Limnol. Oceanogr., 56(3), 2011, 765–774

doi:10.4319/lo.2011.56.3.0765

Krill (*Meganyctiphanes norvegica*) swim faster at night

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Abstract

Krill are key members in marine food webs, and measurement of swimming speed is vital to assess their bioenergetic budgets, feeding, and encounters with predators. We document a consistent and marked diel signal in swimming speed of krill in their natural habitat that is not related to diel vertical migration. The results were obtained using a bottom-mounted, upward-looking echo sounder at 150-m depth in the Oslofjord, Norway, spanning 5 months from late autumn to spring at a temporal resolution of ~1–2 records s^{-1}. Swimming speed was assessed using acoustic target tracking of individual krill. At the start of the registration period, both daytime and nocturnal average swimming speeds of *Meganyctiphanes norvegica* were ~ 3.5 cm s^{-1} (~ 1 body lengths ([bl] s^{-1}) in waters with oxygen concentrations of ~ 15–20% O_2 saturation. Following intrusion of more oxygenated water, nocturnal average swimming speeds increased to ~ 10 cm s^{-1} (~ 3 bl s^{-1}), i.e., more than double that of daytime swimming speeds in the same period. We hypothesize that krill activity during the first period was limited by oxygen, and the enhanced swimming at night subsequent to the water renewal is due to increased feeding activity under lessened danger of predation in darkness.

Krill hold an important role in the world's oceans, especially in the temperate and polar ecosystems. Of particular importance, Antarctic krill, *Euphausia superba*, constitute a biomass that probably surpasses that of mankind (Verity and Smetacek 1996), and krill are the single most important item of food for a variety of predators, including marine mammals, fish, and birds. In the Northern Hemisphere, *Meganyctiphanes norvegica* plays a key role in ecosystems from the Mediterranean to polar seas, being a grazer on phytoplankton, predator on zooplankton, and important prey for fish, birds, and sea mammals (Mauchline 1980).

Studies of krill behavior have largely focused on diel vertical migrations (for instance, Moore 1950; Mauchline 1980; Tarling et al. 2001). Horizontal migrations have been suggested for the large Antarctic krill (Siegel et al. 1990; Sprong and Schalk 1992), and experimental studies show that this species is capable of sustained swimming speeds of at least 4–5 body lengths per second (bl s^{-1}; Kils 1981). For actively swimming krill, energy consumption depends heavily on swimming speed (Torres and Childress 1983). Furthermore, an increase in swimming speed may increase the encounter rates with food items (Gerritsen and Strickler 1977) but also with slow-moving and ambush-type predators (Greene 1985). Individual krill swimming speeds therefore have direct effect on several key aspects of krill biology, but apart from a few studies (Price 1989; De Robertis et al. 2003), swimming speeds have seldom been investigated and therefore remain largely unknown.

We have previously shown that it is possible to record the behavior of individual krill in situ by means of submerging split-beam echo sounders into krill scattering layers (SL) (Klevjer and Kaartvedt 2003, 2006). In the current study, we apply this approach in the Oslofjord, taking advantage of access to a very sheltered krill habitat. Here, we present results on krill swimming behavior from continuous measurements over a 5-month period, with a temporal resolution of 1–2 records s^{-1}. The long-term coverage enabled us to assess the effect of different environmental events on individual behavior; major events included ice covering the fjord, a water renewal that brought more oxygenated waters into the fjord, and the spring bloom. The high temporal resolution made it possible to address short-term patterns, and the results are organized here to detect consistent changes on timescales as short as 30 min.

Methods

Study site—The studies took place at 150-m depth in the deepest part of the Bunnefjord, the inner branch of the Oslofjord (Fig. 1). This is an extremely sheltered location, and the basin is defined by a shallow sill (depth 57 m) at the outlet of this branch, which comes in addition to an outer sill in the Oslofjord (depth 19 m) (Fig. 1). The deep waters in the Bunnefjord therefore have long residence times, and hypoxic and even anoxic waters occur (Beyer 1968; Kaartvedt et al. 2009).

Continuous records—An upward-looking, bottom-mounted Simrad EK60 echo sounder equipped with a 120-kHz ES120-7 depth-resistant transducer was deployed at ~ 150-m depth (59.792171°N, 10.726776°E) (Fig. 1). The submerged transceiver (GPT), kept in a pressure-proof casing, was powered from land via 800 m of cable. The digitized signals were transmitted back over the cable to a laptop computer, where they were stored in raw format for later analysis. The laptop was connected to the internet with mobile broadband technology, allowing remote control and the delivery of real-time echograms via a web-based interface. The echo sounder was calibrated by the standard sphere method near the surface prior to deployment and

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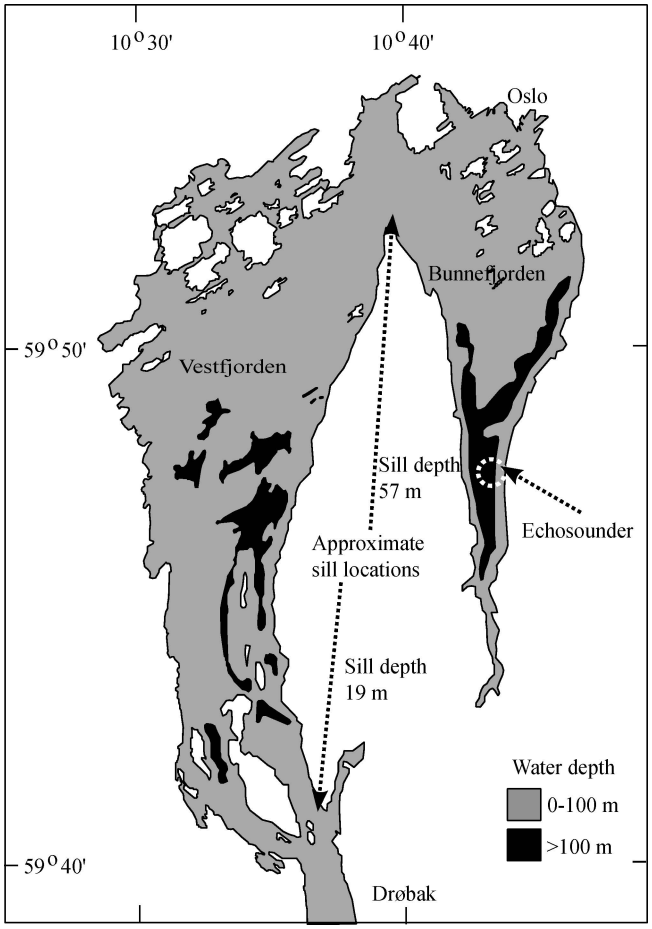

Fig. 1. Map showing the area of the inner Oslofjord, with deployment position of acoustic rig in the Bunnefjord indicated by dotted white circle. Water depths exceeding 100 m are depicted in black, and positions of important sills are indicated.

immediately after retrieval of the acoustic rig. The results for the two calibrations were significantly different, suggesting that performance of the transducer changed over the time of the experiment. Results on target strength (TS; a proxy for size) are therefore only used in assessing the identification of acoustic targets in comparison with catches from trawl sampling.

