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EGG MORTALITY IN RECRUIT- AND REPEAT-SPAWNING COD - AN EXPERIMENTAL STUDY

by

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ABSTRACT

Experiments on the reproduction of individual Norwegian coastal cod and for the Arcto-Norwegian cod were conducted during the years 1989-92, and the year 1995 respectively.
The experimental fish used were held in captivity over several consecutive spawning seasons to investigate differences in egg mortality within and between spawning seasons. Egg mortality was found to be restricted to the first days of incubation. For coastal cod a significant reduction of egg mortality was documented from first to multiple spawning from the same cod female. Similarly, a decreased egg mortality was found in the first egg batches compared to the last ones. Preliminary results on Arcto-Norwegian cod showed similar trends.
The results are discussed in relation to egg surveys, management of spawning stocks and the combined match/mismatch-maternal recruitment variability model.

Introduction

In recent years the effects of maternal factors on eggs and larval viability, and hence on the recruitment variability, have had its renaissance in Western fishery science. This research was started by Soviet scientists during the 1930's on fresh water fish. Nikolskii (1962, a,b) proposed that maternal factors influenced recruitment variability. Studies on cod (Solemdal 1970), winter flounder (Buckley et al.1992 a,b), striped bass (Zastrow et al. 1989) and capelin (Chambers et al.1989) have all demonstrated the significance of the maternal factor on eggs and larvae viability.

Maternal effects on reproductive parameters in cod, egg size, larval activity etc., have been documented on captive Norwegian coastal cod (Kjesbu et al. 1995) and field caught Arcto-Norwegian cod (Solemdal et al.1992 a,b,;1993). The day of first spawning

in cod is probably also influenced by a maternal factor (Kjesbu 1994).
For Arcto-Norwegian cod in the Lofoten area egg mortality during incubation can be as high as 90 % (Fossum 1988).
Experimental studies have demonstrated that the most pronounced egg mortality occurs during the first few days of development (de Braak 1994, Nissling & Westin 1991).
Egg mortality in the field has been attributed to a size-selective predation, the smallest eggs being consumed more frequently than the larger eggs (Rijnsdorp & Jaworski 1990).
The present paper focus on the variability in the natural mortality of cod eggs caused by the maternal effect, both within and between spawning seasons. The significance of these sources of variation in egg mortality for the interpretation of egg surveys and recruitment variability is discussed.

Materials and methods

Brood stock
We used fish produced in a mass rearing programme at the Austevoll Aquaculture Research Station, Norway (Naas 1990, van der Meeren 1993) reared from eggs of local, Norwegian coastal cod.
In addition, Arcto-Norwegian cod were caught in the Bear Island area and transported to the Institute of Marine Research, Bergen.

Fish were stocked in outdoor seawater tanks of 30 m^3, and fed moderately on wet pellets (0.5% wet body weight per day). No food was given to the fish during spawning as they do not normally feed at this time (Kjesbu et al.1991).
The sex of the fish was identified in prespawning specimens which were anaesthetized by means of benzocaine or, more recently, metomidate (Mattson and Riple 1989,Thomas & Robertson 1991), and catheterized (McEvoy 1984 , Kjesbu 1989). The ovarian biopsy samples were placed under a binocular microscope and the mean diameter of the most advanced vitellogenic oocytes was measured to forecast the calender day of first spawning (Kjesbu 1994).

Immediately before spawning, pairs of selected females and males were moved to one of 10 chambers in an indoor circular seawater tank of 200 m^3 with a natural light cycle. The criteria for the selection of a pair of fish included the feeding history, sex, health status and the predicted date for the start of spawning. The females were placed in the same chamber each year.
The ambient water temperature was measured on a weekly basis throughout the whole experiment but every day during spawning. The temperature variation in the 6 months prior to spawning was ±0.5° C.

During the years 1989-92 coastal cod were kept in captivity and their egg characteristics investigated during their spawning period. Each cod female was monitored separately and each egg batch sampled separately (Kjesbu et al 1995). The size of the eggs increased significantly from first to second year of spawning. Subsequent years the egg size increased more slowly.
Parallel to this work experiments on egg mortality were performed.
During 1994 and1995 the broodstock of Arcto-Norwegian cod from the Bear Island

area was monitored in an identical manner to the coastal cod.

Egg mortality

Eggs sampled from the spawning chambers, temperature 8-9 °C, were kept in a refrigator at 5 ° C until the eggs reached developmental stage 1a according to Westernhagen (1970).

