From siphonophores to deep scattering layers: uncertainty ranges for the estimation of global mesopelagic fish biomass

Roland Proud1*, Nils Olav Handegard2, Rudy J. Kloser3, Martin J. Cox4, and Andrew S. Brierley1

1Pelagic Ecology Research Group, Gatty Marine Laboratory, Scottish Oceans Institute, University of St Andrews, St Andrews, Fife KY16 8LB, UK
2Institute of Marine Research, PO Box 1870, Nordnes, 5817 Bergen, Norway
3CSIRO Oceans and Atmosphere Flagship, GPO Box 1538, Hobart, TAS 7001, Australia
4Australian Antarctic Division, 203 Channel Highway, Kingston, Tasmania, 7050 Australia

*Corresponding author: tel: +44 (0)1334 46 3401; e-mail: rp43@st-andrews.ac.uk.


Received 10 January 2018; revised 6 March 2018; accepted 8 March 2018.

The mesopelagic community is important for downward oceanic carbon transportation and is a potential food source for humans. Estimates of global mesopelagic fish biomass vary substantially (between 1 and 20 Gt). Here, we develop a global mesopelagic fish biomass model using daytime 38 kHz acoustic backscatter from deep scattering layers. Model backscatter arises predominantly from fish and siphonophores but the relative proportions of siphonophores and fish, and several of the parameters in the model, are uncertain. We use simulations to estimate biomass and the variance of biomass determined across three different scenarios; S1, where all fish have gas-filled swimbladders, and S2 and S3, where a proportion of fish do not. Our estimates of biomass ranged from 1.8 to 16 Gt (25–75% quartile ranges), and median values of S1 to S3 were 3.8, 4.6, and 8.3 Gt, respectively. A sensitivity analysis shows that for any given quantity of fish backscatter, the fish swimbladder volume, its size distribution and its aspect ratio are the parameters that cause most variation (i.e. lead to greatest uncertainty) in the biomass estimate. Determination of these parameters should be prioritized in future studies, as should determining the proportion of backscatter due to siphonophores.

Keywords: acoustics, DSLs, myctophids, pneumatophore, resonance, scattering models, swimbladder.

Introduction

In this article, we consider, from the standpoint of available acoustic survey data, what the global biomass of mesopelagic fish (fish in the 200–1000 m depth range, including myctophids or "lantern fish") might be.

The importance of the mesopelagic community

The mesopelagic community plays an important role in global biogeochemical cycling and the biological carbon pump, and is attracting increasing attention from commercial fishers (St John et al., 2016). Biogeochemical and ecosystem models which simulate the biological carbon pump require validation of the mesopelagic component to provide confidence in their predictions of vertical carbon flux, which itself feeds into climate/Earth-system models (Giering et al., 2014). To cast light on the "dark hole in our understanding" of the mesopelagic (St John et al., 2016), to progress towards ecosystem-based management in advance of developing fisheries, and to make headway on conservation of water-column habitat in areas beyond national jurisdiction (Roberts et al., 2017), a robust estimate of mesopelagic fish biomass is required.

A substantial amount of mesopelagic biomass in the 1 mm+ size fraction is contained, during the day, within deep scattering layers (DSLs), primarily made up of fish, zooplankton, squid, and jellyfish. DSLs are detected using echosounders, which emit sound waves and record backscatter (see Chu, 2011, for a review). Echosounder
observations (summarized pictorially as echograms) can be analysed and biological features such as layers, schools, and swarms can be identified and quantified (Holliday, 1972; Coetzee, 2000; Cox et al., 2011; Proud et al., 2015). DSL depth varies globally between ~200 and 1000 m and is driven, at least in part, by environmental conditions, e.g. light intensity, oxygen concentration, temperature, and mixing (Bianchi et al., 2013; Kleivjer et al., 2016; Aksnes et al., 2017; Proud et al., 2017). There is often more than one single scattering layer (e.g. Andreeva et al., 2000). DSL backscattering intensity (a proxy for biomass) also varies globally and is correlated with primary production (PP) at the surface and temperature at DSL depth (Neiburn and Koslow, 2015; Proud et al., 2017). Typically, DSL backscatter reduces during the night, as a proportion of the community migrates to the surface to feed (Brierley, 2014).

**Present estimates of mesopelagic fish biomass**

It has been estimated recently that the global biomass of mesopelagic fish could be around 11–15 gigatonnes (Gt) (Irigoin et al., 2014). That estimate arises from analysis of an acoustic survey (38 kHz) transect run west to east around the world through the mid latitudes (the Malaspina 2010 Circumnavigation Expedition). Under that analysis, the acoustic backscatter is attributed 100% to fish and the resulting biomass estimate is ~11–15 times higher than an historic estimate of 1 Gt based on net sampling (Gjøsaeter and Kawaguchi, 1980). Although it is recognized that trawl avoidance by mesopelagic fish may lead to a large underestimation of their biomass by net sampling (Kaartvedt et al., 2012), acoustic energy is not necessarily directly proportional to fish biomass and the acoustic energy is not only from fish and so the disagreement between “historic” and “new” estimates could be due to inaccuracy in both assumptions rather than just to a failing of one.

**Proud et al.** (2017) compiled a quasi-global database of daytime 38 kHz mesopelagic backscattering intensity, and used it to define a mesopelagic biogeography. The biogeography was compiled from completely different acoustic data to the Malaspina study, with a much wider geographic extent, and was based on characteristics of objectively identified DSLs. Total backscatter arising from DSLs in the mesopelagic zone (200–1000 m) was predicted to be 6.02 ± 1.4 × 10^9 m^2 (mean area-backscattering coefficient multiplied by surface area). In previous work, we scaled this prediction to global fish biomass (70°N and 70°S), estimating a value of 9 Gt (Proud, 2016), Irigoien et al. (2014) suggest that their estimate (11–15 Gt for the geographic region between latitudes 40° N and 40° S) could be ~30% higher (i.e. 14.3–19.5 Gt) if expanded to the area between 70° N and 70° S, which is similar to the extent of the Proud et al. (2017) biogeography. That scaled estimate is startlingly high, and begs the question “can it even be sustained given known PP?”

**Gas-bladdered mesopelagic siphonophores and fish**

The mesopelagic zone is occupied by a range of taxa, including crustacean and gelatinous zooplankton and cephalopods. Some of these can be numerically very abundant (e.g. copepods) and some have a high acoustic target strength (TS). Gas-bearing siphonophores (Physonects and Cystonects) and teleost fish, with gas-filled swimbladders are strong acoustic targets (Barham, 1963, 1966; Warren, 2001; Scoulding et al., 2015) and resonant at depth at 38 kHz (Kloser et al., 2016). To estimate plausible ranges of mesopelagic fish biomass with acoustic data the effect of resonant scatter from siphonophores with gas-filled pneumatophores (gas bladders) and fish with gas-filled swimbladders (gas bladders) needs to be considered (Davison et al., 2015).

