Evaluation of sound extinction and echo interference in densely aggregated zooplankton

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KEYWORDS

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Abstract

The investigation of sound extinction and echo interference is important as regards the accurate assessment of the abundance of densely aggregated zooplankton. To study these effects, the analytical model describing sound backscattering by an aggregation of isotropic scatterers (Rytov *et al.* 1978, Sun & Gimenez 1992) has been extended to the case of densely aggregated elongated zooplankton. The evaluation of the effects in the case of a dense krill aggregation demonstrates that they can be significant and should be taken into account.

1. Introduction

The hydroacoustic measurement of fish and zooplankton abundance is based on the echo integration method (Medwin & Clay 1998). The question of the applicability of this method is very important, since it uses the hypothesis of proportionality of the energy backscattered by an aggregation to the scatterer number. The applicability of echo integration therefore depends on the validity of the linearity of the regression. It is known that zooplankton species such as krill form aggregations with densities of approximately 10^3-10^5 individuals per cubic metre (Green *et al.* 1988, Hewitt & Demer 1996). Where biological aggregations reach such a density, the linear relationship cannot be satisfied. In the case of large concentrations the interference of individual echoes, sound attenuation induced by scattering and absorption by zooplankton individuals – hence the shadowing effect, as well as multiple scattering among targets may upset the proportionality.

In the case of fish, theoretical models taking all three interfering effects into account have been derived (Foote 1978, 1983, 1990a, Stanton 1983, 1984, Sun & Gimenez 1992, 1994, Andreeva *et al.* 1994, Andreeva & Belousov 1996, Feuillade *et al.* 1996). A range of acoustic and biological parameters where effects are significant has been defined on the basis of these models. Furthermore, the theoretical analysis has been supplemented by experiments verifying the linearity of the relationship between echo energy and fish abundance (Rottingen 1976, Foote 1983).

The situation is different for sound backscattering by zooplankton populations. As no experimental verification has been carried out, modelling the disturbing effects in dense zooplankton aggregations takes on a fresh significance. Analytical and numerical analysis should be conducted to define the range of acoustic and zooplankton parameters for which the effects are important but a linear relationship not guaranteed. Therefore, a model describing sound scattering by densely aggregated zooplankton is required. It should cover echo interference, sound attenuation and multiple scattering among individuals. Further, it should use a recognised verified description of sound scattering by individual zooplankton animals. Most of the existing models describing sound scattering by zooplankton populations do not take the interference of individual echoes or multiple scattering into consideration (Pieper & Holiday 1984, Kristensen & Dalen 1986, Foote 1990a, Holiday & Pieper 1990, Andreeva et al. 1994, Andreeva & Belousov 1996, Medwin & Clay 1998). Only sound extinction has been considered (Andreeva et al. 1994, Chu & Ye 1999, Gorska 1999). The echo interference has also been analysed (Gorska 1996, 1997), but the model developed in those papers is based on an unverified model of sound scattering by an individual zooplankton target.

In the present paper a theoretical model describing sound scattering by a densely aggregated zooplankton is developed (Section 2), which accounts for two disturbing effects – for sound extinction caused by scattering and absorption by zooplankton individuals, and echo interference. The model employs a verified description of sound backscattering by krill individuals (the uniformly bent cylinder model) (Stanton 1989, Stanton *et al.* 1993, 1998). In Section 3 the conditions of the significance of echo interference and sound attenuation are formulated on the basis of the analytical solutions obtained in Section 2. The range of biological and acoustic parameters for which the considered effects are important is defined for various krill species (Section 3). The analysis is based on experimental data covering measured lengths and swimming angle distributions in zooplankton populations (Sameoto 1976, 1980, Sameoto *et al.* 1977, Kils 1979, 1982, Kristensen & Dalen 1986, Foote *et al.* 1990, Chu *et al.* 1993, Endo 1993, Loeb *et al.* 1993, Miyashita *et al.* 1996). The measured parameters characterising the acoustic properties of the biological tissue of krill are also taken into consideration (Greenlaw 1977, 1979, Kristensen & Dalen 1986, Kogeler *et al.* 1987, Foote *et al.* 1990, Foote 1990b, Chu *et al.* 1993, Medwin & Clay 1998).

