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Comparison of acoustical and optical zooplankton measurements using an acoustic scattering model: A case study from the Arctic frontal zone

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Abstract: High-frequency acoustic measurements supplemented by a modern optical method, Laser Optical Plankton Counter (LOPC), allowed us to perform a comparative analysis through the application of a mathematical model. We have studied the correspondence between measured and modelled echoes from zooplankton aggregations consisted mainly of two *Calanus* species. Data were collected from the upper 50 m water layer within the hydrographical frontal zone on the West Spitsbergen Shelf. The application of a "high-pass" model of sound scattering by fluid-like particles to the distribution of zooplankton sizes measured by LOPC resulted mostly in very good agreement between the measured (420 kHz BioSonics) and modelled values, except for cases with very low zooplankton abundance or with occurrence of stronger scatterers (*e.g.* macrozooplankton, fish). An acoustic model validated for the elastic parameters of zooplankton confirmed that particles smaller than 1 mm in diameter, although highly abundant, did not contribute significantly to the sound scattering process at a frequency of 420 kHz. The implementation of diverse complementary methods has great potential to obtain high spatial and temporal resolution in zooplankton distribution studies; however, their compatibility has to be tested first.

Key words: Arctic, Svalbard, zooplankton, high-frequency echosounding, sound scattering model.

Introduction

Zooplankton constitute a very important link in the marine food web, connecting primary producers and higher trophic levels, *i.e.* consumers. Furthermore, as generally passive drifters, they are good tracers and sensitive indicators of various processes in the marine environment (*e.g.* Hays *et al.* 2005). Collecting data on the abundance of zooplankton and their spatio-temporal distributions is therefore an essential part of marine research, as it forms a necessary base for studies of other phenomena. This is particularly important in the Arctic, where recently observed climate changes and the consequent ecosystem changes are extreme on the global scale (*e.g.* ACIA 2005). Zooplankton distribution in the open ocean is patchy, resulting from a combination of behavioural and environmental characteristics (*e.g.* Haury *et al.* 1978; Omori and Hamner 1982; Folt and Burns 1999). The traditional way of collecting zooplankton by nets demands a huge amount of time and effort and it delivers only depth-integrated, one-dimensional snapshots of zooplankton composition in the water column. Thus, it is necessary to collect high resolution biological data automatically and concurrently with environmental measurements to understand the subsequent patterns and their causal mechanisms.

An alternative approach to traditional net sampling came together with the introduction of acoustical methods into plankton ecology investigations. Echosounders have long been used to map the distribution of zooplankton (*e.g.* Greenlaw 1979; Pieper and Holliday 1984; Wiebe *et al.* 1996). Synoptic studies of zooplankton have been performed by using high-frequency echosounding (Holliday and Pieper 1995; Wiebe *et al.* 1997; Brierley *et al.* 1998; Lavery *et al.* 2007) or multifrequency echosounding (Holliday *et al.* 1989; Pieper *et al.* 1990; Trevorrow *et al.* 2005). In the context of the presented study, four papers contributed especially to comparing acoustic data on the zooplankton distribution with biological and/or optical sampling (Pieper and Holliday 1984; Kirsch *et al.* 2000; Fielding *et al.* 2004; Lavery *et al.* 2007). They were carried out in various basins and with the application of different biological and acoustic tools. To predict volume backscattering, a wide spectrum of acoustic scattering models have been used (*e.g.* truncated fluid sphere, “high-pass” bent cylinder, distorted-wave Born approximation for bent cylinder and prolate spheroid).

Multi-frequency acoustics combined with pump samples was tested for the first time in Californian waters to check the hypothesis that field-recorded scattering is due to zooplankton (Pieper and Holliday 1984). This pioneering work, which utilised three independent models and four distinct frequencies from 0.54 to 3.08 MHz, demonstrated a decreasing trend of correlation between the calculated and measured volume backscattering strength with decreasing frequency. Moreover, a linear relationship between the log-transformed dry weight of zooplankton collected by a Longhurst-Hardy Plankton Recorder and the mean volume backscattering strength measured by 153 kHz ADCP was found in Arabian Sea waters (Fielding *et al.* 2004). Furthermore, the abundance of copepods inferred by both multi-frequency acoustics and 420 kHz echosounder were found to agree with that measured by MOCNESS tows and video records (Kirsch *et al.* 2000; Lavery *et al.* 2007), although there were some discrepancies between the acoustic values and net results.

Simultaneously, optical methods, *e.g.* Laser Optical Plankton Counter (LOPC) have also proven to be highly useful in assessing zooplankton patchiness and size structure (*e.g.* Checkley *et al.* 2008), but a common strategy is to use them with at least one complementary instrument (*e.g.* nets, bathometer) to assess not only zooplankton distribution but also its composition. So far, LOPC has been calibrated with nets (*e.g.* Herman and Harvey 2006; Gaardsted *et al.* 2010 and citations therein), Video Plankton Recorder (*e.g.* Basedow *et al.* 2013) and an Acoustic Doppler Current Profiler (ADCP) (*e.g.* Rahkola-Sorsa *et al.* 2014). Those intercomparisons showed generally good agreement in zooplankton distribution patterns, but the absolute counts usually substantially differed. There is no obvious objective way to calibrate any of those instruments, because their technical specifications limit the direct comparability of absolute estimated abundance. The combination of both methods is to use the LOPC to parameterise models to explain the acoustics over a large distance. Most studies of LOPC in conjunction with conventional methods focused on selecting the proper size ranges of the dominant zooplankton taxa.

At the moment, one of the most promising avenues of obtaining the most complete picture of zooplankton distribution is the use of a synergistic combination of acoustic and optical sensors, which enables continuous measurements in near real time with a two-dimensional perspective. The first attempt to combine an acoustic sounding with the LOPC measurements, to perform multidimensional zooplankton observations in high Arctic waters revealed a high correlation between the zooplankton concentrations detected by these two automatic methods (Trudnowska *et al.* 2012). This investigation encouraged us to verify whether models of sound scattering by zooplankton could be utilised with field-collected data on zooplankton size and abundance as input parameters to predict the volume backscattering strength.

The present study is based on data collected within the hydrographical frontal zone on the West Spitsbergen Shelf (WSS) in two summer seasons (2010 and 2012). Frontal zones are crucial areas for high biological productivity, but due to their dynamic nature, accurate studies of the biota inhabiting them are still scarce and constitute a great challenge (*e.g.* Basedow *et al.* 2014). In the current study, we propose an integrated approach combining three complementary methods: biological (traditional vertical zooplankton net hauls) at the stations vs. optical (high resolution LOPC measurements) and acoustic (high-frequency echosounding) provided along transects between stations. Qualitative data, in the form of zooplankton species composition from net samples and size spectra obtained by LOPC, are needed for ecological interpretation of the results. Whereas, quantitative data in the form of LOPC counts and the acoustic backscattering strength of zooplankton aggregations are needed for distribution pattern analyses.

The main goal of the study was to apply a mathematical model of sound scattering by fluid-like particles to the zooplankton concentrations and sizes measured by LOPC and to solve the forward problem by verifying the relationships obtained between the measured and modelled values of backscattering strength. Implementation of the two methods described above, supplemented by zooplankton composition structure obtained from nets sampling, can be a reliable tool for assessing complex information about the zooplankton distribution in the dynamic ecosystem of frontal WSS waters.

