An evaluation of acoustic and video methods to estimate the abundance and vertical distribution of jellyfish

ULF BÅMSTEDT[1,2,*], STEIN KAARTVEDT[3] AND MARSH YOUNGBLUTH[4]

[1]DEPARTMENT OF FISHERIES AND MARINE BIOLOGY, UNIVERSITY OF BERGEN, PO BOX 7800, N-5020 BERGEN, NORWAY, [2]UMEÅ MARINE SCIENCE CENTRE, NORRBYN, SE-910 20 HÖRNEFORS, SWEDEN, [3]DEPARTMENT OF BIOLOGY, UNIVERSITY OF OSLO, BLINDERN, OSLO, NORWAY AND [4]HARBOR BRANCH OCEANOGRAPHIC INSTITUTION, 5600 US 1 NORTH, FORT PIERCE, FL 34946, USA

*CORRESPONDING AUTHOR: ulf.båmstedt@ifm.uib.no

Four non-invasive methods (three acoustic and one video) were compared to estimate the abundance and vertical distribution of scyphomedusae, using the locally abundant coronate species Periphylla periphylla in Lurefjorden, north of Bergen, Norway, as the test organism. The acoustic methods included single-target quantification by, respectively, a hull-mounted 38 kHz split-beam echo sounder and a 675 kHz scanning sonar mounted on a remotely operated vehicle (ROV). Data from acoustic backscattering provided estimates of abundance and changes in the vertical position of scattering (= aggregation) layers. Vertical migration was also studied by acoustic target tracking, following single individuals as they ascended in the afternoon. The ROV-mounted scanning sonar missed an unidentified part in the lower size distribution of the target population. Vertical video profiles, conducted during ROV dives, provided the most detailed information on abundance and distribution, although uncertainties remained regarding the size distribution in the population.

INTRODUCTION

Gelatinous planktonic predators, including the cnidarian order Scyphozoa, are frequently major predators in pelagic systems, especially in coastal waters (Alldredge, 1984). Proliferations of such animals appear to have increased during the last 10–15 years, at least in some environments (Kovalev and Piontkovski, 1998; Brodeur *et al.*, 1999). However, these fauna are not adequately quantified in most field sampling programmes. Standard plankton nets have relatively small (< 1 m diameter) mouth openings and small (<500 μm) mesh sizes. Traditional fishing trawls have large mouth areas but also large mesh openings. Gelatinous zooplankton are fragile and easily damaged by any kind of net. Their remains are often unidentifiable. Species living in the uppermost part of the water column have been quantified by visual observations from boats or by SCUBA (Hamner *et al.*, 1975; Berstad *et al.*, 1995). Unfortunately, this approach is limited by the restrictions on visibility, such as variation in depth distribution and differences in the size and transparency of various species. The use of manned or remotely operated vehicles (ROVs) eliminates the depth restriction.

Acoustic methods have developed gradually and are used increasingly to quantify zooplankton abundance (MacLennan and Holliday, 1996). A few previous applications also relate to gelatinous zooplankton (Mutlu, 1996; Monger *et al.*, 1998; Brierley *et al.*, 2001). One problem associated with conducting acoustic surveys of gelatinous zooplankton is that there is very little contrast in density between the surrounding water and the jellyfish, as a result of its watery consistence [~96% water, see e.g. (Martinussen and Båmstedt, 1999)]. Also, most jellyfish lack an acoustically reflecting organ, like the gas bladder of a fish. Sound scattering, which is a complex function of size, shape, internal structure, material properties and orientation, as well as of wavelength (Foote and Stanton, 2000), will therefore be low. For example, the mass-specific echo energy of a typical medusa or salp is 1/300th of that of a decapod shrimp or a siphonophore with a gas inclusion (Foote and Stranton, 2000). To verify the utility of acoustic methods for estimating the abundance of gelatinous zooplankton, it was therefore necessary to perform tests *in situ*. Our access to a unique fjord environment near Bergen

afforded opportunities to conduct a variety of experiments. In Lurefjorden, ~40 km north of Bergen, there is a large stationary population of the coronate schyphomedusa *Periphylla periphylla* (Fosså, 1992; Jarms *et al.*, 1999; Youngbluth and Båmstedt, 2001). This jellyfish is present at high abundance throughout the year and a prominent part of the population is composed of relatively large individuals. The fjord lacks mesopelagic fish like *Bentosema glaciale* and *Maurolicus müelleri* (Bagøien *et al.*, 2001). The other dominant pelagic components are calanoid copepods (mainly *Calanus glacialis*), chaetognaths (*Sagitta elegans* and *Eukrohnia hamata*) and euphausiids (*Meganyctiphanes norvegica*) (Bagøien, 1999). The only fish species caught in large trawls is whiting (*Merlangius merlangus*), but the numerical abundance of this species is consistently two or three orders of magnitude lower than that of *P. periphylla*. Acoustic studies have indicated the presence of schooling clupeids (S. Kaartvedt, unpublished results).

Here, we report on the possibility of quantifying scyphomedusae by using an ROV with video camera and scanning sonar, and by using a standard scientific echo sounder with a 38 kHz hull-mounted transducer on the ship, and post-processing software. Results from these techniques are evaluated against direct sampling with more traditional gear. We have restricted the presentation to examples of relevance for the methodological evaluation.

METHOD

Data from four different plankton sampling nets were used for comparison with acoustic and visual methods.

The physical characteristics of these nets and the two ROV-based operations are presented in Table I.

