

In situ target strength and behaviour of northern krill (*Meganyctiphanes norvegica*)

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Target strengths (TS) of individual krill were measured directly *in situ*. The study focused on scattering layers consisting mainly of krill, using a submerged echosounder to resolve individual krill at their daylight depths. Individuals were tracked for extended periods, and the method was capable of discerning differences in TS and behaviour within seemingly homogenous scattering layers. Krill size increased with depth. This was sometimes, but not always, reflected in TS. The relationship between TS and size broke down when larger krill deeper in the water column were prone to more upward swimming than shallow-living specimens, which reduced TS, but there were also unexplained variations in TS by depth. The variability of TS within the krill tracks was generally high, with deviations routinely exceeding 10 dB, further emphasizing the dependence of krill TS on behaviour. Therefore, although measured values of TS were within the ranges previously reported for krill, it was difficult to apply fixed TS–size relationships. The study underscores the need to determine the impact of behaviour on TS, and shows that appropriate methods to do so are now available.

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Introduction

The order Euphausiacea carries an important role in many oceans (Mauchline, 1980), especially in the Antarctic (Nicol and Endo, 1999), but krill are also key components in the northern Atlantic. Estimates of krill abundance are routinely based on acoustic methods (Hewitt and Demer, 2000). In order to convert measured acoustic intensities to biomass estimates, it is necessary to know krill TS (target strength, a measure of sound backscattered from an individual). Recent modelling leading to revised values for TS, combined with a re-analysis of acoustic data, have concluded that earlier biomass estimates for Antarctic krill (*Euphausia superba*) may be in error by a factor of 2.5 (Demer and Conti, 2005). Acoustic studies of the northern krill (*Meganyctiphanes norvegica*) have been motivated by a need to assess its behaviour and role in the ecosystem (Onsrud and Kaartvedt, 1998; Tarling *et al.*, 1998; Liljebldh and Thomasson, 2001), but also by its morphological similarity to Antarctic krill (Conti *et al.*, 2005).

Krill TS can be estimated by several methods. One approach has been to convert total measured backscatter

from an ensemble of krill, for which biomass or abundance is known, into individual backscatter (Sameoto, 1980; Foote *et al.*, 1990; Pauly and Penrose, 1998). Another approach is the direct measurement of the TS of individual krill (Wiebe *et al.*, 1990; Hewitt and Demer, 1991, 1996; McGehee *et al.*, 1998; Lawson *et al.*, 2006). Both approaches have often been coupled with physical models, which allow more detailed inferences of the properties of the backscatter from individuals (McGehee *et al.*, 1998; Stanton and Chu, 2000; Demer and Conti, 2003a; Lawson *et al.*, 2006), i.e. they help to identify the factors important to the TS of individual scatterers. These factors include physical parameters such as size, density, and sound–speed contrast in the organisms, but have also emphasized the importance of krill behaviour, mediated through krill orientation (the tilt angle).

Physical models can adequately describe TS in the laboratory, but the scaling of these results to natural environments is currently hampered by a lack of knowledge about natural behaviour, especially regarding the tilt angle. Theoretical studies suggest a strong influence of it on TS (McGehee *et al.*, 1998), yet lack of knowledge of *in situ*

behaviour has so far often forced investigators either to take this variable from values measured *ex situ* (Kils, 1981; Miyashita *et al.*, 1996), or even to infer the value from acoustic data (Demer and Conti, 2003b).

In a previous study, we showed that it is possible to address the behaviour and TS of individual krill *in situ* by means of submerging split-beam echosounders into krill scattering layers (SL; Klevjer and Kaartvedt, 2003). In the current study, we apply this approach in the Oslofjord, where studies of krill SLs have been carried out over many years (Onsrud and Kaartvedt, 1998; Kaartvedt *et al.*, 2002; Klevjer and Kaartvedt, 2003; Onsrud *et al.*, 2004). Although earlier studies have measured the *in situ* TS of krill directly (Hewitt and Demer, 1991, 1996; De Robertis, 2001; Lawson *et al.*, 2006), this study is, to our knowledge, the first to utilize target tracking to study TS and TS variations of individual krill *in situ*, and to couple details of TS with the behaviour of the same individual.

Materials and methods

The study was conducted in the inner Oslofjord, mainly between November 2003 and February 2004, but with additional sampling performed in December 2004 (Table 1). Most data were collected at stations in the same basin as Station “Steilene” (59°48′N 10°34′E), where several previous studies described the fauna and ecology in detail (Bagøien *et al.*, 2000; Onsrud *et al.*, 2004). Sampling was performed both in the deepest part of this basin, and at a nearby, shallower station (59°48′N 10°32′E).

Pelagic sampling was performed with a modified 3-foot Isaacs–Kidd midwater trawl (IKMT) aimed at different parts of the scattering layers, and with a young-fish trawl. The IKMT has an aperture of 0.66 m², and was equipped with a net of 500- μ m mesh to catch even the smallest krill. The young-fish trawl had a vertical opening of \sim 10 m and

an aperture of \sim 100 m², with a mesh size decreasing from 20 cm at the opening to 1 cm at the rear end. Both gears were directed at specific depths with the help of a SCANMAR depth sensor, attached to the headrope. The small aperture of the IKMT combined with the depth sensor allowed us to aim the catches at different depths, usually with an accuracy better than \pm 2.5 m, although the lack of a closing device on the net meant that some organisms were caught shallower in the water column during launching and retrieval of the gear. The near-bottom fauna was sampled by a bottom (shrimp) trawl. In all, eight tows were taken with the IKMT, four with the young-fish trawl, and two with a bottom trawl during daylight.

