ICES J. mar. Sci., 48: 15–21. 1991

Predation on the eggs of Norwegian spring-spawning herring (*Clupea harengus* L.) on a spawning ground on the west coast of Norway

Reidar Toresen

Toresen, R. 1991. Predation on the eggs of Norwegian spring-spawning herring (*Clupea harengus* L.) on a spawning ground on the west coast of Norway. – ICES J. mar. Sci., 48: 15–21.

Predation on the eggs of demersal spawners has been reported several times, and evidence of haddock (*Melanogrammus aeglefinus*) feeding on capelin (*Mallotus villosus*) or herring eggs is a well-known phenomenon. A spawning ground where herring spawning has been observed over several years was selected as the study area, and investigations on the predation of eggs were carried out in three steps: (a) stomach sampling; (b) controlled experiments to find the rate of gastric emptying of herring eggs; and (c) bioacoustic surveys to study the distribution and abundance of predators. Haddock were found to be the main predator on eggs in the area. The total number of fertilized herring eggs being eaten in a period of 50 days was estimated to be about 2.7×10^{12}, which was about 4% of the total egg production of the herring stock spawning in this area.

Reidar Toresen: Institute of Marine Research, P.O. Box 1870, Nordnes, N–5024 Bergen, Norway.

Introduction

The main spawning grounds of the Norwegian spring-spawning herring are along the west coast of Norway, mainly on the Møre coast north of Bergen (Dragesund *et al.*, 1980). Spawning takes place at depths of 70–180 m close to the bottom, where the eggs are deposited on such substrata as rock, gravel, or sand. The spawning lasts for about 4–6 weeks, with a midpoint in the first weeks of March. The incubation time varies from 18 to 24 days depending on the ambient temperature at the sites (Blaxter and Hempel, 1963).

The eggs are preyed upon during the period before hatching. The fact that haddock eat herring eggs is a well-known phenomenon first described by Bowman (1922). Predation on eggs of other demersal spawners like capelin has been studied by Templeman (1965) on the Grand Banks off Newfoundland. Haddock has also been found to feed on the eggs of capelin in the Barents Sea (Sætre and Gjøsæter, 1975). Dragesund and Nakken (1973) showed that both haddock and saithe (*Pollachius virens*) prey on the eggs of herring off the west coast of Norway. However, it has been difficult to quantify this kind of predation. In 1978 Johannessen carried out studies on the predation of herring eggs in a small fjord basin (Lindåspollene) outside Bergen (Johannessen, 1980). Here, young cod (*Gadus morhua*) were found to be the main predator, feeding heavily on the eggs of the local herring stock.

With the exception of the 1983 year class, recruitment to the Norwegian spring-sprawning herring stock has been at a very low level in the period after the severe reduction in the abundance of this stock in the late 1960s. Predation on the eggs could be one of the factors preventing a recovery in the recruitment to this stock. Pilot studies to test this hypothesis were carried out in spring 1980, followed by main studies in 1981.

One of the most important spawning sites of herring along the Norwegian coast, the bank of Buagrunnen, was chosen as the study area (Fig. 1) and the aim of the investigations was to estimate the total amount of herring eggs being eaten during the spawning season at this locality. This was done by: (1) measuring the quantities of eggs in the stomachs of cod, haddock, and saithe to estimate the quantity of herring eggs eaten by these species; (2) measuring the rate of digestion of herring eggs in the stomachs of the predators in controlled experiments; (3) estimating the abundance of predators in the area by the use of acoustic methods.

Materials and methods

Stomach sampling

Samples of the three potential predators, cod, haddock, and saithe, were taken from trawl catches in the study area. Stomachs were sampled in 5-cm length groups of the

