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Interaction of Norwegian spring-spawning herring larvae (*Clupea harengus*) and Barents Sea capelin larvae (*Mallotus villosus*) in a mesocosm study

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Growth and survival of herring (*Clupea harengus*) larvae released into a 4400-m^3 basin were measured for four months. Schooling was observed at an age of 50 days (32 mm long), and metamorphosis took place at an age of about 60 days (34 mm long). About 3000 yolk-sac capelin (*Mallotus villosus*) larvae were released into the basin when the herring were 34 days old (20 mm long), and another group of about 50 000 when the herring were 46 days old (25 mm long). Both capelin groups met with excellent feeding conditions and showed rapid growth. However, they expired at an age of 30 and 22 days respectively, despite the apparently suitable feeding conditions. The newly schooling herring population had a mean density of 1 to 2 fry/m^3 when the capelin disappeared. Laboratory studies on the ability of juvenile herring (25–35 mm) to prey on food items 6–7 mm in size showed that the herring could prey upon capelin larvae of this size.

Separate survival and growth studies were carried out on another group of capelin larvae which were released into a 2000-m^3 basin, where they met rather marginal feeding conditions. About 2·8 % of these larvae survived to an age of 120 days. Capelin larvae from both groups were transferred to bags suspended in the 4400-m^3 basin containing herring. From 0·5 to 5·5 % of group 1 survived to age 40 days, while survival rates for group 2 to age 31 days were higher, ranging from 10·5 to 30·5 %.

These results are discussed in relation to the distribution of juvenile herring on the spawning grounds of capelin in northern Norway. The sharp decline in Norwegian spring-spawning herring in the mid-1960s coincided with a huge increase in the capelin population in the Barents Sea. Recently the herring population has recovered, and the potential influence of herring predation on the capelin population is assessed.

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Introduction

It is well known that marine fish larvae have very high mortality rates, but the causes of this mortality are still not fully known. Starvation has been suggested as the main causal factor, but starved larvae have seldom been identified from sea samples (Methot and Kramer, 1979; O'Connell, 1980). Mortality caused by predation on marine fish larvae from zooplankton organisms (Bailey and Batty, 1983; Christensen, 1983) and juvenile fishes (Garrod and Harding, 1981; Øiestad, 1985) has recently been extensively studied in the laboratory and field. In a recent paper Sissenwine (1984) concluded: "There are numerous reasons why fish populations vary. Predation plays a much greater role than has been hypothesized until recently", and "Recruitment is likely to be a multiplicative function of highly variable processes occurring throughout the first year of life, including the post-larval stage".

In the Northeast Atlantic two important pelagic fish populations spawn along the Norwegian coast. Norwegian spring-spawning herring spawn on the west coast of Norway in the period from February to April, while the Barents Sea capelin spawn on the coast of Finnmark mainly in April. In the period from 1950 to 1980 there were three good year classes of herring, in 1950, 1959, and 1960 (Olsen, 1968; Dragesund *et al.*, 1980). In the years with strong herring recruitment an obvious decline in the abundance of the corresponding year classes of capelin was observed (Olsen, 1968) followed by a decline in catches to very low levels. Hamre (1984) suggested that there might be a close connection be-

tween recruitment to the herring and the capelin populations: a strong year class of herring results in a weak year class of capelin. Similarly, Cushing (1980) has suggested that the outburst of cod in the North Sea might have been caused by the sharp decline in the North Sea herring, since 1-group herring might prey on cod larvae.

From the mid-1960s to 1983 Norwegian spring-spawning herring year classes were almost nonexistent in Norwegian waters, while the capelin population has had a stable and high recruitment. The herring, which hatch about one to two months before the capelin, drift into the area where the capelin eggs hatch, as observed on a cruise in June 1983, when the distribution of herring larvae partly coincides with that of capelin larvae (H. Bjørke, Institute of Marine Research, Bergen; pers. comm.). Especially in years with high recruitment of herring the two species can be expected to be in the same area (Hamre, 1984). In May and June when the larvae potentially have the same distribution, the herring larvae are about 15 mm longer than the capelin larvae. During June most of the herring larvae start schooling (25–30 mm) in the coastal areas of northern Norway, at a time when the capelin are 6–15 mm in length (Slinning, 1976; Wiborg, 1961). In August herring have a mean length of 80 mm while capelin have a mean length of 50 mm (Anon., 1984, 1985).

To test the hypothesis that schooling herring larvae represent a source of mortality for capelin larvae, a set of experiments was conducted in basins and in the laboratory in 1979 and 1985 respectively. This paper discusses the results of these experiments.

Materials and methods

The 4400-m^3 basin (Basin 1) had a surface area of 1700 m^2 and a maximum depth of 4 m. The 2000-m^3 basin (Basin 2) had a surface area of 600 m^2 and a maximum depth of 5 m. The plastic bags for enclosing fish larvae within the basin were 2-m deep and had a volume of 18 m^3. The basin method has been described earlier (Øiestad, 1982), as has the combined basin and plastic bag method (Øiestad and Moksness, 1981).

Basin and plastic bag experiments

The herring larvae used in the 1979 basin and plastic bag experiments came from eggs stripped on the west coast of Norway and incubated in the laboratory at the Flødevigen Biological Station. The eggs hatched on 4 April 1979. About 25 000 herring larvae were transferred to a 4400-m^3 basin (Basin 1) at an age of 4 days (8 April).

