

# In situ swimming speed and swimming behaviour of fish feeding on the krill *Meganyctiphanes norvegica*

M.S.R. Onsrud, S. Kaartvedt, and M.T. Breien

**Abstract:** In situ swimming speed and swimming behaviour of diel migrating planktivorous fish were studied at a 120-m-deep location. Acoustic target tracking was performed using a hull-mounted transducer and submersible transducers located on the sea bottom and free hanging in the water column. The original data displayed a relationship between distance to transducer and swimming speed. A simplistic smoother applied during post-processing, appeared to break this relationship. Target tracking thus provided robust results on in situ swimming behaviour throughout the water column. Swimming speeds of deep-living fish, mainly Norway pout (*Trisopterus esmarkii*) and whiting (*Merlangius merlangus*), were highest during the day (speeds centred around 14–16 cm·s<sup>-1</sup>) and decreased somewhat by night (modes around 10–11 cm·s<sup>-1</sup>). Fish in the upper 10–30 m swam somewhat faster (speeds ranging from 16 to 24 cm·s<sup>-1</sup>). Fish in the upper layer at night were mainly Atlantic herring (*Clupea harengus*), sprat (*Sprattus sprattus*), and whiting. We ascribe the reduction of swimming speed in deep-living fish at night to a switch from visual feeding during day-time to nonvisual feeding by night. We suggest that shallow-living fish could forage visually even by night. Most tracks were fairly short, but some long tracks unveiled elaborate swimming paths as well as cyclic swimming behaviour.

**Résumé :** Nous avons étudié la vitesse de nage in situ et le comportement de nage chez des poissons planctonophages à migration journalière à site d'une profondeur de 120 m. Nous avons fait un suivi acoustique des cibles à l'aide d'un transducteur monté dans la coque et des transducteurs submersibles sur le fond de la mer et en suspension dans la colonne d'eau. Les données originales montrent une relation entre la distance du transducteur et la vitesse de nage. Une méthode simpliste de lissage durant le post-traitement des données semble faire disparaître cette relation. Le suivi fournit donc des résultats robustes in situ du comportement de nage dans toute la colonne d'eau. Les vitesses de nage des poissons des profondeurs, surtout des tacauds norvégiens (*Trisopterus esmarkii*) et des merlans (*Merlangius merlangus*), sont maximales durant le jour (vitesses concentrées autour de 14–16 cm·s<sup>-1</sup>) et diminuent un peu la nuit (modes autour de 10–11 cm·s<sup>-1</sup>). Les poissons dans les 10–30 m supérieurs nagent un peu plus vite (vitesses allant de 16 à 24 cm·s<sup>-1</sup>). Les poissons des couches supérieures la nuit sont surtout des harengs atlantiques (*Clupea harengus*), des sprats (*Sprattus sprattus*) et des merlans. Nous expliquons la réduction de la vitesse de nage des poissons des profondeurs la nuit au passage d'une alimentation visuelle durant le jour à une alimentation non visuelle la nuit. La plupart des tracés sont relativement courts, mais quelques tracés plus longs révèlent l'existence de trajets élaborés de nage, ainsi que de comportements cycliques de nage.

[Traduit par la Rédaction]

## Introduction

Fish swimming speed is a significant component of foraging and bioenergetics models. Search volumes depend directly on swimming speeds and paths (cf. Eggers 1977), where encounter rates are modelled as a function of prey size and predator swimming speed (Evans and O'Brien 1986; Luo et al. 1996). Food capture, escape from predators, and reproduction are directly related to swimming speed limits and endurance. A diel activity rhythm, with increased swimming speed during the day, is normally ascribed to a more active search for food at daytime (Løkkeborg 1998;

Janssen et al. 1999). Feeding mode (e.g., switching between particulate feeding and filtering) also affects swimming velocity (Gibson and Ezzi 1985, 1992).

To formulate sensible models for predator–prey encounter and individual somatic growth, we need knowledge of natural behaviour (Gerritsen and Strickler 1977; Torres and Childress 1983). However, few in situ studies of swimming speed or behaviour have been performed. Split-beam hydro acoustics have recently shown promise for measuring fish movement under field conditions (Arrhenius et al. 2000; Torgersen and Kaartvedt 2001; Čech and Kubečka 2002). The position of resolved targets (single fish) in the acoustic

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**Table 1.** Technical specifications and parameter settings used during target tracking in November 2000.

Transducer type	ES 38DD	ES 120–7	ES 120–7
Beam type	Split beam	Split beam	Split beam
Location	Bottom or free hanging beneath vessel	Free hanging beneath vessel	Hull-mounted
Parameter settings			
Absorption coefficient (dB·km <sup>-1</sup> )	10	38	38
Two-way beam angle (dB)	-20.6	-20.8	-20.5
Alongship angle sensitivity	21.9	21	21
Athwartship angle sensitivity	21.9	21	21
Maximum transmitting power (W)	1000	1000	1000
Pulse length (ms)	Medium (1.0)	Medium (0.3)	Medium (0.3)
Bandwidth (kHz)	3.8	12	12
Minimum TS value (dB)	-65	-65	-83
Minimum echo length	0.8	0.8	0.8
Maximum echo length	1.3	1.5	1.5
Maximum gain compensation (dB)	6	6	6
Maximum phase deviation	3	3	3
TS transducer gain (°)	21.85	22.13	24.63
Alongship 3-dB beamwidth (°)	6.89	7.27	7.09
Athwartship 3-dB beamwidth (°)	6.65	7.06	6.93
Alongship offset angle (°)	-0.1	-0.15	-0.12
Athwartship offset angle (°)	-0.24	0.27	0.03

**Note:** TS, target strength.

beam can be located (Ehrenberg and Torkelson 1996), and acoustic tracking of targets over time (TT) will provide information on three-dimensional localization and movement of the fish in their natural environment.

In previous studies, we have addressed krill (*Meganyctiphanes norvegica*) vertical distribution and their feeding as well as the distribution and feeding patterns of their predators in the Oslofjord, Norway (Onsrud and Kaartvedt 1998; Kaartvedt et al. 2002; Onsrud et al. 2004). Atlantic herring (*Clupea harengus*), whiting (*Merlangius merlangus*), and Norway pout (*Trisopterus esmarkii*) forage on krill both day and night. Diel migrating herring and whiting largely search for prey in the upper and middle part of the krill assemblage, while Norway pout forage in the lower fringe of the krill assemblage, partly living semidemersally at day and ascending into mid-water at night (Onsrud et al. 2004).