1054–3139/91/010015+07 $03.00/0

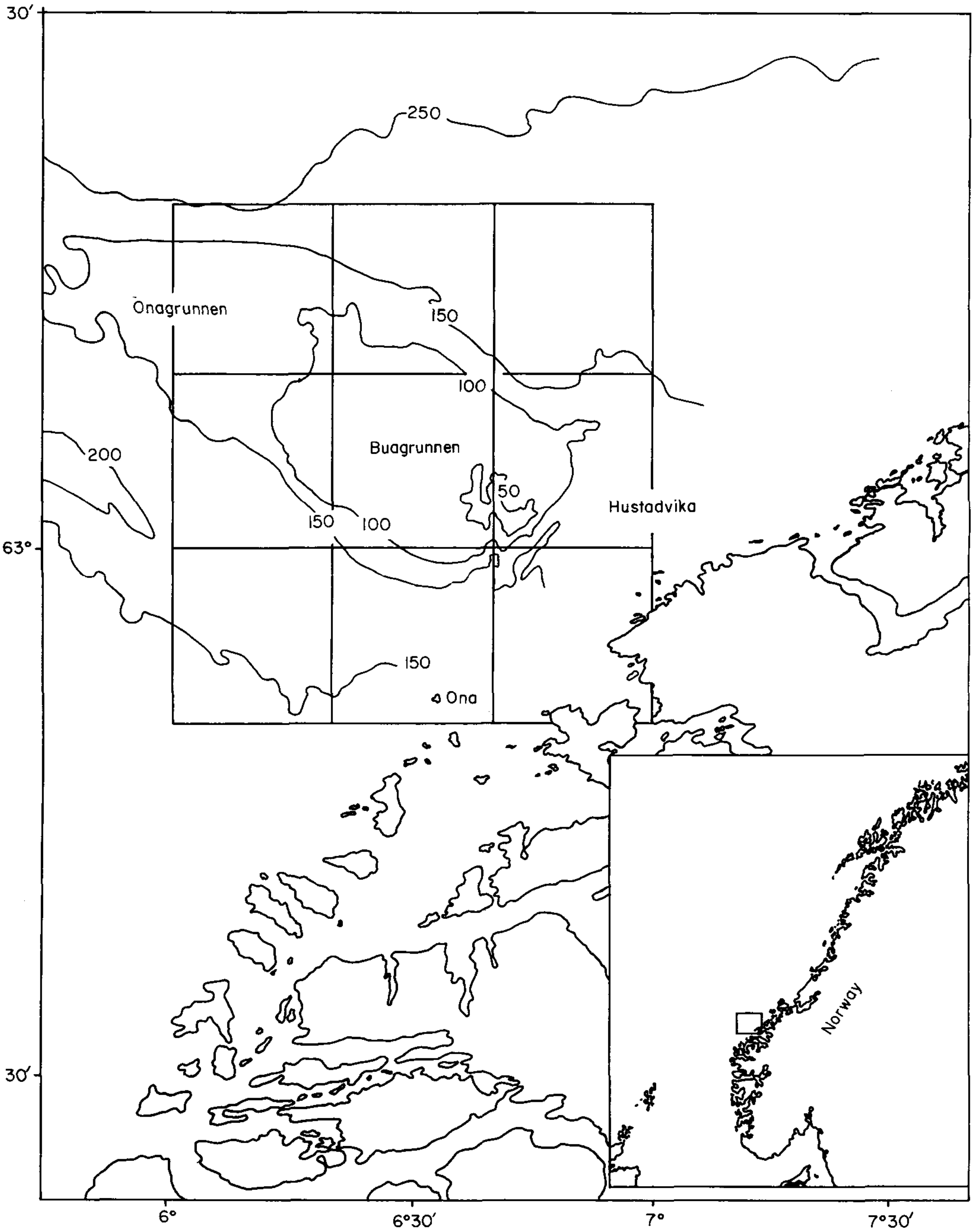

Figure 1. Map covering parts of the Møre coast, western Norway. The squares are the areas investigated to find herring egg predators.

fish. The stomachs and their contents were preserved in formalin for further studies in the laboratory. Here the weight of the various contents was recorded. Herring eggs in the stomach were spread out thinly on a sheet of glass covering millimetre ruled paper and counted and aged in squares of 10 × 10 mm. The number of squares sampled from the content of each stomach was one of ten. The total number of eggs in the stomach was obtained by multiplying the mean number of eggs in the squares by the total area covered by the content of the stomach.

Rate of gastric emptying

The rate of gastric emptying may be studied from samples in the field if the species under study has a very pronounced cycle of food intake. The length of the cycle can

Table 1. Number of stomachs sampled for each of the three species, cod, haddock, and saithe. The numbers and the proportion of stomachs containing eggs of herring are also given.