2. Theoretical approach

Consider the backscattering of an echosounder pulse of length T and angular frequency $\omega(\omega = 2\pi/f)$ by the distribution of N immobile zooplankton targets (the scattering geometry is presented in Fig. 1). Let the echosounder be located at the origin of the co-ordinate system. In zooplankton populations elongated individuals differ in their length l_i , swimming angle θ_i (the tilt angle between the lengthwise axis of an elongated



Fig. 1. Scattering geometry. Scattering of an echosounder signal by a population of randomly distributed and randomly oriented elongated zooplankton animals. The grey area indicates the space occupied by the zooplankton. The vector $\vec{r_i}$ and the distance $\tilde{r_i}$ for the *i*-th scattering target, marked by a black dot, are illustrated

animal and the horizontal plane), and vector $\vec{r_i}$ describing the position of this target in space ($\vec{r_i} = (r_i, \Phi_i, \Theta_i)$). Here *i* denotes the individual number of the zooplankton scatterer. The scattering properties of zooplankton individuals are characterised by the sound speed and density contrasts of the biological tissue, *h* and *g* respectively, with h = c'/c and $g = \rho'/\rho$, where the dash ' refers to the properties within the scattering object, and ρ and *c* are the density and sound speed in the ambient water.

The scattered signal intensity I(t), averaged over an ensemble of aggregation realisations, is considered in the present paper. The different realisations vary in position, swimming angle and length distributions of the zooplankton targets. Taking into account the expression for the far-field intensity of a spherical wave (Medwin & Clay 1998) and summarising echoes from different scatterers, the following expression can be written for the intensity:

$$I(t) = I_{nc} + I_c,\tag{1}$$

$$I_{nc} = (\rho c)^{-1} \left\langle \sum_{i=1}^{N} p_1(t, \vec{r_i}, \theta_i, l_i) p_1^*(t, \vec{r_i}, \theta_i, l_i) \right\rangle,$$
(2)

$$I_{c} = (\rho c)^{-1} \left\langle \sum_{i, j=1; i \neq j}^{N} p_{1}(t, \vec{r_{i}}, \theta_{i}, l_{i}) p_{1}^{*}(t, \vec{r_{j}}, \theta_{j}, l_{j}) \right\rangle,$$
(3)

where t is the time, the symbol * denotes the complex conjugation of the function, and the brackets $\langle \rangle$ refer to the averaging. The function $p_1(t, \vec{r_i}, \theta_i, l_i)$ describes the pressure of the direct echosounder signal scattered by the *i*-th target. The sum corresponds to the superposition of the echoes from N individuals of the population. Here I_{nc} and I_c denote respectively the incoherent and coherent parts of the signal intensity in a single scattering approximation.

Further, the attenuation of the incident and scattered wave induced by scattering and absorption by the targets along the path of the wave propagation (shadowing effect) is taken into account. The attenuation is inserted heuristically in the expression for the pressure $p_1(t, \vec{r_i}, \theta_i, l_i)$ in the same way as it was done by Stanton (1983) and Sun & Gimenez (1992, 1994). The pressure can be expressed as

$$p_1(t, \vec{r_i}, \theta_i, l_i) = P_0(t - 2r_i/c) f(\vec{i}, -\vec{i}) \exp(2ikr_i - 2\int_{\tilde{r}(\tilde{r_i})}^{r_i} \beta(\vec{r}') d\vec{r}') D^2(\vec{r_i}) r_i^{-2}, (4)$$

where the function $P_0(t)$ describes the exciting pulse envelope, k denotes the wave number, $k = \omega/c$, and the function D defines the transmitter and receiver beam pattern (both patterns are the same). Here $f(\vec{i}, -\vec{i})$ is the backscattering amplitude of the target, where \vec{i} is the directional unit vector for the incident wave ($\vec{i} = \vec{r_i}/r_i$ for the *i*-th target). We recall that the backscattering amplitude depends on the individual geometrical form, the animal's swimming angle, the acoustic properties of the biological tissue and the sound frequency (Medwin & Clay 1998). The attenuation coefficient β is integrated over the direction 'echosounder – *i*-th scatterer' from the upper boundary of the aggregation to the *i*-th target. Here $\tilde{r_i}$ denotes the distance between the echosounder and the upper boundary of the aggregation in the direction specified (see Fig. 1). According to Morse & Ingard (1968), the coefficient β is given by

$$\beta(\vec{r}) = 0.5N \langle \sigma_e \rangle_{\theta,l} W_r(\vec{r}), \tag{5}$$

where σ_e represents the extinction cross-section of the individual zooplankton target. The brackets $\langle ... \rangle_{\theta,l}$ denote the averaging over an ensemble of aggregation realisations differing with respect to animal sizes and swimming angles:

$$\langle \sigma_e \rangle_{\theta,l} = \iint d\theta \, dl \, W_\theta(\theta) W_l(l) \sigma_e. \tag{6}$$

In this formula the respective functions $W_r(\vec{r}_i)$, $W_{\theta}(\theta_i)$, $W_l(l_i)$ represent the spatial, swimming angle, and length distributions which, following Stanton *et al.* (1993), are assumed to be independent. The probability density function $W(\vec{r}_i, \theta_i, l_i)$, which describes the probability that the *i*-th target is at position \vec{r}_i and has a swimming angle of θ_i and a length of l_i , can be expressed as

$$W(\vec{r_i}, \theta_i, l_i) = W_r(\vec{r_i}) W_\theta(\theta_i) W_l(l_i).$$
(7)

In accordance with Stanton et al. (1993), the independence of the probability density functions is assumed.

