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IN SITU OBSERVATIONS OF SWIMBLADDER COMPRESSION IN HERRING

by

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ABSTRACT

The hydrostatic function of the swimbladder in herring is experimentally investigated through *in situ* diver-assisted measurements of swimbladder volume on net-caught and caged fish. In agreement with morpho-physiological evidence, the gas volume of the swimbladder was found to change with pressure according to Boyle's law. The volume remained uncompensated at depth, and additional reductions through gas diffusion were observed with time. Besides being depth dependent, the swimbladder volume showed a strong correlation with the condition factor and fat content of the fish. The observations are highly pertinent to the acoustic assessment methods used on this and related species, as they indicate that both depth and seasonal variations in the acoustic scattering properties of herring are likely.

INTRODUCTION

The herring (Clupea harengus L.) is a physostome with a characteristic air-filled connection from the swimbladder to the auditory bullae system and valve-supplied pneumatic ducts leading both to the stomach and directly to the exterior. Morphological and histological description of the system is given by MAIER and SCHEURING (1923) and FAHLÉN (1967). The lack of any rete-organized blood vessels in connection to the swimbladder (FAHLÉN 1967) has made its gas production, and hence its buoyancy control, a more or less unsolved mystery. Other mechanisms for gas production than gas multiplication through a gas gland have been suggested (SUNDNES, ENNS and SCHOLANDER 1958; BRAWN 1962; FAHLÉN 1967), but evidence for this has not been found.

Herring and several other physostomes are known to swallow air at surface and pass it to the swimbladder through the pneumatic duct (BRAWN 1962; HUNTER and SANCHEZ 1976). Although this may be a reasonable technique for filling the swimbladder at surface, it can never bring the herring to neutral buoyancy during extended vertical migrations, where pressure ranges of 40 atmospheres are observed (SUNDNES and BRATLAND 1972).

Measurements of swimbladder gas composition (FAHLÉN 1967; SUNDNES and BRATLAND 1972), which show a low relative amount of oxygen never exceeding that of air, also suggest that the gas is obtained at surface, rather than through the vascular system of the fish. Air swallowed at surface will tend to diffuse out of the swimbladder, at an increasing rate with depth. However, multiple layers of guanine crystals embedded in the swimbladder wall decrease the area available to gas diffusion and increase the path length for gas molecules, making the wall an effective barrier to gas loss (DENTON, LIDDICOAT and TAYLOR 1972).

The only, but indeed strong, indication of gas production at depth is found in observations of gas release when herring schools migrate towards the surface (SUNDNES and BRATLAND 1972). The amount of gas involved, or the physiological and ecological basis for the gas release, is rather poorly understood.

Despite the fact of gas release, several authors have now accepted the physiological evidence for the herring's inability to produce gas for the swimbladder, and claim that its primary function must be to act as a gas reservoir for the acoustico-lateralis system, keeping the gas-filled part of the bullae pressure stabilized with respect to the surrounding water during vertical migrations (ALLEN, BLAXTER and DENTON 1976; DENTON and BLAXTER 1976; BLAXTER, DENTON and GRAY 1979).

Besides leaving the herring in a rather unique buoyancy situation, swimbladder compression will affect the method of acoustic abundance estimation. The conversion factors used to transform integrated echo intensity to fish density are normally established through experimental measurements on surface-adapted fish. If the swimbladder, which is the dominant reflector of acoustic energy in fish, changes in volume and shape with depth, then this will seriously affect the reflection characteristics of the fish. Depth independent conversion factors are now used on several herring stocks in the North Atlantic (BAILEY et. al. 1983; HAGSTRØM and RØTTINGEN 1982; JAKOBSEN 1982).

Swimbladder compression will also modify the current models used in acoustic size-classification experiments based on swimbladder resonance frequency measurements. A general square-root pressure dependence on resonance frequency has so far been applied on all species (LØVIK, DALEN and OLSEN 1982).

The main intention of the present investigation was to make direct observations of swimbladder volume at several depths to give conclusive evidence for one of the two possible adaptation strategies in herring: gas production or gas compression. It was also hoped that the behavioural response to pressure would indicate the buoyancy state of the fish. Continous monitoring of the behaviour of caged herring was therefore an essential part of the experiment. The results from this part of the investigation are reported by ONA (1984).

MATERIAL AND METHODS

Experimental site

The measurements were made in a sheltered fjord west of Bergen. An anchored raft carried both a laboratory compartment and accommodations for the crew. Nearby shore power was carried to the raft through a underwater cable to supply the UTV-camera systems, laboratory equipment, and accommodation necessities with high-quality 230V, 50 Hz AC-current. Diver air bottles were refilled with a fuel-engined air compressor, 3000 psi, on the raft. A bottom depth beneath the raft of 35 meters gave a maximum pressure range for the investigation of 4 atmospheres, which was also assumed to be the maximum safe working depth for the divers when no decompression was applied.

Fish

The herring used in most of the experiments were caught by shore seine in the vicinity of the raft. About 5000 fish from one catch were "herded" into a large (100 m^3) holding pen and carefully towed to the raft. Age and gonad analysis showed that the local stock of herring, found in the area throughout the year, contained both spring and autumn spawners in a 3/1 ratio. Two distinct year classes with one and two winter rings could be separated in the catch with less than 10% admixture of older herring. In situ measurements of swimbladder volume were also made on herring caught in gill-nets at various depths near the raft.

Fish in the length range from 17 to 33 cm are represented in the analysis.