Random subsamples of krill were conserved in 4% formalin; these specimens were later measured for telson–rostrum length (Sameoto *et al.*, 1993) to the nearest millimetre in the laboratory, but not corrected for shrinkage. Length measurements for December are based on random subsamples of frozen krill.

During the acoustic mapping and biological sampling, acoustic data were collected with the ship’s EK500 echosounder, utilizing the hull-mounted transducers at 120 and 38 kHz. During the acoustic sampling of TS data, the 120-kHz transducer was turned off because it interfered with the submersible equipment (see below). The EK500 data were used mainly to identify regions of interest, and to monitor the distribution of fish below the vessel.

“Primary” acoustic data were collected with a SIMRAD EK60 echosounder housed in a pressure chamber, attached to a 120-kHz ES120-7 transducer with a short (\sim 1.5 m) cable, so minimizing signal loss. Digitized signals from the echosounder are transmitted to the vessel via a cable, which also provides the echosounder with power. The transducer and electronics were suspended by cable from the side of the ship, facing downwards, at different depths, but typically close to or inside scattering layers identified from the surface. During acoustic sampling the ship was moored,

Table 1. An overview of sampling and calibration. The calibration days have been italicized, and results presented as distributions are from the days shown in bold type. All night-time sampling has been omitted from the table for the sake of brevity.

Date	Equipment	Depths (m)	Comment
11.11.2003	Pelagic trawl	Several	Ground-truthing, daylight
<i>01.12.2003</i>	<i>EK60</i>	<i>0</i>	<i>Calibration submersible acoustic equipment, 128/256 μs</i>
02.12.2003	EK60, submerged	40, 60, 80, 100	Submerged with calibration sphere, 128 μ s pulse
15.01.2004	EK60, submerged	70, 80	Submerged with calibration sphere, 128 μs pulse
15.01.2004	IKMT	\sim 80 m	Two hauls, before and after acoustic sampling, same depth (\sim 80)
22.01.2004	IKMT	75, 90	Two hauls daylight, different depths
03.02.2004	EK60, submerged	70, 80, 90	Submerged with calibration sphere, 128 μs pulse
03.02.2004	IKMT	75–80	One haul, daytime
04.02.2004	Pelagic trawl	50, 60, 75, 85	Ground-truthing, daylight
05.02.2004	Bottom trawl	—	Ground-truthing, daylight
<i>15.03.2004</i>	<i>EK60</i>	<i>0, 25, 50, 75, 125</i>	<i>Calibration submersible acoustic equipment, only 128 μs</i>
<i>16.12.2004</i>	<i>EK60</i>	<i>0</i>	<i>Calibration submersible acoustic equipment, only 256 μs</i>
17.12.2004	EK60, submerged	55, 60, 65, 70, 80	Submerged without calibration sphere, 256 μs pulse
17.12.2004	IKMT	65, 75, 85	Three hauls, daylight

using three anchors, and the sea state was always calm. The pulse repetition rate (i.e. ping rate) of the echosounder was set to obtain as many echoes per target as possible, and the results presented here were collected at 5–10 pings per second. Data were also collected with the same transducer mounted on the bottom, looking upwards, but these are only included in the analysis of TS variation within tracks.

The submersible echosounder was calibrated prior to and after sampling. Additionally, a calibration sphere was suspended below the transducer on several sampling days. The TS of the sphere showed small, systematic variations with time which could not be explained because the sphere remained at the same position in the beam. Similar discrepancies have been described previously for the EK60 (Jech *et al.*, 2005), albeit at a different frequency. The largest deviations of time-averaged TS of the sphere were <1 dB.

Split-beam transducers provide three-dimensional echo positions, given that individual targets are resolved. By connecting echoes from an individual organism (target tracking), the behaviour of the organism may be established.

Raw data were collected at pulse lengths of 128 or 256 μ s, and subsequently imported to Sonar 5 software (Balk and Lindem, 2000, 2002), where echo detection and target tracking were performed. Several methods were tested, with echoes being detected both by Sonar 5's implementation of SIMRAD's echo-detection algorithm, as well as by the cross-filter detection option in Sonar 5 (Balk and Lindem, 2002). Also, different methods for tracking were tested, both automated and fully manual. In most cases, the TS distributions generated by the different echo-detection methods, as well as the tracking methods, were comparable. Manual tracking on echoes detected by the conventional echo-detection algorithm was selected as the method for obtaining TS distributions, because this algorithm is less likely to include erroneous echoes, and more directly comparable with previous measurements (Hewitt and Demer, 1996). Accepted echoes were in the region 0.6–1.4 relative pulse lengths, having a standard deviation in the phase measurements of <10 phase-steps, as well as having a beam-pattern compensation of <3 dB. For the results used to study TS variations in individual targets, Sonar 5's cross-filter was used for echo-detection, because this algorithm has a higher probability of detection than the SIMRAD algorithm. Again, manual tracking was the preferred tracking method, but in that instance no restrictions were made with regard to beam pattern. For both procedures, no tracks were accepted farther from the transducer than 15 m, most being closer than 10 m.