The extinction cross-section σ_e , including scattering and absorption by a zooplankton individual, can be calculated from the forward scattering theorem (optical theorem) (Ishimaru 1978) and can be given by

$$\sigma_e = (4\pi/k) \mathrm{Im} f(\vec{i}, \vec{i}), \tag{8}$$

where Im denotes the imaginary part of the forward scattering amplitude of the scatterer $f(\vec{i}, \vec{i})$.

To derive an analytical formula relating the terms I_{nc} and I_c to the main parameters, the approach developed by Rytov *et al.* (1978) is employed. Originally it was applied to describe electromagnetic wave scattering by clouds of objects. The approach is based on the statistical independence of scattering targets and on the independence of one-dimensional probability density functions of the target number. This approach has been already employed to describe sound scattering by biological aggregations of isotropic scattering targets and has been presented in detail by Sun & Gimenez (1992, 1994). Using the approach for describing sound scattering by an aggregation of elongated zooplankton, two important discrepancies should be taken into account. Firstly, in a zooplankton population, individuals differ not only in length but also in their swimming angles (Sameoto 1976, 1980, Sameoto et al. 1977, Kils 1979, 1982, Endo 1993, Miyashita et al. 1996). Moreover, the anisotropic character of scattering at a zooplankton individual (see, for example, Stanton et al. 1993) is also significant. These differences result in additional averaging over swimming angles in the derivation.

The application of this approach yields

$$I_{nc} = (\rho c)^{-1} N \Phi_1 \langle \sigma_{bs} \rangle_{\theta, l}, \tag{9}$$

$$I_c = (\rho c)^{-1} N (N-1) \Phi_2 |\langle f \rangle_{\theta,l}|^2,$$
(10)

where the functions Φ_1 and Φ_2 are dependent on the sounding signal geometry and spatial zooplankton distribution. The functions take into account the sound attenuation induced by the scattering and absorption by zooplankton individual. The functions have the following form:

$$\Phi_1 = \int_V |P_0(t - 2r/c)|^2 \exp(-4\int_{\tilde{r}(\vec{r})}^r \beta(\vec{r}') d\vec{r}') D^4(\vec{r}) W_r(\vec{r}) r^{-4} d\vec{r},$$
(11)

$$\Phi_2 = \left| \int\limits_V P_0(t - 2r/c) D^2(\vec{r}) W_r(\vec{r}) \exp(2ikr - 2\int\limits_{\vec{r}(\vec{r})}^r \beta(\vec{r}') d\vec{r}') r^{-2} d\vec{r} \right|^2, \quad (12)$$

where the coefficient β , defined in eq. (5), describes the sound attenuation due to sound scattering and absorption by an individual zooplankton animal. Generally, the integration volume V depends on the spatial dimensions of the zooplankton aggregation and of the sound pulse. However, in the next Section, the case when zooplankton populations are large and the sampling volume is within the domain occupied by zooplankton will be considered (see Fig. 1). For this case, V is defined by the sampling volume.

In eqs. (9), (10) the averaged backscattering amplitude $\langle f \rangle_{\theta,l}$ $(f(\theta_i, l_i) \equiv f(\vec{i}, -\vec{i}))$ and the averaged backscattering cross-section $\langle \sigma_{bs} \rangle_{\theta,l} (\sigma_{bs} = |f(\theta_i, l_i)|^2)$ are given by

$$\langle \sigma_{bs} \rangle_{\theta,l} = \iint_{l=0}^{l} d\theta \, dl \, W_{\theta}(\theta) \, W_{l}(l) \, |f(\theta, \, l)|^{2}, \tag{13}$$

$$\langle f \rangle_{\theta,l} = \iint d\theta \, dl \, W_{\theta}(\theta) \, W_l(l) \, f(\theta, \, l). \tag{14}$$

As was mentioned above, the approximation of uncorrelation among the targets is used to derive eqs. (9)-(12). It is important to analyse the applicability of this approximation. According to Sun & Gimenez (1994), the applicability condition is $n_f < 0.065$, where the fractional number of scatterers $n_f = V_1 n(l)$, V_1 denotes the volume of zooplankton individuals of length l, and n(l) stands for the zooplankton concentration. The analysis has been done for various krill species. The allometric expressions for various krill species are taken from Medwin & Clay (1998). Fig. 2 summarises the results. The curves corresponding to the condition $n_f = 0.065$ are plotted on a graph of concentration n versus length l. For each krill species (for each curve) the uncorrelation assumption is applicable in the domain below the respective curve. The horizontal line represents the highest level of krill concentration quoted in the literature (Green *et al.* 1988, Hewitt & Demer 1996). This analysis shows that the uncorrelation assumption among the individuals is satisfied for concentrations recorded *in situ* (the domain below the horizontal line in Fig. 2).



