Modelling the acoustic effect of swimbladder compression in herring

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Obtaining accurate data on fish target strength (TS) is important when determining the quality of the results from acoustic surveys. However, this requires an improved understanding of both behavioural and environmental influences on the acoustic backscattering by fish. It is well known that the increased pressure with depth compresses the swimbladder of herring, and it has been confirmed by in situ measurements that the TS of adult herring (30–34 cm) is 3–5 dB weaker at 300 m than that of fish close to the surface. Understanding exactly how swimbladder compression may influence herring TS is, therefore, of great interest, and is the main motivation behind this study. Taking account of swimbladder volume changes with depth, we obtained analytical solutions using the Modal-Based, Deformed-Cylinder Model (MB-DCM). The mean-backscattering cross-section is then computed with selected orientation patterns, length distributions, and contrast parameters. The depth-dependence of TS at different acoustic frequencies has been studied. We conducted a sensitivity analysis to show how TS is dependent on the contraction rates of the bladder dimensions and on the fish-orientation distribution. Our theoretical results are compared with TS measured at 38 kHz.

Introduction

The swimbladder of the herring (Clupea harengus L.) compresses with depth in response to the increasing pressure as the fish swims deeper. The acoustic consequences of this phenomenon have to be understood if we are to be able to explain the results from acoustic surveys measuring herring abundance. The effect has been studied both experimentally and theoretically (Vabø, 1999; Gorska and Ona, 2001; Ona et al., 2003; Ona, 2003). Experiments in various seasons on both penned and in situ fish, as summarized by Ona (2003), have confirmed the depth-dependence of herring target strength (TS). Theoretical studies, however, have been limited to bladder-contraction rates that are the same for all dimensions (Ona et al., 2003), and onsonification only in the normal, dorsal-aspect direction (Gorska and Ona, 2001). Nevertheless, the modelling approach has achieved significant results suggesting that TS measurements can be explained by swimbladder compression. One improvement would be to incorporate non-symmetric changes in swimbladder shape, with length reducing less with pressure compared with height.

In this article, the Modal-Based, Deformed-Cylinder Model (MB-DCM; Stanton, 1988, 1989) was used to investigate the herring-backscattering cross-section averaged over typical geometrical and acoustic parameters (σ_bsc). Analytical solutions are presented and the approximations involved in the theory are discussed, leading to numerical evaluation of the main parameters that control the depth- and frequency-dependence of herring TS. Detailed comparison between theory and the measured mean-backscattering cross-sections gives a deeper physical insight into the peculiar acoustic-backscattering characteristics of herring.

Modelling equations

Definition of the mean-backscattering cross-section

For an aggregation of fish, the mean-backscattering cross-section (σ_bsc) is determined by statistical distributions of the geometrical and acoustic variables. We develop an analytical expression for σ_bsc in terms of individual fish
properties described by a seven-parameter array, $\mathcal{A} = \{ d_b, \, \theta_b, \, R, \, e_{ab}, \, e_b, \, g_b, \, h_b \}$. The subscripts $b$ and $sb$ refer to the fish body and swimbladder, respectively; $a$ is half the dorsal width, $l$ is the length (fork length for the body), and $e$ is the aspect ratio $l/a$. Here $\theta$ is the tilt angle and the ratio $R = l_b/l_b$. The body contrasts are $h_b = c_b/c$ and $g_b = \rho_b/\rho$, where $c$ is the sound speed and $\rho$ is the density of the surrounding water. Note that the parameters $l_b, e_{ab}, e_b, R$, and the contrasts may vary with depth.

If $z$ is the depth, the mean-backscattering cross-section can be expressed as:

$$
\langle \sigma_{bzc}(z) \rangle = \frac{\int \int \text{d}\alpha \text{W}_a(\alpha, z)|f_\text{tot}(\alpha, z)|^2}{\int \int \text{d}\alpha \text{W}_a(\alpha, z)}
$$

(1)

where $\text{W}_a(\alpha, z)$ is a multi-dimensional, probability-density function (PDF) covering an ensemble of realizations with different sets of $\{ x_i, \} [i = 1, \ldots, 7]$, geometrical and acoustic parameters of a fish. In general, this function varies with depth (Huse and Ona, 1996; Ona, 2001; Ona et al., 2003). $f_\text{tot}(\alpha, z)$ is the complex, whole-fish, backscattering length (Medwin and Clay, 1998), but depth-dependent due to compression of the herring swimbladder.

