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PHYSIOLOGICAL FACTORS CAUSING NATURAL VARIATIONS IN ACOUSTIC TARGET STRENGTH OF FISH

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The swimbladder is recognized as responsible for a major part of the acoustic backscattering from fish. In most fishes it has the function of a buoyancy regulator but in others its main function is rather unclear. Based on methods for exact mapping of the swimbladder shape, observations of deviations from normal appearance and shape are discussed in relation to possible effects on target strength. Evidence for both periodic variations, as from uncompensated vertical migrations, and seasonal variations, caused by the fat cycle and gonad development, are presented.

INTRODUCTION

In order to obtain absolute acoustic estimates of fish abundance, detailed knowledge of the scattering properties of the measured fish is needed. This information was earlier gathered through experimental measurements on individual, stunned or anaesthetized fish, or on several free-swimming individuals in cage-experiments. A brief summary of the results from such measurements is given by Midttun (1984).

The demand for *in situ* measurements, where the behavioural effects on target strength are incorporated, has been stated internationally for several years (Craig & Forbes, 1969; Ehrenberg, 1972, 1979; Halldorsson & Reynisson, 1982), but high-quality, direct measurements of target strength have so far been restricted by the lack of proper, precise instrumentation. The recently developed dual- and split-beam echo sounders may in the future continuously produce the essential target strength information to be fed into the acoustic fish abundance estimation model. Preliminary use of these systems has already proved that the target strength may vary within the same fish concentration, and that systematic day/night differences occur (Traynor & Williamson, 1983; Ona & Hansen, 1986). Even larger variations in target strength seem to exist between different stocks of herring (Halldorsson & Reynisson, 1982; Foote *et al.*, 1986; Edwards & Armstrong, 1981; Lassen & Stæhr, 1985). This can obviously be explained through different behaviour modes of the herring during the measurements, as shown by Olsen (1979), but it is the intention of this paper to demonstrate that large, periodic variations in target strength must also be expected from cyclic and systematic variations of swimbladder volume and shape.

The fish swimbladder has been identified in several species as the main reflector of acoustic energy. The small specific acoustic impedance of gas compared to that of sea water, fish flesh and bones, makes the gas-filled swimbladder responsible for 90-95% of the total reflected energy from the fish (Foote, 1980b). Acoustic scattering models,

where the exact form of the swimbladder alone is used as the scattering object, demonstrate that this in fact is enough to reconstruct the scattering field from the entire fish (Foote & Ona, 1985; Foote, 1985).

Generally, it is assumed that the swimbladder acts as an ideal buoyancy organ in the fish, and to retain neutral buoyancy its volume and shape should remain independent of the depth. This is only likely to be true for non vertical migrators. Physoclists, such as cod (*Gadus morhua*) and other gadoids, with gas secretion and resorption mechanisms, respond to pressure changes appropriately by secreting gas if the pressure increases or resorbing it if the pressure decreases. Both of these processes are slow, and compensation for depth change is likely to lag behind the rate of vertical migration at dusk and dawn (Tytler & Blaxter, 1973; Blaxter & Tytler, 1978; Harden Jones & Scholes, 1985).

In some of the commercially important physostomatous pelagic species, like herring (*Clupea harengus*), capelin (*Mallotus villosus*), and sprat (*Sprattus sprattus*), on which the acoustic method is widely used for stock assessment, the gas production mechanism, if it exists at all, is still unclear (Maier & Scheüring, 1923; Fahlén, 1967; Brawn, 1962; Sundnes & Bratland, 1972). Herring and other related physostomes are known to swallow air at the surface and pass it to the swimbladder through the pneumatic duct (Brawn, 1962, Hunter & Sanchez, 1976; Blaxter & Batty, 1984). Although this may be a reasonable technique for filling the swimbladder at the surface, it can never bring the herring to neutral buoyancy especially during extended vertical migrations, where pressure ranges of 40 atmospheres are known (Sundnes & Bratland, 1972). Gas loss, however, if required, is among physostomes simply achieved by releasing gas through the duct or ducts leading from the swimbladder.

During development of methods for exact mapping of the swimbladder shape, several examples of deviations from the 'normal' were seen. This paper will present evidence for some physiological factors which affect the shape and volume of the swimbladder to a such an extent that significant changes in target strength are to be expected.

MATERIAL AND METHODS

Methods for this study were developed at the Institute of Fisheries Biology, University of Bergen, in the period 1979-1982. Further work on mapping and swimbladder analysis of herring and cod were done under projects for acoustic size classification of fish at the Institute of Marine Research, Bergen, from 1982 to 1985.

Catch

To prevent decompression damages on the swimbladder, all fish used in the analysis were carefully caught close to the surface by land seine, dip nets or fish pots (Table 1). Herring, *Clupea harengus* and pollack, *Pollachius pollachius* were allowed to swim freely from the land seine to shallow holding pens at the experimental site in Skogsvaag (Figure 1). Large mature cod, *Gadus morhua*, caught in fish pots outside Smøla, were transported to the ring-aquarium at the Institute of Marine Research, Bergen for

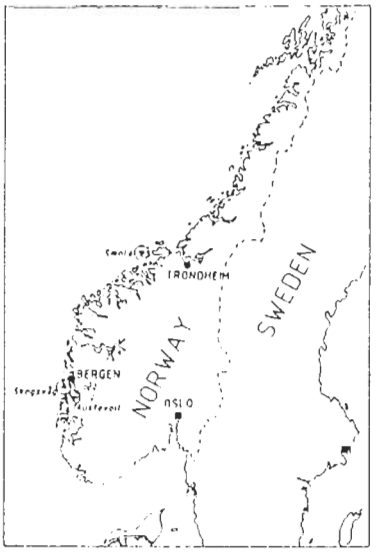

Figure 1. Map of the referred catch and experimental sites.

adaptation, while cod fry were lifted directly from the dip-nets in the rearing ponds at Austevoll to the anaesthetizing bath. Before the measurements, the fish could adapt to surface level for more than seven days.

Of the total background material of 462 fish, only the part needed to focus on swimbladder variability will be presented here.