Fig. 2. The applicability of the uncorrelation assumption $(n_f < 0.065)$. The curves refer to the condition $n_f = 0.065$. The calculations have been done for the allometric expressions relating V_1 and l for various krill species from Table 9.4 in Medwin & Clay (1998). The uncorrelation assumption is applicable in the area below these curves. The horizontal line represents the highest level of krill concentration quoted in the literature (the *in situ* concentrations are in the area below the horizontal line)

The solutions obtained – eqs. (9)-(12) – together with eqs. (5), (6), (8), (13), (14) represent the relationships between the mean intensity of the backscattered signal and zooplankton characteristics. They enable the influence of space, length, swimming angle distributions and the scattering properties of the individual zooplankton targets on the intensity of the backscattered echosounder signal to be analysed. These equations are applicable to any species of zooplankton (fluid-like, gas-filled, elastic-shelled and so on).

3. The influence of sound extinction and echo interference on sound backscattering

3.1. Evaluation of sound extinction

To establish the criterion for neglecting the sound attenuation induced by sound scattering at a zooplankton individual, let us return to eq. (4) for the pressure of the signal scattered by the *i*-th target. Further, a uniform spatial distribution of zooplankton $W_r(\vec{r_i})$ is assumed. This distribution has been used in the models describing sound scattering by a biological population (Stanton 1983, Sun & Gimenez 1994). Taking into account eq. (5), eq. (4) can be presented as

$$p_1 = p_1(\beta = 0) \exp\{-\langle \sigma_e \rangle_{\theta, l} n(r_i - \tilde{r}(\vec{r_i}))\},\tag{15}$$

where $p_1(\beta = 0)$ describes the pressure in the case where the attenuation coefficient β equals 0, and *n* denotes zooplankton concentration, $\tilde{r}(\vec{r_i}) \equiv \tilde{r_i}$. The distances r_i and $\tilde{r}(\vec{r_i})$ are presented in Fig. 1. The equation shows that sound attenuation is more significant with respect to scatterers for which the distances $r_i - \tilde{r}(\vec{r_i})$ are larger.

On the basis of eq. (15) it can be assumed that for the *i*-th scatterer the attenuation can be ignored if the condition $10 \log [p_1/p_1(\beta = 0)] < -3dB$ is satisfied. If the condition is true for scatterers with the largest distances $r_i - \tilde{r}(\vec{r_i})$, it is also applicable to all scatterers, and the expression

$$10\log\exp\{-\langle\sigma_e\rangle_{\theta,l} nL_z\} < -3dB,\tag{16}$$

can be introduced as the criterion for neglecting the extinction effect for the whole zooplankton population. Here L_z denotes the largest characteristic distance covered by sound within a zooplankton population (L_z is the maximum of the distances $r_i - \tilde{r}(\vec{r_i})$). It should be noted that if the condition is not satisfied, extinction is significant at least for scatterers for which the distances travelled by the sound are large. In such cases extinction should be taken into consideration.

We now analyse the applicability of condition eq. (16) to the case of scattering by krill. For this, an analytical expression for $\langle \sigma_e \rangle_{\theta,l}$ is required.



Fig. 3. Scattering by an elongated individual zooplankton animal. Uniformly bent cylinder of constant radius of axis curvature (ρ_c), constant cross-sectional radius (a). The figure has been adapted from Stanton (1989)

Gorska (1999) obtained the analytical formula for σ_e on the basis of the forward scattering theorem (Ishimaru 1978) and the DCM expression for the scattering amplitude of an individual target for the general bistatic sonar case (eq. (8) in Stanton 1989). In this article the model of a uniformly bent cylinder of constant axis curvature radius (ρ_c), constant cross-sectional radius (a) and constant composition has been employed to describe sound scattering by an elongated zooplankton target (see Fig. 3). The model represents the recognised description of sound backscattering by a krill individual (Stanton 1989, Stanton *et al.* 1993, 1998). According to Gorska (1999), the forward scattering amplitude $f(\vec{i}, \vec{i})$ can be written as

$$f(\vec{i},\,\vec{i}\,) = -\frac{i}{\pi} \frac{l}{\gamma_{\max}} \int_{0}^{\gamma_{\max}} d\gamma \sum_{m=0}^{\infty} b_m,\tag{17}$$

