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SPAWNING OF BALTIC HERRING *(Clupea harengus membras)* IN THE WESTERN PART OF THE GULF OF FINLAND

by

P. Oulasvirta[1], J. Rissanen[1] and R. Parmanne[2]

[1] Tvärminne Zoological Station, SF-10850 Tvärminne, Finland.
[2] Finnish Game and Fisheries Research Institute, Fisheries Division, P.O. Box 193, SF-00131 Helsinki 13, Finland.

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Abstract

Spawning of the Baltic herring was studied at 41 sampling sites in Tammisaari archipelago, in the western part of the Gulf of Finland, from April to July in 1982. Eighteen of the sampling sites were established at random, in order to investigate the total egg number deposited in the study area. A bottom rake and SCUBA diving were used to map the spawning sites and collect samples for determining the egg development stage. Quantitative samples were taken on five spawning beds by a SCUBA diver, using a suction sampler and a membrane pump. The diver also observed the spawning substrates and the vertical distribution of the spawn. The proportions of dead eggs and eggs at different development stages were calculated from each sample. The numbers of eggs per square metre were calculated from the quantitative samples. The mortality and development rates of the eggs were also studied in the laboratory and *in situ* in larval incubators.

Spawn was found in altogether 13 localities. The depth distribution of the eggs ranged from 0.2 to 6.5 metres and the most common spawning substrate was vegetation. The largest amounts of eggs were observed at the beginning of spawning, in early May, at which time the maximum egg densities exceeded 10^6 eggs m^{-2}. The mean proportion of dead eggs, weighted by egg numbers, was 13.6 %. The proportion of dead eggs increased during spawning from May to July and the mortality correlated positively with water temperature. However, the temperature of the water alone was not considered to explain the high mortality in June and July. The mortality of eggs in the laboratory was lower than that observed on natural spawning grounds.

Résumé

On a étudié le frai du hareng de la Baltique en 41 sites d'échantillonnage de l'archipel de Tammisaari dans la partie occidentale du golfe de Finlande d'avril à juillet 1982. Dix-huit des sites furent établis au hasard pour étudier le nombre total d'œufs déposé dans la région étudié. Un rateau de fond et un plongeur SCUBA furent utilisés pour caractériser les sites de frai et recueillir des échantillons afin de déterminer l'état de développement des œufs. Des échantillons quantitatifs furent pris en cinq sites à frai par un plongeur SCUBA en utilisant un échantillonneur à succion et une pompe à membrane. Le plongeur observa aussi les substrats du frai et la distribution verticale du frai. Pour chaque échantillon on a calculé la proportion d'œufs morts et d'œufs aux différentes étapes du développement. Avec les échantillons quantitatifs on a pu calculé le nombre d'œufs au mètre carré. La mortalité et le taux de croissance des œufs ont été aussi étudiés en laboratoire et *in situ* dans des incubateurs à larves.

[1] Tvärminne Zoological Station, SF-10850 Tvärminne, Finland

[2] Finnish Game and Fisheries Research Institute, Fisheries Division, P.O.Box 193, SF-00131 Helsinki 13, Finland

Le frai a été observé en 13 endroits en tout. La distribution des œufs en profondeur varie de 0.2 à 6.5 mètres et la végétation constitue le substrat le plus commun du frai. Les plus grandes quantités d'œufs furent observés au commencement du frai, début mai, lorsque les densités maximales d'œufs dépassaient 10^6 œufs/m^2. La proportion moyenne d'œufs morts, pondérée par le nombre d'œufs, était de 13.6 %. La proportion d'œufs morts s'accrut pendant le frai de mai à juillet et la mortalité se corréla positivement avec la température de l'eau. Cependant, la température de l'eau seule ne peut pas expliquer la forte mortalité en juin et juillet. La mortalité des œufs en laboratoire s'avéra inférieure à celle observée sur des sites naturels.

CONTENTS

I. INTRODUCTION

The Baltic herring (*Clupea harengus membras*) is the most important fish species in the Baltic Sea. The total catch of Baltic herring in 1980 was 460 132 tons (Anon. 1982a), or more than half of the total commercial fish catch in the Baltic Sea. The catch of Baltic herring in Finland in 1980 was 83 240 tons (PARMANNE & SJÖBLOM 1982). This was 60 % of the total fish catch in Finland (Anon. 1982b) and its value was 44 % of the total value of the commercial fish catch (Anon. 1982b).

Most herring in the Baltic Sea spawn in springtime. The number of autumn spawners is small, particularly in the northern part of the sea. In the eastern part of the Gulf of Finland, for example, no more than 1-2 % of the Baltic herrings spawn in autumn (OJAVEER 1981a). Spring-spawning Baltic herring are caught with trapnets and trawls during the spawning time. In 1980, 68 % of the Baltic herring catch was caught in May-June (PARMANNE & SJÖBLOM 1982). The catch from trapnets was 43 % of the total Baltic herring catch in Finland.

The studies on the spawning of the Baltic herring include those by SJÖBLOM (1961), RANNAK (1971) and ANEER & NELLBRING (1982). Despite the great economic value of the Baltic herring and the importance of the spawning fishery, little attention has been paid to its spawning off the Finnish coast (see RAJASILTA & RANTA-AHO 1981). The timing of spawning can be observed on the basis of spawning catch data, but insufficient information is available on, for example, the depth, bottom quality and vegetation at the spawning sites, the number of eggs spawned, and the rate of development and mortality of the eggs. Such data are needed, however, for estimating the size of fish stocks and the effects of fishing or for studying the possible effects of environmental changes on Baltic herring stocks. If the number of eggs deposited in a certain area could be determined, it would be possible to calculate the size of the spawning stock, using data on the fecundity and sex ratios. A corresponding method has been used in estimating the size of spawning stocks of Pacific herring in British Columbia, Canada (HUMPHREYS

& HOURSTON 1978). Spawning stock estimates made on the basis of egg numbers demand a large number of representative samples. These are very difficult to obtain for the Baltic herring, because its spawn attaches to the substrate and the number, location and size of the spawning beds are poorly known. The long spawning period of the Baltic herring, the areal dispersal of the spawning and the difficulties in quantitative sampling are obvious reasons for the small number of studies on Baltic herring spawn.

In this study, rake samples, quantitative bottom samples, artificial spawning substrates, SCUBA diving and laboratory experiments were used to investigate the requirements of the Baltic herring as regards its spawning beds, the number of eggs deposited, and the rates of development and mortality of the eggs in the Tammisaari archipelago in the western part of the Gulf of Finland.