A mechanical current meter (SD6000) was deployed together with a salinity, temperature, and depth (STD) probe (SD2000) close to the acoustic rig, directly above the bottom. The current meter gave measurements of current direction and speed, as well as temperature. The mechanical current meter has a precision of 1 cm s^{-1}, and the lowest speed it can measure is 1 cm s^{-1}. The STD probe gave continuous measurements of temperature and salinity.

Ice conditions in the fjord were monitored with a resolution of 1 h via images obtained with a web camera, and the images were stored on a computer. The image records show that the fjord became covered with ice on the morning of 06 February 2006, and thereafter the degree of coverage fluctuated until the evening of 08 February 2006, when the fjord again was completely covered with ice. The fjord thereafter remained fully ice-covered until 12 April 2006.

The Ferrybox (Norwegian Institute for Water Research) project samples chlorophyll *a* (Chl *a*) fluorescence daily throughout the Oslofjord by utilizing fluorometers on ferries in regular traffic. We used chlorophyll values (4-m depth) from the Vestfjord (59.80°–59.83°N, 10.597°–10.558°E) to assess the timing of the spring bloom. Water from this adjacent branch is the source water for the Bunnefjord.

Sampling campaigns—In addition to the continuous measurements, intermittent sampling campaigns were carried out using the University of Oslo vessel *Trygve Braarud*. Conductivity, temperature, and depth (CTD) casts were made with a Falmouth Scientific Instruments CTD equipped with water samplers. Water from these samplers was later analyzed for oxygen content using the Winkler method.

Trygve Braarud is equipped with Simrad EK 500 echo sounders operating at 38 kHz and 120 kHz, which were used when targeting acoustic scattering layers (SL) during pelagic trawling. The pelagic trawl has an aperture of about 100 m^2, and mesh size near the opening is 20 cm, declining to 1 cm in the rear part. Meshes become stretched and smaller during sampling, but absolute quantification of the catch is not trivial, so that we here use the relative unit "liters per minute of trawling" for comparison between tows. The trawl was towed horizontally or obliquely at ~ 2 knots. The depth profile of the trawl was monitored by a Scanmar depth sensor during sampling. The trawl was equipped with a multisampler codend (Engås et al. 1997), allowing vertically stratified samples. In total, 43 depth-resolved hauls were obtained throughout the water column day and night. To create a summary of catches, we divided the water column into three 50-m intervals and averaged the catches from hauls within those intervals. Additionally, benthopelagic organisms were sampled with a bottom trawl on two separate dates. Mesozooplankton were collected via depth-stratified vertical hauls with 200-μm plankton nets (Working Party No. 2, WP2). Mesozooplankton results are not further dealt with here, apart from concluding that this sampling did not provide evidence of alternative acoustic targets to krill.

Acoustic postprocessing—Target tracking (i.e., the process of combining the single echo detections [SEDs] from an organism over time) was performed on SEDs generated by the echo-length–based single echo detector of Sonar5 (Balk and Lindem 2005). Results were analyzed from 01 December 2005 to 25 April 2006. Ping rates were 1–2 pings s^{-1}. In order to accept a track, a minimum of 25 echoes was required, with no more than 5 consecutive echoes missing. Consecutive echoes were required to be within 1 degree in the horizontal dimensions and 5 cm in the vertical dimension in order to be accepted into the track; this gating was allowed to expand by 0.1 degrees for each missing echo. Tracks were accepted in the region from 10 to 25 m from the transducer, with the majority of tracks being recorded within the first 20 m. The effective tracking region therefore spanned the depths from ~ 127.5 to 142.5 m. Tracks with SEDs with target strengths stronger than

−65 dB were removed from the data set in order to separate krill from co-occurring fish (sprat; *Sprattus sprattus*). Additionally, some of the original tracks detected by the Sonar5 software were caused by bubbles released from the bottom mooring (electrolysis); these bubbles had TS values that overlapped with the TS values of krill. These tracks were filtered from the results such that tracks that had changes in the vertical direction of movement were automatically accepted as organisms, whereas tracks that were monotonically rising for more than 0.5 m were discarded as bubbles.

Tracks were then imported from Sonar5 into the software package R (Ihaka and Gentleman 1996), where additional postprocessing was performed before calculations were made of track averages. Noise in the SED positions necessitates smoothing; otherwise, erroneously high estimates of swimming speeds are produced (Mulligan and Chen 2000). Prior to smoothing, the coordinates of the echoes were passed through a filter aimed at removing outliers. This low-pass filter interpolates values for echoes that are not within the range of values for the echoes before and after, working separately on the three dimensions (''along-ship'' angle, ''athwart-ship'' angle, and range). From these filtered positions, net displacement speeds were calculated after doing separate linear regressions on the coordinates of the echoes in the tracks.

To assess swimming speed correctly, the effects of water movements have to be removed. Results from the current meter documented very weak currents, and the current measurements from the deployed rig were generally too coarse to resolve water movements in the very calm fjord environment (1 cm s^{-1} resolution). Also, the storage space of the rig became full during the course of the deployment, and the measurements from this rig therefore only spanned the period from 01 December to mid-March. Currents were therefore additionally estimated from the tracking data. This was done by summing the movements of all tracks for 2-h periods, and dividing by the sum of time in tracks to get the population net movement speeds. These measurements are later referred to as estimated current speeds or population net movement. This population net movement speed was subtracted from the individual tracks. The procedure assumes that the horizontal movements of individuals are uncorrelated (isotropic movements) (Jaffe et al. 1999).

To assess relative abundance of krill in near-bottom waters day and night, acoustic densities of organisms were determined by integration of acoustic measurements over the depth interval from 137.5 to 127.5 m over 30-min periods. Each period was then given a time-coordinate decided by its proximity to sunset, and final estimates were computed by pooling results for the entire measurement series into 30-min bins, with each bin being a fixed amount of time away from sunset. Densities are reported as median mean volume backscattering strength (S_v) values for each time bin.

Results

Physical oceanography, oxygen, and chlorophyll—The records from the submerged current meter (deployed at 155-m depth, close to the acoustic rig; Fig. 1) showed a distinct increase in temperature from 7.5°C to 8.5°C from 19 February to 23 February (Fig. 2), reflecting intrusion of new waters. Temperatures thereafter gradually declined throughout March. Because temperatures measured with the STD showed the same pattern as the temperatures registered with the current meter, only data from the current meter are presented graphically.