The tracks were generated by manually selecting echoes within regions on the echograms containing single targets. The results obtained were subjected to a simple low-pass filter in order to remove the influence of erroneous position measurements and spurious echoes. After tracking, a simple five-point running mean was applied to each of the four variables (range, alongship angle, athwartship angle, and TS) in a track. The difference in position between the running

mean and the original positions was weighted (weights were arbitrarily chosen: range 1; TS 0.1; both angular positions 0.25) and summed over all four parameters, producing a score for each echo in the track. Echoes with scores that exceeded the mean score +2 standard deviations were excluded from the tracks. The procedure therefore mimicked some features of the automated tracking procedure, and tended to reduce the number of outliers that otherwise would be included through the relaxed strictness of the manual tracking procedure. The main argument for selecting that procedure was that it allowed us to verify visually that tracking was restricted to volumes of low density of organisms, therefore minimizing the potential biases introduced by multiple echoes. The method also makes it less likely that single traces left by organisms are "split" and measured several times (Xie, 2000). The tracks from several cruises were used in the overall analysis (Table 1). Only daylight data were included.

In an effort to estimate the influence of vertical behaviour, the average track angle of the krill, defined as \tan^{-1} of the ratio between vertical and horizontal velocities was calculated, with velocities calculated from linear regressions on the positions. This estimate of how much of the total swimming effort is directed at vertical movement is sensitive to the movement of the vessel, currents, and the detailed three-dimensional behaviour of the organism, as well as inaccuracies in the measurements, but nevertheless provided a useful proxy for this study. The measure is not expected to be directly comparable with the angle of body orientation (the tilt angle), because the tilt angle of a krill swimming horizontally will vary according to swimming speed (Kils, 1981).

Measurements of track angle are sensitive to the movements of the ship and the horizontal currents. The impact of these factors was assessed by comparing the track durations, because both a drifting ship and a strong current field would tend, on average, to reduce them. The average track duration is, however, dependent upon the average tracking depth, so additional tests were included. We assessed the influence of currents by computing the net movement in the horizontal plane of all tracked organisms over 15-min periods, and corrected the tracks used for the computation of track angles for movements caused by currents. If higher densities of tracks had been obtained, we would have been able to assess quantitatively the influence of more short-term movements, such as tilting and rotation of the transducer, in the same way, but we had to resort to manual scrutiny of tracks to check whether platform movement influenced the results.

Results

Biological sampling

In late winter (January and February 2004), krill dominated the biomass among the invertebrate organisms in the IKMT catches, which otherwise consisted of chaetognaths and

copepods, plus remnants of a few gelatinous plankton, normally destroyed beyond recognition and enumeration. Random subsamples from the five hauls contained a total of 865 krill, four gobies (*Crystallogobius* sp.), and one pelagic shrimp (*Pasiphaea* sp.).

Krill catches by the IKMT in January and February were dominated by *Meganyctiphanes norvegica*, with some smaller krill belonging to the genus *Thysanoessa*. At least three size modes were found in the catches, the most evident being small krill with a mode around 11–12 mm dominated by *Thysanoessa* sp., a mode centred around 24–25 mm krill (*M. norvegica*), and large krill >30 mm (Figure 1a). Krill were totally dominant also in the catches from December. Subsamples of potential “large” scatterers from three hauls contained 283 krill, one goby, and one *Pasiphaea*. At this time, the small krill mode (<15 mm) was virtually absent from the catches. Krill sizes increased with depth (Figure 1b, c). The larger size group was almost exclusively caught in deeper hauls.

Krill were the dominant invertebrates also in the catches from the larger trawl, which did not reveal any additional major pelagic invertebrate components (not shown). Although not captured pelagically in larger numbers, the bottom trawl revealed that shrimps of the genera *Pandalus* and *Pasiphaea* were moderately abundant at the bottom.

TS distributions and variability within the tracks

TS distributions from the tracks recorded with the transducer within the scattering layer during January and February reveal most tracks with values in the region –77 to

–68 dB (Figure 2a, b). The number of tracks declined rapidly for TS values larger than –70 dB, with peaks of the distributions at approximately –70 dB. In January and February there was an increase in TS by depth (Figure 2a, b, Table 2). This pattern was not replicated in the TS distributions generated in December, when the number of weak TS values increased in the deepest intervals (Figure 2c), although the size of krill from the IKMT catches increased with depth (Figure 1c).

Of a total of 4982 tracks, approximately 3000 were collected with the transducer looking upwards from a firm substratum. Figure 3 shows ping-to-ping variations in selected single targets, along with the resultant TS distribution from single tracks. For clarity, only a subset of the data points have been plotted in the three-dimensional plots. The large range in TS is a prominent feature of some tracks. In one case, the organism was swimming in tight loops (Figure 3, left column). The looping behaviour resulted in relatively rapid, large fluctuations in TS, a feature that can be seen in the echograms as a “pulsation” of the traces. This behaviour was also observed from the bottom-mounted, upward-facing transducer. Another consequence of the three-dimensional looping is that despite swimming actively, the animal may remain within a relatively confined volume for extended periods of time, resulting in tracks of long duration, some track lengths exceeding 2000 pings. Different behaviour may severely affect the resulting TS distributions. For example, the behaviour shown in the middle column of Figure 3 results in a bimodal TS distribution, with peaks centred at –76 and –71 dB. Other invertebrates could be distinguished from krill by their behaviour (and