The TS from individual gas bladders (gas-filled organs of fish and siphonophores), produces >95% of the organism’s total TS (Foote, 1987) and is often used to approximate the TS of a gas-bladdered fish or siphonophore (Warren, 2001; Scoulding et al., 2015). Gas bladder TS can be predicted using acoustic scattering models, typically assuming that the shape of the gas bladder can be approximated by a prolate spheroid (Scoulding et al., 2015). Modelled gas bladder TS increases linearly with size in the Rayleigh zone and plateaus as the size of the gas bladder approaches a value of \( \frac{\lambda}{2\pi} \) in the geometric zone (Figure 1), where \( \lambda \) is the wavelength of the incident sound wave. In the resonant region (Figure 1), the gas bladder vibrates in sympathy with the acoustic wave and radiates more energy than predicted by commonly used log-linear TS-to-length relationships (e.g. Foote, 1987). The degree of the re-radiation is dependent somewhat on the tension of the gas bladder wall and the tissue viscosity (Love, 1978; Bai, 2013; Scoulding et al., 2015). In this study, acoustic data were available at the commonly used fisheries acoustic frequency of 38 kHz. The wavelength at 38 kHz in seawater is ~3.9 cm, and 38 kHz sound scattering by a mesopelagic fish or siphonophore at 500 m, with an in situ gas bladder ~1 mm in length, falls well within the resonant region. Resonant scattering will be provoked routinely in surveys at 38 kHz of mesopelagic fish and siphonophores when the equivalent spherical radius (the radius of a sphere equal in volume to the prolate spheroid) of the gas bladder is within ~0.4–1 mm (Davison et al., 2015; Kloser et al., 2016). Resonant scattering need not be confined just to “small” fish or siphonophores as the investment of fat in the swimbladders of older and larger fish (Neighbors and Nafpaktitis, 1982) may result in swimbladders of larger fish actually containing *smaller* volumes of gas than smaller fish; a reduction in body density with length may also contribute to this effect. Furthermore, compression of the gas bladders of downward-migrating fish, according to Boyle’s Law, may result in the gas bladder volume being substantially smaller than would be suggested by fish length alone, and so diel variability in scattering type/intensity may occur. The issue of mesopelagic fish TS is clearly vexed.

**Approach**

We take the approach here of attempting to attribute received echo energy in plausible proportions to fish and other potential sound-scatterers, and to scale the likely echo energy from fish to
Objectives

The objective of this article is to estimate the likely range of global mesopelagic fish biomass and the drivers of uncertainty. Our method was as follows: (i) define a generalized acoustic biomass model, (ii) obtain a global mean value of mesopelagic backscatter from the literature (Proud et al., 2017), (iii) with reference to acoustic scattering models, review the dominant sources of backscatter found within the mesopelagic zone, (iv) define mesopelagic fish biomass model and identify unknown parameters and possible confounding animal behaviours, (v) define plausible statistical distributions to capture the full range of uncertainty in the unknown parameters and develop scenarios to simulate a range of animal behaviours, (vi) quantify uncertainty across all scenarios of mesopelagic fish biomass estimates, and (vii) run a global sensitivity analysis to quantify the contribution of each parameter to overall uncertainty in the mesopelagic fish biomass model.

Methods

The method presented here follows a generalized approach. We first define general equations used for the conversion of acoustic backscattering intensity to biomass (see also Equation 1 in Kloser et al., 2009 and Equation 9.11 in Simmonds and MacLennan, 2005), and then parameterize them for estimation of mesopelagic fish biomass.

For a given aggregation of organisms, comprising G groups (e.g. taxonomic, functional, or anatomical), each made up of Mt members, over a common area A, the mean area-backscattering coefficient for all groups, sa (m⁻²), is given by

\[
s_a = \frac{1}{G} \sum_{g=1}^{M_t} \frac{M_t}{m} \sigma_{bsg},
\]

where g is the group index, m is the group member index and \(\sigma_{bsg}\) (m²) is the backscattering cross-section for member m of group g. Group biomass, \(B_g\) (kg), is then calculated by

\[
B_g = A \frac{p_g}{\bar{m}} \bar{W}_g,
\]

where \(\bar{W}_g\) (kg) and \(\bar{m}\) are the mean member weight and mean area-backscattering coefficient of group g and \(p_g\), the proportion of \(s_a\) that is produced by group g, is given by

\[
p_g = \frac{n_g \sigma_{bsg}}{\sum_{g=1}^{G} n_g \sigma_{bsg}},
\]

where \(n_g\) is the relative proportion by number of the aggregation represented by group g.

To estimate \(B_g\), the following steps are taken: (i) define the group of interest (g), establish the region and depth range \(z_1\) to \(z_2\) (volume) which contains the group of interest, and define all other known scattering groups found within the volume; (ii) predict or measure \(s_a\) over the volume for a given incident frequency; (iii) define acoustic scattering models to predict \(\sigma_{bsg}\) of each group; (iv) determine which groups contribute substantially to \(s_a\) and estimate \(p_g\); (v) solve (2) for the group of interest, and identify unknown parameters and animal behaviours; (vi) define distributions for unknown parameters and scenarios for unknown animal behaviours; (vii) estimate uncertainty in \(B_g\) over the parameter space for each scenario; and (viii) determine the sensitivity of \(B_g\) to input parameters.

The remainder of the method follows this procedure for the case of the putative global population of mesopelagic fish.

Model definitions and global mesopelagic area-backscattering coefficient

In this study, we define our target group as fish in mesopelagic (200–1000 m) DSLs (Figure 2) during the daytime in the open ocean (seabed depth > 1000 m). Globally, there are c. 900 species of mesopelagic fish and the most abundant and diverse family group is Myctophidae (lanternfish) with c. 250 species (Bone et al., 1995); other fish families which include large
numbers of mesopelagic fish are Gonostomatidae (bristle-mouths), Phosichthyidae (lightfishes), and Sternoptychidae (e.g. marine hatchetfishes) (Bone et al., 1995). The global open ocean has, following Proud et al. (2017), a total surface area, A, of $3.11 \times 10^{14}$ m$^2$ and total global daytime 38 kHz mesopelagic backscatter of $6.02 \pm 1.4 \times 10^9$ m$^2$; at 38 kHz, the signal-to-noise ratio is such that the observable range is at least 1000 m. The global $s_v$ value, determined by dividing the total mesopelagic backscatter by $A$, is $1.94 \pm 0.44 \times 10^5$ m$^{-2}$ m$^{-2}$. We contend that the following taxonomically based scattering groups make possible substantial contributions to mesopelagic $s_v$: copepods; euphausiids; squid; jellyfish; and siphonophores (Physonects and Cystonects, referred to collectively as just siphonophores from here on for simplicity).

Acoustic scattering models

The scattering groups defined here fall into two categories, gas-bearing organisms (mesopelagic fish and siphonophores) and weakly scattering fluid-filled organisms (copepods, euphausiids, squid, and jellyfish). The $s_v$ value of the fluid-filled group was predicted using the distorted-wave-born approximation (DWBA) model (Chu et al., 1993) using parameters from Lavery et al. (2007).

