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The Influence of the Gas-Content of Sea-Water
on Fish and Fish-Larvae.

by
Eva. Henly.

At Flødevigen Sea-fish Hatchery we have, during the last few years, been dealing with the factors which may cause the great mortality of fish-eggs and -larvae in the sea. We have also tried to find out the conditions which are most advantageous for marine eggs and larvae in the laboratory. During this work it has turned out that the gas-content in the sea-water may be of great importance for the larvae.

In our experiments we regularly have used larvae of cod, herring, and plaice. These species are among our most common food-fishes, and they do at the same time represent both the physocliste and the physostome fishes, and also those that do not possess a functioning air-bladder.

We have several times observed in the laboratory that if the gas-concentration in the sea-water becomes high, the mortality will increase. The problem has been to determine the cause of the "gas-disease", and how to prevent it.

By using a sand-filter we were able to remove rather great quantities of gases from the water, and the conditions became somewhat better. The gas absorbed by the sand was analysed, and found to consist of 22.5% oxygen, the rest being nitrogen and inert gases. In this way both oxygen and nitrogen were removed. It is thus impossible to state which gas may cause the "gas-disease". But taking the function of the air-bladder of adult fishes into consideration, the oxygen-concentration must be regarded as a very important factor.

All atmospheric gases are found in solution in sea-water. In addition to nitrogen and oxygen, the most abundant gases in the air, carbon-dioxide is present in large quantities, chiefly as carbonates and bicarbonates. In the absence of dissolved oxygen, hydrogen sulphide may be present.

The dissolved oxygen in the sea-water varies between zero and 8.5 ml/L, although in areas of intense photosynthesis, the content may exceed this upper limit. We have thus sometimes during the spring found more than 20 ml/L in a sea-water pond where the plankton-content was extremely high. Under this condition we have also proved the sea-water to contain some peroxides. Nitrogen, which is apparently unaffected by biological processes, varies between 8.4 and 14.5 ml/L. The total carbon-dioxide in oceanic waters varies between about 34 and 56 ml/L. The distribution of dissolved gases in the ocean is controlled by the following factors: 1) temperature and salinity; 2) biological activity; and 3) currents and mixing processes.

Water in contact with the atmosphere will tend to reach equilibrium either by giving up or absorbing the individual gases until the water is just saturated. Although the zone of contact is a very thin one, convective movements due to cooling, evaporation, or wind action may bring a layer of considerable thickness into equilibrium with the atmosphere. Some of the oxygen may originate from biological processes, but these too take place in the upper part of the ocean. The oxygen in the deep water thus originates from the upper layers, brought down by mixing processes.

If newly hatched cod-larvae (0-7 days old) are kept in an aquarium without water renewal for half a day, and some fresh sea-water of the same temperature and salinity is added, minute gas-bubbles will become attached to the larvae which develop white spots and curl up and die. This new water has evidently too much gas for the cod larvae.

Even older cod larvae are susceptible to an unfavourable gas-concentration. Particularly 3-6 weeks old cod fry are apt to get a "gas-disease". At first the air-bladder expands on account of too much gas. The fry then try to get down towards greater water pressure. The aquaria are, however, usually not deep enough and the fry are forced to stay in a layer where the pressure evidently is too small in regard to the gas-content in the bladder. The air-bladders continue to expand, and after a few

days they become so big that the fry float helplessly at the surface, sometimes swimming on the side and, in severe cases, belly upwards. Their air-bladders become bigger and bigger, and may hinder vital functions. Their jaws are widely separated and the fry refuse to take any food. If nothing is done, the mortality is total. Whether the prime cause of death is choking, starvation, or some other phenomena is unknown.

If such codlings are enclosed in an aquarium provided with a silk-net on the top, and lowered in the sea to 2-5m. below the surface, the air-bladders by the next day have become normal and the codlings are again able to swim in an ordinary manner; the air-bladders function normally. The same will occur if we put cod-fry with expanded air-bladders in a relatively deep aquarium. We have used a cylinder of perspex, 2 metres high, and with a diameter of 13cm. The fry, affected in a reasonable degree, immediately seek the bottom and swim actively; A depth of 2 metres, however, is evidently not sufficient. The fry try to get further down, but stop against the sand on the bottom. Some of the codlings, too much affected, do not succeed; when they get half way they can not get further down; they float up again, and after a while they are found dead at the surface.