The ice cover prevented field campaigns in midwinter, but measurements during the sampling before and after the ice showed that the water renewal introduced more oxygenated water, with near-bottom values below 2 mL L^{-1} in early winter and above 4 mL L^{-1} at the end of the measurements (Fig. 3). Hydrographical conditions below 100 m were otherwise relatively stable in the first period of sampling, with salinities of, respectively, 33.03 and 32.92 on 25 November and 05 January, and corresponding temperatures of 7.45°C and 7.47°C at 150 m (Fig. 4). Measurements made on 19 April registered a salinity of 33.53 and a temperature of 7.69°C, at the same depth, again reflecting the midwinter water renewal.

Daily averages of chlorophyll values measured in the Vestfjord were low throughout December, January, and February (Fig. 2), and monthly averages were below 0.6 mg m^{-3} prior to the water renewal on 19 February. The levels were slightly elevated (0.72 mg m^{-3}, $n = 10$) during the period 19 February to 01 March, though this elevation was only statistically significant when compared to the January average (two-sample t-test: $t = -2.4361$, df $= 11.26$, $p < 0.05$). Around 01 March, the daily averages started increasing, and exceeded 10 mg m^{-3} in mid-March (Fig. 2); the overall March average was 5.03 mg m^{-3}. The April average (2.77 mg m^{-3}, $n = 17$) was significantly different than the March value (two-sample t-test: $t = 2.3497$, df $= 32.766$, $p < 0.05$).

Catches—The sampling identified two components making up the bulk of the acoustic structures, the small clupeid fish sprat (*Sprattus sprattus*) and the krill *Meganyctiphanes norvegica*. These two species dominated the pelagic zone, and in all the trawl samples combined, we caught 3617 sprat and 152 liters of krill. Prior to April, sprat dominated the weight of the catches and were caught in all but 3 of 32 hauls. Krill dominated both numerically and by weight in April, when sprat was lacking in the catches, apart for one shallow (30 m) nocturnal haul (a total of 11 hauls in April). This is in accordance with acoustic data, which show that sprat changed their behavior and left deep waters in February (not shown).

Krill were present in pelagic trawl catches both above and below a depth of 100 m, regardless of date and time of day (Fig. 5). Prior to April, the 100–150-m interval had the highest catches during the day, while *Meganyctiphanes* was fairly equally distributed throughout the water column at night, though with highest catches were found in the upper interval (Fig. 5A). In April, catches were highest in midwater, both day and night, with about half the amount in the deepest interval (Fig. 5B). Catches of alternative invertebrate targets were very low, comprising a total of 15 shrimps (11 *Pandalus* sp. and 4 *Crangon* sp.) and some (not quantified) gelatinous plankton, mainly ctenophores. We

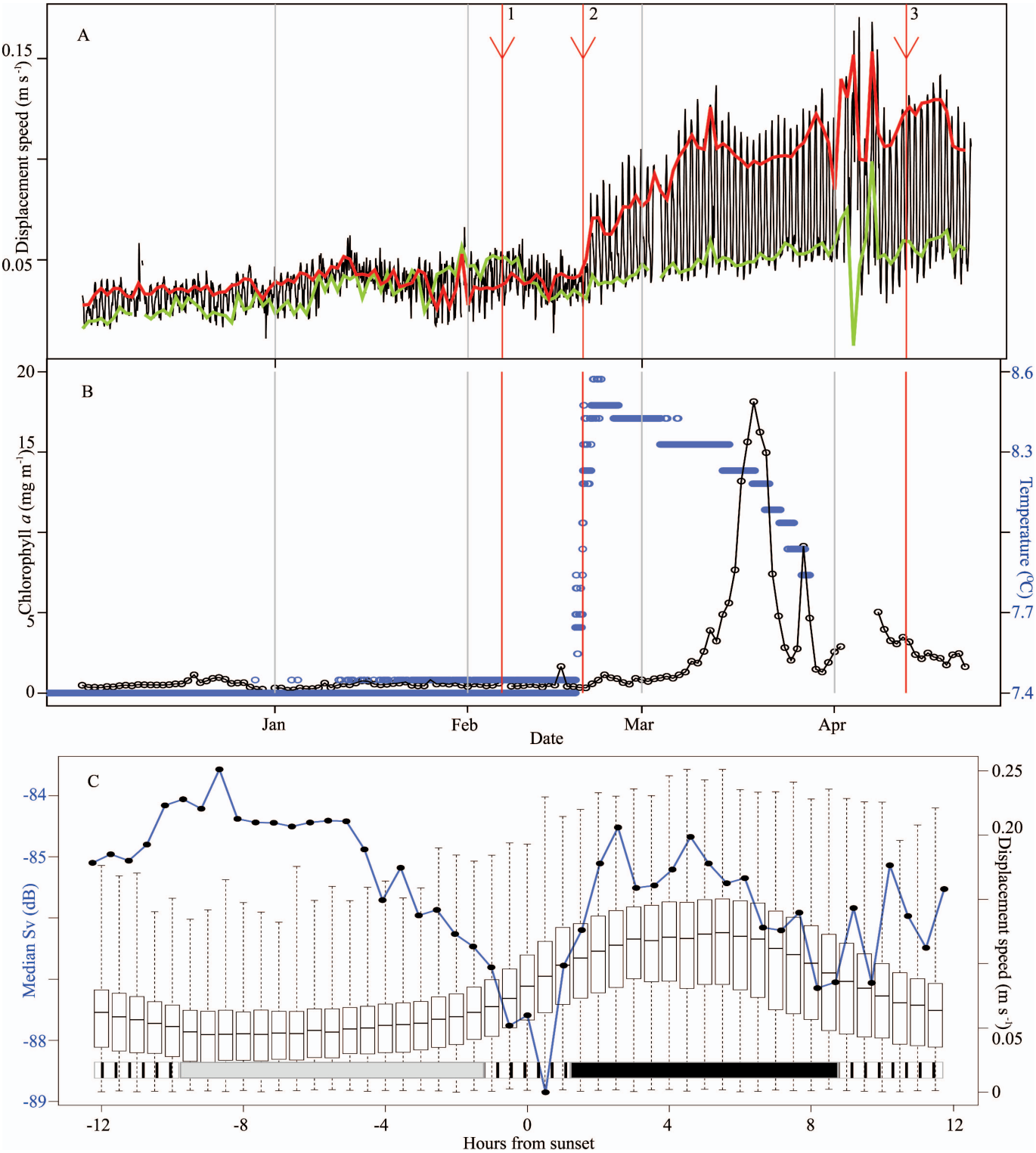

Fig. 2. (A) Krill displacement speeds during the period from 01 December 2005 to 19 April 2006. Thin black line shows values calculated by averaging all individual speeds observed within 2-h intervals. Thick red line shows values calculated by averaging all individuals measured during night, and thick green line shows averages calculated for daytime data. Gray vertical lines indicate new months. Red vertical lines with arrows point to dates of changes in the physical environment: 1–06 February, ice forms on fjord. 2–19 February, water exchange occurs. 3–12 April, ice covers vanishes. (B) Black line with points shows daily averages of chlorophyll *a* (in mg L^{-1}) recorded in the adjacent Vestfjord. Data are courtesy of Ferrybox project (Norwegian Institute for Water Research, NIVA). Blue points are near-bottom temperature at the acoustic rig. Vertical lines are as in A. The incursion of new water masses is clearly visible as an increase in the temperature starting on 19 February. (C) Displacement speeds (box plots) as a function of time away from sunset (30-min