The gas-filled swimbladders of fish (gas bladders) and gas-filled pneumatophores of siphonophores (gas bladders) produce $>95\%$ of the organisms’ backscatter at 38 kHz (Foote, 1980). This figure is likely to be closer to 99% for mesopelagic fish; Foote (1980) refers to much larger and denser epipelagic fish for which backscatter from body tissue makes up a larger proportion of the total. The $s_v$ of the gas bladders of fish and siphonophores can be predicted using the resonance model of Love (1978), including adaptations for shape (Ye, 1998) and directivity (Stanton, 1988). Generally, our resonance model formulation followed that of the prolate spheroid model described by Scoulding et al. (2015), apart from the calculation of the resonant frequency (5) which was taken directly from Love (1978). Resonant scattering is dependent on wavelength of incident frequency, depth range, viscosity of tissue, and size of the gas bladder (Love, 1978; Davison et al., 2015; Kloser et al., 2016). The backscattering cross-section is given by

$$s_v = \frac{a_{esr}^2}{(\omega_0^2/\omega^2 - 1)^{3/2} + \delta^2(\omega, a, b, \beta; \Omega)} D(k, a, \theta, \sigma)$$

where $\omega_0$ is the angular resonant frequency found by solving

$$\left(\omega_0 a_{esr}\right)^2 = C_\beta^2 (a, b) \frac{3\gamma a^\beta P_f}{\rho_l} + \frac{2s}{\rho_l a_{esr}(3\gamma - 1)}$$

$a_{esr}$ is the equivalent spherical radius given by

$$a_{esr} = \left(ab^2\right)^{1/3}$$

where $a$ and $b$ are the semi-major and semi-minor axes of the prolate spheroid, respectively, and are related by the $b$-scaling parameter, $\beta$, given by

$$a = \frac{b}{\beta}.$$
Surface tension at gas cavity-tissue interface N m⁻¹

- Scaling parameter – 0.64 (Yasuma et al., 2015)

Dynamic viscosity kg m⁻¹ s⁻¹

- Mean orientation angle degrees 0° ± 0° (Stasberg, 1953; Weston, 1967)

Mean orientation angle degrees 0° ± 0°

Depth m

- Variable 525 (Proud et al., 2017)

Standard deviation of orientation angle degrees 30° ± 30°

Incident frequency Hz

- 38000 (Scoulding et al., 2015)

Symbol Description Unit Value

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>ω</td>
<td>Incident frequency</td>
<td>Hz</td>
</tr>
<tr>
<td>ρₐ</td>
<td>Density of air</td>
<td>kg m⁻³</td>
</tr>
<tr>
<td>γₐ</td>
<td>Ratio of specific heat for air</td>
<td>-</td>
</tr>
<tr>
<td>cₚₐ</td>
<td>Specific heat at constant pressure for air</td>
<td>cal kg⁻¹ K⁻¹</td>
</tr>
<tr>
<td>κₐ</td>
<td>Thermal conductivity of air</td>
<td>W m⁻¹ K⁻¹</td>
</tr>
<tr>
<td>cₚₛ</td>
<td>Sound speed in sea water</td>
<td>m s⁻¹</td>
</tr>
<tr>
<td>ρₚ</td>
<td>Density of sea water</td>
<td>kg m⁻³</td>
</tr>
<tr>
<td>θ</td>
<td>Mean orientation angle</td>
<td>degrees</td>
</tr>
<tr>
<td>σ</td>
<td>Standard deviation of orientation angle</td>
<td>degrees</td>
</tr>
<tr>
<td>z</td>
<td>Depth</td>
<td>m</td>
</tr>
<tr>
<td>ρₜ</td>
<td>Tissue density</td>
<td>kg m⁻³</td>
</tr>
<tr>
<td>ξ</td>
<td>Dynamic viscosity</td>
<td>kg m⁻¹ s⁻¹</td>
</tr>
<tr>
<td>β</td>
<td>b-scaling parameter</td>
<td>-</td>
</tr>
<tr>
<td>s</td>
<td>Surface tension at gas cavity-tissue interface</td>
<td>N m⁻¹</td>
</tr>
</tbody>
</table>

Comments are referred to using letters.

* At 38 kHz, orientation does not significantly affect backscatter of small targets (Scoulding et al., 2015).

* In the absence of any measurements, we used the mean value from Scoulding et al. (2015).

* Surface tension of a gas bubble.

directivity function (Stanton, 1988) averaged over a normal distribution of orientation angles, N(0, σ), k is the wave number, Cₑ is a spheroidal elongation factor (Strasberg, 1953; Weston, 1967), γₐ is the specific heat ratio for gas, Pₑ is pressure at depth (Pₑ = z/10 + 1, where z is depth in meters), ξ is the dynamic viscosity and Ω is a set of damping constants (Table 1). All constants used in this study are given in Table 1.

Using the constants in Table 1, σₑₑ for a gas-bladdered fish or siphonophore, can be predicted when σₑₑ and z of the gas bladder are known. Swimb bladder volume of a fish, \( V_{swb} \), is related to σₑₑ by

\[
σ_{swb} = \left( \frac{3V_{swb}}{4\pi} \right)^{1/3}. \tag{8}
\]

The proportion of fish body volume, \( p_{swb} \), can be used to calculate

\[
V_{swb} = p_{swb} V_f. \tag{9}
\]

where \( V_f \) is the volume of the fish, given by

\[
V_f = \frac{4\pi}{3} \left( \frac{1}{2} \right)^{3/2}. \tag{10}
\]

Here \( \alpha \) is the fish aspect ratio

\[
\alpha = \frac{l_f}{w_f}. \tag{11}
\]

where fish shape has been approximated by a prolate spheroid and \( l_f \) (mm) and \( w_f \) (mm) are the length and width of the fish, respectively. Therefore, for a given \( \ell_f, \alpha \) and \( p_{swb} \) value, \( σ_{swb} \) can be estimated using (8–10), converted to \( a \) and \( b \) values, using (6 and 7), for a given b-scaling factor (\( β \), Table 1), and used to predict

\[
σ_{hs}(a, b, z, \xi) \cong σ_{hs}(l_f, p_{swb}, \alpha, z, \xi), \tag{12}
\]

from (4). Note that in (12), the constants defined in Table 1 have been omitted for clarity.

Fish weight (\( W_f \) kg) can then be calculated by multiplying fish volume by density and is given by

\[
W_f = V_f ρ_f. \tag{13}
\]

and is therefore a function of length and aspect ratio.

**Mesopelagic echoes**

The gas bladders of fish and siphonophores produce backscatter that contributes to 95% or more of the organisms’ target strength (TS = 10 log₁₀[σₑₑ], dB re 1 m², Maclennan et al., 2002) when sonified at 38 kHz, the frequency used in this study. This proportion may be substantially >95% at certain specific depth-size combinations when resonant backscattering is provoked (Davison et al., 2015) increasing the organisms’ TS by a factor of 10 or more (Figure 3, see also Kloster et al., 2016).

Other large mesopelagic organisms such as squid, which are likely to have similar global abundances to fish (Clarke, 1996), and medusae, have similar, low TSs as the bodies (flesh/bone) of fish (Figure 3) and, as with the bodies of fish, are likely to produce a relatively small proportion of total \( s_{swb} \) (fish bodies might contribute just 5% or less: Foote, 1980; Forland et al., 2014).

Smaller organisms such as copepods, although much more numerically abundant than fish, have TS values that are up to c. 9 orders of magnitude below that of gas-filled structures (Figure 3) so even huge densities of these organisms will not contribute significantly to the total backscatter. For example, even a preposterously high mean global copepod density of 1 million individuals per m² and a size distribution of \( N(μ = 2 \text{ mm}, σ = 0.5 \text{ mm}) \) would equate to a contribution of <1% of the predicted global mesopelagic \( s_{swb} \).
In summary, we assume that backscatter from gas bladders of fish and siphonophores (gas-bearing organisms) produces close to 100% of mesopelagic $s_4$ (Lavery et al., 2010; Irigoien et al., 2014; Davison et al., 2015). This agrees with measurements from a lowered probe that attribute 95% of scatter to gas bladders, many in resonance (Kloser et al., 2007).

