

In situ behaviour and acoustic properties of the deep living jellyfish *Periphylla periphylla*

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The importance of jellyfish in marine systems is increasingly being recognized, and in some ecosystems, jellyfish may now be considered the top predator. We studied the behaviour of individuals of the deep-water scyphozoan Periphylla periphylla in one such location, the Lurefjord, Norway. The study was performed using a combination of submersible acoustics (38 kHz), video and net methods, and the focus was on variation in behaviour and vertical distribution in relation to the diel cycle. A proportion of the population underwent synchronous vertical migrations, but P. periphylla were still recorded throughout the water column both day and night. The majority of individuals were swimming (vertically) at speeds $< 2 \text{ cm s}^{-1}$ irrespective of the time of day. However, occasional vertical swimming events with speeds exceeding 10 cm s^{-1} were recorded. Such events of elevated vertical speeds were of short duration, followed by subsequent periods of no vertical movements. Different size fractions appeared to have different patterns of vertical swimming activity, with smaller jellyfish swimming more continuously than the larger Periphylla. The echo strengths of the individual returns (target strength, TS) peaked at approximately -62 dB , and variability in TS for individuals was high, with the strongest echoes seen in deep water. The results show the feasibility of acoustic methods for studying the in situ behaviour and acoustic properties of these jellyfish, but also that acoustically weak jellyfish are only recorded close to the transducer or the acoustic axis, which will bias acoustic data on vertical size distribution and acoustic abundance estimates.

INTRODUCTION

Gelatinous plankton are major pelagic predators, but their importance in marine ecosystems remains to a large degree unknown (Mills, 1995). Occasionally, members of this group form “blooms”, with exceptionally high densities and biomasses (reviewed in Mills, 2001). The reasons for such occurrences are not fully understood, and a range of factors may be involved, including natural variations (Mills, 2001), eutrophication (Arai, 2001), introductions of alien species (Zaitzev, 1992), climate change (Brodeur *et al.*, 1999) or commercial overfishing (Mills, 1995). In the Lurefjord, Norway, the density of the coronate deep water scyphomedusa *Periphylla periphylla* is persistently several orders of magnitude higher than in their normal, open-ocean habitats

(Fosså, 1992; Youngbluth and Båmstedt, 2001). Its prevalence in this fjord, compared with other, nearby fjords dominated by mesopelagic fish, has been attributed to high light extinction, which makes feeding conditions unfavourable for visual predators (Eiane *et al.*, 1999; Aksnes *et al.*, 2004).

Jellyfish are tactile predators, relying on physical encounters with their prey for food capture. Encounters are mediated either by swimming of the predator or by the prey (Gerritsen and Strickler, 1977). Some hydromedusae seem to employ an “ambush” strategy, in which prey motion leads to encounter (Mills, 1981). However, Costello and Colin (1995) found that for three investigated species of Scyphomedusae, the currents set up by their bell contractions were significant in entraining the

prey. They, therefore, rather suggested that a “cruising predator” strategy, i.e. that the predators own activity brings it in contact with the prey, was common among the Scyphomedusae. *Periphylla periphylla* has 12 strong and sturdy tentacles, usually held upwards along the body in the swimming direction (Søtje *et al.*, 2007). From the behavioural descriptions by Larson (1979) and Youngbluth and Båmstedt (2001), Raskoff (2002) has termed this foraging behaviour as “ramming”. By this mode, the animal minimizes the turbulent disturbance in the swimming direction, thereby reducing the risk of warning the prey.

Most behavioural information on jellyfish has been gathered through observation either in shallow water or in the laboratory (Mills, 1981; Colin *et al.*, 2003; Dawson and Hamner, 2003). The use of ROV’s is likely to improve knowledge of *in situ* behaviour also for deep living species such as *P. periphylla* (Larson *et al.*, 1991; Youngbluth and Båmstedt, 2001). Attaching data loggers to individual jellyfish may also have great utility for describing individual movement patterns over extended periods (Hays *et al.*, 2008). Another method with great potential is acoustics. Acoustic methods for studies of jellyfish have so far mainly been used in a few cases for measuring abundance and distribution (Brierley *et al.*, 2001, 2005; Båmstedt *et al.*, 2003; Alvarez Colombo *et al.*, 2009), but it is also possible to use acoustics to study the behaviour of individual organisms *in situ* (Båmstedt *et al.*, 2003; Kaartvedt *et al.*, 2007).

Whereas the traditional acoustic methods employed in studies of jellyfish have focused on volumetric backscattering (i.e. the total backscattering from a volume containing an assemblage of organisms), split-beam echosounders make it possible to accurately position an organism in the acoustic beam (Brede *et al.*, 1990) and may therefore be used for acoustic sizing by compensating the echo strengths for off-axis position of the target. Acoustic sizes (usually measured as target strengths, hereafter TS) are correlated with physical sizes, but are influenced by swimming activities (Mutlu, 1996; Brierley *et al.*, 2004). Detailed studies of the backscattering of individuals may therefore provide insight into the activity patterns of jellyfish, in addition to being a way of measuring size.

We report results on mesopelagic jellyfish using submersible split-beam acoustic equipment together with net sampling and an ROV. This approach provided independent assessments of jellyfish abundance, their size and vertical distribution and enabled studies of individual jellyfish even in deep water. Specifically, we address vertical distribution, diel vertical migration (DVM) and individual vertical swimming patterns.

