

## ECOLOGICAL INVESTIGATIONS ON THE SPAWNING GROUNDS OF THE BARENTS SEA CAPELIN

By  
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### ABSTRACT

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A programme to study the reproduction of the Barents Sea capelin was conducted by the Institute of Marine Research in Bergen during the period 1971—1974. The present paper deals with the investigations on the spawning grounds along the coast of northern Norway.

During the years of investigations the spawning started between 1 and 15 March, and there was a gradual movement of the spawning area towards north and east during the observation period. The temperature during the incubation has been 1.5 and 6.5° C. The main spawning depth appears to be between 25 and 75 m. The extremes of the spawning depth observed was 12 and 280 m.

The capelin seem to prefer rather coarse substratum as gravel or cobble for spawning. The capelin eggs are mixed with the substratum to a layer up to 15 cm thick. This burying of the eggs is caused by strong current resulting in a sediment transport along the bottom.

Both diving ducks and haddock have been observed feeding on capelin eggs. This predations is probably of little importance although the haddock may consume significant egg quantities on some of the deepest spawning grounds.

### INTRODUCTION

The Barents Sea capelin, *Mallotus villosus*, is one of the most important resources for the Norwegian fisheries. The catch was reaching a peak, 1.6 mill. tons, in 1972. The main fishery is based on the spawning stock approaching the coast of northern Norway and Murman during February—April. The spawning stock is dominated by one or two yearclasses and wide fluctuations in the spawning stock size may therefore be expected. Most of the capelin probably die after the spawning. There is also a spawning during summer and autumn but this seems to be of minor importance and very little data is available (ПРОКХОРОВ 1965).

Capelin has a circumpolar distribution and can be found in the northern regions of the Atlantic and the Pacific. The eggs are demersal

and stick to the bottom substratum. For spawning its preference with regard to depth, temperature and substratum seem to vary geographically, and the published accounts appear to be partly contradictory. Egg development takes 40—50 days at a temperature of 2.8 °C and 30 days at 5 °C (PITT 1958, POZDNJAKOV 1960).

A programme to study the reproduction of capelin was initiated by the Institute of Marine Research in 1971. This programme aimed to give a better understanding of the reproduction biology of capelin and to give data for the management of the fishery. It includes studies on the spawning influx, on the spawning grounds and on the larval drift.

Results from these studies have partly been published by BJØRKE, GJØSÆTER and SÆTRE (1972), GJØSÆTER and SÆTRE (1973), DRAGESUND, GJØSÆTER and MONSTAD (1973) and GJØSÆTER, HANSEN, SÆTRE and WESTERGAARD (1974). Some diving observations from the spawning grounds were presented by BAKKE and BJØRKE (1973) and observations on predation of capelin eggs by eiders by GJØSÆTER and SÆTRE (1975). A method for estimating the spawning stock size based on egg and larval data, and the application of this method on the Barents Sea capelin was described by GJØSÆTER and SÆTRE (1974).

The present paper sums up the results from the spawning grounds investigations.

#### BEHAVIOUR

The behaviour of capelin on the spawning grounds was observed by SCUBA divers and by using echo sounders. Echo recordings indicate that the capelin approach the spawning grounds in dense, pelagic schools (Fig. 1). These schools may contain several hundred tons. Sampling has indicated that males and females often form separate schools. As the schools reach the spawning ground, they may be recorded as settled on the bottom (Fig. 2) or as a continuous layer along the bottom as seen on the left side of Fig. 3. This is a typical spawning layer. A Petersen grab with a 0.1 m<sup>2</sup> opening caught 30 spawning capelin from such a layer. At the right side of Fig. 3 spent capelin are leaving the spawning bed.

Excluding the pelagic migratory schools, the divers observed two types of schools at the spawning grounds. The first type consisted of more or less regularly oriented capelin swimming forward or in circles (Fig. 4). The distance between the capelin was usually between 15 and 30 cm, and the size of the schools was highly variable. The schools

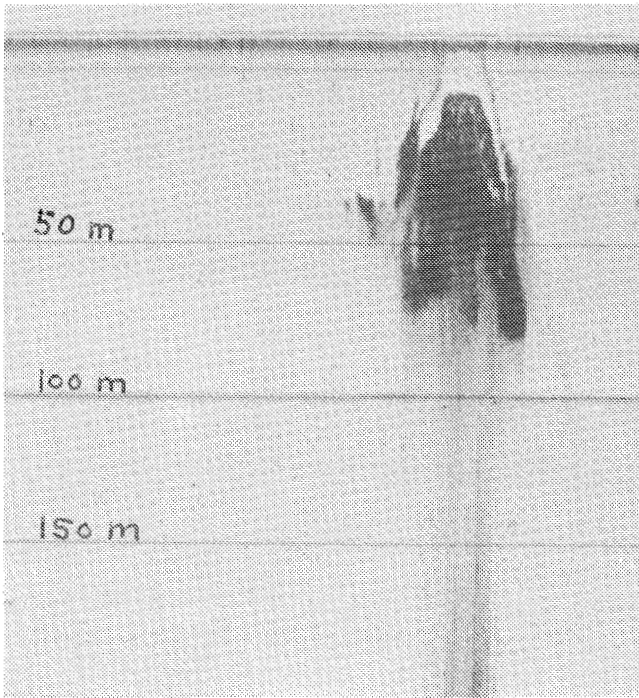


Fig. 1. Pelagic migration school of capelin.

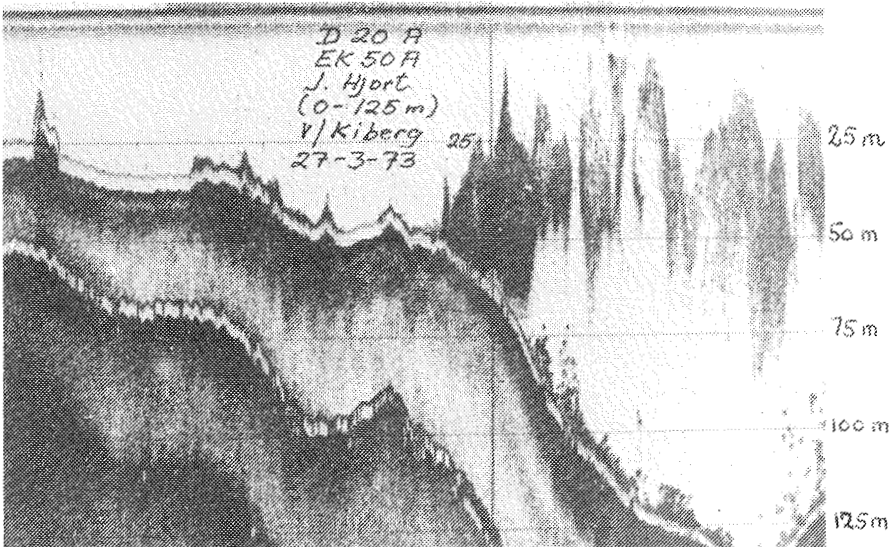


Fig. 2. Schools of capelin settling on the bottom.

