Limnol. Oceanogr., 52(3), 2007, 975–983

Diel vertical migration of individual jellyfish (*Periphylla periphylla*)

Stein Kaartvedt and Thor A. Klevjer
Department of Biology, University of Oslo, P.O. Box 1066 Blindern, 0316 Oslo, Norway

Thomas Torgersen and Tom A. Sørnes
Department of Biology, University of Bergen, P.O. Box 7800, 5020 Bergen, Norway

Anders Røstad
Department of Biology, University of Oslo, P.O. Box 1066 Blindern, 0316 Oslo, Norway

Abstract

Vertical migration of the mesopelagic jellyfish *Periphylla periphylla* (Scyphozoa: Coronatae) was studied by use of hull-mounted and submerged echosounders in a ~440 m deep Norwegian fjord. The research vessel was kept at a fixed position so that individual jellyfish remained in the acoustic beam for prolonged periods in the low advective environment of the deep fjord basin. The population of jellyfish was divided into different vertical modes with different migration behavior. A scattering layer (SL) of *P. periphylla* was located at 150–200 m during the day; it migrated coherently to the upper 50 m at night and returned to depth the next morning. A deeper SL seemed to remain below 250 m both day and night. However, focus on individuals revealed additional, asynchronous migration activity. A pulse of *P. periphylla* left upper layers already a few hours after sunset, and there was interchange of individuals between shallow and deep water throughout the night, including ascent of individuals from the apparent nonmigrating deepest SL. Vertical migration velocities were ~2 cm s^{-1} both during ascent and descent, irrespective of time. Different types of swimming behavior were reflected in the acoustic records, affecting the recorded backscatter.

Most assessments of diel vertical migrations (DVM) of plankton are made by comparing vertical distributions of population means day and night, or through studies of migrating acoustic scattering layers (SL). However, migration of a population integrates the behavior of many specimens, and migration activity may be missed or underestimated when individuals do not act in synchrony (Pearre 2003). Evidence of asynchronous DVM has been gathered from ''tracers'' among gut contents, i.e., presence of food items which likely have been eaten at other depths than the capture of the apparently migrating organism (see Pearre 2003 for a review). Because it is inherently difficult to study DVM of individual plankton organisms in situ (but see DeRobertis et al. 2000), no direct documentation of asynchronous DVM appears to exist.

In this paper, we address the vertical migration behavior of individual jellyfish *Periphylla periphylla* in the ~440 m deep Lurefjorden, Norway (60°41.7′N, 5°08.5′E). Lurefjorden is characterized by an extraordinary large population of this mesopelagic species (Fosså 1992; Youngbluth and Båmstedt 2001; Båmstedt et al. 2003), occurring in concentrations several orders of magnitude greater than in the open ocean (Youngbluth and Båmstedt 2001). The fjord is also exceptional by the virtual absence of mesopelagic fish in the basin water. This has been related to high light extinction, which makes feeding conditions unfavorable for visual predators (Eiane et al. 1999; Aksnes et al. 2004). *P. periphylla* carries out DVM (Fosså 1992; Youngbluth and Båmstedt 2001; Båmstedt et al. 2003), and it has been suggested that 80–90% of the population in Lurefjorden participate in gross migrations from below 100–200 m at day, to upper layers at night (Youngbluth and Båmstedt 2001). However, Klevjer (2006), making acoustic registrations down to 360 m, recently showed that many individuals occurred in deep water, also at night.

It is often claimed that jellyfish are particularly difficult to study. This is because their bodies often are fragile and easily damaged by traditional sampling with plankton nets, because available plankton nets are too small to sample large or dilutely distributed medusae, or because the medusae occur in such large numbers that they clog and burst the nets (e.g., Brierley et al. 2001; Youngbluth and Båmstedt 2001). However, *P. periphylla* is detected acoustically (Båmstedt et al. 2003; Klevjer 2006) and may be easily studied in Lurefjorden because of the absence of alternative targets in the deep water. Although the population density is unusually high compared with oceanic populations of this species, the overall concentrations of jellyfish are sufficiently low to facilitate resolution of individual jellyfish in acoustic studies, largely avoiding problems of multiple targets (cf. Soule et al. 1997). Furthermore, the relatively low swimming activity of jellyfish, and the weak water currents of the enclosed fjord environment, permits studies of single jellyfish for prolonged periods when using a stationary research platform (vessel). In this study, we take advantage of these facts in an acoustic study of *P. periphylla* where we assess vertical migration behavior based on records of individual jellyfish.

Methods

The study was carried out in the deepest part of the fjord on 07–09 November 2004. Maps of the study site and

adjacent regions are given in Fosså (1992) and Youngbluth and Båmstedt (2001).

Hull-mounted SIMRAD EK500, 18 (11.0° nominal 3 dB beam width) and 38-kHz echosounders (7.1° nominal 3 dB beam width) were used in combination with a submerged, 120 kHz EK60 echosounder (7.1° nominal 3 dB beam width). The submerged echosounder was built into a pressure case. It was powered from the ship through 300 m of cable, which also conducted data back to the ship. This echosounder was deployed at different depths to get high-resolution information on *P. periphylla* in deeper layers, and here we present results from transducer depths of 150 m, 100 m, and 75 m. There was a depth limitation of 150 m for the pressure case.

Acoustic raw data were stored for later analysis. Echograms were visualized in Matlab and Sonar5, and additional postprocessing of data was done by the Sonar 5 software (Balk and Lindem 2002).

The RV "Håkon Mosby" was kept stationary by means of automatic satellite navigation (Dynamic Positioning) during most of the acoustic records. This made it possible to follow the slow movements of individual jellyfish in the calm fjord environment, because an individual would remain in the acoustic beam for extended time periods. The behavior of individual jellyfish was derived from echo traces on echograms and by acoustic target tracking (TT). Split-beam echosounders can locate the position of a target in the acoustic beam (e.g., Ehrenberg and Torkelson 1996). By applying software allocating subsequent echoes to the same target (Balk and Lindem 2002), TT provides data on size (TS; target strength), three-dimensional (3-D) swimming trajectories and swimming speed of resolved individuals. Transducer movements can corrupt records of 3-D trajectories (although this can be compensated for; e.g., Handegard 2004), and we here only focus on vertical swimming.

Vertical swimming speeds were assessed in two ways. First, to assess swimming speeds associated with vertical migrations, we manually tracked (selectively picked from echograms) individuals that were seen to be ascending or descending. Vertical speeds less than 1 cm s^{-1} were omitted from analysis of such actively migrating organisms, which likely excluded some migrators. Second, to get data on all resolved targets in the population, we performed target tracking on echoes detected with Sonar5's cross filter detector (Balk and Lindem 2002). The automated tracker was set so that each track should consist of at least 30 echoes, but up to 10 consecutively missing echoes were accepted (ping rate $>$ 5.5 ping s^{-1}). This number of missing echoes was accepted to avoid splitting long tracks and counting them as separate consecutive tracks. The gating of the tracker was set to 10 cm vertically and 1 degree in both horizontal dimensions, increasing in 2-cm vertical increments per missing ping. For an echo to be accepted in a track, it was required to have a 3-D position within this range of the previous echo in the track.