From individuals to populations

The previously defined equations for $\sigma_{bs}$ are applicable only to individuals. To estimate global mesopelagic fish biomass, mean fish population $\sigma_{bs}$ values are needed, which require fish-length distributions. We determined these as follows. We first defined a log-normal distribution:

$$X \sim \ln N (\mu = 0, \sigma_X^2),$$  

where $X$ is a random variable for which the mean $\mu = 0$ and the variance $\sigma^2 = \sigma_X^2$. This distribution describes the shape of the fish-length distribution and can be varied by changing a single parameter, $\sigma_X^2$.

A number sequence was used to define $N$ equal-width fish length–frequency-distribution classes spanning the minimum and maximum fish-length values $l_{\text{min}}$ and $l_{\text{max}}$:

$$L = \text{range}(a = l_{\text{min}}, b = l_{\text{max}}, c = N),$$  

where range($a$, $b$, $c$) is a function, producing a sequence of numbers starting from $a$ and ending with $b$, with total length $c$. Similarly, for a given $\sigma_X^2$, the log-normal distribution range was defined:

$$L_d = \text{range}(ppf_X(0.001), ppf_X(0.999), N),$$  

where $ppf_X$ is the percent point function of $X$, and $L_d$ and $L$ are equal in length.

Backscattering cross-section, $\sigma_{bs}$ values were calculated for each length class and by integrating over the probability density function (pdf) of distribution $X$, using the trapezium rule, the population mean $\sigma_{bs}$ was estimated

$$\sigma_{bs} = \sum_{i=1}^{N-1} \left( \frac{\sigma_{bs_i} + \sigma_{bs_{i+1}}}{2} \right) \left( \frac{p_X(X_i) + p_X(X_{i+1})}{2} \right) (X_{i+1} - X_i) \phi_i,$$  

where $p_X$ is the pdf of $X$ and $\sigma_{bs_i}$ and $\phi_i$ are the $\sigma_{bs}$ value and statistical weight of the ith length class, respectively. The length class weight, $\phi_i$, is included to enable the relative contribution of each length class (i.e. proportion of class with gas bladders) to $\sigma_{bs}$ to be varied. Similarly, mean population weight is given by

$$W_f = \sum_{i=1}^{N-1} \left( \frac{W_{l_i} + W_{l_{i+1}}}{2} \right) \left( \frac{p_X(X_i) + p_X(X_{i+1})}{2} \right) (X_{i+1} - X_i).$$  

Here, the statistical weighting is absent because all fish will contribute to the mean population weight, regardless of whether they possess a gas bladder or not.

Mesopelagic fish biomass model

The backscatter from fish and siphonophores was assumed to produce the majority of mesopelagic $s_4$—a reasonable assumption given Figure 3. Therefore, simplified total area-backscattering

Figure 3. Dominant mesopelagic scatterers and resonance (a) A resonance model (Love, 1978) was used to predict resonant frequency of gas-filled prolate spheroids (ps—approximate shape of inflated fish swimbladders and siphonophore pneumatophores) over a range of sizes and depths; (b) TS values predicted using the resonance model for a prolate spheroid over a range of depths, where size (equivalent spherical radius) was selected to produce resonant backscattering at 38 kHz. Damping ($\zeta$) for prolate spheroid was set to 0, except for the 0.85 mm ps at 1000 m (dashed line) where $\zeta = 20$ (Love, 1978). A DWBA model (Chu et al., 1993) was used to predict frequency response of a fish body (width = 1.63 cm, density contrast $g = 1.023$, sound-speed contrast $h = 1.032$), squid (width = 1.2 cm, $g = 1.043$, $h = 1.053$), medusae ($g = 1.099$, $h = 1.0004$), copepod ($g = 1.058$, $h = 1.02$) and euphausiid ($g = 1.016$, $h = 1.019$). Sizes (lengths) are given in the plot. Sound-speed and density contrast values taken from Lavery et al. (2007).
coefficient \( s^*_a \) is the sum of the contributions of backscattering from siphonophores and fish:

\[
s^*_a = (p_f + p_{siph}) s,
\]

where \( p_f \) and \( p_{siph} \) are the proportion of \( s \) produced by fish and siphonophores, respectively.

Substituting (17 and 18) into (2), mesopelagic fish biomass, for a global population, is estimated using

\[
B_t = A \frac{\sum_i \left( \frac{s_{ih}}{\sigma^2_{bsf}(s_{ih}, \alpha, \sigma_{swb}, z, \zeta)} \right) W_i(\sigma^2_i, \alpha)}{\sigma^2_{bsf}},
\]

where \( s_{ih} \) is the amount of \( s \) produced by fish (\( p_{siph} \)).

**Model scenarios**

All myctophids (a very common and abundant mesopelagic fish) are thought to develop swimbladders during development (Bone et al., 1995; Moser, 1996) and some species of mesopelagic fish are known to keep their swimbladders throughout their lifecycles (e.g., marine hatchetfish). Myctophids caught in the Tasman sea region were found mostly to have gas bladders (Flynn and Pogonoski, 2012) but mesopelagic fish in general have often been reported to have varied swimbladder states, including absent, uninflated, and inflated (Butler and Pearcy, 1972; Neighbors and Nafpaktitis, 1982; Bardarson, 2013), often reported to be linked to ontogeny, where juveniles or young adults possess uninflated or absent swimballders (Yasuma et al., 2010) and late-stage adults have reduced (fat invested) swimballders (Butler and Pearcy, 1972; Neighbors and Nafpaktitis, 1982).

To examine the impact of the observed variability in swimbladder state on acoustically inferred biomass of a global mesopelagic fish population, three scenarios were investigated. Scenario 1 (S1), had equally weighted length classes (\( \phi = 1 \), see Equation 17), i.e., all fish had gas bladders. In scenario 2 (S2), \( \phi \) followed a cosine function (i.e., the smallest length classes always had gas bladders), given by

\[
\phi_i = \begin{cases} 
\phi_{\text{min}} + \cos\left(L_i - L_{\text{min}}\right), & L_i < L_{97.5} \\
\phi_{\text{min}}, & L_i \geq L_{97.5},
\end{cases}
\]

where \( i \) is the length class index, \( \phi_{\text{min}} \) is a constant ranging between 0 and 1 and denotes the minimum proportion of fish per length class with gas bladders (i.e., the proportion of fish that do not lose their gas bladders with age) and \( L_{97.5} \) is the length at the 97.5th percentile of the cumulative distribution function (Figure 4a); the 97.5th percentile was chosen to avoid fitting the cosine curve to extensive tails in the log-normal distributions. In effect, the rate of decay of the curve was controlled by the value of \( \phi_{\text{min}} \). For scenario 3 (S3), \( \phi \) was scaled to a sine curve, similar to the shape observed by Yasuma et al. (2010) for Myctophum asperum, over the population length range:

\[
\phi_i = \sin\left(L_i - L_{\text{min}}\left(90/(L_{\text{cont}} - L_{\text{min}})\right)\right),
\]

where the maximum value of the sine function angle was set to 180 degrees and \( L_{\text{cont}} \) is the length at the centre of the pdf where the cumulative distribution function equalled 0.5 (Figure 4b). This ensured that a large proportion of small (young) and large (old) fish were without gas bladders and that the proportion with gas bladders increased towards the centre of the distribution.

