5.7	0	52.3
1993	88.6	25.2	0	0	113.8

Capelin larvae

Table 2. Capelin larvae abundance estimates (nos. x 10^{-12}), average length (mm) of larvae and median date of survey (in June) in the period 1981-1993 (Anon 1992b, Kjell Bakkeplass pers. comm., IMR, Bergen). *Average length of larvae captured on median date of survey.

Year	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
Index	9.7	9.9	9.9	8.2	8.6	0.0	0.3	0.3	7.3	13.0	3.0	7.3	3.3
St.length	11.6	9.2	12.9	11.0	10.3	*8.8	8.9	10.0	12.1	10.3	10.8	10.0	11.0
Date (mid)	8	11	8	2	5	20	25	22	24	19	22	14	15

The capelin larvae abundance estimate (Table 2) was more than two times higher in 1992 than in 1993. The average capelin larvae abundance estimate for the period 1981 to 1993 was $6.2x10^{12}$. The abundance of larvae in 1992 was thus above average, while in 1993 it was below average.

Predation

1992

The study was carried out by following predetermined course tracks and trawling on acoustic observations in areas with overlap between herring and capelin larvae. The number of herring stomachs containing capelin larvae was 45, which made up 5.6% of the stomachs investigated. In most of these stomachs, few larvae were found, and usually only single observations were made. At one station (St.no. 362), however, one herring (17.0 cm) contained 40 capelin larvae which comprised more than half of the stomach content. A total of 138 larvae was detected in the herring stomachs, an average of 3.1 larvae per stomach in the herring which were found to have eaten capelin larvae. The larvae eaten by herring ranged from 8 to 15 mm in length.

Predation was observed at six stations (Table 3). There was no correlation (r=0.00, p=1.00, n=6) between the number of capelin larvae in the Gulf III samples and the proportion of herring stomachs containing capelin larvae. At one station (St.no. 340), no larvae were caught in the Gulf III while there were several herring containing capelin larvae. Predation occurred in the same areas in both years.

Table 3. Sampling stations at which predation occurred in 1992. The number of larvae in the Gulf III, number of stomachs investigated and the number of stomachs containing larvae.

Date	Time (hrs)	Station	Larvae in Gulf III	Stomachs investigated	Stomachs with larvae
02.06	06.50-07.14	339	0	100	2
02.06	10.08-10.38	340	0	30	28
04.06	08.45-09.05	343	0	60	4
08.06	09.15-09.45	351	2	90	3
11.06	18.51-19.21	360	1	60	4
13.06	20.19-20.49	362	0	4	4
		Sum	3	344	45

1993

The cruise was run following the same procedure as in 1992. Capelin larvae were detected in 77 stomachs of herring, constituting 3.0% of the stomachs examined. Capelin larvae were found in herring stomachs at 19 stations (Table 4). The length of the ingested larvae ranged from 12 to 25 mm. In total, 138 capelin larvae (same as 1992) were found in the herring stomachs, an average of 1.8 larvae per herring containing capelin larvae. There was no correlation ($r=0.16$, $p=0.49$, $n=19$) between the number of capelin larvae in the Gulf III samples and the proportion of herring stomachs containing capelin larvae.

Predation model inputs and results

In order to relate the occurrence of predation to the mortality of capelin larvae, a model was applied. The model was based on the rate of occurrence of larvae in the herring stomachs, on the estimates of herring abundance in the Barents Sea, and a stipulation of the number of "meals" of capelin larvae per day taken by each herring. This stipulation may be based on the observed weight of the stomach content compared to the total amount of expected food intake per day. In the present study, the average observed stomach content was 1.7% of body weight for fish under 9.0 g. This was about 1/3 of the daily ration of 5.0% (at 6.5° C) for comparable sized herring reported by De Silva and Balbontin (1974). Even though the daily ration of food intake is known to decrease with increasing size of the fish (Jobling 1992), the ratio between the observed stomach content and the daily ration should be proportional, independent of fish size (assuming equal daily feeding strategies for all sizes of herring in the study). The relationship between observed stomach content and daily ration from the literature for one year old herring may therefore be adopted to the larger fish. The estimate of the number of meals/day ingested by herring is thus three.

Table 4. Sampling stations at which predation occurred in 1993. The number larvae in the Gulf III, number of stomachs investigated and number of stomachs containing larvae.