All vertical speeds were computed by dividing the vertical distance between the first and last echoes in a track by the track duration. To separate *P. periphylla* from other scatterers in the automatically tracked data, tracks were filtered based on average target strengths, with tracks in the region −80 dB to −50 dB accepted as *P. periphylla*. The lower part of this range overlaps with target strengths of other pelagic invertebrates, like krill, whereas the upper part overlaps with smaller fish. However, we are confident that the majority of tracks represents *P. periphylla*, because automated tracking was restricted to periods and depth regions where the echograms suggested *P. periphylla* was the dominant scatterer. Tracks of other targets may be included but are believed to be scarce enough not to significantly influence the results.

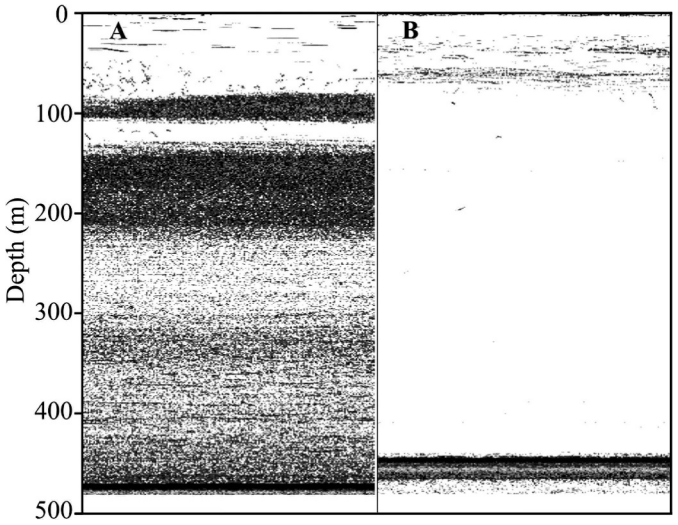

Fig. 1. Daytime echograms (38 kHz) from (A) Masfjorden and (B) Lurefjorden 06 and 07 November 2004, applying a Sv-threshold of −75 dB.

It was necessary to use a low Sv threshold to see the relatively weak jellyfish targets. This is illustrated by echograms by using a threshold of −75 dB in Lurefjorden and in the nearby Masfjorden on two consecutive days (Fig. 1). Mesopelagic fish gave distinct SLs in Masfjorden at this setting, whereas Lurefjorden was almost devoid of backscatter, apart for the upper ~75 m. By lowering the thresholds, echo traces of jellyfish became visible, even at long range (see results). However, results at long range are restricted to large individuals, because echoes from small targets eventually will fall below the noise level (cf. Klevjer 2006).

Lurefjorden has been extensively sampled for many years, so that the main components of the fauna are well known (e.g., Fosså 1992; Bagøien 1999; Bagøien et al. 2001; own unpubl. results). Several previous studies established that acoustic targets deeper than 150 m will be *P. periphylla* (Fosså 1992; Youngbluth and Båmstedt 2001; Båmstedt et al. 2003). The week before our cruise, extensive sampling was carried out in Lurefjorden by a different science crew, reaching the same conclusion (Ulf Båmstedt, pers. comm.). In the trade-off of time use between acoustic and net sampling, we, therefore, prioritized the acoustic studies to obtain uninterrupted time records from a stationary platform. However, vertical plankton tows were taken in 5 depth intervals day and night with a Multinet to establish

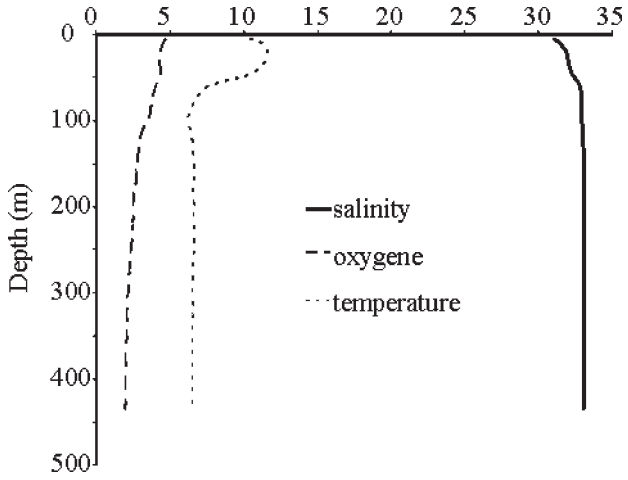

Fig. 2. Vertical profiles of temperature, salinity, and oxygen in Lurefjorden on 07 November 2004.

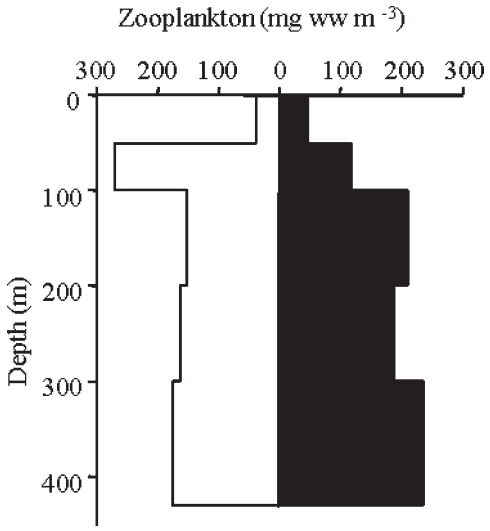

Fig. 3. Vertical profiles of total biomass from Multinet samples day (white) and night (black) in Lurefjorden, 07–08 November 2004.

the potential mesozooplankton prey of *P. periphylla*. We also carried out one tow with a Harstad trawl, one tow with a so-called MIK net with 2 m opening diameter (Munk et al. 1995), and one tow with a 3-foot Isaacs Kidd Midwater Trawl (IKMT) in the upper 150 m, to assess the qualitative composition of the mixture of acoustic targets in this part of the water column.

Krill was a prevailing component of the upper layer. Their biomass was estimated by echo integration based on results obtained by the submerged 120-kHz transducer. In converting acoustic backscatter into biomass of krill, we used literature values for TS-size relationships (Greene et al. 1991) applied on the size distribution of krill from the catches.

Salinity and temperature were measured with a conductivity-temperature-depth (CTD) probe.

