A Bayesian approach to estimating target strength

Sascha M. M. Fässler, Andrew S. Brierley, and Paul G. Fernandes


Currently, conventional models of target strength (TS) vs. fish length, based on empirical measurements, are used to estimate fish density from integrated acoustic data. These models estimate a mean TS, averaged over variables that modulate fish TS (tilt angle, physiology, and morphology); they do not include information about the uncertainty of the mean TS, which could be propagated through to estimates of fish abundance. We use Bayesian methods, together with theoretical TS models and in situ TS data, to determine the uncertainty in TS estimates of Atlantic herring (Clupea harengus). Priors for model parameters (surface swimbladder volume, tilt angle, and s.d. of the mean TS) were used to estimate posterior parameter distributions and subsequently build a probabilistic TS model. The sensitivity of herring abundance estimates to variation in the Bayesian TS model was also evaluated. The abundance of North Sea herring from the area covered by the Scottish acoustic survey component was estimated using both the conventional TS–length formula (5.34 × 10² fish) and the Bayesian TS model (mean = 3.17 × 10² fish): this difference was probably because of the particular scattering model employed and the data used in the Bayesian model. The study demonstrates the relative importance of potential bias and precision of TS estimation and how the latter can be so much less important than the former.

Keywords: acoustic target strength, Bayesian statistics, herring, survey uncertainty.

Received 9 August 2008; accepted 7 November 2008.

S. M. M. Fässler and A. S. Brierley: Gatty Marine Laboratory, University of St Andrews, St Andrews, Fife KY16 8LB, Scotland, UK. P. G. Fernandes: FRS Marine Laboratory, PO Box 101, 375 Victoria Road, Torry, Aberdeen AB11 9DB, Scotland, UK. Correspondence to S. M. M. Fässler: tel: +44 1224 295538; fax: +44 1224 295511; e-mail: s.faessler@marlab.ac.uk.

Introduction

Acoustic-survey techniques are widely used to provide data on fish abundance and distribution (Simmonds and MacLennan, 2005). Such techniques lend themselves particularly well to pelagic fish, which often form well-defined schools in midwater that can be detected efficiently by echosounders. The total error (i.e. random and systematic components of measurements and sampling error) in acoustic surveys is generally not quantified, though work by Tesler (1989), Demer (1994, 2004), Aglen (1994), and Simmonds and MacLennan (2005) are exceptions to this statement. Consequently, the resulting estimates of fish abundance are usually treated as indices to tune population assessment models (Simmonds, 2003). Often, where errors are reported, they are based on random-sampling errors (Rose et al., 2000) and do not account for various sources of systematic measurement and sampling error specific to acoustic surveys (Simmonds et al., 1992). Systematic errors result from the equipment (Toresen et al., 1998), acoustic shadowing (Zhao and Ona, 2003), vessel avoidance (Vabo et al., 2002), and most notably, the uncertainty in the fish target strength (TS; Simmonds et al., 1992). Fish TS quantifies the proportion of incident sound energy that is scattered back towards the transducer and is used to convert the collected echo-intensity data to fish density (Simmonds and MacLennan, 2005). TS is mainly dependent on acoustic frequency (Foote, 1985; Horne and Jech, 1998), fish size (Love, 1977) and fish orientation (Nakken and Olsen, 1977). A simple relationship of the form TS = 20 log₁₀(L) − b₂₀ is conveniently and commonly used to estimate mean TS from fish length (L) using a species-specific value for the intercept b₂₀ (Simmonds and MacLennan, 2005).