In this study, we apply TT in assessing the swimming speed and behaviour of the planktivores performing diel vertical migration and feeding on *M. norvegica*. Specifically, we assess swimming behaviour day and night and in the upper and the lower part of the water column. Detailed acoustical studies of deep-living species have previously been hampered by large distances to the transducer. This problem was overcome by including an upward-looking transducer placed on the bottom at 120 m depth. The location on the bottom provided a solid substrate, facilitating interpretation of fish movements.

## Materials and methods

In situ TT of free-swimming fish was conducted at a 120-m-deep site in the Oslofjord (59°48'N, 10°34'E), Norway, during a full diel cycle and the subsequent evening, 13–14 November 2000. Description of the study site is given in Onsrud and Kaartvedt (1998) and Bagøien et al. (2000).

Acoustic data were collected with a Simrad EK500 echosounder (software version 5.3) (Simrad AS, Horten, Norway) with 38-kHz (7.1°) and 120-kHz (7.1°) split-beam transducers (Table 1). We applied different combinations of hull-mounted and submerged transducers. For each frequency, only one transducer could be used at a given time. The specially designed oil-filled 38-kHz split-beam transducer for use under high pressure (Simrad ES38DD) was placed on the sea bottom, facing upwards, and was coupled to the EK500 onboard the RV *Trygve Braarud* by 300 m of cable (Fig. 1). It was mounted to a steel frame with gimbal couplings to ensure horizontal orientation of the transducer surface. Total weight was ~100 kg. In the afternoon on 14 November, the 38-kHz transducer and a 120-kHz transducer were submerged at 20 m in down-looking mode. Tracking data from the deployed 38- and 120-kHz transducers (10–30 m range) then revealed very similar data on swimming speeds between the two frequencies, mean estimated swimming speed deviating by only 0.2–1.6 cm·s<sup>-1</sup> for three measurement periods. This justified the use of data from the 120-kHz hull-mounted transducer to assess swimming speeds in the upper 10–30 m for the diel cycle.

The transducers hooked up with long cables were calibrated prior to the investigations according to standard target calibration (MacLennan and Simmonds 1992). The ship was moored with three anchors during the diel study. Acoustic data were stored by the software program Echo Receiver (Mork 2000) and later processed by the EP500 postprocessing software (Lindem and Al Houari 1993) and by the Sonar5 postprocessing software (Balk and Lindem 2002).

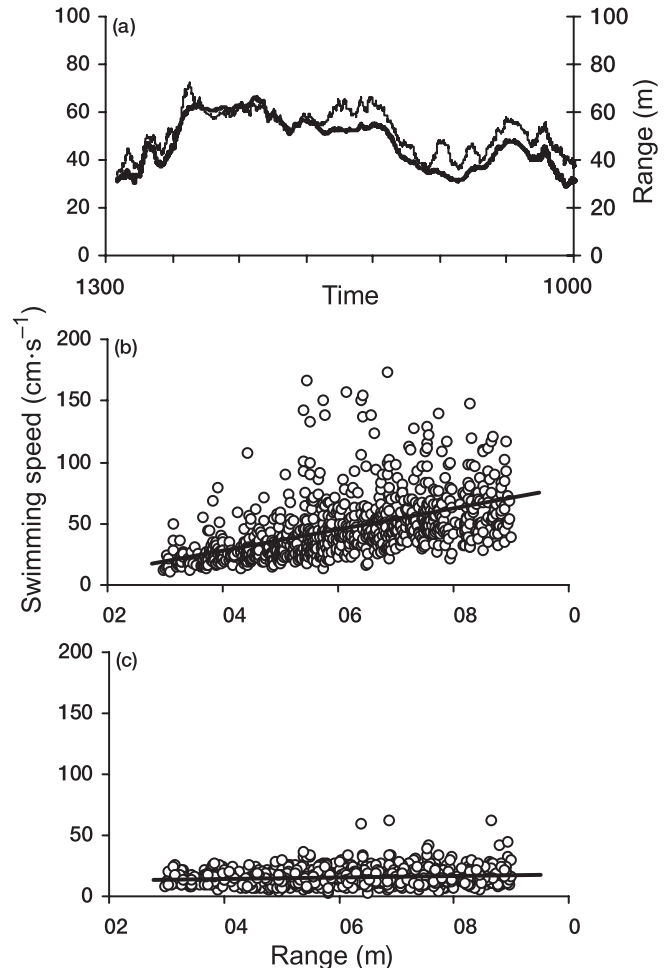
Fish swimming trajectories and velocities were established using TT. Single-fish echo data were logged via the serial port of the echosounder and stored on a personal computer using standard communication software. These data were later analyzed by specially developed software for TT

**Fig. 1.** Survey design illustrating the 38-kHz transducer placed on the sea bottom facing upwards and coupled to the EK500 echosounder onboard the RV *Trygve Braarud* by cable.



(Ona and Hansen 1992), which allows assessment of swimming velocities and trajectories and related variations in target strength (TS). Processed data were imported into Matlab for presentation of track swimming speed and paths. The EK500 was operated at maximum pulse repetition frequency (i.e.,  $\sim 2 \cdot \text{s}^{-1}$  for 120 m depth range). Only tracks containing a minimum of 10 detections were accepted, and maximum depth excursion between detections was set at 0.3 m. Our data were initially analyzed with strong tracking criteria, namely 10 pings, one ping missing. However, data analysis with the Sonar5 postprocessing software showed that the criteria were too strict, as many distinct tracks or parts of tracks with two or three missing pings consequently were rejected. Accordingly, our criteria were changed to 10 consecutive pings, three pings missing. The selected strata for fish

**Fig. 2.** (a) Unsmoothed data; averaged range (thick line) and average swimming speed (thin line) (running mean of 150 tracks) versus time; (b) unsmoothed swimming speed versus range for  $-42 < \text{TS} < -41$  dB ( $n = 919$ ) (linear regression:  $u = 0.76 \times \text{range} + 9.20$ ,  $R^2 = 0.47$ ); (c) smoothed swimming speed versus range for  $-42 < \text{TS} < -41$  dB ( $n = 919$ ) (linear regression:  $u = 0.04 \times \text{range} + 13.33$ ,  $R^2 = 0.007$ ). TS, target strength.



behaviour studies were 10–40 m for the 38-kHz bottom-located and free-hanging transducer and 10–30 m for the 120-kHz transducers. These choices represented compromises between signal to noise ratio, increased angle measurement errors by range, discrimination of fast swimmers, and swimming behaviour in longer tracks.