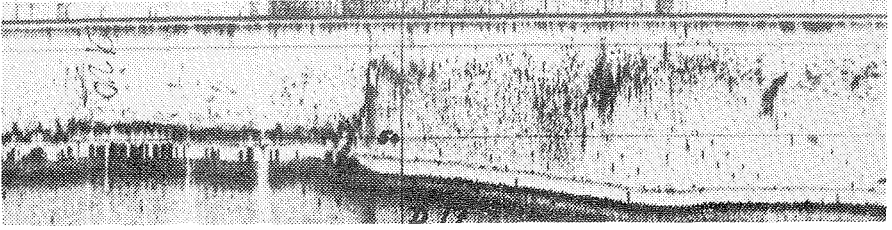


Fig. 3. Spawning capelin forming a layer along the bottom.

reacted collectively to stimuli, and they seemed to be attracted by white and shining objects. As two schools met, the capelin swam upwards in a disorderly manner but they soon gathered in separate schools again.

The second type of schools or masses was often pyramidal and consisted of irregularly oriented fish (Fig. 5). The lower part, having a diameter of about 3—5 m, was close to the bottom. The mean distance between the fishes was only 5 cm, and occasionally they were more concentrated. The activity was highest in the centre of the school.

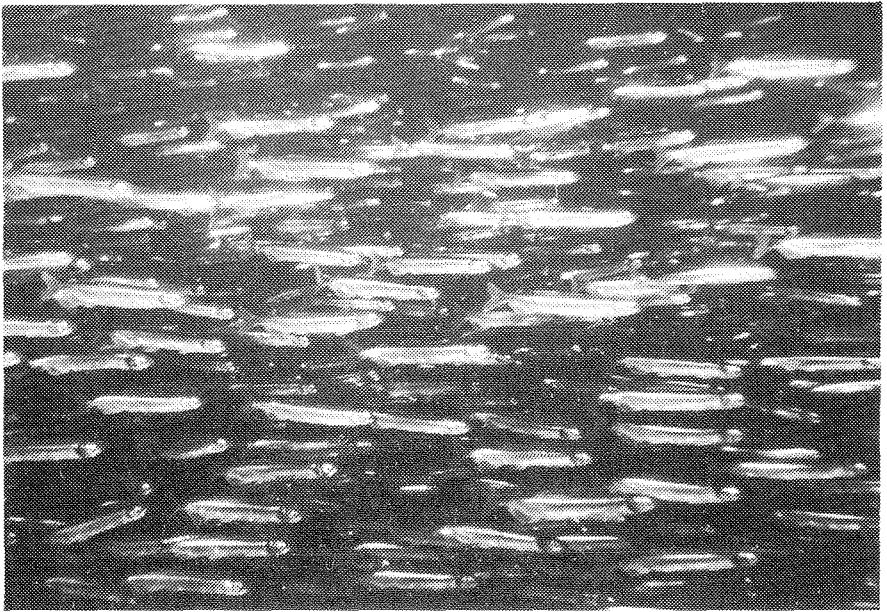


Fig. 4. School of regularly oriented capelin at the spawning ground.

Sometimes capelin from these schools were observed feeding on eggs whirled up from the bottom. Prespawning and spawning males were totally dominant in both types of schools, and females were seldom observed at the spawning grounds.

The spawning act was never observed, possibly because it mainly takes place during the night. The spawning has, however, been described for Canadian beach spawners (e.g. SLEGGs 1933). Male capelin, which had finished spawning, were occasionally observed on the spawning grounds. They seemed to be in a very bad condition. Many of these, and also the dead males found on the bottom, had a permanent deflection on the side. This malformation probably appears during the spawning act when only one male spawns with a female and has therefore to take up a strongly curved position. Spent females were very seldom observed at the spawning grounds.

The two types of schools described here probably correspond with those described by SLEGGs (1933) and BAKKE and BJØRKE (1973). Our observations indicate great variations in the swimming speed of the first type of school. These schools can probably search wide areas to find suitable spawning beds. Both our observations and those of BAKKE and BJØRKE (1973) agree that the schools reacted collectively to stimuli.



Fig. 5. Pyramidal school with irregularly oriented capelin.

The second type, described as «globular masses» by SLEGGs (1933) and as «very dense formations» by BAKKE and BJØRKE (1973), most likely represent the last stage before spawning. These schools appeared to be rather stationary. They reacted only slightly to the presence of divers, and this reaction was individual and not common for the whole school.

#### LOCATION AND TIME OF THE SPAWNING

The spawning grounds were located by a combination of the following methods:

- A) Monitoring the migration of the maturing capelin by echo surveys.
- B) Following the development of the fishery and reports from the fishermen.
- C) Analysing the stomach contents of demersal fishes (e.g. haddock).
- D) Recording concentrations of diving ducks.
- E) Sampling with a 0.1 m<sup>2</sup> Petersens grab.
- F) SCUBA diving.

Methods A to D were used for limitation of the most likely spawning areas and methods E and F for confirmation and detail surveying. To confirm that alle the important spawning grounds had been found, the data from the larval surveys (GJØSÆTER and SÆTRE, unpublished) were consulted.

Eggs, naturally spawned and artificially fertilized, were placed onboard in incubators for hatching at different temperatures. The results obtained, made it possible to calculate the age of the eggs (GJØSÆTER, unpublished). Based on this, the time of spawning was estimated.

Fig. 6 shows the observed spawning grounds during the period 1971—1974. In 1971 the larval distribution indicates that some spawning also occurred farther south. This year concentrations of capelin were located as far south as Vesterålen which is the most southerly area of capelin catches during the last two decades (DRAGESUND *et al.* 1973). For the remaining years all major spawning localities are assumed to be included. These are always situated at the outer part of the coast.