Materials and methods

Study area and sampling design. — The study was carried out during two summer cruises of r/v *Oceania* (July/August of 2010 and 2012) in two hydrographically different regions of the WSS frontal zone: the southern part near the Hornsund fjord and the northern part in the foreground of Magdalenefjorden (Fig. 1). The southern area is influenced by both the cold South Cape Current originating from the northern Barents Sea and the West Spitsbergen Current, which flows northward carrying warmer and more saline Atlantic Water (Walczowski 2013). Whereas, the northern area is under the influence of the interaction between advected Atlantic waters and coastal waters.

We performed and analysed 24 hours of continuous acoustical (echosounder) and optical (LOPC) measurements within the upper 50-meter depth layer recorded along 9 sampling transects crossing the frontal zone (Table 1) together with complementary zooplankton net (WP2, 500 μm mesh size) samples collected from 21 stations arranged along the transects (Fig. 2). The names of the transects were created according to the net station numbers.

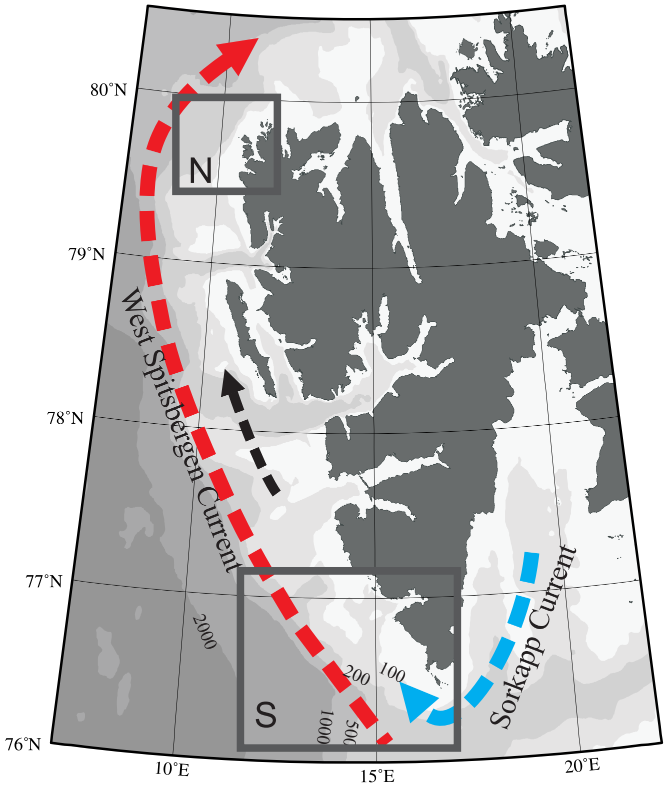

Fig. 1. Map of Spitsbergen with the northern (N) and southern (S) study areas marked with black frames.

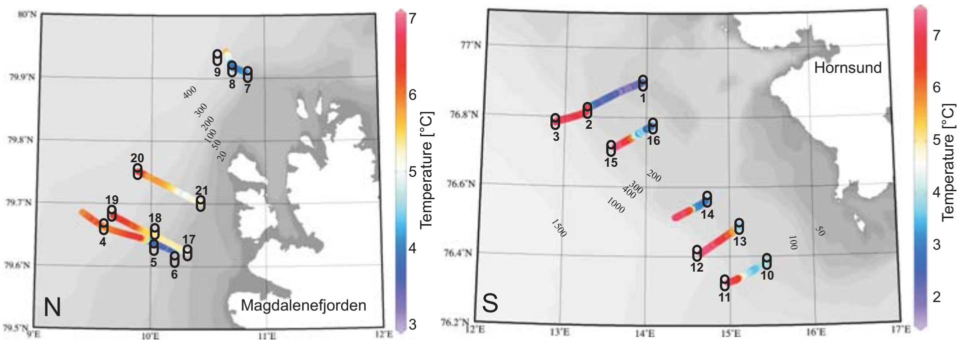

Fig. 2. Northern (N) and southern (S) study areas with temperature values along the transects of LOPC (note the different towing depths, Table 1) expressed in a colour scale. The locations of the zooplankton net stations are indicated by circles.

Data collection and implemented methods. — A DT-X 420 kHz echosounder (BioSonics Inc., Seattle, USA) with a downward looking transducer attached to the side of ship by a special frame (at the depth of 1 m) was used to determine the fine-scale vertical patterns of acoustic backscatter along the studied transect. Echosounder calibration was performed before the first season (2010) by the standard target method. A chosen pulse length of 0.3 ms guaranteed the depth resolution of 22 cm Trigger rate of 2 Hz was established. Theoretically, a working frequency of 420 kHz allows the detection of single individuals with a diameter of more than 1 mm (*ESD*; equivalent sphere diameter: the diameter of a sphere with a volume equal to the volume of an object) according to the commonly applied criterion of detectability: π diameter/wavelength >1 (Medwin and Clay 1998). On the

Table 1

Transects investigated in the WSS waters in 2010 and 2012 with their dates, duration, position, LOPC towing depth and undulating mode ("+" indicate that the LOPC was additionally towed between 0 and 50 m; "–" means that the towing depth was almost constant depending only on the towing speed).

Transect	Date	Duration [min]	LOPC towing depth [m]	Undulating mode	Start position		End position	
					Lat (N)	Lon (E)	Lat (N)	Lon (E)
1-2-3	28.07.2010	320	16–23	–	76°54.5’	13°56.0’	76°46.9’	12°52.6’
4-5-6	06.08.2010	193	9–12	–	79°33.5’	11°08.3’	79°44.6’	08°53.1’
7-8-9	04.08.2010	58	7–12	–	79°56.0’	10°35.0’	79°38.5’	11°19.1’
15-16	29.07.2012	147	23–27	+	76°42.8’	13°36.5’	76°46.6’	14°04.0’
14	28.07.2012	123	24–27	+	76°33.7’	14°43.5’	76°30.7’	14°21.3’
12-13	28.07.2012	166	23–27	+	76°24.6’	14°39.5’	76°29.3’	15°07.2’
10-11	27.07.2012	127	22–28	+	76°22.9’	15°26.4’	76°19.5’	14°58.3’
17-18-19	10.08.2012	144	9–12	–	79°37.4’	10°19.0’	79°40.0’	09°40.0’
20-21	10.08.2012	135	8–12	–	79°45.1’	09°53.0’	79°42.1’	10°26.0’

other hand, such a high frequency seriously reduces the measuring depth range, up to 50 m. The sound absorption coefficient α is proportional to the frequency squared. The automatic function of the time-varied gain (TVG) is utilised in the echosounder to compensate for the spherical spreading and absorption loss:

$$\mathrm{TVG} = 20 \log r + 2\alpha r \tag{1}$$

where r is the range. Consequently, targets of the same size give echoes of the same intensity regardless of their distance from the transducer. However, not only the echo signal but also the surface noise produced by the moving ship are amplified by the TVG. When the signal backscattered in the water column is very weak, the surface noise signal amplified by TVG starts to dominate. This noise signal can be a source of serious errors and has to be treated with the highest caution, more details in the Results and Discussion.

