SURVIVAL OF SPAWN OF THE PACIFIC HERRING
(CLUPEA HARENGUS PALLASII VAL.)
RELATED TO THE ABUNDANCE OF THE SPAWNING STOCK

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The correlation between the abundance of the spawning Pacific herring (Clupea harengus pallasii Val.) and the amount of deposited eggs have been dealt with in considerable detail in literature published in Canada, U.S.S.R. and Japan. Attempts have also been made to predict year-class strength from the number of eggs deposited. It has been established, e.g. at Vancouver (Canada), that there is no direct correlation, and even a negative one is possible, i.e. a great number of eggs can produce in some years a poor resulting year-class (Tester, 1948; Tester & Stevenson, 1949; Stevenson, 1949; Stevenson & Outram, 1952; Taylor, 1955; Taylor, 1963).

Information concerning the survival of Pacific herring eggs on spawning grounds is still insufficient (main investigations in Canada); analysis of the relationship between the survival rate of embryos and the number of spawning fish is almost lacking.

It is very difficult to study the factors which affect the survival of the eggs of the Pacific herring under natural conditions, because the development of eggs occurs within the littoral zone or in the upper part of the sub-littoral, and, as a rule, eggs are affected by the whole complex of variable conditions at the shore.

Continual observations on the spawning grounds of the Pacific herring in various regions of its area, despite a great variety of conditions affecting the eggs, have revealed a major influence of some factors.

The influence of water and air temperatures, silting, depths of spawning grounds, substrate etc. on the development and survival of eggs has been studied during several years (Galkina, 1959, 1960, 1961 and

Figure 7. The spawning grounds of the Pacific herring studied by the author.
Survival of spawn of Pacific herring in relation to spawn thickness and density, it is possible to discuss the correlation between these values and the abundance of the spawning stock.

Observations were carried out on spawning grounds in the Okhotsk (1954-57), Japan (1954-55), Barents (1964) and White Seas (1966) (Fig. 7).

The number of normally developed and viable larvae at hatching was assumed to be a measure of the survival rate of embryos in the eggs deposited. With this in view samples of algae with eggs were taken from parts of the spawning grounds with different spawn density (approximately 3 to 5 cm²) and were transferred to the laboratory 1 to 5 hours before the hatching of the larvae. Not less than 50 samples from each spawning ground were examined. During hatching, dead eggs and abnormal and normal larvae were counted. If in some parts of the spawn the larvae failed to hatch the observations continued.

This method for estimating the survival of eggs under natural conditions differs considerably from the one generally adopted. The method of analysis of preserved spawn is usually used, and the mortality of the eggs is determined by estimating the eggs which become white during fixation. Those eggs which remain transparent are considered to be normally developed. Many pathological changes in the preserved material remain, however, undetected; embryos become deformed, and this technique may lead to wrong conclusions about their viability.

Spawn in a single layer or eggs thinly scattered along the thallus of algae occur in the regions where herring is not abundant, e.g. in the south-eastern Barents Sea, in some parts of the White Sea and also in other seas at 1968). At the same time data were obtained which enabled us to establish the relationship between the development and survival of embryos on the one hand, and density and thickness of eggs deposited on the other. The latter is usually determined by the number of spawners, hence considering the survival of embryos in relation to spawn thickness and density, it is possible to discuss the correlation between these values and the abundance of the spawning stock.

Figure 8. The development of embryos in 3-4 layer thick spawn (embryos are taken from egg membranes, the rolled position of the body is caused by the fixative). 1. Embryos from superficial layer. 2. Embryos from 2nd layer. 3. Embryos from 3rd and 4th layers of spawn.

Figure 9. Abnormal embryos from 2nd layer of 3-4 layer thick spawn (from membrane); the upper layer, strongly bent head and pectoral part, small yolk-sac; the low layer, with underdeveloped body, head lacking.
periods with comparatively poor stocks. Thinly scattered eggs can also be seen in some parts of rich spawning grounds.

If eggs are deposited in the littoral zone they die after the first tide. In the upper sublittoral zone the survival of eggs is, as a rule, about 100% This is true, however, of eggs which are deposited on high vegetation; if eggs are laid on low vegetation some of them die from silting. Some of the eggs die even in single layers of spawn on Laminaria. This may be due to the excretion products of the latter.

Thick and multilayer spawn consist usually of 3 to 5 layers, but sometimes as many as 6 to 15 and even 16 to 20 layers were observed in one of the best littoral spawning grounds in the Okhotsk Sea in 1967 (the total area was 234-4 thousand m²; approximately 18 million spawning fish) and the sublittoral of the White Sea in 1966. The density of egg deposition on such spawning grounds reached 1-2 and even 5 millions per square metre.