There seems to be a gradual movement of the spawning area towards north and east during the observation period. Except for the years 1938—1942 and 1962 the capelin has been an unfailing guest along the coast of northern Norway for at least the last hundred years (MØLLER og OLSEN 1962, OLSEN 1968). The Vardø—Kiberg area seems to be the most regular spawning locality. Spawning west and south of Loppa is considerably less frequent.

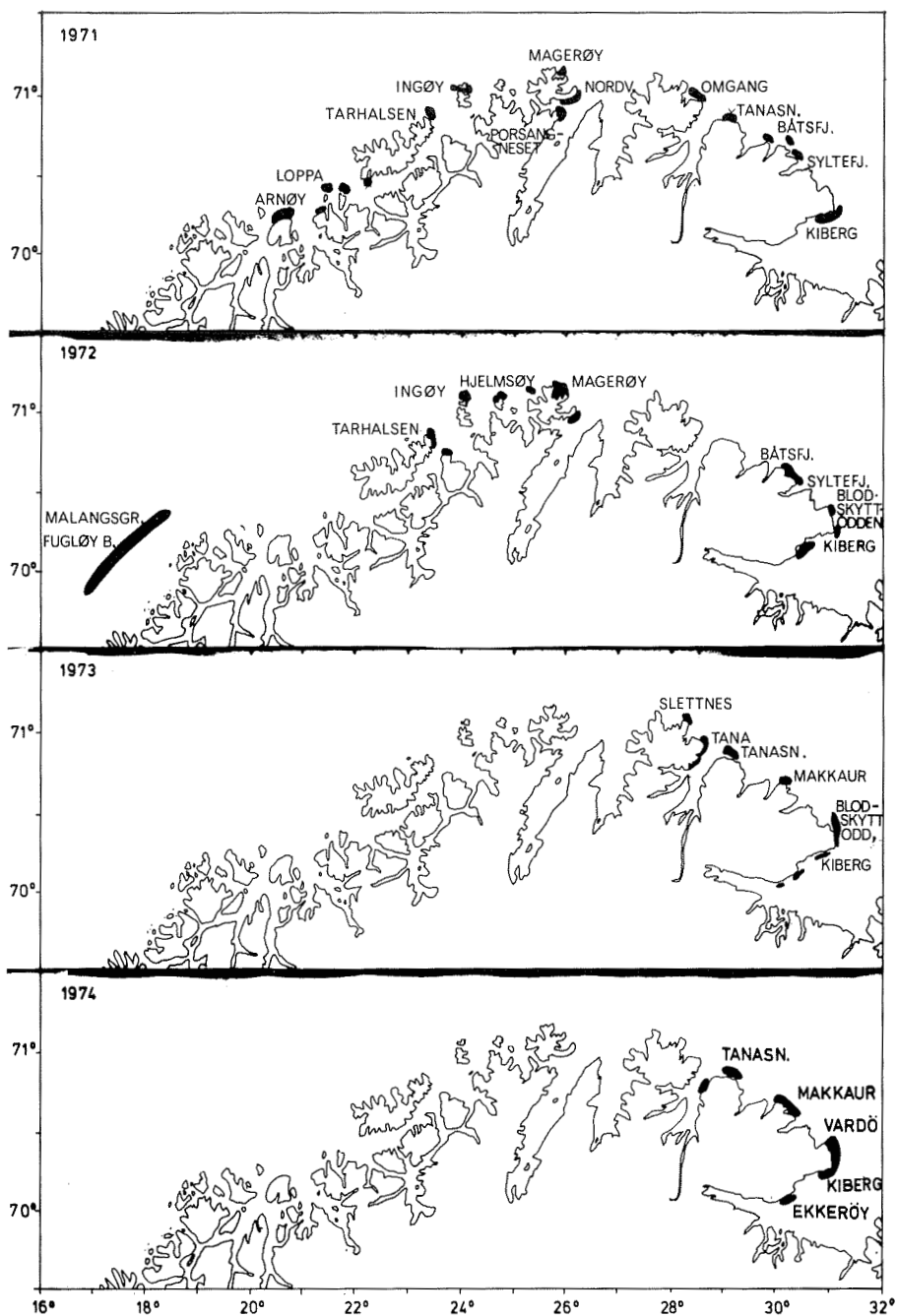


Fig. 6. Location of the observed spawning grounds.