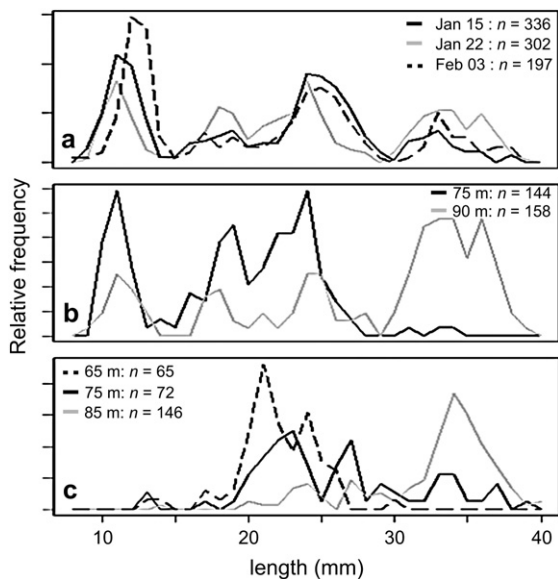


Figure 1. Krill length distribution in catches of the Isaacs–Kidd midwater trawl. (a) From pooled samples on 15 January, 22 January, and 3 February 2004; and from vertically resolved samples on (b) 22 January and (c) 17 December. n denotes number of measured individuals.

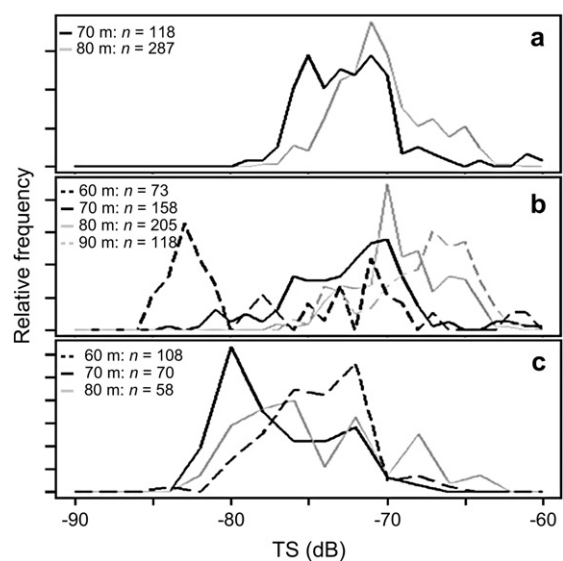


Figure 2. TS distributions for manually tracked individuals recorded by a 120-kHz echosounder lowered into scattering layers on (a) 15 January, (b) 3 February, and (c) 17 December 2004. Depths are transducer depths. The number of tracks is indicated by n .

Table 2. Summary measurements. Average TS was computed by taking the average (in the linear domain) of all tracks with average TS less than -65 dB, and other statistics refer to “full” distributions. Ave KL and SD KL refer, respectively, to average krill length and standard deviation of krill length in the Isaacs–Kidd midwater trawl catches closest to the effective acoustic observation window. All measurements are in mm.

Date	Depth (m)	Average TS (dB)	First quartile (dB)	Median TS (dB)	Third quartile (dB)	Tracks/measured	Ave KL	SD KL
02.12.2003	60	-74.2	-72.1	-74.1	-78.0	133	*	*
02.12.2003	80	-71.7	-69.9	-72.6	-75.5	51	*	*
02.12.2003	100	-72.4	-72.3	-74.3	-76.8	27	*	*
15.01.2004	70	-72.3	-70.8	-72.5	-74.8	104	(19.6/22.1)†	7.8
15.01.2004	80	-70.1	-69.0	-71.0	-72.6	262	(19.6/22.1)†	7.5
03.02.2004	50	-74.2	-72.1	-83.1	-85.7	121	*	*
03.02.2004	60	-75.1	-71.6	-78.4	-83.3	66	*	*
03.02.2004	70	-71.8	-70.2	-71.9	-74.3	135/197	20.94	8.1
03.02.2004	80	-69.3	-68.0	-70.0	-71.1	206	*	*
03.02.2004	90	-68.2	-65.9	-67.8	-70.3	126	*	*
17.12.2004	50	-77.0	-76.4	-77.9	-79.3	98	*	*
17.12.2004	60	-75.1	-74.0	-75.3	-78.3	102/65	22.0	2.8
17.12.2004	65	-74.4	-73.2	-75.5	-77.3	85/72	26.0‡	5.7
17.12.2004	70	-76.6	-75.2	-78.9	-81.2	63/72	26.0‡	5.7
17.12.2004	80	-73.4	-73.2	-76.4	-79.1	55/146	32.4	4.7

*Denotes no suitable observations.

†Refers to pooled catches from two hauls from the same depth, with sampling performed both prior to and after acoustic sampling.

‡Refers to the same haul, the sampled depth was 75 m.

TS). Typical of another type of track, in this case possibly caused by the jellyfish *Cyanea capillata*, which was present in the catches (Figure 3, right column), is both the slow swimming speed (i.e. the length of the track) and the much less variable and stronger TS.

Although the median ping-to-ping variations in TS within the tracks were relatively small (mean 0.84 dB, s.d. 0.54; Figure 4a), the range of TS values ($TS_{\max} - TS_{\min}$) recorded within tracks were fairly high (median 4.5 dB; Figure 4a). Therefore, the average TS for a track may arise from a fairly wide distribution of individual echo strengths (Figure 4b).