The horizontally operated 2 m net, the Beyer's Low-Speed Midwater Trawl (BLSMT), had 0.9 mm mesh size and 2.3 m^2 opening area [e.g. see (Matthews and Sands, 1973)], and the Harstad trawl (Nederaas and Smedstad, 1987) were equipped with a ScanMar depth sensor. The total volume filtered (m^3) was calculated from geographic positions and a simple geometric relationship (T. Brattegard, personal communication):

$$V = \sqrt{(\Delta Lat. \times 1852)^2 + (\Delta Long \times \cos(meanLat) \times 1852)^2} \times OA \tag{1}$$

where ΔLat and $\Delta Long$ are the change in position between start and stop, *meanLat* is the arithmetic mean latitude and *OA* is the opening area (in m^2) of the sampling gear. Positions were given by the differential global positioning system (DGPS) of the ship. The volumes for the vertical net hauls were calculated as the opening area multiplied by the distance (m) of the haul. The calculations thus assumed 100% filtering efficiency and an opening area equal to the theoretical one, with no effects of variable tilting. The figures from this equipment are thus very conservative. The volume for each 1 m^2 MOCNESS net was automatically calculated by the software of the control unit (Wiebe *et al.*, 1985).

Quantification from a hull-mounted echo sounder

A hull-mounted SIMRAD EK500 38 kHz (version 5.0) split-beam echo sounder, operating at a pulse duration of 1 ms, was used for quantification of medusae from

Table I Overview of the different sampling methods and ROV-based methods used in the study

Quantification gear	Screening capacity	Operation
WP3 net	0.8[a]	Vertical
2 m net	3.1[a]	Vertical
2 m net, divided	3.1[a]	Oblique
2 m net, fixed depth	3.1[a]	Horizontal
MOCNESS	1.0[a]	Oblique
BLSMT	2.3[a]	Oblique
Harstad trawl	400[a,b]	Oblique
ROV scanning sonar	8.8–24.7[c]	Vertical
ROV video profiling	2.5 and 6.8[d]	Vertical

The range in screening capacity (m^3 m^{-1}) for ROV scanning sonar is the result of variable speed during descending and ascending, as shown in equation (8). The capacities for ROV video profiling are for a small and a large medusa, respectively (see text).
[a]Theoretical maximum; lower because of clogging and tilting of net during oblique hauls.
[b]Functional capacity different for different sizes of targets because several mesh sizes were used.
[c]This range can be extended by altering sonar settings and speed of ROV.
[d]Dependent on quality of video system and illumination.

R/V 'Håkon Mosby' in December 1995, and February, March and November 1996. Acoustic data from the depth range 0–500 m were logged continuously, and later analysed using the UNIX-based BI 500 post-processing system (Knudsen, 1990; Foote *et al.*, 1991) with a volume backscattering (S_v) threshold setting of −91 dB.

Total acoustic backscattering

The dispersed distribution of individuals in the population, and the scarcity of other interfering targets in Lurefjorden made it possible to obtain *in situ* target strength (TS) measurements of medusae down to at least 100 m depth. TS estimations were obtained using both the BEI 500 software and additional analysis of acoustic records logged on a personal computer (November 1996). These techniques were used to convert acoustic back-scattering into numerical density, with a TS range of −70 to −55 dB. Our numerous acoustic records, taken over many years from the upper 100 m, have shown that this range corresponds to the size range of acoustically detectable medusae in Lurefjorden.

Target tracking

In November 1996 additional analysis of acoustic records logged on a personal computer were performed with a 'target tracking' program that samples and sorts echoes from subsequent pings belonging to single individuals (Ona and Hansen, 1991). Targets recorded by four subsequent pings or more, allowing one missing ping, were included in the analysis. These data were used to study the vertical movements of single targets in the upper 140 m water column.

In the conversion of integrated echo levels (S_A values) into the number of medusae, the peak of the TS–frequency distribution was assigned to all individuals for a given acoustic scattering layer where *P. periphylla* appeared to be the only acoustic target. Numerical abundance (ρ_ν) was obtained using the relationship:

$$\rho_\nu = \frac{S_A}{\sigma} \tag{2}$$

where S_A is the area backscattering coefficient (m^2 nautical mile^{-2}), or depth-integrated echo energy, and σ is the mean area backscattering cross-section of a single target, derived from its relationship to TS:

$$\sigma = 4\pi 10^{TS/10} \tag{3}$$

This treatment produces an artificial number that does not correspond exactly to the actual number in the population, since the formula assumes that all individuals are of the same size (same TS). By using the information on the TS distribution in the population,

we can resolve this value into numbers of each size class (TS value). The total number will then be:

$$\rho_\nu = \frac{S_A}{\sum \lambda_n \sigma_n} \tag{4}$$

where λ_n is the relative proportion of size class n and σ_n is the mean area backscattering cross-section of a single target in the nth size class, derived from its relationship to the TS in this size class, as given from the TS distribution histogram:

$$\sigma_n = 4\pi 10^{TS_n/10} \tag{5}$$

The numerical abundance $(\rho_\nu)_n$ of a given size class will then be:

$$(\rho_\nu)_n = \lambda_n \rho_\nu \tag{6}$$

The size classes are defined as TS classes, and for presentation in real sizes (e.g. length, weight or volume dimensions), a calibration must be made. The TS of given sizes of medusae are recorded. A regression equation is then calculated and used in a final step to determine the size classes.

Quantification from ROV-based methods

Scanning sonar
An 'Argus Rover' (Fami AS, Bergen) equipped with a Simrad Mesotech 675 kHz scanning sonar conducted vertical dives in June and December 1995. The vehicle was outfitted with a video camera (Deep Sea Power and Light Model 2000). Two 250 W halogen lights directed forward provided illumination. Video recordings from preliminary tests were used to verify the signals from the scanning sonar. The sonar was set at 10 m radius, the transducer had a 2° beam and rotated one complete revolution in 25.5 s. The total vertical interval recorded ranged from a 0–27 m starting depth to a 350–445 m ending depth, close to the bottom. The total time for the profile varied between 19 and 48 min. Each time a medusa signal appeared on the sonar screen the depth of its occurrence was recorded manually. Medusa abundance was displayed as number per 1000 m^3 over 10-min intervals. The volume of water scanned by the sonar was calculated according to the formula:

$$\text{Volume} = (2\pi r) \times (r^2 \sin \alpha/2 \times \cos \alpha/2) \times t/T \tag{7}$$

where the volume is given in m^3, r is the radius of the sonar in m (in this case 10), α is the angle of the sonar beam (in this case 2°), t is the time from the start (in s) and T is the time (in s) for a full 360° revolution of the sonar beam (in this case 25.5 s). The 'screening' capacity of this system is given in Table I.