Eggs were then sterilized in 1% Buffodin for 10 minutes and rinsed in seawater. Buffodin is a iodine-based fish farming disinfectant, and used against major fish viruses (Evans Vanodine International LTD).

Seawater used for the experiments was passed through 10 and 30 micron filters and an UV-irradiation system.

The following compounds were added to the seawater used for the experiments: Mycostatin (2500 IU/l), streptomycin sulphate (0.05 gram/l) and doktacillin (0.2 gram/l).

Two hundred eggs were chosen for each egg mortality experiment with coastal cod. All experiments were performed in parallel. The egg pipette and the vial to count the eggs were rinsed in 4 % formaldehyde.

30-40 eggs were inspected at the time under a low power stereomicroscope. Eggs were rejected on the basis of the following criteria: Unfertilized, activated, dead, irregular cleavages and eggs from previous egg batches.

The selected eggs were transferred to one litre glass jars with prepared sea water, and placed in a refrigator at 5° C.The temperature was recorded daily. Dead eggs were removed each day with a pipette specific for each jar, counted and staged. Developmental stage was checked on live eggs every third day. In a few cases bacterial infection developed. These experiments were excluded from the material.

Eggs from Arcto-Norwegian cod were inspected according to the same criteria as for the coastal cod. Each egg was put into a NUNC tray (Roskilde, Denmark), with 2 ml of 70 % autoclaved seawater. Parallels of 24 x 2 eggs were used in each experiment.

From 108 egg mortality experiments with coastal cod eggs in parallels the difference between replicates was less than 10 % in 80 % of the experiments.

Twenty-one egg mortality experiments with eggs from Arcto-Norwegian cod in NUNC-trays had a mean difference between replicates of 2.5 %.

Results

The mean cumulative egg mortality during incubation is shown in Fig.1 for cod females 1,4,5 and 6 (see Fig.2). Mortality was highest during the first five days of development, i.e. the period prior to gastrulation.

In Fig.1 the cumulative egg mortality from cod female 1 (see Fig.2) as first, second and thirdtime spawner are also given. The curves are based on the same egg batches, 1,6,9 and 13 for the first and third spawner and egg batches 2,6,911 and 15 for the second time spawner. Note the similar mortality pattern between the firsttime spawner and the cumulative egg mortality curve from the pooled material, in contrast to the low egg mortality from the second and thirdtime spawner.

In Fig.2 the total egg mortality from the ten studied coastal cod females investigated during several spawning seasons are shown. The egg mortality investigations was a part of a broader study of the reproductive biology of the cod females (Kjesbu et al. 1995).

A normal development of the actual fecundity was considered to be an important paramater for the evaluation of reproductive normality. From Kjesbu et al. (1995) data on age and actual fecundity are shown in Fig.3. Cod females no. 3 and 9 show very irregular trends in actual fecundity, and were excluded from the material. Both cod females developed a 100% egg mortality during their multiple spawning seasons.

In addition two other cod females (no. 2 and 7) were excluded from further analysis. Cod female 2 produced extremely thinshelled eggs giving 100 % egg mortality both seasons (Fig.2). Number 7 had an irregular cycle in the production of the egg batches. Cod females 8 and 10 had a normal development of the actual fecundity, but were not studied as firsttime spawners. From this reason they will not be included in further analysis.

The high, but irregular, actual fecundity of cod female 8 (Fig.3.) was reflected in the egg mortality (Fig.2.).

In Fig. 4 the weighted total egg mortality from first time spawners and repeat spawners are pooled from fish 1,4,5, and 6 judged to have "normal" patterns in egg production and mortality.

Total egg mortality at different stages in the spawning cycle is given in Fig.5.

The results from the egg mortality experiments on Arcto-Norwegian cod, first and second spawners in 1995, are shown in fig.6.

Discussion

Egg mortality experiments have been criticized for being sensitive to microbal infection as well as being sensitive to the antibiotics to reduce microbal growth. The present egg mortality experiments on Norwegian coastal cod and Arcto-Norwegian cod were performed with identical methods throughout the experimental period, and the trend in the results from the two methods were similar. Analyzing the parallels strengthens our conclusion that the results are of biological significance and not only artifacts due to the artificial environment.