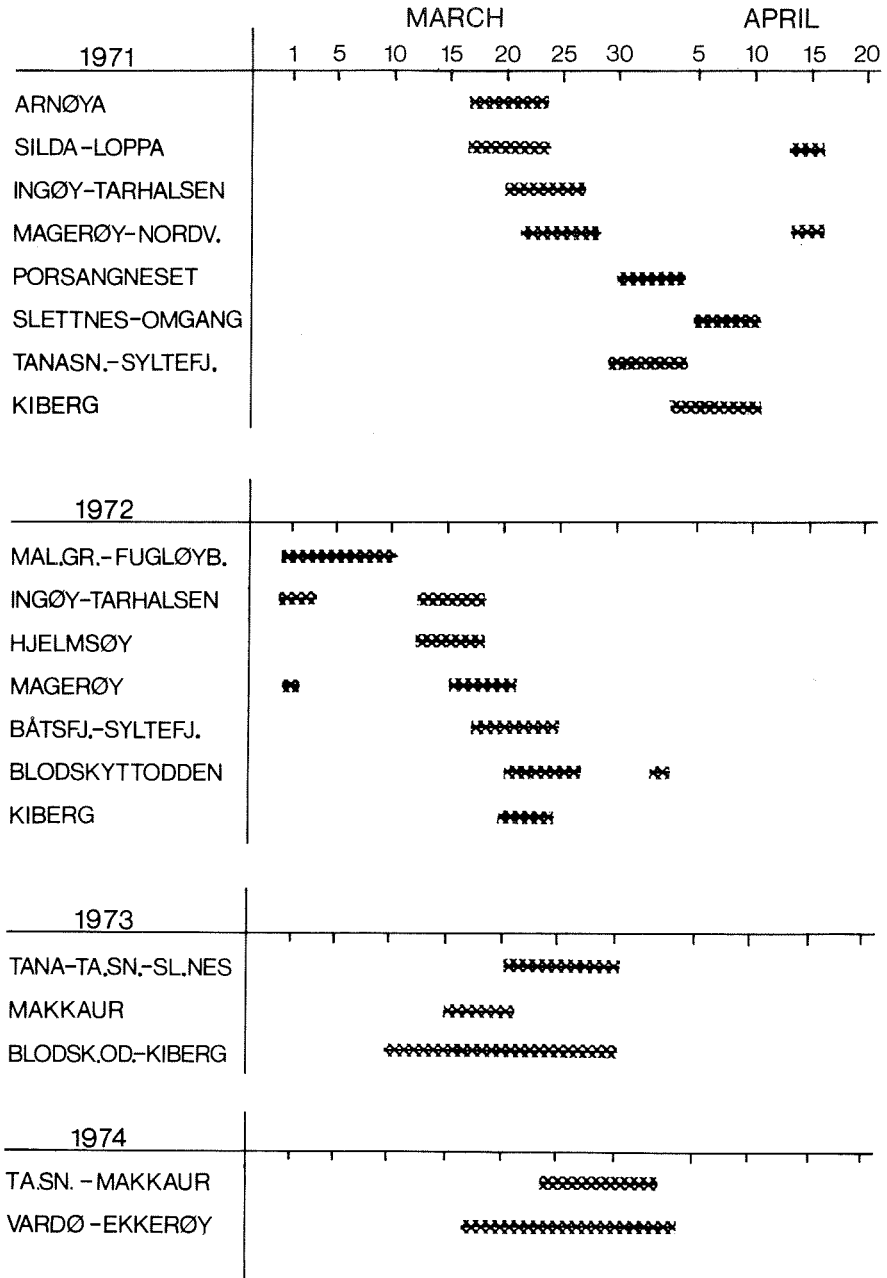


Fig. 7. Time and duration of the spawning.



Fig. 7 shows the time and duration of the spawning for the years 1971—1974. Usually there are several separate spawning runs at the different localities. The year 1971 appears to be somewhat anomalous in that respect. Mature capelin approached the coast in the Ingøy—Magerøy area continuously during February and March and proceeded farther west and south along the coast. (DRAGESUND *et al.* 1973). This may be due to spawning stock size which in 1971 was at a very high level. In the eastern part of the spawning area at Vardø—Kiberg only small concentrations of capelin were recorded. The spawning started in the southernmost area in the middle of March.

In 1972 two separate influxes occurred. The westernmost influx approached the coast in the Ingøy—Magerøy area from the north at the end of January. The capelin moved south and west along a route approximately 20 nautical miles from the coast (BLINDHEIM og MONSTAD 1972). The spawning started at the Fugløybank and Malangsrunden in the beginning of March. In the middle of March a second influx reached the surroundings of Vardø. This part of the spawning stock moved westward.

In 1973 the capelin influx followed the coast of Murman and reached Vardø at the end of February (JACOBSEN og NAKKEN 1973). The spawning started in this area about 10 March.

Three independent spawning runs were present in 1974. The first one approached Omgang from the north and turned eastwards along the coast. The second influx reached Vardø from the northeast, and the third followed the coast of Murman towards Kiberg (ANON. 1974). The spawning started in the Vardø—Kiberg area about 15 March.

During the last century the first spawning run has reached the Norwegian coast between the beginning of February and the end of April. An early arrival of the capelin appears to be associated with a westerly distribution (OLSEN 1968, GJØSÆTER 1972).

#### HYDROGRAPHIC CONDITIONS

The bottom temperature and salinity were measured throughout the whole incubation time. Current measurements with recording instruments of the Aanderaa type were carried out close to the sea floor at several spawning beds.

Table 1 shows the hydrographic conditions during the spawning seasons 1971—1974. The lowest temperature during the time of incubation was recorded in 1971 when the capelin started to spawn in water of 1.5°C. The high upper limit in 1972 is due to the spawning in more oceanic water masses at the Malangsrunden and the Fugløybank. The salinity

Table 1. Hydrographic conditions during the spawning seasons 1971—1974.

Year	t °C during incubation	S ‰ during incubation	t <sub>100</sub> Ingøy	S <sub>100</sub> Ingøy	Temperature anomaly	
					Loppa	Vardø
1971 . . . . .	1.5°—3.5°	34.1—34.4	3.72°	34.470	—1.0°	—0.9°
1972 . . . . .	2.5°—6.5°	34.1—34.6	4.85°	34.560	+0.5°	+0.7°
1973 . . . . .	2.0°—4.0°	34.4—34.6	4.82°	34.658	+0.8°	+0.9°
1974 . . . . .	2.5°—4.0°	34.4—34.6	4.59°	34.651	+0.2°	+0.6°

at the spawning beds during the period 1971—1974 has been between 34.1 and 34.6‰ which is about the normal salinity for the coastal waters along northern Norway.

Table 1 also shows the mean temperature and salinity for the upper 100 m at a fixed oceanographic station off Ingøy during March—April and the temperature deviations from the normal 1936—1970 for the surface layer at Loppa and at Vardø (SÆTRE 1973). It is quite obvious that 1971 is characterized by a small influence of Atlantic water masses along the coast of northern Norway and 1973 as the year of the most marked Atlantic influence.

Previous observations of the spawning temperature of the Barents Sea capelin are rather few. RASS (1933) reports spawning in about 2 °C, and OLSEN (1968) observed spawning in temperature between 2.5 and 5 °C. Listed in Table 2 are spawning temperatures of capelin reported from other areas. It appears that the temperatures at Greenland and on the Grand Banks are very similar to those observed by the present authors.

Table 2. Temperatures in some capelin spawning areas.

Area	Spawning temperature	Author
Newfoundland, beachspawners.	5.6°—10.0°	SLEGGs 1933, TEMPLEMAN 1948
Newfoundland, Grand Banks .	2.8°—4.2°	PITT 1958
British Columbia . . . . .	10.0°—11.0°	HART and McHUGH 1944
Iceland . . . . .	6.0°—7.0°	JESPERSEN 1920, MAGNUSSON 1966
Greenland . . . . .	1.9°—6.6°	KANNEWORFF 1968

#### FLORA AND FAUNA ON THE SPAWNING GROUNDS

The macro flora on the spawning beds included some dispersed *Laminaria digitata*. Various corallinaceae and other red algae were also found. Some eggs were overgrown with small filamentous colonies of diatomea. This occurred only at depths between 10 and 30 m and only

Table 3. Some animals from the spawning grounds.

