# NOTES ON THE GAS CONTENT AND NEUTRAL BUOYANCY IN PHYSOSTOME FISH

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## ABSTRACT

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Field and experimental observations from herring (*Clupea harengus*) and char *(Salmo alpinus)* indicate that the swimbladder gas is not only «swallowed» from the atmosphere, but may also be deposited from the vascular system or tissue around the swimbladder lumen.

## INTRODUCTION

The genera Salmo and Clupea are both physostomes and do not possess any organ or rete formations similar to those of the physoclists (FAHLEN 1967, 1971).

The ethology of the two species is fairly similar. They are schooling fish which live in deeper water during feeding periods but move to shallower areas to spawn. During migration to shallower areas the herring undergo a vertical migration resulting in reduced hydrostatic pressure. The herring avoid overflotation by releasing gas. Prior to the development of acoustical instruments, one of the methods of herring detection in the spawning areas was the observation of the numerous gas bubbles coming to the surface.

The char gas release is of a more complicated nature. The char do not only release gas to compensate for a decreasing hydrostatic pressure. They also release gas by emotional stimuli when the fish are in a steady state of hydrostatic condition (SUNDNES, unpublished observations). A similar behaviour has been described in the European minnow (DYKGRAAF 1932) and in some North American physostome fish (VERHEIJEN 1962).

The gas filling mechanism for herring and char is not known in detail. However, Clupeids are able to swallow gas at the surface (SRIVASTAVA 1964, FAHLEN 1967) and a similar function was described also for Salmonids (JACOBS 1934).

On the other hand, WITTENBERG (1958) has described the refilling of emptied swimbladders of Salmonids in 13 days due to secretion. FAHLEN (1971) was not able to confirm the findings of WITTENBERG (1958), but in his experiment the fish had a gas content of 1.2 cc after 40 days.

The present work intends to give more information about swimbladder function of the fish in their natural environment.


## MATERIAL

Local herring (*Clupea harengus*) from the Trondheims fjord and the Lindåspoll have been used. They are more or less available the entire year and were caught by hook and line or by gillnets. For comparative reasons char (*Salmo alpinus*) from Grimevatnet, Vangsvatnet near Bergen and Øvervatnet in Salangen have been studied. The char were caught by gillnets and beach seine. The reason for using char as a comparative fish in this study is not only the similar ethology with respect to hydrostatic pressure, but also the far better resistance of the char against experimental stress. Both herring and char were transported to the institute of Marine Research for experimental work.


## METHODS AND RELIABILITY OF DATA

The swimbladder gas was analysed using the 1/2 cc analyzer (SCHOLANDER 1947) in the laboratory experiments. In the field work the «water analyzer» (SCHOLANDER, VAN DAM, CLAFF and KANWISHER 1955) was used. The accuracy of the latter is not good enough for $CO_2$ analysis, but accuracy of the values of the gas mixtures found in the physostomes (SUNDNES 1963, SUNDNES, BRATLAND and STRAND 1969) are determined by the accuracy of the analyzer which is $\pm$ 0.3 per cent of the true value.

Buoyancy tests were performed by weighing the gas free fish under water as described by SAUNDERS (1953). The volumetric measurement of the gas content gave the depth of buoyancy by using following equation:

$$\text{Depth of buoyancy} = \frac{\text{Gas volume}}{\text{Weight of the submerged fish}} \cdot$$

A measurement of the buoyancy of physostomes like herring and char by method mentioned above is not precise. By taking the fish from the depth of catch the swimbladder expands and thereby some gas is released.

Buoyancy measurements of char are more problematic as it releases gas even in a buoyant condition by emotional reactions. The buoyancy determinations will therefore always give minimum values. The swim-bladder gas pressure relative to the surrounding hydrostatic pressure was measured by transducers (SUNDNES and GYTRE 1972, in press). These measurements were carried out in aquaria. These results are also influenced by the emotions of the fish. In experiments it is difficult to decide which aspect of the behaviour is imitated in the instinctive system of the fish. To make the fish cooperate in aquaria and obtain data which is relevant to the open sea is, therefore, difficult in many cases. The fish have been observed in field by various types of Simrad echo sounder.

## RESULTS AND DISCUSSION

The value of the $CO_2$ and $O_2$ contents found in the swimbladders of herring in the Trondheims fjord at 8 m depth under a pressure condition where they released gas (millions of gas bubbles reaching the surface over the whole visible area) are given in Table 1.