The high egg mortality during the initital period of incubation can not be caused by artificial means . The eggs used in the mortality experiemnts were carefully selected, such that eggs developing abnormally were rejected. The results in Fig.1 indicate that this early incubation period is very sensitive in a maternal sense. This sensitivity is illustrated by the egg mortality pattern from the first,second and third spawning of cod female 1. The egg mortality pattern of the first spawning cod female shows similar high egg mortality during the first period of incubation as the pooled egg mortality curve. Negligible egg mortality occur during the rest of incubation for both curves. In contrast, the egg mortality from the second and specially the third spawning season of cod female 1 is very low, suggesting a strong maternal influence on the egg mortality during the early sensitive period of incubation. This result corresponds to the significant increase in egg size frem first to muliple spawning (Kjesbu et al. 1995).

In the literature, varying egg mortality patterns and levels are given,for pelagic eggs, both from field and experimental investigations. No similar experimental work on individual spawning fish over several years are found in the literature.

The susceptibility of eggs from Arcto-Norwegian cod to mechanical shock was pronounced during early developmental stages (Rollefsen, 1930,1932,). Later experimental work to evaluate the effect of different environmental parameters on egg mortality also revealed the level of natural egg mortality pattern. Working on cod eggs from the east coast of USA, Bonet (1939) concluded:" At all temperatures an initial period of high mortality decreased with the closing of the blastopore and was followed by a period of low mortality until the embryo was three-quarters the circumference of the egg membranes, when the mortality steadily increased up to hatching".
High egg mortality both during early and later stages were also reported on cod eggs from Rhode Island, USA (Laurence & Rogers 1976). This is contrary to similar investigations on other species, showing high egg mortality during the gastrulation period (Alderdice & Forrester 1971, Blaxter 1969, Holliday & Jones 1967). On this background Laurence & Rogers (1976) conclude:.."the cod appears to be an exception with its increased mortality just prior to hatching". It should be noted, however, that the frequency of abnormal larvae were very high in this material, varying from 27 to 43 % in the different experimental groups.

The egg mortality pattern from Gotland cod in the Baltic, using the same method as the present authors, were similar to the present results, reaching about 50 % during the first 5 days of incubation (Nissling & Westin 1991).
Danielssen & Iversen (1974), studying egg development and mortality in plaice, Norwegian coastal cod and herring in different temperatures concluded that:" Special high egg mortality was not demonstrated in certain stages during incubation". However, looking at the egg mortality patterns in the "normal" temperatures 6,8 and 10° C, clearly show a pronounced egg mortality during the first days of incubation. Using the same method on selecting eggs for the experiments as the present authors, de Braak (1994) also demonstrated the same egg mortality pattern during the first days of incubation in eggs from Arcto-Norwegian cod.

The field investigation on plaice eggs by Brander & Houghton (1982) indicates the same possibility. While the early stages of the plaice eggs did not correlate with recruitment, egg stages just prior to hatching showed higher correlations.

In an investigation of critical larval stages from a large number of species, Vladimirov (1974) concludes:"As experimental data have shown, critical periods of development are revealed only in progony, with morphological and physiological defects inherited from the parents or aquired under the influence of unfavourable conditions of embryonic and postembryonic development". Rothschild (1986) is of similar opinion:" The possible causes of nonpredatory egg death are not well understood, but they might be linked to cytological competence or to unfavourable environmental conditions". Dahlberg (1979) in a rather comprehensive article on survival of eggs and larvae do not mention this type of mortality.
Kjørsvik (1994) states that though egg mortality usually is considered to be a laboratory phenomenon, field investigations have revealed that genetic and other biological factors contribute significantly to natural egg mortality.

From this review we conclude that during the early stages of egg development when mortality rates are highest maternal effects are of significance. The high egg mortality observed during this period, can be called a natural egg mortality. The reduced egg mortality observed in multiple spawners can be classified as a maternal effect changing the magnitude of this natural mortality. This effect is associated with an increase in egg size from first to second spawning but seems to level out for third spawners as also found for the egg size (Kjesbu et al. 1995). Similar studies on other commercial species are lacking, and no physiological explanation of this phenomenon is available.