Two groups of capelin originated from eggs taken by grab sampling off the Finnmark coast in northern Norway and incubated in the laboratory at Flødevigen. The two groups hatched on 5 and 16 May 1979, respectively. From the first group of capelin (C-I) 3000 larvae were transferred to the 4400-m^3 basin on 8 May (age 3 days), and 200 capelin larvae were transferred on the same day to each of nine plastic bags floating in the same basin. From the second group of capelin (C-II) 50 000 larvae were transferred on 20 May (age 4 days) to the 4400-m^3 basin. Approximately 75 000 capelin larvae (C-II) were

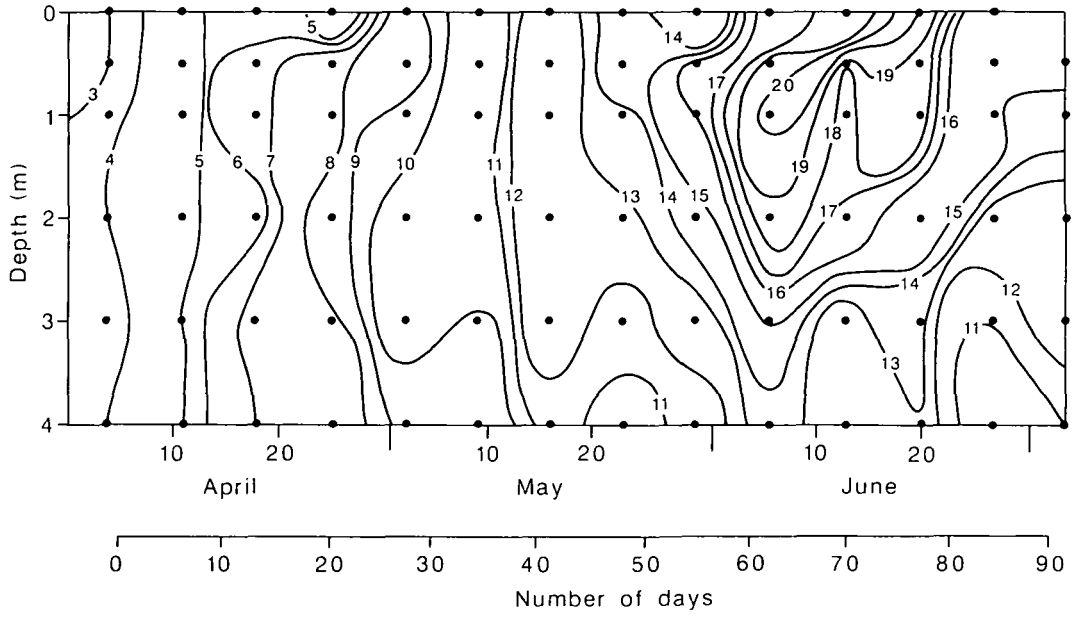

Figure 1. The isotherms in Basin 1 during the experiment. The experimental period is given by date and in number of days.

Table 1. Summary of the different experimental groups of herring and capelin larvae.

Larval group	System	Date of release	Number of days	Age at release	Number released
Herring (H)	Basin 1	8 Apr	4	4	20000
Capelin (C-I)	Basin 1	8 May	34	3	3000
Capelin (C-I)	9 bags	8 May	34	3	200
Capelin (C-II)	Basin 1	20 May	46	4	50000
Capelin (C-II)	Basin 2	19 May	45	3	75000
Capelin (C-II)	9 bags	19 May	45	3	200

transferred to a 2000-m^3 basin, Basin 2 (Moksness, 1982), on 19 May (age 3 days), and 200 capelin larvae (C-II) were transferred to each of nine bags floating in the 4400-m^3 basin on 20 May (age 4 days).

The nine black plastic bags containing capelin larvae of group 1 (C-I) were terminated on 21 May (age 16 days), 30 May (age 25 days), and 14 June (age 40 days), three at a time. The nine plastic bags with capelin larvae of group 2 (C-II) were terminated on 2 June (age 17 days), 16 June (age 31 days), and 2 July (age 47 days), three at a time. A summary of the different groups of larvae is given in Table 1.

All larval lengths quoted are standard lengths. The main net sampling programme was carried out from 2300 to 2400 hours to obtain the best estimates of the larval fish populations and the populations of large zooplankton organisms. The two double-chambered nets used had mesh sizes of 350 μm and 500 μm and openings of 0·1 and 0·3 m^2, respectively. Horizontal hauls at depths of 0 m, 1 m, 2 m, and 3 m were made. Vertical distribution and density of zooplankton organisms were obtained weekly by pump sampling. Measurements of salinity, temperature, and oxygen saturation were made once a week at each metre of depth to the bottom. The experiment in the 4400-m^3 basin was terminated on 12 July when the basin was drained and all surviving juveniles collected. The 2000-m^3 basin was drained on 20 September, when the capelin larvae (C-II) were 120 days old.

All samples were preserved immediately after capture, in 4 % buffered formaldehyde in 10‰ sea water.

The rate of growth of larvae over the experimental period could be approximated sufficiently well by a linear relationship. The mean daily length increment (DLI) from hatching at t_0 to any later time t_i could therefore be calculated as

$$DLI = \frac{L_i - L_0}{t_i - t_0},$$

where L_0 = standard length at hatching (t_0), and L_i = standard length at day t_i.