Results

Physical oceanography—The temperature was highest in upper layers, with a maximum of 11.6°C at 20 m (Fig. 2). There was a marked thermocline from ~45–65 m, with temperatures decreasing from 10.6–7.2°C. The water mass below was fairly homogenous, with temperatures at ~6.5–6.6°C from 120 m to the bottom. Salinity increased steadily from ~31 at the surface to 32.9 at 70 m. Waters below were homogenous, maximum salinities reaching 33.1.

Potential prey and predators—The biomass of mesozooplankton was low in the upper 50 m (<50 mg wet weight m^{-3}; Fig. 3). Catches varied between 100–300 mg wet weight m^{-3} through the remainder of the water column. The highest catch occurred at 50–100 m during the day.

The qualitative catches by trawl, MIK, and IKMT in the upper 150 m consisted of *P. periphylla*, krill (*Meganyctiphanes norvegica*) and a few lightfish *Maurolicus muelleri*. The krill was largely confined to an acoustical SL between 90 and 120 m at day, migrating into the surface layer at night. The average Sv of this layer, as measured by the 120 kHz submerged echosounder was −77 dB, corresponding to a biomass of ~200 mg wet weight m^{-3}. Targets representing larger fish occurred among the krill and were basically restricted to this layer. These fish were easily distinguished by their strong echoes (not shown).

Distribution and behavior of SLs recorded by hull mounted transducers—The highest backscatter was recorded in the upper ~50–120 m at day, congregating in the upper 50 m by night (Fig. 4). This layer would represent a mixture of krill, fish, and *P. periphylla*. No deeper structures were visible when using a Sv threshold of −75 dB (cf. Methods; Fig. 1).

As we lowered the threshold to the values applied for studies of jellyfish, several additional structures became evident at 38 kHz, and at the lowest threshold (−100 dB) also at 18 kHz (Fig. 4). A dielly migrating SL was located below 150 m at day (i.e., beneath the krill layer), swimming into surface waters at night. Vertical swimming speed of the SL was about 1.5 cm s^{-1}, both during ascent in the evening and descent in the morning. Records from this layer were weak during the ascent. A pulse of downward scatter appeared after a few hours of darkness (Fig. 4). Diffuse, weak backscatter was recorded throughout the water column at night. Both frequencies revealed a deep SL, apparent as assemblages of visible single (individual) targets (*P. periphylla*) below ca. 250 m both day and night. Individual, large jellyfish were also recorded more shallowly (Fig. 4). These shallower targets are most clearly revealed by the broad-beam, 18 kHz echosounder.

Migrations of individual P. periphylla *recorded by hull mounted transducers*—Because jellyfish are relatively weak acoustic targets, only large specimens were detected at long range by the hull mounted transducers. Average TS of tracks of individual jellyfish recorded between 75 and 200 m was −60.0 dB (SD 3.6 dB; $n = 598$) at 38 kHz and −50.7 dB (SD 4.1 dB; $n = 328$) at 18 kHz. Behavioral data are based on 38 kHz.

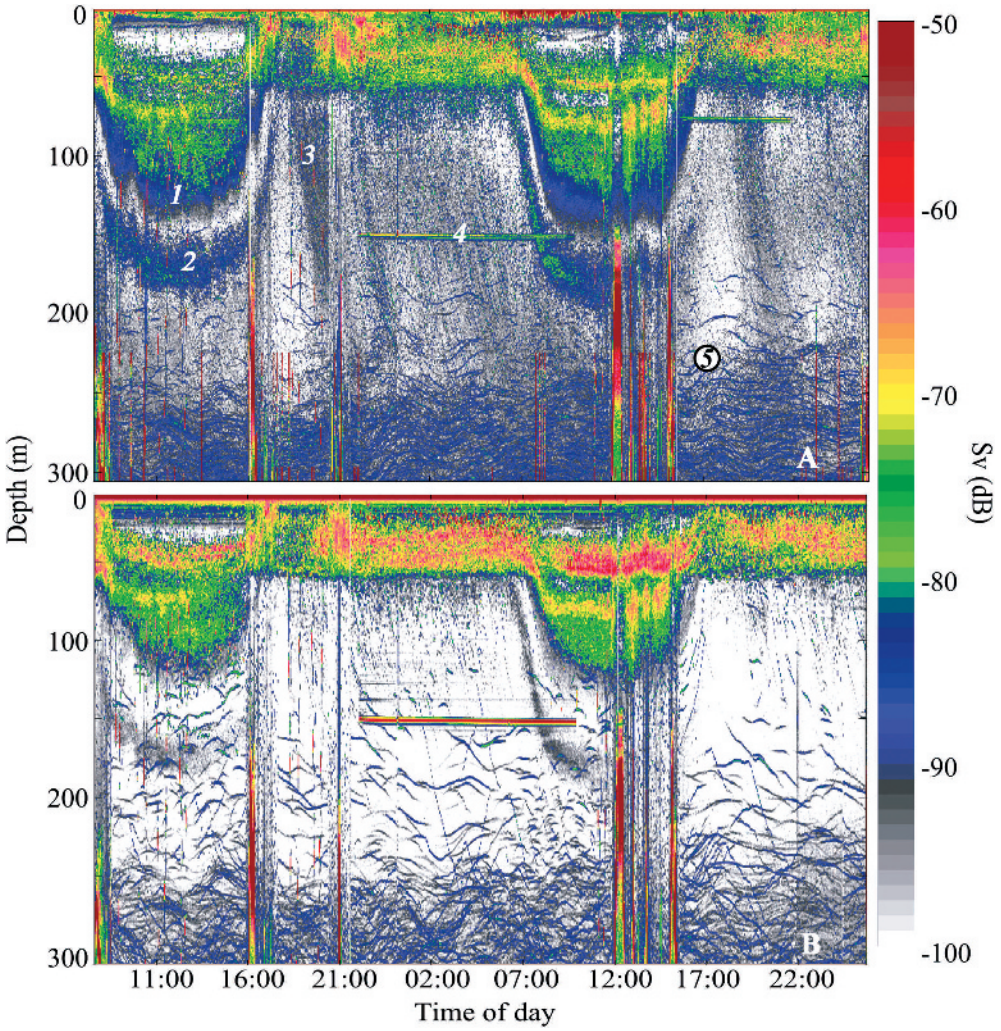

Fig. 4. Echograms for the upper 300 m from hull mounted (A) 38 kHz and (B) 18 kHz transducers spanning the whole study period in Lurefjorden from 07 November to 09 November 2004. Vertical red spikes in these time compressed plots represent bottom signals and relate to events (mainly sampling) when the vessel was not kept stationary. Color scale refers to Sv (dB). Numbers denote: (1) krill SL, (2) SL of dielly migrating *P. periphylla*, (3) downward pulse of *P. periphylla*, (4) submerged echosounder, (5) individual *P. periphylla*

Few ascending individuals were recorded by the hull mounted transducers in the afternoon, whereas individuals leaving upper layers were clearly resolved early at night (Fig. 5A). After this downward pulse, an interchange of individuals between the upper and lower layers became established, continuing throughout the night (Fig. 5B, C).