Video recordings

The ROV 'Aglantha' (Båmstedt and Youngbluth, 2000) conducted vertical video profiles in August 1999 to quantify the abundance and vertical distribution of *P. periphylla* (Youngbluth and Båmstedt, 2001). The medusae encountered were classified as either small or large, with the distinction between the two groups at ∼5 cm coronal diameter. The abundance of medusae was quantified by counting the number of individuals within the field of view of a Sony Hi8 video camera, set at minimum focal length, during descent and ascent through the 440 m deep water column. Initial measurements defined the angle of view and maximum distance of visibility for a small (2 cm diameter) and a large (10 cm diameter) medusa. Two 500 W halogen lights and two HID (high intensity discharge) gas-arc lights (comparable effect 1000 W each) illuminated the field of view. The visibility distance of the small medusa was 2.65 m and that of the larger medusa was 4.30 m. Simple geometric relationships gave the visibility area for these two sizes of medusae (Youngbluth and Båmstedt, 2001). The volume covered was determined by multiplying this area by the distance moved vertically. Each profile of the 440 m water column was completed within 30–35 min. For small medusae, the total volume sampled was ∼1000 m³, whereas large medusae were counted in ∼2700 m³. The depth of occurrence of every medusa was recorded and abundance was calculated per 1000 m³ in 10-m vertical intervals. The main problem with this method was the simplification of defining medusae as either 'small' or 'large' and using one of the two visibility constants in the calculations. Medusae varied from 2 to 17 cm in coronal diameter. The visibility distance therefore also varied over a continuous range.

RESULTS

Total abundance

An overview of the results from sampling with different gear is given in Table II. The total range of abundance estimates obtained with the acoustic and video methods overlapped the results from the different net-sampling methods. These data show that the tested methods were comparable with traditional methods, although rigorous statistical evaluations could not be performed because of variability in sampling times (year, season, time of day) between methods. The highest abundance estimates were usually obtained from the MOCNESS hauls and the two ROV-based techniques, indicating the superiority of these methods.

Echointegration

In February 1996 acoustic backscattering was weak, but scattering layers ascribed to *P. periphylla* (see Discussion) were clearly visible when using the lowest possible volume backscattering (S_v) threshold (−91 dB, meaning that the weakest possible echoes were included). Neglecting the upper 20 m, which was influenced by disturbance from the surface and turbulence from the propellers, three distinct acoustic layers appeared during daytime (Figure 1). The lowest layer, which was uniformly

Table II Summary of abundance estimates of Periphylla periphylla for the whole water column in Lurefjorden, using different methods for small and large medusae

Method	Time	n	Numbers encountered		Abundance (no. per 1000 m³)		
			Small	Large	Small	Large	Total
WP3, divided	Dec. 99	6	10–24	0–5	32–76	0–16	32–92
WP3, undivided	Aug. 99	13	23–56	0–7	67–162	0–20	78–165
2 m net, divided[a]	Feb. 98	2	0–650	0–54	0–526	0–25	0–527
2 m net, undivided	Dec. 99	10	27–97	0–18	21–77	0–14	24–92
2 m net, horizontal	Feb. 98	2	104–272	–	14–35	–	–
MOCNESS[b]	1992, 1998	6 + 4	158–202	20–51	198–206	12–20	–
BLSMT	Dec. 94–Oct. 96	8	–	6–17	–	2–11	–
Harstad trawl[c]	Feb. 96	2	–	410–1530	–	3–9	–
Total backscattering	Nov. 96	–	–	–	–	5–9	–
ROV scanning sonar	June, Dec. 95	9	–	49–185	–	9–23	–
ROV video profiling	Aug. 99	14	150–346	51–140	152–343	19–52	180–364

