

Split-beam target tracking can be used to study the swimming behaviour of deep-living plankton in situ

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Abstract

A scattering layer consisting mainly of krill (*Meganyctiphanes norvegica*) was studied with a submersible transducer, to assess the behaviour of individual organisms in situ by means of split-beam target tracking. Individuals were resolved and tracked, but a rapid increase in average swimming speeds with depth suggested that inaccuracies in the angular estimates affected the estimates. Attempts were made to smooth the tracks during post-processing. Smoothed speeds suggested that most (>78%) invertebrates swam at speeds below 12 cm s^{-1} (mode $\sim 4 \text{ cm s}^{-1}$), with components of speed larger in the horizontal plane than in the vertical.

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1. Introduction

Knowledge of natural behaviour is needed in order to get sensible results from models for predator-prey encounter and individual somatic growth (Gerritsen and Strickler, 1977; Torres and Childress, 1983). However, little is known about the swimming behaviour of individual euphausiids in situ (Jaffe et al., 1999), and until recently no non-intrusive method has been available.

Split-beam target tracking (TT) is a relatively new approach for studying individual behaviour (Brede et al., 1990), and the method has so far mainly been aimed at fish (for instance: Huse and Ona, 1996; Torgersen and Kaartvedt, 2001). TT has the capability to measure swimming speed independently of visibility, with a minimum of disturbance (Arrhenius et al., 2000). The main disadvantages are that the true identity of the studied organisms can only be inferred (MacLennan and Simmonds, 1992), and that the accuracy and precision of the measurements are variable (Ehrenberg and Torkelson, 1996; Mulligan and Chen, 2000).

Røstad (2000) used a hull-mounted 120 kHz transducer to track individual krill in shallow water during nighttime. However, for krill in the deep-scattering layer, the ranges involved preclude the use of hull-mounted transducers for

studies of individual behaviour due to large sampling volumes, low signal-to-noise ratio (SNR) and low spatial resolution. In this study, we explore the possibility of using a submerged transducer to unveil the behaviour of individual macrozooplankton (mainly krill, *Meganyctiphanes norvegica*), at depth.

2. Materials and methods

The study was conducted in the Oslofjord, Norway, at position (59°48'N, 10°34'E) in the period between 15 and 17 March 2000. This particular station was chosen because the calm conditions of the inner Oslofjord facilitated manoeuvring and deployment of a free-hanging transducer, and also because the pelagic community at this 120 m deep location has been described through several previous studies, establishing krill as a major component of the fauna and acoustic targets at 120 kHz (Onsrud and Kaartvedt, 1998; Bagøien et al., 2000; Kaartvedt et al., 2002).

Backscattering data were collected at 38 and 120 kHz with a Simrad EK500 split-beam echo sounder (software version 5.3) from the RV "Trygve Braarud". The ship used three anchors to avoid drift. From the hull-mounted transducers, a scattering layer starting at $\sim 75 \text{ m}$ was observed at 120 (Fig. 1A) but not at 38 kHz.

