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Studies on the High Nitrogen Content in the Physostome Swimbladder

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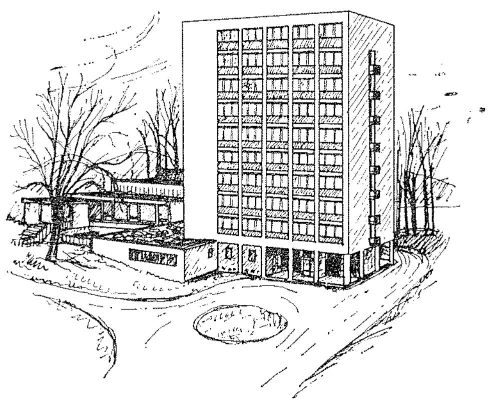

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INTRODUCTION

The finding of Hüfner (1892) showing that the swimbladder of *Coregonus acronius* contained 99 per cent nitrogen pointed to an apparently different mechanism of gas secretion in the physostome and physoclist swimbladder. The high nitrogen content in this and related coregonids has been verified by Saunders (1953), Scholander, van Dam and Enns (1956), and Sundnes, Enns and Scholander (1958). The latter group also showed that the gas mixture in the coregonid swimbladder can be identical with that found in the physoclist swimbladder as *Coregonus lavaretus* from the Randsfjord lake in Norway was found to contain a mixture with a considerable amount of oxygen. The anatomical study made at that time was inadequate, however, and did not show any evidence for a counter-current diffusion process. In a subsequent report (Sundnes 1959) the author found that the swimbladder of *Coregonus acronius* from Bodensee contained 15,2—18,1 per cent oxygen and concluded that the gas secretion mechanism was similar in both physostome and physoclist fishes. This was given further support by the careful study made by Fahlén (1959) of the blood vessels in the coregonid swimbladder. Regarding this counter-current system, one must still postulate that a multiplying effect occurs in these capillaries. The theoretical findings of Kuhn and Kuhn (1961) together with results given in the present paper on the char, *Salmo alpinus,* give a new insight into the fact that the swimbladder of buoyant physostomes contains 99 per cent nitrogen. It is suggested that the high nitrogen content in some coregonid swimbladders and the high oxygen content in others is not due merely to different gas deposition mixtures.

MATERIAL AND METHODS

The deep water fishes used in these studies were the char, *Salmo alpinus,* from the Randsfjord lake in Norway and *Salmo salvelinus* from the Bodensee in Germany. Another char which lives at depths down to 40 meters was obtained from Övervatnet lake in Salangen in North Norway. The fish were caught with gill nets at known depths and the gas samples were taken from the live fish immediately after their reaching the surface. The gas was analysed in a syringe analyzer (Scholander, van Dam, Claff and Kanwisher 1955) and the 0,5 cc. analyzer (Scholander 1947). Some samples for mass spectrometry were transferred to evacuated glass ampules and sealed by melting. The buoyancy determinations were made according to the method of Saunders (1953). The names wich are given to the various species and varieties are those currently in use in the respective countries.

BIOLOGY AND VERTICAL MIGRATION

Being a hydrostatic organ, the swimbladder plays a very important role in the vertical migration of fish. The frequency of an appreciable vertical migration (at least 40—80 meters) in the *Coregonus* and *Salmo* species investigated by the author is only once a year. This is the migration which occurs during spawning. These species are generally found over a relatively small range in depth and while some feed in shallow water and move to deep water to spawn, others behave in an opposite way. Figure 1 shows the relationship between migration and time and it can be seen that there is a different feeding an spawning biology among these coregonids and salmonids.

Coregonus acronius from the Bodensee lives near the bottom in the deepest areas (Nümann 1940). At spawning time it follows the bottom to more shallow areas and then returns to deep water. *Coregonus lavaretus* from the Randfjord lake is different in that it stays mainly in shallow water but goes down to a depth of about 100 meters for spawning in late autumn and winter. After spawning it migrates to more shallow areas. The deep water form of the char, *Salmo alpinus,* in the Randsfjord lake and the *Salmo salvelinus* in the Bodensee are usually found in the deep layers of the lakes. Living at depths of about 80 meters they keep their vertical migration within 20 meters. The char, *Salmo alpinus,* in the Övervatnet lake in Salangen, however, has relatively a wider vertical migration. Like *Coregonus lavaretus* in Randsfjord lake it lives in shallow water and migrates to a depth of about 40 meters for spawning. (Nordeng, H. Personal communication).