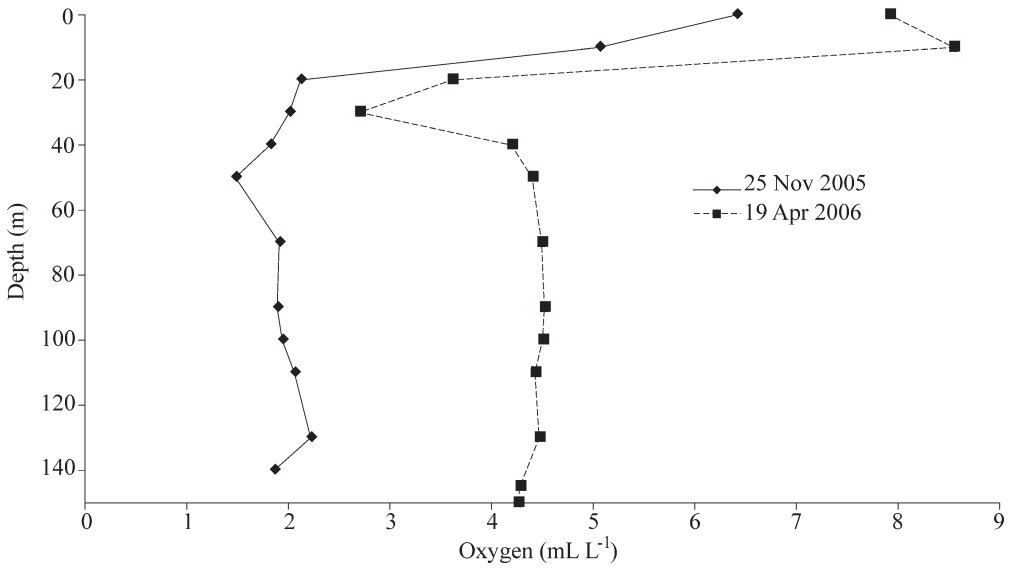

Fig. 3. Oxygen concentrations vs. depth in the Bunnefjord prior to (25 November 2005) and after (19 April 2006) the water exchange.

also caught a total of 33 whiting (*Merlangius merlangus*), 19 four-bearded rocklings (*Enchelyopus cimbrius*), and 1 flounder pelagically, as well as some gobiids. The small gobiids were not properly enumerated in the krill-dominated catches, but they were always vastly outnumbered by the krill. The bottom trawl was used to check for presence of other larger crustaceans. Apart from krill and a few shrimps (*Pandalus* sp.), no large crustaceans were captured.

Lengths of krill—The krill catches were at all times dominated by larger, adult krill, with lengths centered around 35 mm. Very few smaller krill were found in the catches prior to the water exchange. The catches from April introduced an additional, smaller mode of krill, with lengths centered around 30 mm (Fig. 6); however, the April distribution was also dominated by the larger mode.

Currents—Both measurements with the mechanical current meter, and through the population net movements of animals estimated by the split-beam target-tracking method revealed that currents in the deep water were low, with the majority of measurements being below 2 cm s^{-1}, and very few measurements exceeding 3 cm s^{-1}.

Readings from the current meter showed daily averages (movements averaged over entire days) of 1.3 cm s^{-1} prior to 19 February (chosen as a split date due to the water renewal), and 2.0 cm s^{-1} thereafter, a difference that was significant (Mann–Whitney *U*-test = 1061, n_{before} = 80, n_{after} = 36, $p = 0.024$). Tracking-based estimates of current speeds gave speeds of 0.3 cm s^{-1} before and 1 cm s^{-1} after, and once again the differences were significant (Mann–Whitney *U*-test = 187, n_{before}= 80, n_{after}= 36, $p \ll 0.001$). The raw measurements (with a resolution of 30 min for the current meter, and 2 h for the tracking-based current estimates) showed 95% of measured current speeds below a level of, respectively, 4.2 and 2.3 cm s^{-1}.

Swimming speeds—The detected swimming was mostly directed in the horizontal plane, with an average of 15% of the motion directed vertically. Only ~ 10% of tracks were active vertical swimmers, arbitrarily defined as tracks with more than 20% of motion directed vertically. Until mid-February, measured swimming speeds were fairly stable throughout the 24-h period, with averages for daytime and nighttime being, respectively, 3.6 and 3.7 cm s^{-1}, with standard deviations of 2.0 and 1.9 cm s^{-1} and n = 12,324 and 61,622. These speeds are marginally larger than 1 body length per second (bl s^{-1}), applying results from the catches. Despite the minimal diel speed difference, day and night speeds were significantly different (Kolmogorov–Smirnov test, $p \ll 0.001$) (Figs. 2, 7). Swimming speed increased markedly on, and subsequent to, 19 February. Nighttime averages then exceeded daytime speeds by a factor of almost 2 (respectively, 5.1 and 9.9 cm s^{-1} [~ 1.4 to 2.8 bl s^{-1}], with standard deviations of 2.8 and 4.9 cm s^{-1}, n = 87,732 and 93,379); also, these distributions were significantly different (Kolmogorov–Smirnov test, $p \ll 0.001$) (Figs. 2, 7). Average daytime speeds increased slightly toward the end of the registration period; the differences between average daytime speeds before and

←
intervals) for the period 19 February to 25 April. The median is shown as a horizontal line; boxes are bound by 25th and 75th percentiles, and whiskers extend to extreme values. Blue line with black dots depicts a concurrent acoustic proxy for biomass (median of mean volume backscattering values for 30-min intervals). Horizontal bar shows time offset from sunset (0); gray represents hours of daytime and black represents nighttime throughout the > 2-month period; striped areas refer to 2-h periods centered on sunset and sunrise and hours shifting between night and day in course of the registration period.