[a]Composed of a series of five oblique hauls from different depths.
[b]Only large medusae quantified in 1992, only small ones in 1998.
[c]Sampling mainly in, respectively, 200 and 100 m depth.
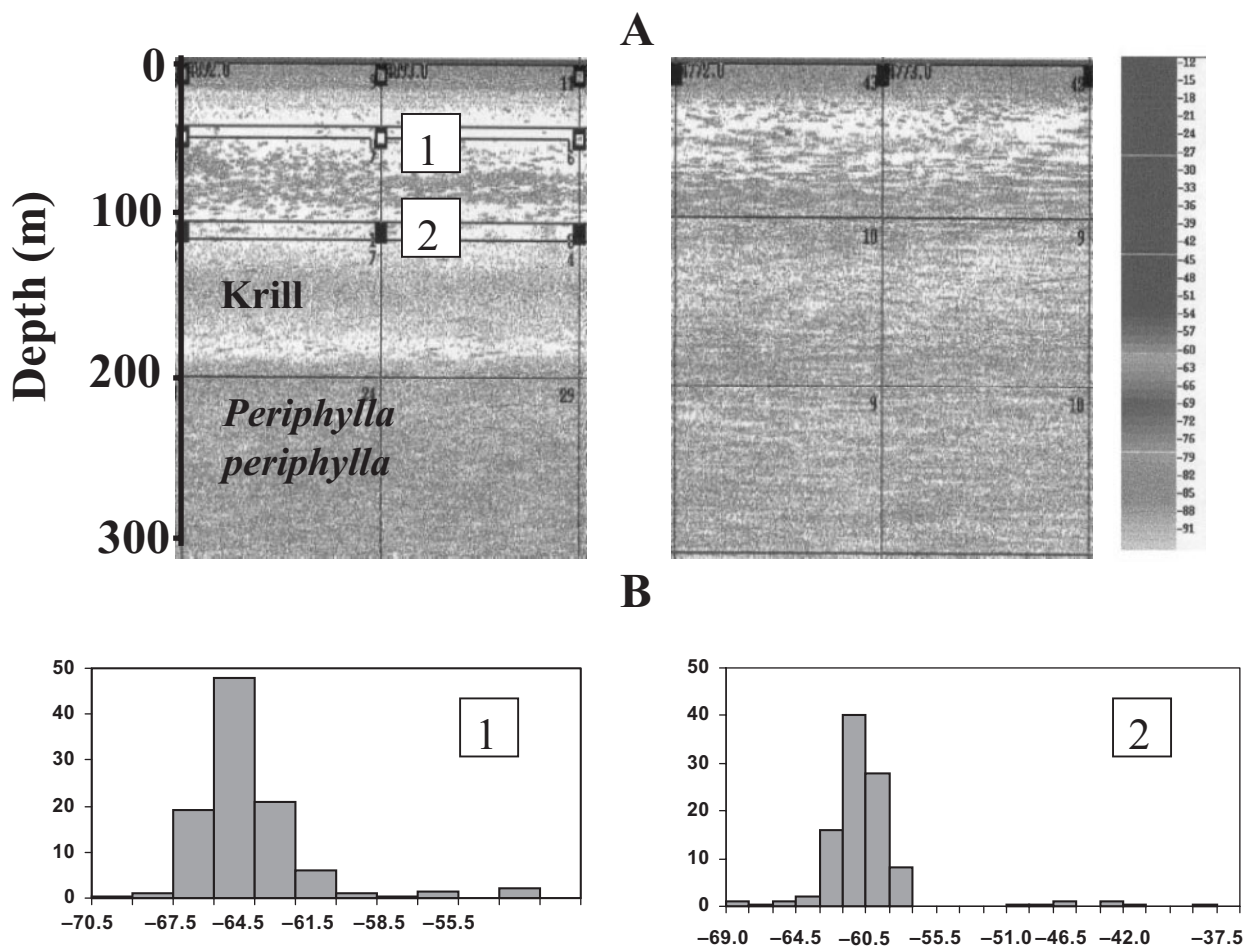
Fig. 1. (**A**) Echograms (EK 500, 38 kHz) from Lurefjorden, February 13–14, 1996 during day (left) and night (right). Colour code refers to volume backscattering strength (dB). Vertical lines delineate ~8-min time intervals. Digits in upper right corners designate integrated echo levels (S_A) for the outlined 'blocks', calculated by the Bergen Echo Integrator (BEI) system (Foote *et al.*, 1991). (**B**) Target strength (TS) distributions from 201 targets in the 46–53 m interval (block 1) and for 160 targets recorded between 105 and 116 m (block 2) during a 38-min time period. Note that the adaptive TS scale in the BEI 500 software adjusts according to the range of registrations so that the scale differs in these two cases. Figure available in colour online as supplementary data at http://www.plankt.oupjournals.org

distributed in the deeper part of the water column, was assigned to *P. periphylla*. The layer above this was assigned to krill. Net sampling during this and other investigations (Viken, 1995; U. Båmstedt *et al.*, unpublished results) has shown a consistent occurrence of the krill species *M. norvegica* above the main distribution of *P. periphylla* during the day, at ~120–180 m. The associated stronger targets probably represented fish such as whiting, *M. merlangus*, and schools of clupeids. The subsurface layer between ~50 and 100 m consisted of animals with TS values corresponding to those of *P. periphylla*, with the smallest individuals in the upper part of this layer (Figure 1B). However, the taxonomic composition of this layer has not been unambiguously identified (see Discussion).

The S_A value for the total deep layer of the population was ~30. Applying a TS value of −61 dB to represent

the deep part of the population gives an estimated abundance of 1 medusa per m² below 200 m during the day, or ~5 medusae per 1000 m³. The S_A level of the total shallow mode (vertical range of ~50 m) was ~6. Depending on which TS is chosen to represent this layer, the abundance estimate varied between 3.5 (TS −61 dB) and 9 (TS −65 dB) ind. per 1000 m³. Assignment into size classes according to the TS distribution in Figure 1, and use of equation (6) gave only slightly different estimates, 4.4 ind. per 1000 m³ in the shallow layer and 4.2 medusae per 1000 m³ in the deeper layer.

ROV-based scanning sonar
The first 20 targets observed with a video camera on the ROV provided the data for an initial test of the efficiency of the sonar. We obtained 100% 'recovery',

i.e. all recorded signals were large *P. periphylla*. However, the lower size limit of the jellyfish for the method could not be determined, and therefore, an unknown part in the lower size range of the population was not included. The average abundance was 17.3 medusae per 1000 m^3 ($n = 6$, SD $= 4.9$) in June 1995 and 19.3 medusae per 1000 m^3 ($n = 3$, SD $= 4.0$) in December 1995. These estimates were similar to the estimates of large medusae from the video profiles (see below), thus showing that the size limit of detectable medusae was about the same as that used to differentiate visually between large and small medusae ($= \sim 5$ cm diameter).