II. STUDY AREA

Samples were taken at weekly intervals in the Tammisaari archipelago during summer 1982, from the break-up of the ice in April to mid July. The number of transects was 41 (Fig. 1). Twenty-three were chosen near the Baltic herring trapnets and in likely areas for spawning grounds. A bottom rope marked at one-metre intervals was laid out perpendicularly to the shore at the sampling sites. The length of the rope was 35-50 m, depending on the place. Eighteen of the transects were established at random. For this purpose the study area was divided into two sub-areas (Fig. 1). The sub-area situated on the south side of the island Älgö lies in the outer archipelago and the sub-area situated north of Älgö belongs to the inner archipelago (HÄYREN 1900). The water area of the northern sub-area is 6.85 km^2 and that of the southern sub-area 7.97 km^2. The areas less than 10 m deep are 6.3 km^2 and 4.7 km^2, respectively, and these were divided into 50 x 50 m squares. Eleven squares were chosen at random in the northern sub-area and seven squares in the southern sub-area. A line (35 m) was drawn from the midpoint of each square to the nearest shore.

III. METHODS

1. Sampling of eggs

Searching for spawn and mapping of spawning sites was done with the so-called Luther-rake (LUTHER 1951). The development stage of the eggs was determinded according to the classification of BRAUM (1978) (Appendix 1). In addition to these rake samples, development stage samples were taken during SCUBA diving in connection with the quantitative sampling.

The samples taken with the rake were used to observe the progress of spawning. When the development stage of the eggs showed that new spawn had been deposited on the transect, quantitative samples were taken by SCUBA diving from one-metre wide transects in different depth zones.

Quantitative samples were taken with a suction sampler below 1.5 m (HISCOCK & HOARE 1973, KANGAS & HÄLLFORS 1978) and with a membrane pump above 1.5 m (TIITINEN 1982). Parallel samples were usually taken, three in each depth zone. The diver also observed the vertical distribution of spawn.

The sampling area was delimited with a tube made of plexiglass with a diameter of 19.3 cm. The height of the tube was 30 cm, which prevented outside algae and eggs from getting into the sample. Plastic foam on the underside of the tube ensured that it fitted tightly to the bottom. The tube was kept in place with lead weights.

2. The artificial spawning substrates

The spawning substrates, made from plastic lawn, had a diameter of 20 cm. They were placed at sites where the quantitative samples were taken, to quantify possible new spawn.

3. *In situ* incubator experiments

Besides development stage samples, the mortality of eggs was also studied by means of *in situ* incubators made from plastic buckets with openings out in the sides to allow free water movement. The holes were covered with 500 µ-mesh nylon net to prevent the hatching larvae from escaping.

Eggs attached to algae were put into the incubators at the spawning site, and the buckets were closed and fastened to the bottom. The algae which

grew on the net were brushed off once during the incubation period.

4. Temperature observations

The water temperature was measured at five places (Fig. 1), using the Ruttner sampler, at depths of 0.2, 2, 5 and 8 m. The temperature was also measured by a diver during sampling.

5. Sample processing

The egg development stage samples taken with the rake and by diving were immediately fixed with a solution of sea water and 2-5 % acetic acid (BRAUM 1978). The proportions of eggs at different development stages, and of dead eggs and deformed embryos, i.e. eggs with no visible cell differentiation, were calculated for each sample. The samples were then preserved in a solution of 10 % formalin and 2 % acetic acid.

The quantitative samples were mainly preserved in the same way, but some were frozen. These frozen samples were also fixed and stained with weak acetic acid before preservation. The number of eggs in each sample was counted. Samples with high egg number were divided with a sub-sampler used in littoral macrofauna surveys (HAAGE 1975).

6. Laboratory experiments

Egg mortality was studied in the laboratory at two different temperatures, 7.6 ^{o}C and 12 ^{o}C. The experiments were done in plastic basins. Fertilization was performed in separate fertilization basins, using the so-called wet method (SHELBOURNE 1964), on 5 x 5 cm pieces of nylon net. Many females and males were used in the fertilization. After an hour the eggs were transferred to the incubation basins. The development stage of the eggs and possible proportion of deformed and dead eggs were determined at intervals. The egg batches, which were placed in separate incubation basins, were allowed to develop until hatching. All the basins were well aerated.

7. Calculating methods

From the quantitative samples the number of eggs were calculated per square metre of bottom. The means and 95 % confidence limits were calculated on parallel samples.

The total number of eggs deposited on the whole transect, and the number of eggs spawned in each depth zone, were calculated, using the width of each zone as a coefficient.

Regression and correlation coefficients were calculated between the proportions of dead eggs in the samples and the highest temperatures observed during the time of egg development. If there was more than one sampling date for the same spawning school, the highest proportion of dead eggs was used in the calculations, because it is presumably closest to the real and final mortality. The mean of the proportions of dead eggs was calculated for the whole study period from all the representative samples. The egg numbers in the quantitative samples were used as coefficients to calculate the mean mortality weighted with the number of eggs. Deformed eggs were counted as dead eggs.

The mortality of eggs in the incubator experiments was determined by calculating the proportions of dead eggs, living eggs and hatched larvae. So-called theoretical mortality was calculated by considering all the eggs that were alive but unhatched at the end of the experiment as hatched (see ANEER & NELLBRING 1982).

The total number of eggs deposited in the sub-area was estimated from the egg numbers observed on the randomly established transects, using the following formula:

$$x = \frac{\sum_{i=1}^{n} a_i/m_i}{n} \cdot b \cdot 10^6$$

where: x = the number of eggs spawned in the sub-area

a_i = the number of eggs on transect i

m_i = the length of transect i in metres

n = the number of transects

b = the water area less than 10 m deep within the sub-area (km^2).

The total egg number was the sum of the egg numbers in the two sub-areas. When the sex ratio in the spawning population is assumed to be 1:1, the spawning stock size in the study area can be calculated with the following formula:

$$Y = \frac{X}{F} \cdot 2 \cdot 10^{-6} \cdot W$$

where: Y = the spawning stock size in tons
X = the number of eggs spawned in the study area
F = average fecundity (eggs/female)
W = the average weight of a fish in grams

Fecundity, in other words the average number of eggs per female before spawning, was calculated with a formula presented by RANNAK (1970) for the Baltic herring of the western parts of the Gulf of Finland:

F = 225W + 4390
F = fecundity
W = average weight of the fish in grams

IV. RESULTS

1. Spawning time

Baltic herrings spawned from the beginning of May, about one week after the break-up of the ice, to mid July or later. Spawning was most intensive in early May.

2. Spawning sites

Spawn was found at 13 of the 41 transects studied. Quantitative samples were taken from five transects. All the spawning sites found were either open littorals or sounds with strong currents, with effective water circulation. The bottom profiles of the spawning sites are shown in Figs. 2-6 a.

3. Bottom quality and the spawning substrates

The eggs were usually attached to vegetation. Common substrates were filamentous algae, such as *Ectocarpus siliculosus* and *Pilayella littoralis*. Spawn was also found on *Monostroma grevillei* and on red algae, e.g. *Ceramium tenuicorne*, *Furcellaria fastigiata* and *Phyllophora sp.* Spawn was found on bladder-wrack (*Fucus vesiculosus*) at only two sites; no stands of bladder-wrack were observed at the other spawning sites. Higher aquatics, such as eelgrass (*Zostera marina*) and *Potamogeton pectinatus*, were also common spawning substrates. Baltic herring eggs were also found on bare stones,

gravel and sand, and on blue mussels (*Mytilus edulis*), but here the egg densities were usually lower than on the vegetation. No spawn was observed on soft bottoms.