where l is the total arc length of the bent cylinder. The value $\gamma_{\text{max}} = l/2\rho_c$ and the integration variable γ are given in Fig. 3. The coefficients b_m can be written in the following form:

$$b_m = -\frac{\varepsilon_m}{1 + iC_m},\tag{18}$$

where the Neumann factor $\varepsilon_m = 1$, for m = 0, $\varepsilon_m = 2$ for m > 0 and coefficients C_m can be expressed as

$$C_m = \frac{[J'_m(k'a)N_m(ka)]/[J_m(k'a)J'_m(ka)] - gh[N'_m(ka)/J'_m(ka)]}{[J'_m(k'a)J_m(ka)]/[J_m(k'a)J'_m(ka)] - gh},$$
(19)

where $k = |\cos \gamma| \, \omega/c$, k' = k/h, the functions $J_m(x)$ and $N_m(x)$ denote the first kind Bessel and Neumann functions respectively and $J'_m(x)$ and $N'_m(x)$ are the first order derivatives of these functions over x.

Here h and g respectively denote the sound speed and density contrast as defined above.

These equations ignore sound absorption by a krill individual. Gorska (1999) has noticed that sound absorption has no influence on the extinction cross-section for a fluid-like zooplankton individual.

The applicability of condition (16) can be analysed on the basis of eqs. (6), (8), (17)–(19). The main problem, emphasised by many authors studying sound scattering by zooplankton, is the lack of a full set of information on the characteristics of zooplankton individuals. In the case of krill, for example, information about the dependence of the contrast parameters g and h on the individual length l is available only for *Thysanoessa* sp. (in the body length range l = 10-25 mm) and *Meganyctiphanes norvegica* (l = 20-50 mm) (Kristensen & Dalen 1986, Kogeler *et al.* 1987). However, for *Euphausia superba* only the dispersion of the contrasts for a limited length range is known (Foote 1990b, Foote *et al.* 1990, Chu *et al.* 1993). Important for the scattering model, the geometrical characteristics, such as the aspect ratio (e = l/a) and the ratio of the radius of cylinder axis curvature to the arc length of the cylinder (ρ_c/l), have been measured only for certain krill species (Macaulay 1994). The information about absorption in zooplankton tissue is not readily available.

We now analyse the applicability of the criterion given by eq. (16) for fluid-like zooplankton. Zooplankton of one size class is considered and the independence of the extinction cross-section on the swimming angle (Chu & Ye 1999) is taken into account.

The condition presented by eq. (16) is analysed by computer for *Thysanoessa* sp. (in the body length range l = 10-25 mm), *M. norvegica* (l = 20-50 mm) and *E. superba* (l = 30-70 mm) at the frequencies 30, 50, 120, 270 and 420 kHz used in acoustic measurements of krill abundance. For *Thysanoessa* sp. and *M. norvegica*, the dependences of the contrast parameters g and h on the length l, presented by Kristensen & Dalen (1986), are employed. They are: $g = 1.058 - 1.3010^{-3} l \text{ [mm]}$,

h = 1.025 for Thysanoessa sp. and $g = 1.063 - 7.29 \, 10^{-4} \, l \, [\text{mm}]$, h = 1.035 for *M. norvegica*. For *E. superba* the analysis has been carried out at the maximum (g = 1.042, h = 1.030) observed contrasts given by Foote (1990b), Foote *et al.* (1990) and Chu *et al.* (1993). The evaluations have been done for a krill density of 1000 individuals per cubic metre, an aspect ratio e = 15 and $\rho_c/l = 2$ (Stanton 1989, Stanton *et al.* 1993, Macaulay 1994). The results are summarised in Figs. 4 and 5. The curves corresponding to the condition $10 \log \exp\{-\langle \sigma_e \rangle_{\theta,l} nL_z\} = -3dB$ are plotted on the graph of vertical thickness of krill aggregation L_z versus individual length *l*. For each frequency (for each curve) the sound attenuation is important in the domain above the curve, but may be negligible below it. It can be shown

Meganyctiphanes norvegica

Fig. 4. Sound extinction. For each echosounder frequency (for each curve), the sound attenuation is significant in the area above the curve but may be negligible below it. The curves correspond to the condition $10 \log \exp\{-\langle \sigma_e \rangle_{\theta,l} n L_z\} = -3dB$. The calculations have been done for the dependence of contrast parameters g and h on the length l from Kristensen & Dalen (1986), for a concentration of n = 1000 individuals per cubic metre, and an aspect ratio e = 15 and $\rho_c/l = 2$. Acoustic frequencies are given in the length

Fig. 5. Sound extinction. For each echosounder frequency (for each curve), the sound attenuation is significant in the area above the curve but may be negligible below it. The curves correspond to the condition $10 \log \exp\{-\langle \sigma_e \rangle_{\theta,l} nL_z\} = -3dB$. The calculations have been done for g = 1.042 and h = 1.030, for concentration n = 1000 individuals per cubic metre, aspect ratio e = 15 and $\rho_c/l = 2$. Acoustic frequencies are given in the legend

that according to eq. (16), these curves are displaced down or up over the vertical axis as the krill densities rise or fall.