ROV-based video records

Preliminary video profiles in 1995–96, using an older ROV, were not successful, mainly because the illumination was too dim and therefore the volume of water viewed was too small. In 1999 with ROV 'Aglantha' we had better video resolution, better illumination and calibrated the visibility area for small and large medusae. These improvements in the method and 'screening volume' indicated that large medusae were actually three times more numerous than estimates based on vertical hauls with a 2-m conical net. The total number of medusae observed in 14 video profiles through the water column during August 1999 ranged from 51 to 140 large medusae and from 150 to 346 small ones (Table II), corresponding to calculated average abundance of 28 large medusae per 1000 m^3 ($n = 14$, 95% CI $= 5.4$) and 232 small medusae per 1000 m^3 ($n = 14$, 95% CI $= 29.5$).

## Vertical distribution and population behaviour

Echo sounder methods

Dynamics of the scattering layers. In February 1996, diel changes in the vertical position of the deep scattering layer of *P. periphylla* (see Figure 1) were studied in order to describe diel vertical migration (Figure 2). Migration velocities could be estimated from the temporal ascent/descent of the upper fringe of the scattering layer. Both the ascent and descent velocities were estimated at 60–70 m h^{-1}, which corresponded to the migration velocity for the krill-layer above.

Vertical migration based on single-target tracking. In November 1996 the vertical movements of *P. periphylla* were studied by target tracking in the afternoon (Figure 3). Single individuals were recorded acoustically as they ascended from waters below 140 m, the greatest depth where single targets could be resolved. The vertical velocity of the front of these ascending single targets was estimated at 60 m h^{-1}
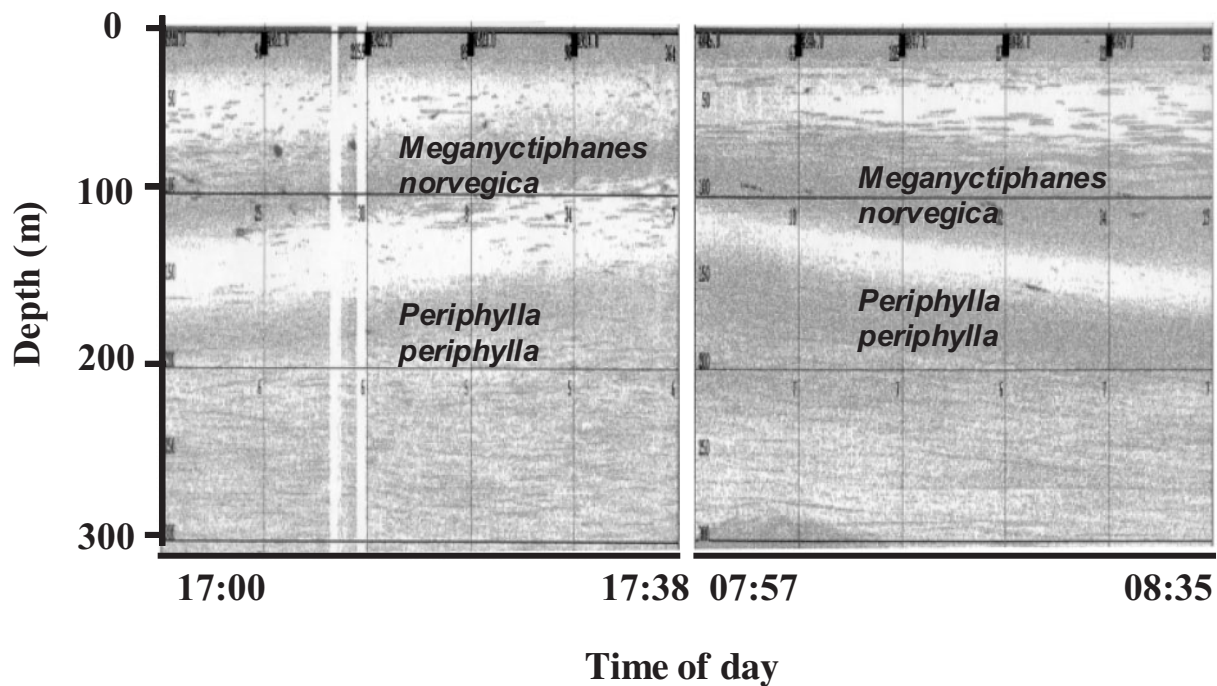
Fig. 2. Diel vertical migration near dusk (17:00–17:38 h; left) and dawn (07:57–08:35 h; right) on February 14, 1996. The scattering layers (SL), descending and ascending in parallel, consist of krill (shallow migrating SL) and *P. periphylla* (deep migrating SL). Acoustic records below 300 m were corrupted by false bottom echoes and are not shown. Colour code and notations as in Figure 1. Figure available in colour online as supplementary data at http://www.plankt.oupjournals.org
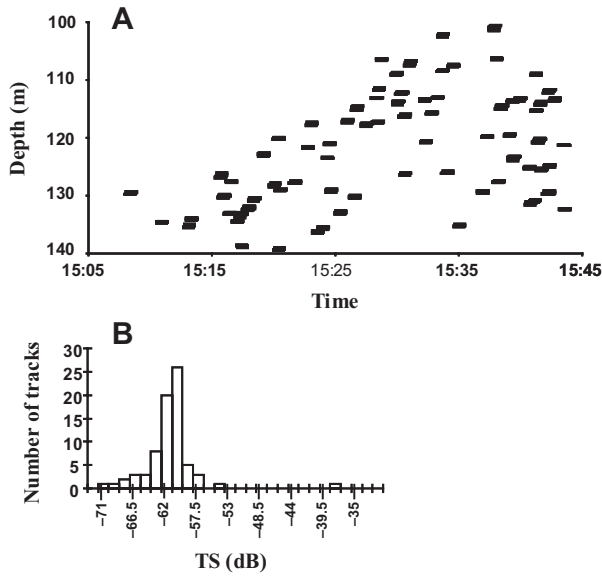
Fig. 3. (**A**) Diel vertical migration of *P. periphylla* in the afternoon of November 8, 1996 as revealed by acoustic target tracking between 140 and 100 m. Each horizontal bar represents a resolved target tracked for at least four pings. (**B**) Target strength (TS) distribution of targets shown in (A).

from the figure, thus corresponding to the velocity of the scattering layer (see above). The majority of the single tracks were moving upwards. Of 74 targets tracked for 4–11 pings, 67 displayed a net upward swimming, five displayed no vertical movement and two showed a net downward movement. The tracking period was too brief to obtain reliable velocity estimates for single individuals.