The TS–L relationship currently applied to estimate abundances of various herring (Clupea harengus) and other clupeid stocks around the world was determined empirically ~25–30 years ago. Nakken and Olsen (1977) insonified 41 stunned and tethered herring at the commonly used frequency of 38 kHz and determined the maximum dorsal-aspect TS at a given fish length. Based on observations of tilt-angle distributions of small herring (mean length = 13 cm), the maximum TS values were reduced by 6 dB to account for the various incidence angles of acoustic waves on the fish, giving a final TS–L relationship of TS = 13.6 log₁₀(L) − 62.8. Edwards and Armstrong (1981) measured the TS at 38 kHz of a total of 565 live herring (L = 21–25 cm) in a cage at 17.5-m depth over a period of 340 h. They obtained a mean TS of −33.8 dB kg⁻¹ of fish. The Planning Group on ICES-Coordinated Herring and Sprat Acoustic Surveys (ICES, 1982) subsequently converted Nakken and Olsen’s (1977) TS–L relationship into TS per kg for a 23 cm herring (−34.6 dB kg⁻¹) to facilitate comparison with Edwards and Armstrong’s (1981) results. It was decided that the mean of the two TS estimates (−34.2 dB kg⁻¹) should be used together with length–weight data from northwestern North Sea herring and the group’s final recommendation was a TS–L relationship of TS = 20 log₁₀(L) − 71.2 dB.

There is evidence that pressure, and therefore fish depth, modulates the TS of Atlantic herring. This dependence could bias survey results if not taken into account (Ona, 1990, 2003; Ona et al., 2003;
Løland et al., 2007) Herring are physostomes and therefore do not have a gas gland that allows them to alter the swimbladder volume actively. As a result, the swimbladders, which can reflect between 90 and 95% of incident sound energy (Foote, 1980a), will change volume with water pressure according to Boyle’s law (Fässler et al., 2009), leading to a steady decrease in TS with increasing depth. Maturity stage or stomach fullness may also have important effects on swimbladder size, shape, and ultimately, TS (Ona, 1990). Additionally, it has been demonstrated that the physical environment can influence the physiology and morphology of herring, leading to geographic variation in swimbladder sizes and mean TS. For instance, herring living in the Baltic Sea have larger swimbladders than their conspecifics in the Northeast Atlantic (Didrikas and Hansson, 2004; Peltonen and Balk, 2005; Fässler et al., 2008). This is linked to their lower fat content and the low salinity of the Baltic Sea, which taken together place increasing importance on the swimbladder for buoyancy regulation.

In this paper, we further develop the backscattering model described in Fässler et al. (2008) that predicts mean TS as a function of fish orientation, size, physical properties, and acoustic frequency, applying Bayesian methods. TS data from Norwegian spring-spawning herring at depth (Ona, 2003) were used to estimate the distribution of the model parameters; namely the relative swimbladder volume at the surface, the tilt-angle distribution, and the s.d. of the estimated mean TS. Bayesian methods were used because these allow parameter uncertainty to be incorporated into estimates of mean TS. The TS model comprised two separate parts: (i) the swimbladder was approximated as a gas-filled, prolate spheroid using the modal-series-based deformed-cylinder model (MS–DCM; Stanton, 1988); and (ii) the fish body was assumed to be a fluid-filled ellipsoid and modelled using the distorted-wave Born approximation (DWBA; Morse and Ingard, 1968; Stanton et al., 1993; Chu et al., 1993; McGehee et al., 1998). Posterior distributions of model parameters were then used with the error-propagation properties of the Bayesian framework to simulate backscattering by herring, while quantifying the precision of the TS estimate. The resulting length- and depth-dependent TS model was applied to estimate random and systematic errors in TS estimation and ultimately to estimate North Sea herring abundance.

This study is an important step towards incorporating the error associated with TS in estimates of total error in acoustically derived abundance estimates of fish. The methods will be advantageous for ecosystem studies and stock assessment where estimates of fish abundance with estimates of total error are required.

### Material and methods

#### Bayesian methods

In Bayesian methods, posterior density functions of model parameters $\theta$ are derived based on the goodness-of-fit of a model to data and on prior information not contained in those data (MacAllister and Kirkwood, 1998). The posterior probability distributions $p(\theta | \text{data})$ of a set of continuous model parameter $\theta$ given the data are determined using Bayes’ theorem (Bayes, 1763) according to

$$p(\theta | \text{data}) = \frac{p(\theta, \text{data})}{p(\text{data})} = \frac{p(\theta) \times p(\text{data} | \theta)}{\int p(\theta) \times p(\text{data} | \theta) d\theta},$$