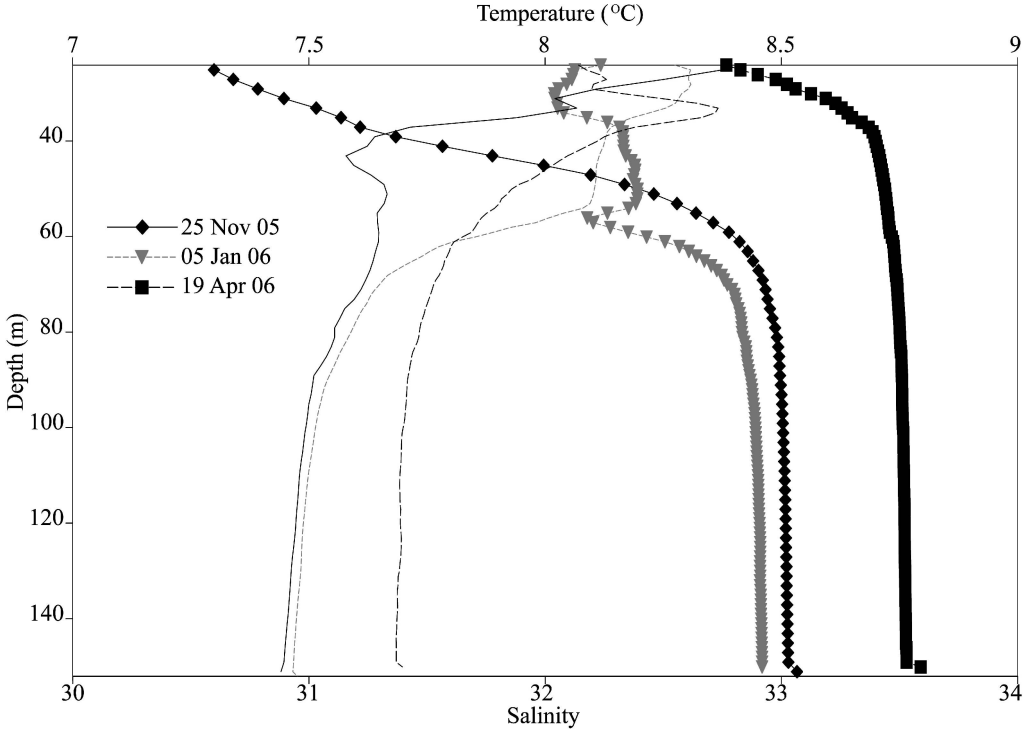

Fig. 4. Physical parameters vs. depth in the Bunnefjord over the season. Lines with symbols show salinities, lines without symbols are temperatures.

after 19 February were significant, as were the differences between nighttime speeds before and after (Kolmogorov–Smirnov test, $p \ll 0.001$).

These measurements are based on averages for whole nights and days (defined as the periods between 1 h prior to and after nautical sunrise and sunset). A histogram of the raw measurements demonstrates that the ''population'' of swimming speeds is actually bimodal, with one group swimming with net displacement speeds very close to zero, and another having higher displacement speeds (Fig. 7). For the night measurements after the water exchange, the median value is 10.4 cm s^{-1}, which for adult krill would correspond to swimming speeds of almost 3 bl s^{-1}, with more than 20% of the population attaining swimming speeds exceeding 4 bl s^{-1} (Fig. 7B). Changes in population average speeds are caused by a varying part of the population being active, as well as changes to the speeds utilized by the active proportion.

The acoustic results suggest that comparable numbers of krill were studied day and night, although densities of organisms in the depth interval 137.5–127.5 m were somewhat higher during daytime (Fig. 2).The near-bottom S_v values dropped abruptly at sunset, but shortly thereafter they returned to levels suggesting that the near-bottom biomass was only reduced by about 20%, compared to daytime levels, during most of the night.

Discussion

The results from this study are to our knowledge the first on long-term in situ individual krill swimming behavior and the first demonstration of diel variations in swimming speed not ascribed to diel vertical migration (DVM). Up until now, little has been known about the actual behavior for any species of krill in situ, with only scant short-term observations reported in the literature (Jaffe et al. 1999; Hamner and Hamner 2000; Klevjer and Kaartvedt 2006). The results were facilitated by the conditions in the Bunnefjord. This is an extremely sheltered environment that still offers access to oceanic species such as *M. norvegica*. The sheltered environment simplifies the practical deployment of gear, and the quality and analysis of the results. The enclosed fjord is characterized by weak currents, so that swimming speeds clearly exceed advection, and they also permit long residence times of targets in the acoustic beam.

The measurements of this study were taken from krill (*Meganyctiphanes norvegica*) living deeper than the main mode of the population distribution, which in the Oslofjord typically is from 75 to 100 m during the day, and in upper waters at night (Fig. 5; Onsrud and Kaartvedt 1998; Kaartvedt et al. 2002). However, the catches confirm that krill were present in the deep water both during night and day (Fig. 5), and we recorded a total of ~ 309,000 tracks assigned to krill during the registration period. Identification of scatterers is an inherent problem in acoustic studies, but a low diversity of species in the deeper waters (e.g., results from the trawl catches) greatly simplifies the interpretations with regard to species composition in acoustic studies. The trawl catches suggest that krill are the only feasible weak acoustic target in the deep water. The potential differences in scattering strength between krill and sprat are large enough that we believe that our approach of using TS in tracks to identify species is valid.

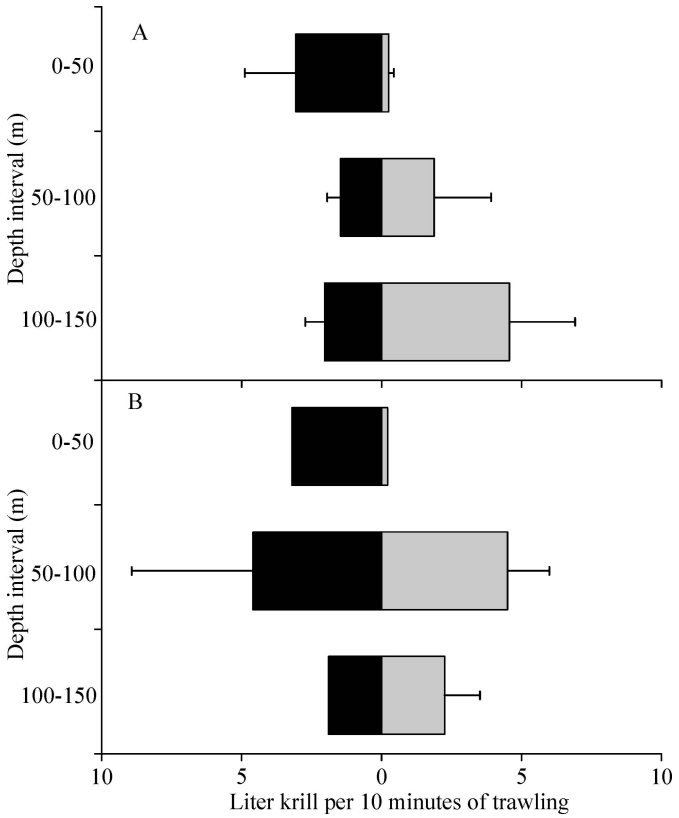

Fig. 5. Krill catches in the Bunnefjord split into day (gray) and night (black) values. Error bars are standard deviations. (A) Catches prior to water exchange, and (B) catches after water renewal.