Date	Time (hrs)	Station	Larvae in Gulf III	Stomachs investigated	Stomachs with larvae
10.06	04.45-05 05	289	208	80	17
10.06	14.57-15.20	290	8	80	2
19.06	17.12-17.42	304	7	60	1
19.06	21.25-21.55	305	1	60	1
27.06	08.55-09.25	315	3	60	3
27.06	18.20-18.40	317	21	60	3
29.06	17.05-18.05	319	18	60	1
29.06	21.15-21.45	320	16	44	5
01.07	12.12-12.50	325	137	5	3
01.07	17.20-17.50	326	160	60	3
01.07	22.10-22.20	328	142	60	22
02.07	11.54-11.58	331	120	60	1
02.07	20.25-20.45	333	14	60	1
10.07	05.30-06.00	-343	1	60	3
10.07	19.00-19.50	345	38	60	5
12.07	20.15-20.45	356	223	60	2
19.07	23.00-24.00	375	92	22	2
20.07	02.20-03.20	376	25	60	1
21.07	01.07-02.17	380	30	50	1
Sum			1264	1061	77

With a daily ration corresponding to three meals/day, and a number of 100 days of exposition to predation, herring would have ingested 37% of the estimated capelin larvae abundance in 1992 and 56% in 1993. In the calculation of mortality in other years than 92 and 93 data of the occurrence of larvae in the stomachs and proportion of herring predators are obtained by calculating the average of the observed 92 and 93 figures. The variables in the model and their input values for all years are shown in Table 5.

Table 5. Variables and their values in the model.

	Input values		
Variables	1992	1993	Other years
X	3.07	1.79	2.43
C	5.6	3.0	4.3
N	$52.4x10^9$	$128.6x10^9$	as estimated
M	3	3	3
D	100	100	100

Different scenarios for capelin mortality attributed to predation by herring , dependent on days of availability of capelin larvae to herring predation (80, 100 or 120 days) for the whole time series of herring and capelin larvae estimates since 1984 are shown in Table 6 and in Figure 5.Other scenarios may also be made showing dependence of other paramaters as e.g. meals/day, which the model is quite sensitive to. The results shows that the impact of predation was much higher in the 90'ies than in the mid 80'ties. This is mainly due to a much higher abundance of juvenile herring in the early 90'ies. The occurrence of predation was higher in 1992, but due to higher abundance of herring and lower abundance of capelin larvae in 1993, the impact of predation on the recruitment of capelin was predicted to be higher in 1993.

