Tilt angle distribution and swimming speed of overwintering Norwegian spring spawning herring

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When plankton production in the feeding areas decreases in the fall, adult Norwegian spring-spawning herring migrate into two fjords in northern Norway. In these wintering areas the herring occupy deeper water. Lacking the ability to refill the swimbladder they are constantly negatively buoyant. This leads to different adaptive behaviour during the day and at night, behaviour which is reflected in swimming angle. Split-beam tracking methods and still-frame photography have been used to study the herring behaviour inside the dense wintering schools. Negative buoyancy seems to be controlled through constant swimming at speeds between 0.25–0.42 ms^{-1} because these are sufficiently high to generate lift when the pectoral fins are used as spoilers. During the day, when the layers aggregate, the average swimming angle is close to horizontal while positive average swimming angles of up to 40° were recorded at night. A bimodal distribution of tilt angles, with one positive and one negative component, indicating a "rise and glide" swimming strategy was also observed at night. Vertically undulating split beam tracks confirmed this particular type of swimming behaviour. As adult herring are directional targets at the echo-sounder frequency used for acoustic assessment of the stock, the possible impact of the observed tilt angles on average acoustic target strength is discussed.

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Introduction

Since 1987, the entire adult stock of spring spawning Norwegian herring has been overwintering in two fjords in northern Norway, Ofotfjord and Tysfjord (68°20′N, 17°E). The herring start to enter the fjords in October when their principal food, *Calanus finmarchicus* L., disappears from the surface layers on the feeding grounds after the summer bloom. They stay in the fjords until the end of January when they start their spawning migration. During the winter the herring barely feed. This period can thus be looked upon as an exercise in predator avoidance and energy conservation. The main predators are cod, saithe and killer whales, which are all predominantly visual feeders on herring. Therefore, in addition to avoiding predators by schooling during the hours of daylight, the herring also prefer to be at depth during the day, in order to avoid the surface-orientated killer whales and to be in waters with the lowest possible illumination to also avoid predatory fish. At night, at least part of the population migrates to the upper water layers. Herring schools are therefore typically observed at depths of 100–400 m during the day and from 50–400 m at night.

Energy conservation means minimizing swimming and basic metabolism. Basic metabolism in this non-feeding situation is mainly a function of temperature. As the temperature profile within the vertical distribution range is quite homogeneous (Røttingen *et al.*, 1994), little can be gained in energy terms through vertical migration. Energy expenditure for herring in this particular situation therefore seems to be mainly related to swimming activity. Herring swim in order to maintain position both vertically and within the school when schooling. Being physostomous, with no gas glands or other known mechanisms of refilling the swimbladder except by surfacing, herring are neutrally buoyant at shallow depths and will expend increasing amounts of energy as their depth increases. The depth of neutral buoyancy will vary with the body density of the

individual fish and the density of the surrounding water. However, at a depth of 100 m, for example, the swimbladder volume will be only 1/11, and at 200 m only 1/21, of the surface volume, thus contributing only marginally to the density of the fish. Herring at these depths are therefore likely to be negatively buoyant and must adopt special swimming strategies in order to maintain a particular depth with a minimum expenditure of energy. Their density may also increase throughout the wintering season as lipid stores are consumed for energy and during gonad development (Røttingen et al., 1994), increasing body density relative to the water masses.

Echo integration is the principal method of estimating the abundance of Norwegian spring spawning herring. Since spawning stock estimates are made during overwintering, it is important to gain knowledge of the behaviour of herring in order to evaluate possible effects of behaviour on acoustic target strength. As dorsal average target strength is very sensitive to changes in tilt angle (Nakken and Olsen, 1977; Foote, 1980), our studies were carried out to evaluate potential bias in stock estimates stemming from such changes in this rather special overwintering situation.

Materials and methods

The investigations were carried out in the wintering area during two surveys in December 1993 (R/V "Michael Sars") and January 1994 (R/V "Johan Hjort"). A steel T-frame holding a 12° beam width, 38 kHz split-beam transducer, a horizontally mounted Photosea-1000 camera with an optional time lapse unit with an Osprey flash gun, and a Simrad FS-3300 Scanning Sonar, was lowered by cable into the herring schools (Fig. 1). The ships were drifting with only navigation lights on during the observation sessions, and vessel movement was logged continuously through the Differential Geographic Positioning System (DGPS) navigational system. The scanning sonar was mounted so that a vertical observation field, $1.7 \times 180°$ parallel to the camera direction was created, and the exact depth of the rig was measured by the depth sensor in the sonar. Photographs were triggered manually during all dives except for a few dives in January when an automatic timer controlled the photography. Photographs were never taken less than 20 s apart and mostly at longer intervals. The herring were observed to scatter when the photographic flash went off but the distribution was normally re-established in less than 10 s. The scanning sonar was used to position the T-frame within the herring shoal and to observe the herring concentration in front of the camera for manual photography. The camera was loaded with 250 frames of film for each dive, and the film (Kodak Tmax, 400ASA) was developed directly after the dive.
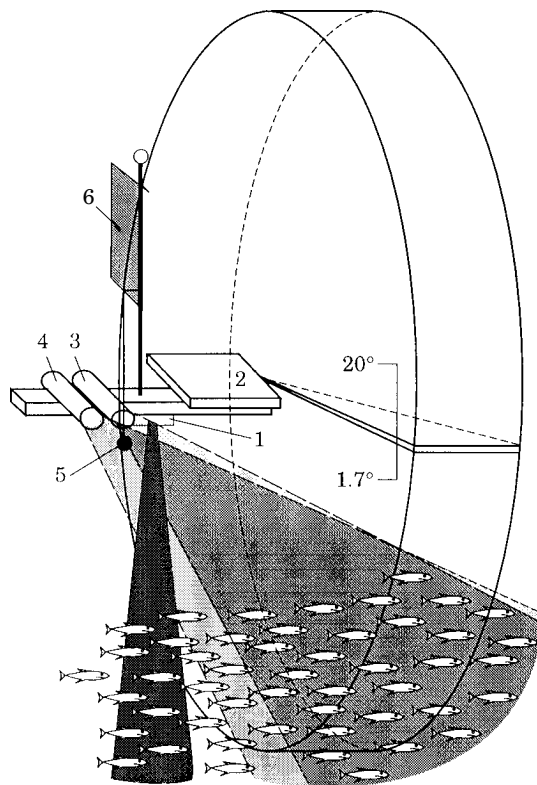

Figure 1. Observation rig. (1) Split-beam transducer; (2) sonar; (3) camera; (4) strobe; (5) vertical line; (6) current sail.