Our studies demonstrate that using captive fish and investigating them over consecutive spawning seasons is the best method for describing maternal factors on egg mortality and larval viability, due to the batch spawning and the individual variability.
The present broodstock of Norwegian Coastal cod were reared from the egg stage, and they were given identical food and environmental conditions throughout the experimental years. It is obvious that long-term investigations on fish reproduction, which is a sensitive process, needs thourough monitoring of the total biological status of the fish. Besides the reproduction parameters like fertilization percentage, egg size, egg batch size, actual fecundity, interval between egg batches etc., the growth , condition and behaviour of the spawning fish were also recorded. Thus, on this basis it was possible to include the history of the egg material tested. Fig. 4 shows a clear effect of a reduced egg mortality from first to multiple spawning. Kjesbu et al. (1991) demonstrated a decreased actual fecundity and an increased atresia in cod starved for a long time. In the present investigation the first spawners were fed equal to the multiple spawners and the condition of the different aged spawners were kept at the same level.
The present results are a contribution to the discussion of the reproductive effects of the composition of the spawning population (Ulltang in press). Data on age/size, condition and fecundity of the spawning females and the maternal influences on the viability of eggs and early stages will improve the knowledge of the reproduction potential of stocks.
Egg mortality also change in a systematic way according to the number of egg batches, being higher at the end of spawning, as Fig. 5 shows. This change follows the general trend of the reduction in egg size, most probably the result from an innate rhythm under hormonal control (Kjesbu et al. 1995). The increased egg mortality at the end of spawning indicates that the cod female is in a state of physiological exhaustion. Investigations on the fatty acids during spawning demonstrated a reduction of 23 % in total fatty acid compound from the first to the eighteenth egg batch (Ulvund & Grahl-Nielsen,1988). Of special interest was the more pronounced reduction in saturated fatty acids compared to monoenic fatty acids. Similarly,the total amount of the main free amino acids in the cod eggs were reduced during spawning from 250-300 to 150-200 nmoles. These effects on egg mortality are uncertain (Mårstøl et al. 1993).

The preliminary results from Arcto-Norwegian cod indicates a similar maternal effect on egg mortality between first and second spawners, but perhaps with a less reduction in egg mortality. The size of firstspawning coastal cod and Arcto-Norwegian cod differ considerable, being about 600 grams,40 cm and 2500 grams and 65 cm, respectively.

Rijnsdorp & Jaworski (1990) introduce a new method in the study of egg mortality, being solely the result of size-selective predation of the smaller cod and plaice eggs.