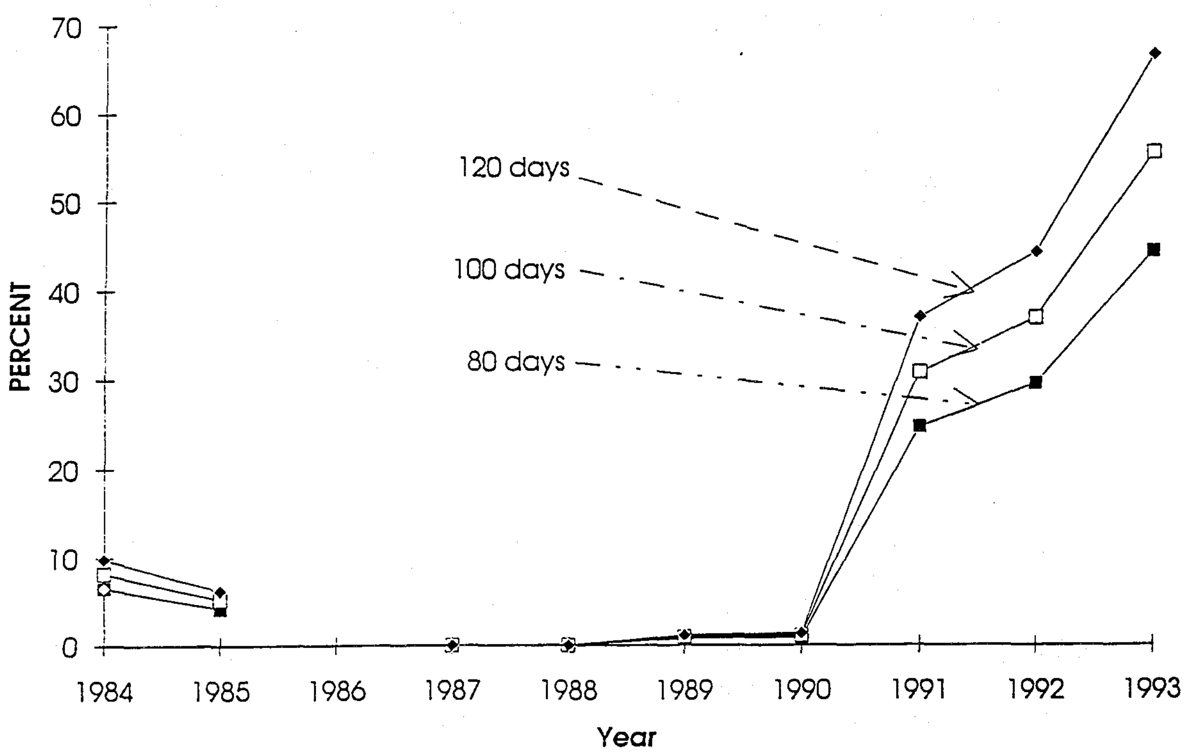

Figure 5. Mortality of capelin larvae in percent of estimated capelin larvae abundance in the years 1984-1993.

Table 6. Estimated number of capelin larvae consumed in the years 1984-1993 in three scenarious of different time-length of predation (80, 100 and 120 days). Proportion of estimated capelin larvae abundance preyed by herring in the same number of days is also given.

Year	TP80	TP100	TP120	TP%80	TP%100	TP%120
1984	0.53	0.67	0.85	7	8	10
1985	0.35	0.45	0.54	4	5	6
1986	0.10	0.12	0.15	-	-	-
1987	-	-	-			
1988	-	-	-			
1989	0.06	0.07	0.08	1	1	1
1990	0.12	0.14	0.17	1	1	1
1991	0.74	0.93	1.11	25	31	37
1992	2.16	2.70	3.24	30	37	44
1993	1.47	1.83	2.20	44	56	67

DISCUSSION

Methodology

Stomach content analysis

In the present study predation by herring on capelin larvae was studied. Ideally, the best way to verify predation in the field is to sample the potential predators and look for prey in their stomachs. Stomach content analysis (SCA) was applied to assess predation by herring on capelin larvae. It has been questioned whether or not this is an appropriate method for investigating predation on fish larvae in the field (Pepin *et al.* 1987; Folkvord 1993). Problems connected with studies of predation on fish larvae using SCA, are those concerned with rapid digestion of larval tissue in fish stomachs, like recognition of larvae and quantification of predation (Bailey and Houde 1989). Several authors have pointed out that fish larvae are digested in less than 30 min. (Hunter and Kimbrell 1980; Christensen 1983). Digestion rate is, however, dependent on the size of the larvae (Folkvord 1993), the temperature (Elliott and Persson 1978; Flowerdew and Grove 1979; Persson 1981) and amount of additional food ingested (dos Santos and Jobling 1991). The studies referred to above were carried out on small larvae (3-6 mm) at higher temperatures than the present study (15°C and 10-11°C for Hunter and Kimbrell 1980 and Christensen 1983 respectively). It is therefore assumed that SCA is applicable under the present conditions.

The surveys

The survey coverage by area was good both in 1992 and in 1993, and the entire distribution area of herring and capelin larvae was covered. In 1992, the area was covered only once, while in 1993, areas of special interest were investigated in more detail. This gave room for a thorough investigation in 1993, and reduced the possibility of missing areas of major importance to predation. However, predation is likely to have continued throughout July and in August in the areas monitored during the survey.

Most of the sampling was carried out in the southern part of the distribution area. As the most abundant locations of herring and capelin larvae were sampled more intensively than other areas, the rates of predation may be slightly overestimated in 1993. In general the concentrations of capelin larvae were relatively uniform within the distribution area of herring, and the estimates of predation are not likely to be systematically overestimated despite the skewed allocation of stations. The total abundance of herring in the Barents Sea was used in the model calculations as potential predators of capelin larvae. This seems reasonable as determined from the spatial overlap in distribution of the predator and the prey.

Abundance estimates

The abundance estimates of herring and capelin larvae used in the model calculations, are likely to be biased. In the survey reports (Anon. 1992a; 1993a), it was concluded that the abundance of the one year old herring may have been underestimated due to avoidance reactions from the vessel. The capelin larvae abundance estimate of 1992 (Anon. 1992b) may have been an overestimate as one station contributed very much to the total estimate. When this station was left out, the capelin larvae abundance estimate was reduced by 25% to 5.6×10^{12}. From this it follows that the predators probably were more abundant and the prey probably were less abundant than the figures applied in the model. If this was the case, the model predictions of the impact of predation are underestimates.