Phylum	
Porifera . . . . .	Various species
Cnidaria . . . . .	Various thecaphore hydroida
Plathyhelminthes.	Turbellaria
Nemertini . . . . .	Various species
Aschelminthes .	Various nonparasitic nematoda
Arthropoda . . . .	Ostracoda
	Copepoda, mainly harpacticoida
	Cirripectida
	Cumacea
	Amphipoda
	Mycidacea
	Decapoda, e.g. <i>Hyas</i> , <i>Pagurus</i> .
Mollusca . . . . .	Polyplacophora
	Gastropoda
	Bivalvia, e.g. <i>Cyprina</i> , <i>Clamys</i> , <i>Modiolus</i>
Annelida . . . . .	Polychaeta
Ectoprocta . . . .	Many species
Brachiopoda . . .	Various species
Echinodermata .	Asteroidea, e.g. <i>Asterias</i>
	Ophiuroidea
	Echinoidea, e.g. <i>Strongylocentrotus</i> , <i>Spataugus</i>
	Holothuroidea
Chordata . . . . .	Pisces: <i>Gadus morhua</i> , <i>Melanogrammus aeglefinus</i> , <i>Pollachius virens</i> , <i>Ammodytes sp.</i> , <i>Anarhichas lupus</i> , <i>Pleuronectes platessa</i> .

on eggs lying on the top of the substratum. Laboratory experiments suggested that these algae had no noticeable effect on the development of the eggs.

The fauna on the spawning grounds was usually sparse and the total biomass very low. No systematic collection was carried out, but some taxa, commonly observed in grab samples or by divers, are listed in Table 3. None of the invertebrates seemed to feed noticeably on eggs or significantly alternate their environment.

#### DEPTH AND SUBSTRATUM OF THE SPAWNING

After the location of the spawning grounds, some of the spawning beds were selected for a more detailed investigation. A Decca map in the scale of 1:5000 or 1:10000 was constructed covering the selected spawning bed. The Decca Navigator System has a high resolution in coastal waters and thus make it possible to navigate with a high relative accuracy. A detailed surveying of the spawning bed was performed using grab and SCUBA divers. The divers were equipped with sampling tubes

0 NO EGGS

1 LESS THAN 10 EGGS

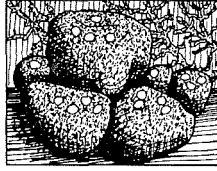
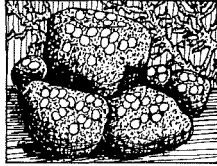
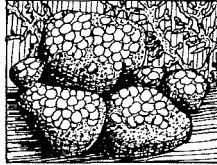
2 SOME EGGS ON  
SUBSTRATA3 SUBSTRATA  
PARTLY COVERED4 SUBSTRATA  
DENSELY COVERED

Fig. 8. Scale for classification of egg quantity.

which enabled them to take samples where the stratification of the bottom substratum was undisturbed. The divers also filmed and photographed on the spawning beds.

The amount of eggs in the grab samples were subjectively classified from 0 to 4 according to the scale shown in Fig. 8. No eggs in the sample were denoted 0 and the highest densities of eggs designated 4. The decisive factor for the classification was the ratio between number of eggs and the quantity of bottom substratum in the sample. The order of size of the egg densities corresponding to the different egg quantities appears in Table 4.

Table 4. Corresponding values of egg quantities and egg densities.

Egg quantity	Egg density eggs/m <sup>2</sup>
0 .....	None
1 .....	10 <sup>1</sup> —10 <sup>3</sup>
2 .....	10 <sup>3</sup> —10 <sup>5</sup>
3 .....	10 <sup>5</sup> —10 <sup>6</sup>
4 .....	10 <sup>6</sup> —10 <sup>7</sup>

The size distribution of the sediment aggregates was classified according to the Wentworth scale (WENTWORTH 1922). This scale is a geometrical one using the particle diameter in mm raised to the powers of 2 as steps between successive elements of the series. KRUMBEIN (1936) used the exponents, that is, the powers of 2 in the Wentworth series as the basis for a logarithmic scale of sediment size. He defined a unit,  $\Phi$ , as the negative logarithm to the base of 2 of the particle diameter in millimeters,  $\Phi = -\log_2 D$ . The logarithmical scale is chosen as most of the physical properties of a sediment are found to vary as some power of sediment size rather than directly with size.

Table 5. Depth distribution of egg quantity 0—4 in grab samples 1971—1974.

Depth in m	Egg quantity					Sum
	0	1	2	3	4	
0—24.....	221	83	32	16	15	367
25—49.....	820	171	100	52	33	1 176
50—74.....	387	69	31	5	5	497
75—99.....	170	16	9	4	1	200
100—124.....	78	5			1	84
125—149.....	51	2	1			54
150—174.....	23	3				26
175—199.....	22	1				23
200—224.....	6	1	1			8
225—249.....	2		1			3
250—350.....	9	1				10
Sum .....	1 789	352	175	77	55	2 448

Table 5 shows the distribution of egg quantities 0—4 at different depths for all the grab samples during the period 1971—1974. Fewer high egg densities are found (i.e. egg quantity 3 and 4) as the depth of the grab samples is increased. In 0—24 m 8.4% of the samples contained egg quantity 3 or 4, in 25—49 m 7.2% and in 50—74 m about 2%. The most shallow spawning bed observed is Nordvågen in 1971 with depths between 12 and 18 m. The deepest sample containing capelin eggs is from 280 m off Vardø in 1973. The samples from the deeper parts are few and the probability of getting a correct sample will decrease with increasing sampling depth. Although the sampling design makes the data unsuitable for statistical treatment they still indicate that the main spawning take place in the upper 75 m.

Information concerning the depth of spawning of the Barents Sea capelin is rather divergent. The suggestions that appear to be in best accordance with our observations are those by RASS (1933) (50—100m) and MOLLER and OLSEN (1962) (10—100 m).

Along the coast of Newfoundland and Labrador the beach spawning is often succeeded by spawning at increasing depth down to at least 55 m (TEMPLEMAN 1948). PITT (1958) reported indications of spawning on the Grand Banks at depths between 46 and 80 m.

The capelin eggs observed by us in the deepest samples may have been spawned at this depth or they may have been transported there from shallower spawning beds. Bottom trawl used at about 250 m depth several times caught haddock with a stomach content of recently swallowed fertilized capelin eggs. This supports the first explanation. Though the main spawning occurs in the upper 100 m, the Barents Sea capelin seems to be able to spawn down to at least 250 m.

Table 6. Distribution of egg quantity 0—4 at different substrata in grab samples 1971—1974.