Upon returning to deep water, several individuals reversed their vertical swimming direction when reaching 150–200 m depth, once again starting ascending (Fig. 5B,C). Single vertically migrating individuals could be followed for extended periods and distances, e.g., one large specimen (TS ~ -51 dB) remained in the acoustic beam as it ascended steadily from 280 m at 03 : 11 h to 140 m at 04 : 26 h. In the morning, ascending individuals were recorded in the lower part of the water column parallel to the descent of the dielly migrating SL of *P. periphylla* (Fig. 5C).

The manually tracked echo traces of dielly migrating jellyfish revealed migration speeds of $\sim$2 cm s^{-1}, regardless of time of night. Average ascent rates were 2.3 cm s^{-1} (SD 0.8, $n = 39$), and average descent rate 2.0 cm s^{-1} (SD 0.7, $n = 92$).

Migration of individual P. periphylla *recorded by the submerged echosounder*—The submerged 120 kHz echosounder provided information of smaller jellyfish than the hull mounted transducer, both because of the higher frequency and because it was used at closer range. In the afternoon, the submerged echosounder (located at 75 m) revealed a coherent ascent (Fig. 6A). Two h later, most individuals were descending (Fig. 6B). Both the ascent and descent rates measured for selected migrating individuals were $\sim$2–3 cm s^{-1}, with average ascent rate of 2.7 cm s^{-1} (SD 1.5, $n = 51$), and descent rate of 2.0 cm s^{-1} (SD 0.8, $n = 80$).

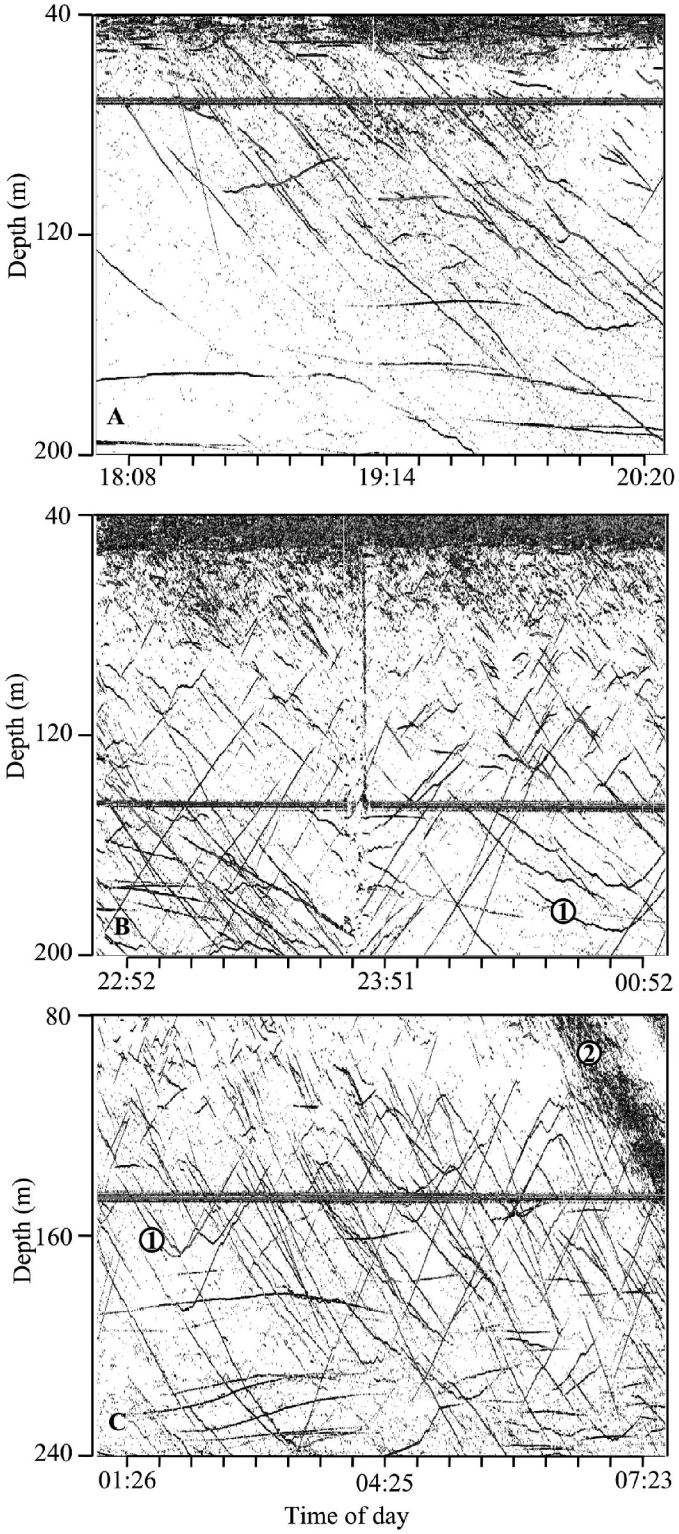

Fig. 5. Echo traces of individual *P. periphylla* (each "line" represents one jellyfish) recorded by hull-mounted transducer (38 kHz) (A) early at night; (B) midnight ±1 h, and (C) latter part of night till return of the dielly migrating SL of *P. periphylla*. Sv threshold −90 dB. Sunset at 16 : 24 h, sunrise at 08 : 21 h. Because of other activities, light on deck was on from 19 : 30 h to 20 : 15 h. The submerged echosounder is seen as a horizontal bar. Numbers