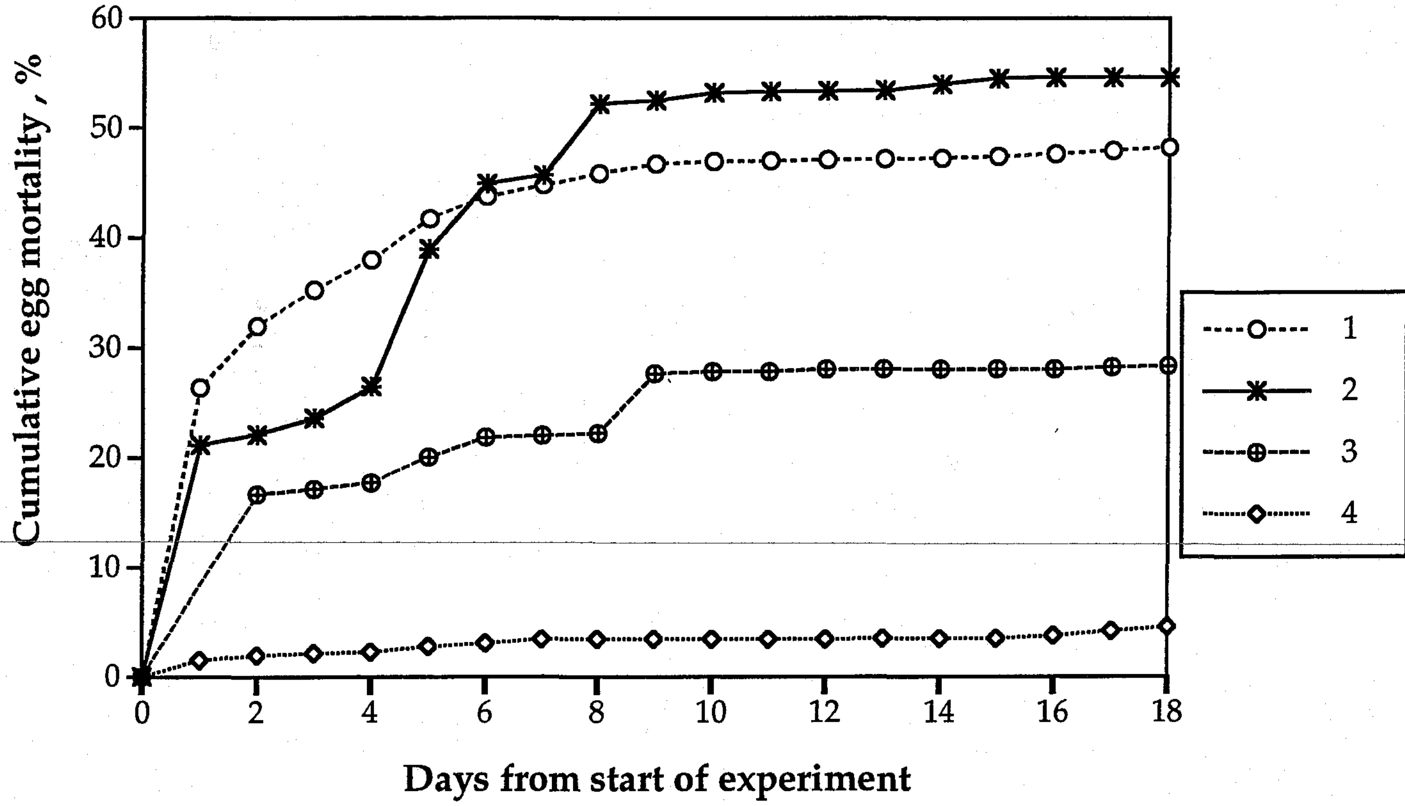
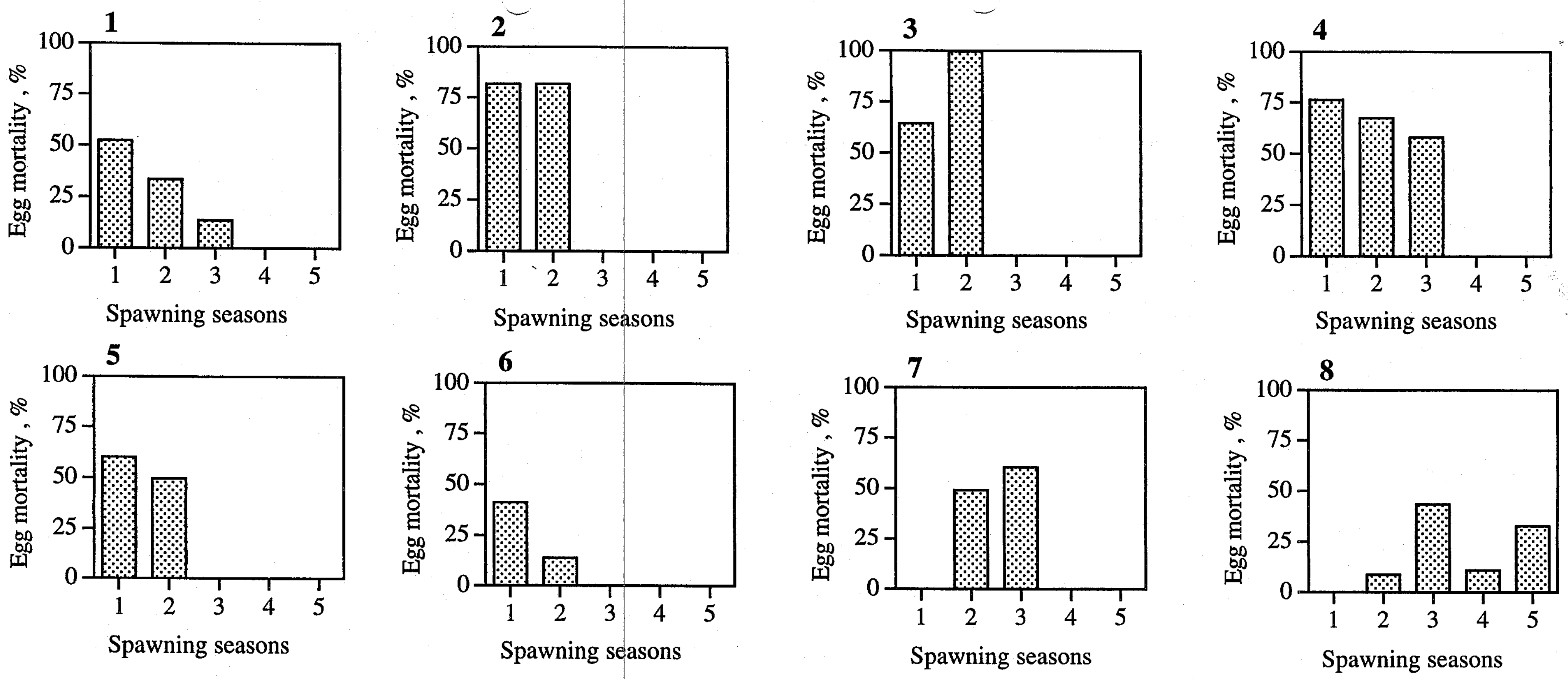