Substrata	Egg quantity					Sum
	0	1	2	3	4	
Pebble-gravel .....	129	39	29	19	27	243
Shell gravel .....	387	71	55	29	15	557
Hard bottom-cobble ...	1 036	192	62	23	12	1 325
Mineral sand .....	144	47	27	6	1	225
Silt-Clay .....	93	3	2			98
Sum .....	1 789	352	175	77	55	2 448

In Table 6 is listed the distribution of egg quantities 0—4 at different substrata. The table shows that gravel or pebbles is the most preferred substratum for spawning. About 19% of the samples from this bottom material contained egg quantity 3 or 4. Shell gravel also occurs as a spawning substratum. About 8% of these samples were classified as egg quantity 3 or 4. At hard bottom and mineral sand between 2.5% and 3% of the grab samples contained egg quantity 3 or 4. Eggs were rarely observed on silt and clay.

Fig. 9 shows a typical size distribution of pebble substratum at Blodskyttodden. The size frequency distribution is represented by a cumulative percent curve of weight. The median  $M_d$ , which is the diameter size at 50% of the cumulative frequency curve, amounts to 8.25 mm. TRASK (1932) defined a sorting coefficient as  $S = V \frac{Q_3}{Q_1}$  where  $Q_1$  and  $Q_3$  are the diameter in millimeters corresponding to the 25th and 75th percentiles, respectively, of the cumulative curve.  $S$  in the distribution shown in Fig. 9 is 1.55 which indicates a well sorted sediment.

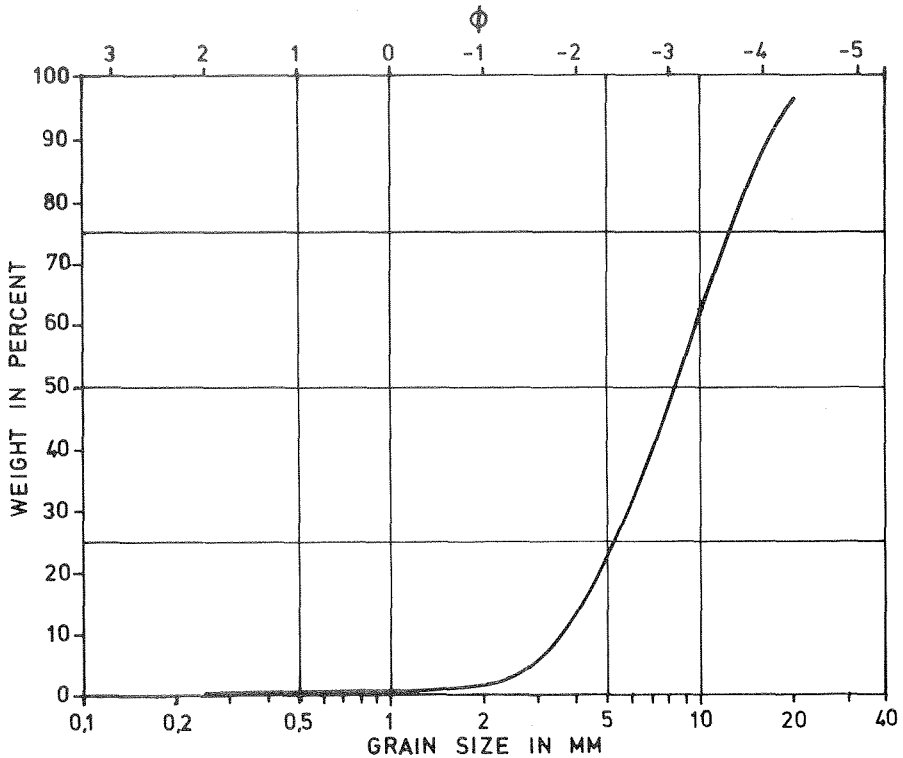


Fig. 9. Typical grain size distribution of pebble substratum from a spawning bed. For explanation see text.

The median of the pebble or gravel substratum where spawning occurred varied between 5 and 15 mm and the sorting coefficient between 1.3 and 1.6. On cobble spawning was observed on substratum up to a size of 60 mm in diameter.

The capelin seem to prefer rather coarse material for spawning. SLEGGs (1933) states that the Newfoundland beach spawning capelin prefer to spawn on gravel beach. TEMPLEMAN (1948) confirms this and observed a grain size from 2.5 to 15 mm to be especially favourable for spawning. For the deeper spawning grounds PITT (1958) reports spawning at a grain size from 0.5 to 2.2 mm at Grand Bank. PROKHOROV (1965) also believes the spawning of the Barents Sea capelin to take place on sandy grounds with shell fragments. The observations of the last two authors are based on recordings of the stomach content of haddock and capelin where swallowed substratum particles were found together with capelin eggs. It is not believed that this method shows representative measure of the grain size at the spawning beds. As shown in Fig. 9 the gravel or pebble substratum also contains particles belonging to the sand fraction. From our investigation it appears that the haddock selects

the eggs attached to the smallest particles (GJØSÆTER and SÆTRE, unpublished). We therefore question the statements of an offshore spawning on a sandy bottom. We have indeed observed high egg densities in grab samples consisting mainly of sand (Table 6). This seems to be due to patches of sand in a substratum of coarser materials.

#### DISTRIBUTION OF EGGS ON AND IN THE SUBSTRATUM

The methods used for these investigations are the same as those described in the section on depth and substratum of the spawning.

As indicated by Table 6, the preferred spawning substratum is gravel, pebble, shell gravel and cobble. Fig. 10 shows egg quantity 4 on gravel



Fig. 10. Eggs at gravel bottom (Egg quantity 4).