METHOD

The study was carried out from the “RV Håkon Mosby” in Lurefjorden (60°41.7’N, 05°08.5’E), Western Norway, in April 2002. Several stations were occupied, in the deep basin of the fjord (i.e. with depths exceeding 290 m) (see Fig. 1, Youngbluth and Båmstedt, 2001, for detailed bathymetry of Lurefjorden). The water properties in Lurefjorden are strongly influenced by a shallow sill of ~20 m, and in the deeper waters where most of this study was performed, physical conditions are relatively constant both within and between years, with salinities in the range 33.1–33.2 psu and temperatures in the range 6–7°C (Eiane *et al.*, 1999; Youngbluth and Båmstedt, 2001; Kaartvedt *et al.*, 2007).

Video profiles

Video profiling to assess abundance and vertical distribution of *P. periphylla* was undertaken with the ROV “Aglantha”, using the same procedures as Youngbluth and Båmstedt (2001). A total of six video profiles were performed within the Lurefjord system during the cruise, but only the results from the deepest station are presented here (Station 4, 60°41.27’N, 05°09.98’E, bottom depth of 439 m). Numerical densities of *P. periphylla* were later determined from the recorded video profiles after the procedure described by Youngbluth and Båmstedt (2001), i.e. dividing the population into small (<5 cm in bell diameter) and large individuals (>5 cm).

Sampling

Periphylla periphylla were collected with a ring net (opening diameter 2 m, a short ring with mesh size 3 mm near the front of the net and the main portion of the net with 500 µm mesh size) with a closed codend, sampling the entire water column in vertical tows. The jellyfish were measured for size (bell height and diameter) shortly after arriving on deck. A total of 10 night-time hauls were made with the ring net, but the size distribution reported here is the pooled results of three hauls, from the deep main basin of the fjord [one at Station 4 mentioned above and two at Station 3 (60°42.62’N, 05°05.77’E, bottom depth 363 m)].

Acoustics

Acoustic data were collected with an oil-filled, pressure stabilized 38 kHz transducer, designed to be operated at depths in excess of 1000 m (ES-38DD), attached to the ships EK500 echosounder via 300 m of cable. Data were collected as echograms with 50 m depth range on

paper printouts, using a threshold of -85 dB. Additionally, resolved echoes (i.e. accepted as single targets by software filters) were logged to a PC over serial connection, using a threshold of -75 dB.

The submersible 38 kHz transducer was calibrated using the standard sphere method at the surface prior to the sampling, on location in Lurefjorden. Two modes of operation were used in collecting the acoustic data, in both the vessel was kept in a fixed position using dynamic positioning (satellite navigation). Vertical profiles were taken by raising the down-looking transducer from a depth of 250 m to the surface in increments of 50 m, keeping the transducer stationary at each depth for about half an hour. This was done both by day and night recording at a range from 10 to 110 m, so that individual jellyfish were registered down to 360 m. In the other mode, the transducer was kept at a constant depth for longer periods, including dawn and dusk. Ping rates during the study were variable, as the echosounder was set to maximum ping rate, and the ranges used were altered regularly, but seldom fell <0.5 pings s^{-1} .

Split-beam transducers can determine the three-dimensional position of targets. The procedure of combining sequential echoes from the same target into so-called tracks is known as target tracking (referred hereafter as TT; Brede *et al.*, 1990). TT was performed with specially designed software (Ona and Hansen, 1991). Note that we use the term “track” when referring to such combinations of sequential echoes from the same resolved target and the term “trace” when referring to individuals on echograms (paper prints). The tracks give information on the three-dimensional movement of the target with respect to the transducer (Brede *et al.*, 1990), but here we only present data on vertical position and swimming since the movements of the freely suspended transducers introduced artefacts in horizontal positioning. Results on vertical position in the calm fjord waters should not be affected by these errors.

Post-processing of video and acoustic data

Vertical profiles of *Periphylla* densities were generated from counts of individuals seen from the ROV “Aglantha”, following the procedure of Youngbluth and Båmstedt (2001). In addition, we estimated relative densities from the acoustic data. As an estimator of organism relative density, we used counts of tracks in the range from 10 to 30 m away from the transducer. This region was split into four regions of equal volume, assuming a cone-shaped acoustic observation volume. With a 7° opening angle for the transducer, the nominal diameter of the sound beam is ~ 1.2 m at 10 m, ~ 3.7 m at 30 m, and 6.1 m at 50 m range. Counts of tracks were

assumed to be Poisson distributed, and a maximum likelihood procedure was used to estimate densities for 10 min periods. In order to reduce the bias introduced by splitting of tracks (i.e. preventing sequences of echoes from a single jellyfish being recorded as several individuals), a high number (10) of consecutively missing echoes were allowed per track. In order not to introduce a bias against fast moving/drifted organisms, only five echoes were demanded to define a track. Vertical excursions of 30 cm were allowed between each recorded echo. Vertical speeds of these tracks were calculated from a linear regression of echo depths versus time.

Vertical speeds were also computed from measurements on echograms (Fig. 1). Only traces closer in range than 60 m from the transducer were used for this approach. For traces having non-uniform vertical speeds, multiple measurements were taken. These data were used for measuring maximum vertical swimming speeds, as a linear regression would tend to reduce the measured speeds of short swimming events.

The vertical swimming speeds recorded with the transducer at 150 and 250 m were pooled, and for comparison, this dataset was split into four parts; night, day, sunrise and sunset. The sunrise and sunset periods were defined as sunset (21:30) and sunrise (05:45) ± 1 h.