**Model input parameters**

To predict mesopelagic fish biomass (\( B_t \), 20) for scenarios 1–3, uniform distributions were assumed for each model variable (\( s_{ih}, \sigma^2_{bsf}, \alpha, \sigma_{swb}, z, \zeta \), Table 2). Scenario 2 also included \( \phi_{\text{min}} \), the minimum proportion of gas-bladdered fish per length class, which was also assumed to have a uniform distribution, with minimum and maximum values of 0 and 1, respectively (Figure 4a). The parameter values have the potential to be widely variable but at present we do not have enough knowledge to predict accurately their global distributions. Here, we use uniform distributions to ensure that we capture the full range of variability that they could potentially contribute to global mesopelagic fish biomass. These parameters and their corresponding distribution ranges were chosen based on the following reasoning.
There are few reported open-ocean observations of siphonophore density or pneumatophore size distributions. Pneumatophores have been reported to have mean lengths ranging between 0.15 mm (Lavery et al., 2007) and 3.27 mm (Barham, 1963), and densities from <1 to >1000 individuals m⁻² (Mackie et al., 1988). Considering the lack of information, p_siph might reasonably be considered to vary from place to place anywhere between 0 and 1, i.e. siphonophores potentially could produce almost all or none of the total mesopelagic xₘ. Mesopelagic fish x_f, x_p, x_s, was drawn from a uniform distribution, where the minimum value was set to 0 (for the case where p_siph = 1, Equation 19) and maximum value of 2.38 × 10⁻⁵ m² m⁻³, the upper bound (mean plus RMSE) taken from Proud et al. (2017).

The variance of the log-normal distributions, σₓ², was varied uniformly between 0.3 and 1. The distribution ranges were then matched with the fish population length range (15), where L_min and L_max were set to 8 mm (approximately the size of a newly developed juvenile myctophid; Moser, 1996) and 315 mm (maximum reported length of any species in the family Myctophidae, www.fishbase.org), respectively, to yield length distributions (Figure 4). As σₓ² was increased from 0.3 to 1, the length distribution shifts from a gaussian-like distribution (μ = c. 88 mm, equal to the median asymptotic length of 219 species of myctophid from www.fishbase.org) to a population dominated by smaller (more likely to produce resonant backscatter) fish, as commonly observed (e.g. Davison et al., 2015). Although L_max was set to 315 mm, the effective maximum length of the fish population was closer to 212 mm (97.5th percentile of broadest log-normal distribution, see Figure 4), which is similar to the 97.5 percentile of the asymptotic lengths of all documented myctophid species (c. 211 mm, www.fishbase.org). For the length distributions used in this study (Figure 4), the majority of fish were smaller than 88 mm, which is consistent with the sizes of common taxa of mesopelagic fish (e.g. Gonostomatidae, Sternoptychidae, Myctophidae, and Phosichthyidae) known to have gas bladders (Marshall, 1971; Bone et al., 1995; Flynn and Pogonoski, 2012).

The aspect ratio, a, a representation of variability in species morphology within the population, was varied uniformly between 4 and 12 (Flynn and Pogonoski, 2012). Changes in a impact both fish mean weight and swimbladder volume (9–13).

During diel vertical migration (DVM), the gas bladders of fish and siphonophores undergo compression on descent and expansion on ascent, following Boyle’s Law. Some species inflate their gas bladders and follow a “constant buoyancy strategy,” whilst others do not, and swim to maintain depth (Denton, 1961; Hersey et al., 1962; Kalish et al., 1986; Thompson and Love, 1996; Love et al., 2003, 2004; Scoulding et al., 2015); this behaviour is likely to vary between and within species, and ontogenetically. Our uncertainty around gas bladder function during and between bouts of DVM stems from the difficulty in making measurements of gas bladder volume at the surface. Bladders of fish brought to the surface from depth may be excessively distended or ruptured following rapid decompression and the measured volumes may not be good indicators of actual volumes in situ at depth. Because of this uncertainty, gas bladder volume as a proportion of body size, p_swb was varied between 0.0001 and 0.0263, equivalent to 0.01 and 2.63% of body volume (Yasuma et al., 2010). The maximum value of p_swb is likely to be limited by neutral buoyancy (body density), which does vary with length for many species (Butler and Pearcy, 1972; Neighbors and Nafpaktitis, 1982; Davison, 2011b). The range of values chosen, result in a broad range of V_swb values (9), which include proportions, both small, representative of gas bladders that do not re-inflate when compressed at depth, and larger proportions, which are consistent with gas bladder sizes required to maintain neutral buoyancy.

Fish (or DSL) depth, z, was varied uniformly in the model between 200 and 1000 m. This parameter affects the resonant frequency (5). For a given gas bladder size, the resonant frequency increases with depth; during DVM, a change in depth will cause a change in gas bladder volume, and this variability is captured by other model parameters (primarily by p_swb) not by depth.

Dynamic viscosity, ζ, (i.e. the viscosity of the gas bladder wall) was set to vary uniformly between 0 kg m⁻¹ s⁻¹, i.e. no damping, resulting in a sharp resonance peak (as might be expected from a gas bubble) up to a value of 20 kg m⁻¹ s⁻¹, which completely dampens the resonance peak (Figure 3). The latter value is as suggested by Love (1978) for midwater fish. There is some contention around this parameter and its validity in modelling the TS of resonant gas bladders (Baik, 2013). Here, we included a broad range of ζ values to ensure that we captured both undamped and damped resonant behaviour in our estimates of global mesopelagic fish biomass.

### Table 2. Assumed fish population input parameter statistical distributions.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Unit</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>s₁₂</td>
<td>Mesopelagic fish area-backscattering coefficient</td>
<td>m² m⁻²</td>
<td>U(0, 2.38 × 10⁻⁵) (Proud et al., 2017)</td>
</tr>
<tr>
<td>σₓ²</td>
<td>Variance of length distribution</td>
<td>–</td>
<td>U(0.3, 1)</td>
</tr>
<tr>
<td>zₐ</td>
<td>Aspect ratio of fish body</td>
<td>–</td>
<td>U(4, 12)</td>
</tr>
<tr>
<td>p_swb</td>
<td>Swimbladder volume as a proportion of fish volume</td>
<td>m</td>
<td>U(0.0001, 0.0263) (Yasuma et al., 2010)</td>
</tr>
<tr>
<td>z</td>
<td>Depth, z</td>
<td>m</td>
<td>U(200, 1000)</td>
</tr>
<tr>
<td>ζ</td>
<td>Dynamic viscosity</td>
<td>kg m⁻¹ s⁻¹</td>
<td>U(6, 20) (Love, 1978)</td>
</tr>
<tr>
<td>qₘₚₗₜₐₖ</td>
<td>Minimum proportion of gas-bladdered fish per length class used in scenario 2</td>
<td>–</td>
<td>U(6, 1)</td>
</tr>
</tbody>
</table>

Distribution of each parameter is given (U, uniform distribution).
Sensitivity of input parameters

A global sensitivity analysis was conducted using a variance based sensitivity metric (Saltelli et al., 2010) to investigate how the different input parameters of the biomass model affected the total biomass. The total effect index is a sensitivity metric that captures both the first order effect as well as higher order effects (interactions). The total effect index for parameter $X_i$ is given as

$$S_{Xi} = \frac{E_{Xi}(VS_{Xi}(B_i|X_{-i}))}{V(B_i)},$$

where $V_{Xi}(B_i|X_{-i})$ is the variance of the biomass estimate when changing the input parameter, $X_i$, $E_{Xi}$ is the mean of $V_{Xi}(B_i|X_{-i})$ and $V(B_i)$ is the total variance of the model. The inner variance estimator captures the variance in the biomass while varying $X_i$ and the outer mean operator takes the mean of these variances.