In nature, when the larva-net, used for pelagic fishing, is hauled from 10-20m: depths to the surface, the opposite phenomenon may occur although it has only been observed by fishes with a closed air-bladder. Some of the larvae turn belly upwards and come to the surface when transferred to a glass-vessel with sea-water. The gas in the air-bladder expands.

As soon as the yolk-sack is resorbed the cod-larvae will respond to changes in water pressure. If they are kept under pressure, say 5 metres of sea-water, they will swim mainly in the upper part of the aquarium. When this pressure is suddenly released, the larvae will sink apathetic towards the bottom.

Several years ago cod-larvae were reared in our salt water pond (34 x 22 x 4 m.) with remarkably good results, and gas-disease was never observed among the larvae reared there.

The experiments just described only apply to larvae of fishes with a closed air-bladder. Larvae of physostome fishes will respond in a somewhat different way when reared in sea water direct from the reservoir. The mortality may be great, but the clinical picture is different. The gas-bubbles are formed in the intestines. When the water comes into contact with the mucous membrane of the herring for instance either in the mouth, the gills, or the intestines, some gas will apparently be liberated. This may probably be explained as a catalytic process. The herring larvae cannot get rid of these gas-bubbles and will sooner or later die from obstruction. This year, however, we have avoided the gas-formation in herring by rearing the larvae in a greater and deeper aquarium. It may be that the great surface permits the excess air to escape.

Regarding the larvae of fishes without a functioning air-bladder, the clinical picture appears to be almost the same. Larvae of plaice, for instance, respond in the same way as the herring larvae do. Here too we find gas-bubbles in the intestines, but the plaice larvae are able to get rid of the gas through the anus, and it does not seem to hurt them at all. The plaice larvae may, however, be killed in an other way if the gas-content is too high.

A couple of years ago we had a great mortality among young flatfish, cross-breed between Pl. microcephalus (female) and Pl. flesus (male). They had been reared in a small aquarium for 5 months and the water had all the time been filtered before entering the aquarium. Then they were transferred to a larger aquarium supplied with unfiltered water. They thrived for about 1 month, and then the water supply was increased. From then on the larvae died in great numbers. By dissection, it was shown that there were rows of small gas-bubbles along the basis of the fin rays of the dead larvae. The tissues were not injured, so the air cannot have been sucked in from bubbles attached to the surface of the larvae; it must have been liberated in the blood. There were also a great number, more or less affected, near the surface, and they showed the same symptoms. The blood circulation in the anal fin and dorsal fin was very slow, but somewhat better in the tail fin. Otherwise they showed no particular sign of illness.

Gas-bubbles are often observed on the fins and gills. If there are any injuries on the fins and the gills the gas will invade the veins and the fish will suffer from gas embolism. In some cases we have proved that when the oxygen content in sea water

becomes extremely high a small amount of peroxide is formed. Some plaice, 3 months old, were held in sea water containing a little hydrogen peroxide and all died within 2 hours. Minute gas-bubbles appeared immediately on the surface, particularly on the fins, the gills, and the head. The bubbles increased rapidly in size and within half an hour they almost enveloped the whole fish. Some of the larvae had injuries on the fins, and on these places the gas formation was extremely high. After a while the gas was sucked in near the basis of the fins up to the backbone and alongside it. The plaice larvae showed an increased respiration and collapsed.

Not only fish larvae are dependant on a normal gas content in the sea water; there is a great mortality also among the oyster larvae if oxygen content becomes too high.

