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THE RELATION BETWEEN THICKNESS OF CHORION AND SPECIFIC GRAVITY OF EGGS FROM NORWEGIAN AND BALTIC FLATFISH POPULATIONS

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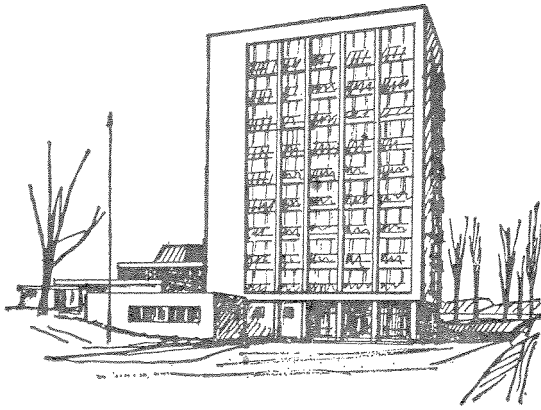
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ABSTRACT

LÖNNING, S. and SOLEMDAL, P. 1972. The relation between thickness of chorion and specific gravity of eggs from Norwegian and Baltic flatfish populations. *FiskDir. Skr. Ser. HavUnders., 16*: 77—87.

Neutral buoyancy, size, and thickness and ultrastructure of the chorion were studied in eggs from populations of flatfish (*Platichthys flesus* and *Limanda limanda*) from western Norway and three localities in the Baltic: Kiel, the Arkona basin and Tvärminne. The observed differences in neutral buoyancy are probably caused by the differing thickness of the chorion and are correlated with the salinity in the area. The differences are thought to be the result of a long term selection process.

INTRODUCTION

Marine teleost species with pelagic eggs are often distributed over a wide range of salinities (APSTEIN 1910, KÄNDLER 1941). Brackish water populations of such species produce eggs of a lower specific gravity, capable of floating in water of reduced salinity. Usually, but not invariably (see e.g. MIELCK and KÜNNE 1932), such eggs are bigger than those of marine populations of the same species.

Most authors have explained the low specific gravity of pelagic eggs in brackish waters as a function of the osmotic conditions, either in the ovary (STRODTMAN 1918, SOLEMDAL 1967), or in the ambient medium (JACOBSEN and JOHANSEN 1908, KÄNDLER and TAN 1965, HOHENDORF 1968). The immediate osmotic effect on the specific gravity is, however, small, and can only explain part of the observed differences between the eggs of marine and brackish water populations. It has therefore been suggested that the existence of pelagic eggs with low specific gravity in brackish water populations is the result of long term selection (SOLEMDAL 1971).