Table 1. Gas content in *Clupea harengus* from Trondheimsfjord caught by hook and line.

| Fish no. | $CO_2\%$ | $O_2\%$ |
|---|---|---|
| 1 ............ | 0.1 | 15.5 |
| 2 ............ | 0.1 | 8.5 |
| 3 ............ | 1.1 | 17.9 |
| 4 ............ | 1.2 | 16.00 |
| 5 ............ | 1.2 | 18.6 |
| 6 ............ | 1.2 | 19.7 |
| 7 ............ | 0.1 | 12.7 |
| 8 ............ | 0.8 | 18.3 |
| 9 ............ | 1.1 | 10.4 |

The oxygen content of the swimbladder varied from 8.5 to 18.3 vol%. In herring from the Lindåspoll the oxygen content varied over the same range as in the Trondheims fjord herring, i.e. 7.7 to 17.7 vol% (Table 2). As far as the gas data are concerned, the oxygen values do not indicate that the swimbladder gas originated from the vascular system of the fish. A gas content of > 21 vol% oxygen would evidently indicate that the oxygen in the haemoglobin of the vascular system of the fish could play an important part as the source of the swimbladder gases. The field studies have not so far indicated the possibility that the oxygen originates from the haemoglobin of the vascular system.

Table 2. Gas content in *Clupea harengus* from
Lindåspollen.

| Fish no. | $CO_2\%$ | $O_2\%$ |
|---|---|---|
| 1 ............ | 0.6 | 14.8 |
| 2 ............ | 0.5 | 16.1 |
| 3 ............ | 2.3 | 17.5 |
| 4 ............ | 1.2 | 16.7 |
| 5 ............ | 0.8 | 17.33 |
| 6 ............ | 0.6 | 16.1 |
| 7 ............ | 0.1 | 9.33 |
| 8 ............ | 0.2 | 16.9 |
| 9 ............ | 0.3 | 10.4 |
| 10 ............ | 0.8 | 7.7 |
| 11 ............ | 0.4 | 10.6 |
| 12 ............ | 0.9 | 13.3 |
| 13 ............ | 0.4 | 17.7 |
| 14 ............ | 0.5 | 17.6 |

Table 3. Gas content in *Salmo alpinus* from
Randsfjorden.

| Depth in meters | $CO_2\%$ | $O_2\%$ |
|---|---|---|
| 70 ............ | 0.22 | 2.91 |
| » ............ | 0.33 | 13.26 |
| » ............ | 0.15 | 3.60 |
| » ............ | 0.17 | 15.87 |
| » ............ | 0.29 | 2.96 |
| » ............ | 0.30 | 15.23 |
| » ............ | 0.18 | 2.88 |
| » ............ | 0.29 | 10.06 |
| » ............ | 0.23 | 3.80 |
| » ............ | 0.27 | 14.30 |

The oxygen content found in the swimbladder of the char is also
lower than the atmospheric value. In general, the oxygen values from
char in normal conditions in nature are lower than those found in herring.
In Table 3, 4 and 5 the $O_2$ content with the respective $CO_2$ values from
different localities and depths are listed.

While the values for the gas mixture found in herring and the char
do not exclude the possibility that the gas has been «swallowed» directly
from the atmosphere, they are more consistent with the findings of
Jacobs (1934), Srivastava (1964) and Fahlen (1967). On the other hand
Wittenberg (1958) and Fahlen have described a refilling of the swim-

bladder in Salmonids independent of an air swallowing function. They found that the gas content of the swimbladder mainly consisted of nitrogen. The refilling process was very slow and incomplete in the fishes used by FAHLEN (1967) compared to those used by WITTENBERG (1958).

Table 4. Gas content in *Salmo alpinus* from Grimevatnet.

| Depth in meters | $CO_2\%$ | $O_2\%$ | Depth in meters | $CO_2\%$ | $O_2\%$ |
|---|---|---|---|---|---|
| 20 ......... | 0.35 | 5.70 | 30 ........ | 0.31 | 3.67 |
| » ......... | 0.70 | 12.02 | » ........ | 0.18 | 9.45 |
| » ......... | 0.42 | 3.99 | » ........ | 0.17 | 4.27 |
| 25 ......... | 0.43 | 2.88 | 32 ........ | 0.62 | 10.77 |
| » ......... | 0.47 | 3.52 | » ........ | 0.55 | 12.96 |
| » ......... | 0.43 | 9.31 | 50 ........ | 0.14 | 4.22 |
| 27 ......... | 0.47 | 11.24 | » ........ | 0.38 | 16.15 |
| » ......... | 0.48 | 1.96 | » ........ | 0.22 | 6.11 |
| 30 ......... | 0.30 | 9.30 | » ........ | 0.26 | 3.32 |
| » ......... | 0.43 | 14.54 | » ........ | 0.13 | 2.47 |
| » ......... | 0.36 | 5.14 | » ........ | 0.12 | 3.10 |
| » ......... | 0.41 | 12.21 | » ........ | 0.13 | 2.87 |
| » ......... | 0.43 | 2.21 | 70 ........ | 0.18 | 0.68 |
| » ......... | 0.40 | 9.08 | » ........ | 0.14 | 4.91 |
| » ......... | 0.20 | 0.51 | » ........ | 0.20 | 4.66 |
| » ......... | 0.42 | 10.20 | » ........ | 0.17 | 6.88 |
| » ......... | 0.48 | 15.60 | | | |