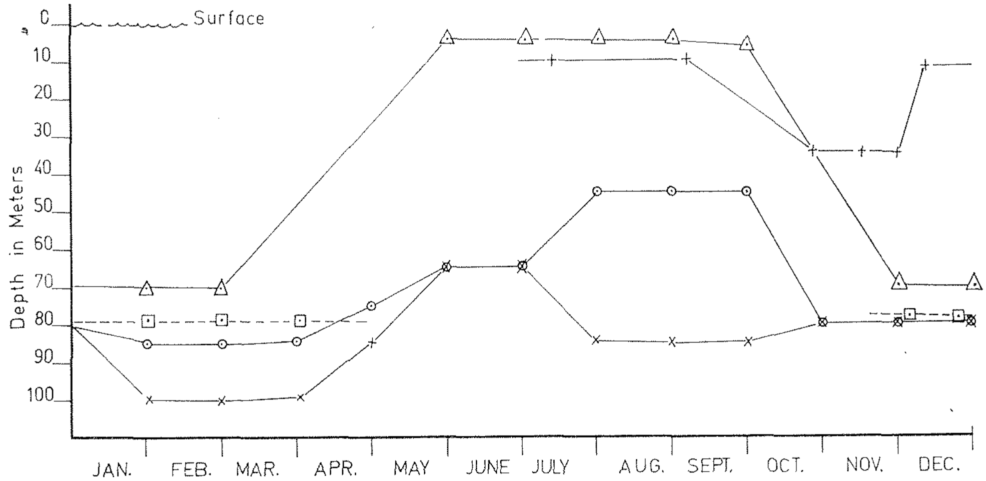

Figure 1. Depths at which the different species are found throughout the year.

△ = *Coregonus lavaretus* from Randsfjord lake.
⊙ = *Coregonus acronius* from Bodensee.
× = *Salmo salvelinus* from Bodensee.
⊡ = *Salmo alpinus* from Randsfjord lake.
\+ = *Salmo alpinus* from Salangen.

THE SWIMBLADDER GAS MIXTURE IN RELATION OF VERTICAL MIGRATION

Values for the swimbladder gas contents are shown in Table I and demonstrate that in both coregonids and salmonids there is a considerable difference in the same species or nearly related forms from different areas. It seems unlikely that there is a different gas deposition mechanism in these fishes and, in addition, a mere difference in location offers little in the way of an explanation for the widely varying gas mixture. By comparing Figure 1 and Table I, however, a connection can be seen between the gas mixture in the swimbladder and the vertical migration of the fishes investigated.

It is seen that the high nitrogen content of up to 99 per cent is found in fish which live in deeper areas of the lakes. If they migrate from these areas once a year the high values are found in the non-migrating period. The finding that *Coregonus acronius* in the Bodensee in autumn has oxygen in the swimbladder (Sundnes 1959) can be understood by the fact that these fish had recently returned to deeper water after spawning in shallow areas. *Coregonus lavaretus* taken near

Table I: *The swimbladder gas content in relation to migration.*

Locality		Bodensee in Germany		Randsfjord lake in Norway		Salangen in Norway
Species		*C. acronius*	*S. salvelinus*	*C. lavaretus*	*S. alpinus*	*S. alpinus*
Total variation in gas content	Non migration period	0,0– 2,9 % O_2 99,9–96,5 % N_2	0,0– 0,7 % O_2 99,9–99,1 % N_2		0,0– 0,8 % O_2 99,7–98,9 % N_2	
	Migration period	15,2–18,3 % O_2 84,7–80,8 % N_2		33,4–69,3 % O_2 63,1–30,5 % N_2		0,0–18,1 % O_2 99,0–85,2 % N_2

the bottom of Randfjord lake (Sundnes, Enns and Scholander 1958) are in this area for spawning as they live in shallow water throughout most of the year. The high oxygen content in their swimbladder results from the fact that these fish at spawning time are in a vertical migration against higher hydrostatic pressure. The same picture is found among *Salmo salvelinus* from Bodensee, *Salmo alpinus* from the Randsfjord lake and *Salmo alpinus* from Salangen. The latter is a shallow water form which migrate to deeper areas for spawning. Table I shows a relatively low oxygen content in this species. This might be due to the termination of the period of gas deposition the subsequent absorption of oxygen. The finding that the argon : nitrogen ratio was from 76,3—82,8 per cent of that in air lends support to this theory.

It is seen that both coregonids and salmonids deposit an oxygen-containing gas mixture into the swimbladder when moving to deeper water. The high nitrogen content is found in the same fish who have been near the bottom for some time and who spend most of the time in these deeper areas.