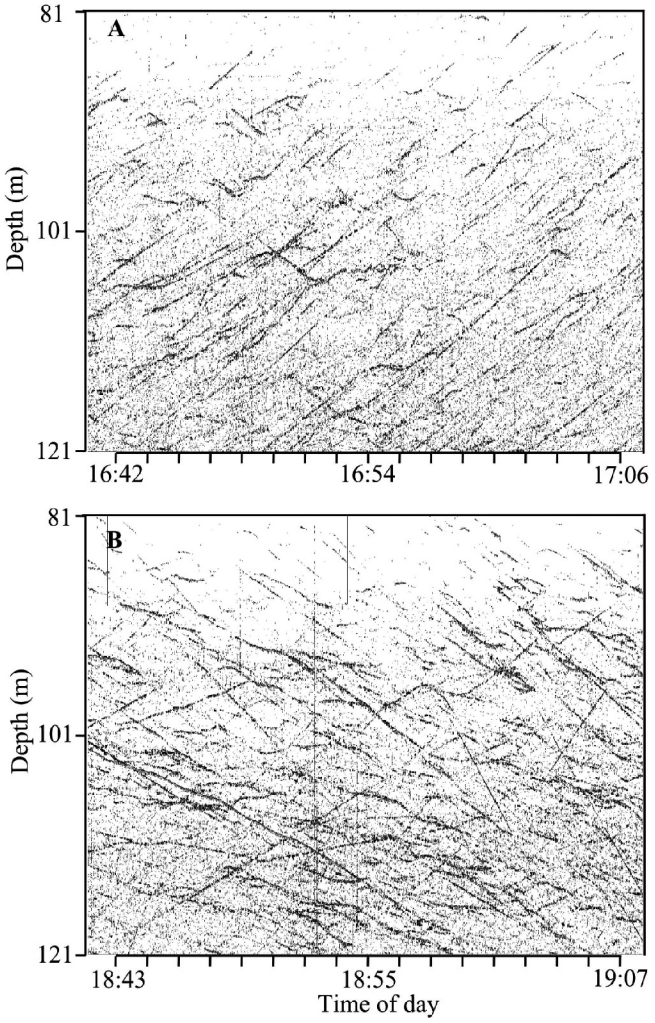

Fig. 6. Echo traces of individual *P. periphylla* recorded by the submerged echosounder (120 kHz) kept at 75 m early at night; (A) records start 20 min after sunset; (B) records start 2 h and 20 min after sunset. Sv threshold −90 dB.

The ascent and subsequent descent in the afternoon was also reflected in the automatic tracking of all targets (Fig. 7). More than 90% of measured speeds were in the range 2.4 (upward swimming) to 2.8 cm s^{-1} (downward swimming). Maximum vertical swimming speed was normally ~4 cm s^{-1} (Fig. 7), both for ascending and descending individuals. Target strengths were generally low, with median TS values of ~ −70 dB to 75 dB (Fig. 7).

The submerged echosounder kept at 150 m from midnight till morning documented a mixture of ascending and descending individuals (Fig. 8). Migrations, as revealed from the automatic tracking, were primarily downwardly directed (Fig. 9). No changes in migration speed were recorded when the dielly migrating SL passed the sub-

←

denote: (1) examples of individual *P. periphylla* reversing migrations from descent to ascent; (2) descending scattering layer of *P. periphylla*

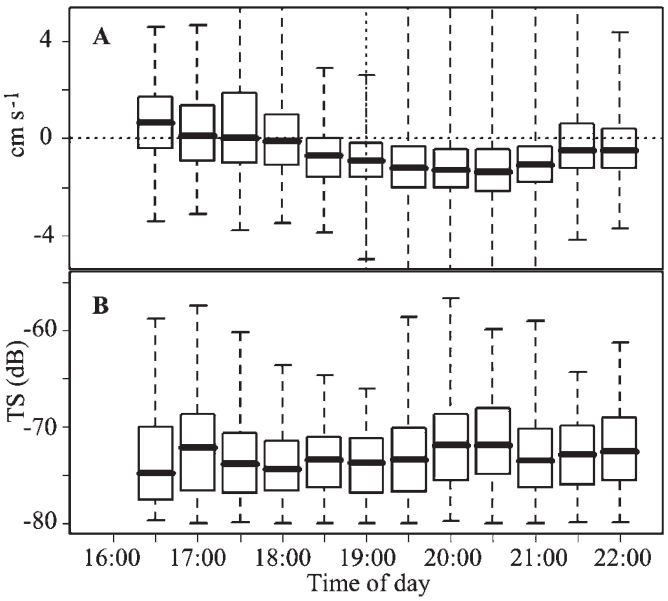

Fig. 7. (A) Distribution of vertical swimming speed (positive is upward swimming) and (B) TS from the submerged 120 kHz echosounder kept at 75 m depth in the afternoon on 07 November 2004. Horizontal axis is local time. The boxes encompass the 25–75 percentiles of registrations for each 30-min registration period, with the median marked by a crossing line. Whiskers denote maximum and minimum values.

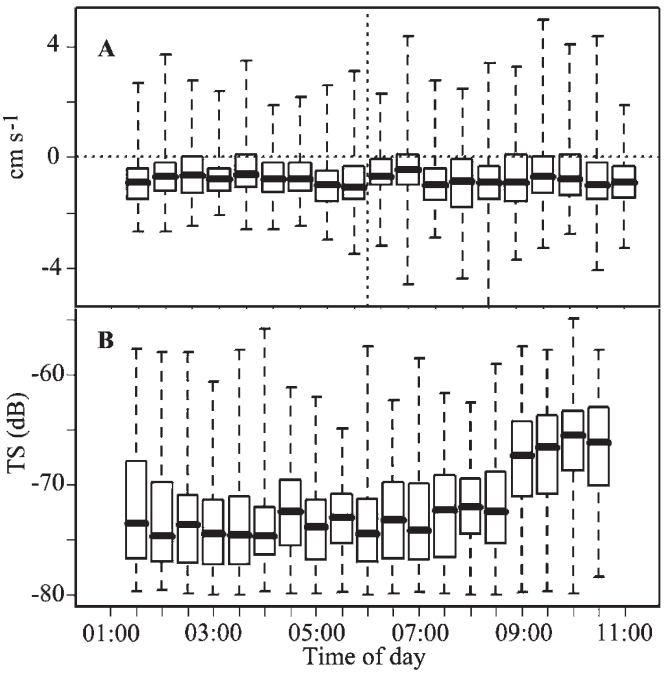

Fig. 9. (A) Distribution of vertical swimming speed (positive is upward swimming) and (B) TS from the submerged 120 kHz echosounder kept at 150-m depth during night and in the morning of 8 November 2004. The boxes encompass the 25–75 percentiles of registrations for each 30-min registration period, with the median marked by a crossing line. Whiskers denote maximum and minimum values.

merged echosounder during its descent in the morning (Fig. 9). The return of this SL to the registration depth did, however, cause a shift to stronger targets, with median TS increasing from ~ −73 dB to ~ −66 dB (Fig. 9).

Acoustic properties related to individual swimming behavior—The behavior of the jellyfish affected the signatures of their echo traces and total backscatter. Individuals observed by the submerged echosounder during the descent of the dielly migrating SL displayed consistently pulsed echo traces. At close range, this gave marked variation in their TS; at a range of 50–60 m animals were not detected during the weak segments of the cycle with the applied threshold of −85 dB (Fig. 10A).

Migration behavior could affect TS. This became evident when ascending individuals occasionally switched swimming mode to an erratic, horizontal phase (Fig. 10B), in which case the TS increased by ~5–10 dB.

Large individual jellyfish in deep water displayed a mixture of swimming patterns. Some long-duration stepwise echo traces stand out in the acoustic records, together with more homogenous traces without such repetitive vertical shifts (Fig. 10C). Weak, pulsed echo traces were also observed but will be underrepresented in the results because of lower acoustic detection at long range.