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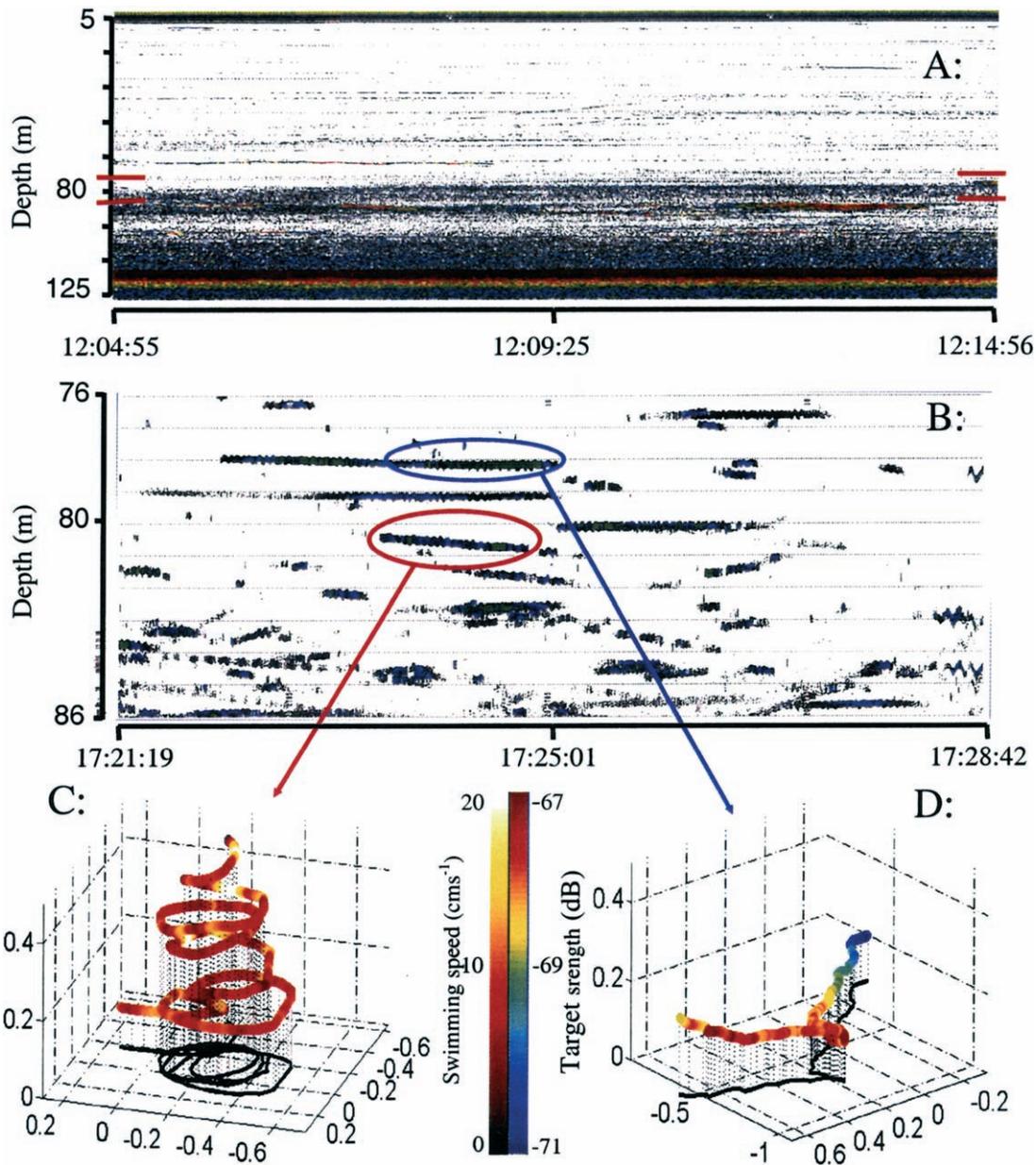


Fig. 1. (A) Echogram from hull-mounted 120 kHz transducer, S_v -threshold = -77 dB, showing the situation shortly after the submersible transducer was raised. The area bounded by horizontal red lines shows the depth-range covered by the printouts from the submersible transducer. (B) Echogram-printout from submersible transducer with 10 m range, showing the depth range of the scattering layer with greater resolution. (B) was printed during daytime on 15th March 2000. (C) Tracking and smoothing performed on targets found within circle in B. The target was tracked for 135 echoes, average smoothed speed was ~ 8 cm s^{-1} , and average TS -74.1 dB. XYZ-scales in meters. Horizontal plane in figure corresponds to the real horizontal plane. (D) Track recorded simultaneously with track in (C); totally 125 echoes, average smoothed speed ~ 3 cm s^{-1} , average TS -68.2 dB.