Vertical behaviour and TS

An evident effect on TS was seen when animals changed their orientation within a track, with the reduction in TS associated with vertical swimming at times being >15 dB (Figure 3c). Using all tracked individuals, there appeared to be a relationship between the estimated track angle and the average TS in tracks (Figure 4c). The echograms shown in Figure 5 were recorded from different parts of the scattering layer, and show how vertical behaviour may vary with depth. Although most individuals in the upper echogram descended, most of those below 100 m maintained depth or were swimming slightly upwards. The differences in behaviour probably go beyond this, however, because closer inspection of the traces reveals that whereas individual traces at 60 m are markedly pulsed, most of those recorded at 100 m are not. Further analysis of track angles plotted against depth is shown in Figure 6, and the corresponding

distributions of track durations are shown in Figure 7. The medians of track angles are generally close to zero, although an exception to this is in the deepest interval on 17 December, where a greater proportion of the population than usual seems to be swimming upwards. The distribution of track angles recorded at 80 m then differed significantly from track angles recorded higher in the water column (two-sided Kolmogorov–Smirnov test, $p < 0.001$ for both depths). The analysis of population net displacement speeds revealed *in situ* current speeds ranging from 0.3 to 4.5 cm s^{-1} (mean $\sim 1 \text{ cm s}^{-1}$), although all estimated current speeds exceeding 3 cm s^{-1} occurred in time-bins containing fewer than 50 tracks.

Discussion

Methodological considerations

This study has shown the feasibility of using target tracking for *in situ* TS measurements of individual krill. Resolved individuals could be followed for more than 2000 pings, because some were swimming in loops and thereby remaining for long periods within the narrow acoustic beam. The TS values were clearly affected by the swimming behaviour. The TS measurements were of sufficient quality to indicate size differences within the population, but the results showed that krill TS is closely linked to *in situ* swimming behaviour, and that this may break the TS–size correlation.

Some technical difficulties were partly, although probably not totally, overcome by the procedures followed. To minimize threshold-induced bias, which reduces detection

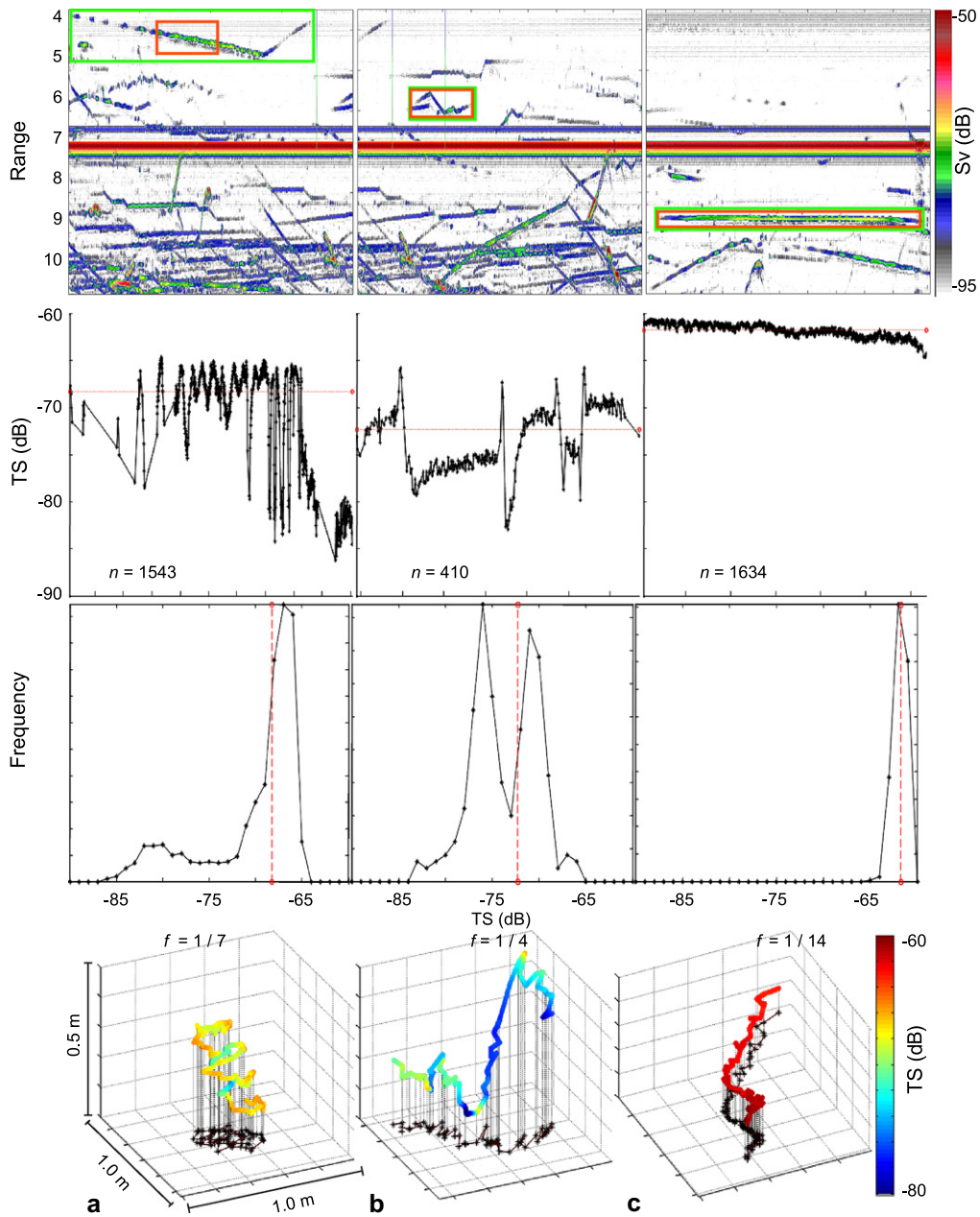


Figure 3. Selected single tracks inside the scattering layer, 2 December 2003. Row 1: Echograms ($200 \text{ s} \times 10 \text{ m}$; TVG, $40 \log R$), with organisms inside green boxes; Row 2: TS plotted against ping (n is the track duration in pings); Row 3: TS distribution; Row 4: three-dimensional (3D) swimming pattern ($1 \times 1 \times 0.5 \text{ m}$). Only a fraction (f) of the data within the bounding red boxes in the echograms is plotted in 3D, and colours are the interpolated TS between echoes. (a) and (b) show krill with the transducer at 100 m, and (c) is a larger scatterer, possibly a jellyfish, with the transducer at 60 m.