Species	n	With eggs	% with eggs
Cod	488	1	0
Haddock	613	293	47.0
Saithe	169	2	1.2

Table 2. Data from trawl stations with catches of haddock showing numbers of stomachs sampled, proportion with herring eggs, and proportion with herring eggs also containing other food items in stomach.

Date	No. of samples	% with eggs	% eggs + sand	% eggs + krill	% other content
16 Mar	170	62	0	12	18
18 Mar	104	68	20	3	14
22 Mar	22	9	0	100	63
25 Mar	28	71	10	35	28
9 Apr	48	19	0	33	48
10 Apr	30	70	0	14	13
11 Apr	11	18	0	0	18
11 Apr	99	19	0	29	30
12 Apr	101	44	5	23	32

then be measured and an estimate obtained of gastric emptying from the average stomach contents through the cycle (Jones, 1974). Haddock, which was found to be the main predator on herring eggs, does not have a very pronounced cycle of food intake, and so it is difficult to measure the rate of gastric evacuation in this way.

There are about as many models of gastric emptying on various food items as there are fish species and scientists, and many investigations have been carried out to shed light on these problems. However, only a few studies have been carried out on gadoid species, e.g. Tyler (1970), Jones (1974, 1976), and Jobling (1981). In these studies the most significant factors determining the rate of gastric emptying were temperature, species and size of the predator, size of meal, and kind of food.

As none of these studies were carried out on haddock, and did not include eggs as food, it was decided to estimate the rate of gastric emptying of herring eggs in the stomachs of haddock by means of a controlled tank experiment. The temperature in the tank was set to the same level as the recorded bottom temperature in the study area (5–6°C).

A total of 49 haddock, ranging in length from 42 to 62 cm (mean length, 49 cm), were used in the experiment and were fed once with fertilized herring eggs. The eggs were inserted in their stomachs through a tube in amounts proportional to the length of the fish; thus, fish in length group 42–49 were given 10 g, those in length group 50–59 were given 20 g, and fish larger than 60 cm were given 30 g of eggs. Every 12 h after the feeding, 5 fish were removed and their length and the quantity of eggs left in the stomach recorded.

In this work a curvilinear regression was performed by computer on the data. The equation used was the linear exponential:

$$P = \exp(a + bt)$$

where P = proportion of food given remaining in the stomach, a = intercept, b = regression coefficient, and t = time after feeding.

Acoustic abundance estimation of predators on the spawning grounds

Estimation of the abundance of demersal fish in the Barents Sea by acoustic survey started in 1970 (Hylen *et al.*, 1972). During the 1970s the methods were further developed and acoustic abundance estimation of bottom-dwelling fish has since become standard (Dalen and Smedstad, 1979). The methods used by Dalen and Smedstad have been used in these investigations.

Two acoustic surveys were conducted in the area, one in the period 16–27 March and one in the period 6–15 April. Pelagic and demersal trawl hauls were carried out to identify the target species and to obtain data for abundance estimation. The echo-recording papers were scrutinized daily and the integrator readings (mm/NM) were divided into two categories of fish (cod/haddock and saithe/other demersal species) from the acoustic and catch data.

The average integrator values (M) for each 5 nautical miles were plotted on maps and the average M for each of the two categories of fish were calculated within the squares shown in Figure 1. This average M was then used to calculate the abundance of fish.

The following functions were used to convert the M values into fish densities:

$$C_{cod} = 5.25 \times 10^6 \times L^{-2.18}$$

$$C_{haddock} = 1.72 \times 10^6 \times L^{-1.69}$$

$$C_{saithe} = 3.64 \times 10^6 \times L^{-2.09}$$

where L is the length of the fish in cm. These functions are products of the target strength functions and the instrument constant of the research vessel "G. O. Sars".