The LOPC (Brook Ocean Technology Dartmouth, Canada) is an optical *in situ* sensor that autonomously provides reliable abundance (number of particles per 1 m^3) and community size structure data on plankton and particles in marine and freshwater environments (Herman *et al*. 2004). It counts and measures each particle (*ESD* range: 0.1–35 mm) passing the laser beam path in a sampling tunnel (7×7 cm wide). During our survey, the LOPC was generally towed at an almost constant depth along the transects (Table 1), but an additional undulating mode within the upper 50 m depth range was also tested for 5–7 minute intervals along 4 transects in 2012 (Table 1). The undulating mode of the LOPC gave us additional, vertical information on zooplankton distribution through the sampled water column and enabled the analysis of TVG effects.

A CTD (SBE 911plus, Seabird Electronics Inc., USA) was connected to the LOPC to provide simultaneous hydrographical data (temperature, salinity). The mesozooplankton samples were collected with a WP2 net (0.25 m^2 opening area) with a 500 μm mesh size in vertically stratified hauls from 50 m to the surface. Each zooplankton sample was preserved with 4% borax-buffered formaldehyde and returned to the laboratory for microscopic analysis, where zooplankton individuals were identified, measured and counted. For each sample, the total number of individuals was converted to a concentration per 1 m^3 using the filtered water volume. The nets delivered detailed point information on overall zooplankton species composition and abundance at 21 sampled stations (Fig. 2). Additionally, a G-test of independence was applied to compare the size structure of the mesozooplankton community between water masses in a specified areas and seasons.

“High-pass” model of sound scattering by zooplankton. — The volume backscattering strength (S_V) delivered by the echosounder is a logarithmic measure of the volume backscattering coefficient (s_V), which in turn represents the total backscattering cross-section of the unit volume of the medium. Target strength (*TS*) is a logarithmic measure of the backscattering cross-section of the individual

(σ_{bs}). It depends mainly on the interrelation between object size and sound frequency as well as on some other factors, such as shape, orientation, material properties and internal structure.

From great numbers of mathematical models describing the *TS* of zooplankters with different degrees of complexity based on various mechanisms of scattering for different types of zooplankton, we have chosen the so-called "high-pass" model of *TS* (Stanton 1989), which describes scattering on the sphere, prolate spheroid, and straight and bent cylinders, of different materials and structures. Its generality makes it especially suitable for *in situ* measurements of the intensity of sound backscattered by a mixture of various species with a range of sizes, shapes, orientations, body composition and structure, in contrast to the specific models applied in laboratory tests on individual plankters (Wiebe *et al*. 1990; Stanton *et al*. 1994).

The sphere model is the simplest one, but zooplankters are obviously not spherical scatterers. The ellipsoid and cylinder models take the shape and spatial orientation of the scatterers into account, so they seem to be better suited to describe the zooplankton scattering. This approach, however, requires some additional parameters like length to width ratio and orientation distribution of the scatterers and is only valid for the orientations close to broadside incidence. Unfortunately, in our case, there is no information concerning these parameters. Benfield *et al.* (2000) found by use of Video Plankton Recorder that over 50 % of *Calanus finmarchicus* on Georges bank took the vertical position, so when measured by vertically directed acoustic beam they cannot be modelled as ellipsoids or cylinders in the broadside incidence approximation. Stanton and Chu (2000) have proved that in some circumstances a very simple model can be used with reasonable accuracy. We used the sphere "high-pass" model as the most reasonable approach. In this model, the backscattering cross-section of any object can be written after Stanton (1989) as the following:

$$\sigma_{bs} = \frac{X}{1+\dfrac{X}{YR^2}} = \frac{XY}{\dfrac{X}{R^2}+Y} = \frac{Y}{\dfrac{1}{R^2}+\dfrac{Y}{X}}, \tag{2}$$

where X and Y are the exact expressions for σ_{bs} valid in specified object size-sound frequency regions of scattering:

$X = \sigma_{bs}(ka << 1, fluid) = a^2 (ka)^4 \alpha_{\pi s}^2$ for Rayleigh scattering, (3)

$Y = \sigma_{bs}(ka << 1, rigid\,/\,fixed) = \frac{1}{4} a^2$ for geometrical scattering, (4)

α – scatterer radius,
k – wave number,

$$\alpha_{\pi s} = \frac{1-gh^2}{3gh^2} + \frac{1-g}{1+2g}, \tag{5}$$

$R = (gh - 1)/(gh + 1)$ – Rayleigh plane-wave plane-interface reflection coefficient, (6)

g – density contrast,
h – sound speed contrast.

According to this model, σ_{bs} depends on the geometrical cross section of the object, and it is modified by $(ka)^4\alpha_{\pi s}{}^2$ in the Rayleigh region ($ka << 1$) and by R^2 in geometric region of scattering ($ka >> 1$). The parameters $\alpha_{\pi s}{}^2$ and R are in control of density g and sound speed h contrasts, so the proper choice of their values is a crucial point. The values of parameters g and h are species-specific, as they depend on organism size, lipid content and occurrence of rigid parts (*e.g.* skeleton and carapace). A literature review gave a wide range of contrast values (Medwin and Clay 1998; Stanton and Chu 2000; Chu and Wiebe 2005; Smith *et al*. 2010; Becker and Warren 2014):

$0.940 < g < 1.051$ $0.949 < h < 1.096$

Acoustical estimates obtained by mathematical modelling are highly sensitive to changes in density and sound speed contrasts. Their impact on TS results in over 20 dB of change when the extreme values are compared. For our calculations, the values $g = 1.0$ and $h = 1.027$, characteristic for *Calanus finmarchicus,* the main representative of the North Atlantic copepods (Kogeler *et al*. 1987), were adopted in the first approach. The influence of various g and h values on the model's results will be discussed further.

Data processing. — To properly correlate the data from the two automatic instruments, only the acoustic scattering returns, averaged over a specified narrow depth layer corresponding to the LOPC towing depth, were taken into consideration. In the case of long transects with rather constant LOPC towing depth (a few-meter differences were caused by variable towing speed, Table 1), the acoustic and laser data were averaged in 30-second time windows. In the short-lasting undulating mode with the LOPC quickly descending and ascending between the surface and 50 m depth, the data were averaged in 5-second time intervals and in 1-metre layers corresponding to the current LOPC depth. S_V values measured by the echosounder were given a manufacturers' threshold of -130 dB. However, due to the averaging over 60 consecutive transmissions and an LOPC tow depth layer with a thickness of 3–7 m, the analysed mean backscattering strength values never fell below -83 dB.

Model-predicted values of the volume backscattering strength S_V were obtained by applying the "high-pass" model of sound scattering to the distribution of zooplankton sizes measured by LOPC. The LOPC abundance dataset was prepared in logarithmic steps of body size intervals, which is a standard way to prepare the biomass spectra. Such an approach provides higher resolution for the extremely abundant and diverse small plankton and particles and lower resolution for the size intervals representing definitely less abundant and occasionally counted large zooplankton. In this way, 49 size classes were created, the first with the smallest *ESD* = 100 µm and the last with the largest *ESD* > 25 mm. The interval widths changed exponentially from 12 µm to 2.7 mm.