probability for the smallest krill (Hewitt and Demer, 1996; Pauly and Penrose, 1998), the sample range for echoes was kept to $<15 \text{ m}$, and only echoes close to the centre of the beam were included in the overall distributions. However, the requirement of several echoes to form a track probably accentuated this problem, and at present we lack

a framework to quantify just how much the measured distributions are biased towards larger values.

We are confident that multiple echoes do not have a significant effect on our results. The manual tracking was conducted only in regions of relatively low target density, in order to minimize the possibility of there being multiple

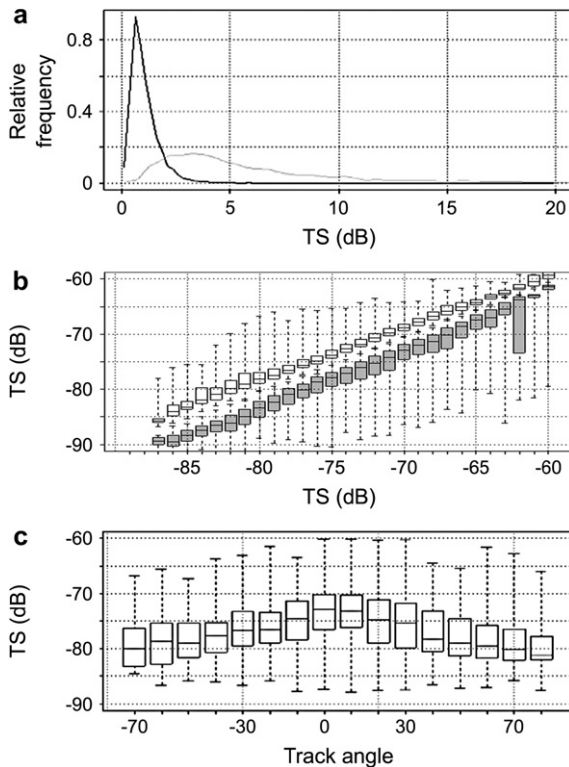


Figure 4. Properties of TS, based on data collected from both free-hanging and bottom-mounted, upwards-looking 120-kHz transducers. (a) Distributions of TS range ($TS_{\max} - TS_{\min}$) (grey line) and average ping-to-ping variations (black line): ($\text{abs}(TS_n - TS_{n-1})$) within tracks, (b) distributions of TS_{\max} (white) and TS_{\min} (grey) plotted against average track TS, and (c) average TS plotted against average track angle. In (b) and (c), the box plots are bounded by first and third quartiles, the central line is the median and whiskers show the range of values. Track angles have not been corrected for currents or movements of the platform.

echoes. Additional analysis done in Sonar 5 showed that the average Sawada index (Sawada *et al.*, 1993) for all data in the region 5–15 m was within acceptable limits (0.045). The low-pass filter ensured that echoes accepted within single tracks were rejected if their three-dimensional position was not relatively close to the preceding echo. This provided an additional filter against echoes resulting from multiple targets. Restricting the echoes used for analysis through the tracking procedure is also expected to lessen artefacts caused by erroneous position estimations, which may influence TS through wrong beam-pattern compensation.

The calibration sphere lowered together with the transducer during several of the sampling operations was used to monitor the performance of the system when it moved into the scattering layer. The TS of the calibration sphere varied slowly with time, and suggests that over time the accuracy of our particular system varied by approximately 1 dB.

The estimated track angles were corrected for the average movement of the population, which we interpret as

the influence of currents, estimated by measuring the net population movement over intervals of 15 min. Manual scrutiny of the tracks has convinced us that rotation or tilting of the transducer is not a problem in our data. Visual controls suggest that most tracks have negligible curvature, and those that do not, such as the first track in Figure 3, can usually be verified by at least partially overlapping tracks.

Identification of organisms

The IKMT and trawl catches corroborate that krill were the main acoustic targets. In the catches of the IKMT hauls aimed at the scattering layers, krill outnumbered other organisms of similar size by 164 to one. The pelagic trawl catches agreed with this, alternative targets such as *Pasiphaea* and jellyfish being caught only in low numbers.

Most of the average TS (Table 2) of the distributions measured here are close to, but slightly higher than, the range of previous TS measurements of Antarctic krill of approximately the same length (Foote *et al.*, 1990; Hewitt and Demer, 1991, 1996; McGehee *et al.*, 1998; Pauly and Penrose, 1998; Lawson *et al.*, 2006) and at the same frequency (120 kHz). However, close to the seabed, where it was not easy to sample with high vertical resolution, the acoustic data for February showed a high proportion of tracks with TS stronger than -65 dB, clearly above previously reported average values (Figure 2c). The only reason to question the identity of these targets would be the higher-than-expected TS. Neither the catches nor the inferred behaviour suggest that taxa other than krill were of major influence in the daytime data. Bottom-trawl catches revealed the presence of both pasiphaeid and pandalid shrimp in the same area, but comparisons with night-time results (not shown) suggested that the pandalids at least formed an acoustically and behaviourally distinct component when they swam up from the bottom during darkness.