The calculations indicate the range of the parameters (f, n, l, g, h) where the sound attenuation is negligible. The insignificance of sound attenuation is demonstrated for small krill species *Thysanoessa* sp. However, for larger organisms (*M. norvegica* and *E. superba*) the effect can be important at higher frequencies. For a krill aggregation approximately one hundred metres thick and a density of 1000 individuals per cubic metre, the sound extinction may be negligible for *M. norvegica* when f < 270 kHz and for *E. superba* when f < 120 kHz. However, for a krill density of 10000 individuals per cubic metre (the highest quoted density) the limit frequencies are 120 kHz and 50 kHz respectively. For thinner aggregations the limit frequencies are higher.

3.2. Evaluation of coherent scattering

In order to evaluate the interference of echoes from zooplankton targets the following function is introduced:

$$K_{\rm int} = \int_{T_r} I_c(t) dt / (\int_{T_r} I_{nc}(t) dt).$$
⁽²⁰⁾

 K_{int} is the ratio of energies of the coherent and incoherent parts of the pulse. Here T_r is the length of the scattered pulse received by the echosounder. The condition

$$K_{\rm int} \le 0.1\tag{21}$$

is introduced as the criterion of applicability of the incoherent approximation (criterion of neglecting the echo interference).

To obtain the criterion in analytical form, the expressions for the incoherent and coherent parts of the intensity eqs. (9), (10) are used. After substituting them in eq. (20), we can derive

$$K_{\rm int} = N \frac{\int\limits_{0}^{T_r} \Phi_2 dt}{\int\limits_{0}^{T_r} \Phi_1 dt} \frac{|\langle f \rangle_{\theta,l}|^2}{\langle \sigma_{bs} \rangle_{\theta,l}}.$$
(22)

For further simplification we now turn to the specific forms of the zooplankton and echosounder characteristics. To transform the second term of the right-hand side of eq. (22) (the functions Φ_1 , Φ_2 from eqs. (11) and (12)), the following simplifications are employed: (i) the uniform zooplankton spatial distribution is used; (ii) the functions describing the exciting echosounder pulse and echosounder beam pattern are chosen in the following form:

$$P_0(t) = \begin{cases} P_0 & t \in [t_1, t_1 + T] \\ 0 & t \notin [t_1, t_1 + T] \end{cases}$$
(23)

and

$$D(\Theta, \Phi) = \begin{cases} 1 & \Phi \in [0, 2\pi], \Theta \in [0, \theta_*] \\ 0 & \Phi \in [0, 2\pi], \Theta \notin [0, \theta_*], \end{cases}$$
(24)

where the exciting pulse begins at the instant t_1 , T denotes the pulse length and θ_* describes the half-width of the echosounder beam. The parameters Θ and Φ represent the vertical and azimuth angles in the spherical co-ordinate system (see Fig. 1).

To derive $\langle f \rangle_{\theta,l}$ and $\langle \sigma_{bs} \rangle_{\theta,l}$ in the third term of the right-hand side of eq. (22) the length and swimming angle distributions should be defined, and the model describing the scattering by a zooplankton individual should be

chosen. Following Stanton *et al.* (1993), the Gaussian length and swimming angle distributions are used:

$$W_l(l) = 1/\sqrt{2\pi} S_l \exp[-(l-\bar{l})^2/(2S_l^2)], \qquad (25)$$

$$W_{\theta}(\theta) = 1/\sqrt{2\pi} S_{\theta} \exp[-(\theta - \bar{\theta})^2/(2S_{\theta}^{-2})], \qquad (26)$$

where \bar{l} ; S_l and $\bar{\theta}$; S_{θ} describe the average and standard deviation of the length and swimming angle distributions respectively.

As in Section 3.1, the model of a uniformly bent cylinder of constant cylinder axis curvature radius, constant cross-sectional radius and constant composition profile are employed to describe backscattering by a krill individual (Stanton 1989, Stanton *et al.* 1993, 1998). The expressions for the backscattering amplitude, eqs. (5), (6), (10), (15), (18), presented in Stanton *et al.* (1993), are used.