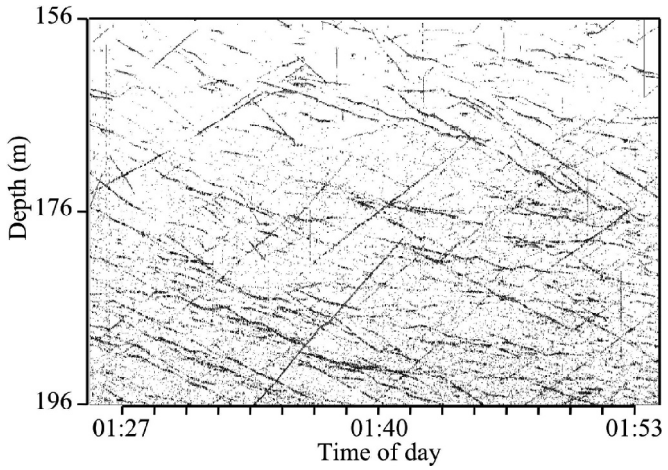

Fig. 8. Echo traces of individual *P. periphylla* recorded by the submerged echosounder (120 kHz) kept at 150 m at night on 08 November 2004. Sv threshold −90 dB.

Discussion

We have shown that the vertical migration behavior of individual jellyfish can be studied in situ by means of echosounders, and that large individuals can be observed at ranges of several hundred meters in absence of other fauna components that mask jellyfish records. This approach has revealed more complex and dynamic diel migration patterns for *P. periphylla* than previously reported. The focus until now has been on coherent ascents in the

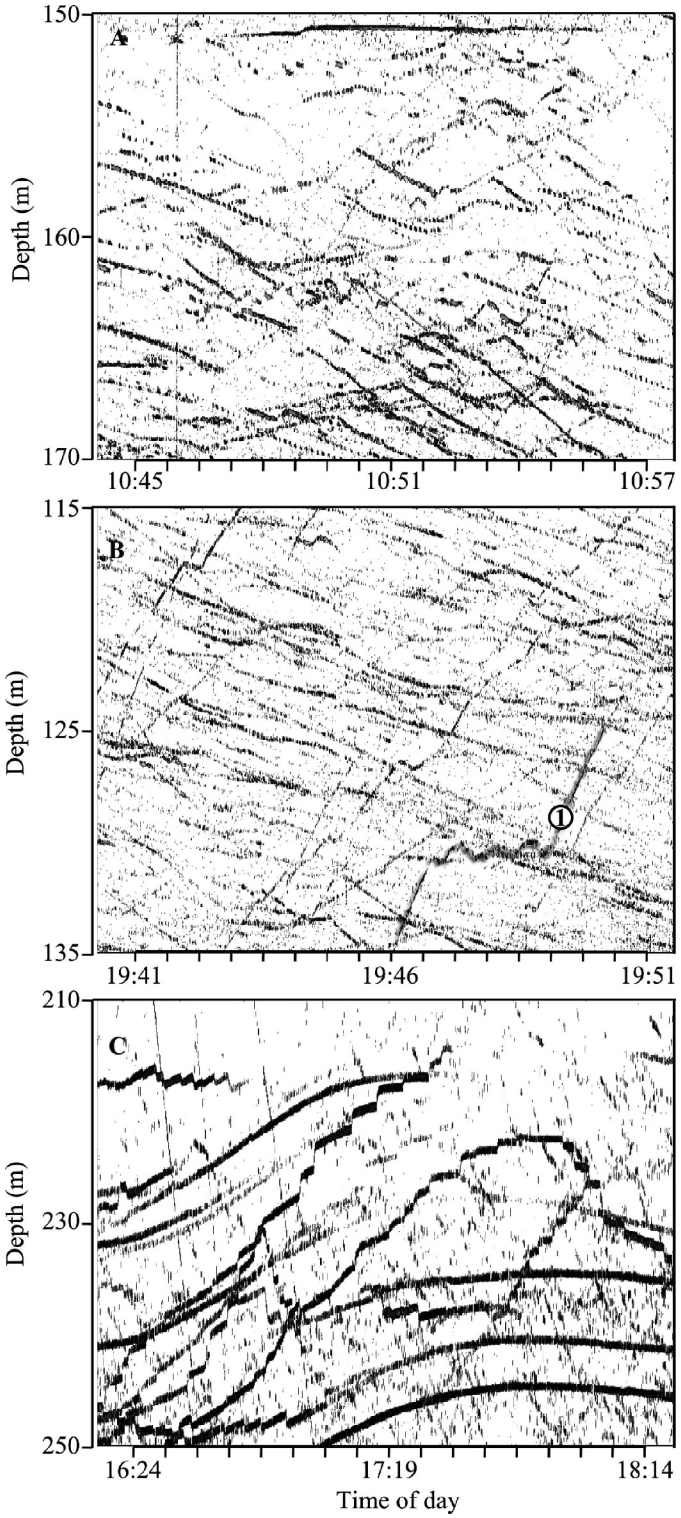

Fig 10. Echo traces of individual *P. periphylla* showing different swimming modes. (A) Records of individual constituting the dielly migrating SL; the 120 kHz echosounder located at 100 m. Note the pulsed echo signatures. (B) Migrating jellyfish, with several examples (one highlighted; marked by "1") of ascending individuals, intermittently changing their swimming behavior; the 120-kHz echosounder located at 75 m; (C) individual jellyfish from the deepest SL recorded by the hull mounted transducer (38 kHz). Sv threshold −85 dB in panels (A) and (B); −90 dB in panel (C).

afternoon and descent in the morning (Youngbluth and Båmstedt 2001; Jarms et al. 2002; Båmstedt et al. 2003), as also observed for part of the population in our study. However, the population consisted of different modes with differing migration patterns, distinct "midnight sinking," with return of individuals to deeper waters early at night, and interchange of individuals between deep and shallow water during the night. To our knowledge, the present study is the first to directly demonstrate such asynchronous vertical migrations by studies of individual plankton organisms in their natural environment. Asynchronous vertical migrations were recorded throughout the water column and for a broad range of size classes, as expressed by TS. We note, however, that TS was strongly related both to acoustic frequency and behavior, and size/TS-relationships of *P. periphylla* remain to be established.

Migrations in relation to food and predators—DVM is normally considered to represent a trade-off between foraging and predator avoidance, amended by temperature effects on metabolic rates (e.g., Lampert 1989; Loose and Dawidowicz 1991). If zooplankton biomass is a useful proxy for potential food, *P. periphylla* did not distribute according to food abundance. Potential food (in terms of biomass) was fairly evenly distributed by depth, with the exceptions of very low biomass in the upper 50 m during the day, and a biomass maximum at the depth of the krill layer during daytime, where biomass of krill added to the relatively high biomass of mesoplankton. The distribution of *P. periphylla*, on the other hand, was vertically stratified into layers, which did not concur with zooplankton biomass maxima. Similar discrepancies were recorded by Sötje et al. (2007).