Interspecific differences in the thickness and ultrastructure of the chorion of pelagic teleost eggs have been described (GÖTTING 1966, HAGSTRÖM and LÖNNING 1968, LÖNNING 1972). As the chorion is the
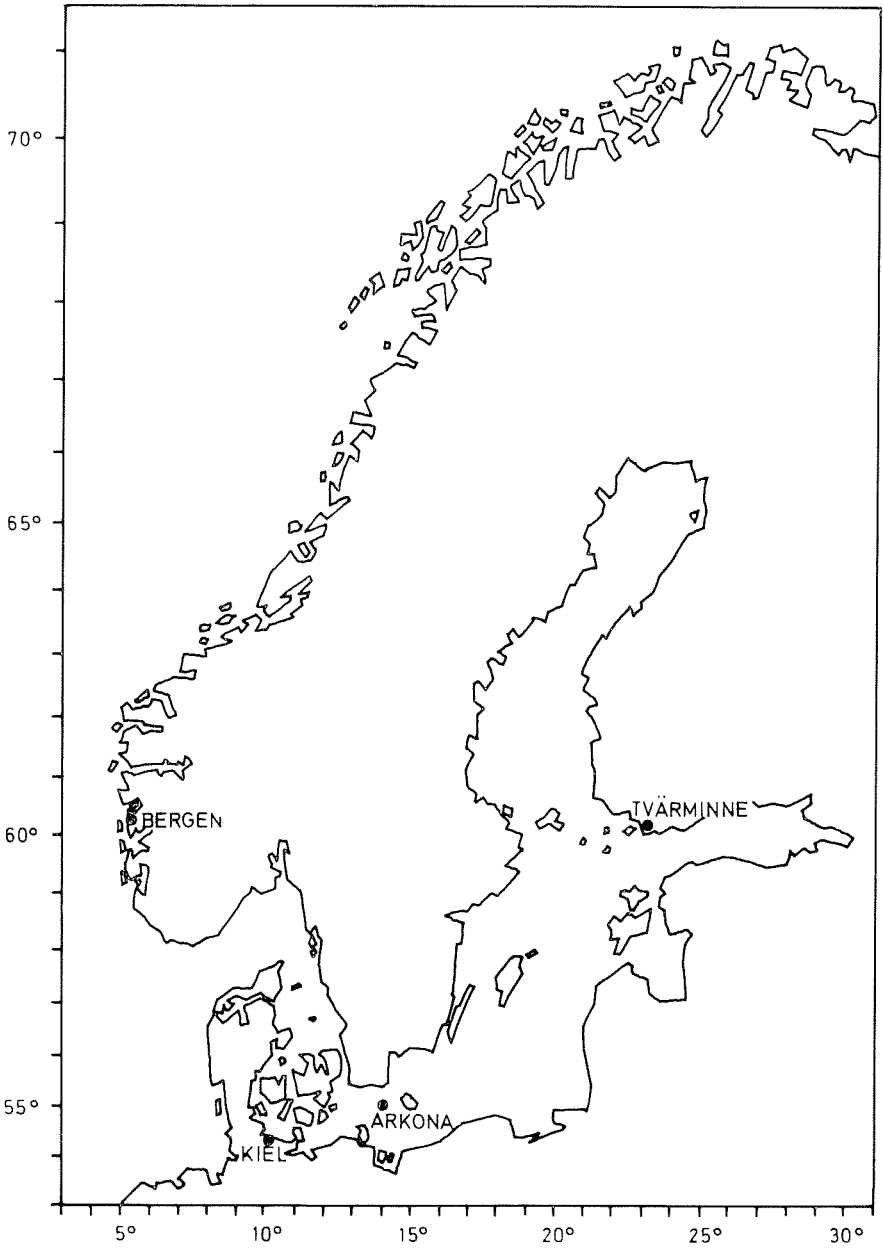

Fig. 1. Sampling localities.

densest part of the egg, such changes have a marked influence on the specific gravity of the egg. To test the hypothesis that intraspecific variation in the chorion between marine and brackish water populations of a given species may be responsible for the observed differences in specific gravity, eggs from flounders [*Platichthys flesus* (LINNAEUS)] and dabs [*Limanda limanda* (LINNAEUS)] caught at Bergen and at different localities in the Baltic have been investigated with regard to size, neutral buoyancy, and thickness and ultrastructure of the chorion.

MATERIAL AND METHODS

Flounders (*Platichthys flesus*) and dabs (*Limanda limanda*) were caught near Bergen in water of 35 $^0/_{00}$ salinity and from Kiel Bay, 22 $^0/_{00}$ S. Flounders were also collected from the Arkona basin, 17—18 $^0/_{00}$ S, and from the area near Tvärminne Zoological Station, 6 $^0/_{00}$ S (Fig. 1).

Diameter and neutral buoyancy were determined on normally developing eggs 24 hours after fertilization, using the methods described by SOLEMDAL (1967).

The fixation and embedding procedure for electron microscopy has been described by LÖNNING (1972). The material was sectioned on a LKB ultrotome III and examined in a Siemens Elmiskop I.

Ultrastructural studies were mainly carried out on eggs fixed 3—5 days after fertilization, and when nothing else is mentioned the micrographs are taken from this material. From the Bergen area unfertilized eggs and eggs fixed immediately after fertilization were also investigated.