where $p(\theta, \text{data})$ denotes the joint probability for a set of parameters $\theta$ and the obtaining of the data. The data used here were derived from a set of extensive in situ TS measurements of Norwegian spring-spawning herring at a range of water depths from 5 to 300 m (Ona, 2003). These were mean TS values standardized to a common fish length $(L)$ of 32 cm (Ona, 2003) at an observed depth $(z)$, each determined from $>2000$ single-fish targets. Suppose that the data represent $j$ samples of a continuous probability density function (PDF) that depends on the unknown parameters $\theta$, in a known way that can be described by a model (Lee, 2004). $p(\theta)$ describes the prior PDF (i.e. the ‘prior’ probability) for $\theta$, $L(\text{data} | \theta)$ is the probability of obtaining the data values if $\theta$ were the true values. $L(\text{data} | \theta)$ is commonly referred to as the likelihood function describing the dependence of the data on $\theta$. The likelihood function of the entire TS dataset is given by the product of the normal density function over all datapoints:

$$L(\text{data} | \theta) = \prod_{j=1}^{n} \frac{1}{\sigma \sqrt{2 \pi}} \exp \left[ -\frac{(Y_j - U_j)^2}{2\sigma^2} \right].$$

where $\sigma$ is the s.d. of the observation error. Likelihood functions can result in small numbers and for that reason the log$_{10}$ (likelihood) was used in the computer program to reduce calculation time and avoid rounding issues (MacAllister and Kirkwood, 1998). Here, $Y_j$ is the $j$th observed TS value in the dataset and $U_j$ is the expected TS, estimated from a theoretical TS model described below. $U_j$ can be described in simple terms as a function of model parameters $(\theta)$, fish length $L$, and depth $z$:

$$U_j = f(\theta; L_j, z_j).$$

The prior distribution for a parameter is based on previous knowledge of the parameter, without incorporating the data used to calculate the likelihood function (Punt and Hilborn, 1997). Priors are usually obtained by consulting experts or historical records. We determined prior distributions for the three parameters that were deemed most important for the outcome of the model. These were the standard deviation of the fish tilt-angle distribution (SDt), relative volume of the swimbladder at the sea surface (V0), and the standard deviation of the observed mean TS (SDTS). Prior distributions of each of these parameters were constructed independently and consequently the joint prior $p(\theta)$ was simply