Table 1. *Catch sites and methods, adaptation depths and treatment of the fish used in the experiments*

AD, pressure adaptation; AN, anaesthetizing; SF, shock freezing; I, swimbladder injection; MS, microtome slicing; SBV, swimbladder volume measurements

Fish	N	Catch method	Site	Depth of catch	Depth of adaptation	Treatment
Large cod	17	fish pots	Smøla	10	0.5	AD, AN, SF, I, (MS)
Cod fry	75	dip nets	Austevoll	1	1	AN, SF, MS
Pollack	20	land seine	Skogsvaag	5	0.5	AD, AN, SF, MS
Herring	257	land seine	Skogsvaag	5	0.5	AD, AN, SBV, (MS)
Herring	90	land seine	Skogsvaag	5	0.2-0.5	AD, AN, SBV, *in situ*

Anaesthetizing and freezing

Before final treatment, either freezing or swimbladder volume measurement, each adapted fish was anaesthetized with 300 ppm benzocaine. Immediately after immobilization, the fish destined for swimbladder shape analysis was transferred to the freezing solution, a bath of ethanol, chilled to a temperature below -50°C by the use of 'dry ice'. During freezing, the fish was held in a normal, horizontal swimming position, stretched between a pair of tongs grasping the snout and tail. Large cod, however, were stretched horizontally in a special frame during freezing. Using this method, the fish was

thoroughly frozen after only a few minutes, and a condition of essentially neutral buoyancy was simulated as closely as possible. The difference between assumed average adaptation depth and 'freezing depth' was less than 25 cm.

Modelling and slicing

Two different methods were used in the modelling process, dependent on the size of the fish. (1) Cod smaller than 50 cm, pollack, and herring were sliced in a large cryomicrotome (LKB -2250) after being encased in blocks of carboxymethyl cellulose (CMC). The block was sliced at 100 µm intervals and, dependent on swimbladder size, photographed at 100-1000 µm intervals with a camera/rack system fixed to the sliced surface at exposure. The edges of the CMC-block were used as an absolute reference, which was needed for the three-dimensional reconstruction of the swimbladder cavity.

(2) Cod larger than about 50 cm could not be sliced properly in the microtome. The swimbladder cavity was therefore modelled by injection. From a transverse cut of the frozen fish, an acrylic resin (Pekatray, BAYER) was injected into the two cavities, and the fish left in a freezer at -5°C for the resin to harden. The two finished casts of the swimbladder cavity were then glued together and embedded in a transparent polyester block, which after exact trimming could be sliced in 1 mm parallel slices on a standard circular saw with precise feeding systems.

Reconstruction

Three-dimensional reconstruction of the swimbladder form was done by digitizing the contour of the inner wall of the bladder from the photographed parallel slices, together with its reference system. This, with the logged information of the actual depth position of the slice, provided the data needed to reconstruct the swimbladder shape in the computer. These point-by-point reconstructions were further used in calculations of the acoustic scattering field from fish by Foote (1985). The volume of the swimbladder in gadoids has been measured either by volume integration in the computer, or by calculations based on the weight of the cast.

Experimental pressure

The effect of pressure on physoclist swimbladders was investigated by an X-ray technique. Anesthetized fish were fastened inside a pressure chamber, almost transparent to X-rays (Plexi-glass), (Figure 2), and photographed from the ventral and dorsal sides during pressure increase. The swimbladder outline on the X-rays was later digitized, and the ventral/dorsal pair used simultaneously by the computer for volume and area integration.

Swimbladder volume measurements in herring

In herring, the swimbladder was emptied for volume measurements immediately after anaesthesia by gentle ventral massage from beneath the pelvic fins towards the anal opening. The gas was collected in an inverted, suspended funnel with a top

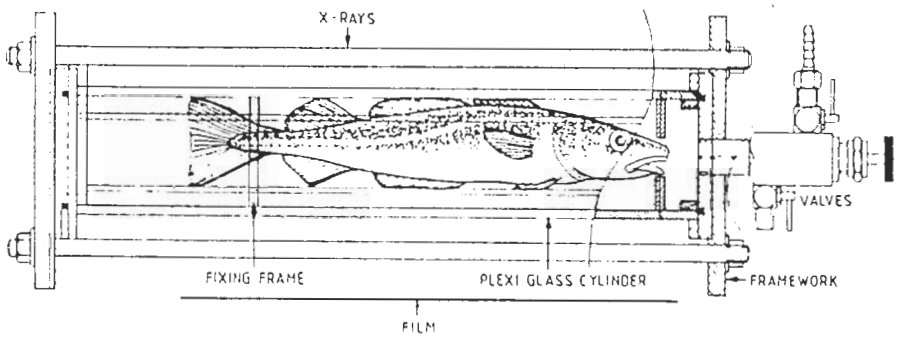

Figure 2. Pressure tank used to observe the change in swimbladder shape during a pressure increase of 10 atm. The X-ray source, Philips (R.I.S), was 112 cm above the tank, with the film cassette placed right below the tank. A stable tank pressure was delivered from a 200 atm air pressure reservoir via a precise pressure reduction valve.

mounted, fine-scaled glass burette. By underwater dissection, this was proved to be an effective way for totally emptying the herring swimbladder, and no residual gas was found in the main chamber or in the anal duct. Residual gas in the auditory bulla system and its precoelomic ducts, which is not measured by this method, represents less than 5% of the total gas volume in surface-adapted adult herring (Allen *et al.*, 1976).

As the main intention of this part of the experiment was to analyze the gas production capacities of the herring swimbladder, only a few herring have at this point been sliced for swimbladder shape analysis.

Fat analysis

After the swimbladder volume measurements, two samples of 60 and 40 herring were saved, and later individually analyzed by standard methods for fat: Na_2SO_4 grinding with ethyl ether extraction (Losnegard *et al.*, 1979).

In situ *swimbladder volume measurements in herring*

To investigate the gas production capacity of herring, the swimbladder volume of caged fish, forced to adapt at 18 and 25 m, was measured *in situ* by scuba divers.

A cylindrical net cage (6 m^3), partly covered by thin, transparent plastic foil was used to control the anaesthetizing of the fish. During depth adaptation, the upper and lower parts of the cage were open to water flow, but could be closed by the divers after having introduced a suitable amount of benzocaine solution from below. Using a cod-end release in the bottom panel of the cage, herring could be individually picked out for swimbladder analysis. Emptying the bladder was conducted as at the surface, one diver carrying the measuring equipment, the other one performing the actual measurement, such as emptying the swimbladder. Underwater television was used to study the fish behaviour, and the adaptation periods were stopped after five days at 18 m and after three days at 25 m as the fish in both cases were still non-buoyant.

In situ measurements on naturally occurring herring, caught in gill nets beneath the experimental raft, were also made using a similar technique. The divers then measured

the swimbladder volume of individual herring still alive in the net, shortly after the entangling was observed from the surface.