Target strengths

The histograms of TS were generated from detected echoes (single echo detection, hereafter SED), as too few tracks were recorded at given depths to use an average from full tracks as a basis for the distributions. The overall TS distribution is, however, based on the tracked individuals, as using the track averages rather than the raw echo counts are expected to lower the overall variance in the distribution. The overall TS distribution is based on tracks recorded deeper than 150 m, at a maximum range of 60 m from the transducer.

RESULTS

Net catches

Size distributions of jellyfish from the three deepest hauls in April (depths ≥ 360 m) were similar and were pooled in Fig. 2. Individuals smaller than ~ 3.5 cm were numerically dominant, with an additional peak in abundance for animals with coronal diameter of around 6 cm.

Video profiles

The video profile was obtained during daytime and showed that the overall numerical density of *Periphylla*

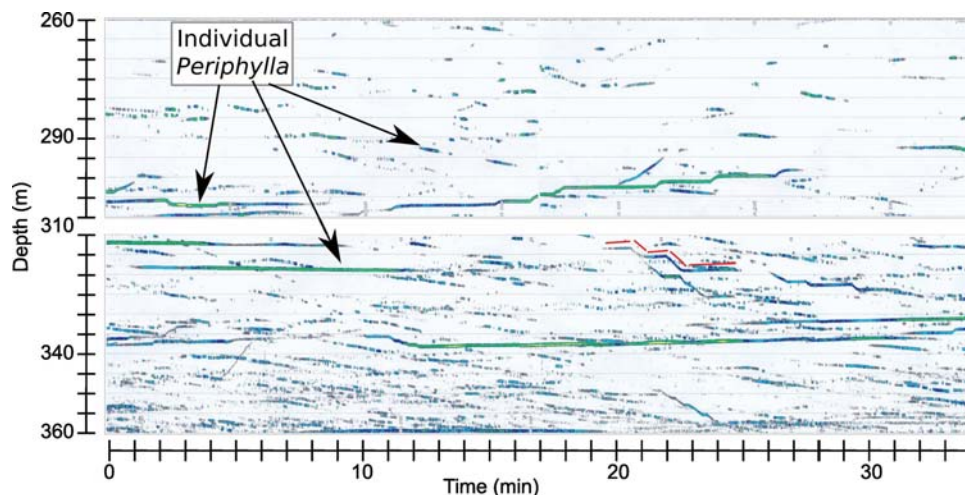


Fig. 1. Echograms showing traces of individual *P. periphylla*, each contiguous coloured stripe representing the depth of echoes returned from a single individual over time. Colours indicate the strength of the returned signals, with stronger echoes represented by warmer colours (i.e. green and yellow). The echograms show 34 min periods during the night with the transducer at 250 m, the upper depicting the range 10–60 m from the transducer, the lower the range 60–110 m, both are taken. The red lines indicate manual measurements taken for vertical speeds.

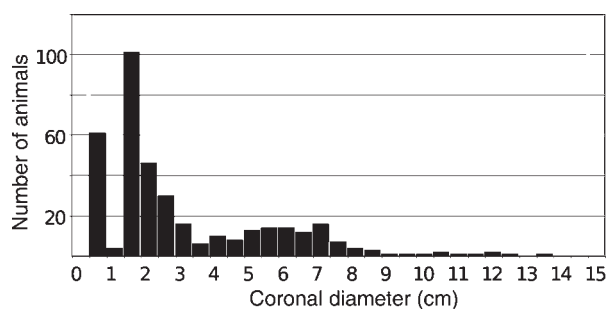


Fig. 2. Integrated distributions of coronal diameters for *P. periphylla* captured in April 2002, with 2 m ring nets hauled from the bottom to the surface.

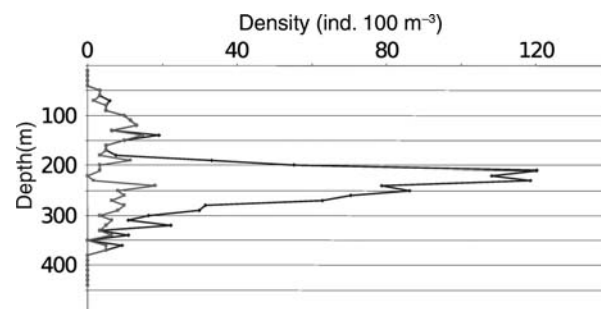


Fig. 3. Vertical distribution of *P. periphylla* (number per 100 m³) computed from the vertical video profile (daytime profile) with densities of large *Periphylla* shown by the grey line and all size groups of *Periphylla* pooled shown by dark line. Densities are reported in number of individuals per 100 m³.

peaked below 200 m depth (Fig. 3). Smaller jellyfish were relatively scarce in the video profile above 200 m, but dominated the population below. Larger individuals were more evenly distributed throughout the water column. On the basis of the vertical video profile, obtained at the deepest station, large *Periphylla* had an average numerical density of 8 ind. 100 m⁻³, whereas the average density of small *Periphylla* (<5 cm) in the same region was 35, with peak densities of, respectively, 18 and 117 ind. 100 m⁻³.

Acoustic assessment of vertical migration and distribution

Acoustic results suggested that part of the population of *P. periphylla* participated in synchronous DVM. We here demonstrate this by presenting echograms based on records from the submerged transducer located at

50 m, showing parallel descent of an assemblage of *Periphylla* and a diffuse scattering layer (SL) of krill [identified from previous sampling (Båmstedt *et al.*, 2003) and its acoustic signature], the latter occurring ~30–50 m shallower (Fig. 4).