Herring tilt angle measurements were made from the photographs, using a high resolution digitizing table. Only fish which were visually evaluated as being in a plane perpendicular to the optic axis and occupying the central third of the picture were selected for measurement. The vertical axis of the picture was determined from the image of a heavily weighted nylon line that hung permanently in front of the camera. Surface illumination readings were logged using a Li-Core LI-1000 light meter with a sensor calibrated in Micro Einstein (ME). The sensitivity of the light meter was 0.0001 ME and logged readings were 15 min averages of readings sampled every 5 s.

The swimming speed of individual herring was measured using the split-beam tracking method on the December 1993 survey. The split-beam transducer was coupled to the Simrad EK-500 echo-sounder through a 200 m-long standard split-beam cable. The system was calibrated with the transducer at 5, 10, 50, 75, 100, and 125 m depth. Real-time tracking software (Ona and Hansen, 1991), running on a HP RS/25C PC, was used to capture target strength and angular position of individual, acoustically resolved targets swimming through the acoustic beam, along with the continuous DGPS data on vessel position. Normal tracking procedures and

settings for such investigations are described in detail by Ona and Hansen (1991). However, working in dense concentrations of fish meant that stringent rejection criteria on track acceptance had to be used. The following thresholds and limitations were set during data capture and post-processing in order to eliminate tracking errors and to isolate incidental tracks of large predatory fish like saithe and cod. First, only tracks containing at least four successive detections were accepted as valid during data capture and only if the depth excursion between each detection was less than 0.1 m. During post-processing, tracks whose average track target strength exceeded $TS = -30$ dB were rejected as belonging to predators. Similarly, tracks outside a range of 20 m were excluded because tracking errors in these densities started to appear at this range. The remaining material was regarded as being more or less uncontaminated by predator tracks and tracking errors. Using these settings, tracking of individual fish at short range, <20 m, could be conducted at densities well above 0.1 fish m^{-3}. However, most of the tracking data were sampled during darkness at densities below this limit. Day-time schools were too dense and often too deep for tracking with this particular transducer.

Only trials during which the drifting speed of the vessel, as averaged from the DGPS system, was less than 2 cm s^{-1} were analysed, and no correction for drift was applied to the swimming speed data. Catch data, herring distribution in the fjord, and preliminary abundance estimates from the two surveys have been reported by Røttingen *et al.* (1994).

Results

Tilt angle measurements

All December dives were in Tysfjord while all January dives were in Ofotfjord. Figures 2 and 3 show graphic representations of herring tilt angles during four representative dives. The two figures include measurements from 296, 1484, 800, and 85 herring, respectively. Measured tilt angles are combined into 10° groups. Night-time shallow-water tilt angles and day-time intermediately deep tilt angles were largely horizontal (Fig. 2a, b), while deep-water tilt angles were positive with head up, often up to 40° (Fig. 3a), or bimodal with one positive and one negative component (Fig. 3b). Photographs of herring in typical shallow-water or intermediate-depth day-time situations are shown in Figure 4a, while Figure 4b features herring at intermediate depths outside of daylight hours or in deep water at all times.

If the threshold for daylight is set at 0.1 ME (5.5 Lux), the earliest morning of the December survey was at 0800 h and the latest evening was at 1330 h, according to the light-meter readings. For the January survey, the
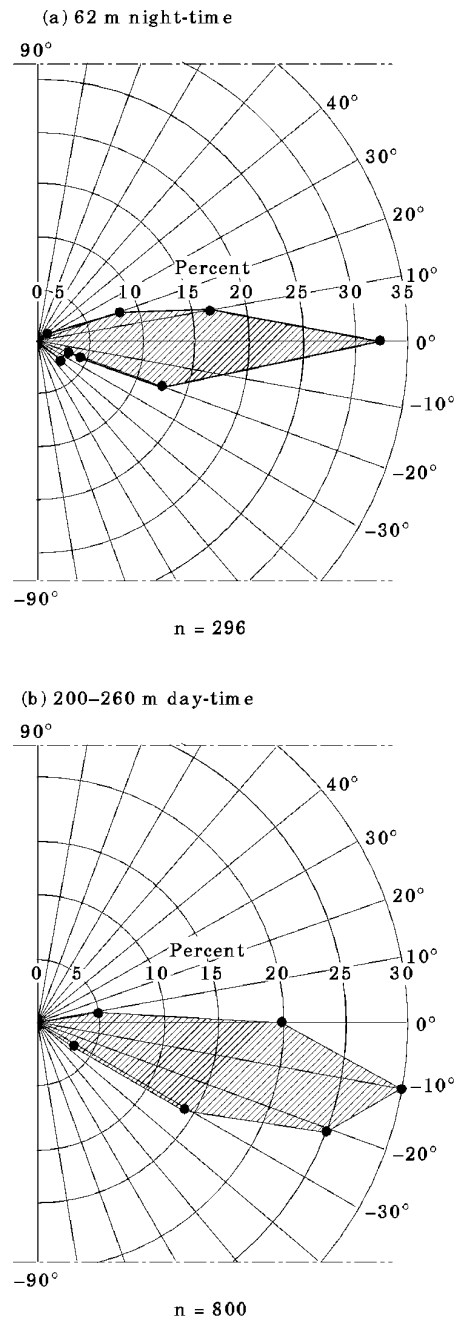

Figure 2. Tilt-angle distributions. (a) December, 2200–0100 h, 62 m depth; (b) January, 1230–1430 h, 200–260 m depth.

corresponding times were 0815 h and 1430 h. Dusk and dawn, defined as readings between 0 and 0.1 ME, normally lasted for 1 h. It should be noted that the fjords in question are north of the Arctic circle and that the sun was below the horizon at all times during the surveys.