DISCUSSION

Since the original finding of Hüfner (1892) concerning the high nitrogen content in the whitefish swimbladder, much thought has been given to the mechanism of gas deposition in physostomes. More recently it has been shown that they deposit a high oxygencontaining gas mixture into the swimbladder (Sundnes, Enns and Scholander 1958; Sundnes 1959). A possible mechanism for this has been put forward

(Fahlén 1959; Kuhn and Kuhn 1961) if one assumes that there exist a multiplying effect of the capillaries in the swimbladder wall. When the fish are moving downward the deposition of gas is fairly high to compensate for increasing hydrostatic pressure and a relatively high oxygen content is found. This is not the case when the fish have been in deeper waters for some time as the oxygen deposited into the swimbladder during the downward migration has been absorbed by respiration of the surrounding tissue.

There is another aspect of the problem which must be taken into account and that is the buoyancy of the fish. The fish, including those with a very high nitrogen content, are buoyant at the depths where they are caught. From the present data, we can assume that the primary gas deposited into the swimbladder was an oxygen-nitrogen mixture. The high nitrogen content of the physostome swimbladder could be explained by an absorption of the oxygen into the surrounding tissue. In order to maintain their buoyancy, however, this loss must be replaced by nitrogen. This is accomplished by a decreasing rate of deposition of the oxygen-nitrogen gas mixture which results in a gradual increase of the relatively poorly absorbed nitrogen and a concomitant decrease in the proportion of the more rapidly absorbed oxygen. Finally the swimbladder contains nearly entirely nitrogen and deposition of the gas mixture is reduced to a low level sufficient to compensate for the slow loss of nitrogen. According to the theoretical conclusions of Kuhn and Kuhn (1961) such a process is possible.

As the physostome swimbladder has been shown to contain as much as 70 per cent oxygen it is considered very likely that the gas mixture deposited in both physostomes and physoclists has a very high oxygen content. It is also unlikely that the gas mixture varies with changes in hydrostatic pressure. The author has recently measured the gas content in the cod, *Gadus callarias.* At a depth of one meter this physoclist fish showed a variation in oxygen content from 3,7—87 per cent and in nitrogen content from 14,5—95,5 per cent. Rather than reflecting a difference in gas mixtures deposited, it seems more likely that these fluctuations arise from variations in the rate of gas deposition. During a period of gas deposition the oxygen content should be very high. The present findings show that the oxygen content can be as high as 70 per cent in physostomes and 87 per cent in physoclists although it is quite probable that the mixture is the same in both types.

SUMMARY

The high nitrogen content in the swimbladder of some coregonid and salmonid fishes has been studied in relation to their different biology and migration. That these fish are found to have high oxygen contents at certain times supports the theory that the gas deposition mixture consists mainly of oxygen. It is suggested that the high nitrogen content often seen is a result of a preferential oxygen absorption by the swimbladder tissue.

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LITERATURE CITED

Fahlén, G., 1959. Rete Mirabile in the Gas Bladder of *Coregonus lavaretus*. *Nature*, 184: 1001—1002.

Hüfner, G., 1892. Zur physikalischen Chemie der Schwimmblasengase. *Arch. Anat. Physiol.* Lpz. 54—80.

Kuhn, W. & H. J. Kuhn, 1961. Multiplikation von Aussalz- und anderen Einzeleffekten für die Bereitung hoher Gasdrucke in der Schwimmblase. *Z. Elektrochem.* 65: 426—439.

Nümann, W., 1940. XIX. Untersuchungen über die Biologie einiger Bodenseefische in der Uferregion und den Randgebieten des freien Sees. *Z. Fisch.*, 37: 637—688.

Saunders, P. L., 1953. The swimbladder gas content of some freshwater fish with particular reference to the physostomes. *Canad. J. Zool.* 31: 547—560.

Scholander, P. F., 1947. Analyzer for accurate estimation of respiratory gases in one-half cubic centimeter samples. *J. Biol. Chem.* 167: 235—250.

Scholander, P. F., L. van Dam, C. L. Claff & J. W. Kanwisher, 1955. Micro gasometric determination of dissolved oxygen and nitrogen. *Biol. Bull, Woods Hole,* 109: 328—334.

Scholander, P. F., L. van Dam & T. Enns, 1956. Nitrogen secretion in the swimbladder of whitefish. *Science,* 123: 59—60.

Sundnes, G., 1959. Gas secretion in Coregonids. *Nature,* 183: 986.

Sundnes, G., T. Enns & P. F. Scholander, 1958. Gas secretion in fishes lacking rete mirabile. *J. Exp. Biol.,* 35: 671—676.