The descent of *P. periphylla* was also evident from the recorded tracks, both by a reduction in estimated track densities in the upper layers and by a subsequent increase in estimated densities recorded in the region 160–180 m depth (Fig. 5).

The recorded pulse of downwardly migrating *Periphylla* reached 160 m between 06:00 and 07:00 (sunrise at 05:45 h) (Fig. 5). The average descent rate measured from the individual traces was -1.03 cm s^{-1} (SD = 1.79 cm s^{-1} , $n = 701$), whereas the leading edge of this layer took ~1.5 h to descend 50 m, corresponding to a speed of 0.93 cm s^{-1} .

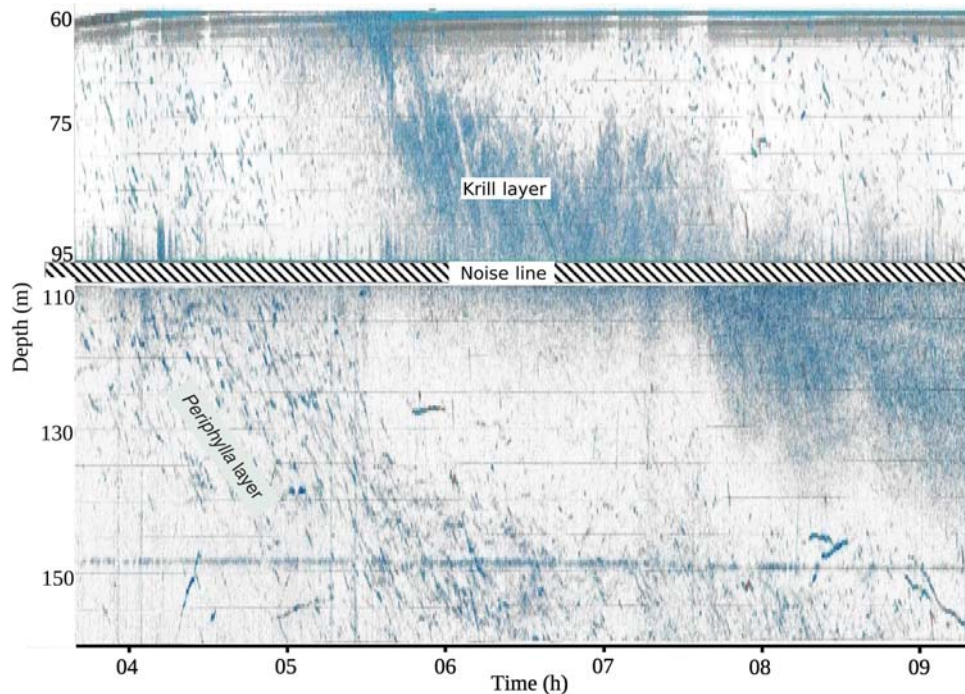


Fig. 4. Echogram recorded with transducer suspended at 50 m depth, showing the depth region from 60 to 160 m between 03:40 and 09:20, local time. Sunrise was at $\sim 05:46$. S_0 threshold -85 dB. Horizontal bar at ~ 100 m masks noise-line caused by sound reflected from the surface. A diffuse SL consisting mainly of krill can be seen migrating above a somewhat less diffuse layer of *Periphylla*.

Although a fraction of *Periphylla* was carrying out coherent vertical migrations, *Periphylla* were still recorded throughout the water column both by day and night (Fig. 6). The size distributions, as visualized in SED echograms (Fig. 6), suggested a higher proportion of strong *Periphylla* echoes above 310 m at night. These individuals typically occurred in long traces, which suggest low net horizontal displacement speeds, and can reflect low swimming activity. Some particularly strong targets seen in the uppermost interval of the SED echograms at night are likely attributable to fish, whereas the daytime results from 110 to 160 could be influenced by multiple echoes, caused by high densities of krill.

Individual swimming behaviour

Ninety percentage of the vertical speeds measured by TT were within $+2.6 \text{ cm s}^{-1}$ (upward swimming) and -3.7 cm s^{-1} (downward swimming). *Periphylla* ascended and descended in all time periods, though the average speeds were negative (downwards) for most of the size classes most of the time (Fig. 7), probably caused by a higher probability of detection of tracks during descent. During sunset, ascent was recorded for individuals with $TS \leq -65$ dB, but stronger tracks had only marginal changes in vertical swimming speeds (Fig. 7). During

sunrise, prevalent descent was recorded for the -65 dB size class.

The behaviour of individuals as derived from echo traces also showed low vertical speeds most of the time. However, a number of traces revealed a distinct step-wise pattern (Fig. 1) with vertical speeds often exceeding 10 cm s^{-1} during short relocation periods. The numbers of organisms showing such elevated speeds were low. This “staircase behaviour” was observed at all times of day and seemed to occur mostly for strong targets in deeper water. A rough estimate based on manually measured speeds showed that $\sim 1.5\%$ of the traces had events exceeding 7 cm s^{-1} ; however, only $\sim 0.12\%$ of the total time measured was spent performing this behaviour.