Fig.1. Cumulative egg mortality curves from captive Norwegian coastal cod.

1. Data from all egg mortality experiments pooled from cod females 1,4,5 and 6.
2. Data from egg batches 1,6,9,13 pooled, cod female 1 as first time spawner.
3. Data from egg batches 2,6,9,11,15, pooled, cod female 1 as second time spawner.
4. Data from egg batches 1,6,9,13, pooled, cod female 1 as third time spawner.



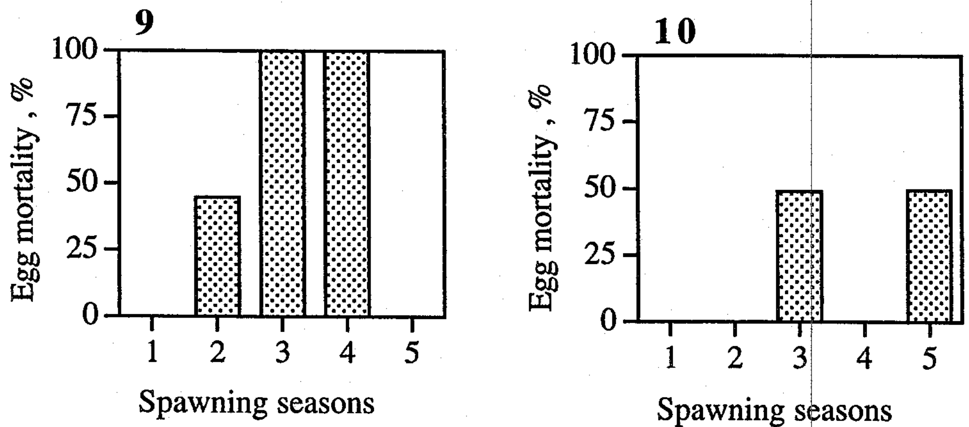


Fig.2. Total egg mortality for ten Norwegian coastal cod females, over succesive spawning seasons. Individuals are identified by number in top left-hand corner.

The present data suggest that variation in mortality and egg size relations between first time and multiple spawners could explain the egg size and mortality given in Rijnsdorp & Jaworski (1990).

A combined match/ mismatch idea (Hjort 1914) with the accumulating facts of the maternal effects, to illustrate the synergistic effect in recruitment variability, has been developed through several publications: Ellertsen et al.(1989), Ellertsen & Solemdal (1990), Solemdal & Kjesbu (1992) and developed further in Kjesbu et al. 1995. The main fact in this idea is the interannual time-stable hatching period for Arcto-Norwegian cod larvae and the interannual time-variable period of the production of Calanus nauplii, due to the temperature variable coastal water where Calanus is spawning.
During warm years, a condition to produce large year classes of Arcto-Norwegian cod, the first hatched larvae are the largest and will hatch during optimal feeding conditions. These newhatched larvae will be large due to two maternal factors:
1. They hatch from the first eggbatches with the largest eggs.
2. Some authers (Sund 1937, Marteinsdottir & Petursdottir 1995) claim the the largest fish start spawning first producing the largest eggs. Hutchings & Myers (1993) found the opposite trend in Canadian cod, and Kjesbu (1994) found no special sizespecific effect of day of first spawning of Arcto-Norwegian cod. However, this material was collected during a relatively short period and from a restricted part of the distribution area of the Arcto-Norwegian cod.
Fitting the present results of the egg mortality studies into the model showed in Kjesbu et al. 1995, the effect of egg mortality on year class strength during a warm year will be as follows:
Egg mortality from the early egg batches being the main contributors to the surviving larval population, will be low. These new facts give extra support of better basis for large yearclasses in warm years.
The situation will be opposite during a cold year. The small newly hatched larvae during the delayed optimal period of feeding are coming from the last egg batches, both giving eggs with high natural mortality.

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