The results up until the end of January might contain some measurements of sprat, but the results were reasonably consistent with the daytime data for the period after sprat left their deep habitat in midwinter. It is therefore unlikely that inclusion of sprat results was a major factor in our results. The other possible alternative targets would be unquantified numbers of jellyfish and ctenophores, which in any case would be slow swimmers and not influence the conclusion on the diel swimming pattern and the effect of the water renewal.

Imperfect positional measurements necessitate smoothing of the results (Mulligan and Chen 2000). While noise in positions tends to bias the results upward, our usage of linear regressions of positions to estimate speeds will tend to give underestimates of the true swimming speeds, because all swimming trajectories will be forced to have no curvature. In previous studies (Klevjer and Kaartvedt 2003, 2006), we have found that northern krill sometimes swim in tight loops. The results on swimming speed revealed a bimodal distribution, and an apparent slow-moving component would be the result of our procedure if part of the population were moving in loops. However, using a running mean–based smoother that allows the tracks to have curvature on the current data resulted in the same overall patterns, even though the average speeds were increased. We therefore opted to use the more conservative average displacement speeds. Average displacement speeds were significantly dependent on ranges, which suggest that the results after the smoothing procedure were still biased. However, the difference between the average speeds at 10 vs. at 25 m was ~ 2 cm s^{-1}. Because the increase in speeds with range was small compared to the night and day differences, and also other factors beside phase jitter of angular measurements may contribute to this increase, this effect is disregarded in the further discussion.

Krill swimming speeds—For most of this study, daytime average krill swimming speeds were on the order of 1 bl s^{-1} (Figs. 2, 7). Krill can attain speeds much higher than this, but swimming speeds of less than 2 bl s^{-1} are in concordance with findings from previous studies (Price

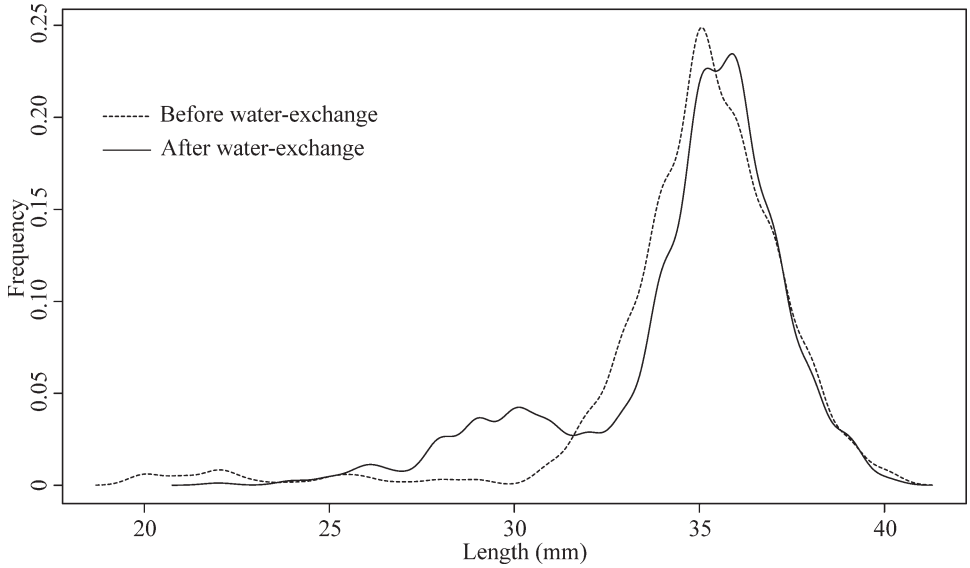

Fig. 6. Length distribution of krill caught deeper than 80 m, split into krill caught before and after the water exchange.