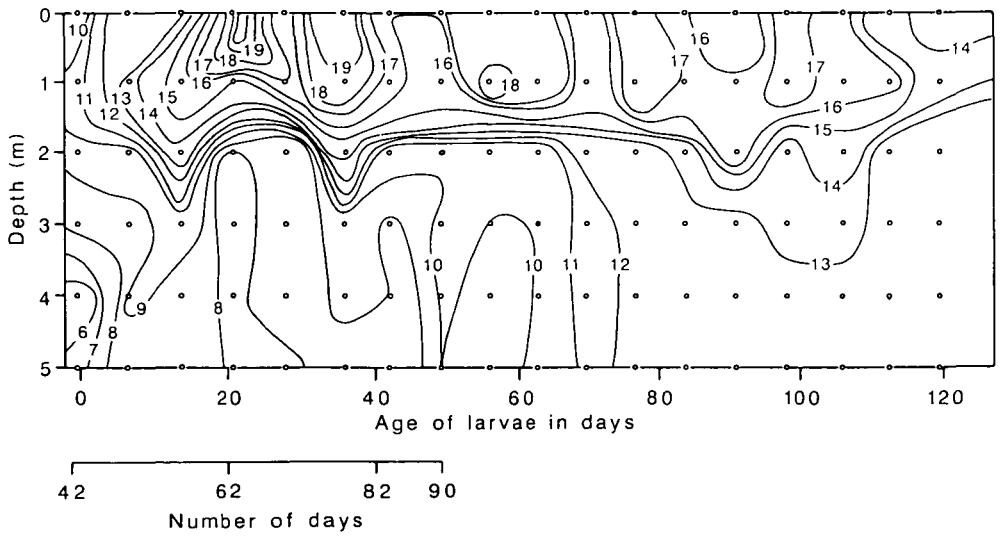

Figure 2. The isotherms in Basin 2 against the age of the second capelin group (C-II). The number of days is shown on the bottom scale (from Moksness, 1982).

In the experimental period from 4 April to 12 July, 4 April has been defined as day 0 referring to the age of the herring larvae.

Laboratory experiments

To test the ability of juvenile herring to consume prey items with the size of capelin larvae, laboratory experiments were performed in 1985. In these experiments herring were reared from eggs until they reached 25–30 mm on live zooplankton. The juvenile herring were kept in 180-l tanks to which were added newly hatched herring larvae, which have the same body dimensions and general body shape as capelin larvae. Control groups of newly hatched herring were kept in 40-l tanks for mortality comparisons. The tanks were under continuous direct observation and herring juveniles were sampled and preserved in formaldehyde for stomach analysis.

Results

Basin and plastic bag experiments

Hydrography

In Basin 1 the temperature increased from 4·6 to 13 °C at 2-m depth and from 5·0 to 11·0 °C at 4-m depth in the experimental period from early April to the middle of July (Fig. 1). The temperature increase in the plastic bags was identical to that at the same depth in the basin. In Basin 2 the temperature increased from 6 to 13 °C below 4-m depth (Fig. 2). Unlike Basin 1, a thermocline was established between 1·5 and 2·0 m from experiment days 42 to 90 (Fig. 2). In all experiments the salinity was between 32 and 34 and the oxygen saturation above 80 %.

Zooplankton

The mean numbers of important prey for the herring and capelin larvae are shown in Figures 3 and 4, for Basin 1 and Basin 2, respectively. The capelin larvae in Basin 1 met excellent feeding conditions, with a prey density of more than 70 organisms/l, which was more than 10 times higher than that available to the first-feeding herring (Fig. 3). The main prey organisms were copepod nauplii (C-II) and rotifera (C-I). The density of the same organisms in Basin 2 (Fig. 4) was on the same level (1–5 organisms/l) as for the first-feeding herring larvae in Basin 1 (Fig. 3). Larval spionidae, which was the dominant organism in the zooplankton community in Basin 2 during the first 60 days of the experiment (Fig. 4), did not play an important role as food for the capelin during the first 20 days of the experiment (see Moksness, 1982).

The density of larger zooplankton organisms in Basin 1 during the experimental period is presented in Table 2. The population of calanoid copepods increased steadily until the middle of May and disappeared almost completely from 28 May (day 54) to 1 June (day 57). The *Podon* sp. population had a similar history, with a collapse some days earlier. *Tisbe ensifer* also disappeared in late May. The population of juvenile amphipods (*Gammarus* sp.) increased in May and continued to be abundant until the end of the experiment. The two dominant hydromedusae, *Sarsia* sp. and *Rathkea octopunctata,* increased rapidly in May and continued to be numerous to the end of June.

In the plastic bags the dominant zooplankton organisms were copepod nauplii and rotifera. The densities of these organisms varied from 10 to 80/l in the different plastic bags.

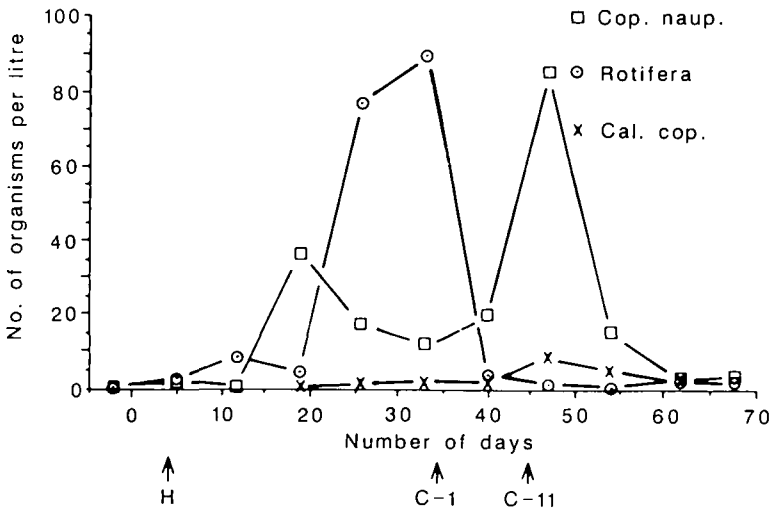

Figure 3. The overall mean density (number/l) of copepod nauplii (cop. naup.), rotifera, and calanoid copepods (cal. cop.) in Basin 1. The experimental period is given in number of days; day 0 = 4 April. Times of release are indicated by arrows. H = herring (8 April), C-I = first group of capelin (8 May), and C-II = second group of capelin (20 May).