False data may be accepted when the built-in filters fail to reject multiple targets within the volume (Ona 1999), and echograms were carefully scrutinized to remove such data. As the first step of the data analyzing process, continuously printed echograms (40 log  $R$ ) from 25-m depth layers (50 m for the uppermost layer, 120 kHz) were evaluated. Only records showing clear fish echo traces and suitable fish densities were selected for further analysis. A suitable fish density for this study was a sufficiently high number of single-fish echoes for collection of a representative sample and a sufficiently low number to avoid the multiple-target echo problem. A total of 8623 individual fish trajectories were tracked with the bottom-located 38-kHz transducer. Trajectories with

averaged TS < -55 dB were excluded to leave out the smallest fish. Hence, eliminating periods with too high fish density, and only including tracks with -55 dB < averaged TS < -30 dB for our selected layer, 2290 tracks from the 38-kHz diel tracking were accepted for further study.

Three-dimensional target positions were calculated from the alongships ( $\alpha$ ) and athwartships ( $\beta$ ) angles and target depth ( $d$ ):  $x = d \tan(\alpha)$  and  $y = d \tan(\beta)$ , where  $d = \text{range} \times \cos \theta$  and

$$\theta = \arctan(\sqrt{\tan^2 \alpha + \tan^2 \beta})$$

This enabled us to calculate and analyze vertical and horizontal motion independently. Averaged swimming speed for a track was calculated as the sum of the ping-to-ping swimming distances divided by the duration of the track:

$$\bar{u} = \frac{\sum_{i=1}^n \Delta l_i}{\sum_{i=2}^n t_i - t_{i-1}}$$

where

$$\Delta l = \sqrt{\Delta x^2 + \Delta y^2 + \Delta d^2}$$

Although the ensonified volume increases with range, ping number in tracks was unrelated to range. However, data from the bottom-located 38-kHz transducer revealed a relationship between swimming speed and range, as exemplified by measured swimming speeds from the fluctuating vertical distribution of the lower edge of the acoustic layer throughout the diel cycle (Fig. 2a). A stepwise linear regression showed that swimming speed was dependent on both range and TS; additionally, there was a correlation between range and TS (model comparison, minimum Akaike's Information Criterion,  $p < 0.01$ ). To establish the dependency between swimming speed and range, which most likely is a result of the system's finite resolution (Brede et al. 1990) and erroneous angle measurement (Mulligan and Chen 2000), we tested swimming speed as a function of range for  $-42 < \text{TS} < -41$  dB (robust least trimmed squares linear regression,  $R^2 = 0.47$ ) (Fig. 2b). To break this dependency, we smoothed the trajectories by a simplistic smoother (Mulligan and Chen 2000; Klevjer and Kaartvedt 2003). The smoothing process removed the evident relationship between range and swimming speed ( $R^2 = 0.007$ ) (Fig. 2c). The regression equations and the correlation coefficients found for our smoothed data lead us believe that measurement error is not a significant factor in our analysis.

To test if measured swimming speeds were influenced by tide currents, we investigated the distribution of swimming direction (horizontal swimming angle, Rao's spacing test) and the relationship between swimming direction and swimming speed for the different periods, transducers, and depth layers (circular-linear correlation). Tests were run for pooled data and data divided into 1- to 2-h periods (or ensuring  $n \geq 100$ ).

To establish the curvature of the trajectories in the horizontal plane, we used the factor net to gross displacement rate (NGDR<sub>xy</sub>), where NGDR is the ratio of the net displace-

ment (linear distance between starting point and end point of a path) to gross displacement (total distance travelled). Thus, linear paths give the highest NGDR. As estimated horizontal movement will be sensitive to pitching and rolling for the hull-mounted and free-hanging transducers, trajectories from periods with heave (passing ships) were excluded. The diel cycle was divided into five periods, day 1, ascent, night, descent, and day 2, to compare swimming speed and behaviour between periods. With transducers deployed at 20 m at the end of the second day, that sampling period was divided into day, ascent, and night.

Four fish species prevailed at the study site (Onsrud et al. 2004): whiting, Norway pout, Atlantic herring, and sprat (*Sprattus sprattus*). Based on the size distributions in the trawl catches (Onsrud et al. 2004), we converted fish lengths to theoretical TS values by applying the formula  $\text{TS} = 20 \log(\text{length (cm)} + b_{20})$  (MacLennan and Simmonds 1992). The  $b_{20}$  values (38 kHz) were taken from the literature and given the values -67.1 for Norway pout (Foote 1987) and -71.2 for sprat (International Council for the Exploration of the Sea 2001). As no  $b_{20}$  literature value was found for whiting, we employed the value -67.4 from the general gadoid equation (Foote 1987). For Atlantic herring, we used the equation:  $\text{TS} = 20 \log L - 2.3 \log(1 + d/10) - 65.4$ , where  $d$  is depth in metres (Ona 2003). Ventral aspect TS might be different from dorsal aspect TS; however, Love (1977) found the acoustic cross section  $\sigma$  from dorsal and ventral aspects to be very similar. The theoretically calculated TS was employed to help identification of species in the acoustic records based on the target tracking data and data from the EP500 and Sonar5 postprocessing software.