Swimbladder volume measurements

i) Control groups

The swimbladder volume of surface-adapted fish was obtained by transferring small samples of about 10 fish from the upper part of the holding pen to a 250 l tank, on the raft, containing a strong 200-300 ppm benzocacin solution. When fully anesthetized, a fish's buoyancy was roughly classified as floating, neutral or sinking. The swimbladder was then immediately emptied under water by gentle ventral massage from beneath the pelvic fins towards the anal opening, with the gas being collected in an inverted, suspended funnel with a top-mounted, fine-scaled glass burette.

With trained personnel, this was shown by underwater dissections to be an effective method for totally emptying the herring swimbladder. No residual gas was found either in the main chamber or in the anal duct of the swimbladder. Residual gas in the auditory bullae system and its precoelomic ducts, which is not measured by this method, represents less than 5% of the total gas volume of the system in surface-adapted, adult herring (ALLEN, BLAXTER and DENTON 1976). The accuracy of the swimbladder gas volume measurements is estimated to be within ±0.1 ml.

ii) <u>In situ measurements</u>

The swimbladder gas volume in herring at depth was measured both on fish caught with gill nets and on caged, depth-adapted fish.

Several earlier tests in the ring tank (250 m^3) of the Institute of Marine Research, Bergen, had shown that herring could be caught in gill nets without releasing gas from the swimbladder as a stress reaction on detainment, as observed in some other physostomes (VERHEIJEN 1962; SUNDNES and BRATLAND 1972). These results indicated that representative observations of swimbladder volume at depth could be made by skillful divers trained at surface.

Herring gill nets with varying mesh sizes from 45 to 52 mm (stretched), which spanned the depth range near the raft, were inspected each morning by two divers. The swimbladder volume of all entangled herring that were still alive was measured using the same equipment and technique as at surface, but with the herring still in the net, immobilized by a firm grip over the skull. This operation made it necessary to strip some meshes near the fish, but also minimized direct handling of the fish before the gas measurements. Depth of catch, state of the fish, and swimbladder volume were recorded on underwater log-sheets, and the fish individually saved for further surface measurements.

The observations on depth-adapted caged herring were obtained using a similar technique. A cylindrical net cage (6 m^3) partly covered by a thin, transparent plastic foil was used to control the anesthetizing of the fish. During depth adaption, the upper and lower part of the cage were open to water flow, but could be closed by the divers after having introduced a suitable amount of benzocaein solution from below. Using a cod-end release in the bottom panel of the cage, herring could be individually picked out for swimbladder analysis, since these were, without exception, negatively buoyant, and sank to the bottom when anesthetized. Adaptation depths of 18 and 25 meters were used for five and three days, respectively, in both cases with a density of 6 fish/m^3.

During all operations the divers were connected with buddy-lines, one carrying the measuring equipment, the other one performing the actual measurement, such as emptying the swimbladder. Special precautions were taken to assure the security of the divers during the gill net inspections.

Fat analysis

To examine possible sources of swimbladder volume variance, a sample of 60 herring was stored after the measurements for fat analysis. These were later individually analysed by standard methods for fat; namely, Na_2SO_4-grinding with ethyl ether extraction (LOSNEGARD et al. 1979). A sample of 40 herring from a later catch was also analysed to monitor swimbladder volume-to-fat content on the estimated top of the fat cyclus of the spring spawners.

RESULTS

General observations

Herring is known to be extremely sensitive towards direct handling, with increased mortality when scales are lost. The catch and herding prosesses in this investigation were most successful as a mortality of 0,2% was observed over the experimental period of seven weeks. The samples to be used as control groups were taken directly from the upper part of the holding pen at less than 1 meter depth. About 95% of the fish were classified as neutral or positively buoyant when anesthetized, indicating that the observed swimbladder volume gives the herring a perfect hydrostatic stability in the upper meter. Gas bubble-release via the post anal opening was observed in several herring after 6-8 minutes in the anesthetic solution, probably due to sphincter relaxation when dying. When gas release appeared during swimbladder measurements, the rest of the sample was discarded.

Control groups

The swimbladder volume of surface-adapted herring showed a high degree of variance, increasing with fish size. The swimbladder volume-to-fish weight ratio decreased slightly with increasing fish size (Fig. 1, Table 1.).

Normally, a swimbladder volume of about 5% of the total body volume is neccesary to give a marine teleost neutral buoyancy (ALEXANDER 1966). The density of the fish tissue was not checked here, and the values reported are therefore not directly comparable with BRAWN's (1962) values, where total body volume is used as reference. Using the reported mean density for herring, 1.026 g/ml, our values are slight under-

estimates when compared to Brawn's. From the common regression (Table 1) it can be estimated that among the measured herring the mean swimbladder volume is 2.9% of the body weight at 100 grams, decreasing to 2.3% at a weight of 200 grams.

As the herring was found to be at neutral or slight positively buoyant when anesthetized, the great variance in swimbladder volume could only be caused by a variable fat content, or other possible boyancy regulators. Individual fat analyses after the swimbladder measurements were made to explain the variance. (Fig. 2, Table 2). Surprisingly, almost the entine fat-spectrum naturally observable in herring, from 6% to 28% is covered by the two samples, taken from two separate but distinct schools. As is evident from the regression analysis, the swimbladder volume and fat content of the fish are strictly correlated, with 1 ml gas being replaced by about 7.5 ml fat (density 0.926). When this relation is used to normalize the swimbladder volume with respect to the fat content of the fish, almost the entire variance seems to be explained (Fig. 3, Table 3).