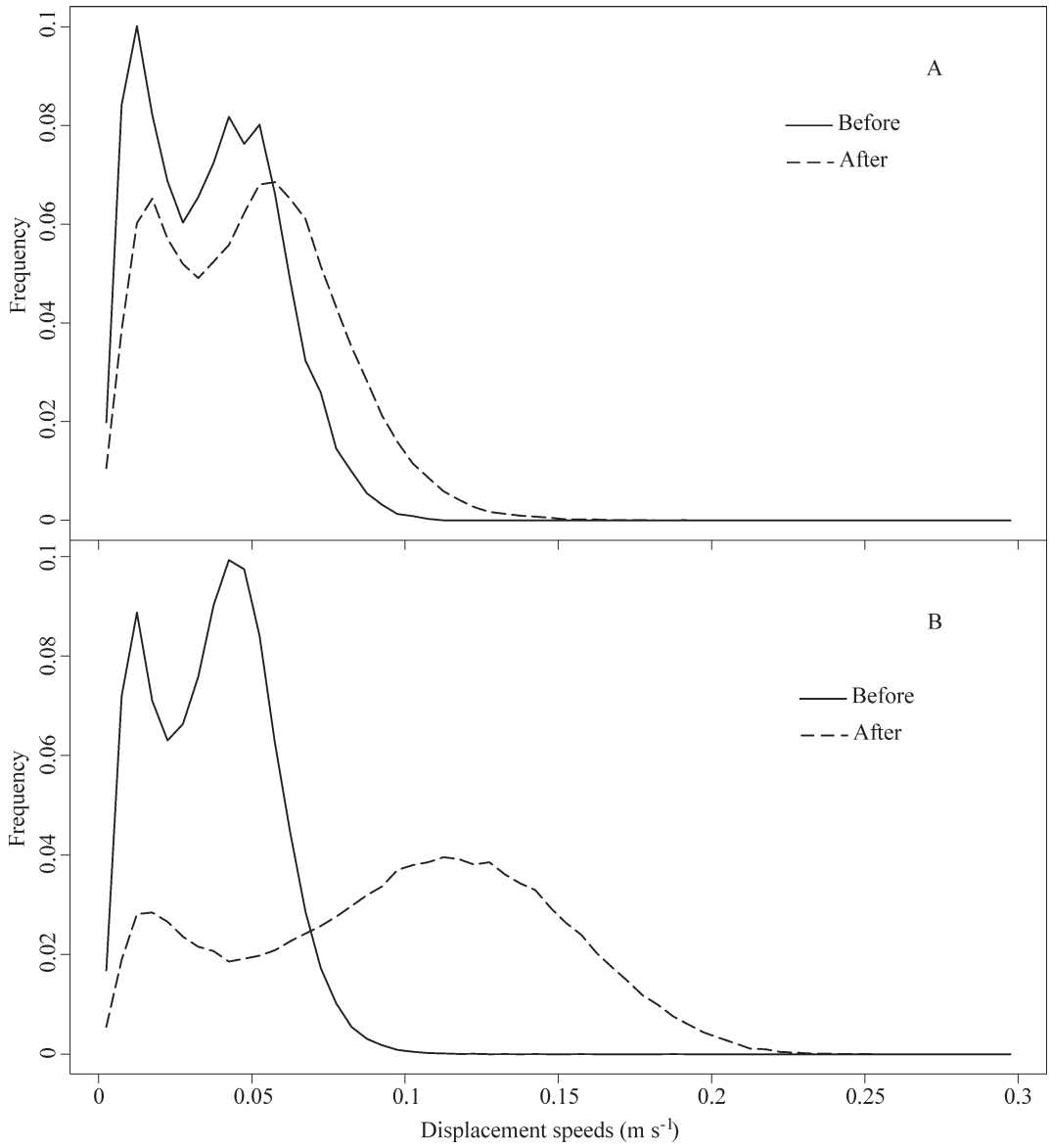

Fig. 7. (A) Distributions of daytime displacement speeds for tracks collected prior to and after water exchange. (B) Distributions of nighttime displacement speeds for tracks collected prior to and after water exchange.

1989; De Robertis et al. 2003; Klevjer and Kaartvedt 2006). Krill oxygen consumption, and therefore energy needs, increases rapidly with increased swimming activity (Torres and Childress 1983). We interpret the depressed swimming speeds prior to the water renewal in midwinter as a behavioral adaptation to low oxygen concentrations in the environment. Krill are negatively buoyant and therefore depend on swimming more or less continuously merely to maintain a given depth (Kils 1981). It has been suggested that an increase in swimming speed up to a certain level does not actually increase the metabolic costs incurred by krill, as the hydrodynamic lift generated by the forward propulsion balances the need for vertical swimming (Kils 1981). Kils found this level to be around 13 cm s^{-1} for a 49-mm *Euphausia superba*, or about 2.7 bl s^{-1}, but this level is likely to vary with factors such as density of both krill and water, as well as krill body shape.

Price (1989) found that *Thysanoessa raschii*, a species with adults 20–25 mm long, swam with average speeds below 5 cm s^{-1}, i.e., below approximately 2 bl s^{-1}. In a more recent study of *Euphausia pacifica*, De Robertis et al. (2003) found that during daytime, this krill species generally moved at speeds approaching 1 bl s^{-1}, but swimming speeds increased (medians up to 2 bl s^{-1}, but with some up to 4–5 bl s^{-1}) in relation to the ascent phase of the DVM. Swimming speeds recorded during night in the Bunnefjord after the water renewal (up to $\sim$ 4 bl s^{-1}; Fig. 7) are therefore toward the higher end of speeds reported for krill in other mesocosm or in situ studies. These increased swimming speeds were not directly connected to the ascent phase, as swimming speeds in the deep waters generally peaked well after sundown, with the highest velocities recorded after individuals returned to deep water subsequent to a short-term ascent at dusk (Fig. 2). Also, in general, most of the movement was directed

horizontally, with an average of only 15% of the movement being in the vertical direction. Acoustic numerical densities were only ~ 20% lower than during day, so we do not believe that high nocturnal speeds are caused by a few ''freak'' swimmers remaining in the deep during night.

The main pattern in our data is the markedly increased nighttime speeds after 19 February. This change was brought on or triggered by one or more factors associated with the water exchange that was recorded on this date. We exclude changes of fish abundance and ice conditions as explanations because these events took place before the abrupt change in krill behavior, which was perfectly synchronized with intrusion of new water (Fig. 2). Also, krill sizes appeared to have been roughly similar prior to and after the water exchange (Fig. 6), so size-related differences in swimming capacity are unlikely to have influenced our results.

The water exchange on 19 February altered the temperature and oxygen content in the deep waters of the Bunnefjord (Figs. 2–4). We reject increased temperature as an explanation for the increased nocturnal swimming speed because the temperature declined in the following period, while swimming speed instead continued to increase. The intrusion of water occurred prior to the spring bloom in the outer source water, so the spring bloom could not explain the sudden increase in activity, although it may have contributed to the subsequent increase through spring. As suggested earlier, we rather ascribe the abrupt behavioral change to intrusion of more oxygenated water. Spicer et al. (1999) found that krill may utilize anaerobic respiration at low oxygen levels, thus remaining in hypoxic waters. During daytime, they found krill down to ~ 15% saturation, which corresponds well with conditions at depth in the Bunnefjord during the first part of our study (15–20%). However, *Meganyctiphanes* proved to have a poor anaerobic capacity, and individuals encaged overnight (i.e., prevented from carrying out DVM) at ~ 30% saturation suffered 70% mortality. The adaptations that allow krill to inhabit hypoxic waters therefore appear to be behavioral. Reduction of activity is an obvious way of minimizing oxygen consumption in sublethal oxygen concentrations. Increases in oxygen levels after the water exchange released the krill from this constraint, and the krill particularly increased their nighttime swimming speeds during this period.

While the higher oxygen saturation after the water exchange enabled the krill population to increase their (nocturnal) swimming speeds, the actual factor(s) that motivated this change in behavior remains uncertain. Diel patterns in behavior are usually considered to be ultimately caused by trade-offs between feeding activities and reduction of risk of predation (Stich and Lampert 1981; Loose and Dawidowicz 1994), which also may apply in the case of the diel patterns in krill swimming activity. Swimming enhances encounters both with prey and predators (Gerritsen and Strickler 1977). Swimming speeds of planktivorous fish measured in situ are commonly 4 to 5 times higher than the in situ swimming speeds of krill during daytime (Onsrud et al. 2005), so that the potential effect of the measured krill swimming on predator encounter rates are moderate during daytime. Being visual predators, fish species present in the Bunnefjord are less efficient at night, which might release deep-living krill from predation, favoring enhanced nocturnal swimming speeds, thereby enhancing encounters with food particles and prey organisms.