ROV-based methods. Both ROV-based methods provided information on the vertical distribution of the population. Results from these methods are shown in Figure 4, together with results from two combined MOCNESS hauls. The MOCNESS tows from February indicated aggregation of small medusae at ∼200 m depth in the afternoon, with very few individuals occurring above 140 m depth. Large medusae, sampled with a MOCNESS system during early night in March, showed a strong aggregation in the uppermost layer. The scanning sonar from the morning in winter indicated a peak in abundance at ∼250 m depth, similar to the surface value from the MOCNESS. The summer distribution in the morning, as given by the video profiles, showed aggregation of both small and large medusae at ∼250 m depth (Figure 4). The 14 video profiles showed that
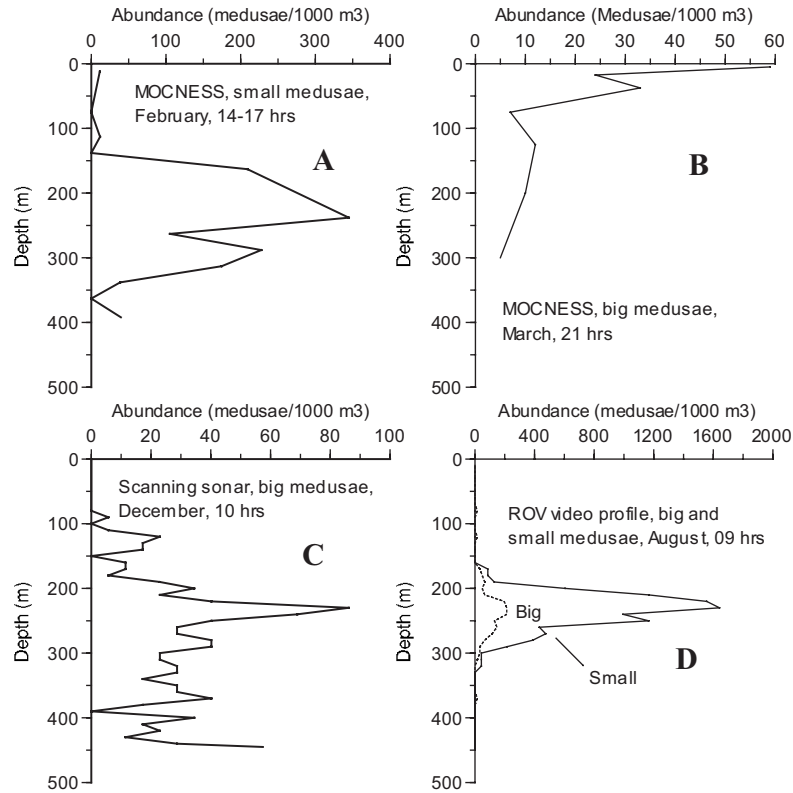
Fig. 4. Examples of results on vertical distribution of *P. periphylla* obtained by using a 1 m² multi-net (MOCNESS; **A** and **B**), an ROV-mounted scanning sonar (675 kHz; **C**), and video registration of small (∼<5 cm diameter) and large medusae (**D**). Note that the results are not directly comparable, since they represent different field studies. See text for further explanations.

abundance in the densest layer exceeded 2 ind. m^{-3} for small medusae, and up to 0.6 ind. m^{-3} for large ones.

Profiling with video and scanning sonar was also used to investigate the diel change in vertical distribution. The distribution patterns from two scanning-sonar profiles in June did not reveal any strong modal distribution, and the change in average depth was therefore used. This average depth changed from 156 m at 01:00 h to 179 m at noon. Thus the average descent of the population was only 23 m. Large medusae detected by video in August showed a pronounced peak at 110 m in the night, but the vertical distribution was more uniform during the daytime (Figure 5). The average depth of large medusae changed from 128 m at 23:30 h to 287 m at 16:30 h the following day. Small medusae showed a very pronounced unimodal distribution, with a change of the peak from 100 m in the night to 230 m in daytime (Figure 5). The average depth of small medusae changed from 129 m in the night to 260 m during the daytime, closely corresponding to the behaviour of the large medusae.

DISCUSSION

A basic requirement for quantification of pelagic fauna is that a sufficiently large water volume is sampled to obtain statistically reliable estimates of abundance. This rule is true irrespective of the sampling method, i.e. direct collection, acoustic profiling or video recording.

Fig. 5. Vertical distribution of small (**A**) and large (**B**) *P. periphylla* during night and day, respectively, in August 1999. The results are based on video profiling with 10 m vertical resolution (see text).

If there is a pre-knowledge of the abundance (X, in numbers per m^3) of a target organism, it is relatively easy to determine which screening capacity (Y, in m^3 m^{-1}) the gear should have. The formula: $Y = n/(D \times X)$ is used where n is the minimum number needed for sound statistics and D is the distance in metres (e.g. depth interval or horizontal distance hauled with a net). For a species with an abundance of 10 ind. 1000 m^{-3} or less, huge nets or trawls are obviously needed, especially if the water column has to be sampled in intervals. The time constraints in conducting repeated hauls with nets make them unsuitable for rigorous temporal studies of the vertical distribution. Multi-nets, such as the 1 m^2 MOCNESS system, can provide more reliable data, since each net can be towed long enough to filter a sufficient volume from any depth interval when it is towed obliquely. The array of several nets will provide abundance data from several contiguous intervals during a single haul. An adequate multi-net system is therefore the appropriate gear for comparison and calibration purposes when using the methods we have described here.