RESULTS

For comparative reasons, the 'normal' shape of the swimbladder will in this paper be defined as that found in immature, surface-adapted individuals with an empty stomach and normal liver size. The boundaries of the swimbladder are defined from the outlines of the gas-filled cavity, and not from the swimbladder wall itself. There are only three areas where these are not identical: (1) In physoclist swimbladders, the gas gland part of the inner wall is strongly vascularized, and the contour is drawn above the capillaries, excluding the gland itself from the gas filled cavity. (2) In the vascular area dorsally in the physoclist swimbladder, known as the oval, the inner wall is modified into a muscular sphincter overlaying the vascular plexus (Ross, 1979). The gas resorbing blood vessels are here imbedded in the wall itself, which with the sphincter excluded, have been used as the boundary. (3) The thin anterior extensions, or horns, of the gadoid swimbladder, are partly filled with fluid, and have not been defined as a part of the gas-filled, acoustically important region of the swimbladder. Likewise, in the physostome swimbladder of herring, *Clupea harengus*, the narrow extensions of the swimbladder forward to the bulla system, the pre-coelomic ducts, and the pneumatic duct to the stomach have also been excluded.

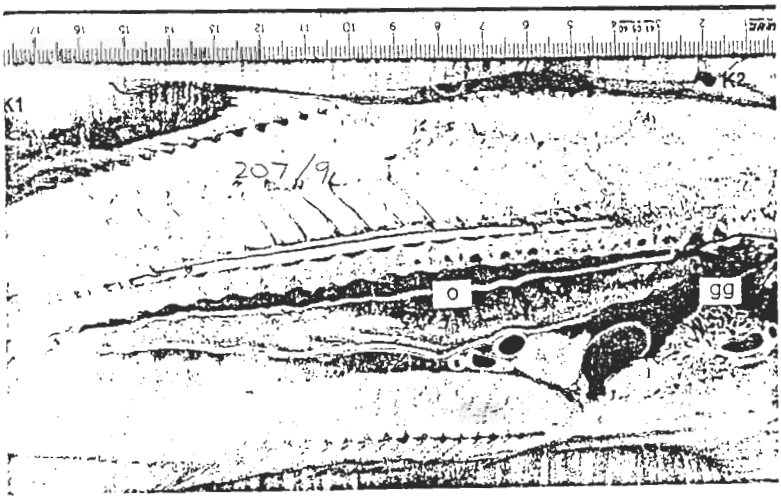

Figure 3. Central microtome slice through the swimbladder of a 44·5 cm pollack (*Pollachius pollachius*), showing references, K1, K2, scale, and the general shape of the bladder. Note the oval area (O), dorsally, and the gas gland (GG) in the ventral, anterior part of the bladder, where the contour is indicated by a black line.

In Figure 3, an example of a 'normal' swimbladder shape is shown. This is a 44·5 cm pollack (*Pollachius pollachius*), with central exposure by the microtome. For cod, the swimbladder is more lobular, with ventral lobes expanding between the pleural ribs, and the 'normal' shape is seen in Figure 4. Note that even without food in the stomach,

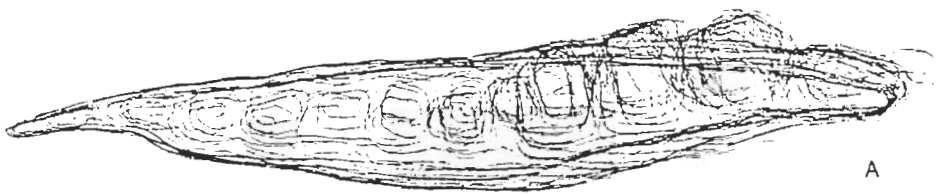

Figure 4. Reconstruction of a 'normal' swimbladder in a 68 cm immature cod (*Gadus morhua*), with empty stomach. Swimbladder volume is 146 ml, or 3·7% of the total weight of the fish. The drawing is three-dimensional with no hidden lines. A, anterior part.

the area below the gas gland is formed by the organs in the body cavity. The swimbladder in small cod, starved for two days (Figure 5), is quite similar to the adult bladder, but with a smaller length/height/width ratio. The ventral lobes on the bladder are not yet very prominent.

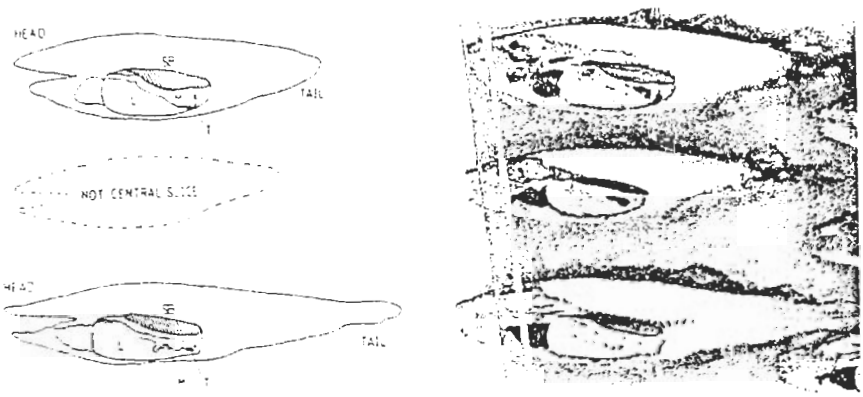

Figure 5. Approximate central slice through two small cod, 11·5 and 12·0 cm, starved for two days with corresponding small stomach content. The contours of the swimbladders are indicated. SB, swimbladder; M, stomach; L, liver; T, intestine.

Deformations from the gonads

At a certain age, dependent upon sea temperature and general growth conditions, the fish becomes mature and gonad development starts. For the Arcto-Norwegian cod stock, the age of first spawning is 5-7 years, generally one year earlier for the male fish. When the gonads develop, a gradual ventral deformation of the swimbladder occurs. Eventually, in the late-maturity stages before spawning, the belly musculature is stretched, and, obviously, the swimbladder must also be influenced by this internal pressure. Figures 6 and 7 show examples of dorsoventral deformations of the posterior part of the bladder. In particular, the ovaries, which are less flexible than the testes, drastically reduce the length and posterior width of the bladder, making it a smaller acoustic target. Compared to the mean volume of 3·6 ±0·3%, of the total wet body weight in the 'normal' situation (Ona, 1982), the mean volume for six cod in maturity stage V is 2·2 ±0·7%, with observations as low as 1·3% (35% of normal swimbladder volume). The mean value for the normal situation is identical to the one reported for immature cod by Sand & Hawkins (1974).