4. Vertical distribution of the spawn

The depth range of the eggs was 0.2-6.5 m. In May, spawning mainly occurred at 1-3 m. In the summer, when the water temperatures increased, the deposition of spawn moved downwards, the densest egg mats and highest egg number being observed at depths of 2-6 m (Fig. 7).

5. Number of eggs spawned

The densities of spawn at different sampling sites and the total egg numbers deposited on different transects during the whole study period are presented in Figs. 2-6 and in appendix 2.

The highest spawn densities, approximately 10^6 eggs m^{-2}, were observed at Ängholmen. Of all the spawn observed on the five quantitatively surveyed transects during the whole study period, 72 % was deposited at Ängholmen.

Spawn occurred on only two of the 18 random transects. According to the formulas presented above, the number of eggs spawned in the northern sub-area was 444.98 m^{-2} and in the southern sub-area 1861.14 m^{-2}, which corresponds to 1.155×10^{10} eggs in the two areas. According to data of the Finnish Game and Fisheries Research Institute the average weight of the mature Baltic herring in the Gulf of Finland in 1982 was 29.6 g. From these values, the amount of Baltic herring spawning in the whole study area can be estimated at 62 tons.

6. Mortality of spawn

Calculated from the development stage and quantitative samples taken from different spawning groups, the proportion of dead eggs were 6.5 % in May, 31.1 % in June and 94.7 % in July. The mean for the whole study period was 30.9 %.

The mean proportion of dead eggs calculated by using the number of eggs on the five quantitative transects as coefficient was 13.6 %.

The proportion of dead eggs correlated positively with temperature (Fig. 8). The correlation coefficient ($r = 0.61$) is significant at the 0.1 % risk level.

The proportions of dead eggs found in the quantitative samples are presented in Figs. 2-6 c.

7. Eggs lost by wave and current action

Spawn was observed to be washed away from the transects at Ängholmen, Stuguholmen and Trelänningen (Fig. 1). At Ängholmen the reason was a strong current, at Stuguholmen the wave action and at Trelänningen a combination of both, though neither was as strong as at Ängholmen or Stuguholmen.

At Ängholmen the strong current moved eggs that were attached to loose algae. It appears that most of the eggs on a transect change their position between the sampling dates.

At Stuguholmen eggs were observed to be dislodged from the transect and also to be washed from shallow points on the transect to deeper ones. Between 10.5. and 15.5., 14.5 % of the spawn on the transect drifted away. Loosening of vegetation and eggs was greater on shallow parts of the transect, 25.4 %, but more than half of these eggs merely shifted to a deeper part of the transect.

At Trelänningen spawn was observed to sink from shallow to deeper water and also to shift from surrounding areas to the transect. The amount of spawn on the transect increased by 16.6 % between 4.6. and 11.6. However, at the same time the number of eggs on shallow parts of the transect decreased by 27.9 %. No deposition of new spawn or hatching of eggs occurred during this period.

Drifting algae, detached from their substrates and bearing eggs, were observed on the north side of the island Skedö and in front of Mattgrund on 28.5. and in Storfjärden on 11.6. (Fig. 1).

8. Mortality and hatching rate *in situ* in larval incubator experiments

The experiments at Ängholmen were performed in mid May, when the water temperature was 6.4-8.3 °C. The experiments at Trelänningen were performed

between 4. and 20.6. The water temperature on the estimated spawning dates was 8.7 °C and 9.5 °C, but after the start of the experiment the temperature soon decreased to 6.5 °C, due to strong water mixing. The egg mortalities at the beginning of the experiments were 0.5 % at Ängholmen and 1.9 % at Trelänningen. The eggs at Trelänningen had already reached stage f, whereas those at Ängholmen were at stage c (BRAUM 1978) (Appendix 1).

There were clear differences in the mortality and hatching percentage between the two localities; 2.3 % of the eggs died at Ängholmen and 96.6 % at Trelänningen.

9. Development and hatching rate of eggs in the laboratory

At 7.6 °C, the development of Baltic herring eggs from fertilization to hatching took about 12-15 days and at 12 °C about 6-11 days (Fig. 9).

At 7.6 °C, the hatching success was 97.3 % and at 12 °C, 92.8 %. At the end of the experiment all the eggs that had not yet hatched at 12 °C were still alive and 67.6 % of those at 7.6 °C. Thus the theoretical hatching percentage at 7.6 °C was 99.1 % and at 12 °C 100 %.

V. DISCUSSION

1. Methods

Because of the small effort required, the method of sampling spawn with a rake is good for surveying large areas. On the other hand, small amounts of spawn and small spawning beds will easily escape notice, the method does not give an exact picture of the number of eggs per unit area, and it is difficult to sample spawn lying on bare sand or gravel.

SCUBA sampling requires a great deal of equipment and many divers are needed for a large number of samples. However, it seems that diving is the only way to obtain quantitative data on spawn densities on Baltic herring spawning grounds.

Baltic herrings often spawn on hard exposed bottoms and the eggs stick to the spawning substrate. Because of this, the membrane pump used alone from the surface, without a diver handling the mouthpiece, is unsuitable for sampling Baltic herring spawn. The suction sampler does not work efficiently above 1.5 m, but below this depth it proved more effective than the

membrane pump.

The number of eggs on each transect was calculated using weighting values for the different depth zones estimated by the diver. This method is subjective and demands self-criticism of the observer.

The mortality values obtained for the incubator experiments agree with the values calculated from samples taken near the incubators. Thus, it seems that the incubators do not affect the survival of the eggs.

The artificial spawning substrates did not give an exact picture of the number of spawned eggs, especially in places with strong currents and strong algal growth, because eggs and algae drifted from the surroundings on to the substrates. The Baltic herring possibly also selects its spawning substrate, and the amount of eggs on artificial spawning substrates may not be comparable with the amounts in nature.

2. Spawning time

Spawning began in early May in the inner parts of the archipelago, and later in the summer in the outer archipelago. However, spawning continued in the inner archipelago to as late as mid summer.

According to data given by local fishermen catching spring-spawning Baltic herring with herring trapnets, Baltic herring occured near the spawning site at Ängholmen as early as the end of April. However, spawn was not found on the transects at Ängholmen or Stuguholmen until 7.5., when the eggs were about two days old. According to SJÖBLOM (1961), the first Baltic herring that reach the shore are not mature fish but so-called ice fish, coming to feed in shallow waters.