To evaluate Equation (1), we require the analytical solution for $f_\text{tot}(\alpha, z)$, along with information on the multi-dimensional distribution and the physics of swimbladder compression.

### Backscattering formulation for individual fish

The total backscattering length of a fish can be expressed as:

$$
f_\text{tot}(z) = f_{sb}(z) + f_b
$$

(2)

where $f_b$ and $f_{sb}(z)$ are the backscattering lengths of the fish body and the swimbladder, respectively. The corresponding backscattering cross-section is $\sigma_{bzc}(z) = |f_\text{tot}(z)|^2$. Note that by “fish body” we mean all parts of the body (flesh, skeleton, scales, and internal organs) excluding the swimbladder.

When the swimbladder is the dominant scatterer, Equation (2) is a good description of whole-fish backscattering, but possibly not otherwise (Ding and Ye, 1997). Accounting for the herring-swimbladder compression and the increased, relative, fish-body contribution with depth, a different approach considering the swimbladder and body as a coupled system might be more satisfactory. However, their interaction has not yet been studied in detail and we limit our analysis in this study to a simple summation of the two components, which may then be evaluated separately.

The directivity of the backscattering is incorporated through the equations:

$$
f_{sb}(z) = f_{sb}^{0}(z)D_{sb}(\theta, z)
$$

(3)

$$
f_b = f_b^{0}D_b(\theta)
$$

(4)

where $f_{sb}^{0}(z)$ and $f_b^{0}$ denote the backscattering lengths of the swimbladder and body, respectively, for the normal, dorsal-incidence case. The directivity patterns $D_{sb}(\theta, z)$ and $D_b(\theta)$ are the solutions for a straight cylinder (Medwin and Clay, 1998). We generalize the formulae by including a depth-dependent, swimbladder length to account for pressure-induced compression. Thus:

$$
D_{sb}(\theta, z) = \frac{\sin^2[kl_{sb}(z) \sin(\theta + \Delta \theta)]}{[kl_{sb}(z) \sin(\theta + \Delta \theta)]^2} \cos(\theta + \Delta \theta)
$$

(5)

for the swimbladder and

$$
D_b(\theta) = \frac{\sin^2(kh_b \sin \theta)}{(kh_b \sin \theta)^2} \cos \theta
$$

(6)

for the fish body. $\Delta \theta$ is the tilt of the swimbladder axis relative to the snout–tail axis of the fish. In herring, however, this angle is close to zero and can be ignored.

The swimbladder-directivity formula (Equation (5)) was tested against measurements reported by Foote and Nakken (1978). These were obtained at 38 and 120 kHz for large herring near the surface, where the swimbladder contribution is certainly dominant. For the fish body, we compared our predictions with calculations using the Distorted-Wave, Born Approximation (DWBA), as described by Stanton and Chu (2000), assuming the body was a prolate spheroid. The comparisons showed that our simpler models were reasonable approximations.

### Backscattering solution for individual fish and normal dorsal incidence

From the MB-DCM (Stanton, 1989), analytical solutions for the backscattering lengths $f_{sb}^{0}(z)$ and $f_b^{0}$ are obtained by modelling the swimbladder and fish body as gas- and liquid-filled, prolate spheroids, respectively. Incorporating depth-dependent terms, the backscattering lengths for normal dorsal incidence are:

$$
f_{sb}^{0}(z) = -\frac{i}{R}l_{sb}(z)\int_0^1 du \sum_{m=0}^{\infty} b_m^{sb}(z, u)
$$

(7)

for the swimbladder and

$$
f_b^{0} = \frac{i}{l_b} \int_0^1 du \sum_{m=0}^{\infty} b_m^{b}(u)
$$

(8)

for the fish body. The variable $u$ is the length fraction $x/(l_b(z)/2)$ in Equation (7) and $x/(l_b/2)$ in Equation (8), where $x$ is the distance along the major axis of the respective prolate spheroid.