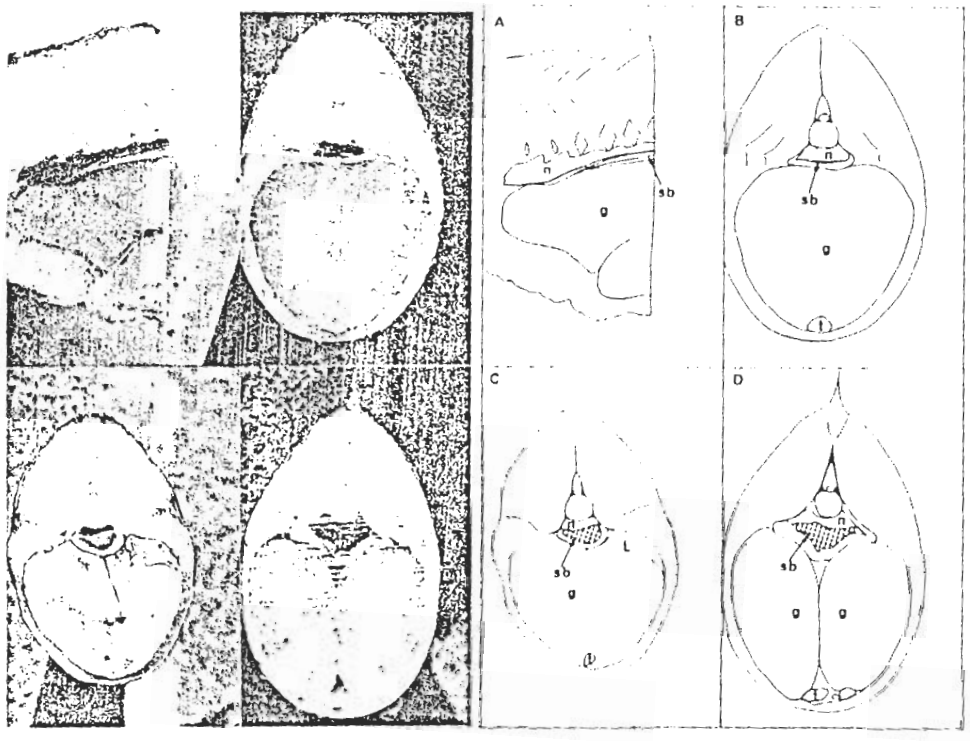

Figure 6. Examples of transverse cuts through mature cod before injecting the plastic resin into the swimbladder cavity. (A, B & D) Female cod, 61 cm. (C) Male cod, 71 cm. (n, kidney; sb, swimbladder; g, gonad; t, intestine; l, liver.)

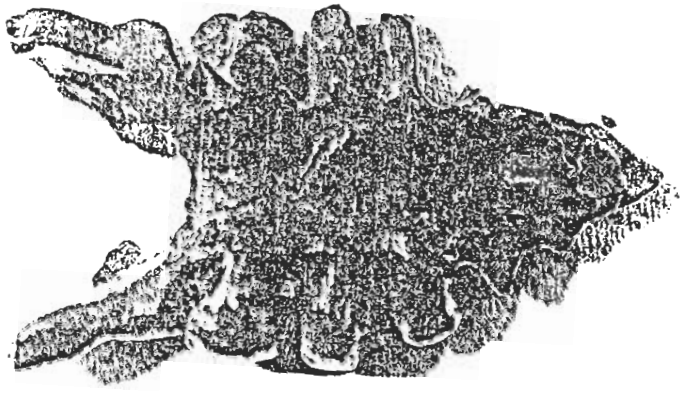

Figure 7. Cast of the swimbladder in the female cod shown in Figure 6, dorsal view. The swimbladder volume is reduced to 1.3% of the total body weight. The posterior part of the bladder is compressed, as well as the central part between the paired frontal lobes which lie anterior.

Deformations from the stomach

When food is available in great quantity, the fish will feed until the stomach is fully expanded. For the so-called 'capelin-cod' in the Barents Sea, where young cod feed heavily on capelin, the degree of stomach filling can often be judged from outside,

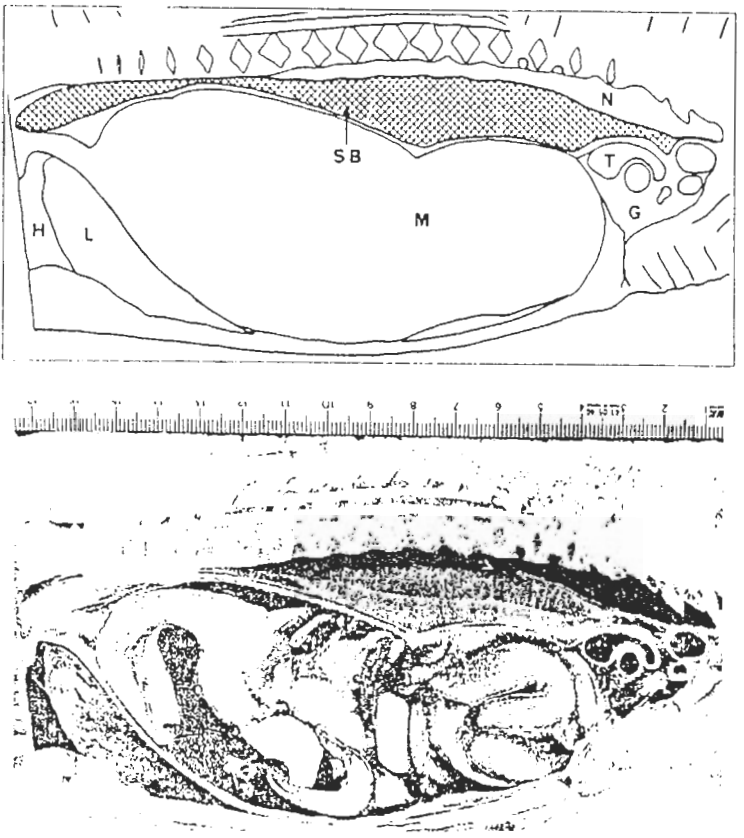

Figure 8. Central slice through the swimbladder of a 54 cm cod with stomach three-quarters full. Stomach content is squid. SB, swimbladder; N, kidney; L, liver; G, gonad; M, stomach; H, heart.

without opening the fish. To demonstrate how this affects the swimbladder shape, cod adapted to the 1 m deep ring-aquarium were fed with sliced squid, and anaesthetized three hours after feeding. As is evident from Figure 8, showing the central slice through a 54 cm cod with stomach classified as three-quarters full, the swimbladder is dramatically deformed at both ends. In particular the anterior part of the bladder is squeezed against the dorsal wall of the body cavity, reducing the length of the bladder by 30% and the volume by 50%. In fish with full stomachs, the swimbladder is deformed so as to be almost unrecognizable (Figure 9) and the volume is reduced to about 10% of the original. Two examples of similar stomach-related deformations of the swimbladder in small cod are presented in Figure 10.

Combined effects

The combined deformation of the bladder from both gonads and stomach is shown in Figure 11. The anterio-ventral part of the swimbladder is squeezed upwards by the stomach, and the posterior part by the gonads. A more moderate combined deformation in a male fish is shown three-dimensionally in Figure 12.