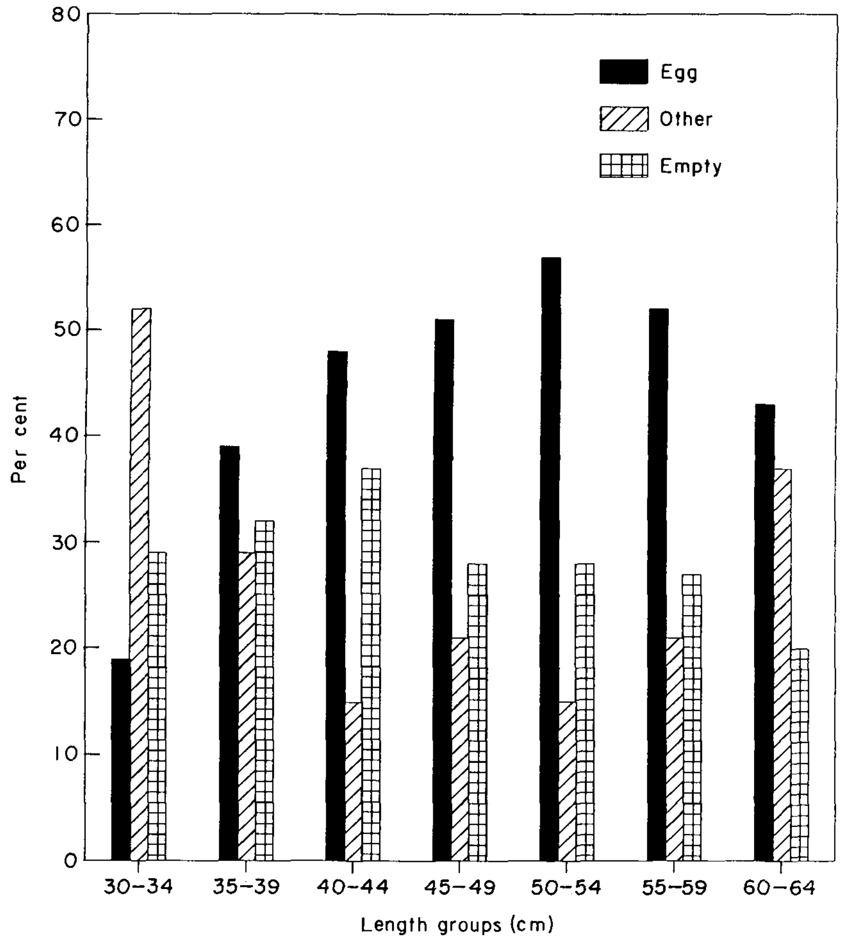

Figure 2. Proportions of haddock stomachs containing eggs, other food items, or that were empty.

Results and discussions

Stomach contents

Table 1 gives the number of stomachs sampled for each of the three species, cod, haddock, and saithe, and also the number and proportion of stomachs that contained herring eggs for each of the three species. White eggs were found in only a few cod and saithe stomachs, they were found in about 50% of haddock stomachs.

Results from the trawl stations where haddock containing herring eggs were caught in 1981 are given in Table 2. Stations where no predators were found are not included. At trawl stations where haddock were caught, 47.8% of them (haddock >30 cm) had eggs in their stomach. At two of the stations, 70% contained herring eggs. Of the stomachs containing eggs, 24% had other food items as well. About 26% were empty.

The contents of the stomachs of cod and saithe indicate that these species tend to search for food in the more open water. Herring and krill were the dominant food for these species. The samples were taken at the same trawl stations as those at which haddock with eggs were caught.

The proportion of haddock stomachs containing herring eggs, other food items, or found to be empty is shown in Figure 2. Haddock in the size interval from 30–65 cm ate herring eggs, while no eggs were found in the stomachs of fish shorter than 30 cm. The highest incidence of eggs was found in fish of length 50–54 cm.

Table 3 gives the mean and standard error of the number of eggs found in the stomachs of haddock in the various length groups.

Rate of gastric emptying and daily ration

The following parameters were recorded for each of the fish examined during the experiment: L = length (cm); F = amount of food given/kg bodyweight; x = amount of food left in the stomach; t = number of hours between feeding and sampling.