## Results

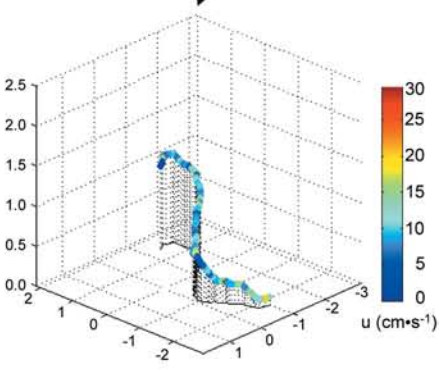
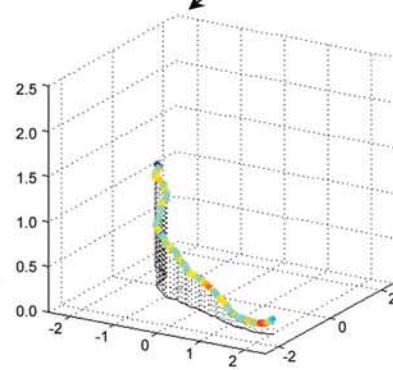
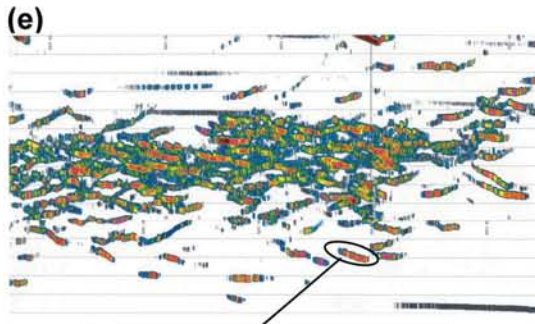
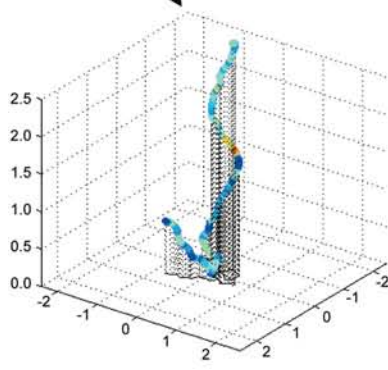
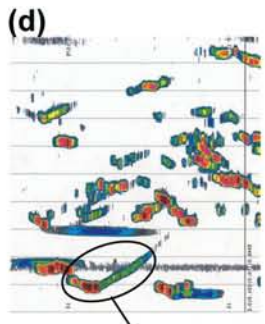
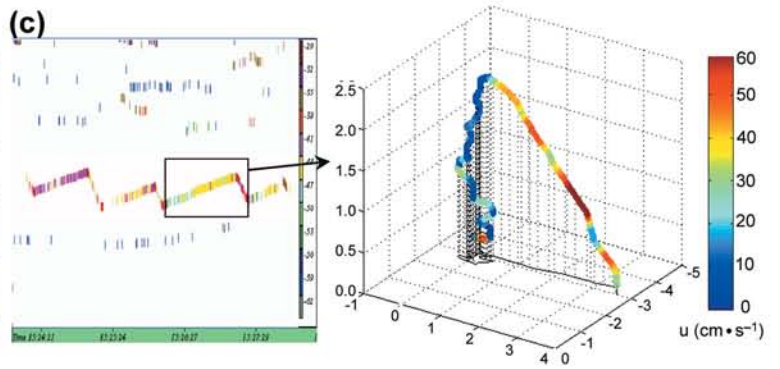
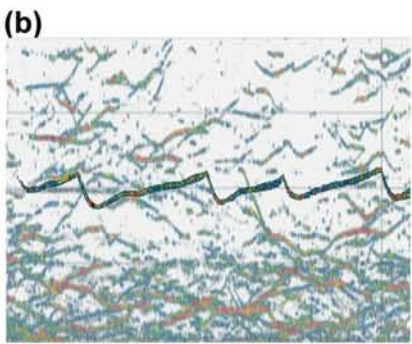
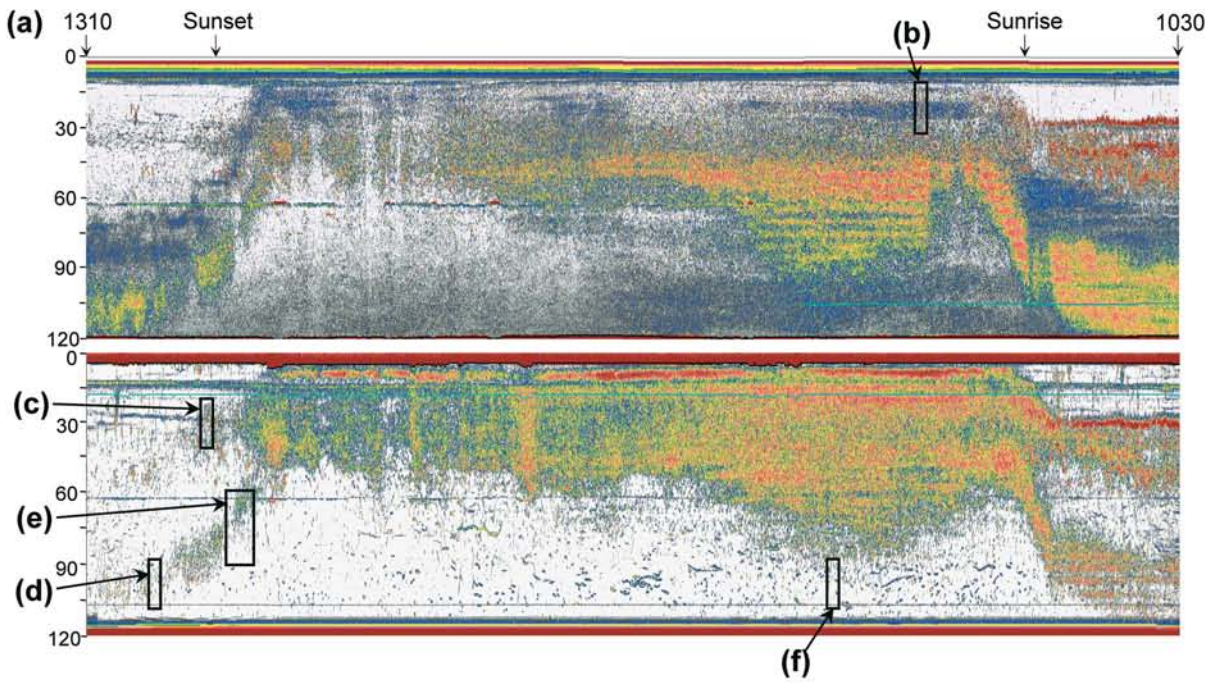
Fish records (apparent on both frequencies) (Fig. 3) indicated a deep scattering layer (below ~90 m at day, migrating into midwater at night) and more shallow-living fish being confined to various structures in the upper 60 m at day, migrating into the upper 30 m at night. These structures were most evident the second day, including marked records of schooling fish. Dielly migrating krill were displayed as a blue scattering layer at 120 kHz, being situated at ~70-90 m at day, migrating into the upper 30 m at night (Fig. 3).

Single fish could be resolved throughout the water column (e.g., Fig. 3): individuals in the upper part by the hull-mounted transducer and in deep water by the bottom-mounted transducer. Single fish in midwater were resolved the second afternoon by the transducers deployed at 20 m (not shown).