RESULTS

Neutral buoyancy and egg diameter have been measured for eggs of populations of *Platichthys flesus* and *Limanda limanda*, living under different salinity conditions, and the results are given in Table 1. From this it can be seen that, in general, neutral buoyancy decreases with salinity, with the exception of the flounders from the most brackish area, Tvärminne, which have eggs of somewhat higher neutral buoyancy than those from the Arkona basin. In the Arkona basin the buoyancy is only just enough to keep the eggs from sinking, at Tvärminne flounder eggs sink and develop demersally. Similarly, egg diameter in both flounder and dab increases with decreasing salinity. Here again the sole exception are the flounders from the Tvärminne area, which have significantly smaller eggs than those from the Arkona basin.

Table 1. Neutral buoyancy and diameter of flatfish eggs from marine and brackish populations.

Species	Locality	Salinity $^0/_{00}$	Neutral buoyancy $^0/_{00}$ S	Pelagic: P Demersal: D	Egg diam. mm		Number of eggs	Individuals
					Mean	Range		
Platichthys flesus	Bergen	35	31.8	P	0.884	0.78—0.94	1 760	14
	Kiel	22	—	P	0.959	0.89—1.02	339	2
	Arkona	17—18	16.2	P	1.185	1.01—1.29	1 470	14
	Tvärminne	6	19.9	D	1.008	0.88—1.11	1 723	19
Limanda limanda	Bergen	35	30.9	P	0.770	0.75—0.87	332	7
	Kiel	22	17.5	P	0.928	0.84—1.04	485	7

In electron microscopic studies the chorion of the fish egg is usually described as consisting of a thin outer layer and a thick, lamellar inner layer. The nomenclature of these layers varies among authors; in this paper the purely descriptive terms «outer layer» and «inner layer» will be used.

Recent studies of the eggs of *Platichthys flesus* and *Limanda limanda* from the Bergen area have shown that the chorion of the egg has about the same thickness in these two species, viz. about 2.5 μ; the ultrastructure of the chorion, on the other hand, shows clear species-specific differences (LÖNNING 1972).

In eggs of *P. flesus* from Bergen the inner lamellar layer of the chorion consists of 6 lamellae and the distance between the lamellae varies, being largest between the mid-lamellae. Outside the lamellar part a reticular layer is present. The outer layer of the unfertilized egg is rather homogeneous whereas in the 3—5 days old larvae this layer is fenestrated or subdivided into several layers (Fig. 2, see also LÖNNING 1972, figs. 10, 12).

Eggs of *P. flesus* from Kiel Bay show a somewhat thinner chorion, viz. about 1.8 μ. Also in these eggs the number of lamellae is 6, but these lamellae seem to be more equidistant than in the Bergen material. The reticular layer and the outer layer are in these eggs more homogeneous and not so distinct (Fig. 3).

Eggs of *P. flesus* from the Arkona basin have a quite different chorion from those from the Bergen and Kiel area. The diameter is only ca. 1.1 μ and there are but three lamellae, of which the two outer are furthest apart. As in the Kiel material the outer and reticular layer are rather homogeneous, but in the Arkona population these layers are thinner (Fig. 4).

In eggs from Tvärminne, finally, the chorion is nearly as thick as in the Bergen material, viz. 2.3 μ. The number of lamellae, however, is only 4. Outside the lamellae a rather distinct, reticular layer is present, followed by the outer layer, which is often somewhat subdivided (Fig. 5). As mentioned above the eggs in this population are demersal.

The chorion of the egg of *Limanda limanda* from the Bergen area has been described earlier (HAGSTRÖM and LÖNNING 1968, LÖNNING 1972). As already mentioned the diameter is 2.5 μ. In this species the lamellar part consists of 9 equidistant lamellae and the outer layer is subdivided into several homogeneous layers of different electron density (cf. Fig. 6, which shows an unfertilized egg).

Eggs of *L. limanda* from Kiel (Fig. 7) have a thinner chorion, viz. 1.6 μ. The number of lamellae is 8 or 9, and also in this population the lamellae are equidistant. The outer layer is less homogeneous than in

the Bergen material, and is somewhat broken up. As the Kiel material consisted of 5 days old larvae, some of these differences, especially in the outer layer, may be due to morphological changes during development (cf. LÖNNING 1972).