Inserting the distributions $W_r(\vec{r})$, $W_\theta(\theta)$, $W_l(l)$, the echosounder characteristics $P_0(t)$ and $D(\Theta, \Phi)$ and the expressions for σ_{bs} and $f(\vec{i}, -\vec{i})$ in eq. (22), we obtain

$$K_{\text{int}} = \pi^{1/2} \theta_*^2 n z^2 k^{-2} \tau^{-1} s^{-1} \sin^2 k \tau \Re, \qquad (27)$$
$$\Re = \frac{\left| \int_0^\infty du \exp[-(u-1)^2/s^2] u^{1/2} [1+2\varphi(u)]^{-1/2} \times \right|}{\int_0^\infty du \exp[-(u-1)^2/s^2] u [1+4\varphi(u)]^{-1/2} \times \left| \frac{\exp[-\phi(u)/(1+2\varphi(u))] \Psi(u)}{|x|} \right|^2}{|x|} \qquad (28)$$

Here the function \Re refers to the ratio of the square of the modulus of the averaged backscattering amplitude to the averaged backscattering cross-section (the third term on the right-hand side of eq. (22)). The backscattering amplitude and backscattering cross-section have already been averaged over the swimming angle in the derivation of \Re . However, the averaging over the length cannot be done analytically, and the integral over $u(u = l/\bar{l})$ refers to the averaging. In eqs. (27), (28), $k = \omega/c$, $\tau = cT/2$ and $s = 2^{1/2}S_l/\bar{l}$. In the formula z denotes the distance between the echosounder and the upper zooplankton layer border (Fig. 1). The functions $\phi(u)$, $\varphi(u)$ and $\Psi(u)$ are substituted for the following analytical expressions:

$$\phi(u) = 3.2 \,\bar{\theta}^2 \,\rho_c^2 \bar{l}^{-2} \,u^{-2},\tag{29}$$

$$\varphi(u) = 3.2 \, S_{\theta}^2 \, \rho_c^2 \bar{l}^{-2} \, u^{-2}, \tag{30}$$

$$\Psi(u) = \exp(-i\Omega(u)) \left[1 - T_{12}T_{21} \exp\left(2i\Omega(u)h^{-1} + i\frac{\pi\Omega(u)}{2\Omega(u) + 1.6}\right) \right], (31)$$

where $\Omega(u) = 2klu/e$. The transmission coefficients can be expressed as $T_{12} = 2gh/(1+gh)$ (for transmission from seawater to the body medium) and $T_{21} = 2/(1+gh)$ (for the reverse transmission).

Eqs. (27) and (28) are limited by three approximations. Following Stanton *et al.* (1993), the relation $S_{\theta} \geq \bar{\theta} + w$ is used to average the backscattering characteristics over θ (eq. (28)). Here w denotes the typical width of the directional characteristics of the zooplankton individual backscattering amplitude (see Stanton *et al.* 1993). Moreover, the expression for K_{int} is obtained for thin zooplankton layers, where sound attenuation can be neglected (the condition given by eq. (16) is applicable). The depth zis also presumed to be much larger than the characteristic vertical thickness of the domain occupied by zooplankton.

Eqs. (27) and (28) for K_{int} show that echo interference is more significant for a larger zooplankton concentration, a broader echosounder beam and a deeper zooplankton layer. It can also be proved that if

$$s\bar{l}k/e \ll 1,\tag{32}$$

the function $\Psi(u)$ does not have any influence on the integrals in eq. (28) (its change is negligible for the range of u important in the integration). However, this very function defines the dependence of the coefficient K_{int} on the contrast parameters g, h, the aspect ratio e and the mean length \bar{l} of an individual animal. This means that K_{int} is not sensitive to these parameters and depends only on one single parameter of a krill individual – the ratio ρ_c/\bar{l} . In this case the dependence of K_{int} on k obviously becomes $K_{\text{int}} \propto k^{-2} \sin^2 k\tau$. In the general situation, where the condition given by eq. (32) is not satisfied, the dependences on the zooplankton parameters $\bar{l}, \bar{\theta}, S_l, S_{\theta}, g, h, \rho_c, e$ and on the sound wave number k are not obvious and should be investigated by computer.

On the basis of the criterion introduced (eqs. (21), (27), (28)), the range of the parameters $(n, \bar{l}, S_l, \bar{\theta}, S_{\theta}, g, h, e, \rho_c, z, f, T, \theta_*)$ where the individual echo interference can be neglected is investigated in the case of krill. The evaluation has been carried out for *Thysanoessa* sp., *M. norvegica* and *E. superba*. The same values for krill parameters \bar{l}, g, h are used as in the previous Section. The values of $\bar{\theta}$ and S_{θ} are taken from Sameoto (1976, 1980) and Kristensen & Dalen (1986) for *Thysanoessa* sp. and *M. norvegica*, and from Kils (1979, 1982), Foote *et al.* (1990), Chu *et al.* (1993), Endo (1993), and Loeb *et al.* (1993) for *E. superba*. The calculation is made for $S_l = 0.1 \bar{l}$. Note that the inequality $S_l \ll \bar{l}$ is applicable to krill (Sameoto 1976, 1980, Stanton *et al.* 1993).