3. Spawning substrates

The most common spawning substrate was vegetation. Spawn was also observed on bare gravel, on stones and on blue mussels (*Mytilus edulis*). Vegetation is the main spawning substrate reported in most other studies (RANNAK 1971, OJAVEER 1981b, RAJASILTA and RANTA-AHO 1981, ANEER and NELLBRING 1982). In the studies by ANEER and NELLBRING (1982) in the Askö area in Sweden, the most important substrates were the filamentous algae *Pilayella littoralis* and *Ectocarpus sp.*, which agrees with our own observations. Contrary to our observations, however, the authors did not find Bal-

tic herring eggs on substrates other than vegetation. However, in the Southern Baltic Sea spawning has been observed on stones and gravel in addition to vegetation (BIESTER et al. 1979), as also in the Gulf of Riga (RANNAK 1959).

Although spawn was mainly found on vegetation, this does not necessarily mean that Baltic herring search for vegetation. It is more probable, as suggested by ANEER and NELLBRING (1982), that the spawning substrate itself is not so important but rather an environment rich in oxygen.

4. Spawning temperature

The Baltic herring attempts to spawn in shallow water, probably because of the better circulation. Another factor determining the depth of spawning is the water temperature. According to OJAVEER (1981b), in the Gulf of Riga the spring-spawning sea herring spawns in temperatures of 5-13 ^{o}C and the gulf herring in 9-17 ^{o}C. In this study the temperature at the beginning of spawning time at a depth of 0-2 m was about 5-6 ^{o}C. According to SJÖBLOM (1961), Baltic herring start to spawn in Finnish waters when the water temperature has risen to 6-7 ^{o}C. A rapid rise in temperature in the surface water in early June clearly affected the spawning depth at Stuguholm. At this time the greatest amounts of spawn were deposited in depths of 4-6 m, where the temperature was only about 6 ^{o}C, compared with 18 ^{o}C at the surface. Spawning was not observed in temperatures higher than 15 ^{o}C.

5. Vertical distribution of spawn

The upper and lower limits of the vertical distribution were 0.2 and 6.5 m. These agree with the spawning depths reported by RAJASILTA and RANTA-AHO (1981) in the Archipelago Sea, SW Finland: 0.2-3 m in May and 1-4 m later in the summer. According to our SCUBA observations in the Archipelago Sea in 1981, the spawn distribution range was 1-6 m. In an extensive study by ANEER and NELLBRING (1982) in the Askö area in Sweden, the spawning depth ranged between 0.4 and 11 m. According to observations by OJAVEER (1981b) in Pärnu Bay, Estonia, spawning occurred at 3-10 m.

Only a slight downward shift could be seen in the depth of the densest spawn deposits as the spawning time proceeded (Fig. 7); the downward shift in the lower limit of spawn deposition was more pronounced.

6. The number of eggs spawned

The total number of eggs and egg densities varied greatly between the spawning beds and sampling dates (Figs. 2-6).

According to the great standard deviation between parallel samples, the aggregation of the eggs was high. In spite of the wide confidence limits of the mean (Appendix 2), the mean egg densities agreed fairly well with the visual observation made by the divers.

The maximum egg densities, approximately 10^6 eggs m^{-2}, were high compared with the maximum densities presented earlier, 1.3×10^4 eggs m^{-2} (RAJASILTA and RANTA-AHO 1981).

The size of the stocks of spawning Baltic herring in the study area calculated from the egg numbers on random transects (62 tons) is too small. The Baltic herring catch from six trapnets near Stuguholmen and Ängholmen was as much as 98.6 tn. For estimates of the spawning stock size based on estimates of the total egg numbers in a certain area, the number of random transects and the number of egg samples taken from each transect should evidently be much greater.

7. Mortality

When egg mortality is considered, attention should be paid to the following factors, which cause under or overestimation of the real and final mortality. The estimate is lowered by taking samples before the hatching stage, decomposition of dead eggs, predation and washing away of spawn from the spawning grounds. The estimate is raised by old dead eggs derived from previous spawnings and hatching of eggs before sampling. Account should also be taken of inter-sample variation in the ages of the eggs.

The proportion of dead eggs increased as the spawning time progressed from May to July. The increase of mortality in the samples taken from Stuguholmen after May is partly due to the presence of old dead eggs, left

from previous spawnings.

The deleterious effect of high water temperature can be seen in the high mortalities after a heatwave in early June. RANNAK (1971) also observed a rise in herring egg mortality in the Gulf of Riga with increasing water temperatures, but there the maximum proportion of dead eggs was only 15 %, in a water temperature of 18 °C. The reason for the high mortalities in our study in early June may have been both the high temperature and the rapid fall of temperature after the heatwave. Laboratory experiments with Baltic herring and Atlantic herring embryos have also showed higher egg survival in cold than in warm water (BLAXTER 1956, OJAVEER 1981c), but in OJAVEER's study (1981c), low temperature, 3 °C, was observed to be harmful as well. As the mortality in our own laboratory experiments was negligible at both temperatures, the increase of water temperature in the summer evidently does not alone explain the clear increase of mortality in June and July. A further explanation of the high mortality might be an unfavourable environment for the eggs. When the temperature of the water rose in early June, the herrings spawned at greater depths. When vegetation was lacking the eggs were deposited on gravel and on blue mussels (*Mytilus edulis*). The water circulation at such depths may be expected to be weaker than in shallow water, particularly for eggs that have fallen between grains of sand or gravel. *In situ* experiments with Pacific herring eggs have shown an increase in mortality with increasing depth (TAYLOR 1971).

Mortality was high among the eggs attached to abundant filamentous algae in late June and early July. ANEER and NELLBRING (1982) observed that almost all of the eggs died in places where the old parts of filamentous algae were decomposing and hydrogen sulfphide formed. A low oxygen content can thus be the reason for the high mortality in the summer, though no hydrogen sulphide could be observed in our study. A strong increase of filamentous algae and decrease of bladder-wrack (*Fucus vesiculosus*) have been observed off south-western Finland in the last few years (KANGAS et al. 1982). The effects of this change on the spawning of Baltic herring are unknown, but the oxygen content is probably higher on bladder-wrack than on dense filamentous algae.

In many studies the rate of development and mortality of eggs have been found to relate to the thickness of the egg layers (BLAXTER 1956, TAYLOR 1971, GALKINA 1971, BAXTER 1971, OJAVEER 1981b). In thick layers the lowest eggs are found to thrive poorly; their develoment slows down and the hatching rate falls. This is thought to be because of the poorer supply of oxygen and difficulties in getting rid of possible metabolic products among the undermost eggs (GALKINA 1971). OJAVEER (1981b) has also found lower ferti-

lization in the lowest eggs in egg mats 4-5 layers thick. Such thick layers of eggs were not observed in this study. Clusters with tens of eggs were occasionally found, but no differences in rate of development, fertilization or mortality were observed between the innermost and outermost eggs. On the contrary, in early May, when the egg densities were highest, the mortality was very low at Ängholmen and Stuguholmen.

