

ANGULAR DISTRIBUTION OF OVERWINTERING NORWEGIAN SPRING SPAWNING HERRING

By

Ingvar Huse, Kenneth Foote, Egil Ona, and Ingolf Røttingen
Institute of Marine Research
P.O.Box 1870, N-5024 Bergen, Norway

ABSTRACT

When plankton production drops off in the fall, adult Norwegian spring spawning herring migrate to two fjords in northern Norway with stable water masses with low temperature and predation. In the wintering areas, the herring occupy deeper water. Thus, without the ability to refill the swim bladder, they are constantly underflotated. This leads to different adaptive behaviour day and night, which is reflected in swimming angle. As the swimming angle is very important for the directivity of acoustic backscattering, this behaviour could have substantial impact on acoustic measurement of fish density. Results from extensive photographic observations are discussed in this respect.

INTRODUCTION

Over the last few years, the entire adult stock of spring spawning Norwegian herring has been overwintering in two fjords in northern Norway, Ofotfjord and Tysfjord. The herring start to enter the fjords in October, when their principal feed, *Calanus finmarchicus*, disappears from the surface layers after the summer bloom. They stay in the fjords until the end of January when they start their spawning migration. During these more than three months, the herring barely feed. Consequently this period can 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 light hours, the herring also stay in deep waters during the day, both to avoid the surface-oriented killer whales, and to stay in waters with lowest possible illumination to avoid predatory fish. At night, at least parts of the population migrate to the upper water layers. Accordingly, the herring schools are observed at depths from 100 to 400 m during daytime, and from 50 to 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 in the vertical distribution stratum is quite homogenous, nothing is gained energy wise through vertical migration. Energy expenditure is therefore directly related to swimming activity. Herring swim to maintain position both vertically and in the school when schooling. Being physostomous with no gas glands or other means of refilling the swimbladder except by surfacing, herring will expend increasing amounts of energy with increasing depth greater than where neutral buoyancy can be maintained. This depth will vary with the body density of the individual fish and the density of surrounding water masses. However, at a depth of e.g. 100 m the swimbladder volume will be only 1/11 and at 200 m only 1/21 of the surface volume, thus only contributing marginally to the density of the fish. Herring at these and greater depths are therefore probably underflotated and have to adapt special swimming strategies in order to maintain vertical position with a minimum of energy expenditure. The problem also probably increases through the wintering season as lipids are consumed (Røttingen et al. 1994), with increasing total body density as a result.

Echo integration is the principal method of estimating the abundance of Norwegian spring spawning herring. Since the estimation is carried out during overwintering, it is of course important to gain knowledge of the behaviour of herring in order to evaluate possible behavioural effects on single fish acoustic target strength (TS). TS is very much a function of fish tilt angle (Nakken & Olsen, 1977). The present investigation was therefore carried out in order to find possible variations in distribution, vis-a-vis TS, and tilt angle adaptations to the rather special overwintering situation.

MATERIALS AND METHODS

The investigation was carried out during two surveys in December 1993 (R/V "Michael Sars") and January 1994 (R/V "Johan Hjort"). A T-frame with a horizontally mounted Photosea-1000 camera with an automatic release unit, an Osprey strobe and a Mesotech 330 SONAR was lowered by the SONAR cable into the herring shoals (Figure 1b). The SONAR was mounted to

set up a vertical observation field parallel to the camera direction. Manual exposure was used in all December dives and in the last dive in January. For the other dives the automatic release was applied with an exposure interval of 24 seconds. With manual exposure the minimum interval was 20 seconds, but most manual release intervals were much longer. The SONAR was used to position the T-frame in the herring shoal and to observe the herring concentration in front of the camera for manual release.

The herring were observed to scatter when the strobe went off, but the registration was normally re-established in less than 10 seconds. The ships were drifting with only navigation lights on during the photographic sessions. In December, the SONAR registrations showed that there were less herring in front of than behind the camera. In January, a current sail was mounted to the vertical rod of the T-frame in order to have the camera face the drift direction. Now there were less herring behind than in front of the camera, showing that the hole in the registration was produced by the rig drifting through the herring shoal, and not by the strobe light.