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(a) 330–370 m night–time
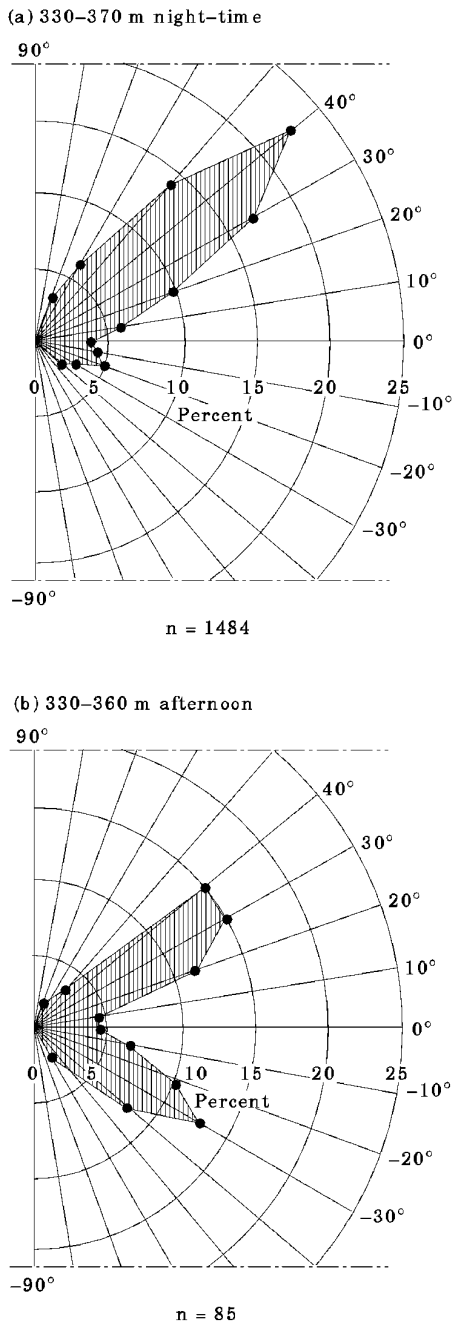

n = 1484

(b) 330–360 m afternoon

n = 85

Figure 3. Tilt-angle distributions. (a) January, 0130–0230 h, 330–370 m depth; (b) January, 1600–1715 h, 330–360 m depth.

Swimming speed measurements

An example of a typical herring layer at night, as recorded from the hull mounted transducer, is shown in Figure 5, with ideally resolved targets for tracking by the rig transducer in Figure 6a. In Figure 6b, a more dense concentration was only partly resolved, and effective

tracking range was only 25 m. Table 1 summarizes the average recorded swimming speed of herring in the selected dives, and Figure 7a, b show examples of the frequency distribution of swimming speeds recorded at depths of 62 and 107 m. A major component of the herring recorded were swimming at speeds around 0.25–0.35 m s^{-1}. This is close to 1.0 bl s^{-1} for this particular herring, with average length between 26–36 cm, depending on the actual catch data used (Røttingen *et al.*, 1994). Note that very few herring were swimming at low speeds and that a few herring were swimming at about twice the average recorded speed. Stringent threshold criteria, particularly regarding range, removed most of the tracked data in all series but particularly in the last three series, where less than 100 tracks were accepted. This was done in order to stabilize the mean swimming speed, as only a few tracking errors giving high speeds tended to affect the mean value. The average swimming speed and its distribution was similar at all depths, and the differences observed did not seem to be depth related. The highest recorded average was 0.41 m s^{-1} at a depth of 140 m, and the lowest was 0.27 m s^{-1} at 107 m. At the shallow recordings, 60 and 62 m, the average swimming speeds were 0.31 and 0.33 m s^{-1}, respectively. Constant current at the measuring depth may affect the tracking data because recorded speed is measured relative to the transducer. However, current speeds in these fjord basins were very low and should have moved the targets in one particular direction relative to the rig. Although some preferred swimming directions were naturally seen in some of the data sets, swimming speed was generally independent of tracked swimming direction (Fig. 8). Figure 9 shows some echogram traces of herring alternately swimming and gliding.