The coefficients $b_m^{sb}(z)$ and $b_m^{b}$, which are also functions of $u$, can be expressed as:

$$
b_m^{sb}(z) = \frac{e_m(-1)^m}{1 + iC_m^{sb}(z)}
$$

(9)

$$
b_m^{b} = \frac{e_m(-1)^m}{1 + iC_m^{b}}
$$

(10)
where the Neumann factor $\varepsilon_m = 1$ for $m=0$, and $\varepsilon_m = 2$ for $m > 0$. The coefficients $C_m^a(z)$ and $C_m^b$ are:

$$C_m = \frac{|J_m(k'a)N_m(ka)|/|J_m(k'a)J'_m(ka)| - gh[N'_m(ka)/J_m(ka)]}{|J_m(k'a)N_m(ka)|/|J_m(k'a)J'_m(ka)| - gh}$$  \hspace{1cm} (11)

where $C_m = C_m^a$, $a = a_a$, $g = g_a$, $h = h_a$ and $C_m = C_m^b$, $a = a_b$, $g = g_b$, $h = h_b$ for swimbladder and fish body, respectively. Here $g_a$ and $h_a$ are the density and sound-speed contrasts, $g_b = \rho_a/\rho$ and $h_b = c_a/c$, where $\rho_a$ and $c_a$ are the gas density and sound speed in the swimbladder, respectively. Note that $a_a$ and $a_b$ are the cross-section radii of the respective prolate spheroids and are therefore functions of $u$. $J_m(x)$ and $N_m(x)$ are Bessel functions of the first and second (Neumann) kinds of order $m$; $J'_m(x)$ and $N'_m(x)$ are the corresponding first-order derivatives with respect to $x$. For the swimbladder $k' = k/b_a$ and for the fish body $k' = k/b_b$, where $k = 2\pi f/c$ is the wave number in the surrounding seawater and $f$ is the echosounder frequency.

Modelling dependencies

Multi-dimensional distribution

The multi-dimensional PDF has not been sufficiently studied. Only some general information on orientation and fish-length variations is available (Huse and Ona, 1996; Ona, 2001; Ona et al., 2003). We constructed PDFs that include only these two parameters. Gaussian PDFs were assumed for fish orientation and length. These assumptions are supported by experimental work (Nakken and Olsen, 1977; Foote and Ona, 1987; Huse and Ona, 1996; Ona, 2001; Ona et al., 2003), and by early theoretical studies (Foote, 1980, 1985; Foote and Traynor, 1988).

Assuming statistical independence of the $\alpha_i$, the multi-dimensional PDF is:

$$W_a(\bar{\alpha}, z) = \prod_{i=1}^{2} \left[ \frac{1}{(2\pi)^{1/2}S_{\alpha_i}(z)} \exp\left[-(\alpha_i - \bar{\alpha}_i(z))^2/(2S_{\alpha_i}^2(z))\right] \right]$$ \hspace{1cm} (12)

where $\bar{\alpha}_i(z)$ and $S_{\alpha_i}(z)$ represent the means and standard deviations (SD) of the respective distributions. The cases $i = 1$ and $i = 2$ refer to the averaging over fish length and orientation, respectively.

Depth-dependence of swimbladder dimensions

Differential changes in the linear, swimbladder dimensions with depth could have important implications for the backscattering. This feature is not yet established, although Ona (1990) found that the volume of the herring swimbladder $V(z)$ decreases with depth according to Boyle’s law. Thus, $V(z) = V_0(1 + z/10)^{-\eta}$, where $V_0$ is the volume at the surface and $z$ is the depth in metres. We, therefore, assume that the swimbladder dimensions change in the following manner:

$$a_b(z) = a_b(0)(1 + z/10)^{-\alpha}$$ \hspace{1cm} (13)

$$h_b(z) = h_b(0)(1 + z/10)^{-\beta}$$ \hspace{1cm} (14)

where $\alpha$ and $\beta$ are the compression factors for the corresponding dimensions. Boyle’s law requires that $2\alpha + \beta = 1$.

Results and discussion

All the simulations (Figures 1–4) relate to herring of mean total length 32 cm, with a swimbladder length 0.26 times the total length, and mean dorsal widths of swimbladder and fish body 1 and 2 cm, respectively. The fish-length distribution is unimodal with 10% SD. The density and sound-speed contrasts are (1.04; 1.04) and (0.00129; 0.23) for the fish body and the swimbladder, respectively. We used orientation distributions with a mean of $\theta = 0^\circ$ and SD of 5° or 10° (see the subsequent discussion). Our results for the spherical-scattering cross-section $4\pi(\sigma_{b_{sc}}(z))$ are presented in Figures 1 and 4.