### Target strength

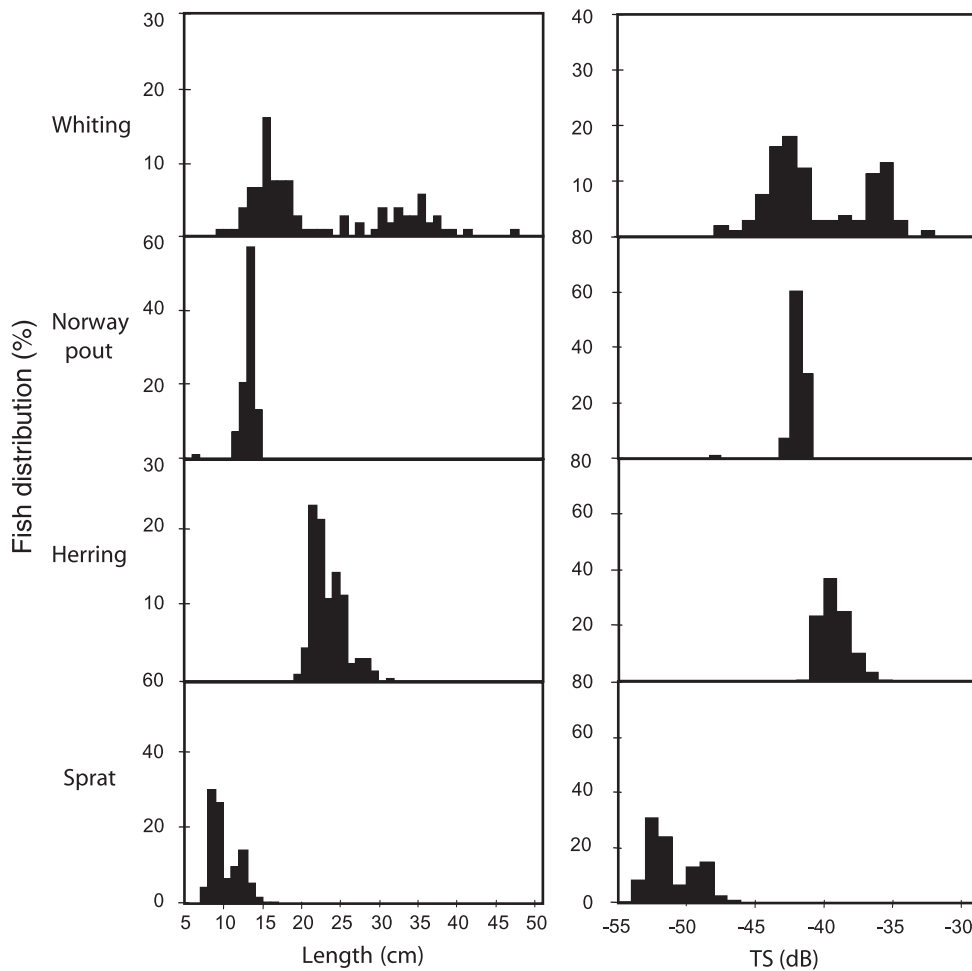
Size distribution and theoretically calculated TS indicated that sprat could be separated from whiting, Norway pout, and Atlantic herring based on TS (Fig. 4). The three krill-feeding species, however, had partly overlapping TS values (Fig. 4).

Tracking data obtained from the bottom-located transducer were restricted to the 80- to 110-m depth layer. The TS distribution in this layer was fairly constant throughout the diel cycle (Fig. 5a), with a mean TS of -43.4/-42.5 and -42.1 dB for day 1/day 2 and night, respectively. The TS



**Fig. 3.** Acoustic registrations and processed data for a diel cycle in November 2000. (a) Backscattering from the 120-kHz hull-mounted transducer (upper) and the 38-kHz bottom-located transducer (lower) during the diel cycle in November 2000; (b) paper printout (120 kHz, 40 log R), 20–45 m, 0440–0449, swimming trajectory highlighted; (c) Sonar5 processed data, 25- to 50-m depth layer, 1523–1528, and three-dimensional plot of selected swimming trajectory (x, y, and z axes in m, colorbar for swimming speed in cm·s<sup>-1</sup>); (d–f) paper printouts (38 kHz, 40 log R) and three-dimensional plot of selected trajectories: (d) 85- to 110-m depth layer, 1357–1401, (e) 60- to 95-m depth layer, 1553–1604, and (f) 85- to 110-m depth layer, 0307–0312.

**Fig. 4.** Fish length distribution for whiting (*Merlangius merlangus*) (n = 106), Norway pout (*Trisopterus esmarkii*) (n = 82), Atlantic herring (*Clupea harengus*) (n = 196), and sprat (*Sprattus sprattus*) (n = 1083) from trawl catches in November 2000 and the calculated target strength (TS) distribution.



distribution in the deepest layer was narrower than for the other depth layers (Fig. 5).

**Swimming speed**

Average swimming speed for the trajectories (hereafter called swimming speed) calculated from tracking data ranged from 2.0 to 61.0 cm·s<sup>-1</sup> (Table 2). Very few tracks had swimming speeds above 50 cm·s<sup>-1</sup>. Likewise, few tracks had swimming speeds below 5 cm·s<sup>-1</sup>. Note, however, that swimming speed could vary greatly within long tracks (Fig. 3).