Acknowledgments

T.A.K. was funded by the Norwegian Antarctic Research Expedition (NARE). Anders Røstad provided Fig. 1. Norwegian Institute for Water Research (NIVA) kindly provided previously unpublished chlorophyll values for the Oslofjord. The comments of two anonymous reviewers improved the manuscript.

References

Balk, H., and T. Lindem. 2005. Sonar4 and Sonar5-Pro postprocessing systems (operation manual). Univ. Oslo.

Beyer, F. 1968. Zooplankton, zoobenthos, and bottom sediments as related to pollution and water exchange in the Oslofjord. Helgoland Mar. Res. **17:** 496–509.

De Robertis, A., C. Schell, and J. S. Jaffe. 2003. Acoustic observations of the swimming behavior of the euphausiid *Euphausia pacifica* Hansen. ICES J. Mar. Sci. **60:** 885–898, doi:10.1016/S1054-3139(03)00070-5

Engås, A., R. Skeide, and C. W. West. 1997. The 'MultiSampler': A system for remotely opening and closing multiple codends on a sampling trawl. Fish. Res. **29:** 295–298, doi:10.1016/S0165-7836(96)00545-0

Gerritsen, J., and J. Strickler. 1977. Encounter probabilities and community structure in zooplankton: A mathematical model. J. Fish. Res. Board Can. **34:** 73–82.

Greene, C. H. 1985. Planktivore functional groups and patterns of prey selection in pelagic communities. J. Plankton Res. **7:** 35–40, doi:10.1093/plankt/7.1.35

Hamner, W. M., and P. P. Hamner. 2000. Behavior of Antarctic krill (*Euphausia superba*): Schooling, foraging, and antipredatory behavior. Can. J. Fish. Aqaut. Sci. **57:** 192–202, doi:10.1139/cjfas-57-S3-192

Ihaka, R., and R. Gentleman. 1996. R: A language for data analysis and graphics. J. Comput. Graph. Stat. **5:** 299–314, doi:10.2307/1390807

Jaffe, J. S., M. D. Ohman, and A. De Robertis. 1999. Sonar estimates of daytime activity levels of *Euphausia pacifica* in Saanich Inlet. Can. J. Fish. Aquat. Sci. **56:** 2000–2010, doi:10.1139/cjfas-56-11-2000

Kaartvedt, S., T. Larsen, K. Hjelmeseth, and M. S. R. Onsrud. 2002. Is the omnivorous krill *Meganyctiphanes norvegica* primarily a selectively feeding carnivore? Mar. Ecol. Prog. Ser. **228:** 193–204, doi:10.3354/meps228193

———, A. Røstad, and T. A. Klevjer. 2009. Sprat *Sprattus sprattus* can exploit low oxygen waters for overwintering. Mar. Ecol. Prog. Ser. **390:** 237–249, doi:10.3354/meps08196

Kils, U. 1981. Swimming behavior, swimming performance and energy balance of Antarctic krill, *Euphausia superba*. Biomass Sci. Ser. 3.

Klevjer, T. A., and S. Kaartvedt. 2003. Split-beam target tracking can be used to study the swimming behaviour of deep-living plankton in situ. Aquat. Living Resour. **16:** 293–298, doi:10.1016/S0990-7440(03)00013-5

———, and ———. 2006. In situ target strength and behaviour of northern krill (*Meganyctiphanes norvegica*). ICES J. Mar. Sci. **63:** 1726–1735, doi:10.1016/j.icesjms.2006.06.013

Loose, C., and P. Dawidowicz. 1994. Trade-offs in diel vertical migration by zooplankton: The costs of predator avoidance. Ecology **75:** 2255–2263, doi:10.2307/1940881

Mauchline, J. 1980. The biology of mysids and euphausiids. Adv. Mar. Biol. 18.

Moore, H. B. 1950. The relation between the scattering layer and the Euphausiacea. Biol. Bull. **99:** 181–212, doi:10.2307/1538738

Mulligan, T., and D. Chen. 2000. Comment on 'Can stationary bottom split-beam hydroacoustics be used to measure fish swimming speed in situ?' by Arrhenius et al. Fish. Res. **49:** 93–96, doi:10.1016/S0165-7836(00)00260-5

Onsrud, M. S., and S. Kaartvedt. 1998. Diel vertical migration of the krill *Meganyctiphanes norvegica* in relation to physical environment, food and predators. Mar. Ecol. Prog. Ser. **171:** 209–219, doi:10.3354/meps171209

———, ———, and M. T. Breien. 2005. In situ swimming speed and swimming behaviour of fish feeding on the krill *Meganyctiphanes norvegica.* Can. J. Fish. Aquat. Sci. **62:** 1822–1832, doi:10.1139/f05-090

Price, H. J. 1989. Swimming behavior of krill in response to algal patches: A mesocosm study. Limnol. Oceanogr. **34:** 649–659, doi:10.4319/lo.1989.34.4.0649

Siegel, V., B. Bergström, J. O. Strömberg, and P. H. Schalk. 1990. Distribution, size frequencies and maturity stages of krill, *Euphausia superba*, in relation to sea-ice in the northern Weddell Sea. Polar Biol. **10:** 549–557.

Spicer, J., M. A. Thomasson, and J. O. Strömberg. 1999. Possessing a poor anaerobic capacity does not prevent the diel vertical migration of Nordic krill *Meganyctiphanes norvegica* into hypoxic waters. Mar. Ecol. Prog. Ser. **185:** 181–187, doi:10.3354/meps185181

Sprong, I., and P. H. Schalk. 1992. Acoustic observations on krill spring–summer migration and patchiness in the northern Weddell Sea. Polar Biol. **12:** 261–268, doi:10.1007/BF00238268

Stich, H., and W. Lampert. 1981. Predator evasion as an explanation of diurnal vertical migration by zooplankton. Nature **293:** 396–398, doi:10.1038/293396a0

Tarling, G. A., J. B. L. Matthews, P. David, O. Guerin, and F. Buchholz. 2001. The swarm dynamics of northern krill (*Meganyctiphanes norvegica*) and pteropods (*Cavolinia inflexa*) during vertical migration in the Ligurian Sea observed by an acoustic Doppler current profiler. Deep-Sea Res. I **48:** 1671–1686, doi:10.1016/S0967-0637(00)00105-9

Torres, J., and J. Childress. 1983. Relationship of oxygen consumption to swimming speed in *Euphausia pacifica*. Mar. Biol. **74:** 79–86, doi:10.1007/BF00394278

Verity, P., and V. Smetacek. 1996. Organism life cycles, predation, and the structure of marine pelagic ecosystems. Mar. Ecol. Prog. Ser. **130:** 277–293, doi:10.3354/meps130277

Associate editor: Thomas Kiørboe

Received: 01 July 2010
Accepted: 18 December 2010
Amended: 12 January 2011