A synoptic comparison of the data on the ultrastructure of the chorion in the investigated populations of *P. flesus* and *L. limanda* is given in Table 2.

Table 2. Diameter of chorion and number of lamellae of flatfish eggs from marine and brackish populations.

| Species | Locality | Chorion | | Number of eggs measured |
		Thickness μ Mean	Number of lamellae	
Platichthys flesus	Bergen	2.5	6	13
	Kiel	1.8	6	5
	Arkona	1.1	3	5
	Tvärminne	2.3	4	6
Limanda limanda	Bergen	2.4	9	11
	Kiel	1.6	8—9	6

DISCUSSION

The low specific gravity of pelagic fish eggs in brackish areas is of survival value as it will cause the eggs to float in water of lowered salinity.

Short term experiments with flounders which were transferred from high to low salinity showed that the specific gravity of the eggs was little affected (SOLEMDAL 1967). Similarly, Baltic flatfish kept for two years in water of full marine salinity still produced eggs of low specific gravity (SOLEMDAL, in press). The differences in neutral buoyancy in pelagic eggs of marine and brackish water populations of the same species can thus not be explained by water absorption by the eggs due to osmotic conditions in the ovary or the surrounding medium.

Of the different egg components, the chorion is by far the densest. In herring the chorion amounts to 15—30% of the total dry weight (BLAXTER and HEMPEL 1963), in plaice 19—33% (SOLEMDAL 1970).

Generally the Baltic populations have eggs with a thinner chorion than the marine populations (Table 2). In *Platichthys flesus*, fishes from the Arkona basin have the thinnest chorion, while at Tvärminne, in still

more brackish water, the chorion is much thicker and has in fact nearly the same value as in the marine populations. However, at Tvärminne the eggs develop at the bottom, so that a thick, tough chorion is a definite advantage.

Both the thin chorion of the most brackish populations, and the thick chorion of the Tvärminne flounders, may thus well be the result of a long term selection process. This hypothesis is supported by the experiments mentioned above, in which it was shown that in Baltic flatfish kept at high salinity for as much as two years the eggs still were of the low gravity Baltic type. Differences in e.g. feeding conditions, hydrography or spawning season in the Baltic populations can thus be ruled out as a possible explanation for the differences in egg structure.

In both *Platichthys flesus* and *Limanda limanda* there is an inverse correlation between diameter of the egg and its specific gravity (Table 1). Such a correlation does not exist, on the other hand, in *Pleuronectes platessa*. In this species the Baltic populations have the smaller eggs (SOLEMDAL, in press). Egg size per se is thus not likely to be the main cause of the observed differences in specific gravity.