As determination of the fat content of individual fish is a tedious operation, it was hoped that the condition factor could be used as a fat-indicator. From Fig. 4 it can be shown that the parameters are significantly correlated, but it was concluded that the variance was too high to base a multiple regression on the form

$$V_{sb}=W\cdot\hat{m}+CF\cdot\hat{m}_2+\hat{b}$$

As the fish sampled <u>in situ</u> not were analysed for fat, the expected swimbladder volume at surface for these are estimated from the merged control-groupdata by simple linear regression (Table 1). Merged data from all samples in this table were used in an F-test (ZAR 1974). Testing of both slopes and elevations indicated no significant difference among the samples ($P>0.50$).

In situ measurements

During 20 inspections, the divers measured the swimbladder *in situ* of 25 herring caught in the gill nets, and later 18 herring from the cage experiment.

Of the herring caught in gill nets, about 15% were still alive and in good condition; the rest were classified as dead or dying, and therefore discarded. The cage-adapted herring were in excellent condition, and were measured within five minutes of anesthetizing. As only a few of the total number of herring within the cage were measured, it is important to note that every herring (about 60), without exception, was negatively buoyant when anesthetized. At the surface, 95% of the fish were neutral or positively buoyant.

The observed swimbladder volume relative to its estimated surface value is plotted against depth of catch in Fig. 5. Compression of the gas according to Boyle's law is indicated by a heavy continous line. The herring caught in gill nets are individually marked, while the samples from the cage are indicated with mean value, standard deviation and total range.

As both the observed and the expected volumes contain an unknown factor of variance from individual differences in fat content, the cage measurements are entirely consistent with Boyle's law. The fish at 18 meters depth was allowed an adaptation time of five days, the samples from 25 meters, three days. This was in both cases considered to be sufficient even if the gas-producing capacity were extremely low. Slightly lower volumes than predicted from free-compression theory in both samples indicates rather a low gas diffusion out of the swimbladder at depth.

Several of the measurements from the gill nets are also consistent with this theory, but a high percentage of low values was also recorded. If this is due to passive gas diffusion, the herring must have spent weeks at depth without surfacing, or some gas must have been released before inspection. The expected and observed, pressure-corrected swimbladder volumes are shown in Fig. 6.

DISCUSSION

The investigation seems to confirm earlier physio-morphological evidence for the absence of a gas production mechanism in the herring swimbladder. Of 43 herring measured in situ at depth of catch, or at adapted depth, no value exeeding the swimbladder volume expected from free-compression theory was recorded. Bearing in mind that just a single observation of a surface-comparable volume at depth would have confirmed the opposite hypothesis, the statistical power of the data is evident. The observations were made at moderate depths, but as the pressure gradient is strongest here, little was considered to be gained by working deeper. At 30 meters, the swimbladder volume is already reduced to 25% of its original, surface volume.

An extremely low gas-producing capacity in salmonids has been recorded at surface levels by WITTENBERG (1958). A similar mechanism was considered to be unlikly in herring, as this is contraindicated by its vertical migration pattern. As measurements of the gas diffusion rate from the swimbladder was not implemented in the project, longer adaptation periods were not applied. The results indicate that gas diffusion rates can actually be estimated by this technique, and plans for such investigations have already been made.

Preliminary estimates of the gas diffusion rate from the cage measurements were made. Discarding one observation of a large swimbladder volume at 25 meters depth, the herring being very slender (CF=0.582), the estimated rates are

1.8μl STP/h/atm at 18 meters depth
1.0μl STP/h/atm at 25 meters depth

(Mean values for fish size 22,8±3.1 cm.)

This is about twice the observed rate in small, 13 cm, herring in BLAXTER & BATTY (1984), but even at this rate, the swimbladder gas in adult herring will be maintained for weeks at depth. The gas diffusion rate seems to be strongly related to fish size, and Blaxter & Batty conclude that the juvenile herring are likely to lose their swimbladder gas at a much higher rate than the adults. This may explain the difference in migration pattern between juvenile and adult herring. The small herring performs more or less daily migrations, while the vertical migration pattern among adults can be very irregular, with weeks between each ascending.

There seems to be no reasonable explanation for the phenomenon of gas release when herring schools are ascending. If gas were produced at depth, this would obviously be a practical way to avoid over-inflation of the swimbladder as the pressure is reduced. When no measurable gas production occurs at depth, the release may have a different functional meaning. Several earlier suggestions have been made, but as neither the amount of gas involved, nor the frequency of the phenomenon is unknown, good explanations are lacking.

The observations of a time-lag between pressure equalization between the auditory bulla system and the swimbladder (BLAXTER & HOSS 1979), due to the narrow gas duct connecting the two chambers, may indicate that gas is released from the swimbladder to increase the speed of this process. The hearing sensitivity will this way be kept undisturbed by pressure. If this is done by creating a minor negative pressure inside the swimbladder, held in a few seconds by muscular tension of the body cavity, release of small quantities of gas would be a reasonable way to create a negative pressure. The problem is then more or less comparable to the method used by divers when equalizing the pressure in the inner ear when descending and ascending. Further studies must be made to clarify this aspect of the swimbladder function in herring.

Even if the swimbladder gas were compressed, the herring seemed to have no problem in compensating for the negative bouyancy (ONA 1984). Increased swimming activity, extended pectoral fins, and slight positive tilt angles were observed as compensatory responses.

The main incentive for this investigation was to further increase the precision of acoustic abundance estimates on herring. As the swimbladder represents a high density contrast to the fish-flesh and surrounding sea water, it is responsible for about 90-95% of the backscattered acoustic energy by the fish (FOOTE 1980). These investigations indicate that the acoustical scattering properties of herring will be depth dependent. The buoyancy balance regulation between gas and fat also indicate that seasonal variations are likely. The magnitude of both depth and seasonal changes will depend on the shape stability of the swimbladder during gas compression and fat investment.