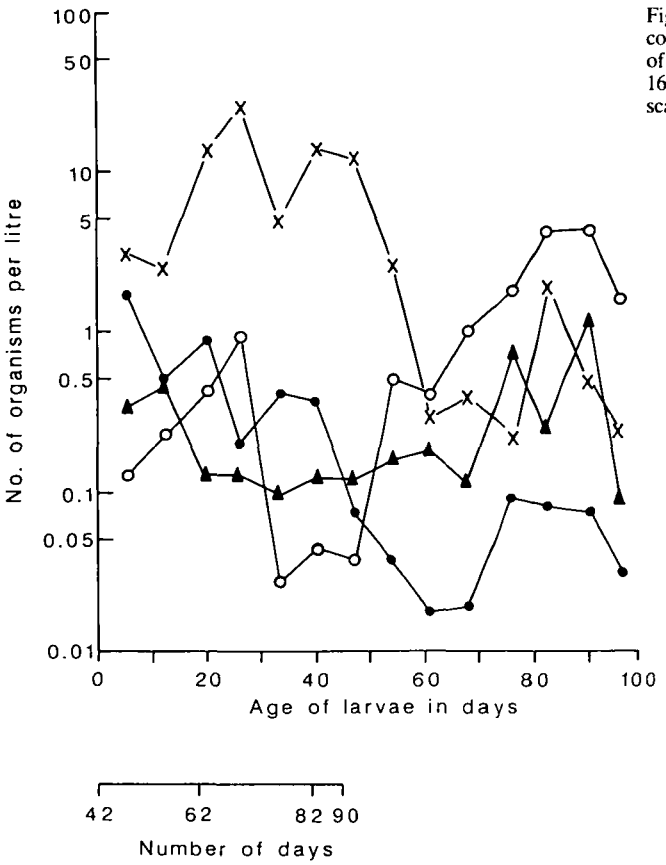

Figure 4. The overall mean density (number/l) in Basin 2 of copepod nauplii (●—●), veliger of *Littorina* (○—○), larvae of spionidae (×—×), and calanoid copepods (▲—▲) from 16 May onwards. The number of days is shown on the bottom scale (from Moksness, 1982).

Table 2. The mean density of zooplankton (number/l) in Basin 1 estimated from the catches with a 500-μm mesh size net. Highest density in italics.

Date (1979)	Number of days	Calanoid copepods[a]	*Podon* sp.[a]	*Tisbe ensifer*[a]	Amphipod juveniles	Hydromedusae[b]
14 Apr	10	3·0	0	0·3	0	2·4
19 Apr	15	10·7	0·1	0·7	0·1	2·5
23 Apr	19	19·8	0·3	1·1	0·1	4·5
26 Apr	22	31·8	1·8	0·9	0·3	3·5
30 Apr	26	44·8	2·9	2·0	0·2	7·3
3 May	29	45·7	6·0	3·3	0·8	13·0
7 May	33	39·8	33·6	1·6	2·0	13·2
10 May	36	27·8	22·4	1·9	3·5	7·7
15 May	41	*114.0*	*73·0*	2·0	7·7	35·6
21 May	47	34·7	18·2	*4·1*	29·6	55·4
24 May	50	25·5	0·3	1·0	28·3	115·7
28 May	54	22·1	2·6	0·5	*79·0*	149·6
1 Jun	57	4·8	3·7	0·3	22·1	309·3
5 Jun	61	1·6	2·5	0·2	28·5	*323·9*
8 Jun	64	0·5	5·1	[c]	22·0	100·9
11 Jun	67	0·1	1·5	0·1	23·2	103·9
18 Jun	74	0	1·5	0·2	6·6	31·5
2 Jul	90	0	13·0	0·5	13·1	0

[a]Underestimated owing to the coarse mesh size.
[b]*Sarsia* sp. and *Rathkea octopunctata*.
[c]Present at low density.

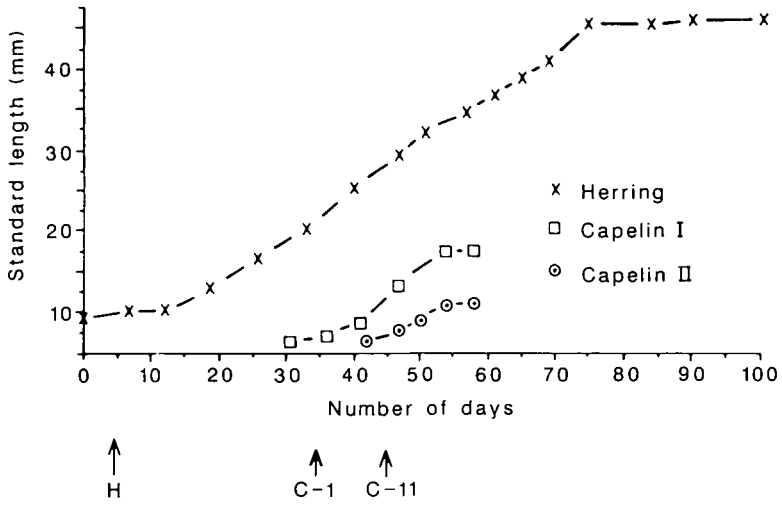

Figure 5. The mean standard length of herring and the two capelin groups in Basin 1. The experimental period is given in number of days; day 0 = 4 April. Times of release are shown by arrows. H = herring (8 April), C-I = first group of capelin (8 May), and C-II = second group of capelin (20 May).

Growth of herring and capelin larvae

The growth of the three larval groups in Basin 1 is shown in Figure 5 as mean standard length. The herring larvae had reached a length of 20 mm (age 34 days) when the first group of capelin (C-I) were released in the basin.