$$p(\theta) = p(\text{SDt}) \times p(V_0) \times p(\text{SDTS}),$$

where $p(\text{SDt})$, $p(V_0)$, and $p(\text{SDTS})$ are the priors for the respective parameter values. These priors are assumed to be independent of each other and of both fish length and water depth. A prior can be either informative or uninformative. An uninformative prior provides little information relative to the data (Box and Tiao, 1973) and usually has the form of a uniform distribution or one with a large variance, giving all reasonable parameter values approximately equal probabilities. Informative priors provide precise information based on previous evidence and may have a considerable affect on the result. Priors for parameters SDt, and $V_0$ were based on published values (Table 1), whereas an uninformative prior was chosen for SDTS. Because of the complexity of the model, integration of the denominator (i.e. the normalization constant) in Equation (1) was not feasible. Instead, values were sampled directly from the posterior distributions of the model parameters using Markov Chain Monte Carlo (MCMC).
<table>
<thead>
<tr>
<th>Description</th>
<th>Value or prior distribution (source)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Physical properties</td>
<td></td>
</tr>
<tr>
<td>Sound speed contrast water-fish body</td>
<td>$h_b = 1.04$ (Fässler et al., 2008)</td>
</tr>
<tr>
<td>Density contrast water-fish body</td>
<td>$g_b = 1.04$ (Fässler et al., 2008)</td>
</tr>
<tr>
<td>Sound speed contrast swimbladder-fish body</td>
<td>$h_{bs} = 0.23$ (Fässler et al., 2008)</td>
</tr>
<tr>
<td>Density contrast swimbladder-fish body</td>
<td>$g_{bs} = 0.00128$ (Fässler et al., 2008)</td>
</tr>
<tr>
<td>Fat density</td>
<td>$\rho_f = 0.926$ g cm$^{-3}$ (Brawn, 1969)</td>
</tr>
<tr>
<td>Scales density</td>
<td>$\rho_a = 1.966$ g cm$^{-3}$ (Brawn, 1969)</td>
</tr>
<tr>
<td>Bones density</td>
<td>$\rho_b = 1.93$ g cm$^{-3}$ (Brawn, 1969)</td>
</tr>
<tr>
<td>Fish flesh density</td>
<td>$\rho_h = 1.057$ g cm$^{-3}$ (Brawn, 1969)</td>
</tr>
<tr>
<td>Sound speed in water</td>
<td>$c_w = 1500$ m s$^{-1}$</td>
</tr>
<tr>
<td>Echosounder frequency</td>
<td>$f = 38$ kHz</td>
</tr>
<tr>
<td>Fish behaviour and dimensions</td>
<td></td>
</tr>
<tr>
<td>s.d. of tilt-angle distribution</td>
<td>$\Delta \theta = 5.56^\circ$ (measurements)</td>
</tr>
<tr>
<td>Relative swimbladder volume at sea surface</td>
<td>$V_{bs} = \text{Normal (5.0, 0.7)}$ (Harden Jones and Marshall, 1953; Ona, 1990)</td>
</tr>
<tr>
<td>Swinbladder minor-axis compression factor</td>
<td>$\alpha = 0.42$ (Fässler et al., 2009)</td>
</tr>
<tr>
<td>Swinbladder minor-axis compression factor</td>
<td>$\beta = 0$ (Fässler et al., 2009)</td>
</tr>
<tr>
<td>Precision</td>
<td>s.d. of mean TS estimate $\sigma_{TS} \sim \text{Gamma (0.001,1)}$ (uninformative prior)</td>
</tr>
</tbody>
</table>

The fish-body component was modelled using the DWBA, with the model routines described in Fässler et al. (2007). The swimbladder was modelled with a MSB–DCM (see Gorska and Ona, 2003; Fässler et al., 2008, for details). All input parameters for the model, including their sources, are listed in Table 1.

**Survey analysis**

Echo-integration data were taken from the Scottish component of the North Sea herring acoustic survey in summer 2007 (Figure 1). Details of survey procedures can be found in individual survey reports (e.g., ICES, 2008). Acoustic data were collected using Simrad EK60 echosounders operating at 18, 38, 120, and 200 kHz with split-beam transducers mounted on the drop keel typically at depths of 5 m. The transducers had nominal beam widths of 11, 7, 7, and 7°, respectively, and were located in proximity to each other. The maximum offset of 0.6 m was between the centres of the 18 and 38 kHz transducers. Data were collected between 02:00 and 22:00 GMT from 29 June to 18 July 2007, with integration starting at a depth of 12 m. Post-processing and analysis were done using Myriax EchoView software (v 4.40). Biological samples were collected from some of the more dense aggregations observed throughout the survey using a PT160 pelagic trawl for identification purposes and to generate length frequency distributions for the herring in the various survey subareas. Fish lengths were recorded in 0.5 cm intervals to the nearest 0.5 cm below total length. Integrated volume-backscattering coefficients $s_A$ were averaged over distances surveyed each 15 min (~2.5 nautical miles). Numbers of fish in length group $i$ in a given area were estimated by

$$N_i = \frac{s_A}{\sigma_{bs}} p_i A,$$

where $N_i$ is the number of herring in length group $i$ and $s_A$ the nautical-area-scattering coefficient (NASC) with units m$^2$ nautical