Discussion

Buoyancy regulation in most teleosts is accomplished by swimbladder volume regulation (Horn, 1975). The swimbladder in herring has been thoroughly described by Brawn (1962) and Fahlen (1967). Although data have been presented which indicate that herring are able to refill their swimbladder without access to the surface (Sundnes and Bratland, 1972), most authors seem to agree that herring do not possess this ability (Brawn, 1962; Fahlen, 1967; Blaxter and Hunter, 1982; Blaxter and Batty, 1984; Ona, 1984a). The herring swimbladder thus compresses and expands with ambient pressure according to Boyle's law. Brawn (1969) carried out extensive experiments and calculations on the buoyancy of both Atlantic and Pacific herring. Her conclusion was that herring, with its high lipid content and reduced skeleton, was well adapted for its extensive vertical excursions because of rather than in spite of its physostomous swimbladder. Thorne and Thomas (1990) used
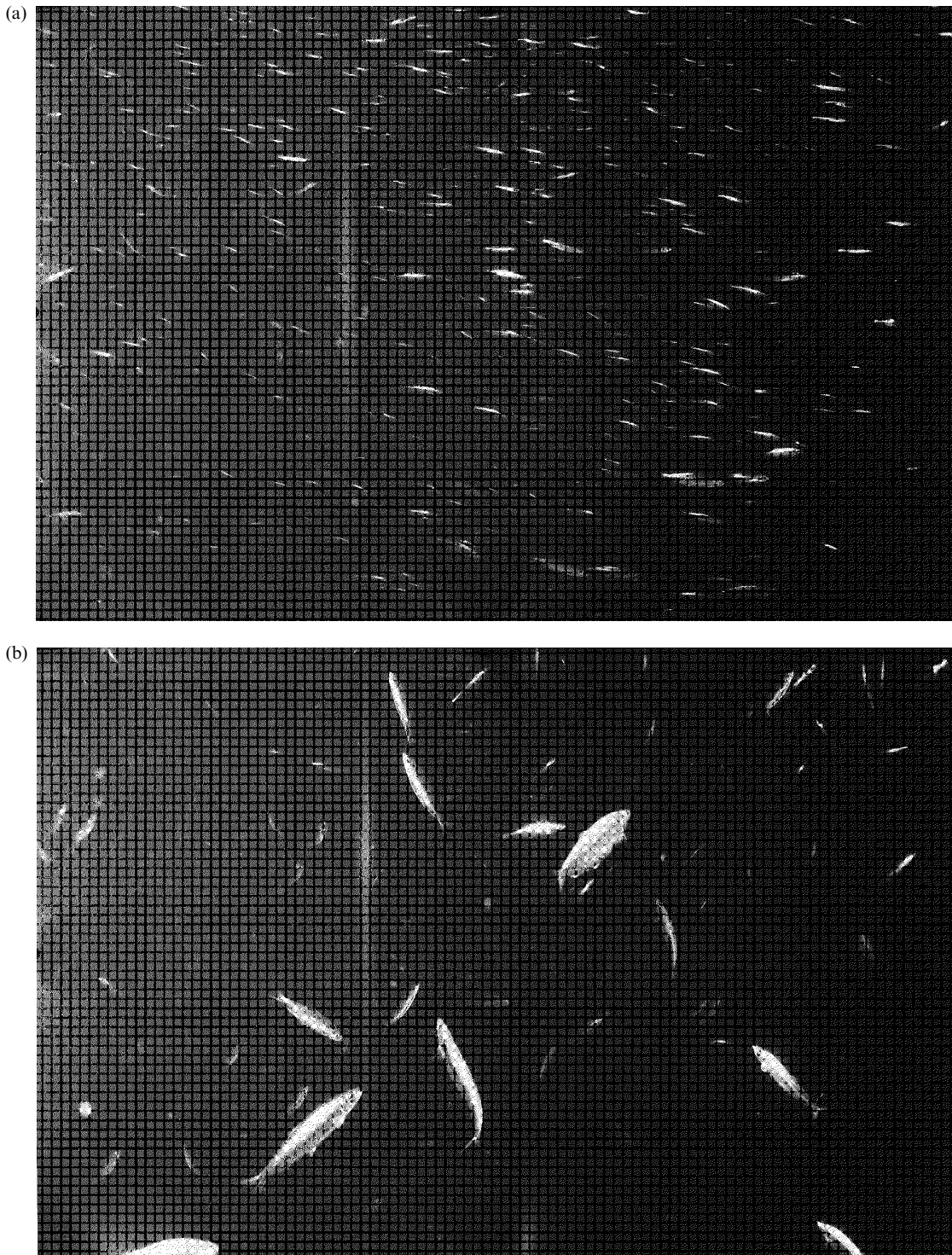
(a)

(b)

Figure 4. Photographs of herring in day-time/shallow water (a) and night time/deep water (b) situations.

data from Brawn (1962) to conclude that the herring they observed in Puget Sound would have been adapted to neutral buoyancy at a depth of about 60 m.