Calculations of backscattered energy based upon the swimbladder being a simple geometrical shape can only be approximate, as the dorsal surface of the swimbladder is quite stable under pressure changes, due to its dorsal and lateral attachment to the body cavity, at least in gadoids (ONA 1982).

The acoustic effect of swimbladder compression in herring may be investigated by in situ target strength measurements, as in HALLDORSSON (1983). To isolate the effect of vessel avoidance, which will tend to act in the opposite way, being strong near the surface and reduced at depth, cage calibrations with continuous behavioral observations should be made at several depths.

Before the combined effect of vessel avoidance and gas compression is elvcidated, the best way to obtain integrator conversion factors for herring is through in situ techniques, either by target strength measurements, e.g., HALLDORSSON 1983, or by purse seine techniques, e.g., HAGSTRØM & RØTTINGEN (1982).

REFERENCES

ALEXANDER, R. McN. 1966. Physical aspects of swimbladder function. Biol. Rev. Cambridge Philos. Soc., 41: 141-176.

ALLEN, J.M., BLAXTER, J.H.S. & DENTON, E.J. 1976. The functional anatomy and development of the swimbladder - inner ear - lateral line system in herring and sprat. J. Mar. Biol. Assoc. U.K. 56: 471-486.

BAILEY, R.S., AGLEN, A., CORTEN, A. and SIMMONDS, J.E. 1983. Report on the 1983 herring acoustic survey in the northwestern North Sea. ICES. C.M. 1983 (H:52), 1-8. (Mimeo).

BLAXTER, J.H.S., BATTY, R.S. 1984. The herring swimbladder; loss and gain of gas. J. Mar. Biol. Ass. U.K., 64(2):441-459.

BLAXTER, J.H.S. & HOSS, D.E. 1979. The effect of rapid changes of hydrostatic pressure on the Atlantic Herring Clupea harengus L. II. The response of the auditory bulla system in larvae and juveniles. J. exp. mar. Biol. Ecol., 41:87:100.

BLAXTER, J.H.S. DENTON, E.J., & GRAY, J.A.B. 1979. The herring swimbladder as a gas reservoir for the acousticolateralis system. J. Mar. Biol. Ass. U.K., 59: 1-10.

BRAWN, V.M. 1962. Physical properties and hydrostatic function of the swimbladder of herring (Clupea harengus, L.). J. Fish Res. Board Can., 19: 635-656.

DENTON, E.J. & BLAXTER, J.H.S. 1976. The mechanical relationship between the clupeid swimbladder, inner ear and lateral line. J. Mar. Biol. Assoc. U.K., 56: 487-807.

DENTON, E.J. LIDDICOAT, J.D. & TAYLOR, D.W. 1972. The permeability of gases of the swimbladder of the conger eel (Conger conger). J. Mar. Biol. Assoc. U.K., 52: 727-746.

FAHLEN, G. 1967. Morphological aspects on the hydrostatic function of the gasbladder in Clupea harengus L., Acta. Univ. Lund. Sect. 2(1): 1-49.

FOOTE, K.G. 1980. Importance of the swimbladder in acoustic sattering by fish: A comparison of gadoid and mackerel target strengths. J. Acoust. Soc. Am., 67(6):-2084-2089.

HAGSTRØM, O. RØTTINGEN, I. 1982. Measurements of the density coefficient and average target strength of herring using purse seine. ICES. C.M., 1982 (B:33), 1-13. (Mimeo).

HALLDORSSON, O. 1983. On the behaviour of the Islandic summer spawning herring (Clupea harengus L.) during echo surveying and depth dependence of acoustic target strength in situ. ICES. C.M. 1983 (H:36), 1:35.

HUNTER, J.R. & SANCHES, C. 1976. Diel changes in swimbladder inflation of the larvae of the northern anchovy Engraulis mordax. . Fishery Bulletin. Fish and Wildlife Service. United States Department of the Interior, 74: 847-855.

JAKOBSSON, J. 1982. Echo surveying of the Icelandic summer spawning herring 1973-1982. Symposium on fisheries acoustics, Bergen, Norway, 21-24 June 1982, ICES. NO 22: 1-36 (Mimeo).

LOSNEGARD, N., BØE, B. and LARSEN, T. 1979. Undersøkelse av ekstraksjons-midler for bestemmelse av fett. Fiskeridirektoratet, Rapporter og meldinger, Nr. 1/79; 1-4. (In norwegian).

LØVIK, A., DALEN, J. & OLSEN, K. 1982. Acoustical remote sensing of fish size. *Symposium on fisheries acoustics, Bergen, Norway, 21-24 June 1982, ICES. NO 52*: 1-24 (Mimeo.)

MAIER, H.N. & SCHEURING, L. 1923. Entwiklung der Schwimblase und ihre Beziehungen zum statishen Organ und der Kloake bei Clupeiden, spez. beim Hering. *Wissenshaftliche Meeresuntersuchungen der Kommission zur wisseuchaftlichen Untersuchung der deutchen Meere. (Abteilung Helgoland), no.6*, 23 p.

ONA, E. 1982. Mapping of the swimbladder shape and shape stability for theoretical calculations of acoustical reflection from fish. *Thesis, Univ. of Bergen, Bergen, Norway*. 231 pp (In norwegian).