**Figure 1.** Map of the northwestern North Sea showing the survey area (grey) covered by the Scottish component of the North Sea Herring Acoustic Survey. Numbers represent the ICES acoustic-survey estimates by statistical rectangle from 2007: absolute numbers (millions of fish; white, upper part of the figure) and biomass (thousand tonnes; black, lower part of the figure). The vertical axis shows degrees of latitude (N), and the horizontal axis shows degrees of longitude [East and West (−)] of the Greenwich Meridian.
mile\(^{-2}\) (MacLennan et al., 2002). The analysed area (A) covered a total of 38 769.5 nautical miles\(^2\). The survey area was divided into seven subareas characterized by fish with similar length frequencies. For each area, \(p_i\) is the proportion of herring in length group \(i\), and \(\sigma_{bs,i}\) is their backscattering cross section, so that

\[
\tilde{\sigma}_{bs} = \frac{\sum_{i} \sigma_{bs,i} \cdot p_i}{\sum_{i} p_i}.
\]  

Distributions of expected \(\sigma_{bs}\) were calculated concurrently in the Bayesian framework by directly using all the model parameter values sampled from their posterior distributions in the Markov Chain. In that way, the uncertainty in the model parameters was propagated through to the “predicted mean backscattering cross section”, and the distribution of the parameters and any correlation between them was taken into account. Samples of \(\sigma_{bs}\) were then drawn from a lognormal distribution with estimated precision based on SDTS. Hence, the methods applied in this paper differ from those of previous investigations (Demer, 1994, to 200 m. Numbers of herring were estimated as follows: all length groups of herring in depth bins of 5 m ranging from 0

\[
\text{Distributions of expected } \sigma_{bs} \text{ were calculated concurrently in the Bayesian framework by directly using all the model parameter values sampled from their posterior distributions in the Markov Chain. In that way, the uncertainty in the model parameters was propagated through to the “predicted mean backscattering cross section”, and the distribution of the parameters and any correlation between them was taken into account. Samples of } \sigma_{bs} \text{ were then drawn from a lognormal distribution with estimated precision based on SDTS. Hence, the methods applied in this paper differ from those of previous investigations (Demer, 1994, to 200 m. Numbers of herring were estimated as follows: all length groups of herring in depth bins of 5 m ranging from 0 to 200 m. Numbers of herring were estimated as follows:}

\[
(i) \quad \text{TS} = 20 \log_{10}(L) - 71.2 \quad \text{to convert fish length (L) into TS;}
\]

\[
(ii) \quad \text{estimated distributions of } \sigma_{bs} \text{ for every depth bin and length group; and}
\]

\[
(iii) \quad \text{the } \text{TS} = 20 \log_{10}(L) - b_{30} \quad \text{relationship with } b_{30} \text{ based on calculations in (ii) for depths of 10–20 m [following the methods used by Nakken and Olsen (1977) and Edwards and Armstrong (1981)].}
\]  

Results
Computations were done on 45 000 samples from the posterior distributions. Posterior distributions converged after ~200 iterations, but a more conservative “burn-in” interval (i.e. discarded values at the beginning of the MCMC chain) of 2000 iterations was chosen. The plot matrix of samples from posterior distributions of the model parameters revealed no severe autocorrelation between parameters (Figure 2). Possible autocorrelation could have influenced mixing and convergence of the sampled posteriors. Figure 3 shows the results from the Bayesian estimation of the three model parameters. The mean and s.d. of the posterior distribution for the relative swimbladder volume at the surface \(v_{bs} \) (mean = 4.95\%, s.d. = 0.72\%) were approximately equal to those of the prior distribution; this suggests that the prior had a considerable effect on the parameter estimation. However, the posterior for \(SD\) had a smaller mean and a considerably narrower distribution (mean = 7.14\%, s.d. = 0.50\%) than the prior. Because of the uninformative prior assigned to \(SD\), all the information used to construct the posterior distribution came from the data \(SD = 1.64 \text{ dB, s.d. = 0.12 dB}\). Results from the Scottish component of the North Sea Herring Acoustic Survey can be found in ICES (2008). The herring abundance estimated by ICES (2008) for the survey area (Figure 1), applying \(\text{TS} = 20 \log_{10}(L) - 71.2\), was \(5.34 \times 10^9\) fish. Figure 4 shows a comparison of estimated herring abundances using the three different methods applied in this study to determine the herring TS. Using model values based on the Ona (2003) dataset to determine the TS for herring in surface waters between 10 and 20 m, following the methods applied by Nakken and Olsen (1977) and Edwards and Armstrong (1981), the mean TS is 4.0 dB higher than the one used to generate the ICES (2008) biomass estimate. As a result, the estimated herring abundance calculated here is reduced by >50\% to \(2.45 \times 10^9\) fish. In comparison, the estimated normal distribution of abundance based on TS distributions by length group and depth bin had a mean and s.d. of \(3.17 \times 10^9\) and \(3.02 \times 10^7\) fish, respectively. This is also less than the current estimate, but suggests higher estimated abundances if the depth-dependent TS is applied.