Radakov and Solovjev (1959) visited the traditional wintering areas for Norwegian spring spawning herring east of Iceland in a submarine. They observed herring
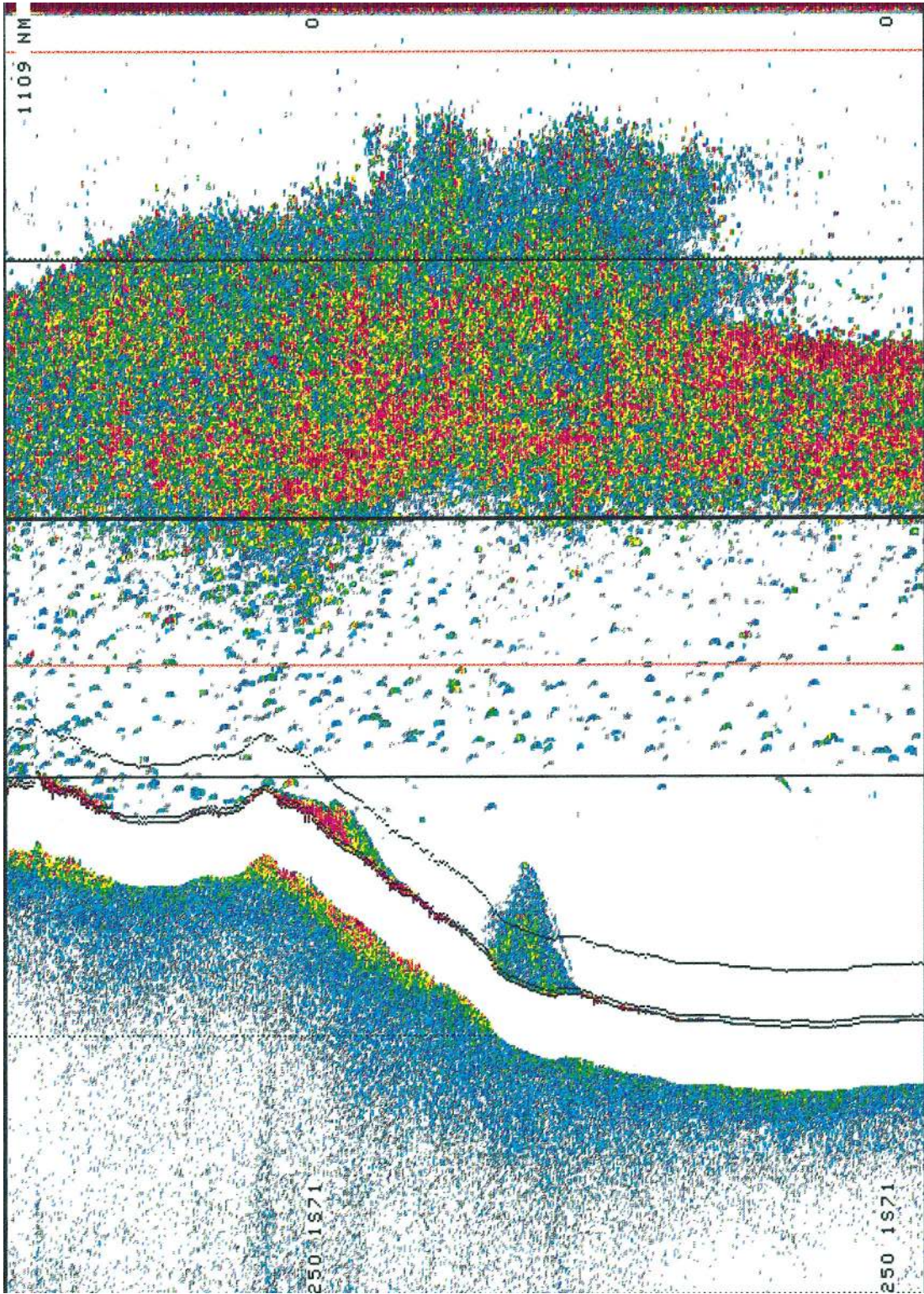
Figure 5. Typical herring layer at night, as seen from the hull-mounted transducer. Depth range shown is 0–250 m, with 50 m between individual horizontal lines.
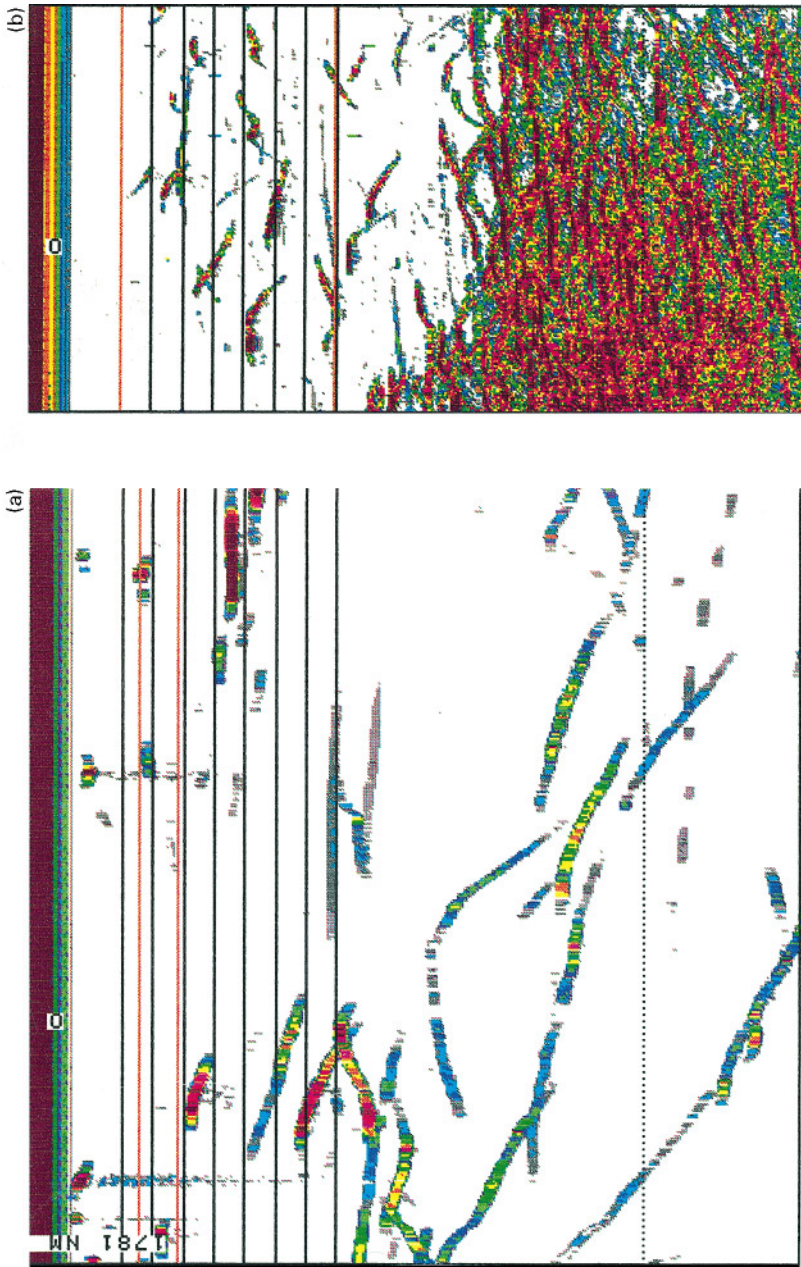
Figure 6. (a) Resolved individual targets within layer as observed from the rig transducer at 90 m depth. Displayed range 0–50 m. (b) Resolved tracks of individual fish in the upper part of the layer. Displayed range 0–50 m.

Table 1. Measured average swimming speed of herring at selected stations.