TS distributions

The TS distribution based on all tracked individuals below 150 m peaked at -62 dB, tapering rapidly off for larger values, but with moderate numbers of tracks detected down to the threshold of -75 dB (Fig. 8A). TS distributions based on single echo strengths for the depth intervals 160–210 m and 260–310 m, both peaked at about -60 dB, whereas an additional smaller peak of approximately -55 dB appeared in the deepest interval (Fig. 8B).

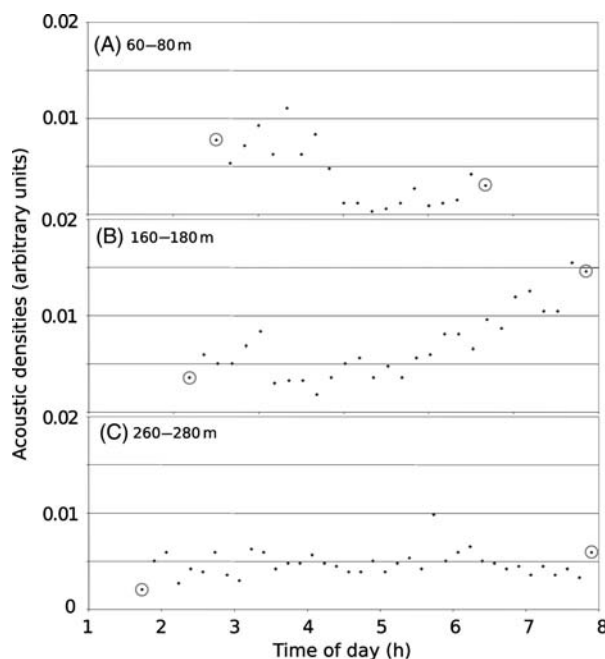


Fig. 5. Evolution of track densities (arbitrary units) versus time of day, recorded at three depths, each point is the average estimated track density in a 10 min interval, estimated in the range 10–30 m from the transducer. Deployment at different depths differed in lengths, the first and last points of each series are marked with a circle. (A) With transducer at 50 m, deployment lasting 3 h and 20 min. (B) Transducer at 150 m, deployment lasting 4 h and 50 min. (C) Transducer at 250 m, deployment lasting 6 h and 20 min.

In comparing results for targets from the same depth interval in the water column, but recorded at different range from the transducer (10–60 versus 60–110 m), we highlight two points. First, the weak targets (left part of the distribution) were no longer recorded as the range increased (Fig. 8B). The implication is that the smallest jellyfish were only recorded close to the transducer or the acoustic axis. Second, the distributions recorded at longer ranges shifted to the right, either because of the effects of multiple echoes or because the larger volume of the beam increases the chances of observing sparsely distributed large organisms.

Some *Periphylla* showed large systematic variations in TS; however, in most of the inspected tracked individuals, the variation appeared more random. The high average variability in TS (defined as $TS_{\max} - TS_{\min}$) within tracks (Fig. 9A) peaked for organisms with a TS of -63 dB. Although the slope on the left-hand side of this graph is influenced by the TS threshold at -75 dB, the decline at average TS higher than -60 dB should not be influenced by methodical constraints, so that variation in TS within tracks indeed was smaller for acoustically large organisms. The detailed plot of average TS versus vertical swimming speed showed a

dome-shaped relationship, with highest TS for animals swimming downwards at $\sim 1 \text{ cm s}^{-1}$ (Fig. 9B), though the magnitude of change was small compared with the variation within tracks.

DISCUSSION

The results of this study demonstrate that echo sounders can be used to reveal the behaviour of jellyfish, even for individual specimens in deep water. Identification is perhaps the biggest problem affecting ecological applications of acoustic studies. In this respect, Lurefjorden offers a unique environment, due to low abundance of alternative acoustic targets. Albeit both pelagic crustaceans and fish occur, their vertical distribution and acoustic properties are such that identification is generally not a problem in this particular habitat. However, only a part of the population of *P. periphylla* was detected acoustically, with a bias against small organisms which increases with range and off the acoustic axis. The comparisons of TS distributions for a given depth measured at different ranges (Fig. 8) (respectively, 10–60 and 60–110 m range), clearly show the effects of the so-called “threshold-induced bias” (Weimer and Ehrenberg, 1975). This reduction in the detection of weak echoes with range is caused by weak echoes falling below the detection threshold. Similar effects have been found in other studies of gelatinous scatterers (Alvarez Colombo *et al.*, 2009). Larger jellyfish would be seen at longer range from the transducer and more off the acoustic axis before the threshold-induced bias would make them acoustically invisible. To obtain a crude measure of what size ranges of organisms were actually sampled, we used the model of Monger *et al.* (1998) (with their parameters for *Aequorea victoria*). This approach suggested that individuals with diameters smaller than ca. 2.5 cm would not have been included at 38 kHz at the settings utilized, even in the centre of the acoustic beam and close to the transducer. On the basis of the *in situ* size distribution (Fig. 2), a large proportion of the *Periphylla* population was therefore acoustically “invisible” at 38 kHz.