For the central value of the particle radius in each size class, the backscattering cross-section s_{bs} was calculated (eq. 2) and then multiplied by the number of particles detected in this class by the LOPC. This manipulation yielded a backscattering coefficient s_V for each class of individuals, which represents the contribution of the size class to the total backscattering. Finally, the resultant backscattering strength $S_V = 10\log \Sigma s_V$ was computed and compared with the value directly measured by the echosounder.

The relationship between the measured and modelled values of acoustic backscatter along each transect was investigated with linear regression. Correlation coefficients were determined for whole transects as well as for their consecutive fragments by use of a 10-minute sliding window.

Results

Temperature gradients along the studied transects were more distinctive (4–5°C difference) in the southern part of the WSS than in its northern part (2.5–3.5°C difference) (Fig. 2). Net data confirmed that copepods of the genus of *Calanus* clearly dominated the zooplankton community, especially the boreal species *C. finmarchicus* (Table 2). Larger *Calanus* species (*C. glacialis* and *C. hyperboreus*) and other zooplankters (*e.g.* Amphipoda or Chaetognatha) contributed only slightly to the total zooplankton abundance. The analysis of the whole plankton size spectrum (0.1–35 mm *ESD*) indicated two abundance peaks, one represented by the very finest size fractions (up to 0.3 mm *ESD*) and the other with a predominant middle size fraction (0.5–1.6 mm *ESD*) comprising mainly *Calanus* individuals (Fig. 3A). A close-up of the limited size fraction, mesozooplankton (0.3–3.2 mm *ESD*), enabled to present various patterns in size distributions (Fig. 3B). In the Magdalenefjorden region, we found prevailing small plankters (< 0.5 mm *ESD*) in the coastal waters, whereas a clear domination of large zooplankton individuals (*ca*. 1.0 mm *ESD*) was observed in the open Atlantic waters (Figs 3.1 and 3.3B). In the Hornsund region, we found either a high contribution of the *Calanus* size fraction (Fig. 3.2B) or the domination of small plankton particles (Fig. 3.4B). The size structure of Arctic and Atlantic waters as well as of coastal and open waters differed significantly (G test, $p < 0.001$). Generally higher total plankton abundance was found in Atlantic waters compared to Arctic waters at most investigated transects (Fig. 3).

Comparison of the acoustically measured values of S_V with those calculated by the model indicated a generally close relationship between the two analysed approaches. In the vast majority of cases, good or even very good agreement

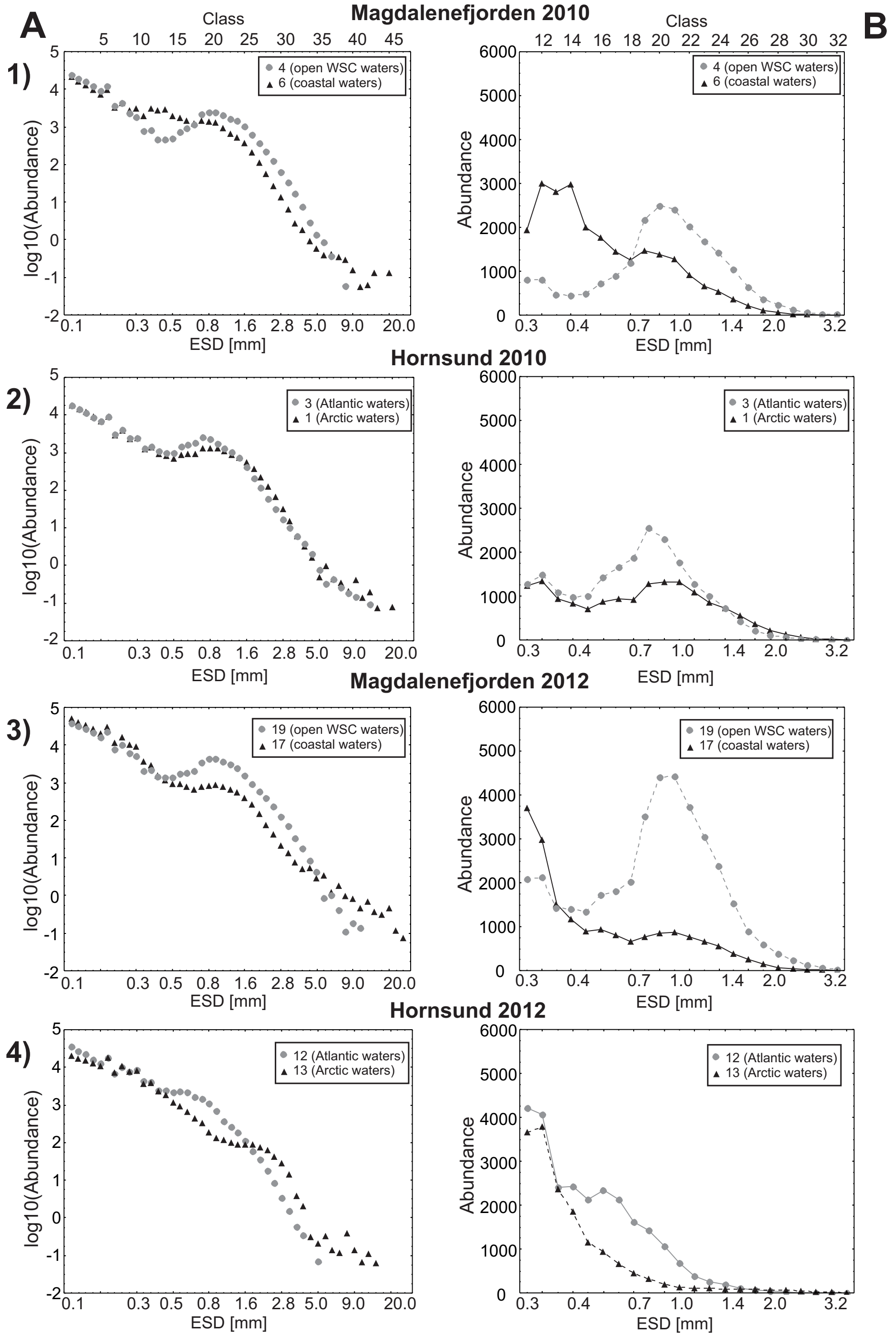

Fig. 3. Examples of zooplankton size spectra determined by LOPC. **A**. Zooplankton abundance in logarithmic scale for all 49 size classes (0.1–35 mm). **B**. Zooplankton abundance in linear scale for the mesozooplankton size fraction (0.3–3.2 mm).

Table 2

Relative composition of most important zooplankton taxa in net samples at stations.