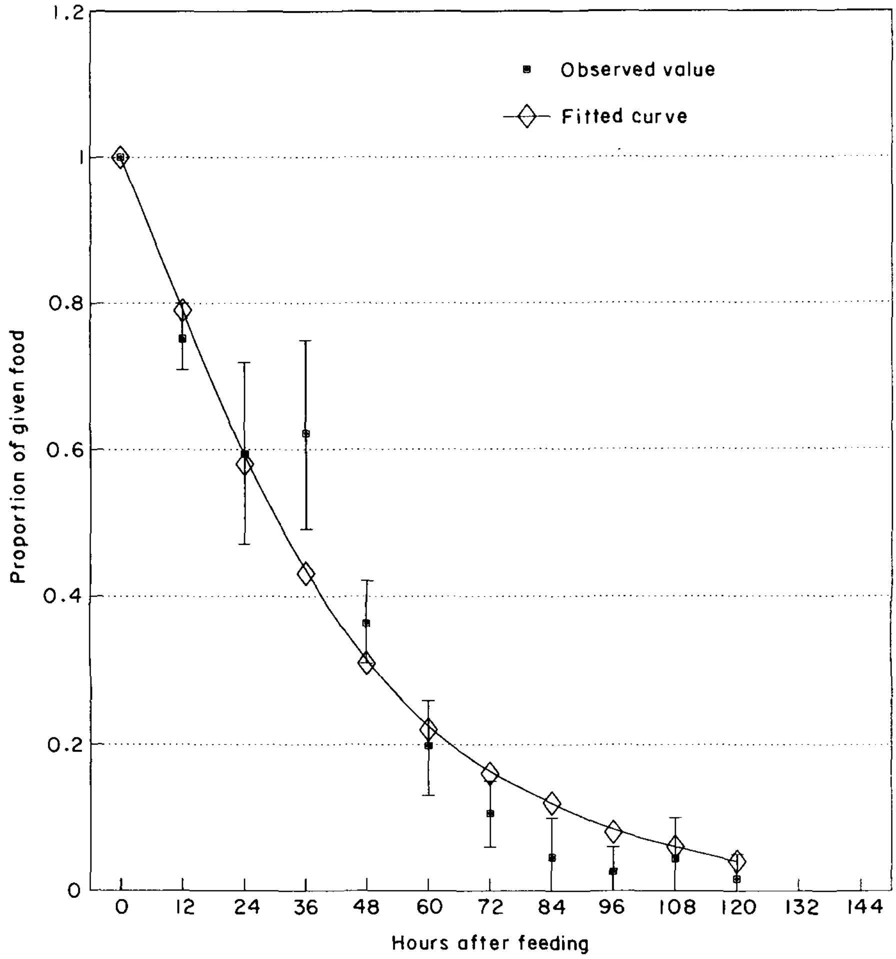

Figure 3. Mean proportion of given food (with 95% confidence limits) left in the stomachs of haddock after 12-h steps of feeding. The curve fitted by the equation P = exp (a + bt) is also shown (see p. 5).

Table 3. Mean number of herring eggs in the stomachs of haddock divided by length groups ($n \times 10^3$). The standard error of the mean (s.e. $\times 10^3$) is also given.

Length (cm)	n	s.e.
30–34	2.4	0.41
35–39	4.1	0.37
40–44	7.0	0.62
45–49	13.6	0.78
50–54	21.0	1.14
55–59	24.6	1.72
60–64	35.9	2.48

Table 4. Estimated number of haddock ($n \times 10^6$), proportion preying on herring .ggs, number preying on eggs ($n \times 10^6$) per length group, and consumption per ($C \times 10^9$ eggs) per day.

Length	$n_{haddock}$	Prop	$n_{preying}$	C/d
30–34	0.89	0.19	0.17	0.17
35–39	2.02	0.39	0.79	1.36
40–44	3.06	0.48	1.47	4.32
45–49	3.21	0.51	1.64	9.37
50–54	3.08	0.57	1.76	15.52
55–59	2.76	0.51	1.41	14.57
60–64	1.43	0.41	0.59	8.90

The relationship between the proportion of food remaining in the stomach and time after feeding was not linear (Fig. 3). An exponential least squares regression was performed relating the proportion of given food remaining in the stomach to time after feeding. The "linearization" was achieved through logarithmic transformation. The regression resulted in the following parameter values:

$$P = \exp(0.098 - 0.027t)$$

Table 5. The estimated number ($N \times 10^6$) of each year class in the 1981 spawning stock of the northern component of the Norwegian spring-spawining herring (Anon., 1982). The mean individual fecundity ($F \times 10^3$) for the respective year classes (Serebryakov, 1988) is also shown.