Depth-dependence: echosounder frequency

Figure 1a illustrates the depth-dependence of $4\pi(\sigma_{b_{sc}}(z))$ at 18, 38, 120, and 200 kHz frequencies often used in acoustic surveys of herring. The SD of the orientation distribution was 5°, and the contraction factors $\alpha$ and $\beta$ were 1/3. The mean-backscattering cross-section of the whole-fish decreases with depth because of the swimbladder contraction. The decrease is stronger at the lower frequencies, 18 and 38 kHz.

Depth-dependence: orientation-distribution width

Figure 1b shows the effect of the orientation-distribution width. The non-averaged, backscattering cross-section for maximum dorsal incidence is also shown for comparison. The reference frequency is 38 kHz and the contraction rates are as previously noted. The wider the distribution, the smaller is the backscattering strength. It is interesting to note that the case of maximum-dorsal incidence has a stronger depth-dependence than the stochastic examples.

Depth-dependence: contraction rates, $\alpha$ and $\beta$

The computations (Figure 1c) were made for three selected cases: (i) $\alpha = 1/3$, $\beta = 1/3$; (ii) $\alpha = 2/5$, $\beta = 1/5$; and (iii) $\alpha = 1/2$, $\beta = 0$. Other parameters are as in Figure 1a. In the first case, the swimbladder dimensions have symmetrical reduction factors, while the length reduction is relatively small ($\alpha > \beta$) in cases (ii) and (iii).

It is important to note that the dorsal-geometric cross-section of the swimbladder changes with depth as $(1 + z/10)^{-\eta}$, where the contraction factor $\eta = \alpha + \beta$. The $\eta$ is
largest (2/3) and smallest (1/2) for cases (i) and (iii), respectively. Case (ii) is intermediate, with $\eta = 3/5$. Figure 1c demonstrates that the dorsal-contraction rate controls the depth-dependence of the mean-backscattering cross-section; the contraction rate of the dorsal cross-section is described in the legend. The larger the contraction factor $\eta$, the greater is the depth-dependence.

Frequency-dependence: sensitivity analysis
The depth-dependence of the ratio $\langle \sigma_{\text{bsc}}(f) \rangle / \langle \sigma_{\text{bsc}}(38 \text{ kHz}) \rangle$ at frequencies $f = 18, 120, \text{ and } 200 \text{ kHz}$ is presented in Figure 2. The upper and lower plots are for $5^\circ$ and $10^\circ$ SD of the tilt-angle distribution, respectively. Other parameters are as for Figure 1a. Both plots show the ratio $\langle \sigma_{\text{bsc}}(f) \rangle / \langle \sigma_{\text{bsc}}(38 \text{ kHz}) \rangle$ changing with depth at all frequencies. The inter-frequency differences also depend on the depth, and we find that the curves and their relative positions are sensitive to the width of the tilt-angle distribution.

The body contribution to whole-fish backscattering
The backscattering from the fish body as a proportion of the whole-fish backscattering is presented in Figure 3. The upper and lower panels of the figure show the results
for different orientation-distributions and swimbladder-contraction rates, respectively.

The relative importance of the body increases with depth due to the decreased contribution of the gradually contracting swimbladder. Thus, the ratio \( \frac{\sigma_b}{\sigma_{bsc}(z)} \) is very small at the surface, only a few percent, increasing to nearly 60% at 300 m in the case of maximum-dorsal incidence (Figure 3a).

These results help us to understand which of the parameters control the fish-body contribution. A wide-orientation distribution reduces the proportion of total backscattering due to the fish body (see Figure 3a, which is obtained for identical contraction rates of swimbladder dimensions, case (i)). In the case of the variation of contraction rate of the dorsal cross-section of the swimbladder, Figure 3b is drawn for the same parameters as Figure 1c and the same examples of swimbladder-dimension changes, cases (i)–(iii) as previously described. The proportional, fish-body contribution is sensitive to the nature of the swimbladder deformation. The larger the contraction factor of the dorsal cross-section, the larger is \( \frac{\sigma_b}{\sigma_{bsc}(z)} \).