In the latter experiments, the high nitrogen content does not indicate the source of the gas. It is doubtful that the primary gas deposited in the swimbladder consists mainly of nitrogen. As long as the composition of the residual gas in the swimbladder is unknown, any refilled gas will be «contaminated» by the residual gas (SUNDNES et al. 1969). Also, the delay between the deposition of gas and the gas sampling is important (SUNDNES et al. 1969). In the present work char have been emptied of swimbladder gas to the degree which is possible by puncture and then kept in aquaria with no access to the surface. The fish were then emptied of gas in intervals varying from 3 to 9 days. The results of the gas analysis for a char are shown in Table 6.

Table 6 shows a high degree of variation of the oxygen content in the refilled gas. The oxygen content of the primary refilled gas is not known as long as the residual gas volume is unknown.

The high nitrogen content found in the refilled gas by WITTENBERG (1958) is possibly caused by the secondary effect described by SUNDNES et al. (1969). The relatively high oxygen content found in the present

Table 5. Gas content in *Salmo alpinus* from Øvervatnet.

| Depth in meters | $CO_2\%$ | $O_2\%$ | Depth in meters | $CO_2\%$ | $O_2\%$ |
|---|---|---|---|---|---|
| 6 ......... | 0.39 | 15.39 | 23 ........ | 0.11 | 5.56 |
| » ......... | 0.28 | 19.07 | » ........ | 0.06 | 11.86 |
| 9 ......... | 0.59 | 13.24 | » ........ | 0.10 | 14.36 |
| » ......... | 0.75 | 16.32 | » ........ | 0.12 | 6.10 |
| » ......... | 0.45 | 12.00 | 25 ........ | 0.73 | 19.88 |
| » ......... | 0.40 | 16.64 | » ........ | 0.53 | 19.68 |
| 12 ......... | 0.34 | 15.77 | » ........ | 1.48 | 19.40 |
| 15 ......... | 0.39 | 15.46 | » ........ | 0.11 | 20.83 |
| 18 ......... | 0.42 | 20.10 | » ........ | 0.06 | 19.53 |
| » ......... | 0.03 | 6.78 | » ........ | 0.11 | 18.69 |
| » ......... | 0.11 | 8.47 | » ........ | 0.17 | 15.39 |
| » ......... | 0.29 | 16.49 | » ........ | 0.17 | 18.46 |
| » ......... | 0.17 | 17.19 | » ........ | 0.10 | 17.09 |
| » ......... | 0.06 | 18.61 | » ........ | 0.06 | 18.10 |
| » ......... | 0.22 | 5.86 | » ........ | 0.06 | 16.07 |
| 20 ......... | 1.50 | 13.10 | » ........ | 0.16 | 17.56 |
| » ......... | 0.80 | 3.90 | » ........ | 0.02 | 19.70 |
| » ......... | 0.10 | 18.10 | » ........ | 0.12 | 15.66 |
| 23 ......... | 0.18 | 9.66 | » ........ | 0.04 | 17.94 |
| » ......... | 0.10 | 19.44 | » ........ | 0.14 | 2.49 |
| » ......... | 0.18 | 18.62 | » ........ | 0.19 | 5.33 |
| » ......... | 0.14 | 17.56 | 30 ........ | 1.00 | 0.00 |
| » ......... | 0.30 | 12.53 | » ........ | 0.44 | 3.40 |
| » ......... | 0.07 | 8.57 | » ........ | 0.35 | 7.20 |
| » ......... | 0.18 | 10.72 | » ........ | 0.70 | 2.30 |
| » ......... | 0.11 | 18.85 | » ........ | 1.30 | 4.20 |
| » ......... | 0.31 | 18.41 | | | |

Table 6. Gas content of char with no excess to surface.

| Date | | vol. of gas sample | $CO_2\%$ | $O_2\%$ |
|---|---|---|---|---|
| 16/11 | original gas | 5 | 0.93 | 15.81 |
| 25/11 | refilled gas | 6 | 1.05 | 9.90 |
| 1/12 | refilled gas | 6 | 0.65 | 12.93 |
| 3/12 | refilled gas | 6 | 0.61 | 9.93 |
| 6/1 | refilled gas | 8 | 0.79 | 4.05 |
| 10/1 | refilled gas | 5 | 1.05 | 9.79 |
| 13/1 | refilled gas | 5.5 | 1.13 | 9.65 |

experiments and also the oxygen content found in herring by FAHLEN (1967) may indicate that the vascular system or tissue surrounding the swimbladder are also a source of swimbladder gas.