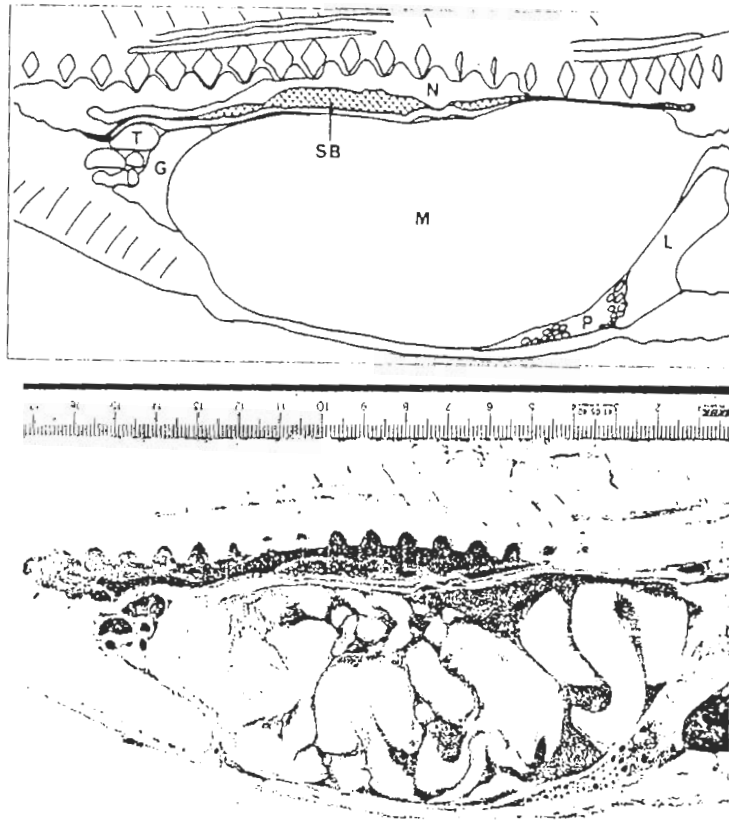

Figure 9. Dramatically squeezed and reduced swimbladder in a 51 cm cod with full stomach. Swimbladder volume is estimated to only about 10% of 'normal' volume.

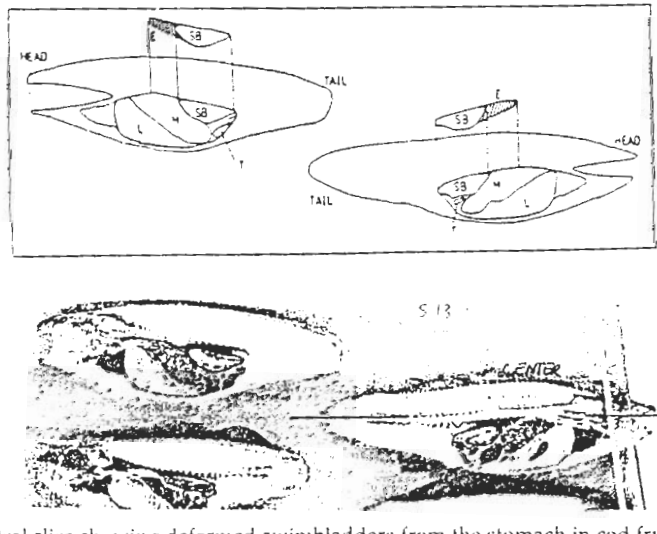

Figure 10. Central slice showing deformed swimbladders from the stomach in cod fry, 13·5 and 12·5 cm. SB, swimbladder; M, stomach; L, liver; T, intestine; E, part of swimbladder emptied by the stomach.

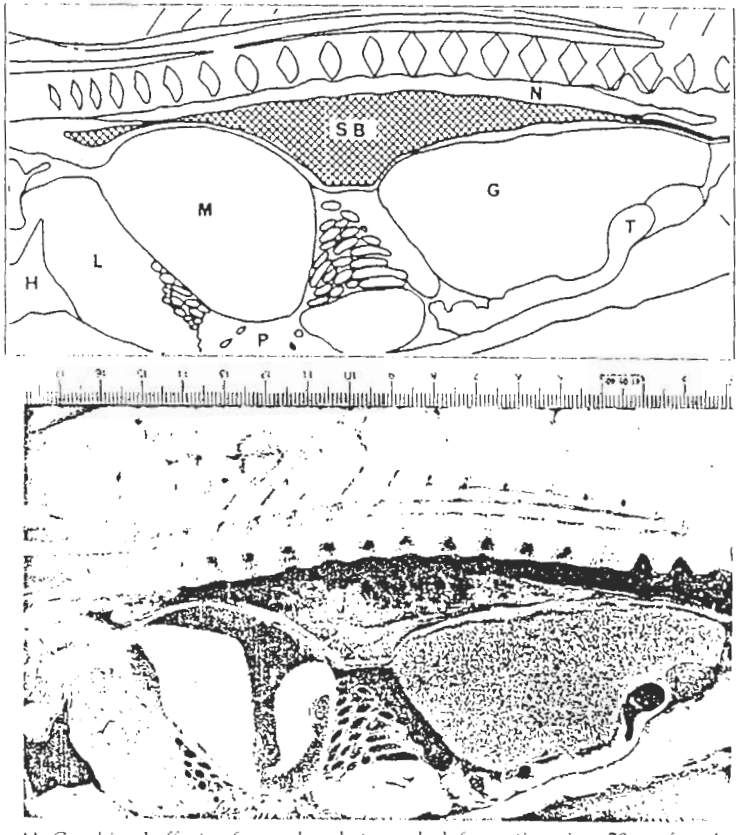

Figure 11. Combined effects of gonad and stomach deformations in a 59 cm female cod. Swimbladder volume is reduced to 1·5% of body weight.

Effects of pressure

For gadoids, the pressure tank experiments were performed in order to simulate a rapid downward migration that would not be compensated for by gas production. Figure 13 shows an X-ray of cod at the surface (1·0 atm). From the digitized outline of the swimbladder, the area and volume is determined by computerized, 1 mm parallel sagittal slices. The swimbladder volume (Figure 14) follows the gas law with pressure increase, while the dorsal area of the bladder, at least at moderate pressures, is quite resistant. Most of the change in shape must therefore take place in the vertical plane of the bladder. When the swimbladder eventually collapses, at about 2 atm, the ventral wall is squeezed towards the dorsal in the anterior end of the bladder, emptying this part of the bladder. From this point, the area-reduction more nearly resembles that theoretically expected.