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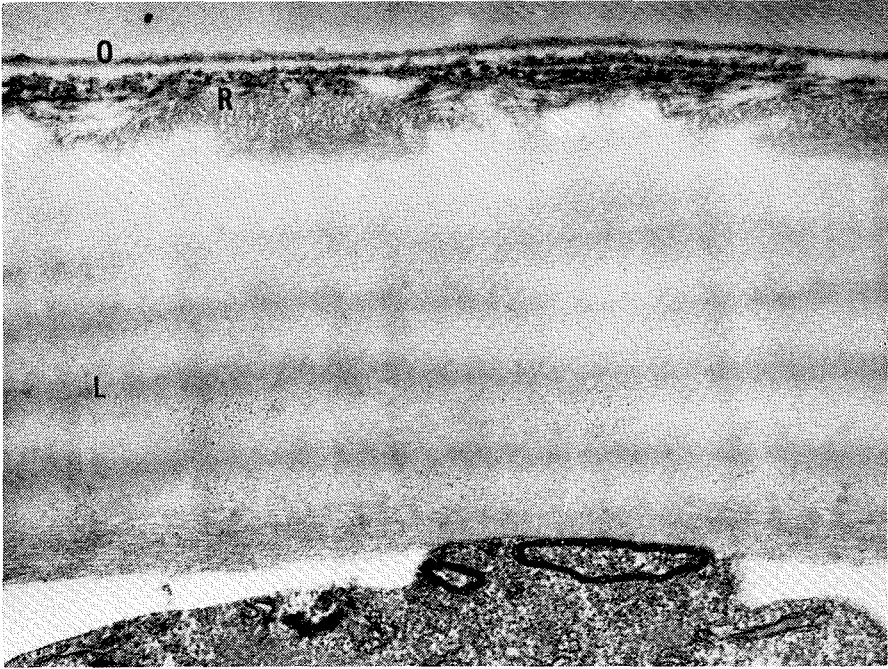Fig. 2. Chorion with outer layer (0) and inner layer consisting of a reticular part (R) and 6 lamellae (L). 30 000x. *Platichthys flesus* from the Bergen area.
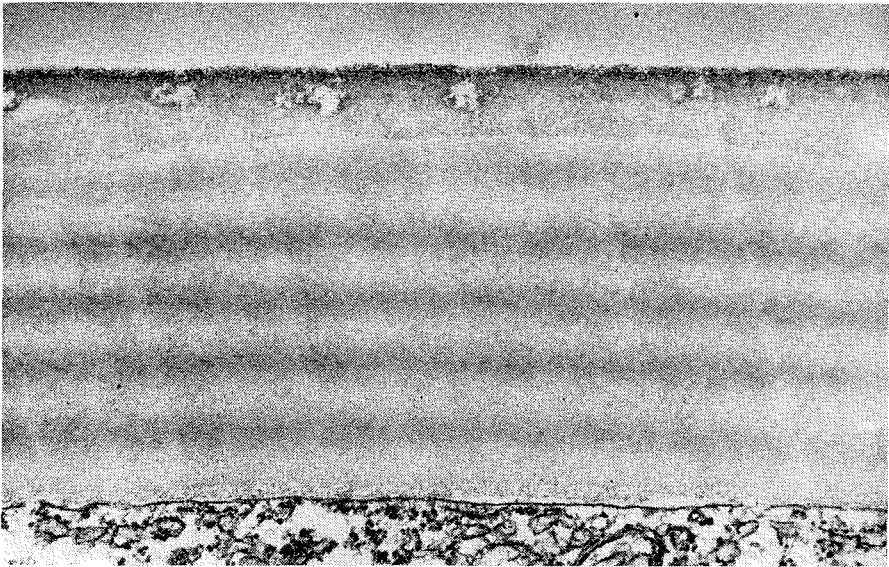

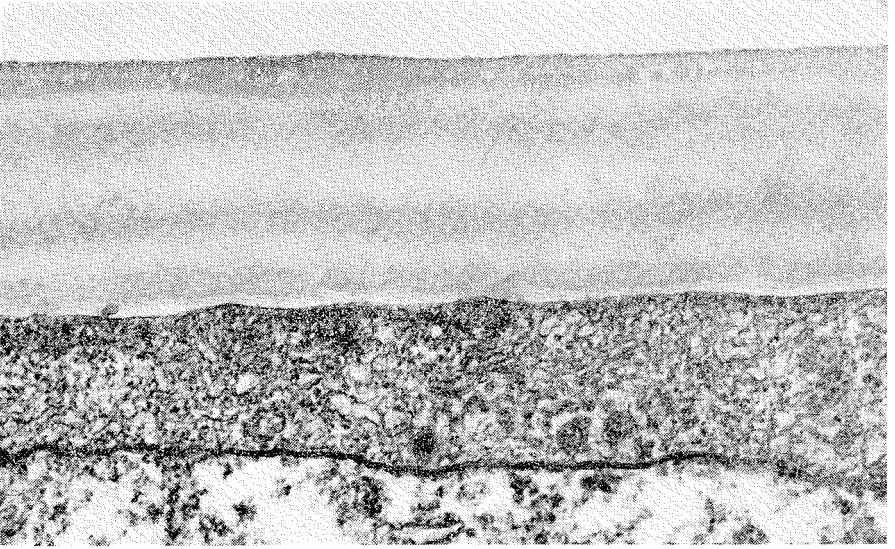Fig. 3. *P. flesus* from Kiel Bay. 30 000x.