We used simulations to estimate the sensitivity indices. The total effect index

$$S_{Xi} = \frac{\frac{1}{2N} \sum_{j=1}^{N} \left( B_i(C_j) - C(D) \right)^2}{V(B_i)}$$

is estimated using the Jansen (1999) estimator (Saltelli et al., 2010, Table 2). Here, $N$ is the number of simulations, $C$ is a set of $N$ sets of parameters drawn from a Sobol sequence (rows are realizations $j$ and columns are the parameter $i$), $C(D)$ is identical to $C$ except that parameter $i$ is replaced from a similar but independent resampling set $D$. $S_{Xi}$ was calculated for 100 model runs, where for each run, $N$ was set to 5000.

Results

A fish biomass model was constructed and parametrized by seven input factors ($\delta_s^0$, $\sigma_s$, $\alpha$, $p_{swb}$, $z$, $\phi_{min}$, the latter of which was used only in scenario 2, see Table 2 for definitions) and run for three different scenarios: S1, which assumed the fish population was comprised solely of fish with gas bladders; S2 where all fish had gas bladders as juveniles, and a minimum proportion of fish kept their gas bladders throughout their life, whilst a growing proportion (following a cosine curve) lost their gas bladder with increasing length, and S3, a population with a large proportion of small and large fish without gas bladders. Five thousand biomass estimates were generated for each model run to capture the range of possible variability and to illustrate uncertainty (Figure 5).

Fish biomass uncertainty

Model results for S1–S3 were summarized using box plots (Figure 5). Median values of $TS$ decreased from $-53.8$ dB re 1 m$^2$ (lower quartile, $Q_1 = -55.6$; upper quartile, $Q_3 = -52.4$) to $-56.8$ dB re 1 m$^2$ ($Q_1 = -59.1$; $Q_3 = -55$) and median biomass increased from 3.833 Gt ($Q_1 = 1.812$; $Q_3 = 7.374$) to 8.292 Gt ($Q_1 = 3.670$; $Q_3 = 15.962$) from S1 to S3. Since the proportion of gas-bladdered fish per length class has no impact on fish weight, it was constant for all three scenarios and had a median value of 4.51 grams ($Q_1 = 2.25$; $Q_3 = 8.64$).

Maximum fish biomass and contributions of fish and siphonophores to global mesopelagic backscatter

Maximum mesopelagic fish biomass was estimated for each scenario. The minimum lower (25%) and maximum upper (75%)
Table 3. Median mesopelagic fish biomass predictions (Gt) by siphonophore contribution for each scenario.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>0</th>
<th>10</th>
<th>20</th>
<th>30</th>
<th>40</th>
<th>50</th>
<th>60</th>
<th>70</th>
<th>80</th>
<th>90</th>
<th>99</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>7.082</td>
<td>6.373</td>
<td>5.665</td>
<td>4.957</td>
<td>4.249</td>
<td>3.541⁺</td>
<td>2.832⁺</td>
<td>2.124⁺</td>
<td>1.416⁺</td>
<td>0.708⁺</td>
<td>0.071⁺</td>
</tr>
<tr>
<td>2</td>
<td>8.588</td>
<td>7.729</td>
<td>6.870</td>
<td>6.012</td>
<td>5.153</td>
<td>4.294⁺</td>
<td>3.435⁺</td>
<td>2.576⁺</td>
<td>1.788⁺</td>
<td>0.859⁺</td>
<td>0.086⁺</td>
</tr>
</tbody>
</table>

⁺Value closest to a food-web model estimate of mesopelagic fish biomass (2.4 Gt, Anderson et al., 2018).
⁺⁺Value closest to a food-web model estimate of mesopelagic fish biomass calculated for a trophic efficiency of 10% per trophic level (3.363 Gt, see Figure 6).
⁺⁺⁺Value closest to a food-web model estimate of mesopelagic fish biomass (2.4 Gt, Anderson et al., 2018).

Siphonophore contribution (%)

- For any given siphonophore density and gas bladder size distribution, global fish biomass values can be predicted for each gas bladder scenario using Figure 6, e.g. for a global population of siphonophores with normally distributed gas bladder lengths with a mean < 0.6 mm (e.g. as in Lavery et al., 2007), equivalent to a a₉₀ of c. 0.15 mm (6 and 8), fish biomass would make up close to 100% of mesopelagic sₐ for any given mean global density of siphonophores (<1000 individuals m⁻²). Conversely, for a mean gas bladder a₉₀ larger than 1 mm (e.g. Barham, 1963; Pickwell, 1966), siphonophores are dominant, contributing almost 100% of mesopelagic sₐ for a given mean open-ocean siphonophore density, larger than c. 6.5 individuals per m³ (e.g. Robison et al., 1998).

At 10% TE per trophic level, mesopelagic fish biomass is c. 3.363 Gt (Figure 6)—a value which falls between a fish contribution of 40 and 50% under S1, between 30 and 40% for S2 and between 20 and 30% for S3 calculated from model median fish biomass values (Table 3). Non-acoustic estimates of global mesopelagic fish biomass values between 1.812 (lower quartile of S1) and 15.962 Gt (upper quartile of S3). The median biomass value of S1, 3.833 Gt, is our equivalent of a previous median acoustic biomass estimate of between 14.3 and 19.5 Gt (Irigoin et al., 2014, extrapolated from those authors’ 40° N geographical range, to “our” 70° S to 70° N range). Our lower values are a consequence of acknowledging that a proportion of the total acoustic backscatter is resonant (high intensity echoes from low biomass targets), that siphonophores contribute to the total backscatter, and the uncertainty in population characteristics (i.e. species’ morphology and length distribution). For S3, where the proportion of gas-bladdered fish is reduced for small and larger fish, our prediction of median biomass of 8.292 Gt differs from Irigoin et al. (2014) by only a factor of two. Due to escapement and avoidance, the global biomass estimate by trawling of 1 Gt (Gjøsaeter and Kawaguchi, 1980) could be out by factor of seven or more (Koslow et al., 1997; Kloser et al., 2009; Yasuma and Yamamura, 2010; Davison, 2011a), which allows a prediction of c. 7 Gt or more: that is very close to the median value of S3. Conversely, a recent simple food-web model predicted mesopelagic fish biomass to be just 2.4 Gt (Anderson et al., 2018), which is within the biomass ranges of S1 and S2. Considering that S2 is probably the more likely of our scenarios (Butler and Peary, 1972; Neighbors and Naefpaktitis, 1982; Davison et al., 2015), the uncertainty in our acoustic derived estimate could be reduced to between 2.091 and 8.903 Gt (lower quartile to upper quartile). This range also overlaps with the range derived using a macroecological model, i.e. a median biomass of 1.4 Gt for all consumers, with 95th percentile of 8.1 Gt (Jennings and Collingridge, 2015).