Despite a considerable geographical separation of these two seas and the different location of spawning grounds, the development of the embryos within the eggs has so much in common that one may speak of regular features of these processes.

In multilayer spawn deposited on algae with a branched thallus and in double layers on Laminaria the development of eggs in various layers of spawn proceeds irregularly. Variations in the morphogenesis rate of embryos in spawn depend on the microregime which is caused by two main processes, the degree of oxygen penetration and the possibility for removal of the products of metabolism. Differences in the development rates of embryos in the various layers therefore depend on the thickness of spawn and the density of the egg deposition. In dense spawn with as little as 3 to 4 layers, the difference in the rate of morphogenesis may be considerable; in the superficial layer morphogenesis is just on the point of hatching, in the second one they are less developed with the eyes poorly pigmented, in the third and fourth layers the tail is just beginning to grow or it hardly reaches the head (Fig. 8). In thick spawn abnormal embryos were already seen in the second layer. They have a rudimentary head or it may even be lacking; they have a shortened, often spirally bent body, and a very small yolk-sac (Fig. 9). In the case of spawn with a greater number of layers the lack of development of the embryos in deeper layers may be more considerable. These processes depend on the substratum on which the eggs were deposited. (Galkina, 1961).

Asynchronism in the morphogenesis rate of embryos is apparently characteristic for the spawn of herring of the genus Clupea as it has been recorded for its subspecies (Lea, 1930; Runnström, 1941; Kryzhanovsky 1956; Altukhov, 1957). Kryzhanovsky believes that such irregularity in the development only slows down hatching of eggs situated in deeper layers of the spawn. Observations have shown, however, that as well as the delay in development of the embryos in deeper layers, death can also take place (Fridland, 1951; some notes of Lea and Runnström).

According to the author's observations the mortality rate of eggs depends not only on the thickness and den-

Figure 10. Larvae from multilayer spawn. 1. Normally but unequally developed. 2. With slightly bent body. 3. With spirally bent body. 4. Dead or semidecayed; they fall out during the hatching of normal larvae.
sity of spawn but also on the influence of some other factors such as substratum, where eggs develop, temperature, depth of spawning grounds etc.

In addition to dead eggs, the author found for the first time, when examining living spawn, many abnormal and non-viable embryos, although viewed through the egg membrane they seemed to be normally developed. The reason is that most such embryos show abnormalities due to various kinds of curvature of the body (Fig. 10). Such defects are hardly visible as in the egg membrane the embryos are normally in a bent position. The deviations can be detected only at hatching or when dissecting living eggs. The latter is very difficult, however, and gives poor results. During hatching of normal larvae from superficial layers, abnormal embryos hatch or rather they fall out from membranes together with the normal ones. As well as larvae with bent and twisted bodies, dying and partly decaying embryos fall out of the membranes (Fig. 10). The hatching of abnormal embryos from membranes is favoured by the hatching enzyme of neighbouring normal embryos and their own enzyme, because, despite abnormalities in the general structure, the hatching glands in many embryos are well developed. The number of such embryos can exceed 2 to 3 times the number of dead eggs.

After hatching, the remains of empty egg membranes from which have hatched normal, abnormal and even dying embryos, are left behind. Therefore, the presence of empty membranes is far from being a reliable indicator of the hatching of viable and normal larvae.

A great variety of micro-regimes of spawn closely associated with their micro-structures causes different relationships between the normally developed embryos, those with a slow morphogenesis rate, and dead eggs. The mortality of eggs and the occurrence of non-viable embryos caused both by the density and thickness of spawn and by the accompanying influence of other factors in rich spawning grounds can reach 70 to 80%.

Thus, the higher the abundance of spawning fish and the thicker the spawn, the higher the relative mortality of embryos as compared with the mortality of embryos in scattered and thin spawns deposited by scarce spawners. This is possibly one of the clues as to how the existence is maintained of the comparatively poor populations of the Pacific herring on the subarctic and Arctic Basins, where the amount of eggs deposited is low and the rate of survival (in the sublittoral zone) is high. This is perhaps one of the explanations of the negative correlation between the number of eggs deposited and the abundance of a resulting year-class.

It should, however, be kept in mind that with the high relative egg mortality in rich spawnings the absolute number of surviving embryos can be much higher than in poor ones. That is why the analysis of the relationship between the number of eggs deposited and the abundance of the resulting year-class (TAYLOR, 1963) reveals both negative and positive correlations. The factors discussed, which cause a definite tendency in the processes of survival of herring embryos are also accompanied by many other factors. In some years these are apparently dominant.

REFERENCES