An artificial increase in size by range would also be the case with inclusion of so-called multiple echoes (e.g. Gauthier and Rose, 2001), caused by software algorithms failing to reject composite echoes originating from more than one individual. This could also be the case if the performance of the transducer changed with depth; however, the oil-filled transducer used in this study is not expected to have this problem, but this was not verified. We ascribe the additional peak of strong targets in the deepest interval (this interval was only

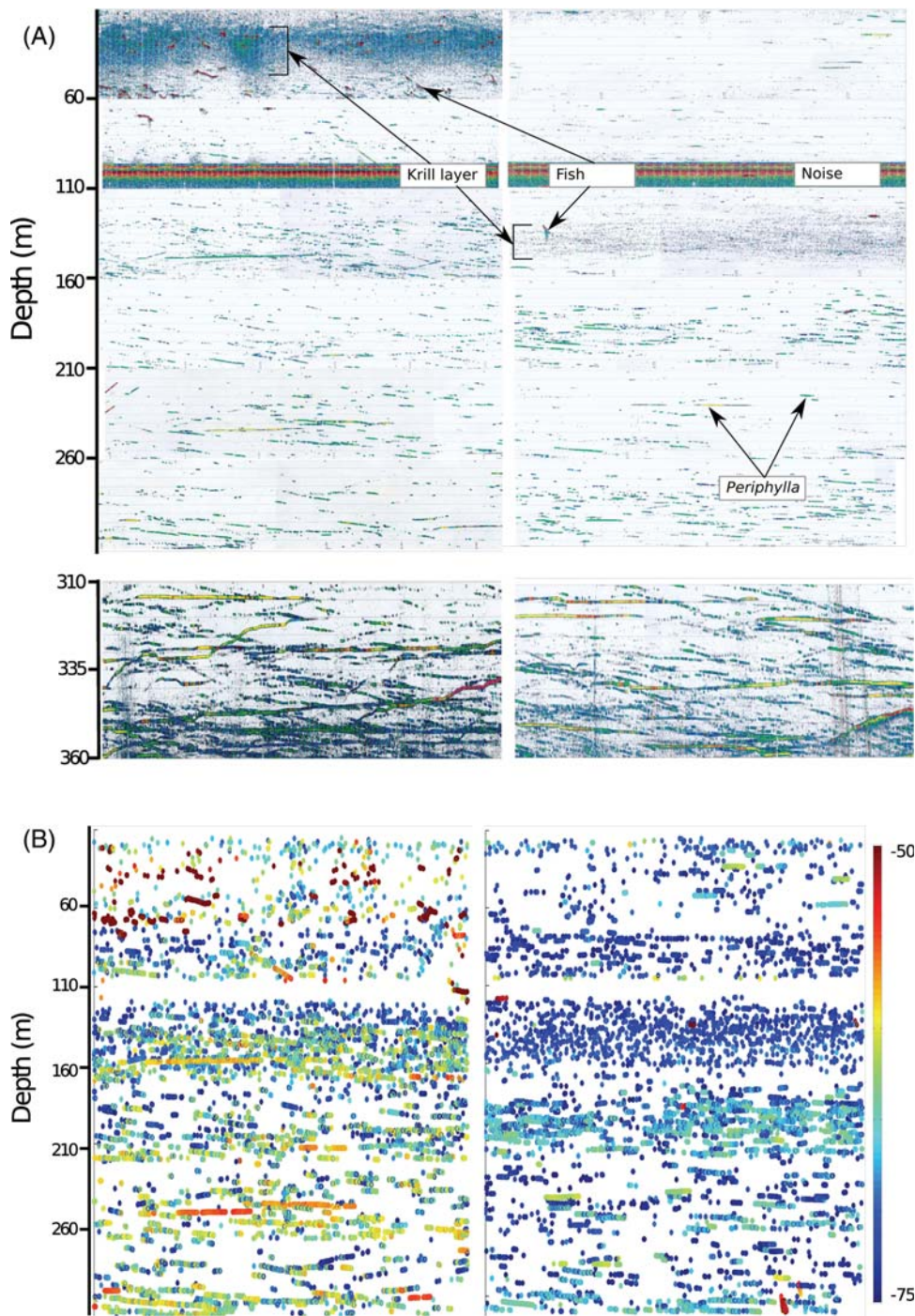


Fig. 6. Composite echograms from Lurefjorden, April 2002, generated by aligning echograms recorded at several depths, but not simultaneously (sequential depths separated by ~30 min). Colours indicate echo strengths, with red and yellow traces being stronger than green and blue echoes. Left side: night-time distribution (23:50–02:30). Right side: daytime distribution (~08:30 to ~11:00). (A) Upper panels (10–310 m): composite of echograms with 10–60 m range from the transducer. Lower panels (310–360 m): echograms with 60–110 m range from the transducer. During daytime, a SL consisting mostly of krill can be seen between 110 and 160 m, and during night, the krill layer is mixed with *Periphylla* and fish in the upper 50 m. (B) Based on single echo detections. The composite image shows single echoes detected in the same periods as in A (transducer range 10–60 m). Echoes detected in the depth ranges occupied by the krill layer are probably influenced by multiple krill echoes (“single” echoes that are actually the combined echoes of several scatterers). Echoes exceeding -50 dB (brown in colour) in the upper 150 m are most likely caused by fish.