The proportion of deformed embryos, in which no cell differentiation or cell organisation could be seen, increased from May to July. OJAVEER (1981c) has reported that a very cold incubation temperature, 3 °C, causes disturbances in the development of Baltic herring eggs in their early stages. It is possible that high temperatures or lack of oxygen have the same kind of effect on the first cell divisions of fertilized eggs. According to the literature, the mortality in natural spawning grounds is low. In samples of Baltic herring eggs collected in the Archipelago Sea, the proportion of dead eggs was below 10 % (RAJASILTA and RANTA-AHO 1981). According to RANNAK (1971), the mortality of Baltic herring spawn is well below 10 %. OJAVEER (1981b) reports that the proportion of dead eggs in Baltic herring spawn ranges between 0.2 and 31 %, depending on the environmental conditions and the stage of embryo development. The mean egg mortality of the Baltic herring in Rügen in the southern Baltic Sea was 9.9 % (BIESTER et al. 1979). In the studies of ANEER and NELLBRING (1982) the mean hatching rate of eggs moved from natural spawning grounds to the laboratory was 54 %. As the authors admit though, the transfer to the laboratory may have increased the mortality. Compared with the above values, the mean proportion of dead eggs in the samples in this study, 30.9 %, is rather high. The estimate of 13.6 % obtained from the egg numbers for the five transects that were quantitatively surveyed agrees better with the values obtained earlier.

8. Eggs lost by wave and current action

Detachment of eggs and increase of mortality by wave action have been observed in Pacific herring spawn in British Columbia, Canada (TAYLOR 1964). In our own study spawn was observed to be washed away at Stuguholmen, Trelänningen and Ängholmen, and this probably often occurs, though the data for the other spawning grounds are insufficient.

At Stuguholmen and Trelänningen algae and spawn detached from shallow sites were observed to accumulate in deeper waters. At Ängholmen the water current changed its direction, apparently moving loose *Monostroma* algae and

the attached eggs back and forth in the strait, although without causing an increase in the proportion of dead eggs.

Drifting rafts of algae with Baltic herring eggs were found twice. In spite of the high temperature and exposure to solar radiation, the eggs on these algal rafts were alive. Algae drifting in the archipelago are soon washed ashore, and these algae had probably only recently become detached, which would explain the low proportion of dead eggs. As Baltic herring spawn in very shallow and usually rather exposed localities, particularly in early spring, displacement by wave action may be of considerable importance.

Part of the eggs assumed to have been washed away from the transect may of course have been eaten. Gulls were observed to gather in shallow water at some spawning sites. It is probable that the gulls ate eggs which had become detached from their substrates and drifted ashore. Fishermen consider that gathering of gulls is an indication of Baltic herring spawning sites (ANEER and NELLBRING 1982). Among the fishes, the eelpout (*Zoarces viviparus L.*) (RANNAK 1959), cod (*Gadus morhva*) and whitefish (*Coregonus lavaretus*) are predators on eggs of Baltic herring.

9. Rate of development

In laboratory experiments eggs developed faster at 12 °C than at 7.6 °C. At 12 °C OJAVEER (1981c) observed the first Baltic herring larvae 150 hours after fertilization. In our experiment the first larvae were observed 154 hours after fertilization. The hatching times were shorter than those found in Atlantic herring (BLAXTER 1956). However, in the laboratory hatching experiments carried out by VUORINEN and AXELL (1980) the Baltic herring eggs hatched during 7-14 days at 14 °C.

As the temperature varies in the sea, the rate of development of eggs in natural conditions cannot be directly compared with the rates of development in the laboratory. Development was slow in early May. Hatching began approximately two weeks after spawning. During development the average temperature at 2 m was 6-6.5 °C. In the summertime, however, development was usually so rapid that weekly collecting yielded only one sample of eggs before they hatched. According to observations made both in the laboratory and in nature the hatching time varies greatly between individual eggs spawned at the same time.

VI. ACKNOWLEDGEMENTS

The personnel of Tvärminne Zoological Station gave us all the practical help needed during this study and took care of the important preparatory arrangements with the owners of the water areas and the fishermen. Local fishermen, particularly Paul and Per Nyholm, gave us valuable information on the spawning of the Baltic herring in the study area. Mr. Pentti Kangas (Lis.phil.) kindly lent us the suction sampler. Ms. Mervi Heinonen and Mrs. Anna Damström checked the English language. We are deeply grateful to all of them and to the many other people who contributed to this study.

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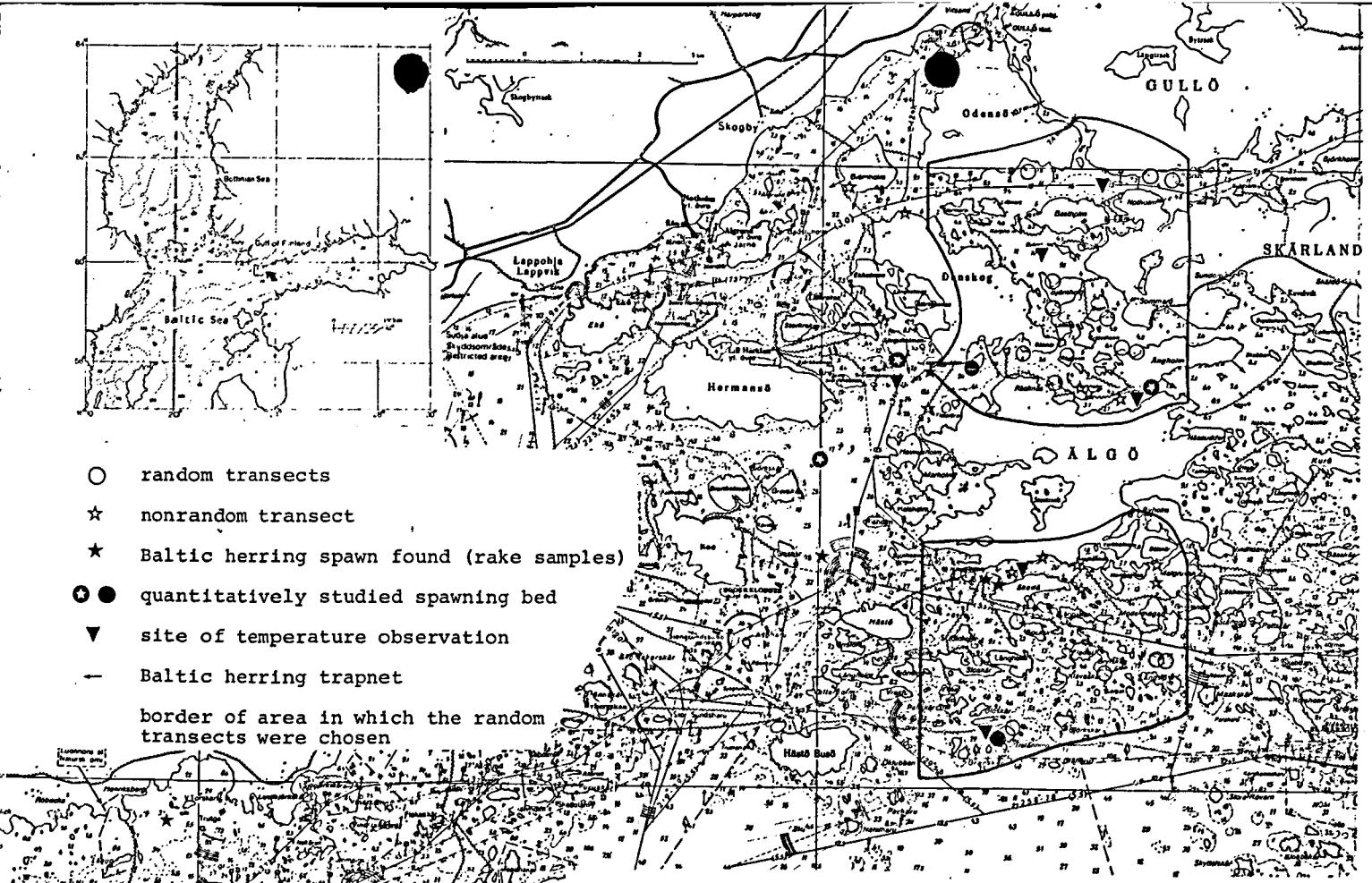