When the second group of capelin (C-II) were released the herring had reached a mean length of 25 mm. The herring larvae had a daily length increment of 0·25 mm till an age of 16 days, while the two capelin groups had a daily length increment of 0·39 and 0·27 mm till age 16 days, as shown in Table 3. The daily length increment in C-I varied from 0·39 to 0·43 mm and in C-II from 0·27 to 0·29 mm. Herring in the same period (age 30 to 50 days) had a daily length increment of about 0·65 mm. At an age of 50 days and a mean length of about 32 mm the herring were observed to be schooling for the first time in the basin. The metamorphosis of herring larvae took place at an age of 56 days at a standard length of 34 mm.

The control groups of C-I in plastic bags showed growth equal to that observed for C-I in Basin 1 (0·35–0·47 mm/day) (Table 3), while C-II in Basin 1 had a better growth (0·27 mm/day) than that observed for C-II in the plastic bags (0·20–0·27 mm/day). The growth of the C-II group was slightly better in Basin 1 (0·27 mm/day) than that observed in Basin 2 (0·25 mm/day) (Fig. 6).

Mortality of herring and capelin larvae

Estimates of the population size of herring and the two capelin larval groups in Basin 1 are presented in Figure 7. The herring decreased from 25000 to about 7000 within the first 30 days. At termination of the basin experiment 4400 juvenile herring were left in the basin, giving an overall survival rate of 17·6 % and a density of 1/m^3. The two groups of capelin expired before day 60 of the experiment (age 30 and 22 days, respectively). The first group of capelin (C-I) showed little mortality during the first 20 days after release, followed by a sudden decrease, while the second group of capelin (C-II) disappeared within the first 18 days following release.

The survival rates in the control groups of capelin in plastic bags are shown in Table 4. The survival of C-I in the plastic bags was 11·5 % while it was almost 100 % in Basin 1 (day 47). Although the capelin disappeared in the basin, 5·5 % survived to age 40 days in one of the plastic bags. The survival of C-II in the plastic bags was as high as 41·5 % (age 17 days), when they had dis-

Table 3. The daily length increment (mm/day) of the capelin larvae from hatching till age 17 and 25 days respectively, in the different basin and plastic bag experiments. C-I = capelin group one, C-II = capelin group two.

Capelin group	System	Daily length increment (mm/day) to age (days)					
		16	17	25	31	40	47
C-I	Basin 1	0·39	–	0·41	–	–	–
C-I	Plastic bags	0·35	–	0·47	–	0·43	–
C-II	Basin 1	0·27	–	–	–	–	–
C-II	Plastic bags	–	0·20	–	0·27	–	0·20
C-II	Basin 2	0·25	–	0·24	–	–	–

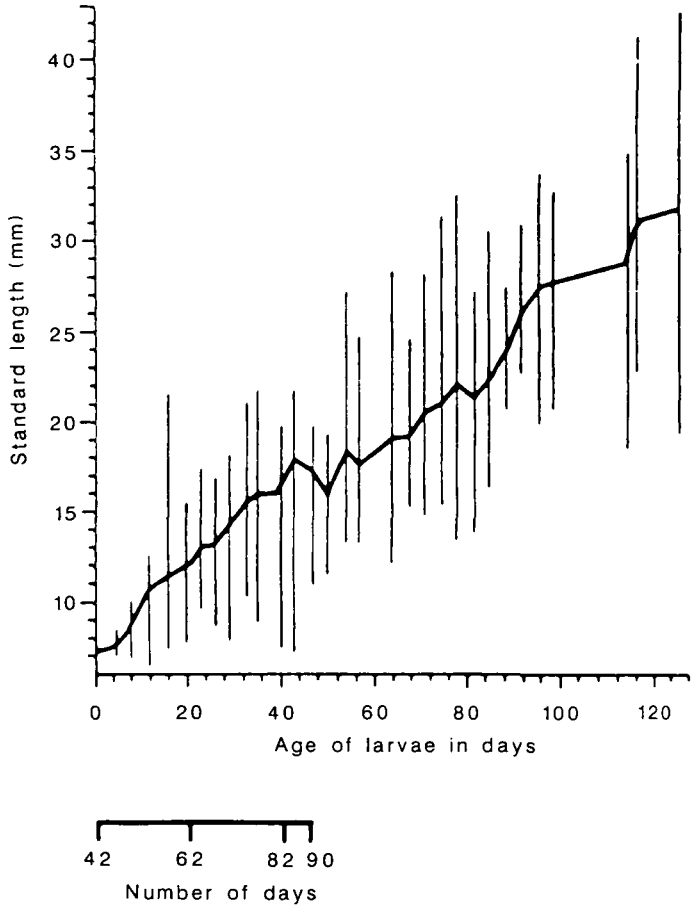

Figure 6. The mean standard length of capelin larvae in Basin 2. Vertical bars = range (N = 10257). The x-axis gives the age of the capelin larvae in Basin 2, where age 0 = 16 May. The number of days is shown on the bottom scale (from Moksness, 1982).