The camera was loaded with 250 frames of film for most dives, giving a total time in the herring shoal of 100 minutes with automatic exposure. The film (Kodak Tmax, 400ASA) was developed directly after the dive. Prints of frames with herring were made either on the ship (December) or after the survey (January).

Herring tilt angle measurements were made using a specially developed AUTO CAD routine and a digitising tablet. Only fish in the central 1/3 of the picture were measured. Also, only fish which were visually evaluated to be in a plane perpendicular to the optic axis were selected to be measured. The vertical axis of the picture was decided from a heavily weighted nylon gut line hanging in front of the camera, showing in all pictures. 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 minute averages of readings sampled every 5 seconds. Computations were made with SAS software, and graphs with UNIGRAPH.

RESULTS

Figure 1a shows the wintering area and the photographic dive stations. All December dives were in Tysfjord, while all January dives were in Ofotfjord. Figures 2-8 show a graphic representation of the tilt angles of the herring during the two surveys. Each figure represents one dive, and the dives are presented sequentially, starting with the first dive in December as Figure 2, and presenting the last dive in January as Figure 8. The three first dives are from December, while the four last dives are from January. Measured tilt angles are combined into 10° groups. The A-figures are a full representation of all angles, with $0/180^\circ$ as the horizontal plane, 90° being upwards and 270° being downwards. The B-figures give a direct representation of the tilt angles. The A-figures are given to present symmetry. Four of the distributions (Figures 2, 4, 5, 6) appear to be fairly symmetrical around the vertical axis, indicating that the azimuth distribution of the fish can be considered to have been random. The three others are somewhat skewed, meaning that the azimuth distribution of the fish probably was slightly influenced either by the ship, the rig, or by environmental conditions (current, predators, illumination).

If the threshold for daylight is set at 0.1 ME (5.5 Lux) the earliest morning of the December survey was at 0800 hrs, and the latest evening was at 1330 hrs. For the January survey the corresponding times were 0815 hrs and 1430 hrs. Dusk and dawn, defined as readings between 0 and 0.1 ME, normally lasted for one hour. 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.

Figure 2 shows a dive to 150 m between 1700 and 2100 hrs. There are three tilt angle peaks: +40°, +10° and -20°. The number of observations, N, was, however, rather small. Figure 3 shows a shallow distribution, only 62 m, at 2200-0100 hrs. Here the majority of the fish were swimming horizontally, but not schooling. N is fairly large (296). This is the only night-time distribution where the fish were swimming horizontally. Figure 4 is comparable to Figure 2. The time of day and depth is about the same, but the negative tilt component is not as pronounced as in Figure 2. Figures 5, 6 and 7 all show fish distributed between 300 and 370 m at night. The herring in Figures 5 and 7 show strong positive tilt, while Figure 6, like Figure 2, has a stronger negative component. Common for these two dives were that they were made in the early evening and that N was quite low. Figure 8 shows a daytime observation (1230 to 1430 hrs) taken at 200-260 m depth in Ofoten in January. The tilt angles in this dive averaged around -10°. The herring in the pictures from this dive were schooling. None of the pictures from the other dives showed any sign of schooling. Figures 9 and 10 show examples of herring photographs at day and night respectively. Figure 11 shows a typical daytime echogram, while Figure 12 shows an example of a night-time echogram.

The latest observations (Figures 8 and 9) were recorded 15 January in the mouth of Ofoten. At this time there was a considerable emigration out of the fjord by mature herring which had commenced their spawning migration (Røttingen et al., 1994), and the observations were made in the middle of the migrating concentration of fish. Still, the tilt distributions seemed to be basically the same as for the other observations.

DISCUSSION

Buoyancy regulation in most teleosts is accomplished by swimbladder volume regulation (Horn, 1975). The swimbladder in herring is thoroughly described (Brawn, 1962; Fahlen, 1967). Although there have been data presented indicating that herring are able to refill their swimbladder without access to the surface (Sundnes & Bratland, 1972), most authors seem to agree that herring do not possess this ability (Brawn, 1962; Fahlen, 1967; Blaxter & Hunter, 1982; Blaxter & Batty, 1984; Ona, 1984a). Consequently, the herring swimbladder will compress and expand with ambient pressure according to Boyle's law. The depth range over which herring can regulate buoyancy will therefore be a function of body tissue density, surrounding sea water density and the amount of air being swallowed at the surface. Brawn (1969) did 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 documented extensive vertical excursions, more because of than despite its physostomous swimbladder. Thorne & Thomas (1990) used 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, which conforms well with the results in the present investigation (December dive 8, Figure 3).