ONA, E. 1984. Tilt angle measurements on herring. *ICES. C.M. 1984 (B:19)*, 1-13. (Mimeo.)

SUNDNES, G. & BRATLAND, P. 1972. Notes on the gas content and neutral boyancy in physostome fish. *Fish Dir. Skr., Ser. Havunders., 16*: 89-97.

SUNDNES, G., ENNS, T. & SHOLANDER, P.F. 1959. Gas secretion in fishes lacking rete mirabile. *J. Exp. Biol., 35 (3)*: 671-676.

VERHEIEN, F.J. 1962. Gas splitting by alarmed fish disturbs their hydrostatic equilibrium. *Science, 137 (3533)*: 864-865.

WITTENBERG, J.B. 1958. The secretion of inert gas into the swimbladder of fish. *J. Gen. Physiol.,41*: 783-804.

ZAR, J.H. *Biostatistical analysis*. Preutice-hall inc., New York, 1974, 670 pp.

Table 1. Coefficients and associated statistics of linear regression of swimbladder volume on weight, $Sb.vol. = \hat{m} \cdot weight + b$, for surface adapted herring. Number of observations, the estimated regression constants $\hat{m}$ and $\hat{b}$, estimated standard error of $\hat{m}$, standard error of regression (SE) and the correlation coefficient (r) are shown.

Sample no.	Date	Regression coefficients					
		N	$\hat{m}$	SE($\hat{m}$)	$\hat{b}$	SE	r
3+4	27.6.83	52	0.016	1.8E-3	1.416	0.506	0.791
5	28.6.83	51	0.019	1.7E-3	0.983	0.539	0.845
6	29.6.83	63	0.017	1.6E-3	1.065	0.626	0.804
7	5.7.83	60	0.017	2.1E-3	1.132	0.661	0.718
common		226	0.017	9.1E-4	1.157	0.589	0.786

Table 2. Coefficients and associated statistics of linear regressions of swimbladder volume (as percentage of body weight) on its fat content (also expressed as percentage of body weight). Sb.vol.= $\hat{m}\cdot$fat content + $\hat{b}$, other symbols as in table 1.

Sample no.	Date	Regression coefficients					
		N	$\hat{m}$	SE($\hat{m}$)	$\hat{b}$	SE	r
7	5. 7.83	60	-0.147	0.013	5.52	0.433	0.840
8	7.10.83	31	-0.137	0.014	5.74	0.255	0.872

Table 3. Coefficients and associated statistics of linear regressions of swimbladder volume on weight for surface-adapted herring, before and after normalizing for individual variations in fat content.

Sample no.	Date	Regression coefficients					
		N	$\hat{m}$	SE($\hat{m}$)	$\hat{b}$	SE	r
7	5. 7.83	60	0.017	2.1E-3	1.132	0.661	0.718
8	7.10.83	31	0.047	3.4E-3	-0.649	0.580	0.917
7	Fat-normalized	60	0.029	9.3E-4	1.127	0.282	0.971
8		31	0.034	5.2E-3	0.149	0.279	0.967