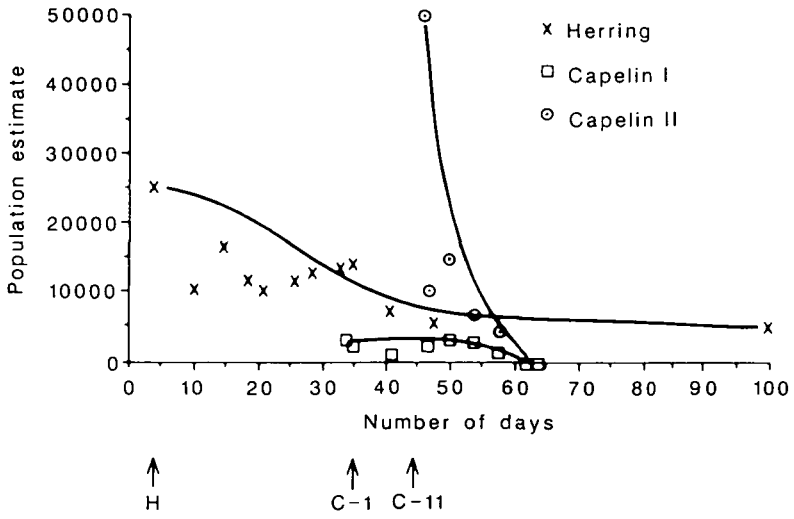

Figure 7. Population estimates of herring and the two groups of capelin in Basin 1. The number of days in the experimental period is shown on the bottom scale. Times of release are indicated by arrows.

Table 4. Survival, in percentage, of the capelin larvae in groups C-I and C-II, in the 18 plastic bag experiments.

Date (1979)	Capelin group	Number of days	Age of larvae in days	Survival (%)		
				Bag 1	Bag 2	Bag 3
21 May	C-I	47	16	11·5	10·0	6·0
30 May	C-I	56	25	2·5	2·5	2·0
14 Jun	C-I	71	40	0·5	1·0	5·5
2 Jun	C-II	59	17	22·0	41·5	40·0
16 Jun	C-II	73	31	10·5	13·5	30·5
2 Jul	C-II	89	47	0·0	0·5	4·0

appeared in the basin (day 59), and even at age 31 days a survival of 30·5 % was observed in one of the plastic bags. Figure 8 shows the population estimates of the control group of C-II in Basin 2. High mortality was observed between age 20 (day 62) and 35 days (day 77), but 2 % survived to the end of the experiment, when the capelin juveniles were 128 days old, at a density of 1/m^3.

Laboratory experiment

The newly hatched herring larvae (8–9 mm) disappeared from the tank within 3–4 days even when a high density of zooplankton was present as alternative food for the herring juveniles (25–30 mm). When the zooplankton concentration in the tank was reduced to a low level the herring larvae (8–9 mm) disappeared within 24 h. The control groups of starving herring (8–9 mm) survived to an age of about 25 days. Stomach contents were investigated in some juvenile herring, but no larval herring were identified.

Discussion

The main spawning area of herring lies to the south of the spawning area of capelin. Hatching of herring takes place from 40 to 60 days before the hatching of capelin. The herring larvae drift northwards with the coastal current, and thus the distribution of herring larvae in June/July partially overlaps that of capelin larvae, as shown in Figure 9. In a study of the recruitment of the Barents Sea capelin, Gjøsæter (1972) concluded that there is a connection between eastern spawning and strong year classes. Hamre's (1984) suggestion, referred

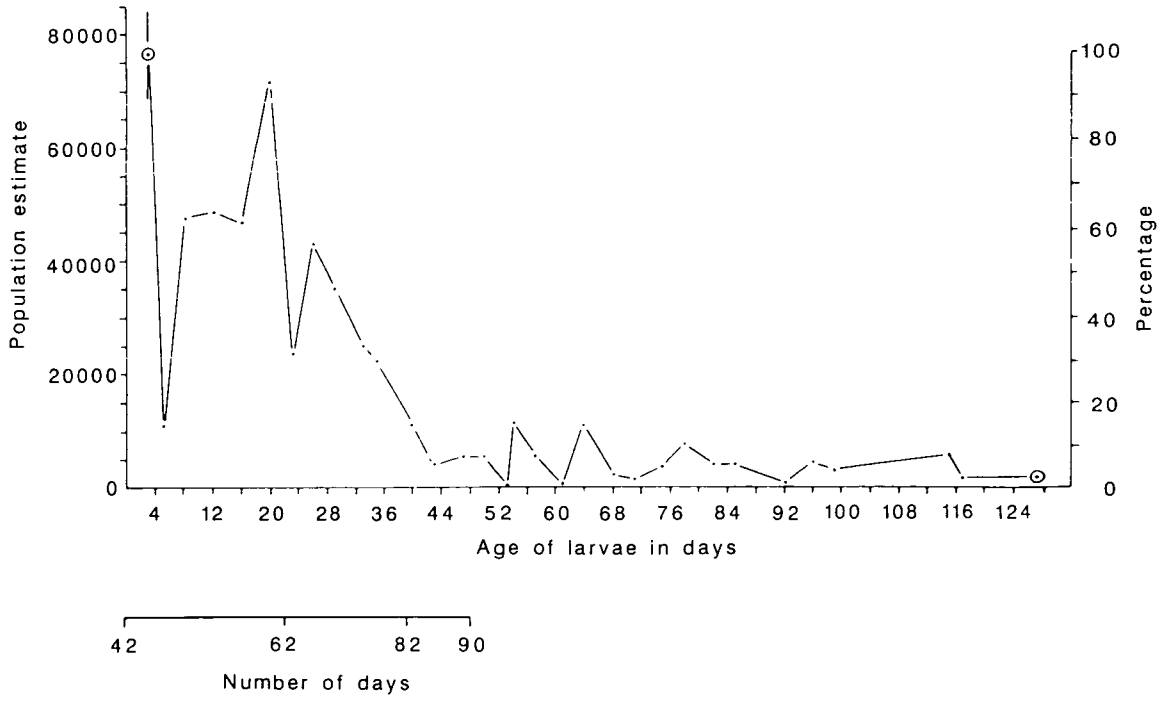

Figure 8. Population estimates of capelin larvae in Basin 2 against the age of the second group of capelin larvae. The number of days is shown on the bottom scale (from Moksness, 1982).