Sensitivity analysis

The total effect index S₁₃ was calculated for input parameters used in the maximum fish biomass model run for each scenario (Figure 7). The area-backscattering coefficient for mesopelagic fish, s_f, was set to the global mean value, 1.94 × 10⁻⁵ m² m⁻² (Proud et al., 2017). This constraint was applied because the model would be very sensitive to a distribution that varies the total s_f value between 0 and the maximum value, 2.38 × 10⁻⁵ m² m⁻²; including s_f as a distribution rather than a constant in the sensitivity analysis leads to unclear results, as S₁₃ for s_f tends to 1 and the values for the other parameters are very small. For scenarios S1 and S2, the results show that swimbladder volume (as a proportion of body size), p_swbl, is the most important parameter, followed by the aspect ratio, α, and length distribution parameter, σ_sw. Fish depth (z) and viscosity (ζ), affecting the resonant frequency (5) and damping of the resonant peak (Equation 4 and Figure 3), respectively, contribute relatively little to the overall model uncertainty. At an individual level, these parameters are very important (Scoulding et al., 2015) but this importance reduces substantially when considering the full range of the parameter space, which includes, for example, variability in population structure (e.g. shape of length-frequency distribution). For S3, p_swbl and σ_sw are the most important parameters, i.e. α has a reduced impact on model uncertainty.

Discussion

By exploration of likely echo energy levels arising from mesopelagic organisms, characterized using acoustic scattering models, it became apparent that siphonophores and fish were likely to be the dominant scatterers in the mesopelagic zone during the daytime (Figure 3). Our model results predict a range of global mesopelagic fish biomass values between 1.812 (lower quartile of S1) and 15.962 Gt (upper quartile of S3). The median biomass value of S1, 3.833 Gt, is our equivalent of a previous median acoustic biomass estimate of between 14.3 and 19.5 Gt (Irigoin et al., 2014, extrapolated from those authors’ 40° N geographical range, to “our” 70° S to 70° N range). Our lower values are a consequence of acknowledging that a proportion of the total acoustic backscatter is resonant (high intensity echoes from low biomass targets), that siphonophores contribute to the total backscatter, and the uncertainty in population characteristics (i.e. species’ morphology and length distribution). For S3, where the proportion of gas-bladdered fish is reduced for small and larger fish, our prediction of median biomass of 8.292 Gt differs from Irigoin et al. (2014) by only a factor of two. Due to escapement and avoidance, the global biomass estimate by trawling of 1 Gt (Gjøsaeter and Kawaguchi, 1980) could be out by factor of seven or more (Koslow et al., 1997; Kloser et al., 2009; Yasuma and Yamamura, 2010; Davison, 2011a), which allows a prediction of c. 7 Gt or more: that is very close to the median value of S3. Conversely, a recent simple food-web model predicted mesopelagic fish biomass to be just 2.4 Gt (Anderson et al., 2018), which is within the biomass ranges of S1 and S2. Considering that S2 is probably the more likely of our scenarios (Butler and Peary, 1972; Neighbors and Naefpaktitis, 1982; Davison et al., 2015), the uncertainty in our acoustic derived estimate could be reduced to between 2.091 and 8.903 Gt (lower quartile to upper quartile). This range also overlaps with the range derived using a macroecological model, i.e. a median biomass of 1.4 Gt for all consumers, with 95th percentile of 8.1 Gt (Jennings and Collingridge, 2015).
Model sensitivity

Given that the relative proportions of fish and siphonophore backscatter are known, swimbladder volume (as a proportion of body size), \( p_{\text{swb}} \), was the most sensitive parameter in the mesopelagic fish biomass model for all three scenarios (Figure 7). This is not surprising, since the gas bladders of mesopelagic fish are predominantly smaller than the wavelength of sound at 38 kHz (c. 4 cm) and therefore volume, not shape or orientation, drives TS (i.e. Rayleigh scattering, see Figure 1). Other parameters in the model, such as the aspect ratio (\( \alpha \)) and distribution variance (\( \sigma^2 \)) were also important (Figure 7). To reduce the uncertainty caused by \( p_{\text{swb}} \) in the model, we must first resolve the issue of compression during DVM, i.e. do fish inflate their bladders at depth (constant buoyancy strategy), to remain neutrally buoyant, or not? Evidence in the literature is mixed (Denton, 1961; Hersey et al., 1962; Kalish et al., 1986; Thompson and Love, 1996; Love et al., 2003, 2004; Scoulding et al., 2015). The problem can only be solved by making more observations of the mesopelagic community at depth, using for example, paired optical/acoustic systems (e.g. Marouchos et al., 2016), which will improve our knowledge and help narrow the distributions of the other model parameters.
Figure 7. The total effect index $S_{T1}$ of the mesopelagic fish biomass model input parameters for scenarios S1–S3: distribution variance ($\sigma^2_x$), swimbladder volume as a proportion of body volume ($p_{swb}$), depth ($z$), aspect ratio ($\alpha$), dynamic viscosity of gas bladder wall ($\xi$), and minimum proportion of gas-bladdered fish ($\phi_{min}$). In this model run, mesopelagic fish $sippets$ is constant, set to the global mean value of $1.94 \times 10^{-2}$ m$^2$ m$^{-2}$.

Model caveats

The mesopelagic fish biomass model (20) derived here assumes that siphonophores are the only other significant contributor to mesopelagic $sippets$. In most cases, this is probably a valid assumption (Barham, 1963; Lavery et al., 2007; Kloster et al., 2016) but, where fish densities are low, other scatterers such as squid and jellyfish will become more prominent (Clarke, 1996; Pauly et al., 2009; Haraldsson et al., 2012). In some instances, e.g. the polar regions, zooplankton populations may dominate (Murphy et al., 2007).

At a global scale, the assumption is reasonable but to follow a similar approach as made here at regional or smaller scales, the contribution of other scatterers will need to be considered. Fortunately, our approach can readily incorporate contributions from other scatterers, indeed we started with multiple scatterers (Figure 3) and eliminated groups that contributed little to total scattering. We recommend this approach is adopted at regional scales and that results arising from such analyses are not extrapolated to other regions that likely contain different mesopelagic communities.

We made a number of assumptions when selecting model parameters and distributions (Tables 1 and 2). We depended heavily on the literature which, in most cases, describes observations made only over small spatial ranges (i.e. local studies; e.g. Neighbors and Nafpaktitis, 1982; Yasuma et al., 2010). This reflects the paucity of data concerning mesopelagic fish and siphonophores, and highlights the pressing requirement for increased sampling at depth. The validity of our analysis results is also dependent upon our present level of knowledge, which is relatively poor (St John et al., 2016). For example, the density of mesopelagic fish ($\rho_f$) was assumed to be $1050$ kg m$^{-3}$, a reasonable median value taken from Love (1978). The value of $\rho_f$ for mesopelagic fish varies between $1030$ and $1080$ kg m$^{-3}$ (Cepen, 1967; Butler and Pearcy, 1972; Davison, 2011b; Davison et al., 2015). Inputting this range of $\rho_f$ values into our biomass model did not substantially change estimates of fish biomass (±2.5%). However, fish with higher densities are more likely to have inflated swimbladders, and that possible interaction is not considered in our analysis. As our understanding develops and we obtain more observational data, we may need to include additional parameters into our model framework.

The largest source of uncertainty in the mesopelagic fish biomass model is the unknown contribution of siphonophore to mesopelagic $sippets$. It is likely that fish produce most of the backscatter at 38 kHz but the proportion remains largely unknown.