Fig. 1. Study area, sampling sites and the locations of Baltic herring trapnets.

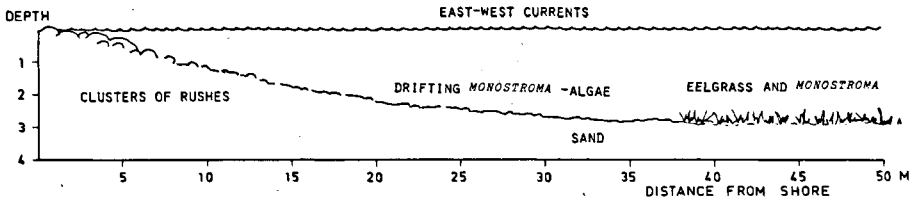


Fig. 2a. Bottom profile at Ängholmen.

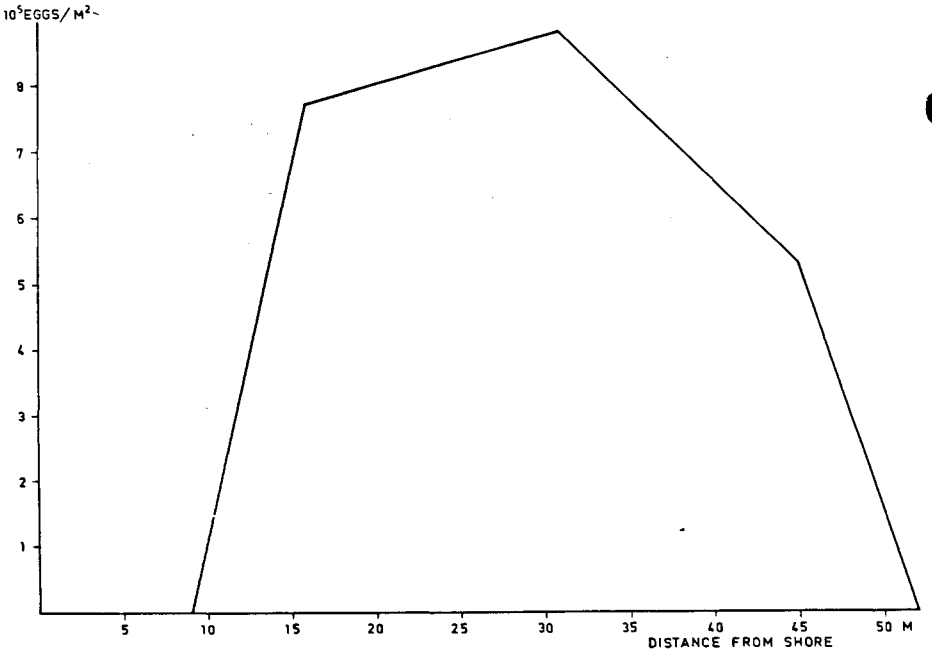


Fig. 2b. Total number of eggs deposited on the Ängholmen transect during the study period according to the samples taken on 16.5.

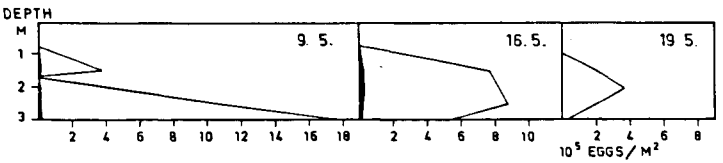


Fig. 2c. Egg density at different depths and dates at Ängholmen. White areas: living eggs, black areas: dead eggs.

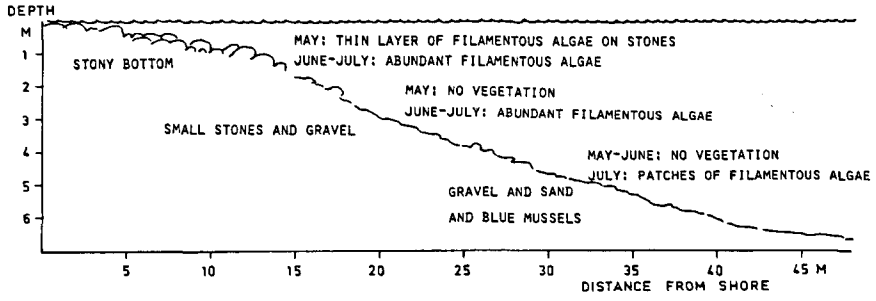


Fig. 3a. Bottom profile at Stuguholmen.

Fig. 3b. Total number of eggs deposited on the Stuguholmen transect during the study period.

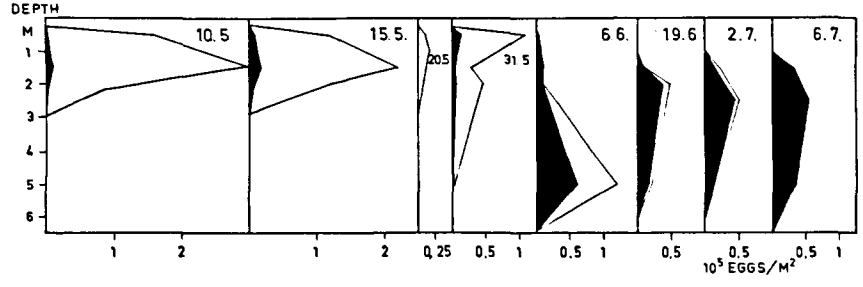


Fig. 3c. Egg density at different depths and dates at Stuguholmen. White areas: living eggs, black areas: dead eggs.