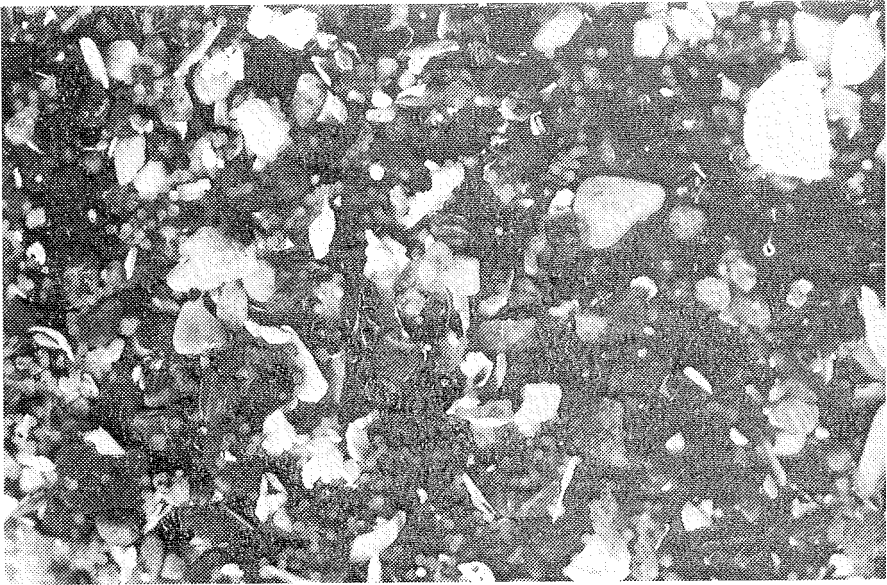


Fig. 11. Eggs at gravel bottom with shell fragments (Egg quantity 3).

bottom. A more detailed picture is shown in Fig. 11. Fig. 12 shows eggs on bottom consisting of shell gravel. A conspicuous feature of the egg distribution on these substrata is that the eggs are attached to the single particles. The layer of bottom substratum with eggs can reach a thickness of 15 cm, but 5—7 cm is the most usual.



Fig. 12. Eggs at shell gravel.



Fig. 13. Layers of eggs at cobble.

On cobble the eggs are less mixed with the substratum and more attached to each other. Fig. 13 shows eggs on such a bottom together with empty shells. Fig. 14 gives a more detailed picture of the egg distribution. The egg layer of the cobble rarely exceeds 3 cm. The egg distribution is usually homogenous within a spawning bed. An abrupt change in egg density corresponds with a transition of the bottom substratum.



Fig. 14. Eggs and fauna from hard bottom.

The capelin eggs, found in gravel and shell gravel, are mixed with the substratum to a layer up to 15 cm thick. Although the capelin may be capable of doing some active burying, they certainly are not able to bury them to this depth. On most of the gravel and shell gravel spawnings beds the SCUBA divers observed periodic undulation in the bedding plane (Fig. 16). These so-called ripple marks are commonly observed in sand, but appear to be rather seldom in coarser materials (ALLEN 1968). The ripple marks observed had a wave length of 1.0—2.0 m and an amplitude of 0.2—0.5 m. According to the classification of ALLEN (1970) they are called dunes. The gravel dunes were longcrested and usually elongated transversely to the dominant current directions. The current is the generating force of these dunes, and they will move with the water flow. Due to erosion the material on the crests is coarser than in the troughs. The lighter material, such as eggs, is accumulated in the troughs which are therefore visual as light parts in Fig. 11. Along the coast of northern Norway there is a rather strong and alternating tidal current approximately parallel to the coast. The dunes thereby will move back and forth and thus mix the eggs into the substratum.

Though the mechanism governing the formations of ripples and dunes is still not fully understood, the appearance of these is evidence of sedimentary displacement along the bottom.



Fig. 16. Ripple marks on a gravel spawning bed.

The mean egg density at egg quantity 4 is calculated within 95% confidence limits to  $4 \cdot 10^6 \pm 1 \cdot 10^6$  eggs/m<sup>2</sup>. If a fecundity of  $10^4$  eggs (GJØSÆTER and MONSTAD 1973) and a sex ratio of 1 : 1 are assumed, this will correspond to approximately 800 spawning capelin per square meter. The egg density expressed in eggs/cm<sup>3</sup> substratum, will decrease with depth in the mixture of eggs and substratum. Typical examples of vertical distributions are shown in Fig. 15.

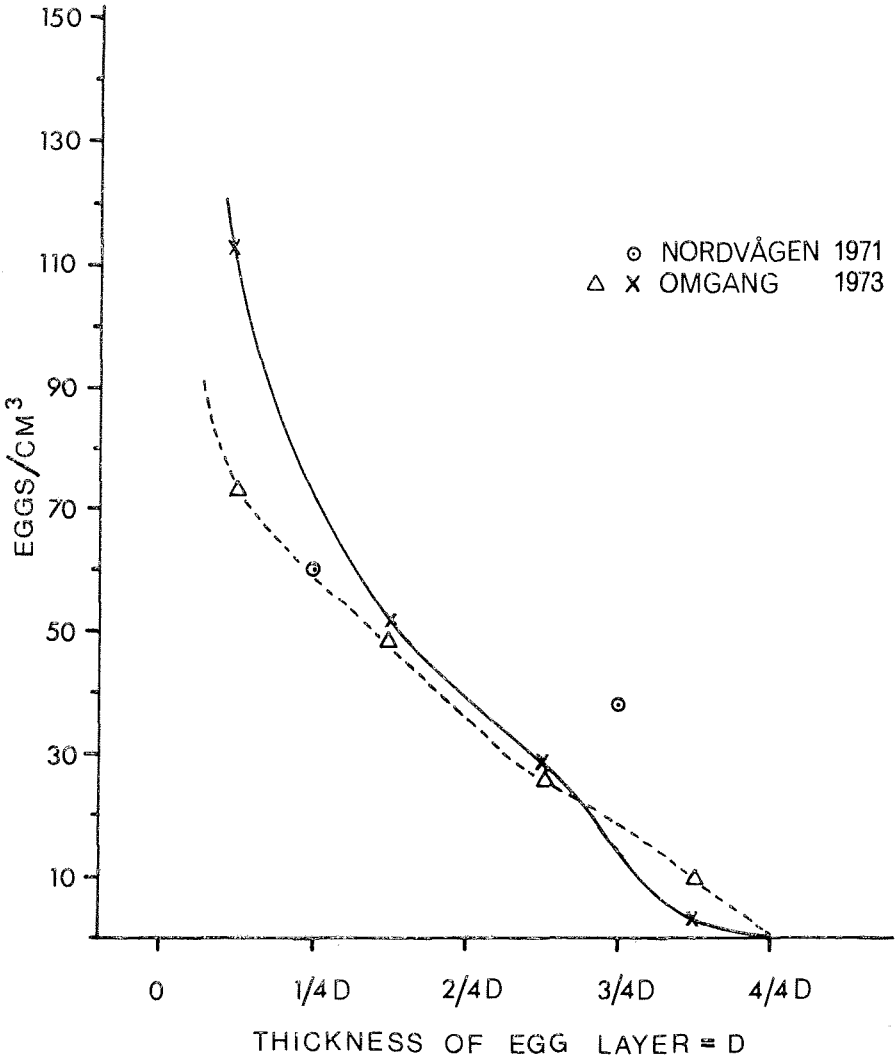


Fig. 15. Vertical distribution of eggs in the substratum.