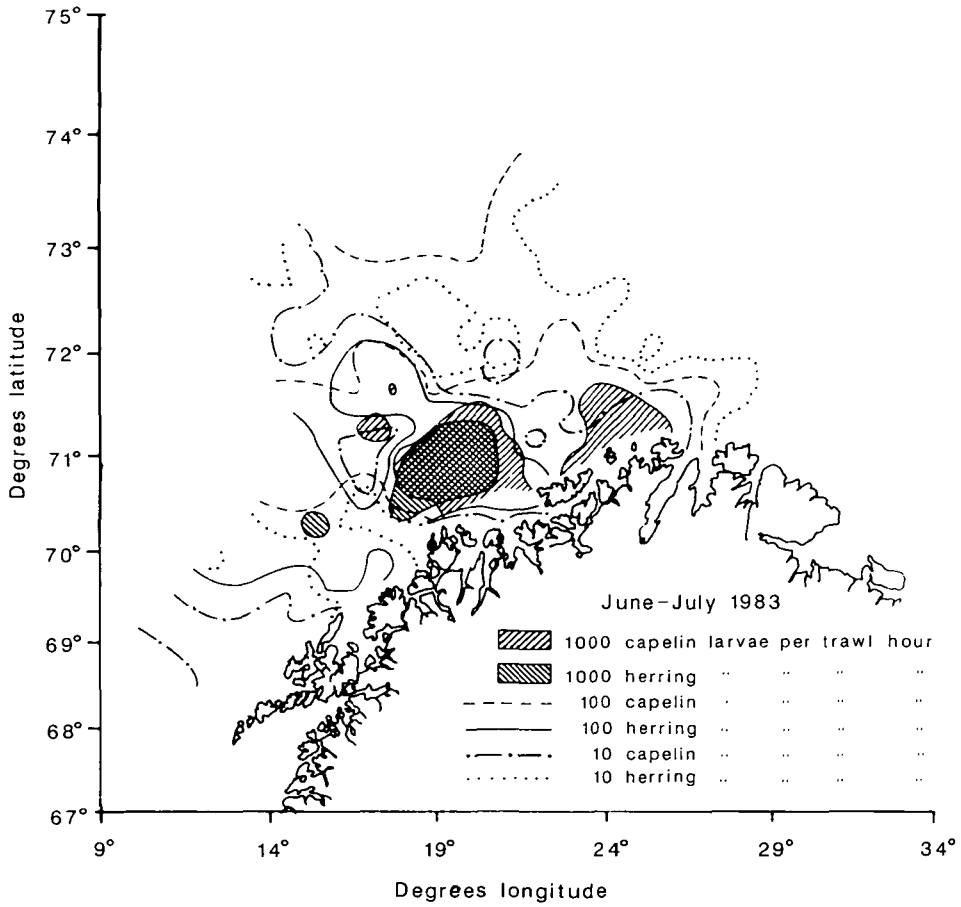

Figure 9. The geographical distribution of herring and capelin larvae off the coast of Finnmark in June 1983. (Björke, Institute of Marine Research, Bergen. Unpubl. data).

to earlier, is that there is a relationship between the recruitment of Atlanto-Scandian herring and Barents Sea capelin, where a high recruitment of herring results in a low recruitment of capelin. Both authors might be right in that when capelin have a western spawning their larvae have a greater possibility of being in the same water masses as the herring, while with an eastern spawning the capelin and the herring larvae are likely to be in two different areas.

In the present experiments herring and capelin larvae were brought together in a 4400-m^3 basin (Basin 1). The two groups of capelin in Basin 1 died out at the same time at an age of 30 and 22 days, respectively. This sudden and complete mortality was not observed in the control groups (plastic bags and Basin 2), where capelin larvae of both groups survived until the end of the experiments. The hydrographic conditions (temperature, salinity, and oxygen) in both basins and in the plastic bags were almost identical in all experiments, and the species did well at the rather high temperatures.

The densities of prey organisms in Basin 1 were more than 10 times higher than those observed in Basin 2 (Figs. 3 and 4) during first feeding of the capelin larvae. A higher observed growth rate was expected in Basin 1 owing to the higher densities of prey organisms (Table 3). The first group also had a very high survival to age 20 days, far higher than in the parallel plastic bags. For the second group the survival was higher in the plastic bags although the growth rate was lower. The high numbers of some of the larger zooplankton organisms, such as amphipods and hydromedusae, observed in Basin 1 at the time the two capelin groups disappeared, could have influenced the survival rate of capelin. However, these organisms could not cause a total mortality of the larvae within the short time observed. In other basin experiments it has been observed that hydromedusae might be a heavy predator on fish larvae, but the densities of hydromedusae in those experiments were from 200 to 1500/m^3 (Øiestad, 1985). Besides, the C-I larvae, being 17 mm long, were too big to be an easy prey for the hydromedusae.

The first-feeding herring larvae met poor feeding conditions (below 5 organisms/l), resulting in a daily length increment of 0·25 mm over the first 16 days and a reduction of the numbers of herring to about 50 % over the first 14 days after release. When the first schooling of

herring was observed at an age of 50 days (24 May; mean length 31 mm), the corresponding age and length of the two capelin groups were 18 days, 13·3 mm, and 8 days, 7·3 mm, respectively. Schooling of herring was observed frequently from then onwards, and the herring schools exploited the total water column. During this period the herring larvae were very efficient predators, and the mesozooplankton was greatly reduced during the following two weeks. During the same period the two capelin groups disappeared.