	Year classes									
	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978+
N	86	0	7	7	343	157	21	86	7	714
F	108	95	94	99	94	82	92	73	63	

$\Sigma N \times F = 64.4 \times 10^{12}$ eggs.

where P = proportion of given food remaining in the stomach and t = hours after feeding. The correlation coefficient between the dependent and independent variables is −0.89, while the standard errors of the intercept and slope are 2.3×10^{-3} and 0.14 respectively.

The curvilinear shape (Fig. 3) means that the rate of stomach evacuation is greater in the first few hours than towards the end of digestion. About 42% of the given food amount left the stomach during the first 24-h period. Time for complete gastric emptying (less than 10% of given food left in the stomach) was 96 h.

In nature, the fish probably feed more or less continuously. The average quantity of eggs in the stomachs from the study area was also found to be much higher than the amount of food given in the experiment. A daily reduction in the average stomach content of 42% per day will therefore be used as an estimate of the rate of emptying of fertilized herring eggs from the stomachs of haddock.

Total consumption of herring eggs by haddock on the spawning ground

An acoustic abundance estimate of haddock was made from the two surveys conducted in the area. The results are given in Table 4. The estimated number (haddock > 30 cm) was 16.45×10^6 individuals, about half of which were in the length interval 40–54 cm.

To calculate the total amount of eggs consumed, it is first necessary to estimate the proportion of the haddock stock that preyed on eggs, and for how long.

It cannot be assumed that all the haddock in the area eat eggs. Some haddock prefer other kinds of food, and herring spawning does not take place over the whole area in which haddock are present. Table 4 gives the proportions of haddock (by length group) in the trawl catches with herring eggs in their stomachs; these proportions were used to obtain an estimate of the number of active egg-predators in the area (also given in Table 4).

The time of exposure to predation may be seen from studying the age composition of the eggs in the stomachs. The incubation time for herring eggs at temperatures of 5–6°C is about 21 days (Blaxter and Hempel, 1963). By establishing the age of the oldest eggs from the first catches of egg predators and the age of the youngest eggs from the last catches of predators, an estimate of how long the eggs must have been exposed to predation was obtained.

In 1981 there were eggs on the seabed in the period from 7 March to 29 April. However, the concentration of eggs is unlikely to have been constant throughout the period. The intensity of the spawning varies and by the end of the period many eggs have been hatched. Predation on eggs probably occurred before and after these investigations were conducted. The estimate of about 50 days (7 March to 29 April) of exposure to predation will therefore be used in the computations of predation in the area.

The following equation expresses the total amount (in numbers) of eggs consumed by the predator:

$$C = t \times N_i \times p \times n_i$$

where C = total consumption of herring eggs eaten by the predator (number); t = time of exposure to predation; N_i = number of predators in length group i; p = proportion of food passing through the stomach per day; n_i = mean number of eggs in the stomachs of fish in length group i. Applying this model, the daily consumption of eggs is estimated as 5.4×10^{10} eggs and the consumption in 50 days as 2.7×10^{12} eggs. The daily consumption per length group is given in Table 4.

Conclusions

The ultimate question is how large a fraction of the total amount of spawn in this area is eaten by haddock. To answer this, the fecundity of the herring population spawning in this area must be estimated.

In 1981, Buagrunnen was the only spawning site of the northern component of the Norwegian spring-spawning herring. The estimated number (in millions) per year class in the spawning stock of the northern component is given in Table 5 (Anon., 1982).

The individual reproductive capacity of herring depends on fish length, weight, age and year-class strength (Lyamin, 1966). Lyamin studied the reproductive capacity (population fecundity) of the spawning stock of the Norwegian spring-spawners as a whole. Serebryakov (1988) analysed the dynamics of the population fecundity of this stock in terms of spawning stock size and structure. Seliverstova (1989) calculated the average individual fecundity per age group divided into three groups of year-class strength: poor, average, and rich (for the years 1951–1975). The year classes in the spawning stock in 1981 may all be rated as poor ones and the average fecundity (thousand eggs) of individuals comprising the various year classes is given in Table 5.