Date	Time (GMT)	Transducer depth (m)	Number of tracks	Swimming speed (m s^{-1})	Position
5 December 1993	0100–0300	60	356	0.31 ± 0.012	68°12.57′N 16°27.04′E
8 December 1993	2330–0032	62	237	0.33 ± 0.008	68°06.19′N 16°24.92′E
9 December 1993	0150–0244	107	427	0.27 ± 0.005	68°06.28′N 16°24.91′E
9 December 1993	0544–0630	140	85	0.41 ± 0.019	68°06.24′N 16°24.94′E
11 December 1993	0740–0834	70	90	0.36 ± 0.013	68°06.16′N 16°24.95′E
12 December 1993	1637–1840	120	78	0.37 ± 0.019	68°12.93′N 16°25.91′E

visually with artificial light and with an echo-sounder. They found herring at 80–100 m depth to be quite immobile in the evening with increasing swimming activity towards dawn. Tilt angles were mostly horizontal in the evening but with a dominant downwards tilt towards dawn. The depths of these observations were not properly recorded, but they seem to have been between 80 and 100 m. A total of 84% horizontal non-swimming herring were reported in the evening of 11 January, probably at 100 m. If this observation is correct, it could mean that the herring were neutrally buoyant at this depth. Of course, among other factors, the use of artificial illumination leaves some questions about the observations. Ona (1990) found that herring with a fat content of 16.8% all sank when being anaesthetized *in situ* at a depth of 30 m. Brawn (1969) calculated a sinking factor for herring as the ratio of herring body density, including the swimbladder, to sea-water density multiplied by 1000. For depth-adapted herring, she found sinking factors between 1001 and 1008 for ten herring with varying lipid content. In other words, all the herring she studied were negatively buoyant.

On the basis of these contradictory observations it is difficult to conclude at which depths, if indeed any at all, herring are able to attain neutral buoyancy.

Using a photographic technique similar to the one used in this study, Aoki and Inagaki (1988) found that Japanese anchovies had an average positive tilt angle of 10° at 20–30 m at night. Ona (1984b) investigated tilt angles of herring in pens and found a positive tilt angle at 30 m, which he assumed to be compensatory regulation of negative buoyancy resulting from swimbladder compression. He and Wardle (1986) found that negatively buoyant mackerel, swimbladder absent, at swimming speeds lower than 0.8 body lengths s^{-1}, tilted their bodies with the head up. The maximum recorded tilt was +27° in a 32 cm-long fish swimming at 0.45 body lengths s^{-1}. He and Wardle also found that tilt angle was positively correlated with fish body density and that tilting occurred only at swimming speeds lower than the preferred speeds of around one body length per second. A calculation of sinking factors for the data of He and Wardle (1986) gives 1007 for the fattest mackerel and 1013 for the leanest. Brawn (1969) also calculated sinking factors for overwintering Norwegian spring-spawning herring based on data given by Devold (1963). She found that at 500 m a herring with 15% lipid content would have a sinking factor of 1027. Reducing the depth to 250 m only marginally decreased the sinking factor, since the swimbladder volume at 250 m depth would already be reduced to 1/26 of the surface value as compared to 1/51 at 500 m, meaning that an adapted swimbladder volume of 6 ml at the surface for a 300 g herring (Ona, 1984a) would have been reduced to 0.2 ml at 250 m and to 0.1 ml at 500 m. The mean fat content of the herring observed in our investigation was 16% in December and 15% in January (Røttingen et al., 1994). The herring in the deeper waters of the wintering area would therefore have sinking factors well in excess of those of the mackerel described by He and Wardle (1986), and might therefore be expected to swim horizontally at speeds of at least one body length s^{-1}, to swim with a positive tilt angle at lower speed, or intermittently swim upwards and sink/glide in order to maintain vertical position. This is indeed what was observed. Day-time horizontal orientation is probably induced by the elevated swimming speeds associated with schooling, which suggests that sufficient light for schooling can penetrate down to 200–250 m even in the winter time at these high latitudes. This is also indicated by the high fish densities observed in the day-time compared to lower densities observed during the dark hours in this investigation.
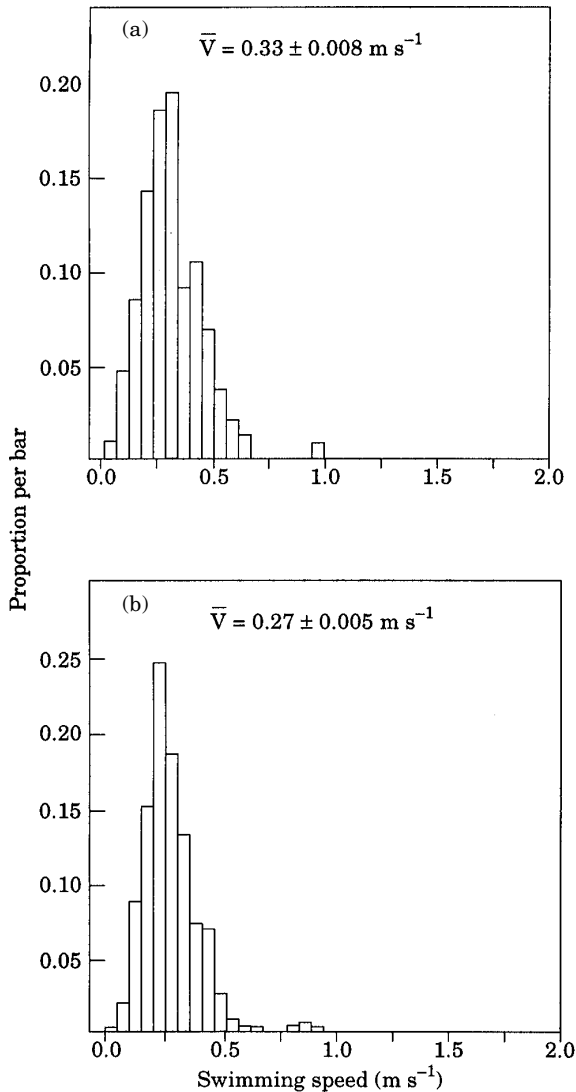
Figure 7. (a) Recorded swimming speeds of 237 individual herring at depth of 62 m, 2330–0032 h, and (b) recorded swimming speeds of 427 herring at 107 m, 0150–0224 h.
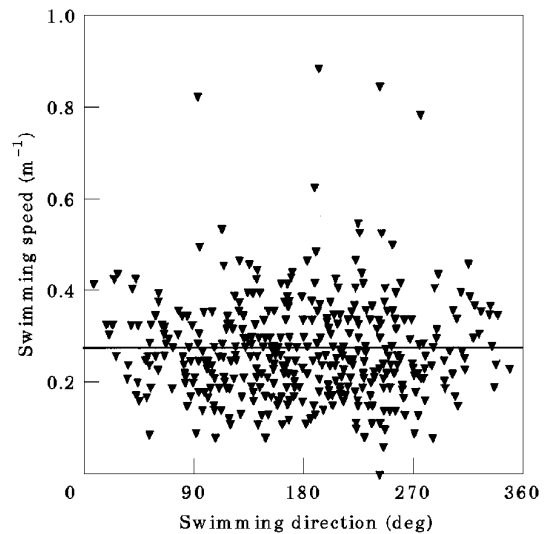