Fig. 4. *P. flesus* from the Arkona basin. 30 000x.
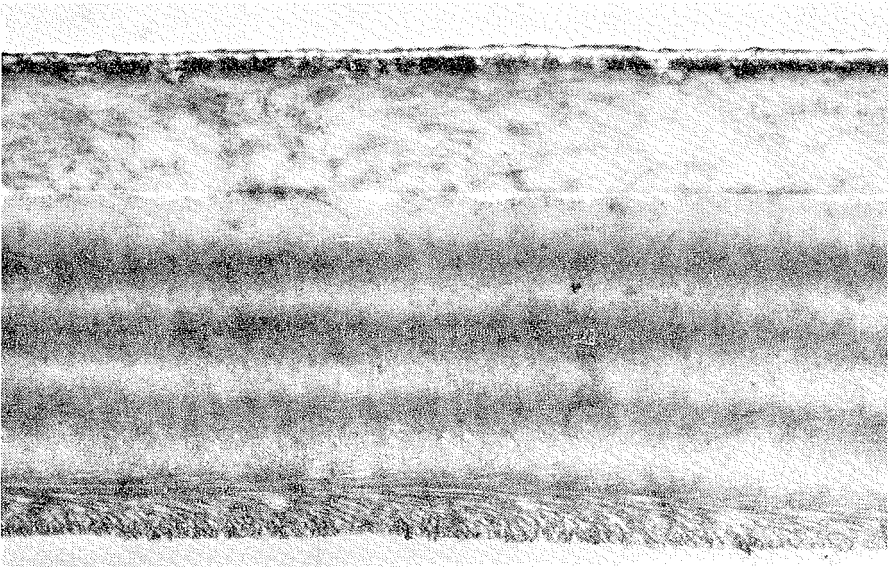

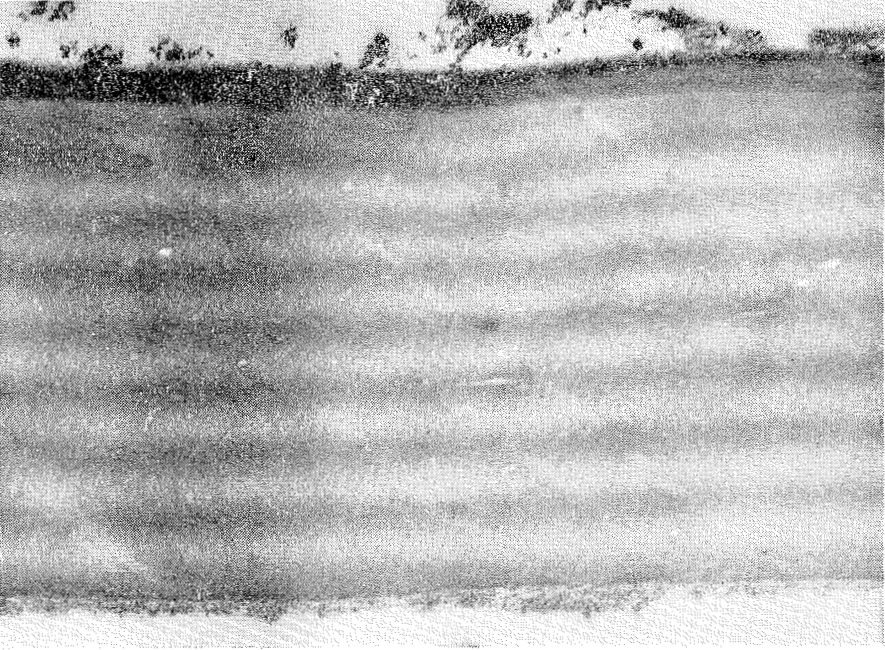Fig. 5. *P. flesus* from the Tvärminne area. 30 000x.