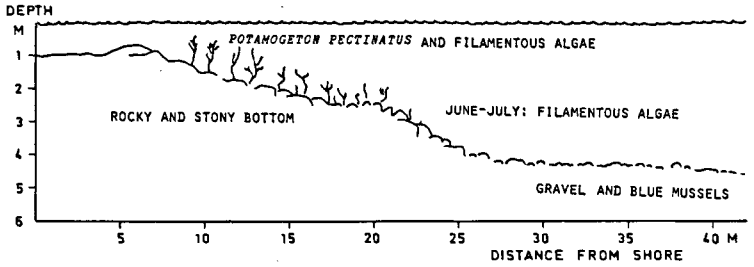


Fig. 4a. Bottom profile at Rönngrundet

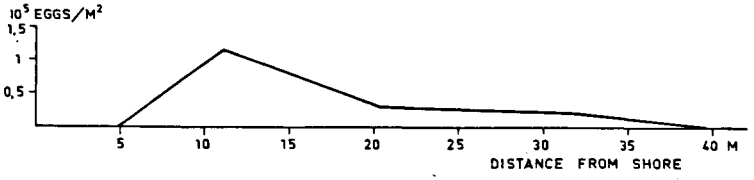


Fig. 4b. Total number of eggs deposited on the Rönngrundet transect during the study period.

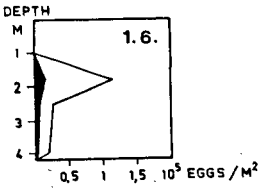


Fig. 4c. Egg density at different depths at Rönngrundet. White areas: living eggs, black areas: dead eggs.

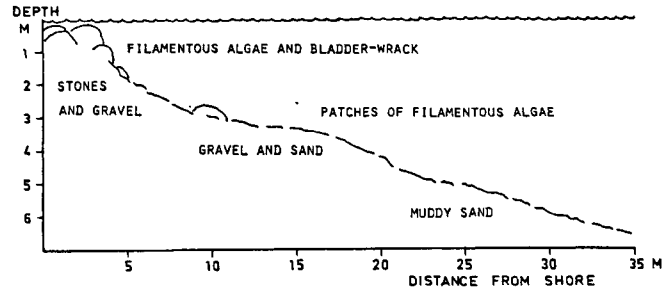


Fig. 5a. Bottom profile at Lindesholmen.

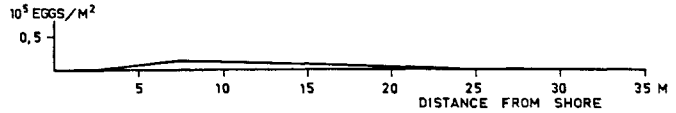


Fig. 5b. Total number of eggs deposited on the Lindesholmen transect during the study period.

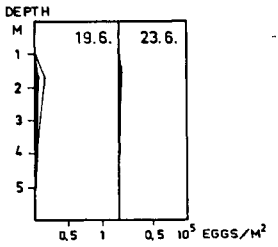


Fig. 5c. Egg density at different depths and dates at Lindesholmen. White areas: living eggs, black areas: dead eggs.

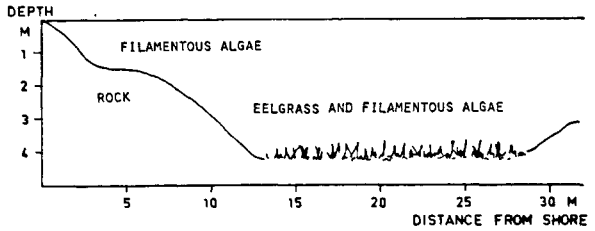


Fig. 6a. Bottom profile at Trelänningen.

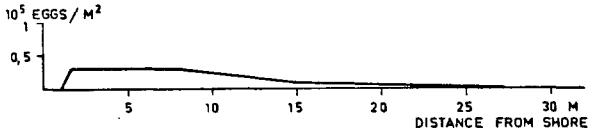


Fig. 6b. Total number of eggs deposited on the Trelänningen transect during the study period.

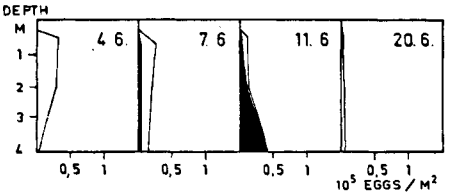


Fig. 6c. Egg density at different depths and dates at Trelänningen. White areas: living eggs, black areas: dead eggs.

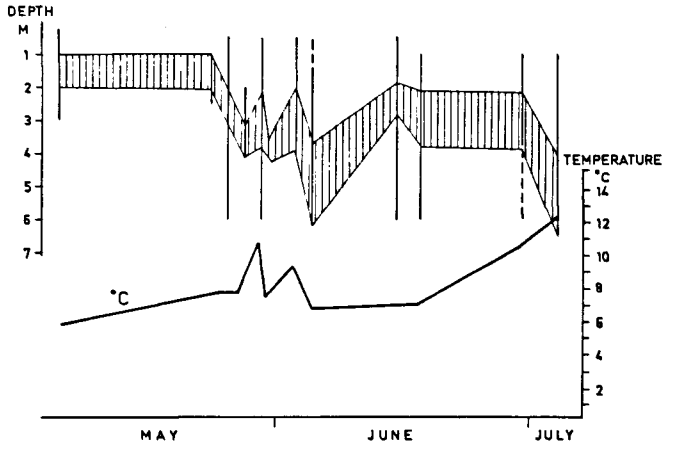


Fig. 7. The most common spawning depth and the water temperature at this depth. The upper and lower limits of the spawn distribution are marked with vertical lines. Broken line: occurrence of new spawn not certain.

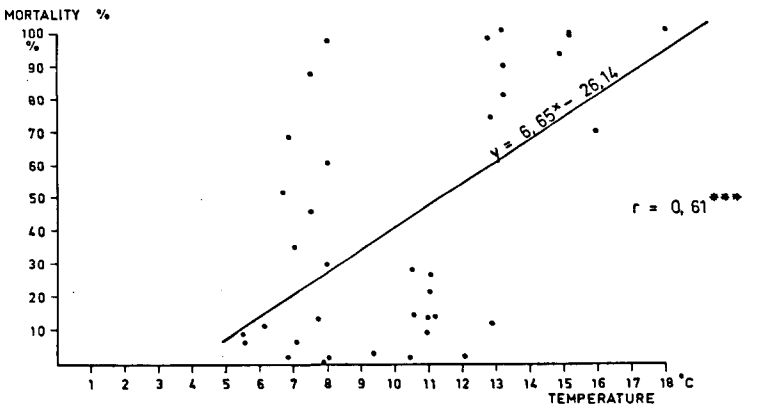
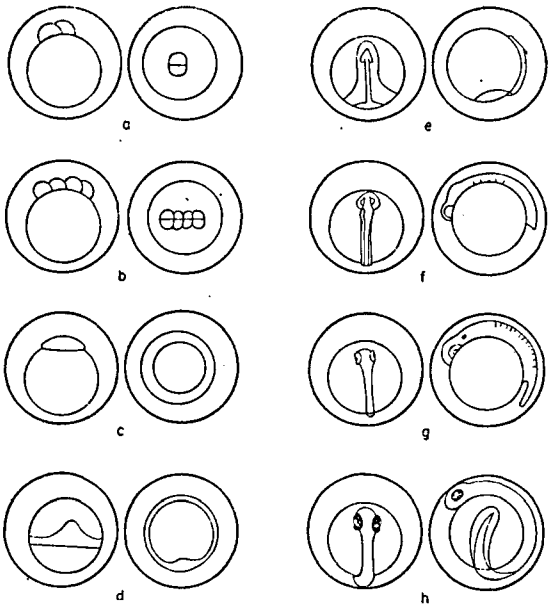


Fig. 8. The relation between water temperature and the proportion of dead eggs in samples.