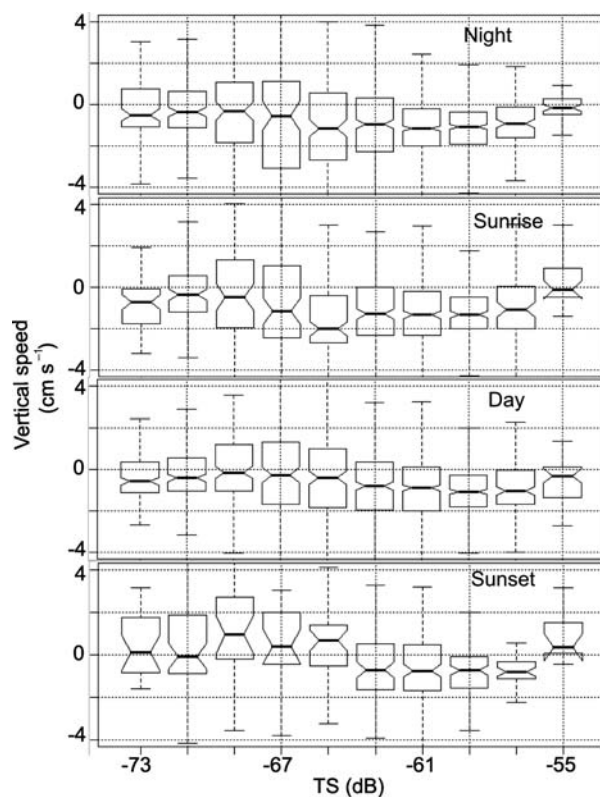


Fig. 7. Distribution of vertical swimming speeds vs. TS for all tracks recorded deeper than 150 m, April 2002, night, sunrise, day and sunset. Records for sunrise and sunset span sunrise (05:46) and sunset (21:30) $\pm$ 1 h. Boxes span first to third quartile, horizontal line is the median and whiskers extend to the maximum speeds.

observed at long range) to a real increase in target size from the addition of some particularly large jellyfish at depth. A visual inspection of the echograms shows some particularly strong echoes from jellyfish above 300 m (Fig. 6), leading us to believe that the additional peak in the data is caused by a deep-living group of jellyfish. Also, there was a diel variation in the proportion of strong echoes, with more seen at night, including more strong single traces (Fig. 6B), which suggests that the cause of the additional strong peak is caused by biology rather than systematic errors.

The dependence of TS on organism size is well recognized. The variability in TS is expected to increase as the size of the scatterer relative to the wavelength (acoustic frequency) increases (Stanton *et al.*, 2004). On the contrary, variability in TS of *P. periphylla* seemed to decrease for the (acoustically) larger animals (Fig. 9). One interpretation is that the apparently less active behaviour of large jellyfish influences TS to a lesser extent than their smaller conspecifics. Youngbluth and Båmstedt (2001) indeed found more active swimming among smaller than larger specimens. Previous

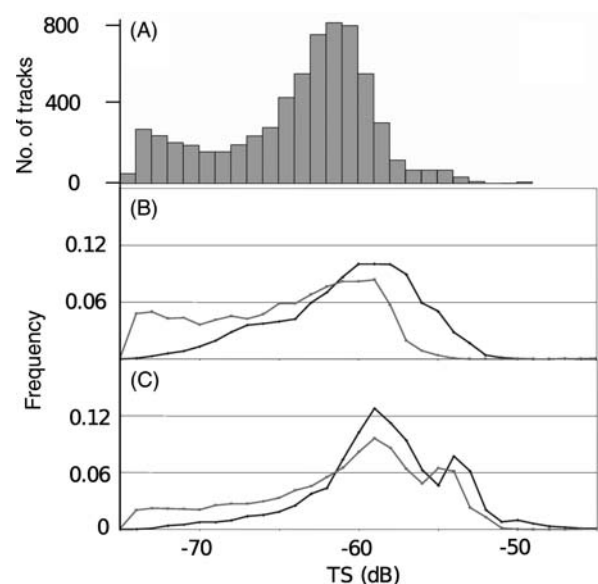


Fig. 8. (A) Distribution of TS for all tracks recorded below 150 m, in the range 10–60 m from the transducer. (B and C) Distributions (daytime) of registered single echoes from overlapping depth intervals, but differing in range from transducer, respectively, 10–60 m (grey line) and 60–110 m (dark line). Paired distributions are separated by $\sim$ 30 min in time. (B) Between 160 and 210 m, and (C) between 260 and 310 m depth.

acoustic studies of jellyfish have connected variations in TS to swimming movements of the animal, i.e. bell contractions (Mutlu, 1996; Brierley *et al.*, 2004). For some of the *Periphylla*, clear cyclic patterns could be found in TS; however, in other tracks, the TS varied in a seemingly haphazard way. The acoustic properties of jellyfish and their relation to behaviour are poorly described and clearly need further study.

Vertical distribution and migration

A high proportion of the jellyfish that formed an acoustic layer from 160 to 180 m during the daytime carried out synchronous DVM. On the basis of the density profiles, at least 75% of the individuals in this layer ascended at night. This deviated from records deeper in the water column, where comparisons of day and night echograms showed no evident difference in abundance of jellyfish. As we did not survey the entire water column (we were restricted by a cable of 300 m) and could not efficiently sample the prevailing small size classes acoustically, we do not know how large a fraction of the total population actually performed DVM. However, the relatively high density of targets in the deep at night suggests less participation in synchronous migrations than the 80–90% reported by Youngbluth and Båmstedt (2001). Yet, the enhanced number of