It can be demonstrated that the condition eq. (32) is satisfied for the range of krill parameters considered here. The coefficient K_{int} , therefore, does not depend on the contrast parameters and aspect ratio different for

Fig. 6. Incoherent scattering. The curves correspond to the condition $K_{\text{int}} = 0.1$. The calculations have been done for the parameters z = 20 m, $\theta_* = 8^\circ$, T = 0.0015 s, $\rho_c/\bar{l} = 2$ and $S_l = 0.1 \bar{l}$. The numbers in the legend refer to the values of parameters $[\bar{\theta}, S_{\Theta}]$ of swimming angle distribution. For each $[\bar{\theta}, S]$ the coherent scattering is significant in the area above the curve but may be negligible below it

various krill species. Hence, the results of the calculation, illustrated in Fig. 6, apply to all three investigated krill species for the given range of the mean length \bar{l} . The results are not critical with respect to the contrast parameters g, h and aspect ratio e.

In Fig. 6 the curves correspond to the condition $K_{\text{int}} = 0.1$. The echo interference is significant in the field above the curves but can be neglected below the curves. The calculations have been done for z = 20 m, $\theta_* = 8^\circ$, T = 0.0015 s, $\rho_c/\bar{l} = 2$. The numbers in the legend to Fig. 6 correspond to the values of the parameters $[\bar{\theta}, S_{\theta}]$. Note also that the evaluation has been done for the largest value of the sine function in eq. (24), which is equal to 1.

It can be inferred from the analysis of the results presented in Fig. 6 that for an aggregation concentration of approximately 10 000 individuals per cubic metre, the interference is negligible for frequencies f > 240, 190, 160, 140 kHz when $S_{\theta} = 30^{\circ}$, 50° , 70° , 90° respectively. For more dispersed

aggregations these limit frequencies are lower. For example, the respective limit frequencies are 70, 60, 50, 40 kHz for aggregation concentrations of 1000 individuals per cubic metre. However, for concentrations smaller than 150 individuals per cubic metre, the echo interference is negligible for the entire range of parameters considered.

4. Summary

A model describing the scattering of echosounder signals by a dense zooplankton population has been developed. Sound attenuation induced by scattering and absorption by individual zooplankton animals, and the interference of individual echoes are taken into account. An analytical relationship between the mean intensity of the backscattered signal and zooplankton characteristics has been obtained. These expressions are applicable to any species of zooplankton (fluid-like, gas-filled, elastic-shelled *etc.*) and arbitrary distributions over animal space position, animal length and swimming angle. Sound extinction and echo interference have been evaluated on the basis of the equations.

The range of acoustic and zooplankton parameters in which these effects are of importance have been defined for krill. This analysis is based on a recognised verified description of sound backscattering by krill individuals. The experimental data concerning the acoustical properties of krill individuals and the orientation and length distributions in krill populations are also taken into account.

The analysis shows that:

- 1. In the case of a krill aggregation approximately one hundred metres thick (the thickness does not exceed one hundred metres) the sound attenuation can be neglected for small krill species (*Thysanoessa* sp.). However, for larger species *M. norvegica* and *E. superba* the effect is significant at the high frequencies used. For example, for a krill density of 1000 individuals per cubic metre the sound attenuation should be taken into account at f > 270 kHz and f > 120 kHz for *M. norvegica* and *E. superba* respectively. In case of the highest quoted krill concentration of 10 000 individuals per cubic metre the effect is important for sound frequencies higher than 120 kHz and 50 kHz for *M. norvegica* and *E. superba* respectively. For a smaller aggregation thickness these limit frequencies are larger.
- Coherent scattering increases for larger zooplankton concentrations, a broader echosounder beam, a deeper zooplankton layer, a smaller mean swimming angle and a narrower swimming angle distribution. In the case of the krill species considered here – *Thysanoessa* sp.,

M. norvegica and *E. superba*, the interference can be important with respect to concentrations larger than 150 individuals per cubic metre where the swimming angle distribution of zooplankton is narrow. For example, in the case of aggregation concentrations of approximately 10 000 and 1000 individuals per cubic metre the echo interference is significant at the respective frequencies f < 240 kHz and f < 70 kHz when $S_{\theta} = 30^{\circ}$.

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