The difficulties mentioned in connection with the gas content of the sea water have lately been avoided ^{to a certain degree} at the Flødevigen Sea-Fish Hatchery, as we now are filtering the water twice through sand-filters. The oxygen content is in this way reduced by about 20%. The oxygen content in the reservoir may, for instance, one day be 114%, After it has passed filter no. 1 it falls to 102.5%, and when it is entering the aquaria the concentration is 95%. Whether this gas removal is a purely physical process, or whether the sand may act as a catalyst, being able to catalyse the liberation of gases from the water, is unknown. But if some iron is present in the sand the oxygen liberation is greatly increased. This gas removal by means of the sand-filters has been a great improvement, but the difficulties are not entirely overcome, at least not for the rearing of cod larvae.

Plaice and other flat fishes (and cross-breed) are now reared in great numbers at the Flødevigen Sea-Fish Hatchery without any trouble. Plaice and soles have been hatched and kept in aquaria till they are more than three years old. Herring too have been kept for a couple of years. We have also succeeded in rearing mackerel up to considerable sizes, but here cannibalism is an interfering factor. Rearing of cod larvae too has been successful for the first three weeks after hatching, but then the "gas disease" appears, and the mortality between 3 and 6 weeks is much too great, although reduction of the oxygen content has improved the results somewhat.

There is also another factor that probably affects the survival of cod larvae in the laboratory, this is their heredity. If the parents originate from the littoral region the chance for the larvae to survive will probably be greater than if the parents are accustomed to deep water. This problem will be further investigated next year.

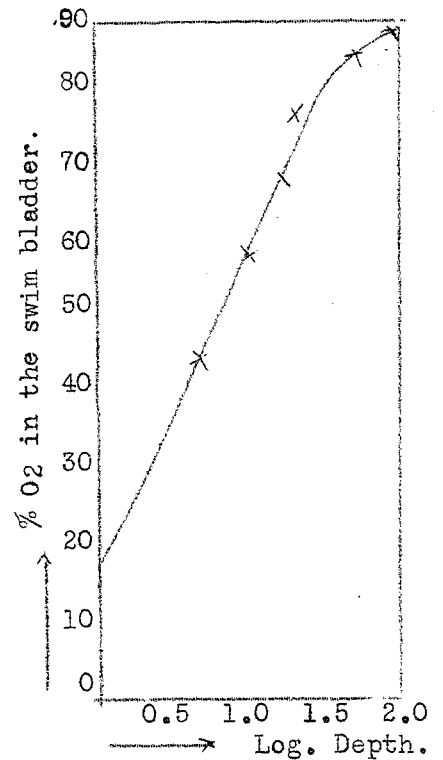
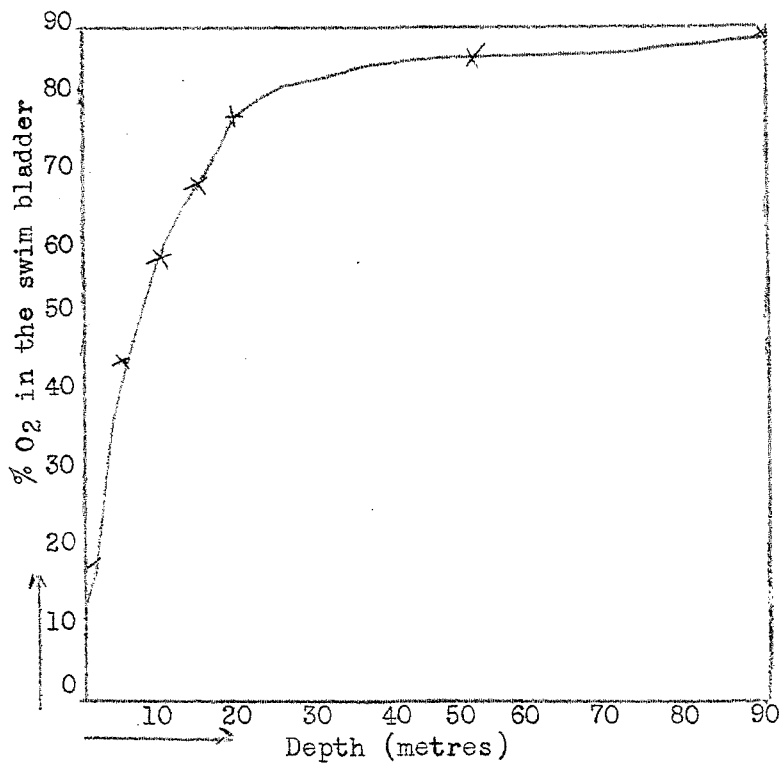
Pelagic fish larvae are usually found in nature at greater depth than expected. In the laboratory pelagic cod larvae are buoyant in sea water of specific weight about 1.022; in nature, however, they are found in water of a far higher specific weight. They are found at a depth of 10-20m. The depth (water pressure?) is apparently of the greatest importance.