For this particular study, ground-truthing was performed within and above the observed scattering layer with a pelagic trawl. The trawl had an aperture of about 100 m^2 , mesh size near the opening was 20 cm, declining to 1 cm near the cod end, and was towed horizontally at two knots for about 30 min. All the fish and subsamples of krill were frozen from the catch, for later species determination and length measure-

ment (for fish tail-fork length, for krill telson-rostrum length, Sameoto et al., 1993) in the lab.

A downward-looking, submersible 120 kHz transducer was deployed at ~ 66 m to allow close inspection of the scattering layer and resolution of individual targets (Fig. 1B). Their swimming trajectories were established using specially made software for split-beam TT (Ona and Hansen, 1992),

and data were imported into Matlab for presentation of three-dimensional (3D) swimming tracks and target strengths (TS) (Fig. 1C,D). The submersible transducer was connected to the echo sounder via 100 m of cable. Due to logistic problems, the transducer was not calibrated prior to the deployment.

The transducer had a vertical resolution of 3 cm, while the angular resolution was 0.13° . Pulse duration was set at 0.3 ms, while the average ping rate was $\sim 2.3 \text{ s}^{-1}$.

Echo data interpreted by the EK500 as originating from a single source and with TS (uncalibrated value) higher than -83 dB , were collected from this transducer in the period from 14 h 52 on the 15th to 09 h 23 on the 16th (local time), most of the tracks were therefore recorded during nighttime. The settings used required a minimum of 10 returned echoes to define a track, allowing for one missing echo (except for the illustrations presented in Fig. 1C,D) and a (arbitrary) maximal vertical excursion of 10 cm between echoes.

Registrations of single individuals were easily identified from printouts with high vertical resolution, showing the depth range 10–20 m from the transducer (Fig. 1B). This allowed a manual check of whether wave-movement corrupted the estimated swimming speeds. Also tracks recorded deeper than this were accepted. Swimming speeds were calculated by dividing the sum of movements in a track by the track duration.

Comparisons between day and night relative invertebrate numbers were made from counts of individual traces on echogram-printouts, the traces were identified as invertebrates on the basis of trace-colour on the 40LogR paper-prints. These numbers were then converted to numerical densities.

Since a free-hanging transducer was used, the swimming speeds estimated through the TT-procedure were subjectively examined for the effect of wave-motion generated by passing ships. Tracks recorded in periods with the passing ships were discarded. Since three anchors moored the vessel, the drift was assumed to be minimal. The potential influence of currents at depth was not accounted for.

Bias against fast swimmers may be introduced by requiring a minimum of 10 echoes to define a track (Torgersen and Kaartvedt, 2001). Errors are also introduced through the systems finite resolution (Brede et al., 1990), and by erroneous angle measurement (Mulligan and Chen, 2000), both factors expected to increase ping-to-ping swimming speeds. Since the resolution is inversely proportional to depth, and the angular error increase with decreasing SNR (Ehrenberg and Torkelson, 1996), it was expected that the average of estimated swimming speeds would increase with depth.

Interpolation of position by using adjacent echoes may increase the precision of the measurements (Fleischman and Burwen, 2000). We tried to remove the effect of the finite resolution and erroneous angle measurements by assuming that small, rapid fluctuations in positions were caused entirely by these error sources. This was done by further post-processing the tracks with a simple three-step routine, effec-

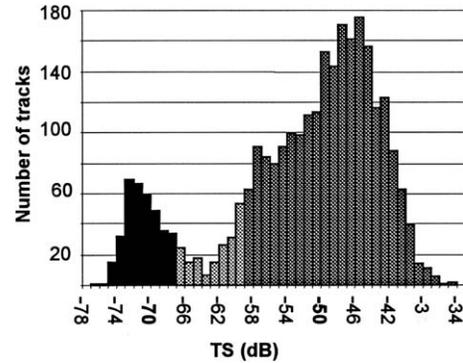


Fig. 2. TS-distribution of tracked organisms; black interpreted as invertebrate, dark grey as fish, light grey not included in any group.