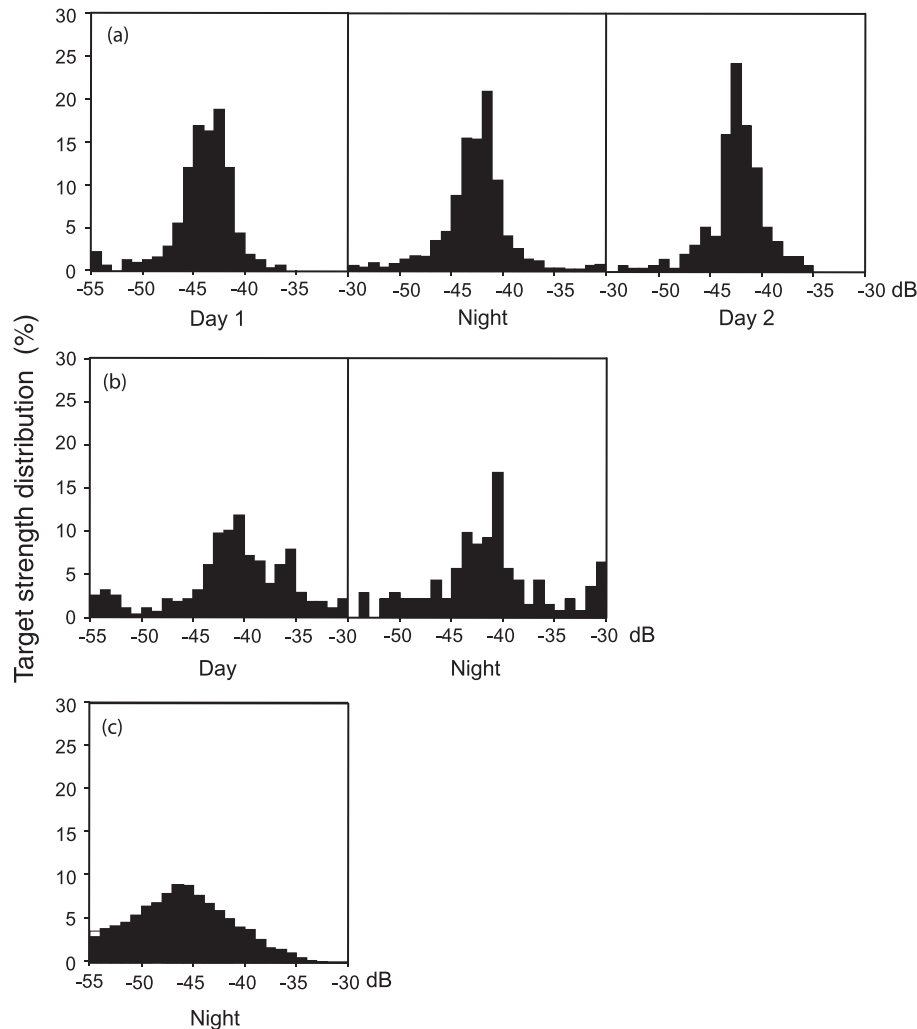
Swimming speed in deep water decreased significantly from day to night (Kruskal Wallis  $\chi^2$ ,  $p < 0.017$ ) (Fig. 6). Tracking data obtained from the bottom-located transducer (80- to 110-m interval) unveiled modes of 15–16 cm·s<sup>-1</sup> prior to and during ascent, decreasing to 10 cm·s<sup>-1</sup> by night (Table 2). Tracking with the downward-looking 38 kHz, de-

ployed at 20 m depth during the following afternoon, revealed similar results for the 30- to 60-m layer (Fig. 6; Table 2).

Owing to the schooling behaviour and the vertical distribution of the fish by day, tracking of individual fish in upper waters (10–30 m) could only be done from dusk until dawn. The nocturnal swimming speed and range were significantly higher than in deeper water (Kruskal Wallis  $\chi^2$ ,  $p < 0.01$ ), most fish swimming at speeds ranging from 16 to 24 cm·s<sup>-1</sup> (Fig. 6).

As the calculated swimming speeds might be influenced by tide currents, the data were tested for uniform distribution of swimming direction (horizontal swimming angle) and correlation between swimming direction and swimming speed. Swimming angles in the 10- to 30- and 80- to 110-m layers showed bimodal distribution when all data were pooled (Fig. 7). However, by dividing data into 1- to 2-h pe-

**Fig. 5.** Average target strength (TS) (dB) distribution for the given periods during a diel cycle and the following afternoon in November 2000. (a) 80- to 110-m depth layer (38-kHz bottom-located transducer); (b) 30- to 60-m layer (38-kHz transducer deployed at 20 m depth); (c) 10- to 30-m layer (120-kHz hull-mounted transducer).



riods, most periods (65%) showed a uniform distribution of swimming angles. Where data showed a significant correlation between swimming direction and swimming speed, the relationship was generally weak,  $r$  at all times  $\leq 0.22$ .

### Swimming behaviour

The majority of tracks were short (10–20 pings), and the  $NGDR_{xy}$  largely revealed straight (portions of) swimming paths with little vertical excursions. By day and also during ascent, most tracks in the deepest layer were horizontal or slightly sinking. During dusk, the recorded behaviour was inconsistent with the population behaviour revealed by the scattering layer, as the fish scattering layer ascended steadily. In the period from 1400 to 1716, throughout migration, 245 tracks were descending, while 109 tracks were ascending. Only in the 10- to 30-m layer did we find a consistent, positive net movement during dusk.

However, more elaborate swimming trajectories were also suggested by the echograms, including trajectories with slow, upward swimming lasting for more than 1 min followed by rapid descents (Figs. 3b and 3c). Only one cycle was successfully tracked, displaying slow, spiralling, upward

swimming ( $v_{avg} \sim 11 \text{ cm}\cdot\text{s}^{-1}$ ) (Fig. 3c) and straight, rapid, downward swimming ( $v_{avg} \sim 39 \text{ cm}\cdot\text{s}^{-1}$ ).

After midnight, the lower edge of the fish scattering layer was sinking continuously at a velocity of about  $0.3 \text{ cm}\cdot\text{s}^{-1}$ . Single fish with somewhat higher sinking rates were seen to sink out at the fringe of the layer with little horizontal movement, thus staying in the beam for extended periods (Fig. 3f).

### Discussion

Swimming speeds below 30 m were higher during day than at night. Estimates from the bottom-located and free-hanging 38-kHz transducer were fairly consistent, with respective modes of 16 and  $14 \text{ cm}\cdot\text{s}^{-1}$  during daytime and 10 and  $11 \text{ cm}\cdot\text{s}^{-1}$  by night. Klevjer and Kaartvedt (2003) similarly found a mode around  $12 \text{ cm}\cdot\text{s}^{-1}$  for the horizontal component of fish swimming at depth during nighttime in March 2000 at the same location. The bimodal distribution of swimming direction (horizontal swimming angle) in the pooled data suggests that tidal currents may have influenced swimming direction, while swimming speeds were generally

**Table 2.** Average swimming speeds ( $\text{cm}\cdot\text{s}^{-1}$ ) for the various periods and layers during the diel study in November 2000.

	Day				Night				
	10–30 m	30–60 m	80–110 m	10–30 m	30–60 m	80–110 m	10–30 m	30–60 m	80–110 m
Mean	—	16.2	16.0	22.6	17.3	16.9	19.5	13.0	13.3
SD	—	5.7	5.2	8.9	7.2	5.3	7.0	5.1	6.4
Mode	—	14	16	21	14	15	18	11	10
Min.	—	6.4	2.5	10.0	4.4	6.1	3.6	2.6	2.0
Max.	—	45.0	43.6	53.3	54.1	46.0	58.8	27.2	61.0

unrelated to swimming angle and thereby tide currents. Later current measurements at the study site have generally shown weak currents ( $1\text{--}5\text{ cm}\cdot\text{s}^{-1}$ ) throughout the water column.