Effects from variable fat content

In gadoids, variation in fat content is mainly related to the size of the liver, and does not vary seasonally to the same extent as in herring and related species. A highly variable swimbladder volume was observed in herring (Figure 15) despite the fact that

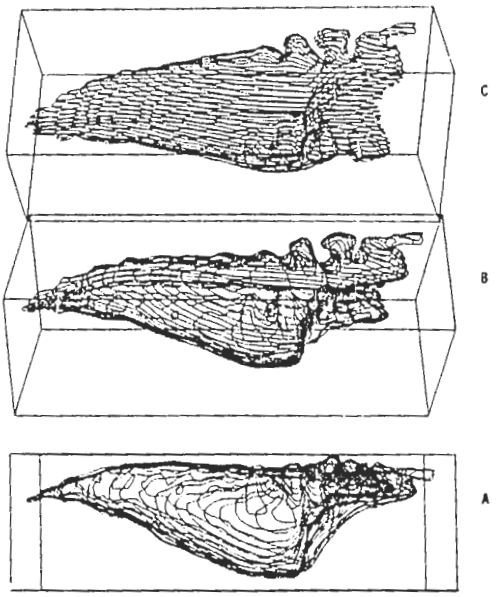

Figure 12. Moderate, combined deformations in a male, 54 cm cod. Swimbladder volume is 2·1% of body weight. The three-dimensional box containing the drawing is rotated first -10° around the z-axis (A), and then 30 (B) and 60 (C) degrees around the x-axis. The seven last lateral lobes on each side of the bladder are emptied, and the stomach deformations are evident below the frontal lobes.

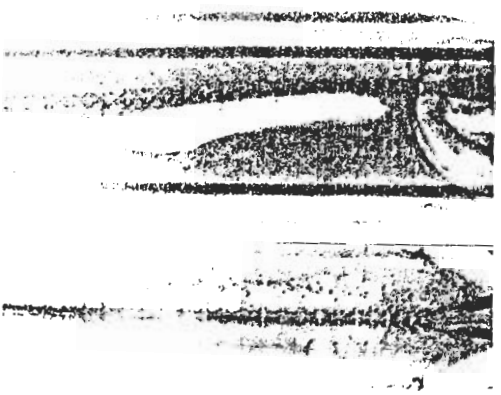

Figure 13. Dorsal and ventral X-rays showing a cod, 27 cm, inside the pressure tank at surface level, 1·0 atm.

all were at ideal neutral buoyancy in the anaesthetizing bath. Individual swimbladder volume measurements and fat analysis showed that the two variables were closely correlated (Figure 16) and that nearly all the variance in swimbladder size could be explained by this relation (Figure 17). From the regression analysis, it is calculated that 1 ml of swimbladder gas is equivalent to 7·5 ml of fat (density 0·926 g cm^{-3}). From this factor alone, the swimbladder volume in herring giving neutral buoyancy at the surface may naturally vary from nearly 5% down to well below 2% of the total body volume.

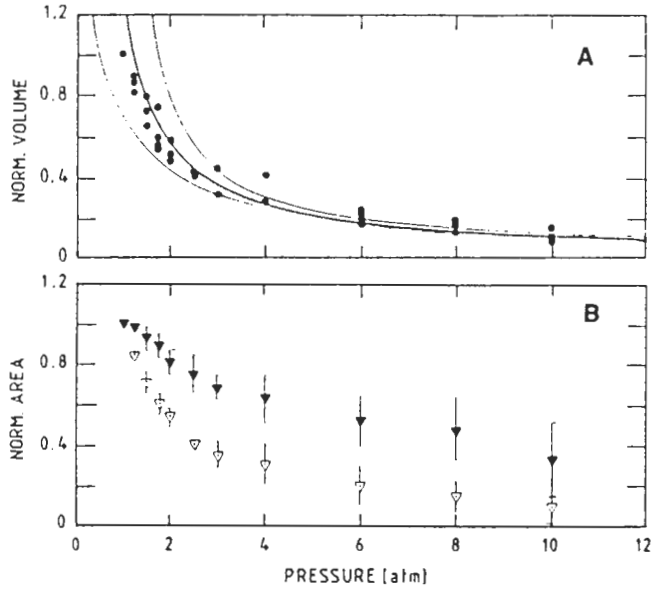

Figure 14. (A) Normalized swimbladder volume in three gadoids as a function of pressure. The regression shows a nearly ideal volume reduction. (B) Dorsal (closed symbols) and lateral area of the swimbladder as a function of pressure. Standard deviations are shown.

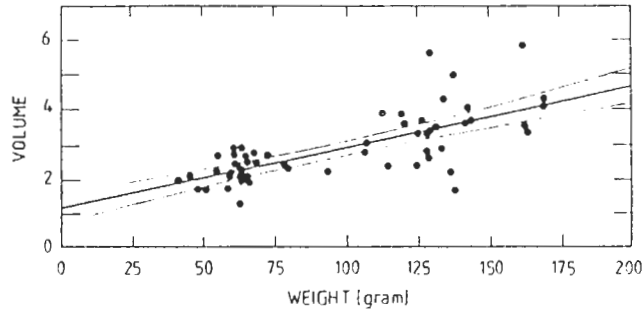

Figure 15. Swimbladder volume (ml) related to fish size in 60 herring, with 95% confidence belt for the regression line. Y = 0·017 X + 1·18, n=60, s.e=0·66, r=0·72.

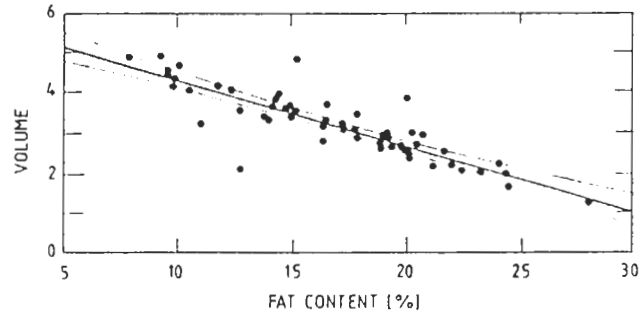

Figure 16. Swimbladder volume per unit wet body weight of the herring, related to fat content. Y = -0·17 X + 6·00, n=60, s.e.=0·43, r=-0·87.

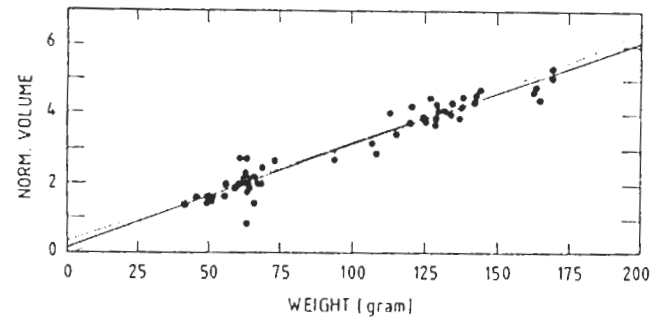

Figure 17. Fat-normalized swimbladder volume related to fish size. All herring normalized to the mean fat content of the sample, 16·8%, according to the regression in Figure 16. Y = 0·030 X + 0·17, n=60, s.e.=0·31, r=0·97.