Station	*Calanus finmarchicus*	*Calanus glacialis*	*Calanus hyperboreus*	Amphipoda	Chaetognatha	Others
1	84.8	13.9	0.2	0.0	0.1	1.0
2	95.1	2.3	0.0	0.1	1.4	1.1
3	96.1	1.4	0.0	0.1	0.8	1.6
4	94.3	3.5	0.4	0.1	1.3	0.4
5	82.3	16.7	0.4	0.2	0.2	0.2
6	78.3	20.1	1.1	0.1	0.2	0.2
7	96.3	2.9	0.2	0.1	0.2	0.2
8	85.4	13.0	0.7	0.2	0.5	0.3
9	97.1	2.6	0.0	0.1	0.2	0.1
10	99.4	0.5	0.0	0.0	0.1	0.0
11	98.6	0.4	0.0	0.0	0.5	0.5
12	57.7	42.1	0.0	0.0	0.1	0.2
13	16.7	83.2	0.0	0.0	0.0	0.1
14	98.9	0.1	0.0	0.0	0.3	0.7
15	99.5	0.0	0.0	0.0	0.3	0.2
16	33.4	66.5	0.0	0.0	0.1	0.1
17	91.3	6.7	0.0	0.0	1.7	0.3
18	98.6	1.0	0.0	0.0	0.3	0.1
19	98.6	0.8	0.0	0.0	0.3	0.2
20	94.4	3.3	0.0	0.0	1.7	0.6
21	88.2	10.3	0.0	0.0	1.5	0.0

was achieved. The correlation coefficients (R_{corr}) calculated for the measured and predicted values of S_V along the entire transects were statistically significant ($p < 0.0001$); R_{corr} ranged from 0.3 to 0.96, except for transect 14 where $R_{corr} = -0.03$.

The best agreement between measured and modelled values of backscattering strength was achieved for the northern waters in 2010 (Fig. 4A). Although, the measured values were slightly lower than the modelled ones (Fig. 4B), there was a very high correlation $R_{corr} = 0.96$ between the two sets of data.

The worst agreement characterised by the coefficient of correlation between the measured and predicted S_V values $R_{corr} = -0.03$ was recorded in the southern transect 14 in 2012. It is presented in Fig. 5, together with a local correlation coefficient determined for the 10-minute sliding window. The possible reasons for these dramatic discrepancies are discussed in the next section.

The local correlation with a sliding window of 10-minute interval was calculated for consecutive fragments of all nine of the analysed transects (Table 1) in the same way as presented in Fig. 5B. The distribution of the 172 values of R_{corr} calculated for the 15-minute sliding window is characterised by a small number (less than 9%) of

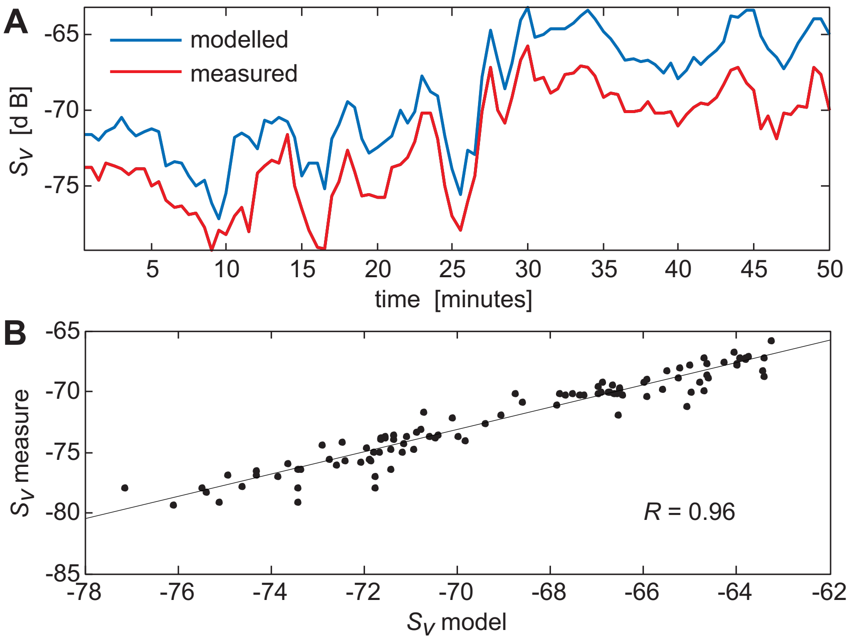

Fig. 4. **A**. Echosounder record of the volume backscattering strength (S_V) (red curve) and S_V predicted by the model on the basis of zooplankton concentration measured by LOPC (blue curve) at the LOPC depth along the northern transect 4-5-6 from 2010. Both signals were averaged over 60 transmissions (30 s). **B**. Correlation between measured and modelled volume backscattering strength S_V along the 4-5-6 transect.

near zero values connected with echo signal contaminants (Fig. 6). The maximum of this distribution is located at R_{corr} = 0.8, and its median is equal to 0.64.

Despite some differences in absolute S_V values, synchronous minima and maxima were detected by both approaches (Fig. 7A) along all studied transects of both seasons. Direct comparison of measured and modelled S_V curves with the echogram (Fig. 7B) showed that the S_V peaks corresponded well with the yellow patches indicating high zooplankton concentrations. There are, however, some time shifts in corresponding peaks, which can be explained by the distance from ship-mounted transducer to LOPC, which was hauled behind the stern. This can be a potential cause of difference.

Distribution of differences between modelled and measured values of S_V calculated for all transects from both seasons (Fig. 8) shows that most of the predicted values is higher than observations. The total number of samples analysed for 2010 and 2012 was 2815. The median value is 1.89 dB and over 60% of difference values is within the range [-3,+3] dB.

An undulating mode (within 50–0 m water layer) of the LOPC route was performed at several fragments of transects 10, 12-13, 14, 15-16 recorded in 2012 (Table 1) to provide the zooplankton size spectra at different depth strata. The track of the LOPC route was marked on the background of a pre-processed echogram

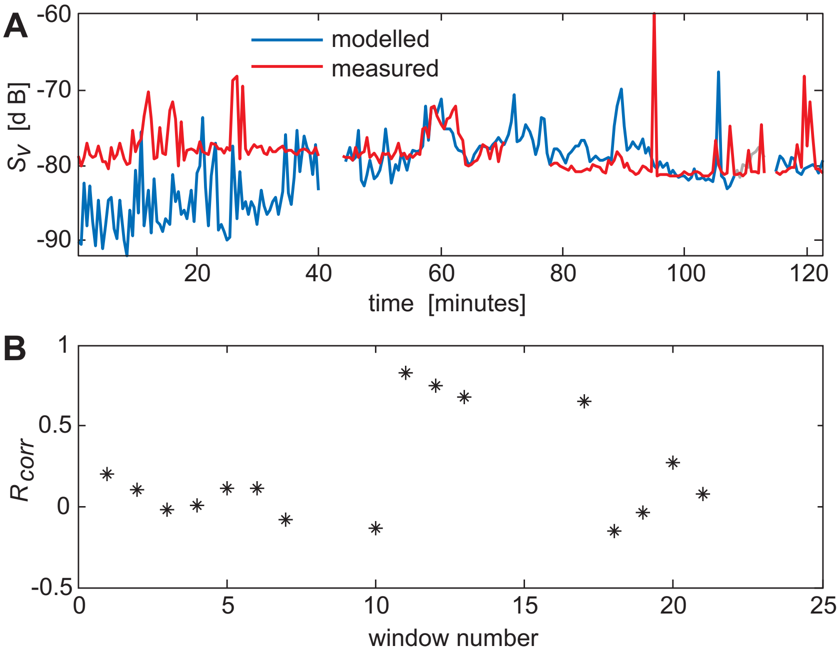

Fig. 5. An example of the impact of noise and fish on the measured echo detected along transect 14 (2012). **A**. Echosounder record of the volume backscattering strength (S_V) (red curve) and S_V predicted by the model on the basis of zooplankton concentration measured by LOPC (blue curve). **B**. Local correlation coefficient calculated along the whole transect with a sliding window 20 units (10 minutes) wide.