App. 1. Stages of development of fish eggs (Braum 1978). a: 2-cell stage, b: 8-cell stage, c: embryonic disc, d: early gastrula, with embryonic shield formed, e: embryonic shield enlarged, blastopore still open, f: blastopore closed, the embryo half surrounds the yolk, myomeres appear in the middle of the trunk, g: tip of tail free of the yolk sac, eyes well developed, myomeres numerous, h: larva before hatching.

Appendix 2. Egg number per m^2, 95 % confidence limits of the mean and the proportion of different egg development stages (BRAUM 1978), larvae, deformed eggs and dead eggs in different samples. Weigh. = Weighting value of the sample, e.g. width (m) of the depth zone, N = Number of parallel samples.

						Egg development stages									
Date	Place	Depth	Eggs/m^2	95 % confidence limits of the mean	N	c	d	e	f	g	h	larvae	dead eggs	deformed eggs	Weigh.
9.5.	Ängholm	1,5	385.836		1	95,6							4,4		4
		2	366.611		1	95,5							0,5		17
		3	1.761.925		1	98,6							1,4		14
10.5.	Stuguholm	0,5	158.365 ±	144.962	5			97,4					2,3	0,3	6
		1,5	299.455 ±	431.980	3			95,9					3,7	0,4	4
		2,2	84.689 ±	121.868	3			95,4					4,3	0,3	5
15.5.	Stuguholm	0,5	119.939 ±	48.735	3				0,8	93,0			5,4	0,8	6
		1,5	220.795 ±	145.760	3					91,8			7,7	0,5	4
		2	118.948 ±	203.490	2					93,8			6,1	0,1	5
16.5.	Ängholm	1,5	769.876 ±	1.057.411	3					97,7			2,0	0,3	14,5
		2,5	881.098 ±	1.314.788	3					97,7			2,3		14,5
		3	528.151 ±	1.024.974	3					97,7			2,3		14
19.5.	Ängholm	1	196.640 ±	347.882	3						98,0	1,1	0,9		11,5
		2	357.364 ±	1.058.113	3						98,4	0,9	0,7		17,5
		3	35.442 ±	42.245	3						98,6		1,4		14
20.5.	Stuguholm	0,5	12.415 ±	20.212	3						99,1	0,5	0,4		6
		1	17.374 ±	29.138	3						89,9	2,4	7,7		4
		2,5	7.458 ±	11.491	3						89,4		10,6		5

Appendix 2., cont.

Date	Place	Depth	Eggs/m^2	95 % confidence limits of the mean	N	Egg development stages c	d	e	f	g	h	larvae	dead eggs	deformed eggs	Weigh.
31.5.	Stuguholm	0,5	109.645 ±	128.456	4	70,8				15,6			13,6		4,5
		1,5	28.010 ±	30.985	3	67,7				4,4			27,9		4
		2	47.606 ±	90.630	3	66,0				20,0			14,0		11,5
		5	7.763 ±	14.877	3	1,1			76,7	1,1			21,1		17
1.6.	Rönngrund	1,8	114.980 ±	374.695	3						86,7		13,3		12
		2,5	27.086 ±	67.291	3				20,6	50,0	2,9		26,5		7
		4,2	18.023 ±	32.216	3				70,6				29,4		16
4.6.	Trelänning	0,5	33.516 ±	53.694	3	0,5		97,9					1,6		1
		2	30.198 ±	55.062	3	98,4							1,6		11
		4	6.019 ±	1.539	3	3,1			95,0				1,9		15
6.6.	Stuguholm	0,5	2.755 ±	3.235	3								100,0		4
		1,5	10.214 ±	18.942	3	19,9				0,2			79,8		4
		2	11.400 ±	21.540	3	30,5							69,5		11
		5,5	121.858 ±	113.261	3	46,6			0,6	1,7			51,1		18
7.6.	Trelänning	0,7	26.687 ±	46.951	3				0,2	82,6			17,0	0,2	1
		2	21.553 ±	9.147	3				78,4				21,0	0,6	11
		4	17.875 ±	5.963	3				77,7	0,8	0,5		17,8	3,2	15
11.6.	Trelänning	0,5	12.175 ±	28.933	3						76,7		23,3		1
		2	15.968 ±	15.453	3				1,1	5,7	25,9		67,3		11
		4	40.227 ±	38.561	3				0,6		6,3		93,1		15
19.6.	Lindesholm	1	832 ±	566	3				40,0				60,0		1,5
		1,7	14.330 ±	24.658	3				53,2				45,2	1,6	7
		4	3.488 ±	3.010	3				60,5				34,8	4,7	20

Appendix 2., cont.

Date	Place	Depth	Eggs/m^2	95 % confidence limits of the mean	N	Egg development stages c	d	e	f	g	h	larvae	dead eggs	deformed eggs	Weigh.
19.6.	Stuguholm	1,5	21.572 ±	20.532	2					0,2	2,0	0,2	97,5	0,1	5
		2	45.418 ±	290.495	2	9,0	1,4		0,2				87,2	2,2	11
20.6.	Trelänning	1	992 ±	2.223	3						22,0	7,3	70,7		1
		2	1.474 ±	1.443	3						2,5		97,5		11
		4	5,728 ±	4.303	3						1,4		98,6		15
23.6.	Lindesholm	1,5	2.155 ±	12.168	2						8,7		91,3		1,5
		4	1.043 ±	1.956	2						31,1		68,9		27
2.7.	Stuguholm	1,5	21.727 ±	30.322	3			19,7					74,5	5,8	5
		2,5	49.658 ±	37.001	3			10,6					82,6	6,8	11
		5	16.211 ±	7.654	3								100,0		14
6.7.	Stuguholm	1,5	30.537 ±	47.931	3			0,4	0,6				91,6	7,4	5
		2,5	56.697 ±	80.397	3			1,3	0,6				96,7	1,4	11
		5	36.784 ±	16.084	3			7,1	0,8				83,7	8,4	21,5