tively forming a filter against short, rapid movements. The first step was aimed at reducing the effect of the discrete resolution, and gave echo (n), the same position as echo ($n - 1$) if echo ($n - 1$) had the same position as either of echoes $n + 1$ to $n + 3$. The second step was aimed at reducing the effect of erroneous measurements, and interpolated the position of echo (n) if the position was not between positions ($n - 1$) and ($n + 1$). The last step fitted a 3 (5 point for vertical data) point running mean to the data, further smoothing the effect of the resolution. In all steps, the first and last measurements of a track were kept unchanged, and the corrections were performed separately on both of the angular measurements (and steps 1 and 3 on the depth-data).

Swimming speeds were then recalculated on the basis of these estimated positions.

3. Results

The system had the capability to resolve individual plankton scatterers at their daytime depth, enabling the study of behaviour of individuals (Fig. 1C,D). A largely bi-modal TS-distribution of tracked individuals (Fig. 2) suggested that fish could be separated from invertebrates on the basis of average TS. Conservatively, tracks with average TS less than -68 dB were ascribed to invertebrates, and tracks above -60 dB to fish. A total of 2253 tracks passed the criteria, of which 359 were interpreted as originating from invertebrates. Fish tracks were mostly obtained at night. Only four invertebrate tracks were observed beyond 20 m from the transducer. Invertebrate tracks lasted from 3.7 to 82.1 s, with an average track duration of 10.4 s.

The invertebrates of the daytime trawl-catches from the depth of the scattering layer were dominated by the krill *M. norvegica*, with some ctenophores present in the catch (Table 1). The trawl-catches also contained fish (Table 1), but no fish larvae were found. Average daytime densities of invertebrates in the depth interval of 76–86 m were $0.30 \text{ individuals m}^{-3}$ (S.D. = 0.15, $N = 62$), while nighttime densities were $0.09 \text{ individuals m}^{-3}$ (S.D. = 0.05, $N = 80$). Roughly 70% of the invertebrates therefore performed diel migration.

Table 1

Total trawl catch. Maximum depth is the average depth of the bottom rope of the trawl. Trawling distance refers to the horizontal distance the trawl covered at the designated depth. Small gobies were not discerned among the krill in haul 2, but they may have been present. The presence of gelatinous plankters was noted in both hauls, but these organisms were destroyed beyond recognition or enumeration. Krill volumes were measured with 0.25 l jars

Species	Number caught	Mean length	Range
Haul 1		Maximum depth	
Trawl distance ~0.675 nmi		~77 m	
Sprat (<i>Sprattus sprattus</i>)	10	9.8 cm	7.3–11.2 cm
Crystal goby (<i>Crystallogobius linearis</i>)	>50	3.0 cm	3.4–3.7 cm
Krill (<i>Meganyctiphanes norvegica</i>)	0.25 l	^b	^b
Haul 2		Maximum depth	
Trawl distance ~0.8 nmi		~89 m	
Sprat (<i>Sprattus sprattus</i>)	5	9.0 cm	5.5–11.0 cm
Crystal goby (<i>Crystallogobius linearis</i>)	^a	^b	^b
Mueller's pearlside (<i>Maurollicus muelleri</i>)	6	5.3 cm	2.6–6.2 cm
Whiting (<i>Merlangius merlangus</i>)	2	^b	33–39.5 cm
Krill (<i>Meganyctiphanes norvegica</i>)	9.75 l	3.1 cm	2–4 cm

^a Probably present, but could not be separated from the krill.

^b Not measured or not applicable.

The average uncorrected horizontal component of the swimming speed in average increased rapidly with range (Fig. 3A), though variations between tracks were large. The filtered (corrected) estimates also increased with depth, albeit at a much lower rate. The effect of the smoothing procedure on two simultaneous tracks is illustrated in Fig. 3B,C.