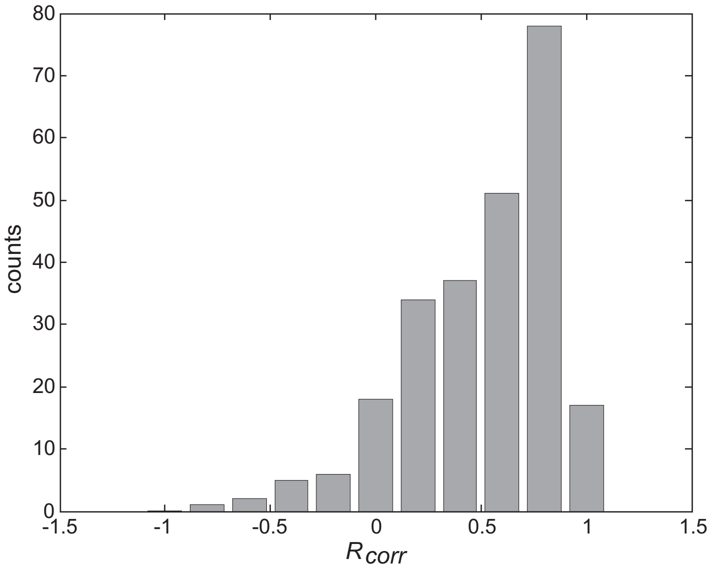

Fig. 6. Histogram of the local correlation coefficients calculated along all 9 transects with a sliding window of 20 units (10 minutes) wide.

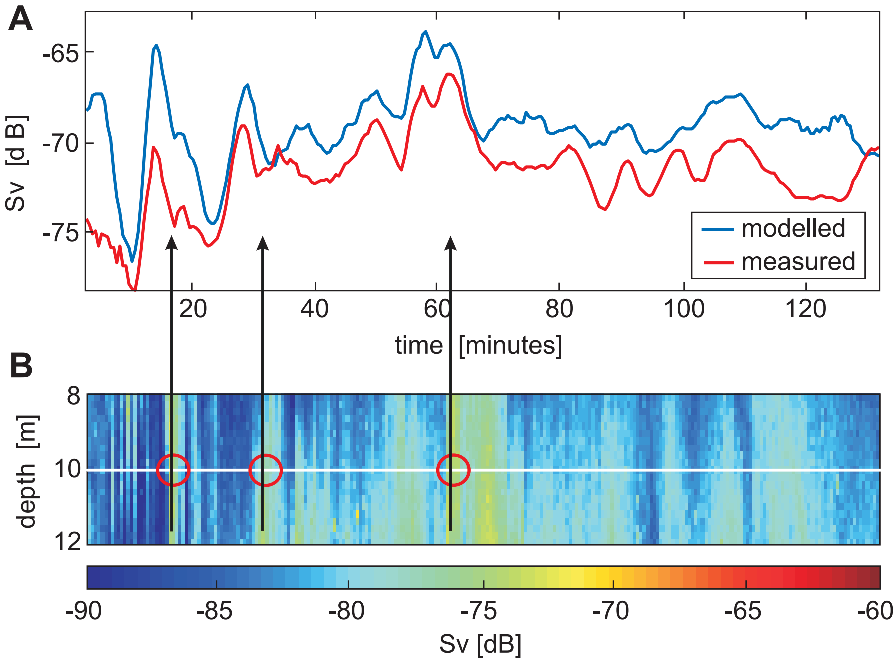

Fig. 7. **A**. Echosounder record o fthe volume backscattering strength (S_V) (red curve) and S_V predicted by the model on the basis of zooplankton concentration measured by LOPC (blue curve) along the northern transect 20-21 (2012). **B**. Echogram of a limited depth layer corresponding to the LOPC towing depth, marked with a white line.

(Fig. 9A) to follow the effect of TVG and characteristic features along the transect. Good agreement between the modelled and measured values was obtained within the fragments representing moderate zooplankton abundance at mid-depth layers, whereas there was a lack of agreement between data points at depths below 40 m (Fig. 9B). There was almost no zooplankton below 40 m depth (Fig. 9A), but this layer was spuriously spoiled by subsurface noise, as the echosignal kept the noise level dependent on the depth due to TVG amplification, analogously to the situation observed in the first part of transect 14, see Discussion.

Discussion

Comparison of measured and modelled values. — According to the net results, copepods of the genus of *Calanus* dominated zooplankton assemblages in the studied area of the Arctic frontal zone. Therefore, our choice of the scattering model for fluid-like particles seems to be fully justified. A comparison of optical and acoustic measurements of zooplankton in the Arctic frontal zone has shown that the spatial profiles of backscattering strength values S_V calculated from the model on the basis of size distributions determined by LOPC have a shape analo-

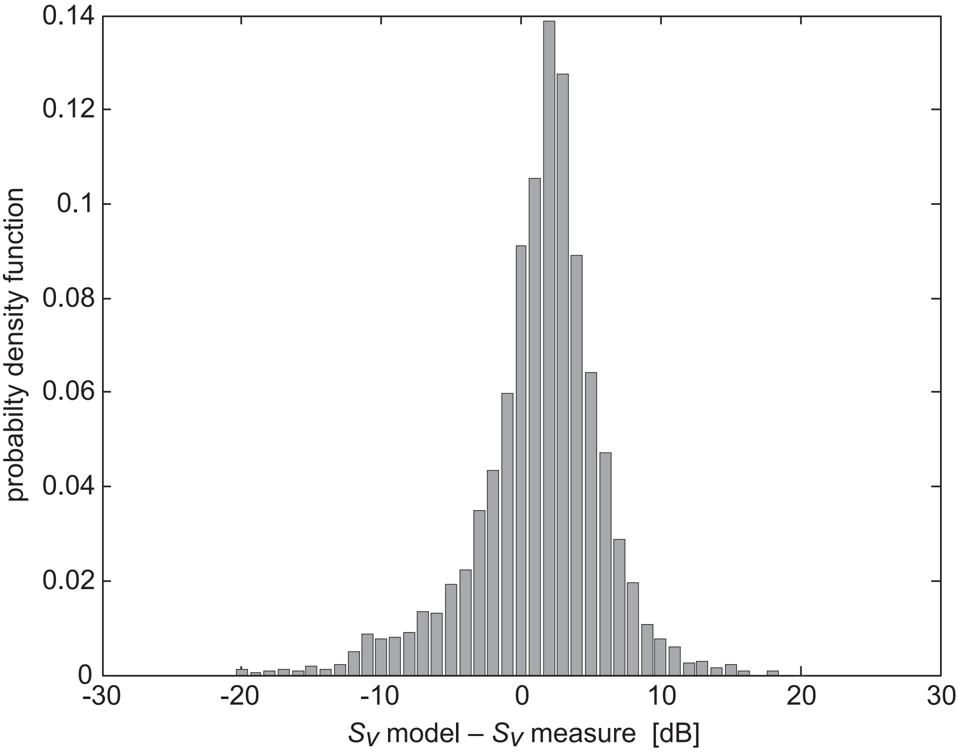

Fig. 8. Histogram of the differences between model predicted and directly measured values of backscattering strength computed for all transects made in 2010 and 2012.