Predation

Horizontal distribution

There was extensive overlap in the distributions of herring in the two years. In 1993 the herring had a more easterly distribution than in 1992. This was probably due to the migration of the three year old herring out of the Barents Sea prior to the survey in 1993, as only few individuals of this age group were caught. In both years studied, the capelin larvae distribution area encompassed the herring distribution, and the predation potential was therefore large. In 1992, the highest concentrations of herring and capelin larvae were in the same areas. This coincided, especially for the area east of Vardø, with high biomass of zooplankton (Anon. 1992d). This is similar to what Helle (1993) found for the larval stages of cod and -capelin in the Barents Sea.

Vertical distribution

Consistent variations of vertical overlap between herring and capelin larvae would influence on the predation model. The capelin larvae abundance estimates are based on the larval abundance in the 0-60 m interval (Gulf III). The larvae found below 60 m would thus have no impact on the predation model, and lack of vertical overlap between the two species is therefore limited to this depth interval. As there seemed to be a high degree of vertical overlap between the species in the 0-60 m interval, the model was not adjusted for this parameter.

The predation model

The number of herring stomachs containing capelin larvae has some value in itself, but it is more interesting if it can be related to the impact of predation on recruitment of capelin. That was the basis for using a predation model.

The time span in which capelin is susceptible to predation by herring is uncertain, but findings in the present study show that herring (13-25 cm) is capable of ingesting relatively large juvenile fish such as 5 cm sand eel. The susceptibility of capelin larvae to predation by herring was here set to be constant for a given number of days while in the predatory field, in order to simplify the model calculations.

The total number of herring in the Barents Sea increased markedly from 1992 to 1993. This was mainly due to a strong herring year-class in 1992 (Anon. 1993a) which was estimated to be 4 times stronger at the one group level than the 1983 year-class, the strongest year-class since the 1960s (Røttingen 1990). The size of the herring did not seem to be important to the predation, as most of the herring stomachs contained few larvae regardless of size of the herring.

It has been shown on several occasions (Fossum 1992) that despite high capelin larvae abundance estimates, the abundance obtained during the 0-group surveys in September have been extremely low. This was the case both in 1992 and in 1993 (Anon. 1992c, 1993b). Predation is therefore probably most important prior to September, and in the model calculations 100 days of predation were applied (May, June, July and early August).

The model predicted that the impact of predation on capelin larvae survival was much higher in the nineties than in the mid eighties. This is probably due to a much higher abundance of herring in recent years combined with a significantly lower abundance of capelin larvae. In addition, the distribution of the 1983 year-class as one year olds was very easterly (Røttingen 1990) and the capelin larvae distribution that particular year therefore did not encompass the distribution of juvenile herring. The impact of predation is therefore overestimated in 1984.

A weakness of the model may be that it does not take into account the reduction in available capelin larvae due to predation. As the capelin larvae are removed by predation, herring will encounter fewer capelin larvae. The model should therefore not be linear, but descending corresponding to the number of larvae left. However, if the predation is assumed to be restricted to a certain size group of larvae, then there would be a steady supply of larvae into the size ranges vulnerable to predation due to differences in hatching time and in growth rate of the larvae. In this case the linear model will be less biased.

The biomass of zooplankton in the Barents Sea was above average for both years studied (Arne Hassel pers. comm., IMR, Bergen). Starvation has thus possibly not been responsible for the extremely high mortality observed for capelin larvae in 1992 and 1993 (according to the 0-group abundances). The presence of herring in the Barents Sea ecosystem seems to be incompatible with normal recruitment of capelin. Fossum (1992) states that there seemes to be two different regimes for recruitment of the Barents Sea capelin, one with herring present and one without herring. Although the number of stomachs containing capelin larvae in the present study were moderate, the model suggests that predation may have severe influence on the survival of capelin larvae. It is therefore likely that predation is the main cause of the high mortality observed for the larvae in years when juvenile herring distribute in the southern Barents Sea. This study thus supports the hypothesis that predation by juvenile herring on capelin larvae has significant impact on capelin recruitment.

CONCLUSIONS

-The capelin larvae abundance encompassed the entire herring distribution area in both years, and there was generally a high degree of vertical overlap.

-In most of the herring stomachs where capelin larvae were found, only a few specimens occurred.

-It is estimated that predation by herring may have strong influence on the survival of capelin larvae when high abundance of herring occur. Predation of capelin larvae was higher in the early nineties than in the mid eighties. This is explained by the much higher abundance of herring and a significant lower abundance of capelin larvae in recent years than in previous years.

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