The distributions of corrected swimming speeds showed a mode around 4 cm s^{-1} (Fig. 4) for the invertebrate tracks and a mode around 12 cm s^{-1} for the fish, both distributions being positively skewed with means 9 and 21 cm s^{-1} . Most invertebrates only had small vertical velocities, and the vertical components of swimming speed were below 1.6 cm s^{-1} in more than 90% of the tracks, with an average vertical component of 0.9 cm s^{-1} (Fig. 4). The fish showed more vertical mobility, the average vertical component was 2.9 cm s^{-1} , these behaviours were confirmed by visual inspections of the echogram-printouts.

4. Discussion

The results showed the possibility of describing the in situ behaviour of individual macrozooplankton with existing technology. Based on the trawling and the results from previous investigations at the sampling site (Onsrud and Kaartvedt, 1998; Kaartvedt et al., 2002), the tracks ascribed to invertebrates were probably dominated by krill. However, some of the tracks showed very low swimming speeds coupled with systematic changes in TS. Though also these observations may have been of krill, they could alternatively be explained by ctenophores or jellyfish slowly changing their orientation while swimming through the beam (cf. Fig. 1D). The gelatinous invertebrates were not sampled quantitatively with the gear used, and their relative importance is therefore uncertain. Since nighttime trawling was not performed, the identity of the non-migrating proportion remains uncertain.

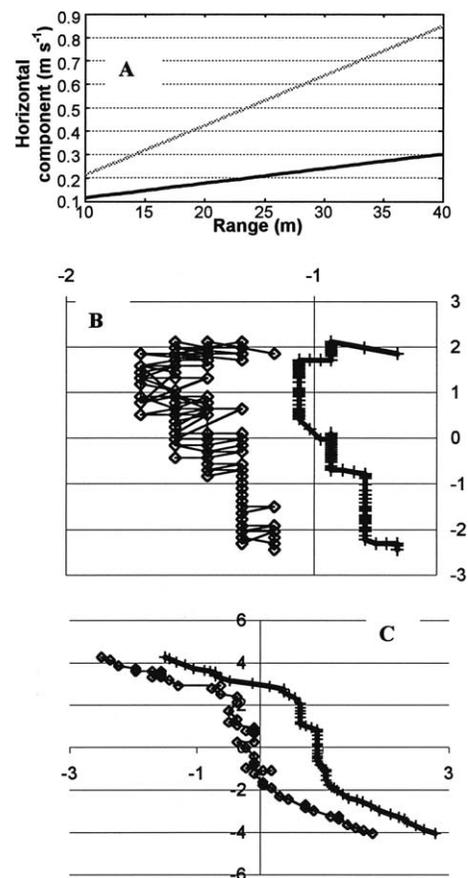


Fig. 3. (A) Regression of horizontal speed component vs. average range to track, all data (except periods of wave-action). Grey line: Unsmoothed estimates: $y = 0.0212x - 0.002$, $R^2 = 0.0588$. Black line: Smoothed estimates: $y = 0.0062x + 0.0526$, $R^2 = 0.0611$. $N = 2253$. (B) and (C) depict the effect of the smoothing on two simultaneous tracks, track (B) is an invertebrate and C is a fish. Only the horizontal projections are shown, with scales in degrees, smoothed tracks (marked by +) offset from the original positions (marked by diamonds). (B) Range 16 m, average TS -71.0 dB, track consists of 177 echoes recorded during 82.07 s, average speed without smoothing 8.4 cm s^{-1} , with smoothing 2.5 cm s^{-1} . (C) Range 19 m, average TS -45.1 dB, track consists of 63 echoes recorded during the first 28.73 s of track in (B), average speed without smoothing 13.7 cm s^{-1} , with smoothing 11.0 cm s^{-1} .