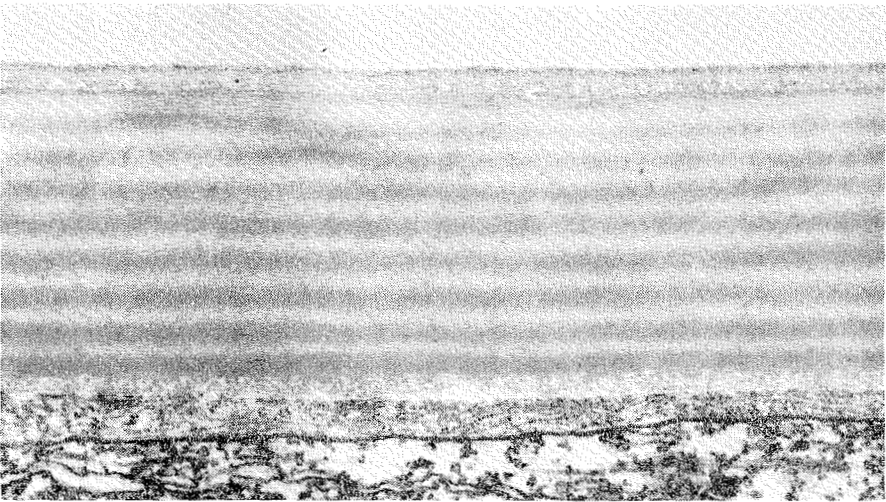Fig. 6. *Limanda limanda* from the Bergen area. 30 000x.

Fig. 7. *L. limanda* from Kiel Bay. 30 000x.

NOTES ON THE GAS CONTENT AND NEUTRAL BUOYANCY IN PHYSOSTOME FISH

By

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ABSTRACT

SUNDNES, G. and BRATLAND, P. 1972. Notes on the gas content and neutral buoyancy in physostome fish. *FiskDir. Skr. Ser. HavUnders., 16* : 89—97.

   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 equa-

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

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 swimbladder 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 dif-
ferences 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
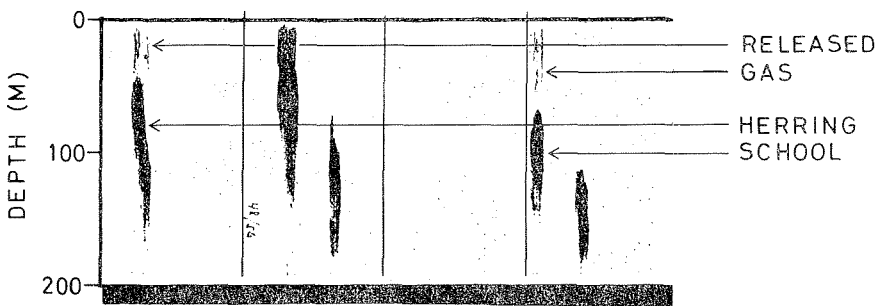

Fig. 1. Echogram showing gas release from migrating herring. (Photo: G. Vestnes).

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).
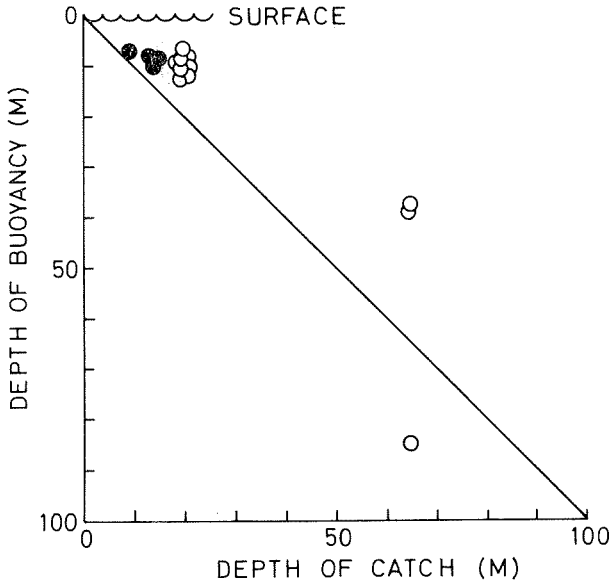

Fig. 2. Depth of buoyancy of *Clupea harengus* (●) and *Salmo alpinus* (○) in relation to depth of catch. The diagonal is the line of perfect buoyancy, i.e. where depth of buoyancy equals depth of catch.

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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