Figure 8. Recorded swimming speed as a function of swimming direction for 427 herring at depth of 107 m. Average swimming direction is measured relative to split-beam transducer orientation.

large proportion of the tracks may be recorded as almost stationary (Ona, 1994).

From the above discussion, the results of this investigation, and those of Huse *et al.* (1994), who presented more extensive data on angular distribution as a function of depth and time, we suggest that overwintering Norwegian spring spawning herring have adapted the following swimming strategies:

- In shallow waters (0 to at least 62 m) herring swim approximately horizontally day and night.
- At intermediate depths (around 100–200 m), where sufficient light for schooling seems to be available in the middle of the day, herring swim horizontally during the period with sufficient light and at lower light levels swim with an upward tilt, or alternate between swimming upwards and gliding.
- In deep water (300–400 m) where even day-time illumination seems to be insufficient for schooling, herring always either swim with an upward tilt or alternate between swimming upwards and gliding.

Many authors have dealt with the topic of variation in target strength as a function of tilt angle (e.g. Olsen, 1971; Nakken and Olsen, 1977; Foote, 1980; Edwards *et al.*, 1984; Foote and Ona, 1987; Blaxter and Batty, 1990). Foote and Nakken (1978) present target strength diagrams for various herring tilt angles. These data suggest that a large difference in average target strength should be expected between the shallow- and deep-water orientations observed in this investigation. The decrease in swim bladder volume with increasing depth should further accentuate this difference. The possibility also

As herring become less buoyant with depth, a slight increase in swimming speed would be expected over the depth range observed. The recordings made at night during this investigation do not support this. On the contrary, the observed trace velocities were significantly slower at 107 m than at 62 m. Rather than increasing swimming speed, the herring evidently adapt a tilted swimming strategy, no doubt because this is favourable in terms of energy. Contrary to the observations made by Radakov and Solovjev (1959), no herring were recorded at very low swimming speeds or immobile. Swimming speeds of neutrally buoyant fish with closed swimbladders, as measured by tracking, show a larger spread of speeds than herring in this situation, and a
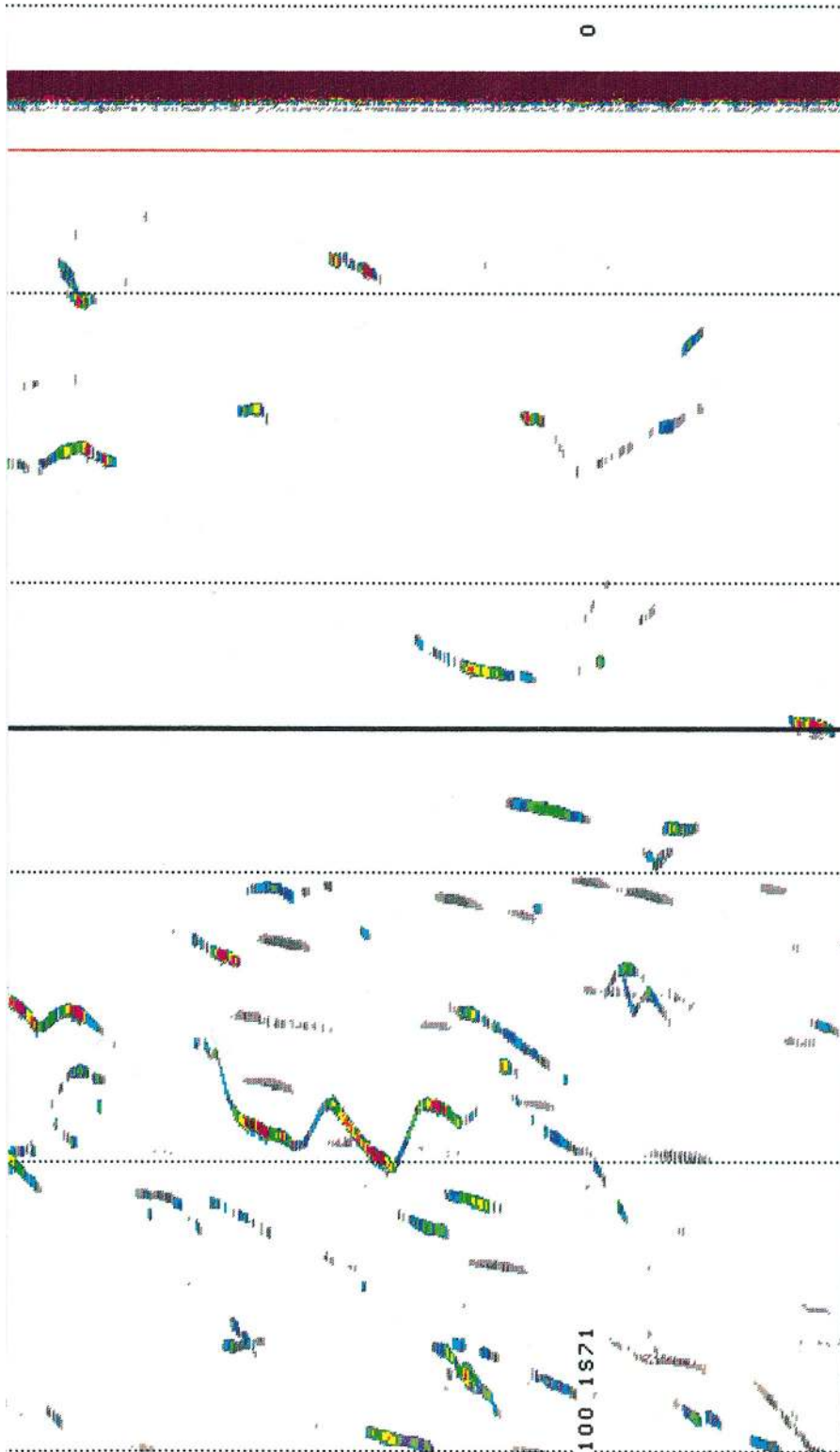
Figure 9. Swim-glide tracks of individual herring. Displayed range 0–100 m.