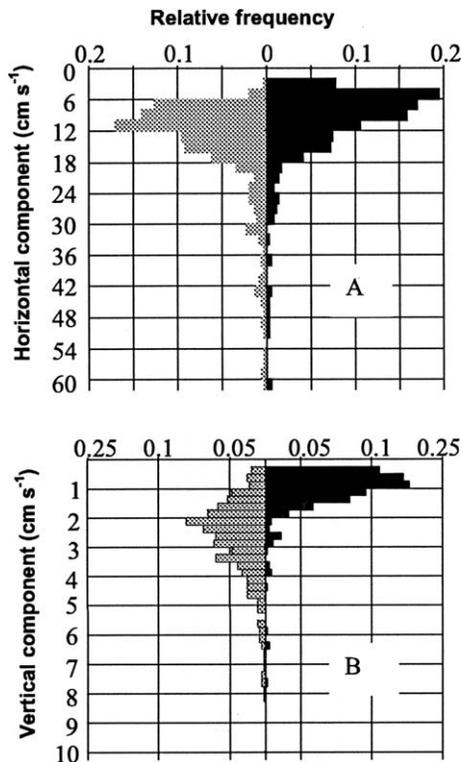


Fig. 4. (A) Distributions of horizontal component of swimming speed for the invertebrate group, left (grey) uncorrected average speeds, right (black) smoothed estimates. (B) The same distributions for the vertical component.

The uncalibrated peak TS-values obtained for invertebrates seemed relatively high compared to values measured for Antarctic krill (Foote et al., 1990), but were in accordance with previous calibrated measurements of *M. norvegica* at the same location (Røstad, 2000). Regardless of the absolute accuracy of the measurements, the bi-modal distribution of TS suggested that there was little possibility of misinterpreting fish as invertebrate.

4.1. Validity of single-echoes and tracks

Due to physical limitations of the single-echo detection-filters in the EK500, an unknown proportion of the accepted echoes stems from noise and multiple scattering (Soule et al., 1997). Since the probability of accepting such false registrations in consecutive pings is low, TT is commonly employed to sort out the echoes created by valid single sources (Ehrenberg and Torkelson, 1996). The relatively strict settings used for the TT procedure and the relatively low densities observed made us believe that false registrations of echoes were not a major problem within our tracks.

There was a restricted range of observation for the weak targets, effectively 10–18 m, probably related to the strict settings used in the single-echo detection-filters (Soule et al., 1997) and decreasing SNR. During day, this restricted range was also influenced by higher numerical densities, but even at night, when the numbers of organisms were lower, few invertebrate tracks were recorded beyond 20 m.

Ping-to-ping velocities estimated directly from the positions given by the echo sounder are biased high, and as long as there is measurement error this will always be the case (Mulligan and Chen, 2000). A lower estimate can be gained by calculating the speed between the first and the last positions in the track (Arrhenius et al., 2000), but since many of the tracks sampled in situ are bound to have some curvature, this method tends to underestimate the real speeds. Mulligan and Chen (2000) suggested that a better estimate could be obtained by fitting a smoothed trajectory to the data, and suggested that further post-processing of the positional data was needed when describing the swimming behaviour of organisms using acoustic data.

The smoothing procedure used made the estimated swimming speeds less dependent on range (Fig. 3A). A certain increase in average estimated speeds with depth was expected, due to the increasing proportion of fish tracks with range, as well as bias against fast swimming fish closer to the transducer, due to the narrowing beam. However, it may have introduced artefacts in the tracks by filtering out small scale and rapid within-track behaviour, as there is a possibility that some of the perceived errors in the positions are in fact caused by actual behaviour, though we believe that this generally was not the case (Fig. 3B,C).

The measured swimming speeds ascribed to krill seem to be reasonable. Assuming a length corresponding to the mode of the observed length distribution (3.5 cm), the mean and modal swimming speed were ~ 2 and ~ 1.1 body-lengths (BL) s^{-1} , respectively. All observed swimming speeds for invertebrates were within the bounds of the swimming capabilities of krill (up to 11 BL s^{-1} ; Kils, 1982). Jaffe et al. (1999) recorded a swimming speed of 0.5–1 BL s^{-1} for the krill *E. pacifica* in Saanich Inlet.

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