P. periphylla are nonvisual predators and are not constrained by low light levels in searching for food (apart for potential direct harmful effects of light in upper layers at day; Jarms et al. 2002). The light level may still be essential, as potential prey may perceive the predator by visual cues. There was no prominent vertical overlap between *P. periphylla* and krill during the daytime. Possibly, krill may be a suitable food at night but less so during the day. *Meganyctiphanes norvegica* has well-developed eyes and may be able to visually spot, and avoid the slowly swimming jellyfish in daylight (cf. Browman 2005). Fish associated with the krill layer might also represent a potential danger of predation for *P. periphylla*.

M. norvegica became the dominant prey component in terms of biomass in upper waters at night. *M. norvegica* is reported in the diet of *P. periphylla* in Lurefjorden (Youngbluth and Båmstedt 2001), and, in terms of food availability, the vertically migrating krill would represent the most likely driving force for the nocturnal ascent of *Periphylla*. Other potential prey was scarce in the upper layer (apart for a potential contribution by unquantified amounts of small lightfish *M. muelleri*), whereas the migrating jellyfish left relatively high concentrations of mesozooplankton in the deep water.

Some *P. periphylla* left the surface layer early at night, and a pulse of descending individuals was recorded a few hours after sunset. So-called midnight sinking has often

been explained in terms of the hunger–satiation hypothesis, which states that individuals return to deeper water once fed (see Pearre 2003 for a review). Satiation-based descent is usually asynchronous, because each animal is stimulated to descend individually once satiated. In such cases, hungry individuals are present near the surface, whereas well-fed individuals are encountered at depth (Pearre 2003). According to this scenario, satiated *Periphylla* would leave upper waters, whereas individuals remaining in surface waters would be expected to be unfed. *P. periphylla* that is sampled at the surface indeed often (but not always; Sørnes 2006) has little stomach content, which Youngbluth and Båmstedt (2001) ascribed to very low metabolic demands. We suggest that our acoustic approach in combination with sampling with a remotely operated vehicle (ROV) can be used to test if the hunger–satiation hypothesis applies to *P. periphylla* in Lurefjorden. This would allow discriminate sampling of descending, and ascending individuals, respectively, as identified in acoustic records.

Enhanced near-surface risk of predation is normally seen as the ultimate reason for descent once fed (Pearre 2003). In the case of *P. periphylla* in Lurefjorden, the only potential nocturnal predator in upper water would be fish, which accumulated in the upper layers at night. The fish predators recorded among the krill in Lurefjorden were most likely whiting *Merlangius merlangus* (Fosså 1992; own unpubl. results). Gadoids are known to prey on jellyfish (Arai 1988). The existence of predators on *Periphylla* in Lurefjorden is suggested by disfigurement of a small portion of medusae collected in net tows (Youngbluth and Båmstedt 2001). They found that dome mesoglea was damaged but healing on a few medusae and that parts of, or whole, tentacles were missing on other individuals. Preferential feeding on tentacles of jellyfish has been noted for various fish (Arai 1988). There is, however, a paucity of information of fish in Lurefjorden. Fish trawls rapidly become filled with several tones of *Periphylla* (see Fosså 1992), which has hampered studies of fish in this fjord. It appears necessary to address the role of fish predation to correctly evaluate the behavior of *P. periphylla* in Lurefjorden. An alternative driving force for leaving upper waters could relate to advection, because an early descent would reduce the risk of being transported away from their confined (limited) habitat. These arguments do, however, imply that *P. periphylla* has become adapted to this particular environment. The jellyfish has been present in large quantities in Lurefjorden through decades (Fosså 1992) but may still be considered an expatriate. Little is known about phenotypic plasticity in behavior among simple organisms like jellyfish.

A considerable number of descending individuals reversed their descent when reaching 150–200 m (cf. Fig. 5). This roughly corresponds to the daytime depth of the migrating SL. The daytime distribution of the SL is believed to be governed by light, but, in case the observations of nocturnal reversals of migrations in this depth interval are not merely incidental, some other cue would be responsible at night. It has been documented that jellyfish may show behavioral responses to pressure (Graham et al. 2001), but whether or not pressure may play a role for the vertical positioning of *P. periphylla* in Lurefjorden remains to be investigated.

Migrations in relation to hydrography—The vertically homogenous hydrography in the deep daytime habitat had no explanatory power for the distribution of *P. periphylla*, which included vertically segregated modes of the population. However, the distribution of all targets in upper waters at night was confined to relatively warm water, with a persistent and sharp lower edge of the SL coinciding with the steep thermocline (cf. Figs. 2 and 4). High temperature may be beneficial for food digestion when availability of food makes digestion time the limiting factor (e.g., Wurtsbaugh and Neverman 1988). However, we cannot distinguish between any direct impact from temperature or other factors, like distribution of prey organisms.

Swimming behavior—The migration speeds of *P. periphylla* appeared to be uncorrelated to acoustic sizes, and the asynchronous migrators exhibited the same vertical speed as those migrating in response to sunset and sunrise. Neither isolumes nor the rates of change of light intensities (cf. Ringelberg 1995) were the zeitgeber for these migrations, darkness apparently being the only necessary environmental cue for ascent. Motivation for undertaking synchronous migrations will vary among taxa and environmental settings. Visual predators may follow an isolume when this enables them to scan the water column for prey during the upward and downward ascent (Clark and Levy 1988; Baliño and Aksnes 1993), leading to synchronous migrations. This would not apply to a nonvisual predator like *P. periphylla*. Otherwise, migrations related to dusk and dawn might be motivated to obtain the longest possible period in upper waters, either related to feeding or temperature (cf. Wurtsbaugh and Neverman 1988).

P. periphylla displayed different types of swimming behavior, evident from vertical migration patterns, but also revealed from the acoustic signatures of individuals. This concurs with conclusions derived from previous video observations, where different modes of behavior have been identified in the population (Youngbluth and Båmstedt 2001). Jellyfish are tactile predators, relying on collisions with prey for food capture. Encounters are mediated either by swimming of the predator or by the prey (Gerritsen and Strickler 1977). Based on in situ video observations with red light, Youngbluth and Båmstedt (2001) found that large, deep-living *P. periphylla* in Lurefjorden appeared to be drifting for prolonged periods, followed by more rapid shifts in vertical position. Smaller individuals ($<$6 cm) seemed to be swimming haphazardly and continuously. They suggested that swimming behavior was related to depth, size, and time of day, apparently connected to feeding.