Acoustic methods

Acoustic methods were applied to estimate the abundance and the behaviour of *P. periphylla*. Medusae were clearly discernible at 38 kHz, both as acoustic scattering layers and as single individuals in the upper 100–140 m of the water column.

Lurefjorden is an ideal environment for *in situ* TS measurements of *P. periphylla* because of the spatially dilute population, which reduces the probability of recording multiple (overlapping) targets, and because of the paucity of interfering targets. Narrow TS distributions with distinct peaks were recorded, and the inclusion of target tracking (which reduces the probability of accepting multiple targets) did not alter the TS distributions (Soule *et al.*, 1997). However, the TS distribution may be positively biased due to software discrimination against weak targets. Weak targets fall earlier into the noise range than strong targets; the latter may therefore be resolved further off the acoustic axis. This treatment gives a larger efficient sampling volume for strong targets and thus a numerical over-representation resulting in an artificial size increase with depth.

Quantification of scattering layers through echo integration
The abundance of medusae was probably underestimated in deep water because of threshold-induced bias in the integration (Reynisson, 1996). This bias may particularly underestimate the abundance of weak targets in deep water (where the signal-to-noise ratio is comparatively low). This result occurs because the effective sampling volume, given by the effective equivalent beam
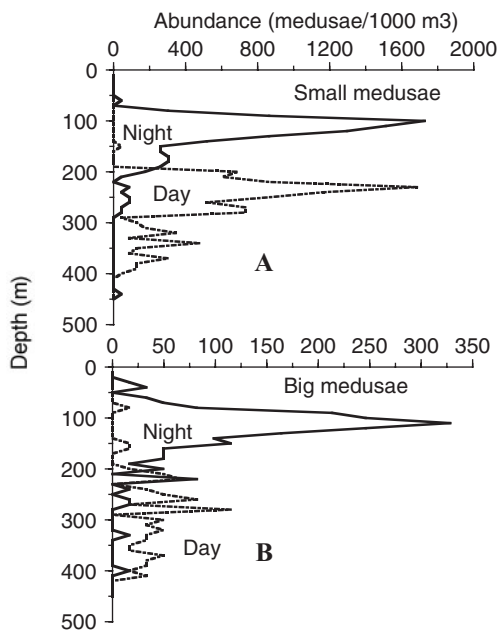
angle, becomes progressively smaller than the nominal, full volume of the acoustic beam as weak targets in the outer fringes fall below the noise level (Reynisson, 1996). The magnitude of this bias has not been assessed.

The scattering layer below ∼200 m could unambiguously be ascribed to *P. periphylla*, since studies for many years have documented the paucity of alternative scatterers (Fosså, 1992; Nesse, 1994; U. Båmstedt *et al.*, unpublished results). The upper mode recorded acoustically in February 1996 was not identified in the present investigation, and a corresponding peak was not documented by the video in our investigation from August 1999. However, previous and subsequent results from our numerous cruises to Lurefjorden have shown that *P. periphylla* commonly migrates up to the surface at night during the winter. This behaviour was also documented by the MOCNESS haul from March (see Figure 4). The actual depth of aggregation seems to be dependent on the physical conditions, e.g. a brackish surface layer or turbulence as a result of strong wind can inhibit the ascent to the surface. The swimming behaviour and acoustic characteristics further suggest that medusae were responsible for the echoes. The free-drifting ship was almost stationary in the calm fjord environment during the acoustic study, and single targets could be kept within the acoustic beam for up to 15 min (not shown), documenting low swimming velocity. The stronger targets (more actively swimming fish) were recorded for shorter periods, and displayed a different behaviour with more vertical movements (Figure 3). Furthermore, target tracking suggested very little ping-to-ping variation in the TS of targets in the upper mode, as would be expected for a coronate medusa since its swimming mode involves only small fluctuations in size and direction. Their directivity would also be much less important than for a fish with a swim bladder. It is still possible that other targets intermingled among the shallow acoustic mode since unidentified targets of corresponding TS are often recorded in the upper layer of fjords (U. Båmstedt *et al.*, unpublished results). Still, our difficulty in ascribing this acoustic layer definitely to *P. periphylla* shows the importance of using a visual method like video profiling as a form for verification.

The wet weight to dry weight ratio of *P. periphylla* corresponded to that of other medusa (Fosså1992) it was compared with (Arai, 1997; Martinussen and Båmstedt, 1999), so therefore, other large jellyfish may be studied acoustically at 38 kHz. However, the basin water of Lurefjorden is unique compared with other deep-water habitats because of the absence of mesopelagic fish. Corresponding densities of jellyfish elsewhere would be masked by other targets and would not be observable acoustically. In a comparative study

between four fjords, we used a S_v threshold of −82 dB. In essence, *P. periphylla* in Lurefjorden became acoustically invisible at this setting, while strong acoustic fish layers were seen in the other fjords (Bagøien *et al.*, 2001). Nevertheless, in many field situations, other jellyfish such as *Aurelia aurita* occur in much higher concentrations than *P. periphylla* in Lurefjorden, [e.g. (Olesen *et al.*, 1994; Berstad *et al.*, 1995; Ishii and Båmstedt, 1998)], and could be quantified with acoustic methods.