HJULSTRØM (1939) has constructed a diagram to predict the critical conditions for the beginning of sediment movement as a function of current velocity. According to his diagram particles of size 5 mm are transported at a current of 40 cm/sec and particles of size 10 mm at 70 cm/sec. Current measurements on the spawning beds confirm that these values quite often are exceeded. It is obvious that the critical conditions for the commencement of the sediment transport cannot be deduced entirely from the grain size. The critical water velocity also varies with the excess density ( $\rho_s - \rho$ ) of the grain where  $\rho_s$  is the density of the solid grain and  $\rho$  is the density of the water. Shell fragments therefore demand a lower velocity to move than pebbles of the same size. Eggs attached to the particles will reduce their density. This effect will increase with decreasing particle size. Therefore, to move a particle covered with eggs the strength of the current will be less than that deduced by the diagram of HJULSTRØM (1939), and this discrepancy will increase as the grain size is reduced.

The eggs of the Newfoundland beach spawning capelin are also mixed with the gravel. The thickness of this mixture can exceed 30 cm (SLEGG 1933). In this case it is the wave action which is the causal factor governing the burying.

At the spawning beds with egg layers thicker than approximately 5 cm there was a retardation in the development of the eggs from the deepest layers. This retardation became more pronounced during the incubation period. This is probably due to decreased availability of oxygen in the deepest layer. However, the viability did not appear to be influenced by this.

#### EGG MORTALITY

The reduction in number of eggs at the spawning grounds can be attributed to factors as rate of fertilization, drift of eggs and predation.

The rate of fertilization seems to be very close to 100% both in natural environment and in the laboratory. Outside the main spawning beds lower rates of fertilization were sometimes observed. Very little is known about the fate of the eggs that drift away from the spawning beds. LILLELUND (1961) has, however, shown that eggs of the closely related *Osmerus eperlanus* usually survive although they drift freely in the water masses. BAKKE and BJØRKE (1973) observed a reduction in egg density on the surface of the substratum in Nordvågen in 1971, and they believed this to be due to drift of eggs. Later investigations indicate, however, that drift of eggs is usually of little significance, and the observed reduction

in egg density on the surface was probably due to the eggs being buried in the gravel.

Water from the fish pumps used onboard the fishing ships often contains large number of eggs. Samples from this water, which go back to the sea, contained fertilized eggs. These eggs had retained their ability to stick to other objects. Most of them survived till the experiment was concluded at the blastula stage.

Predation by fish is often the most significant cause of mortality in demersal eggs. The most important predator is haddock.

In 1971 spawning was mainly observed in shallow water (less than 80 m), and only an insignificant number of haddock and other fish were found at the spawning grounds.

In 1972 part of the spawning took place in deeper waters, and at spawning grounds deeper than 150 m haddock was abundant. Seventy percent of the haddock caught at Malangsgrunnen contained capelin eggs. The number of eggs in each stomach ranged between 5000 and 10 000. Saithe and cod were also observed on the spawning grounds, but they did not feed on eggs. In trawl catches in the Malangsgrunnen area there were more haddock compared to saithe and cod at stations where capelin eggs were found. The mean length of haddock was lower and the degree of filling of their stomachs higher at stations with eggs than at stations without. The material available is too sparse to decide whether the haddock, and especially the small haddock, concentrates at the spawning grounds.

In 1973 and 1974 predation by haddock was also recorded at the deeper spawning grounds, but the predation was less than in 1972. It is not possible to assess the quanta of capelin eggs consumed by haddock, but it may be a significant part of the eggs spawned in water deeper than 100—150 m.

Haddock feeding on capelin eggs have been observed both in the Barents Sea and in Canadian waters, and it is supposed to constitute an important part of the haddock's diet during the capelin spawning season (ZENKEVITZH 1963, TEMPLEMAN 1965). TEMPLEMAN (1965) observed haddock feeding on capelin eggs at spawning beds lying as shallow as 40 m.

At spawning beds shallower than approximately 50 m flocks of ducks were observed feeding on capelin eggs. In 1972 the flocks consisted of about 3/4 king eiders (*Somateria spectabilis*) and 1/4 common eider (*Somateria mollissima*) and long-tailed duck (*Clangula hyemalis*).

In 1973 and 1974 king eiders were even more dominating and long-tailed ducks very sparse.

The ducks concentrated over the spawning beds as soon as the spawning started, and they disappeared during the hatching period. Although

the ducks were numerous, calculations indicate that the quanta of eggs consumed were less than 2—3% of the total egg production (GJØSÆTER and SÆTRE 1975).

Common eiders have also been observed feeding on herring eggs (SOLEIM 1942, CANTIN, BEDARD and MILNE 1974).

Capelin have often fertilized capelin eggs in the stomach, and in 1974 the divers saw capelin feeding on eggs. This predation is, however, probably of little importance.

Table 7. Mortality of capelin eggs at different egg quantities.

Mortality %	Egg quantity				Sum
	1	2	3	4	
<5%.....	10	19	14	13	55
5<10%.....	2	10	10	8	31
10<20%.....	7	3	4	1	15
20<50%.....	6	8	—	—	15
≥50%.....	12	2	3	—	17
Sum .....	37	43	32	21	133

The percentage of dead eggs was recorded in 132 samples from various parts of the spawning area (Table 7). In general the mortality was lowest where the egg density was highest. Even where the mixture of egg and gravel was as thick as 15 cm, no vertical gradient in mortality could be observed. Many of the eggs recorded as dead were mechanically destroyed. Parts of these eggs were probably destroyed by the sampling process.

Eggs which had completed approximately 2/3 of their developmental time (embryo with pigmented eyes and capable of strong movements), showed no increase in mechanical destruction, but slightly reduced viability when trawl bobbins were towed through the spawning beds (BAKKE and BJØRKE 1973, DRAGESUND *et al.* 1973).

Laboratory experiments (unpublished) also indicate that the eggs can endure fairly strong mechanical stress. The experiments indicate, however, that the susceptibility to mortality varies with the age. It seems to be high until the closure of the blastophore, then it decreases, but it apparently increases again during the last period before hatching. Comparable development in the vitality has also been observed for other species (e.g. RILEY 1974, POMMERANZ 1974).

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