If the strong targets indeed represent krill, one possibility for the apparent disparity with previous assessments may be that the estimation of krill TS is made under the assumption that krill will present themselves in dorsal aspect, and this may or may not hold true in a natural environment. The values presented here are well within the values measured *in situ* for the side aspect of Antarctic krill (Hewitt and Demer, 1996). Inclusion of lateral TS measurements in the data may also be a contributing factor to the large variance in TS seen in these tracks, with measurements routinely varying by >10 dB within tracks.

TS variation and behaviour

The TS measured within tracks had a wide range, the modal difference between the largest and the smallest TS measured for single tracks being 4 dB. It was expected that the average range of TS measurements ($TS_{\max} - TS_{\min}$) would increase with average TS of the track, because there is both a bias against weak echoes and an expectation that

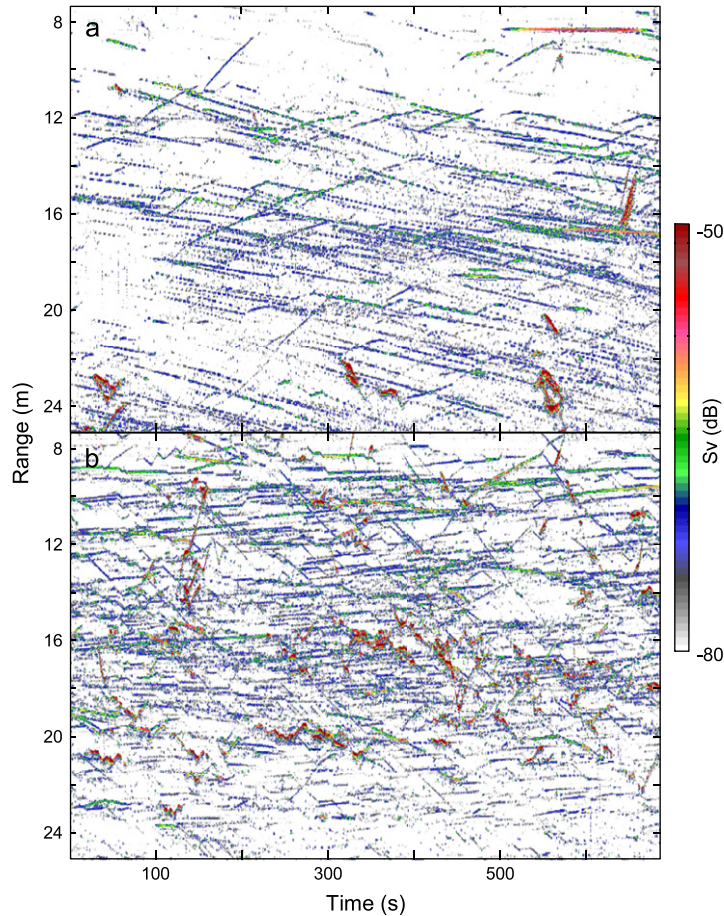


Figure 5. Echograms showing differing vertical behaviour in different parts of the scattering layer (2 December 2003), with the transducer at (a) 60 m and (b) 100 m, separated by about 40 min. Both echograms recorded with the same range to the transducer.

there should be less fluctuation in TS from a smaller organism than from a larger organism (Stanton *et al.*, 2004). From the distributions of TS ranges (Figure 4b), such a pattern is not evident in the ranges between -85 and -65 dB. While this may reflect true variations in TS for these organisms, i.e. variations introduced by both behaviour and physical scattering properties, it is also influenced by weaker targets being less accurately positioned, and so being more prone to receiving an incorrect beam-pattern compensation. Ping-to-ping variability in TS showed dependence on track average TS (not shown), which was particularly noticeable for tracks weaker than -77 dB. Therefore, the inclusion of echoes from only a relatively narrow portion of the beam did not fully eliminate this bias.

Despite variability introduced by the method, we ascribe most variation to behaviour. Much of the variability in the selected tracks is systematic, particularly for tracks where the krill appeared to swim in relatively tight loops. Moreover, the largest deviations in TS were in those tracks where krill changed their vertical orientation within the tracks: a krill changing from a slightly downward direction

(sinking/swimming downwards) to upward swimming could have its TS reduced by at least 15 dB, and this range is probably restricted by the effective detection threshold. The large variance of TS in single krill underscores the need to obtain numerous echoes from each organism in order to size it accurately by acoustic methods (Wiebe *et al.*, 1990).

The krill comprised at least three size groups (Table 2; Figure 1a), with the largest individuals being captured in the deepest tows (Figure 1b, c). Krill within a population may segregate according to size (Mauchline, 1960), larger individuals staying deeper in the water column. In the Oslofjord, sampling over several years has revealed that trawls from the deeper parts of the scattering layers usually have a higher proportion of large krill than shallower hauls (unpublished data). In some data (Figure 2a, b), there is a trend of increasing TS with increasing depth. However, in data from December 2004 (Figure 2c), the initial trend of increasing TS is reversed in the two deepest intervals. Median krill TS recorded with the transducer at 70 and 80 m was lower than records at 60 m, despite the larger