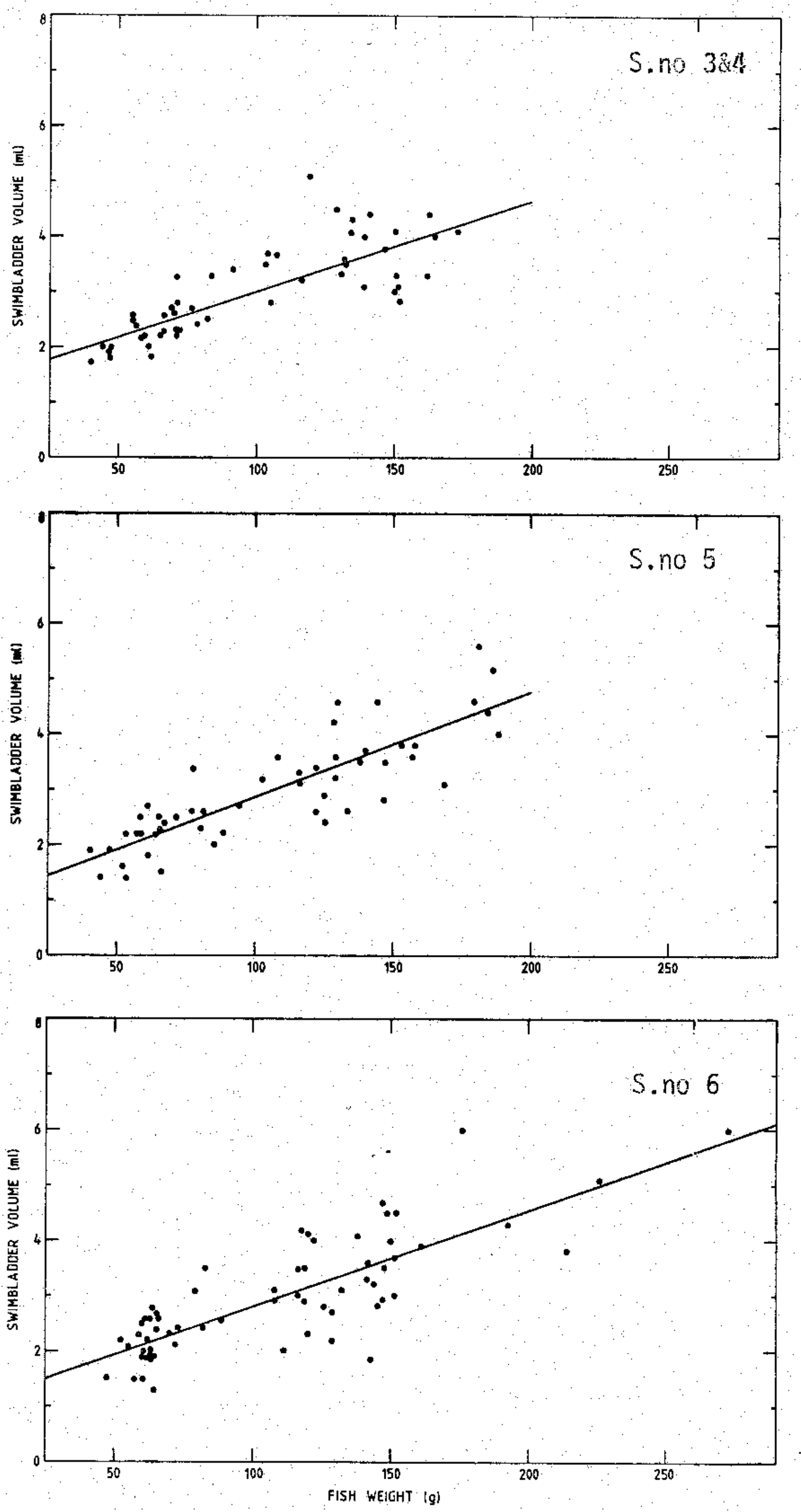

Fig.1. Swimbladder volume in ml related to fish size for three independent samples of herring from the holding pen.

The relation $w(\text{grams}) = 4.95 \times 10^{-3} \cdot L(\text{cm})^{3.131}$

can be used to transform the weight axis. The estimated regression coefficients are found in Table 1.

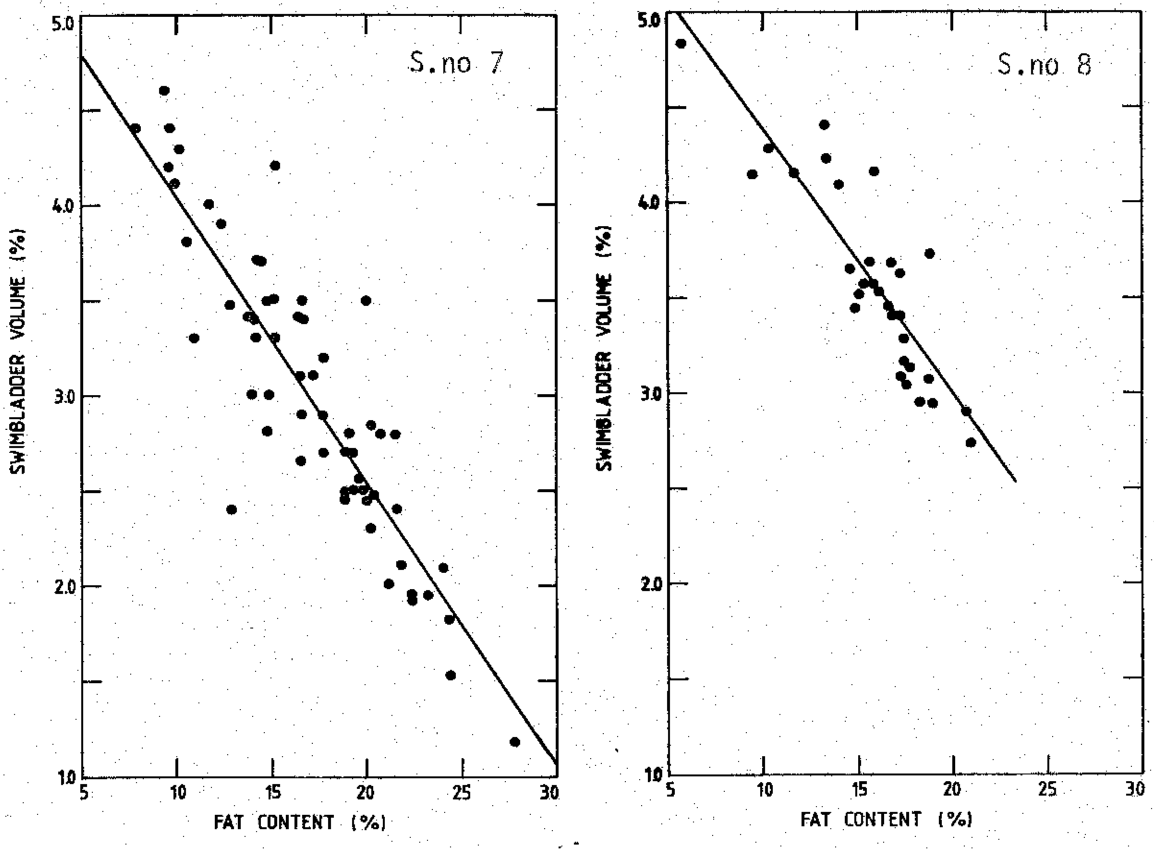

Fig.2. Swimbladder volume per unit wet body weight of herring related to its fat content. Sample no.7 was taken in the experimental period, no.8 in October 1983