Discussion
When interpreting results from an acoustic survey of fish, it is important to recognize the stochastic nature of the TS and its possible dependence on many factors. It has long been known that TS is influenced significantly by fish length (e.g. Love, 1977; Foote, 1979), fish orientation (e.g. Nakken and Olsen, 1977; Foote, 1980b), and acoustic frequency (e.g. Haslett, 1965; Love, 1977). Because of a lack of suitable alternatives, acoustic surveys still rely on empirically determined, frequency-specific TS–L relationships, which may be biased, particularly for physostomous fish. Many experiments from which these relationships were derived for herring were done in only one season and neglected important biological effects such as feeding state and gonad development (Ona, 1990; Ona et al., 2001) or the fact that dead or stunned fish may have a different TS from live fish (e.g. McClatchie et al., 1996). On the other hand, because for the same size and species of fish the observed TS can cover a wide range, acoustic surveys have relied on the expected values of the mean TS (Simmonds and MacLennan, 2005; Foote, 1987). It is difficult to quantify the effect of any one factor on TS by empirical observations, so theoretical TS models have been used to approximate fish backscatter and investigate its dependence on various input parameters (Clay and Horne, 1994; Foote and Francis, 2002; Gorska and Ona, 2003). This theoretical modelling approach...
offers the most promise if uncertainty arising from TS variability is to be estimated and incorporated into the acoustic stock assessments (Demer, 2004).

Total error in acoustic surveys is rarely quantified (Rivoirard et al., 2000; Rose et al., 2000; Tjelmeland, 2002), despite its obvious advantages and widespread use in fish-stock assessment. Bayesian methods have been identified as a valuable tool to estimate the total uncertainty in trawl surveys (Punt and Hilborn, 1997; MacAllister and Kirkwood, 1998; Meyer and Millar, 1999) and could be used in acoustic surveys to quantify and incorporate uncertainty into abundance and biomass estimates. The results of these methods provide estimates of the random and systematic components of measurement and sampling error, which are important for managing fisheries. Uncertainty in the advice provided by fishery scientists can be based on a combination of data from the stock in question and prior information on population model parameters based on data from similar fish populations (MacAllister and Kirkwood, 1998). Another advantage of Bayesian methods is that the uncertainty associated with model parameters can easily be propagated through the framework to estimate distributions of model outcomes. Based on these properties, we have proposed a Bayesian system that allows unknown parameters, or those that are difficult to estimate, to be incorporated into a conventional fish-backscattering model to estimate distributions of expected TS. This can then provide a basis for estimating the uncertainty associated with TS in an acoustic survey and contribute to the overall estimate of uncertainty.