Radakov & Solovjev (1959) visited the traditional wintering areas for Norwegian spring spawning herring east of Iceland in a submarine. They observed herring 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 dominating downwards tilt towards dawn. Depths of these observations are not properly stated, but seem to have been between 80 and 100 m. 84% horizontal non-swimming herring were reported in the evening of 11 January, probably at 100 m. If this observation can be assumed to be correct, it could mean that the herring were buoyancy-adapted at this depth. The use of artificial illumination leaves of course a questionmark with that report.

Aoki & Inagaki (1988) found that Japanese anchovy had an average positive tilt angle of 10° at 20-30 m at night using a photographic technique similar to the one used in this investigation. Ona (1984b) investigated tilt angles of herring in pens and found a positive tilt angle at 30 m depth which he assumed to be a compensatory regulation of negative buoyancy from swimbladder compression. He & Wardle (1986) found that negatively buoyant mackerel at swimming speeds lower than 0.8 body lengths per second 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 per second. He & 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.

Brawn (1969) calculated sinking factors for herring which was 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. Calculating sinking factors for the data of He & 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 depth a herring with 15% lipid content would have a sinking factor of 1027. Reducing the depth to e.g. 250 m would only marginally decrease the sinking factor since the swimbladder volume at 250 m depth already would be reduced to 1/26 of the surface value as compared to 1/51 at 500 m, meaning that a neutral buoyancy-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 observed herring in the present investigation was 16% in December and 15% in January (Røttingen et al., 1994). Accordingly, the sinking factor of the herring in the deeper waters of the wintering area would have sinking factors well in excess of the mackerel described by He & Wardle (1986), and should therefore be expected to swim horizontally at speeds of at least one body length per second, swim with a positive tilt angle at lower speed, or intermittently swim upwards and sink/glide in order to maintain vertical position.

Based on the above and the results in this investigation it is proposed that overwintering Norwegian spring spawning herring have adapted the following swimming strategy:

- Inside the range of potential neutral buoyancy (0 to at least 62 m and not more than 120 m) the herring will swim or rest/glide approximately horizontally day and night.
- Outside the range of potential neutral buoyancy the herring will swim horizontally at speeds greater than one body length per second during the day, and slower with an upward tilt at night.

- Outside the range of potential neutral buoyancy the herring will, in the evening and with a decreasing frequency through the night, intermittently swim upwards and subsequently sink/slide with a negative tilt angle.

Many authors have covered the subject of variation in target strength (TS) as a function of tilt angle (e.g. Olsen, 1971; Nakken & Olsen, 1977; Foote, 1980; Edwards et al., 1984; Foote & Ona, 1987; Blaxter & Batty, 1990). There are, however, few data readily available on TS of herring as a function of tilt angle. Nakken & Olsen (1977) presented TS diagrams for cod and saithe as a function of tilt angle. If the TS-tilt angle relationship for herring is similar, a reduction in the order of magnitude of 10 dB in mean TS could be expected if the deep water day time orientation is compared to the night-time orientation observed in this investigation. A similar reduction is also reported by Olsen (1976) for sprat. It remains, however, to be clarified whether the tilt angle distribution in the survey situation is in fact the same as observed in this investigation. The possibility exists that the surveying ship polarises the fish in terms of tilt angle distribution. If such an avoidance reaction exists, its extension and magnitude will also probably be a function of depth and vessel specific characteristics. It is therefore quite clear that the results of this investigation call for a closer look at the behaviour in the acoustic survey situation of deep dwelling herring in particular and deep dwelling physostomous fish in general.