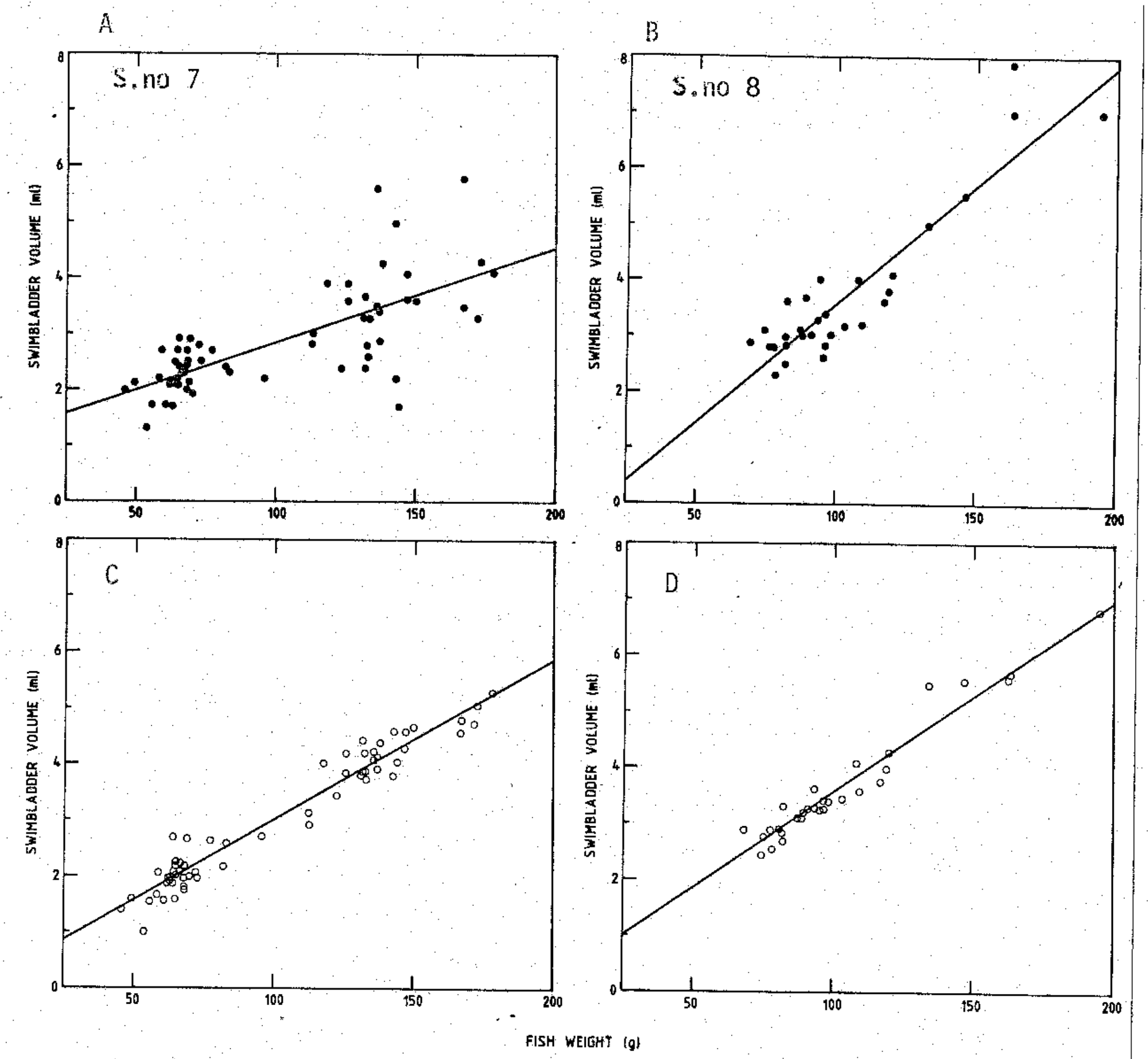

Fig.3. Swimbladder volume in ml related to fish size (A,B) for the samples subjected to fat analysis nos.7 and 8. Using the relation from Fig.2 the swimbladder volume in C and D is normalized with the mean fat content of the samples as reference. Evidently, most of the swimbladder volume to weight-variance is explained through individual difference in fat content. The regression coefficients are found in Table 3.

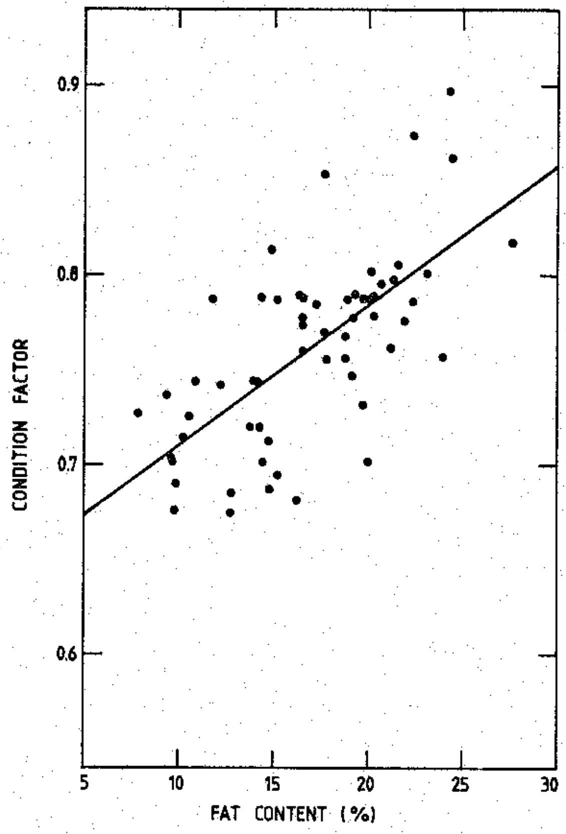

Fig.4. Condition factor versus fat content of herring from sample no.7. Condition factor is estimated as