P. periphylla in Lurefjorden apparently is foraging on both moving and nonmoving prey with krill, copepods (particularly *Calanus* spp.), chaetognaths, and ocstracods being identified among the stomach contents (Båmstedt and Youngbluth 2001; Sørnes 2006). The krill *M. norvegica*, the dominant nocturnal biomass component in upper waters, is an active swimmer (Klevjer and Kaartvedt 2003), and moving prey would be more vulnerable to capture by

ambush feeders (Greene 1986). In contrast, the prevailing prey below 150 m would largely be nonmoving, dormant copepods (overwintering *Calanus* spp.), although there are also active, potential prey, like the ostracod *Concoecia* and the mysid *Hemimysis abyssicola* (Bagøien 1999). Linking of particular swimming patterns to particular modes of feeding behavior will have to await future studies. We here limit our analysis to demonstrating that jellyfish behavior also has implications for their acoustic properties.

In conclusion, individual jellyfish, as well as SLs, could be studied in situ by using acoustic techniques. The current approach has revealed a mixture of synchronous and asynchronous diel vertical migration patterns. Options for future studies include in situ assessment of 3-D swimming behavior, and relation of individual swimming and migration behavior to particular feeding modes.

References

Aksnes, D. L., J. Nejstgaard, E. Sædberg, and T. Sørnes. 2004. Optical control of fish and zooplankton populations. Limnol. Oceanogr. **49:** 233–238.

Arai, M. N. 1988. Interactions of fish and pelagic coelenterates. Can. J. Zool. **66:** 1913–1927.

Bagøien, E. 1999. Predatory impact of invertebrates and fish on overwintering *Calanus*.Dr-thesis. Department of Biology, Univ. of Oslo.

———, S. Kaartvedt, D. L. Aksnes, and K. Eiane. 2001. Vertical distribution and mortality of overwintering *Calanus*. Limnol. Oceanogr. **46:** 1494–1510.

Baliño, B. M., and D. L. Aksnes. 1993. Winter distribution and migration of the sound scattering layers, zooplankton and micronekton in Masfjorden, western Norway. Mar. Ecol. Prog. Ser. **102:** 35–50.

Balk, H., and T. Lindem. 2002. Sonar4 and Sonar5-Pro post processing systems. Operator manual. Lindem Data Acquisition.

Båmstedt, U., S. Kaartvedt, and M. Youngbluth. 2003. An evaluation of acoustic and video methods to estimate the abundance and vertical distribution of jellyfish. J. Plankton Res. **25:** 1307–1318.

Brierley, A. S., B. E. Axelsen, E. Buecher, C. A. J. Sparks, H. Boyer, and M. J. Gibbons. 2001. Acoustic observations of jellyfish in the Namibian Benguela. Mar. Ecol. Prog. Ser. **210:** 55–66.

Browman, H. I. 2005. Application of sensory biology in marine ecology and aquaculture. Mar. Ecol. Prog. Ser. **287:** 266–269.

Clark, C. W., and D. A. Levy. 1988. Diel vertical migration by juvenile sockeye salmon and the antipredation window. Am. Nat. **131:** 271–290.

Derobertis, A., J. S. Jaffe, and M. D. Ohman. 2000. Size-dependent visual predation risk and the timing of vertical migration in zooplankton. Limnol. Oceanogr. **45:** 1838–1844.

Ehrenberg, J. E., and T. C. Torkelson. 1996. Application of dual-beam and split-beam target tracking in fisheries acoustics. ICES J. Mar. Sci. **53:** 329–334.

Eiane, K., D. L. Aksnes, E. Bagøien, and S. Kaartvedt. 1999. Fish or jellies—A question of visibility? Limnol. Oceanogr. **44:** 1352–1357.

Fosså, J. H. 1992. Mass occurrence of *Periphylla periphylla* (Schypozoa, Coronatae) in a Norwegian fjord. Sarsia **83:** 103–116.

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

Graham, W. M., F. Pagés, and W. M. Hamner. 2001. A physical context for gelatinous zooplankton aggregations: a review. Hydrobiologia **451:** 199–212.

Greene, C. H. 1986. Patterns of prey selection: Implications of predator foraging tactics. Am. Nat. **128:** 824–839.

———, T. K. Stanton, P. H. Wiebe, and S. McClatchie. 1991. Acoustic estimates of Antarctic krill. Nature **349:** 110.

Handegard, N. O. 2004. Cod reaction to an approaching bottom trawling vessel investigated using acoustic split-beam tracking. Ph.D. thesis, Univ. of Bergen.

Jarms, G., H. Tiemann, and U. Båmstedt. 2002. Development and biology of *Periphylla periphylla* (Scyphozoa: Coronatae) in a Norwegian fjord. Mar. Biol. **141:** 647–657.

Klevjer, T. A. 2006. *In situ* acoustic studies of individual krill and jellyfish.Ph.D. thesis, Univ. of Oslo.

———, and S. Kaartvedt. 2003. Split-beam target tracking can be used to study the swimming behavior of deep-living plankton *in situ*. Aquat. Liv. Res. **16:** 293–298.

Lampert, W. 1989. The adaptive significance of diel vertical migration of zooplankton. Funct. Ecol. **3:** 21–27.

Loose, C. J., and P. Dawidowicz. 1991. Trade-offs in diel vertical migration by zooplankton: the costs of predation avoidance. Limnol. Oceanogr. **75:** 2255–2263.

Munk, P., P. O. Larsson, D. S. Danielssen, and E. Moksness. 1995. Larval and small juvenile cod *Gadus morhua* concentrated in the highly productive areas of a shelf break front. Mar. Ecol. Prog. Ser. **125:** 21–30.

Pearre, S., Jr. 2003. Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. Biol. Rev. **78:** 1–79.

Ringelberg, J. 1995. Changes in light intensity and diel vertical migration: A comparison of marine and freshwater environments. J. Mar. Biol. Ass. UK **75:** 15–25.

Sørnes, T. A. 2006. Visual or tactile zooplanktivores.Ph.D. thesis, Univ. of Bergen.

Sötje, I., H. Tiemann, and U. Båmstedt. 2007. Trophic ecology and the related functional morphology of the deepwater medusa *Periphylla periphylla* (Scyphozoa, Coronata). Mar. Biol. **150:** 329–343.

Soule, M., M. Barange, H. Solli, and I. Hampton. 1997. Performance of a new phase algorithm for discriminating between single and overlapping echoes in a split-beam echosounder ICES J. Mar. Sci. **54:** 934–998.

Wurtsbaugh, W. A., and D. Neverman. 1988. Post-feeding thermotaxis and daily vertical migration in larval fish. Nature **333:** 846–848.

Youngbluth, M. J., and U. Båmstedt. 2001. Distribution, abundance, behavior and metabolism of *Periphylla periphylla*, a mesopelagic coronate medusa in a Norwegian fjord. Hydrobiologia **451:** 321–333.

Received: 23 June 2006
Accepted: 23 November 2006
Amended: 14 December 2006