Siphonophores

A range of siphonophore densities and gas bladder sizes have been observed, from very small siphonophores in the Gulf of Maine (0.15 mm mean gas bladder length, Lavery et al., 2007) and low-density populations <1 individuals m$^{-2}$ (Mackie et al., 1988), to large Nanomia biijuga in the San Diego Trough (3.27 mm length, Barham, 1963) and high densities in the east Indian Ocean (>1000 individuals m$^{-2}$, Musayeva, 1976). Siphonophores are often less abundant in open ocean than in neritic regions, for example Kloster et al. (2016) observed, using a lowered probe, just 2.5 individuals m$^{-2}$ in the open Southern Ocean (Kloster et al., 2016). The total size of siphonophores varies from a few cm to several m but there is presently no understanding of how this size relates to gas bladder size at depth: variability in siphonophore size by cryptic species, population genetic variation, seasonality, or ecological conditions are also unknown (C. Dunn, pers. comm.). Against this background of uncertainty, to attribute legitimately large proportions of global mesopelagic $sippets$ to fish biomass, one of the following must be true: (i) in the open ocean, siphonophore densities are relatively low in the mesopelagic zone; (ii) after descent to depth, during DVM, a lot of gas-bearing siphonophores are not able to re-inflate their gas bladders at the now-high ambient pressure, or (iii) the majority of siphonophore gas bladders do not produce resonant backscatter at 38 kHz in the 200–1000 m depth range (e.g. 0.4 mm $> \phi_{swb} >$ 1.0 mm, Kloster et al., 2016).

Presently, we are limited to small-scale visual estimates of siphonophores, from SCUBA to ROVs and submersibles (e.g. Rogers, 1978; Robison et al., 1998); the Monterey Bay Aquarium Research Institute does have an extensive database called the Video Annotation and Reference System (VARS), which contains records of siphonophores observed in ROV dives, since before 2000 (Schlining and Stout, 2006). To reduce uncertainty in estimates of fish biomass, more data on global variability in siphonophore density and size distribution are needed.

Swimbladders

The swimbladder state (present/absent/reduced/inflated) and volume (with respect to body size) of mesopelagic fish is highly variable between species (Butler and Pearcy, 1972; Neighbors and Nafpaktitis, 1982; Yasuma et al., 2010) and within species (Scoulding et al., 2015). Swimbladder function during DVM is also not well understood (Denton, 1961; Hersey et al., 1962; Kalish et al., 1986; Thompson and Love, 1996; Love et al., 2003, 2004; Scoulding et al., 2015). It is likely that some species adopt the “constant buoyancy strategy,” as observed by Barham (1971) from a submersible, where fish reside in a torpid state and remain neutrally buoyant during the daytime. The alternative is the “tread-water strategy,” whereby fish maintain depth by swimming...
From siphonophores to deep scattering layers

(Love et al., 2004). The trade-off between the two strategies is the energetic cost of absorption and secretion of gas, which can be high (Bone et al., 1995) vs. the energetic cost of swimming to maintain depth. In addition, a fish in a torpid state, vs. a fish in constant movement, may be more difficult to detect visually, and hence, at lower risk of predation from deep-diving predators (e.g. King penguins and Elephant seals). Strategy may also change during the life cycle of mesopelagic fish, since density reduces with size (via lipid investment, e.g. Gee, 1983) and therefore, older, larger fish, are more likely to opt for the constant buoyancy strategy (Butler and Pearcy, 1972; Neighbors and Naapaktitis, 1982; Davison, 2011b). An additional complication is that “residential” DSLs have often been observed (Figure 2) presumably containing some species that do not migrate, and the proportion of species that migrate do so seasonally with different proportions and length classes (Koslow et al., 1997; Flynn and Kloster, 2012).

In the absence of any known environmental drivers of swimbladder volume and state in mesopelagic fish, our method is useful because it provides a mean view of a likely very complex system. To move forward and reduce uncertainty in estimates of mesopelagic fish biomass, a better understanding of variability at the individual level is required (e.g. TS variation with depth). If DVM behaviour, swimbladder state, and volume can be related to the environment, we will not only make more accurate estimates of mesopelagic fish biomass but also will gain a better understanding of how community-scale properties, such as vertical depth structure, emerge from the behaviour of individuals.

Wider implications for ecosystem models

The analysis framework developed here could be used to build an acoustic observation model (Handegard et al., 2013), to predict the expected acoustic “views” of simulated ecosystems, e.g. Atlantis, SEAPODYM, MIZER, and size-based ecosystem models (Lehodey et al., 2008, 2014; Fulton et al., 2011; Trebilco et al., 2013; Scott et al., 2014), and to compare those predictions with actual acoustic observations. This would serve to provide ecosystem models with a method to validate the mesopelagic component of their models. This is of particular importance for ecological/biogeochemical models that simulate the biological carbon pump and provide carbon fluxes for coupled climate models (Giering et al., 2014).

Moving forward

The predicted global mesopelagic $s_g$ used here was based on 38 kHz observations (Proud et al., 2017). A lot of data are available at a frequency of 38 kHz, but use of single frequency data alone does not enable frequency–response analyses that can identify scattering type (e.g. Kloster et al., 2002; Lavery et al., 2010). Data at 18 kHz, the only other commonly used frequency that has a high enough signal-to-noise ratio to provide useful observations from the entire mesopelagic zone, are often collected alongside 38 kHz data (www.imos.org.au). Using 18 and 38 kHz data together could enable resonance peaks to be identified, and the mean size of the target to be predicted. Performed at a global scale, this would at least provide some information concerning regional-scale size structure of gas-bearing organisms.

Increased in situ optical and acoustic sensing in the ocean will advance the understanding of the depth distribution and abundance of siphonophores. As an example, profiling probes are being proposed (Handegard et al., 2010) and developed (Kloster et al., 2016). The gelatinous community (including siphonophores) is woefully under sampled and the incorporation of cameras on profiling probes will greatly increase our understanding of their distribution and abundance. In the future, combining such probes with acoustic and optical sensors could be done on a global scale in an ARGO float style of approach (Handegard et al., 2010).

Concluding remarks

We used predicted global 38 kHz DSL backscattering intensity (from Proud et al., 2017) to estimate global mesopelagic fish biomass. Our range of possible estimates spanned 1.812–15.962 Gt (lower and upper quartile). This range of values lends credence to the idea that there may be a substantial biomass of fish in the mesopelagic zone. Such a biomass could play a substantial role in the biological carbon pump, and could potentially bolster future food security.

Uncertainty in mesopelagic fish biomass estimates could be reduced by (i) including more frequencies in the analysis to aid in determining size structure of resonant scatterers; (ii) development of an individual-based model to link DVM behaviour, weight/condition, swimbladder state, and volume to the environment, and (iii) obtaining more information on the size and depth distribution and density of siphonophores, both by collation of existing data and through the use of new technologies such as profiling acoustic optical systems (Marouchos et al., 2016).

Acknowledgements

This study has received support from the European H2020 International Cooperation project Mesopelagic Southern Ocean Prey and Predators (MESOPP, http://www.mesopp.eu/). The authors thank Ben Scoulding for providing code, Philip Pugh for helpful discussions concerning siphonophores, Gareth Lawson for help with jellyfish modelling, and Samuele Lo Piano and Sindre Vatnhol for assistance with the sensitivity analysis. We also thank the reviewers for helpful and informative comments.

Funding

Horizon 2020 Framework Programme, (Grant/Award Number: “692173”).

References


Neighbors, M. A., and Nafpaktitis, B. G. 1982. Lipid compositions,

Mackie, G. O., Pugh, P. R., and Purcell, J. E. 1988. Siphonophore


Marrouchos, A., Sherlock, M., Kloeser, R. J., Ryan, T., and Cordell, J. 2016. A profiling acoustic and optical system (pAOS) for pelagic studies; Prototype development and testing. In OCEANS 2016 - Shanghai. IEEE. pp. 1–6.


Handling editor: David Demer