Capelin larvae were not found in the stomachs of the herring, either in samples from the basin or in the laboratory. This does not, however, mean that the disappearance of capelin in the basin was not due to predation by herring. Larval fish generally do not have hard structures and are rapidly digested, although Theilacker *et al.* (1986) have recently published a method using immunoassay for detecting yolk-sac larvae in the gut of other fish, which offers a powerful new technique for the future. Moreover, the laboratory experiments clearly showed that schooling herring of equivalent size can prey upon larvae similar to capelin, especially when their zooplankton food is scarce. Again, in a basin experiment with Pacific herring in 1986 (Wespestad and Moksness, in prep.), 30-mm metamorphosed herring were observed attacking smaller herring, and stomach analyses showed that 30-mm herring had indeed eaten herring of about 20-mm in length.

Although we lack direct evidence of predation in the form of stomach contents we think that the evidence resulting from the control experiments using plastic bags, the laboratory observations, and the consumption of herring by herring in recent experiments, offer strong circumstantial evidence that herring can be a predator on other species of larval fish and quite likely caused the demise of the capelin that coinhabited the basin. It is also noteworthy that in Basin 1, both crops of capelin and zooplankton were reduced at the same time, indicating that both were preyed upon at the same time.

During the last five years the recruitment of Norwegian spring-spawning herring has improved, and the 1983 year class in particular has been estimated as a very strong one, while the 1984 year class was estimated as above average relative to the 1970s (Anon., 1985). The recruitment of capelin in the same two years was poor, especially in 1983 (Anon., 1985). A cruise in April/May 1985 confirmed that the 1983 year class of adult capelin was very poor (S. Tjelmeland, Institute of Marine Research, Bergen; pers. comm.). Yet the larval indices for the 1983 and 1984 year classes of capelin were as high as for the previous strong year classes (Alvheim, 1984). These observations are consistent with the hypothesis that if herring and capelin are distributed in the same water masses, the schooling 0-group herring prey on the capelin larvae, and that if the year class of herring is a strong one the subsequent recruitment of capelin is reduced.

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References

Alvheim, O. 1984. Investigations on capelin larvae off northern Norway and in the Barents Sea in 1981–1984. Joint Soviet/Norwegian Symposium, Bergen, Norway, August 1984.

Anon. 1984. Preliminary report of the International 0-Group Fish Survey in the Barents Sea and Adjacent Waters in August–September 1984. ICES CM 1984/H:36.

Anon. 1985. Report of the Working Group on Atlanto-Scandian Herring and Capelin. ICES CM 1985/Assess:4.

Bailey, K. M., and Batty, R. S. 1983. A laboratory study of predation by *Aurelia aurita* on larval herring (*Clupea harengus*): Experimental observations compared with model predictions. Mar. Biol., 72: 295–301.

Christensen, V. 1983. Predation by sand eel on herring larvae. ICES CM 1983/L:27.

Cushing, D. H. 1980. The decline of herring stocks and the gadoid outburst. J. Cons. int. Explor. Mer, 39: 70–81.

Dragesund, O., Hamre, J., and Ulltang, Ø. 1980. Biology and population dynamics of Norwegian spring-spawning herring. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 164: 15–29.

Garrod, C., and Harding, D. 1981. Predation by fish on pelagic eggs and larvae of fishes spawning in the west central North Sea in 1976. ICES CM 1981/L:11.

Gjøsæter, J. 1972. Recruitment of the Barents Sea capelin 1951–1961. ICES CM 1972/H:24.

Hamre, J. 1984. Assessment and management of Barents Sea capelin. Joint Soviet/Norwegian Symposium, Bergen, Norway, August 1984.

Methot, R. D. Jr., and Kramer, D. 1979. Growth of northern anchovy (*Engraulis mordax*) larvae in the sea. Fish. Bull. U.S., 77: 413–423.

Moksness, E. 1982. Food uptake, growth and survival of capelin larvae (*Mallotus villosus* Müller) in an outdoor constructed basin. Fisk. Dir. Skr., Ser. Havunders., 17: 267–285.

O'Connell, C. P. 1980. Percentage of starving northern anchovy (*Engraulis mordax*) larvae in the sea estimated by histological methods. Fish. Bull. U.S., 78: 475–489.

Øiestad, V. 1982. Application of enclosures to studies on the early life history of fishes. *In* Marine mesocosms, pp. 49–62. Ed. G. D. Grice and M. R. Reeve. Springer-Verlag, New York.

Øiestad, V. 1985. Predation on fish larvae as a regulatory force, illustrated in mesocosm studies with large groups of larvae. NAFO Sci. Coun. Studies, 8: 25–32.

Øiestad, V., and Moksness, E. 1981. Study of growth and survival of herring larvae (*Clupea harengus* L.) using plastic bag and concrete enclosure methods combined. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 178: 144–149.

Olsen, S. 1968. Some results of the Norwegian capelin investigations 1960–1970. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 158: 18–23.

Sissenwine, M. P. 1984. Why do fish populations vary? *In* Exploitation of marine communities, pp. 59–94. Ed. by R. M. May. Springer-Verlag, New York.

Slinning, A. E. 1976. Undersøkelser på kondisjonsfaktoren og lengde–vekt forholdet hos loddelarver ved kysten av Nord-

Norge i tiden Mai–Juni, 1971 og 1973. Thesis. Univ. of Bergen, Norway, 1976. 91 pp.
Theilacker, G. H., Kimball, A. S., and Trimmer, J. S. 1986. Use of an ELISPOT immunoassay to detect euphausiid predation on larval anchovy. Mar. Ecol. Prog., Ser. 30: 127–131.
Wiborg, K. F. 1961. Forekomst av egg og yngel av fish i vest- og nord-norske kyst- og bankfarvann våren 1960. Fiskets Gang, 9: 190–195.
Wespestad, V., and Moksness, E. Observations of the early life history of Pacific herring (*Clupea harengus pallasii*) from Bristol Bay, Alaska, in a large basin (in prep.).