REFERENCES

- Aoki, I. and Inagaki, T. 1988. Photographic observations on the behaviour of Japanese anchovy *Engraulis japonica* at night in the sea. *Mar. Ecol. Progr. Ser.*, 43: 213-221.
- Blaxter, J.H.S. and Batty, R.S. 1984. The herring swimbladder: loss and gain of gas. *J. Mar. Biol. Ass. U.K.* 64: 441-459.
- Blaxter, J.H.S. and Batty, R.S. 1990. Swimbladder "behaviour" and target strength. *Rapp. P.-v. Réun. Cons. int. Explor. Mer.*, 189: 233-244.
- Blaxter, J.H.S. and Hunter, J.R. 1982. The biology of clupeids. *Adv. Mar. Biol.*, 20: 1-223.
- Brawn, V.M. 1962. Physical properties and hydrostatic function of the swimbladder of herring (*Clupea harengus* L.) *J. Fish. Res. Bd Canada*, 19(4): 635-656.
- Brawn, V.M. 1969. Buoyancy of Atlantic and Pacific herring. *J. Fish. Res. Bd Canada*, 26: 2077-2091.
- Devold, F. 1963. The life history of the Atlanto-Scandian herring. *Rapp. Proc. Verb. Réun. Couns. Perm. Explor. Mer.*, 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 CM 1984/B:34*. 23 pp.
- Fahlen, G. 1967. Morphological aspects on the hydrostatic function of the gas bladder of *Clupea harengus* L. *Acta Univ. Lund II*, 1967(1). 49 pp.
- Foote, K.G. 1980. Effect of fish behaviour on echo energy: the need for measurements of orientation distributions. *J. Cons. int. Explor. Mer.*, 39(2): 193-201.
- Foote, K.G. and Ona, E. 1987. Tilt angles of schooling penned saithe. *J. Cons. int. Explor. Mer.*, 43: 118-121.
- He, P. and Wardle, C.S. 1986. Tilting behaviour of the Atlantic mackerel, *Scomber scombrus*, at low swimming speeds. *J. Fish. Biol.*, 29(Suppl. A): 223-232.

- Horn, M.H. 1975. Swimbladder state and structure in relation to behaviour and mode of life in stomateoid fishes. *Fish. Bull.*, 73(1): 95-109.
- Nakken, O. and Olsen, K. 1977. Target strength measurements of fish. *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, 170: 52-69.
- Olsen, K. 1971. Orientation measurements of cod in Lofoten obtained from underwater photographs and their relation to target strength. *ICES CM 1971/B:17*. 8pp. [Mimeo].
- Olsen, K. 1976. Some experiments on the effect on target strength of fish undertaking vertical migrations. *ICES CM 1976/B:42*. 14 pp.
- Ona, E. 1984a. *In situ* observations of swimbladder compression in herring. *ICES CM 1984/B:18*. 24 pp.
- Ona, E. 1984b. Tilt angle measurements on herring. *ICES CM 1984/B:19*. 13 pp.
- 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 CM 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 pallasii*). *Can. J. Fish. Aquat. Sci.*, 47: 1920-1928.