The herring abundance estimates obtained in this study indicate that the uncertainty associated with this particular model is largely systematic. Assuming that the ICES (2008) assessment of herring abundance, which is based on the conventional TS–L relationship, is correct, the associated accuracy of the acoustic estimate based on the Bayesian TS model is 40.6%. This error is in accordance with previous upper estimates of the systematic error of the TS component in acoustic estimates of absolute abundance, where values of $+26$ to $+41\%$ (Tesler, 1989), $0$ to $+50\%$ (Simmonds and MacLennan, 2005), or $0$ to $+40\%$ (Simmonds et al., 1992) have been reported. Factors that may have affected the accuracy of the abundance estimate in this study were the dataset used to derive the model parameters and the TS model itself. It must be noted that the herring TS data used in this study might not have been entirely appropriate, being based on Norwegian spring-spawning herring as opposed to North Sea herring. Although these stocks are the same species and live in broadly similar environments, in contrast, for example, to herring living in the Baltic Sea, which have an entirely different salinity regime, the two herring stocks may have a different morphology (Sinclair and Solemdal, 1988). It is evident that the TS–L relationship fitted to the whole Ona (2003) dataset ($TS = 20 \log_{10}(L) - 71.2$) is $3.9$ dB higher than that currently applied to estimate abundance of North Sea herring. In terms of fish numbers, referring to the 2007 acoustic survey, this difference would cause a $59.3\%$ reduction in estimated abundance of North Sea herring and ultimately bring the results...
more in line with estimates using the Bayesian model. It follows that, because the accuracy of the Bayesian TS model is strongly dependent on the input data, acoustic-survey analyses should be based on reliable TS data. Further work will involve collection of appropriate in situ TS data to tune the TS model, providing results more applicable to North Sea herring.

Additionally, the TS model used may have been unsuitable for the species in question, because it is based essentially on the coherent addition of backscatter from simple approximations of the herring swimbladder and fish-body shapes. This improves computational efficiency, but neglects structural details of the herring anatomy. Moreover, the model does not take account of the boundary conditions at the swimbladder wall, because it ignores the fish-body components when calculating the swimbladder backscatter. Nonetheless, coherent addition is applicable in the present case, because the swimbladder is the dominant source of backscatter (Ding and Ye, 1997; Gorska and Ona, 2003). In contrast to the low accuracy of the herring abundance estimate, it is very precise (CV = 1.0%), so the random error associated with the TS component is negligible. This high precision, however, can be attributed to the central-limit theorem, because absolute fish abundance was derived by averaging a large number of estimates (Demer, 2004).

Another advantage of the Bayesian model is the ability to apply a specific TS distribution to all herring schools encountered in the survey. This is of particular importance when dealing with the depth-dependence of herring TS. In the survey area, NASCs were highest at depths between 100 and 150 m (Figure 5). At these depths, swimbladder volumes are only ~6–9% of those at the surface, resulting in greatly reduced TS values (Fässler et al., 2009). As a result, extending the TS dataset from values at the sea surface (10–20 m) to include values down to 300-m depth resulted in an abundance estimate that was higher by about one third (Figure 4).

There are disadvantages of the Bayesian approach linked with the selection of prior probabilities. Unless carefully chosen, the selection of prior probabilities may cause bias, and their construction can be tedious and require considerable effort (MacAllister and Kirkwood, 1998). Prior distributions estimated for two of the model parameters in this study were based on reliable measurements on herring and are assumed valid. However, the TS-model evaluation indicates a particular need for accurate data on tilt-angle distributions. Fish behaviour, as reflected in the distribution of tilt angles within an aggregation of fish, is the most important factor influencing TS and hence the accuracy of subsequent abundance estimates (Foote, 1980c; Blaxter and Batty, 1990; Horne and Jech, 1999; Hazen and Horne, 2003). Other potential limitations of the more complex Bayesian model are the demand on computing resources, as well as posterior distributions that may sometimes be too complex to estimate. Nonetheless, given appropriate input data, these methods can provide an important step towards opportunistically incorporating the variability associated with factors affecting TS, to give an overall estimate of the expected TS distribution. The resulting probabilistic abundance, density, and biomass estimates could become essential components in ecosystem studies and resource management.

**Acknowledgements**

The authors are grateful to Dezhang Chu and Gareth Lawson from the Woods Hole Oceanographic Institution, Woods Hole, MA, for providing the MATLAB code for the fish-body model. We thank Dave Borchers (CREEM, St Andrews University, UK), Liz Clarke (FRS, Aberdeen, UK), and Colin Millar (CREEM and FRS) for their expert advice and help with Bayesian statistical methods. SMMF acknowledges the support received through an ORSAS award of the British government, a studentship of the University of St Andrews (Scotland), and an Ausbildungsbeitrag of the Kanton Basel-Landschaft (Switzerland).

**References**


INHIBITION


doi:10.1093/icesjms/fsp008