Pelagic fish larvae will, like other forms of zooplankton, avoid places where the phytoplankton content is great. It is reasonable to assume that the cause might be a too great oxygen content produced by the phytoplankton. We must of course be aware of the fact that there also may be some antibiotic compounds produced by the phytoplankton that may keep the zooplankton away.

We have carried out some analyses on the air-bladders of cod. We found that cod caught near the surface have an oxygen content in the air-bladder of about 10%, whereas fish caught at a depth of 25m. contained 80% oxygen, and at 100m. 90%.

(see diagrams next page)

During the last 50 years a rather extensive literature has been produced concerning the gas disease. The symptoms are always the same; as to the cause the opinions diverge. Marsh & Gorham (Washington 1905) described gas disease among larvae and several adult marine fishes very accurately. They came to the conclusion "that nitrogen excess is more important than oxygen excess, and can singly cause the disease process". Semper (abstract) described how he watched sticklebacks, white fishes, and axolotls succumbing when the animals were kept in water rich in gas. He observed gas liberation in the veins and the muscles. Roth (Stuttgart 1922) explained how a great mortality occurred when the water contained a great amount of finely suspended air (because of leaky pumps which began to suck air). The air was liberated into the water as minute air-bubbles. Some eels showed a very characteristic clinical picture.



The figures show the relation between the oxygen content in the air-bladder and the depth.

Their skin became unevenly swollen and the epithelium was penetrated with small shiny air-bubbles. Gudgeon, gold-fish and minnows also succumbed. The author did not make any statement to whether the air that penetrated the muscles originated from small air-bubbles present in the water or from dissolved air liberated in the body. But according to his experiences the gas disease only occurs when finely suspended air is present in the water. Plehn (abstract 1922) has often found trout with gas-disease in sunlit ponds with great photosynthesis. She also described the symptoms, and they fully agree with those found here regarding the plaice larvae. She stated the cause of death to be gas-embolism. The larvae would survive, she said, if the fishes were transferred into normal water. Haempel (abstract 1937) has proved (using young salmonids) that an increased oxygen content at first causes dyspnoea (difficulty of breathing), after which the respiration stops (apnoea). A secretion of slime together with great sensibility follows, and finally a spasm (caused by oxygen narcosis) occurs, so that the fish choke. Mrsic (abstract 1933) described a very interesting case of gas-disease (and hopes to prove the cause to have been a supersaturation with carbon dioxide). All fishes living in the water reservoir of Zagreb were attacked by the gas-disease. They tried to transplant trout larvae, but these died too. When, however, the water was aerated, the fishes survived. Mrsic was convinced that the cause was a supersaturation with carbon dioxide.

In this way several theories have been put forward as to the cause of the disease. The most important are oxygen excess, nitrogen excess, carbon dioxide excess, pH variations, temperature variations, and irritations from associated plants, or compounds liberated from the plants, or the effect of two or more of these factors.

At Flødevigen Sea-Fish Hatchery we assume the main trouble to originate from: 1) the oxygen concentration; 2) the water pressure. Whether these factors may be of importance in nature or not is uncertain. It appears reasonable to expect, however, that if newly hatched larvae are brought into contact with sea water containing a high amount of oxygen, they will be heavily affected. Further, if young individuals of physoclistic species, at the age when the air-bladder is formed, are brought from 10-20m. by the current to the surface, a gas-disease will occur.