exists, however, that a surveying ship may influence the distribution of tilt angle by initiating an avoidance reaction.

References

Aoki, I. and Inagaki, T. 1988. Photographic observations on the behaviour of Japanese anchovy *Engraulis japonica* at night in the sea. Marine Ecological Progress Series, 43: 213–221.

Blaxter, J. H. S. and Batty, R. S. 1984. The herring swimbladder: loss and gain of gas. Journal of the Marine Biological Association of the U.K., 64: 441–459.

Blaxter, J. H. S. and Batty, R. S. 1990. Swimbladder "behaviour" and target strength. Rapports et Procès-verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 189: 233–244.

Blaxter, J. H. S. and Hunter, J. R. 1982. The biology of clupeids. Advances in Marine Biology, 20: 1–223.

Brawn, V. M. 1962. Physical properties and hydrostatic function of the swimbladder of herring (*Clupea harengus* L.). Journal of the Fisheries Research Board of Canada, 19: 635–656.

Brawn, V. M. 1969. Buoyancy of Atlantic and Pacific herring. Journal of the Fisheries Research Board of Canada, 26: 2077–2091.

Devold, F. 1963. The life history of the Atlanto-Scandian herring. Journal of the Fisheries Research Board of Canada, 154: 98–108.

Edwards, J. I., Armstrong, F., Magurran, A. E., and Pitcher, T. J. 1984. Herring, mackerel and sprat target strength experiments with behavioural observations. ICES C.M. 1984/B:34, 23 pp. [Mimeo].

Fahlen, G. 1967. Morphological aspects on the hydrostatic function of the gas bladder of *Clupea harengus* L. Acta Univ. Lund II 1967. 49 pp.

Foote, K. G. 1980. Effect of fish behaviour on echo energy: the need for measurements of orientation distributions. Journal du Conseil International pour l'Exploration de la Mer, 39: 193–201.

Foote, K. G. and Nakken, O. 1978. Dorsal aspect target strength functions of six fishes at two ultrasonic frequencies. Fisken Hav. Series B, 3: 1–96.

Foote, K. G. and Ona, E. 1987. Tilt angles of schooling penned saithe. Journal du Conseil International pour l'Exploration de la Mer, 43: 118–121.

He, P. and Wardle, C. S. 1986. Tilting behaviour of the Atlantic mackerel, *Scomber scombrus*, at low swimming speeds. Journal of Fish Biology, 29(Suppl. A): 223–232.

Horn, M. H. 1975. Swimbladder state and structure in relation to behaviour and mode of life in stomateoid fishes. Fisheries Bulletin, 73: 95–109.

Huse, I., Foote, K., Ona, E., and Røttingen, I. 1994. Angular distribution of overwintering spring spawning Norwegian herring. ICES C.M. 1994/B:19, Ref. H, 14 pp. [Mimeo].

Nakken, O. and Olsen, K. 1977. Target strength measurements of fish. Rapports et Procès-verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 170: 52–69.

Olsen, K. 1971. Orientation measurements of cod in Lofoten obtained from underwater photographs and their relation to target strength. ICES C.M. 1971/B:17, 8 pp. [Mimeo].

Olsen, K. 1976. Some experiments on the effect on target strength of fish undertaking vertical migrations. ICES C.M. 1976/B:42, 14 pp. [Mimeo].

Ona, E. 1984a. *In situ* observations of swimbladder compression in herring. ICES C.M. 1984/B:18, 24 pp. [Mimeo].

Ona, E. 1984b. Tilt angle measurements on herring. ICES C.M. 1984/B:19, 13 pp. [Mimeo].

Ona, E. 1990. Physiological factors causing natural variations in acoustic target strength of fish. Journal of the Marine Biological Association of the U.K., 70: 107–127.

Ona, E. 1994. Detailed in situ target strength measurements of 0-group cod. ICES C.M. 1994/B:30, 9 pp. [Mimeo].

Ona, E. and Hansen, D. 1991. Software for target tracking of single fish with split beam echo-sounders. User manual. Institute of Marine Research, Bergen, Norway, Oct. 1991.

Radakov, P. V. and Solovjev, B. S. 1959. The first experiences with the use of a submarine for observation of the behaviour of herring. Rybnoe chozjajstvo, 7: 16–21 (in Russian).

Røttingen, I., Foote, K. G., Huse, I., and Ona, E. 1994. Acoustic abundance estimation of wintering Norwegian spring spawning herring, with emphasis on methodological aspects. ICES C.M. 1994/B+D+G+H:1. [Mimeo].

Sundnes, G. and Bratland, P. 1972. Notes on the gas content and neutral buoyancy in physostome fish. FiskDir. Skr. Ser. HavUnders, 16: 89–97.

Thorne, R. E. and Thomas, G. L. 1990. Acoustic observations of gas bubble release by Pacific herring (*Clupea harengus pallasi*). Canadian Journal of Fisheries and Aquatic Sciences, 47: 1920–1928.