gous to that measured by echosounder. Despite some differences in the absolute terms, there are strong correlations between the trends in the predictions and measurements. Both approaches revealed the same and synchronous zooplankton maxima and minima in S_V values. There are, however, several potential causes of non-compliance in our comparative studies, *e.g.* the sporadic presence of fish or larger zooplankters, very low zooplankton abundance and/or improper choice of the density and sound speed contrasts g and h.

In general, our investigations showed a good correlation and a close correspondence between measured and modelled zooplankton abundance peaks and distribution patterns. However, as acoustic estimates delivered by model are highly sensitive to changes in density and sound speed contrasts, some differences in the absolute S_V values were observed. In most of the analysed cases, the measured values were slightly lower than those predicted by the model. This difference could indicate that values of density and sound speed contrasts adopted in the calculation were generally too high. To check this option, some additional model test calculations were conducted. The values of g and h depend on the species and stage of development of individuals included in the sound scattering mixture that is studied (Stanton and Chu 2000). However, in model analyses mean g and h values for all scatteres have been

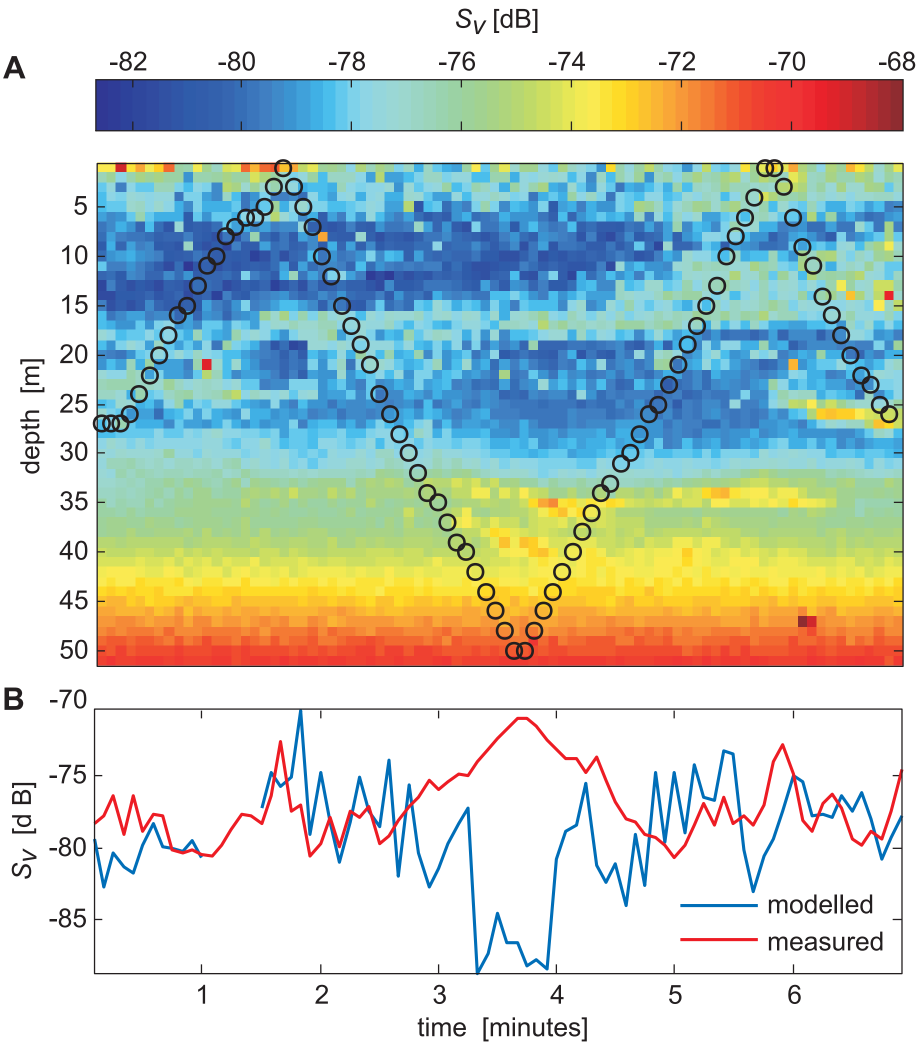

Fig. 9. **A**. Echogram with LOPC depth location (indicated by circles) during undulating mode operation. **B**. Echosounder record ofthe volume backscattering strength (S_V) (red curve) and S_V calculated by the model on the basis of zooplankton concentration measured by LOPC (blue curve) at varying depths. A 7-minute fragment of the southern transect 10-11 (2012).

assumed. In this study, literature values (Kogeler *et al.* 1987) were incorporated into our model calculations, and we then changed the value of one or both parameters by matching the measured S_V results to the results of modelling. In this way, we could determine the optimal value for each transect or for its selected fragments. In the first approach, $g = 1$ was assumed, and h was changed over the range of 1.01 to 1.03. For all studied transects, the difference between measured and modelled S_V was estimated, and its minimum value was found. When we neglected the noise-contaminated parts of S_V curves associated with acoustically undetectable zooplankton, the best fitting was obtained for *h* values between 1.012 and 1.0275. In most cases, this value was lower than the value of *h* previously applied in our modelling. The relationship between *g* and *h* for zooplankton is not known, but it can certainly be assumed that both parameters, which depend on the physical properties of zooplankton tissue and the surrounding medium, are changing in the same direction. Therefore, in the second approach, a regular increase in both parameters was applied from the minimum value $g = h = 1.0025$ to the maximum value $g = h = 1.05$. The best fit was obtained by using the value of $g = h = 1.013$, resulting in value of the Rayleigh reflection coefficient (eq. 6) $R = 0.0129$, which is significantly lower than the *R* applied in other studies (Pieper and Holliday 1984; Kirsch *et al*. 2000; Fielding *et al*. 2004; Lavery *et al*. 2007;) ranging from 0.0178 up to 0.1. But the value applied in this study was close to the reflection coefficient *R* (max = 0.0124) obtained by Smith and others (2010) for copepods from the Bering Sea. Unfortunately, the current state of our knowledge does not permit directly determining *g* and *h* values. In the case when the elastic properties cannot be measured in a direct way (Chu and Wiebe 2005), they have to be implemented from published data. The proper choice of these parameters is the most sensitive part of these analyses because it is crucial for getting reliable values, which in turn may influence any obtained agreement between the measured and modelled results.