$$CF = \frac{w(g) \cdot 100}{L(cm)^3}$$

Simple linear regression analysis gives

$$CF = 0.0073 \cdot FC + 0.638 \quad , r = 0.669, P < 0.001$$

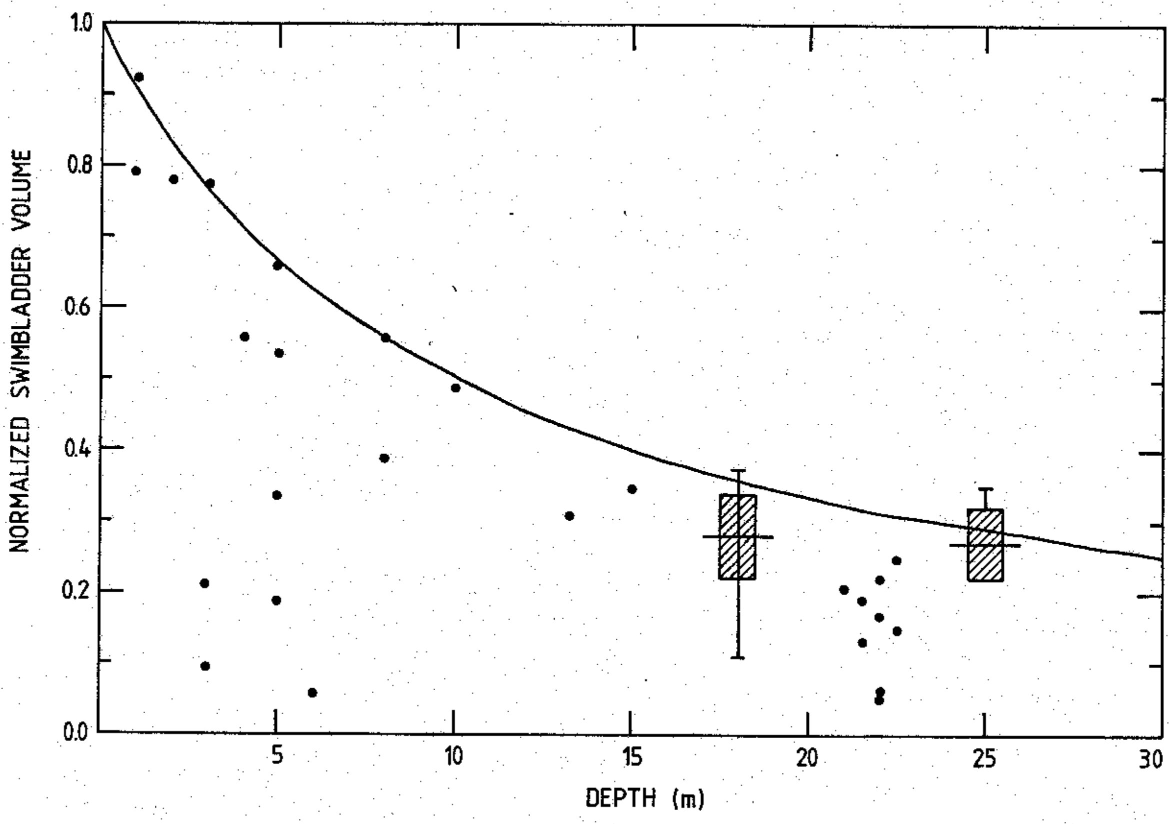

Fig.5. Swimbladder volume of herring measured by divers *in situ*, normalized with respect to the expected surface volume (Regression no.5, Table 1). Free compression of the gas according to Boyle's law is indicated by the heavy line. Data from the cage experiment is given as mean value, one standard deviation and observed range. The measurements on herring in gill nets are marked individually.

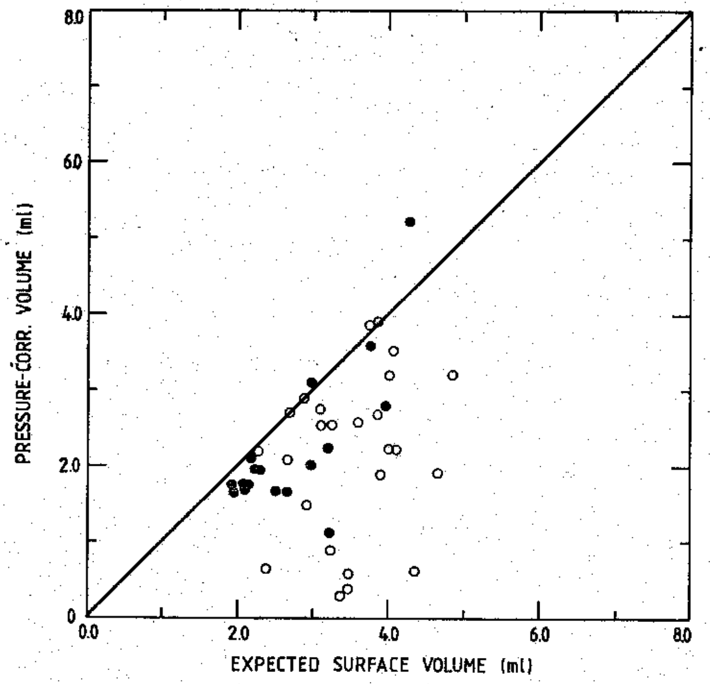

Fig. 6. Estimated expected swimbladder volume (from regression no. 5, Table 1) related to observed, pressure-corrected volume e.g. observed value multiplied by the actual pressure in atm. at the depth of catch . Caged herring are indicated by closed symbols, net-caught by open.