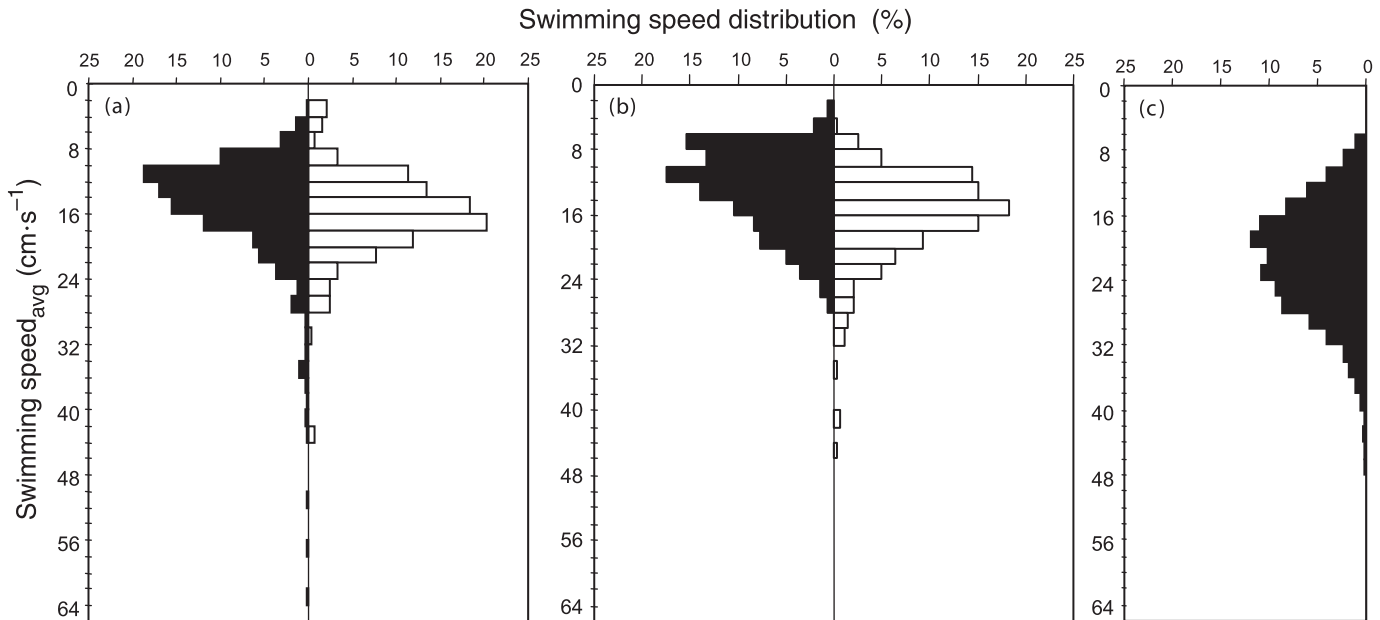
Sprat were the most common fish in the trawl catches below 90 m (Onsrud et al. 2004), but TT revealed stronger acoustic targets in this layer than would be suggested from the sprat in the trawl catches. The formula used for estimating TS distributions (relating TS to length) refers to the dorsal aspect. However, measurement from the ventral aspect of a positively identified, deep-living sprat assemblage (another part of the fjord; Volan 2004) also revealed weaker targets than in the deepest layer of the current investigation. Length distribution from that population peaked at  $\sim 12.5$  cm long specimen, TS values peaking at about  $-47$  dB (Volan 2004), which also agrees with the theoretically calculated TS from fish length for sprat. If TS can be trusted in distinguishing between species, we suggest that whiting and Norway pout were the main fish components in the 80- to 110-m layer. Fish size from trawl catches and TS distributions suggests a swimming speed mode of about 1 body length $\cdot\text{s}^{-1}$  by day and 0.7 body length $\cdot\text{s}^{-1}$  by night. This estimate of in situ swimming speed in deep-living planktivores thus concurs with experimental, laboratory, and in situ swimming speed estimates for adult fish of similar size (Gibson and Ezzi 1985; Huse and Ona 1996; Čech and Kubečka 2002). The somewhat higher swimming speeds registered by day compared with nighttime values might be related to feeding, as visual feeding normally entails increased swimming speed (Løkkeborg 1998). Swimming speed of planktivores is of relevance for prey encounter. For visual planktivores, encounter rate is proportional to the product of swimming speed (ignoring the much lower prey speed; Gerritsen and Strickler 1977), prey abundance, and reactive field (proportional to irradiance, at least at low and moderate levels; Aksnes and Giske 1993; Aksnes and Utne 1997).

The 30- to 60-m layer consisted of both Atlantic herring and whiting by day (Onsrud et al. 2004); however, most single targets possibly stem from whiting because of the daytime schooling behaviour in Atlantic herring. Backscattering in this layer by night mainly stemmed from the gadoids, as the clupeids then had migrated to the upper layer. Although the size range for whiting caught in this layer was 12.3–47 cm, most fish lengths were  $\sim 14\text{--}15$  cm, indicating swimming speeds in terms of body length comparable with those below 80 m. However, for the larger fish, somewhat lower swimming speeds were indicated. Previous reports suggest that swimming speeds in terms of body lengths per second are normally slower for larger than for smaller fish (e.g., Videler 1993).

After sunset, when individual fish could be tracked in the upper 10–30 m, most fish swam at speeds ranging from 16 to 24  $\text{cm}\cdot\text{s}^{-1}$ . Catches in this layer mainly consisted of Atlantic herring and whiting as well as sprat (Onsrud et al. 2004), the fish species caught at midwater by day. The length distributions (trawl catches) of Atlantic herring and whiting in this layer ranged from 18.7 to 24.2 cm and from 13.2 to 37 cm, respectively, most whiting, however, in the size range 15–19 cm, again suggesting swimming speeds of about 1 body length $\cdot\text{s}^{-1}$ , comparable with swimming speeds at depth by day. Feeding on *M. norvegica* in the uppermost layer in November is assumed to be visual even by night (Onsrud et



**Fig. 6.** Swimming speed distribution for the (a) 80- to 110-m layer, (b) 30- to 60-m layer, and (c) 10- to 30-m layer during the day (open bars) and night (solid bars).