Diversified zooplankton assemblages at the frontal zone. — We are aware that the zooplankton populations on both sides of investigated by us frontal area might differ with respect to species composition and diet, so their elastic parameters could also be slightly different. It is highly recommended to validate any theoretical assumption or model on a diversified dataset in order to test it under various conditions and we are satisfied that the model proved to be suitable in both hydrographical regimes. Therefore, we chose the frontal zone of the WSS waters to apply and test our acoustical-optical model for zooplankton distribution data. We observed various zooplankton assemblages in terms of their abundance, taxonomic composition and size spectrum. The colder less saline waters were generally full of small particles, possibly of mineral origin, as those particles dominate the suspensions in the coastal waters (Trudnowska *et al*. 2015). The inflow of Atlantic waters was associated with highly abundant *C. finmarchicus* assemblages, especially in the northern Magdalenefjorden region. These peaks were also observed in previous seasons (Trudnowska *et al*. 2012). They could also occur in the WSC waters near Hornsund in parallel with the relatively high contribution of the larger and lipid-rich copepod species *C. glacialis* often observed in waters on the eastern part of the front near Hornsund (Kwasniewski *et al*. 2012; Jakubas *et al*. 2013). Such co-occurrence of distinct zooplankton assemblages has proven to be of great importance for our model calculations. Diverse taxonomy, *i.e.* smaller or bigger species that have different lipid content, can require the usage of different values for the contrasts *g* and *h,* and size composition variation may in turn determine whether some zooplankters are detectable by acoustic backscattering.

Cases of discrepancy. — The low negative correlation R_{corr} = -0.03 between the modelled and measured S_V values throughout transect 14 could be explained by two recognised phenomena, a lack of zooplankton and the presence of fish. In the first part of the described transect (first 40 minutes), characterised by extremely low concentrations of zooplankton, the measured S_V reached the level of noise amplified by TVG, which was evidently higher than the S_V calculated from the model (Fig. 5). It is worth mentioning that, at the LOPC towing depth of approximately 25 m chosen for this transect (Table 1) and the absorption coefficient a = 0.1 dB m^{-1} (calculated for T = 2°C, S = 35 and f = 420 kHz), the signal amplification rate introduced by TVG (eq. 1) achieved a value of 33 dB (2000-fold). The high acoustically detected peaks in the last part of the analysed transect (last 30 minutes) were most probably associated with the presence of fish. These peaks could not be predicted by the model of sound scattering by zooplankton, but they were presented as examples of model disturbances, which had to be filtered out in further analysis. The local correlation calculated for consecutive fragments with a sliding window of 10-minute interval varied significantly along the studied transect (Fig. 5B). High local correlation (R_{corr} = 0.7) was obtained for the middle part of the analysed transect (50–90 minutes), which was affected by neither noise nor the presence of fish. After deleting the first part of the record dealing with low concentration of zooplankton, the correlation coefficient for the whole transect substantially increased (from -0.03 up to 0.30). After removing both “contaminated” parts, the first one with interfering noise and the last one laden with echoes from fish, the correlation coefficient reached a satisfying level (0.66).

Plankton size relevance. — The results obtained by comparison between measured and modelled S_V values allowed us to compare LOPC counts with echosounder recordings to establish a size threshold for acoustic detection. It could be expected that due to very weak scattering in the region $ka << 1$, the smallest particles detected optically could not be recorded by the echosounder. Therefore, a special test was conducted to examine the effect of neglecting the influence of small plankters on the modelled values of S_V by elimination, one by one, of the smallest size classes from the model calculations. In most cases, the omission of the first 10 classes (neglecting particles of ESD smaller than 300 μm) resulted in a difference in computed S_V smaller than 0.2 dB. Omission of the first 16 classes (neglecting particles of ESD smaller than 1.2 mm) gave a difference of no more than 0.5 dB. It was proven that the smallest particles with the highest abundance (< 1.0 mm ESD) were not relevant in the process of sound scattering and were not detected by the echosounder working at a frequency of 420 kHz. According to our model, one particle with a radius of 1 mm gives S_V = -103.6 dB, whereas one thousand particles 10 times smaller with radii of 100 μm give S_V = -115 dB, indicating that one bigger particle scatters 13 times more energy than one thousand smaller ones.

Methods specification. — Many methods of studying zooplankton distribution exist (*e.g.* net sampling, optical and video measurements, echosounding), and each of them is specific and characterised by an inherent bias in its sampling procedure. They all differ in resolution, sampling volume, counting accuracy, selectivity, identification capabilities and measured size range, so it is worth verifying and supplementing different techniques to develop, refine and validate individual approaches. The three methods used in our zooplankton investigations: biological, optical and acoustical are complementary but not equivalent. Therefore, we have not attempted to directly compare the zooplankton densities measured acoustically and optically with the net collected data. Each of the instruments used in our study sampled a different volume of water because of its construction and rules of operation. In addition, each of these devices detects a somewhat different component of the zooplankton community. We are aware that no single net or mesh size is suitable for sampling the broad size range of zooplankton species from mesozooplankton (mainly copepods ranging from 200 μm to 5 mm) to macrozooplankton. The net used in our survey (WP2) is adapted for collecting *Calanus* dominated communities, and it most likely undersamples both larger zooplankton, which can avoid net capture, and smaller zooplankters, which may be extruded or escape through the mesh openings (500-μm). The LOPC has a small entrance and also can substantially underestimate larger fast moving zooplankters such as euphausiids. In contrast, the acoustic measurements will detect these larger organisms (euphausiids, siphonophores and pteropods) as well as fish and gas bubbles. In addition, a portion of the small particles detected by the LOPC may have been of mineral origin, giving a much stronger acoustic echo than fluid-like particles. All of these differences seriously complicate the interpretation of the data and could be a source of the observed bias.

Therefore, it is a key matter to realise that direct comparison of zooplankton density detected by various tools is hazardous, as none of the known methods is perfect and gives unquestionably accurate results. What is really important is to verify whether the heterogeneity patterns in zooplankton distribution and composition structure have been accurately detected. A mathematical model of sound scattering by the collection of zooplankters can be a useful tool joining the abundance and size distribution of zooplankton as measured by LOPC with their scattering strength as measured by the echosounder.

Conclusions

This study is the first attempt to use Laser Optical Plankton Counter (LOPC) to paremeterise the mathematical model of sound scattering by zooplankton and to compare the results provided by a model supplied by LOPC assessed zooplankton size distribution with echosounding results. The measurements were carried out for the *Calanus* dominated zooplankton assemblages in the upper 50-metre depth layer of the West Spitsbergen frontal zone.

In summary, our study indicated good agreement between the measured and modelled values of backscattering strength in the epipelagial (0–50 m) zone of frontal West Spitsbergen Shelf waters, but to create a complete report of the model application, we demonstrated examples of good agreement and disagreement between the two values. Using two complementary methods of counting zooplankton, LOPC and echosounder, supported by mathematical modelling of sound backscattering and supplemented by net sampling, can be a useful tool for resolving spatial scales over which biological and physical factors are associated. This strategy can be especially important because planktonic organisms that respond relatively quickly to changes in their environment can be very good indicators of the state of a particular ecosystem, especially in the changing Arctic region.

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