Scanning sonar

This method was used with an underwater vehicle, but it would be possible to make blind profiles with an instrument sent down on a cable, although the possibility of verifying targets by video is then lost. In other environments it might be more difficult to distinguish the different sources. There is a possibility of increasing the range (radius) of the scanning sonar, although the backscattering signal decreases quickly with distance, thereby increasing the risk of losses. Our choice of a 10-m radius was optimal for the environment in Lurefjorden, with *P. periphylla* as target. Like the other acoustic methods we have surveyed, there is an uncertainty in that we cannot define the detectable lower size range. This fact means that abundance values are reliable over only part of the size range, missing an unknown proportion of the small medusae. This problem is shared by all the acoustic methods that we have used. Thus, when abundance data for a greater proportion of the population are needed, the acoustic methods must be combined with either video profiles or sampling with nets. Like the video recordings for large medusae, the scanning sonar also gave many 10-m intervals with zero numbers in between non-zero intervals, and this limited the possibility of investigating small-scale changes in vertical distribution. Since detection of small-scale variation is a direct function of a low search volume in relation to the abundance, this problem can be partly compensated for by reducing the speed of the ROV during profiling. However, the speed cannot be so low that the sonar scans over the same target several times. The critical speed (v, m s^{-1}) is given by:

$$v > \sin(\alpha/2) \times 2 \times r/t_{\text{sonar}} \qquad (8)$$

where α is the beam angle (2° in our case), r is the radius setting of the sonar (10 m in our case) and t_{sonar} is the time for one complete revolution of the transducer (25.5 s in our case). If the target is moving in the same direction as the ROV, this problem also has to be accounted for in the formula. With our settings the critical speed was 0.014 m s^{-1}, whereas our actual speed varied between 0.15 and 0.31 m s^{-1} during ascent and descent. Thus, the volume searched could actually

be increased by a factor of 10 or more by just slowing down the speed of the ROV. However, then the swimming speeds of targets and behavioural reactions to the light might appear as new problems. This problem can easily be solved by switching off the light, but then no information will be provided from the video cameras.

Video recordings

Our results for video recordings showed that this method gave detailed information on the abundance and vertical distribution of the medusa population. With the illumination and camera settings used on ROV 'Aglantha' the search volume was between 2.5 and 6.8 m^3 m^{-1} descending or ascending, depending on the size of the medusa (Youngbluth and Båmstedt, 2001). Although the distributional data for small *P. periphylla* showed a high resolution, that for large medusae was poorer, with frequent occurrence of zero numbers in 10-m intervals in between non-zero intervals. By moving obliquely through the water column the search volume can easily be increased. However, when doing this, it is important that the distance travelled can be quantified. Precise logging from a Hydroacoustic Positioning Reference (HPR) system is one way of accomplishing this task, but this method does not compensate for movements of the water. The limited accuracy of the position, being 1–2% of the depth, according to the producer's manual, might also be a problem, and short-term failure in acoustic communication between the ROV and the mother ship is another problem frequently experienced in this study. A mechanical flow meter, as used by ROV 'Aglantha', is not sufficiently sensitive and precise for this purpose, but very sensitive and precise Doppler current meters are available.

The main problem with the video-recording method is the lack of reliable estimates for the size of each medusa. Only two categories (large and small) have been used hitherto (Youngbluth and Båmstedt, 2001). One possible improvement would be to use an illuminated frame in front of the camera (cf. Bergstrøm *et al.*, 1992) and count only those medusae passing through the frame. A precise measurement of the size can then easily be obtained for each individual by direct measurement from a video monitor. However, quantitatively, the method has the same limitations as net sampling since the mouth area needs to be fairly large. Alternatively, the vehicle can make oblique dives, to increase the volume scanned per depth interval. If all sizes of medusa should be recorded, it might be necessary to use two counting frames (one that is smaller, close to the camera, for the small medusae and a larger one, more distant, for the large medusae) and use one frame at a time or two different video cameras. Paired, parallel laser beams can be used to scale any target (Tusting and Davis, 1993), and have also been used extensively by us. However, this device does not work for multiple targets that quickly pass through the field of view during continuous ascent or descent of the ROV.

An additional problem in the video-based methods is the potential behavioural effects from the illumination that might disturb the distributional data. We observed strong negative phototaxis of *P. periphylla* when exposed to white light, whereas red light (670 nm) did not have that effect (Youngbluth and Båmstedt, 2001). The speed of the ROV during vertical transects in this study was sufficiently fast that we could neglect this factor in the distributional studies, but we recommend that red or infrared light be used whenever recording the behaviours of deep-water medusae or other gelatinous zooplankton.

Conclusions

The two methods based on a hull-mounted echo sounder are considered to be very accessible since most research ships have research-quality acoustic equipment. All the acoustic methods are highly time efficient. Since the method can quantify how the population changes in the uppermost part of the water column, the data are useful for estimating vertical migration. Deployment of a submersible echo sounder or transducer would eliminate depth limitations both for single target detection and echo integration and provide a suitable improvement for studies of vertical distribution. Subsequent preliminary studies with this technique have already shown very promising results.

The ROV-based scanning sonar method requires access to an ROV with scanning sonar. Small-sized medusae are not recorded, but accurate data on total abundance and depth distribution of the large-sized medusae, as evidenced from the high abundance estimates, are possible.

As with the previous method, ROV-based video profiling has low accessibility, but if an adequately equipped ROV is available, this method is the best approach, because of the detailed information provided about the targeted population. Observations from ROVs can also provide information on the abundance and distribution of other members of the community, and together with the simultaneous recording of environmental parameters, this concept can generate reliable data for ecological studies. Hitherto, insufficient documentation of individual size and thereby also size-related abundance has been a weak factor in the method. A new method, based on a constant speed during vertical profiling, and use of simple geometric relationships in the field of view, is now being tested (U. Båmstedt, personal communication). This approach will provide

information on object size and distance between object and camera, and will eliminate this major limitation of the system. This method already works, but it is an extremely time-consuming task to extract all information from a vertical video profile. We hope to develop a computer-based image-analysis system that can automatically calculate individual sizes from the video frames.

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