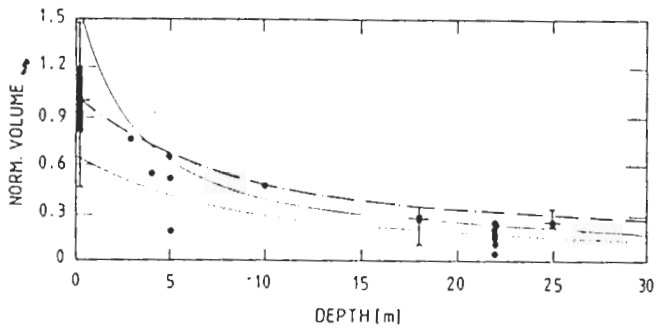

Figure 18. Normalized swimbladder volume measured *in situ* as a function of depth. Controlled measurements, in which the herring were anaesthetized, 60 at surface and a total of 17 cage adapted at 18 and 25 m, are shown with mean, standard deviation and total spread. Individually marked fish (closed circles) were measured at depth of catch in gill nets. Theory (Boyle's law), is indicated by the broken line, together with the 95% confidence belt for the regression estimate.

Gas production in herring

A total of 42 herring was measured by scuba divers at depths from 3-25 m, including 17 herring which were forced to adapt in cages. The swimbladder volume of the remaining 25 was measured shortly after they were trapped in gill nets. Only 13 of these, classified as fully alive in the net are presented here.

Herring should physiologically not be able to secrete gas to the swimbladder, and the *in situ* measurements of swimbladder volume at depth (Figure 18), entirely support this hypothesis. As the recorded volumes are not corrected for a variable fat content, all values are consistent with free-compression theory. Instead of gas secretion to restore neutral buoyancy, both cage experiments indicate rather gas resorption from the bladder. In particular the free swimming herring, trapped in gill nets at 22 m depth had small swimbladders, only 16% of the surface adapted value. For the caged fish, where the adaptation time is known, it is possible to calculate the gas resorption rate. Discarding one observation of a large swimbladder volume at 25 m depth, the herring being

very slender (condition factor 0·53) the estimated rates for 12 fish at 18 m and four at 25 m are: (for a mean fish length of 22·8 ± 3·1 cm)

1·8 ± 1·8 µl STP h^{-1} atm^{-1} at 18 m depth
1·0 ± 0·6 µl STP h^{-1} atm^{-1} at 25 m depth

This is significantly higher than earlier reported for adult herring by Blaxter & Batty (1984), and nearly twice the rate they found for 15 g fish. As the main intention of the experiment was to confirm or invalidate the gas production hypothesis, and not to measure gas resorption in herring, longer adaptation periods were not considered.

DISCUSSION

The observations of high variability in swimbladder shape and volume seem to reduce the general importance of the swimbladder as an ideal buoyancy regulator. Similar but weaker deformations of the ventral part of the bladder can be observed on X-rays as presented by Molnár & Tølg (1960, 1962), and on autoradiographs by Ingebriktsen & Bergsjø (1979).

In the modelling and reconstruction process, it is of course assumed that deformation effects caused by the methodology are insignificant compared to the real deformations. Three possible sources of errors have been evaluated: pressure-induced errors, gas exchange in the period of treatment, and freezing artefacts. With the swimbladder adapted at an assumed depth of 50 cm, the immediate volume increase is 5% when lifting the fish out of the water, half of which is compensated for during freezing at 25 cm depth. From this, the actual swimbladder volume, expressed as a percentage of total body volume, may be positively biased by about 0·1%. As gas production and resorption in physoclists is a slow process (Blaxter & Tytler, 1978; Harden Jones & Scholes, 1985), no significant adjustment of volume is expected in the handling process of less than 3 min. For cod, Harden Jones & Scholes (1985) have indicated a pressure dependent resorption rate of 0·06 ml O_2 kg^{-1} min^{-1}, and a lower, pressure independent secretion rate.

The shock-freezing of the fish is performed with nearly natural loading, considering the weight distribution and buoyancy. The fixation of the outer shape of the fish is immediate, with a gradually growing frozen 'shell' surrounding the swimbladder and body cavity. The shape of the bladder is then already determined, as the adhesion forces in the water film covering the organ surfaces resist separation. The swimbladder wall in frozen state is thus always tightly connected to the other organs in the body cavity. As the later cooling of the swimbladder gas cannot be compensated through a volume change, a reduction in the pressure seems to occur instead. The suction created by a temperature difference of 35-40°C may be 0·13 atm, and can be heard when puncturing the bladder shortly after the freezing.

The volume expansion for clean freshwater during freezing is approximately 9%, dependent on freezing speed. This is more than for water-rich tissues, where the water content is about 80% and some of the expansion will be taken up by the tissue.

Practical density measurements on fresh and frozen gonads and muscle from cod indicate that the expansion is less than 6%. The linear effect of the expansion, as observed on a transverse or longitudinal section through the fish, may then be 1·8%, or 0·9 mm on a gonad or stomach height of 5 cm. On this basis, it is reasonable to assume that more than 95% of the observed deformations are real, while the remaining part may be explained through the experimental method. Freezing artefacts of similar magnitude will also be found on normal state swim bladders.

The described deformations are all more or less periodic, the stomach content varying on a daily or short-periodic cycle, the gonad development and fat content varying on a seasonal cycle. The intake of food is commonly connected with the vertical migration pattern, and the largest deformations should be expected immediately after the morning descent, coinciding with possible pressure-induced deformations.

In relation to the primary role of the swimbladder as a hydrostatic organ in the fish, it may be interesting to note that even with substantially reduced swimbladder volume, the effect of the reduction could hardly be detected in the general behaviour pattern of the fish. Harden Jones & Scholes (1985) suggest 55% as a limit for volume reduction of the swimbladder in cod, if the fish must compensate for the negative buoyancy in a small chamber by fin strokes only. The present study indicates that large cod, in a free-swimming situation, easily compensate for 70-90% of the swimbladder lift. The additional lift seems to be created by the use of pectoral-fin extension, as in scombroids lacking swimbladder (Magnuson, 1978). The mackerel (*Scomber scombrus*) must swim at a 'minimum sustained speed' of 0·88 bodylengths s^{-1} when compensating for a density of 1·06 in 1·025g cm^{-3} sea water (Magnuson, 1978). The maximum sustained speed for cod is suggested to be near 3 bodylengths s^{-1}, while tagging experiments indicate an average speed during the spawning migration of 34 cm s^{-1} (Harden Jones, 1968). Even though cod and scombrids are not hydrodynamically comparable, it seems reasonable that cod can compensate for negative buoyancy in a similar manner.