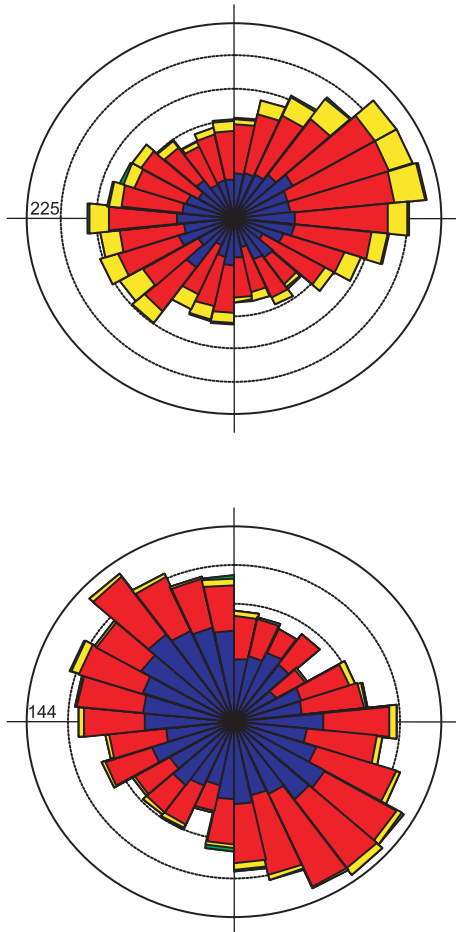
al. 2004). Similar swimming speeds (body lengths per second) at depth by day and in the upper 30 m by night could support this assumption. Gibson and Ezzi (1985, 1992) reported swimming speeds of 1–1.5 body lengths·s<sup>-1</sup> for Atlantic herring feeding by biting, not very different from our results.

Some fish at the upper extension of the krill layer (including records by night) employed a swimming pattern of repeated slow ascents and rapid descents. The behaviour might be related to the visual search pattern, where fish spot their prey in the downwelling light. The upward rising phase would enhance the contrast between the incident light and the prey and thus be adaptive in visual search for prey. Transparency of zooplankton is an excellent strategy for staying invisible to horizontally scanning eyes (Thetmeyer and Kils 1995). Planktonic prey may appear more visible against the bright light of the sky (darker owing to absorbance at opaque parts of the body) or dark depths (brighter owing to light scattered in their tissue) compared with the less contrasting background directly in front of straight-swimming fishes (Lazzaro 1987; Thetmeyer and Kils 1995). Janssen (1981) and Thetmeyer and Kils (1995) found that blueback herring (*Alosa aestivalis*) and Atlantic herring searched for prey in the downwelling light just outside Snell's window, at the same time reducing their own conspicuousness. Janssen (1982) assumed swim-search feeding behaviour for continually feeding, obligatory planktivores. The slow upward motion and fast downward swimming, repeated in cycles, would maximize time of optimal search regarding visual detectability. We were unable to establish which fish species adopted the up-and-down swimming strategy. However, the same slow upward swimming followed by rapid downward swimming was seen during day-time for small schools of clupeids at the upper extension of the krill layer in a later study in the Oslofjord (M.S.R. Onsrud, personal observation). Atlantic herring are

also described as attacking their prey predominantly from below (Batty et al. 1990; Gibson and Ezzi 1990; Thetmeyer and Kils 1995), leading us to believe that Atlantic herring adopted this strategy in their search for *M. norvegica* at the study site. Although little information exists on cyclic swimming patterns in situ, Čech and Kubečka (2002) found sinusoidal cycling patterns in cyprinid fish feeding on zooplankton, and up-and-down swimming has been reported in roaches (*Rutilus rutilus*) that consume plankton (Haberlehner 1988). Janssen (1981) also noted up-and-down cycling for blueback herring where the fish only fed during the ascending phase of the cycle.

In the deepest layer during day and during ascent, most tracks were directed towards the bottom, although during dusk, the fish scattering layer was steadily ascending. The inconsistency between the scattering layer behaviour and the individual fish behaviour could be ascribed to a swimming behaviour of stepwise ascent followed by a sinking phase. Possibly the ascent was not recorded, while the sinking phase was detected acoustically. A tilt angle, especially with the head up, generally results in a dramatically reduced TS (e.g., Nakken and Olsen 1977; Foote 1980; MacLennan et al. 1990). The track tilt angle for the ascending phase in Fig. 3d is about 35°, very similar to trajectory angles described for fish searching for zooplankton around the boundary of Snell's window (Janssen 1981; Thetmeyer and Kils 1995). Estimating the tilt angle in this manner assumes that the displacement of the fish is due to active swimming in the direction of the measured displacement (McQuinn and Winger 2003). The krill layer in our study slowly ascends at about 1 cm·s<sup>-1</sup>. Given a search pattern where the fish spot their prey in the downwelling light, and swimming speed differences, a stepwise ascent would keep the fish associated with the ascending krill layer and enable attacks from below. Torgersen and Kaartvedt (2001) ascribed similar patterns in studies of diel migrating mesopelagic fish to short rapid

**Fig. 7.** Rose diagrams showing swimming speed distribution versus swimming direction (horizontal swimming angle) for the hull-mounted (upper) and bottom-mounted (lower) transducers. All data are pooled for the 10- to 30-m interval and the 80- to 110-m interval, respectively. Blue, 0–12 cm·s<sup>-1</sup>; red, >12–24 cm·s<sup>-1</sup>; yellow, >24–36 cm·s<sup>-1</sup>; green, >36 cm·s<sup>-1</sup>. Note that the bearing of the bottom-located transducer is not known so that the displayed swimming directions for the two transducers are not comparable.



ascents that often were not recorded acoustically followed by a longer sinking period (i.e., the opposite allocation of time between rising and descending to that described above).

Norway pout appeared to forage on krill in the lower part of the water column, even by night when visual predation is unlikely (Onsrud et al. 2004). We hypothesize that prey detection was then by tactile means. Fish relying on hydromechanical stimuli in prey detection behave in a way that minimizes self-generated noise caused by their own movements (Rowe et al. 1993; Janssen et al. 1999). Swimming trajectories, generally curved paths with no velocity fluctuations, with swimming speed as low as 0.3 body length·s<sup>-1</sup>, were derived from the tracking data. A gliding swimming behaviour would reduce noise for the lateral line system (Janssen 2004), and this behaviour suggests that prey movement may contribute in mediating encounters. *Meganyctiphanes norvegica* are active prey organisms, and previous in situ studies at the same study site have suggested

krill swimming speed with mode ~4 cm·s<sup>-1</sup> (Klevjer and Kaartvedt 2003), which corresponds to 30%–40% of the measured modes for deep-living fish at night.

Our study has shown that a bottom-located transducer facilitates target tracking of deep-living fish. Combined with free-hanging and hull-mounted transducers, we were able to obtain robust in situ results of swimming speeds and behaviour at a deep location throughout the water column. Tracking of fish from stored raw data, increased sampling rate, and enhanced resolution enabled by the latest echosounders hold promise of increased accuracy in swimming speed estimates and the ability to reveal the full aspect of swimming behaviour.

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