The total egg production of herring spawning in the area in 1981 can now be calculated as the sum of the products N × F of Table 5, which is 64.4×10^{12} eggs. The estimated total consumption of eggs by haddock (2.7×10^{12}) is therefore only 4.2% of the total reproductive capacity of the herring spawning on this ground.

The calculations are based on an acoustic estimate of fish close to the seabed. Although it is difficult to establish variance estimates in acoustic biomass computations, and acoustic estimates of bottom-living fish can generally be characterized as lacking in precision, it is reasonable to conclude that predation by haddock on herring eggs in this area at this time was not such as to significantly impair the survival prospects of the eggs before hatching. However, in the 1980s the Arcto-Norwegian haddock stock and its coastal components were at a low level, and still are.

Acknowledgements

I thank K. Korsbrekke, Institute of Marine Research (IMR), Bergen, Norway for worthwhile comments on the statistical treatment of the data. Thanks are also extended to the International Council for the Exploration of the Sea for permission to cite the ICES papers. I also acknowledge the assistance of Ole Gullaksen (IMR) who kindly corrected the English text.

References

Anon. 1982. Report of the Working Group on Atlanto-Scandian Herring and Capelin. ICES CM 1982/Assess: 12.

Blaxter, J. H. S., and Hempel, G. 1963. The influence of egg size on herring larvae (*Clupea harengus* L). J. Cons. perm. int. Explor. Mer, 28: 211–240.

Bowman, A. 1922. The occurrence of "spawny" haddock and the locus and extent of herring spawning grounds. Fish. Scot., Sci. Invest. 1922, IV.

Dalen, J., and Smedstad, O. M. 1979. Acoustic method for estimating absolute abundance of young cod and haddock in the Barents Sea. ICES CM 1979/G: 51, 24 pp.

Dragesund, O., Hamre, J., and Ulltang, Ø. 1980. Biology and population dynamics of the Norwegian spring-spawning herring. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 177: 43–71.

Dragesund, O., and Nakken, O. 1973. Relationship of parent stock size and year class strength in Norwegian spring-spawning herring. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 164: 15–30.

Hylen, A., Jakobsen, T., Lahn-Johannessen, J., Smedstad, O. M., and Sætre, R. 1972. Bunnfiskundersøkelser ved Bjørnøya, Spitsbergen og i Barentshavet med F/F "G. O. Sars" 3–20 November 1970. Fisken Hav., 1977 (2): 3–15. (In Norwegian).

Jobling, M. 1981. Mathematical models of gastric emptying and the estimation of daily rates of food consumption for fish. J. Fish. Biol., 19: 245–257.

Johannessen, A. 1980. Predation on herring (*Clupea harengus* L.) eggs and young larvae. ICES CM 1980/H: 33, 12 pp.

Jones, R. 1974. The rate of elimination of food from the stomachs of haddock, cod and whiting. J. Cons. int. Explor. Mer, 35: 225–243.

Jones, R. 1976. Estimates of the food consumption of haddock (*Melanogrammus aeglefinus*) and cod (*Gadus morhua*). J. Cons. int. Explor. Mer, 38(1): 18–27.

Lyamin, K. A. 1966. Fecundity of the spring race of Atlanto-Scandian herring (*Clupea harengus harengus* L.) in the Norwegian Sea. Trudy PINRO, Moscow, 17: 147–191. (In Russian).

Seliverstova, E. I. 1989. Spawning stock structure and population fecundity of the Atlanto-Scandian herring. Contribution to the IV Soviet-Norwegian Symposium in Bergen, 1989, on "Biology and fishery of blue whiting in the Northeast Atlantic and the Norwegian spring-spawning herring".

Serebryakov, V. P. 1988. Population fecundity and yearclass strength of some commercial fish species. ICES 1988 ELHS/No.14.

Sætre, R., and Gjøsæter, J. 1975. Ecological investigations on the spawning grounds of the Barents Sea capelin. FiskDir. Skr. Ser. HavUnders., 16: 203–227.

Templeman, W. 1965. Some instances of cod and haddock behaviour and concentrations in the Newfoundland and Labrador Seas in relation to food. Int. Comm. NW Atl. Fish. Spec. Publ. No. 6: 449–461.

Tyler, A. V. 1970. Rates of gastric emptying in young cod. J. Fish. Res. Bd. Can., 27: 1177–1189.