The present observations on herring support earlier physio-morphological evidence for the absence of a gas-producing mechanism in the herring swimbladder. In addition to the presented *in situ* cage-measurements, made within 4 min after anaesthesia, the remaining 48 anaesthetized herring were clearly non-buoyant, sinking rapidly towards the bottom of the cage. At the surface however, 95% of the fish were neutral or positively buoyant. The remaining data from gill nets are clearly less reliable than data from the controlled experiments, as the chances for unobserved gas release from the swimbladder is larger. However, these data give important information on the natural swimbladder state of herring, which, by any method, is difficult to obtain from depths below the surface level. As only one single observation of a normal swimbladder volume at depth would support the hypothesis of an alternative method for gas production in herring, data on dead herring may also be usable. Experiments in a ring aquarium showed that even 40% of the dead herring had normal swimbladder volumes one hour after the catch. The rest released some gas from the swimbladder when moribund or dead, probably due to relaxation of the sphincter muscle surrounding the pneumatic duct. If the morpho-physiology of the herring swimbladder was unknown, and we open-mindedly support both the gas production and the free compression

alternatives with equal probability, the observed frequencies of 0 and 25, respectively, yield a probability level of 3×10^{-8} for gas production. Inclusion of the dead herring would decrease the probability further.

The indicated gas resorption rate is higher than reported by Blaxter & Batty (1984), who found a slow gas diffusion out of the swimbladder of small herring, forced to adapt in similar cages. On adult herring, however, no significant reduction of the swimbladder volume occurred after six days at 20 m. If the estimated rate from this experiment is used, 0·42 ml gas should have been lost during the adaptation period. A very high variance in swimbladder volume for equally sized adult herring, caused by the variable fat content, may easily mask minor volume reductions in both experiments. Using fat-normalized swimbladder volumes will improve the precision of the estimates of gas diffusion rates in the herring swimbladder.

Even without any gas diffusion, the herring will be negatively buoyant at any depth below surface. At 100 m deep, only a fraction of the original lift from the swimbladder is present, and the fish must actively prevent sinking. In a large, 35 m^3 circular cage, herring easily compensated for the negative buoyancy at 30 m depth by increased swimming speed, slightly positive tilt, and increased pectoral fin extension (Ona, 1984b).

Acoustic effect

Any reduction of the dorsal surface of the swimbladder will reduce the maximum acoustic back scattering cross section or target strength of the fish. Experimental data on target strength are often gathered during the summer months on surface-adapted fish, with no systematic feeding prior to the measurements. The bulk of the available data are on immature fish, and no information on fat content has been recorded. Midttun (1984) has summarized the results from earlier investigations. There is reason to believe that most of these experimental target strength data were obtained on fish in which the swimbladder resembles the 'normal' state of the bladder.

In order to estimate the average acoustic effect of swimbladder deformations or changes, the actual shape of the bladder must be used as input in a scattering model, as in Foote (1985), and a large amount of comparative material should be available. At this moment, however, only rough estimates can be made, using the actual reductions of the back scattering surface as an index.

If the experimentally obtained average target strength relation on cod,

$$\langle TS \rangle = 21{\cdot}8 \log L - 68{\cdot}3 \text{ [dB]},$$

(Foote, 1980a, based on Nakken & Olsen, 1977), is used, it is possible to substitute fish length (L) with the length of the swimbladder (SBL), using

$$SBL = 0{\cdot}23\ L$$

as an average value for cod (Ona, 1982). The target strength related to swimbladder length is then:

$$\langle TS \rangle = 21{\cdot}8 \log SBL - 54 \text{ [dB]},$$

which, with caution, may be used to estimate the effect of the observed deformations of the bladder.

The change of swimbladder shape reported here, both for high degrees of stomach filling and for ripe gonads, will reduce the average target strength by 2-5 dB when using this relation. If additionally the swimming behaviour changes when the fish is compensating for negative buoyancy, as reported by Ona (1984b), the average backscattering is further decreased. An acoustic biomass estimate will be negatively biased by 20-70% due to reported deformations on gadoids. For herring, only the variance in fat content can bias the estimate both ways by 30-40% if a nominal target strength relation is used. This may explain some of the variance in target strength data obtained on herring in different areas. Lassen & Stæhr (1985) have in fact observed a significant difference in target strength between herring in the low-salinity Baltic Sea and in the higher-salinity Skagerrak, probably caused by a difference in swimbladder size.

Besides the expected variance from fat, depth corrections may be necessary for herring and related species if the free-compression theory can be acoustically confirmed. Several attempts to make repeated *in situ* target strength measurements on herring at different depths have, however, not confirmed this fairly obvious dependence. Halldorsson (1983) reports a significant depth dependence in his data on herring, but his method of averaging individual target strength observations in the logarithmic domain is incorrect.

The actual reduction of dorsal swimbladder surface with pressure is more conservative than indicated from a simple volume to area conversion, as suggested by Harden Jones & Scholes (1985) or Halldorsson (1983). In particular among gadoids, the dorsal surface is quite stable, being directly and indirectly connected to the muscles, kidneys and bones through a massive mantle of connective tissue (Hagman, 1921). This tends to reduce the effect of pressure on dorsal target strength.

In low-frequency size classification models (Holliday, 1977; Løvik *et al.*, 1982), however, all mentioned deformations will reduce the apparent size of the fish, as the volume of the resonance chamber, the swimbladder, is reduced.

The swimbladder of a specific species and fish length in the 'normal' state is ideally of the same size and shape, and much of the observable variance in earlier experimental single-fish data may originate from differences in swimbladder state. For herring at the surface, the total variance in maximum target strength for 30 cm fish is 7 dB (Nakken & Olsen, 1977). If the fat content during the target strength measurements on the local Skogsvaag stock were similar to the ones reported here and by Ona (1984a), most of this variance could be explained through the variance in fat content.

CONCLUSIONS

1. Natural variations in swimbladder volume and shape will cause variations in fish target strength.

2. Four important factors which may alter the target strength significantly are: stomach content, gonads, fat content and pressure.

3. The idea of a 'standard', fixed target strength relation with a precision level of 0·1 dB for each species has no biological foundation, and should be used only as a reference or guideline.

4. As the target strength of the fish may vary with time of day, season, and region, absolute acoustic abundance estimates are best obtained when the *in situ* target strength of the fish is monitored continually.

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