If the gas in the swimbladder is deposited there only by swallowing or other injecting processes direct from the gaseous atmosphere, it means that the fish must be heavily overinflated at the surface in order to be buoyant at, e.g. 100 m depth. On the other hand the fish can have a gas volume which is able to keep them buoyant in the upper few meters and thereby be in negative buoyancy at any depth below that.

Herring may carry out extended vertical migrations, i.e. over pressure ranges up to 40 atmospheres. Herring in the present investigation caught at 10 m depth had a gas volume of 6 cc. If one assumes that the herring was buoyant at that depth, it must then take in another 458 cc of air at the surface to be buoyant at 400 m depth. Such a situation of the herring has so far not been observed in our investigations.

The other possibility is to keep the swimbladder volume constant by the rigidity of the swimbladder or the body wall. By using a transduser technique (SUNDNES and GYTRE 1972, in press), the pressure of the swim-bladder gas in live herring was measured in relation to the surrounding hydrostatic pressure. The internal gas pressure of the herring followed the hydrostatic pressure on the outside. Whether minute pressure differences are possible in herring which are «cooperating» during the experiment is unknown, but it is clearly evident that no physical rigidity exists in the herring which can keep the swimbladder volume constant over those pressure ranges where herring perform vertical migrations. This means that only by access to atmospheric gases at the surface will herring not be buoyant in the major depth area of their distribution. Against this opinion numerous echo sounding observations of gas release indicate an overflotation of the herring from all depths when migration occurs toward decreasing hydrostatic pressure. At the surface this is also
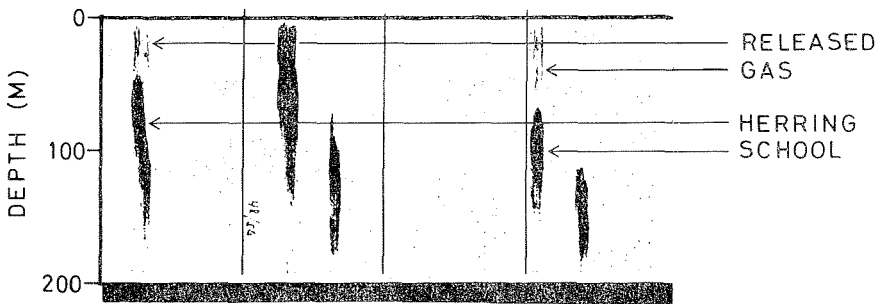


Fig. 1. Echogram showing gas release from migrating herring. (Photo: G. Vestnes).

visible by eye as previously described in the present chapter. In Fig. 1 gas release situation of herring is shown.

As previously discussed, buoyancy measurements of herring and char are problematic, but a few observations indicate that both species are buoyant at their depth of catch (Fig. 2).
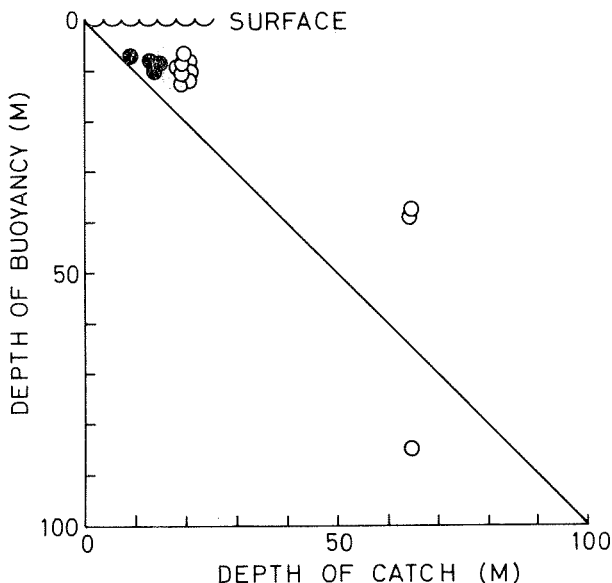


Fig. 2. Depth of buoyancy of *Clupea harengus* ( ● ) and *Salmo alpinus* ( ○ ) in relation to depth of catch. The diagonal is the line of perfect buoyancy, i.e. where depth of buoyancy equals depth of catch.

The findings presented here indicate that both the herring and the char are able to compensate for the volume loss of the swimbladder due to hydrostatic pressure and without access to the surface.

Another question which is related to this type of swimbladder concerns their compressibility due to the effect of migration towards higher hydrostatic pressure as previously described. There are no indications that the herring compensate for the increased hydrostatic pressure as fast as the vertical migration takes place. As the swimbladder and its geometry are known to play an important part of the target strength in acoustical methods (McCartney and Stubbs 1971), further investigations must elucidate an eventual effect on the target strength of Clupeids and Salmonids due to vertical migration and during the restoration of neutral buoyancy at a certain depth.

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