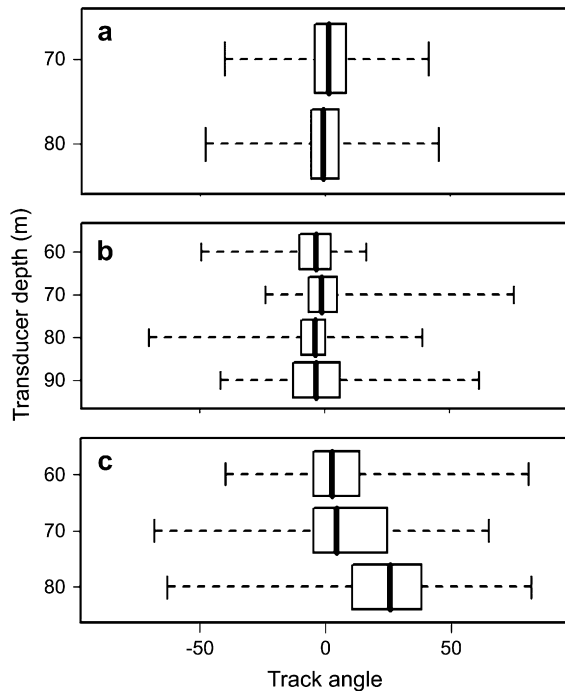


Figure 6. Track angles plotted against transducer depth, with the track angles corrected for current speeds inferred from average population movements. (a) 15 January 2004, two transducer depths, (b) 3 February 2004, four transducer depths, and (c) 17 December 2004, three transducer depths. Box plots are bounded by first and third quartiles, with the median shown as the central line and whiskers extending to extremes of measurements.

size of the krill in the deepest interval (Table 2; Figure 1b). The average TS at 80 m is slightly higher, but the average will be markedly influenced by the few stronger targets found there (Figure 2c). Different behaviour among the vertically segregated krill is one possible explanation for this discrepancy with the catch data. At least in the deepest part of the water column, the population has a distribution of track angles different from that of the shallower part of the population (Figure 6c), which, as might be expected, leads to reduced TS (Figure 4c). However, the distribution recorded at 70 m also has a much reduced TS when compared with the shallowest distribution, despite comparable track angles, and we are not able to explain all the variation in the data. Modelling has shown that TS is non-linearly related to krill length, so variation in TS may also be caused by the scattering properties of krill.

In the data collected on other dates (Figure 2a, b; Table 2) TS increased with depth, along with the krill size distribution, without any obvious differences in the simple measure of krill behaviour used. The differences in TS found here probably reflect a change in the size distribution. Recent modelling of krill TS (McGehee *et al.*, 1998; Demer and Conti, 2003a) has simplified krill behaviour to a “static” distribution of aspect angles, describable through a mean and a standard deviation for the population as a whole.

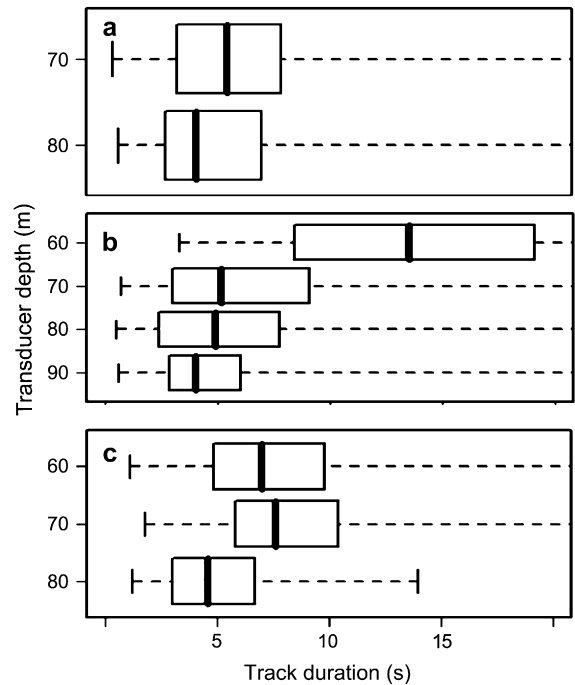


Figure 7. Durations of tracks plotted against transducer depth. (a) 15 January 2004, two transducer depths, (b) 3 February 2004, four transducer depths, and (c) 17 December 2004, three transducer depths. Box plots are bounded by first and third quartiles, with the median shown as the central line and whiskers extending to extremes of measurements.

Previous investigators have attributed large differences in krill scattering between day and night to changes in behaviour and orientation (Everson, 1982), and have recommended that acoustic surveys of krill biomass be corrected for biases introduced by migration (Demer and Hewitt, 1995).

Our results show that the behaviour of krill may vary with both time and depth, adding further complexity to the relationship between krill size and TS, even in periods where the behaviour perceived from the surface may seem homogenous. Krill swimming in loops has been described previously (Widder *et al.*, 1992; Figure 1C of Klevjer and Kaartvedt, 2003), and during the course of this study was the dominant behaviour on some occasions, though at other times it was not much in evidence. As TS fluctuated strongly during a loop, the prevalence of this behaviour could influence the results of krill acoustic surveys.

The acoustic properties of krill have generated much interest, particularly because of the importance of krill in the Antarctic ecosystem. Many studies on krill TS have focused on physical properties, and much recent progress has come through modelling studies (Demer and Conti, 2005). Although such studies emphasize krill aspect angle as a crucial factor for TS, little is known about natural behaviour *in situ* (although see De Robertis *et al.*, 2003). The results of the current study suggest that krill behaviour, including aspect angle, is highly dynamic and may vary

both with depth and time. We have shown that methods are now available to focus on behavioural aspects *in situ* and to allow us to discover to what extent TS is related to size and to behaviour.

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