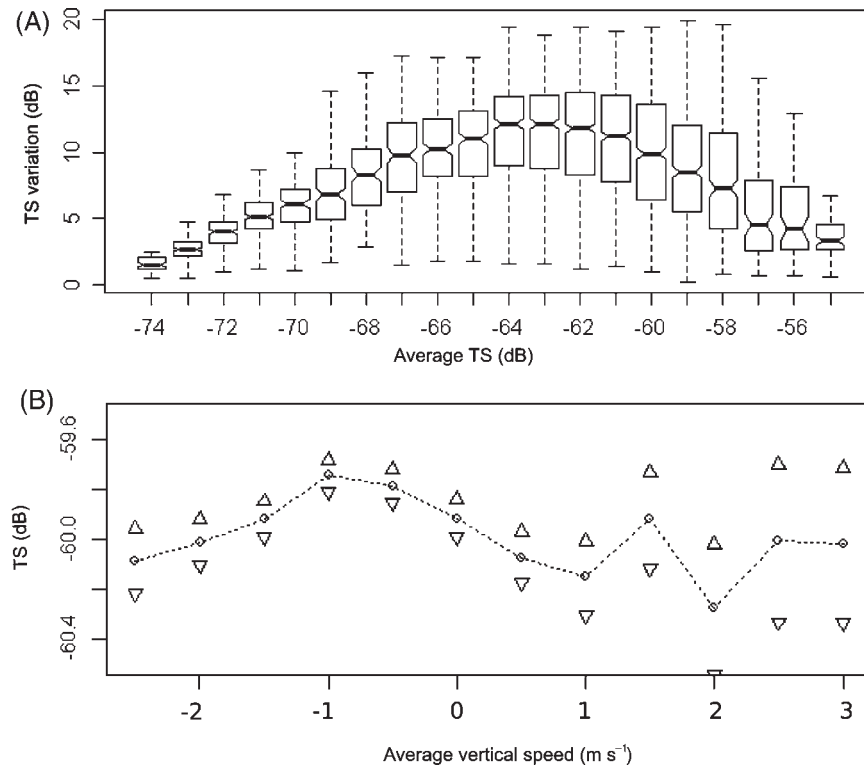


Fig. 9. (A) Average TS of track vs. variation ($TS_{\max} - TS_{\min}$) of TS within track. Boxes span first to third quartile, horizontal line is the median and whiskers extend to the maximum and minimum measurements, respectively. (B) Vertical speeds versus average TS, based on a subset of tracks with mean TS in the region -58 to -62 dB, believed to represent *Periphylla* of similar sizes. Triangles represent 1 SD.

large jellyfish in the upper 300 m of the water column at night, as recorded in the SED echograms (Fig. 6B), suggest ascent from deeper layers and vertical migration that was not revealed by our other analyses. It is well established that a focus on mean population behaviour may underestimate the proportion of migrating individuals (Pearre, 2003). In a recent study, Kaartvedt *et al.* (2007) found that while the mid-water SL of *Periphylla* followed the classical pattern of DVM, individual jellyfish were found to both leave and arrive the shallow layers during night-time. This pattern is consistent with asynchronous vertical migrations (Pearre, 2003), which also may relate to ascending and descending tracks recorded during night in this study.

(Individual) swimming behaviour

The leading edge of the *Periphylla* SL used ~ 1.5 h to descend 50 m. This represents an average descent rate of $< 1 \text{ cm s}^{-1}$, slightly less than the average swimming speeds measured directly from the traces inside the migrating layer. It is also approximately equal to the “overall” average speed determined from TT. *Periphylla* certainly has the capacity to swim much faster, even for extended periods (Youngbluth and Båmstedt, 2001),

though this capacity appeared to be utilized rarely during the course of this study.

While the migration of the layer was evident in the echograms and in the density plots (Fig. 5A and B), the patterns were less clear in the distributions of swimming speeds detected through tracking (Fig. 7). Increased upwards swimming during sunset periods were indeed found for jellyfish in the TS range -69 to -65 dB, and signs of descent in the morning were found for jellyfish around -65 dB, but no systematic patterns in swimming speeds and direction could be found for the majority of tracks. Evidently, individuals in deep waters descended and ascended regardless of the time of day, as also recently reported from video records by Sötje *et al.* (2007).

For all size classes of *Periphylla*, except the largest, the spread in vertical speeds, and possibly also the high variability in TS, suggests that the organisms are swimming actively throughout the diel period. This observation concurs qualitatively with differences in behaviour between different sizes of *Periphylla* as noted by *in situ* video observations (Youngbluth and Båmstedt, 2001). Large individuals varied between the periods of quiescence and active swimming, i.e. after the periods

of active swimming they turned their aboral sides upwards and hung motionless with extended tentacles. Smaller individuals swam more or less continuously.

As outlined previously, aquatic predators have been coarsely separated into those who actively seek out their prey (“cruising” predators), and those who employ a “sit-and-wait” strategy (“ambush” predators) (Greene, 1985), although O’Brien *et al.* (1990) argued that cruising and ambush modes are two extremes along a continuum of search strategies. According to this scheme, the continuous swimming observed among the small jellyfish concurs with the cruising (in this case called “ramming”) mode, whereas a schematic presentation of ambush feeding given by O’Brien *et al.* (1990) virtually mirrors the acoustic traces of the large deep living medusae (Fig. 1). These individuals occasionally changed their vertical distribution in small steps. Plankton may be distributed in vertical microlayers with local elevated concentrations (McManus *et al.*, 2003), and this behaviour may represent a strategy in search for such layers (cf. Soto *et al.*, 2008).

In conclusion, our results have shown the feasibility of using submerged acoustic equipment for studying the *in situ* behaviour and acoustic reflectivity of individual jellyfish. In this way, we could distinguish different vertical migration behaviour among parts of the population, as well as assessing individual swimming behaviour by depth, by size and related to the time of the day.

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