Comparison with measurements and discussion
A comparison between theory and experiment has been done to interpret the observed TS and for a better understanding of the nature of backscattering by herring. The data used in our analysis were collected during several TS experiments on herring, described in Ona (2003). The depth-dependence of the mean-backscattering cross-section was carefully studied in these experiments.

Figure 4 shows the comparison of results at 38 kHz sounder frequency. The measurements are indicated by triangles with different colours for the various experiments. The data comprise measured backscattering cross-sections, some averaged over one complete fish track and some over a large number of tracks. Here, a fish track means a sequential series of accepted, valid TS measurements on the
same fish, collected as the fish passes through the acoustic beam.

The data presented are the actual measurements adjusted to correspond to a common fish length of 32 cm. The narrow length distributions of the observed fish suggest that it is reasonable to standardize the results in this way, using the relationship \( \text{TS}_A = \text{TS} - 20 \log(l_b \text{ (cm)}/32) \), where \( \text{TS}_A \) is the adjusted TS.

A simple, swimbladder-compression model was fitted to the empirical data by non-linear regression (Ona, 2003). The regression is the red line in Figure 4 for which the equation is:

\[
\sigma_{\text{back}}(z) = \sigma_0(1 + z/10)^\gamma,
\]

where the fitted parameters are \( \sigma_0 = 37.1 \text{ cm}^2 \) and \( \gamma = -0.23 \).

MB-DCM computations, shown in Figure 4, were made at 38 kHz for \( 5^\circ \) SD of the tilt-angle distribution. Theoretical curves are drawn for two contraction rates of the dorsal cross-section of the swimbladder. The dark-blue curve refers to the smallest contraction rate (case (i), no change in the swimbladder length). The light-blue curve corresponds to case (i), equal contraction factors \( \alpha = \beta = 1/3 \) for all swimbladder dimensions. These are the extreme cases. We found that for any case \( 0 < \beta < \alpha \) (swimbladder length-contraction factor less than that of swimbladder width), the resulting curve, generated under otherwise similar assumptions, would lie in the domain between two blue curves.

We conclude from these results that the observed decrease of mean-backscattering cross-section with depth can be explained by the compression of the herring swimbladder. It is interesting to observe that most of the measurements are located within the domain between the blue theoretical curves (Figure 4). However, exactly how the swimbladder is compressed is still an open question. According to the fit with the model results, it is most likely that the diameter of the bladder reduces more rapidly than its length. This conclusion agrees with the findings of Blaxter (1979) and Ona (1990), who showed that the swimbladder length of herring and cod changed more slowly with depth compared with the height. Our results, however, also suggest that more information on fish-orientation distributions and on the mechanics of swimbladder compression is needed to explain field measurements of TS.

Summary

Analytical expressions describing the fish-backscattering cross-section, averaged over various geometrical and bio-acoustic parameters, have been obtained. Employing these solutions, the depth-dependence of the mean-backscattering cross-section of herring has been analysed numerically. Sensitivity to the acoustic frequency, the fish tilt-angle distribution, and the contraction rates of the individual bladder dimensions have been investigated.

Summarizing the results of the analysis, we can conclude that, for herring:

(a) The depth-dependence of the mean-backscattering cross-section for both swimbladder and the whole-fish can be substantial over the considered frequency range.
(b) The depth-dependence of the mean-backscattering cross-section is sensitive to a number of parameters, including the frequency, tilt angle, and the deformation rate of the individual swimbladder dimensions.
(c) These parameters also control the proportion of whole-fish backscattering contributed by the fish body. This contribution may be important at large depths.
(d) The frequency-dependence of the mean-backscattering cross-section varies with depth and is also sensitive to the spread of the tilt-angle distribution.

As the mean-backscattering cross-section is sensitive to the fish-orientation distribution, and to the manner of swimbladder compression with depth, we suggest further investigation of both these topics. Better knowledge on these may greatly improve the modelling results.

The model fits the experimental data best when the length-contraction factor of the swimbladder is made smaller than that of the width. This suggests that the real swimbladder may contract in that manner as the ambient pressure increases.

The present model is based on a highly simplified geometry of the herring swimbladder and body. Acoustic scattering is dependent on the structure of the scatterer. To improve the model, we should use the true morphology resolved to a small fraction of a wavelength. This should provide further insight into the characteristics of acoustical backscattering by herring.

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