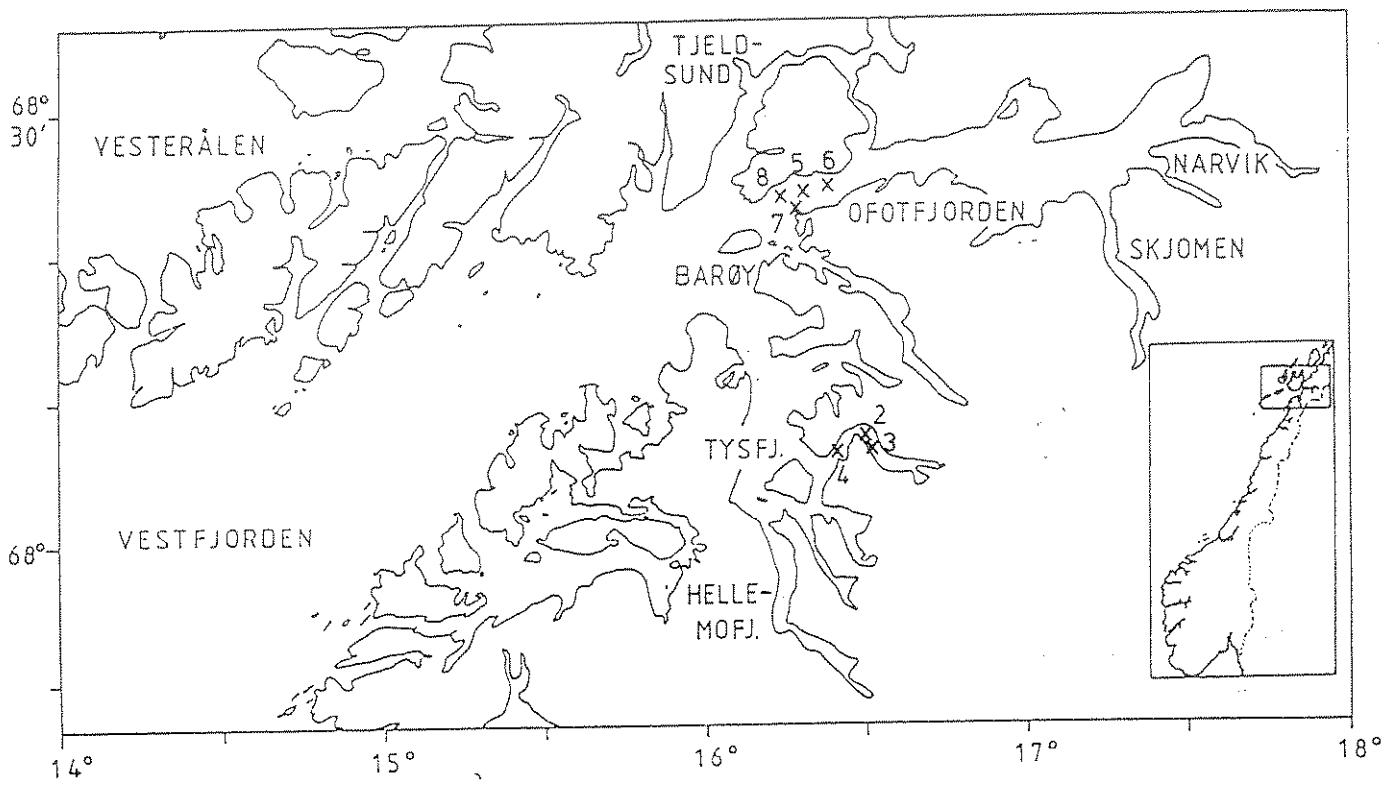


Figure 1a. Map of wintering area with stations (dives).

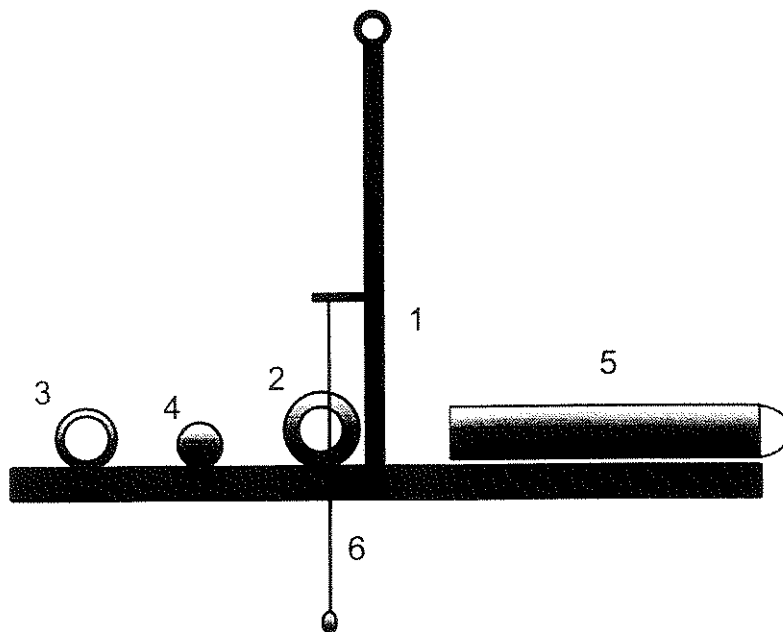


Figure 1b. Observation rig. 1) T-frame; 2) Camera; 3) Strobe; 4) Timer; 5) Sonar; 6) vertical line.

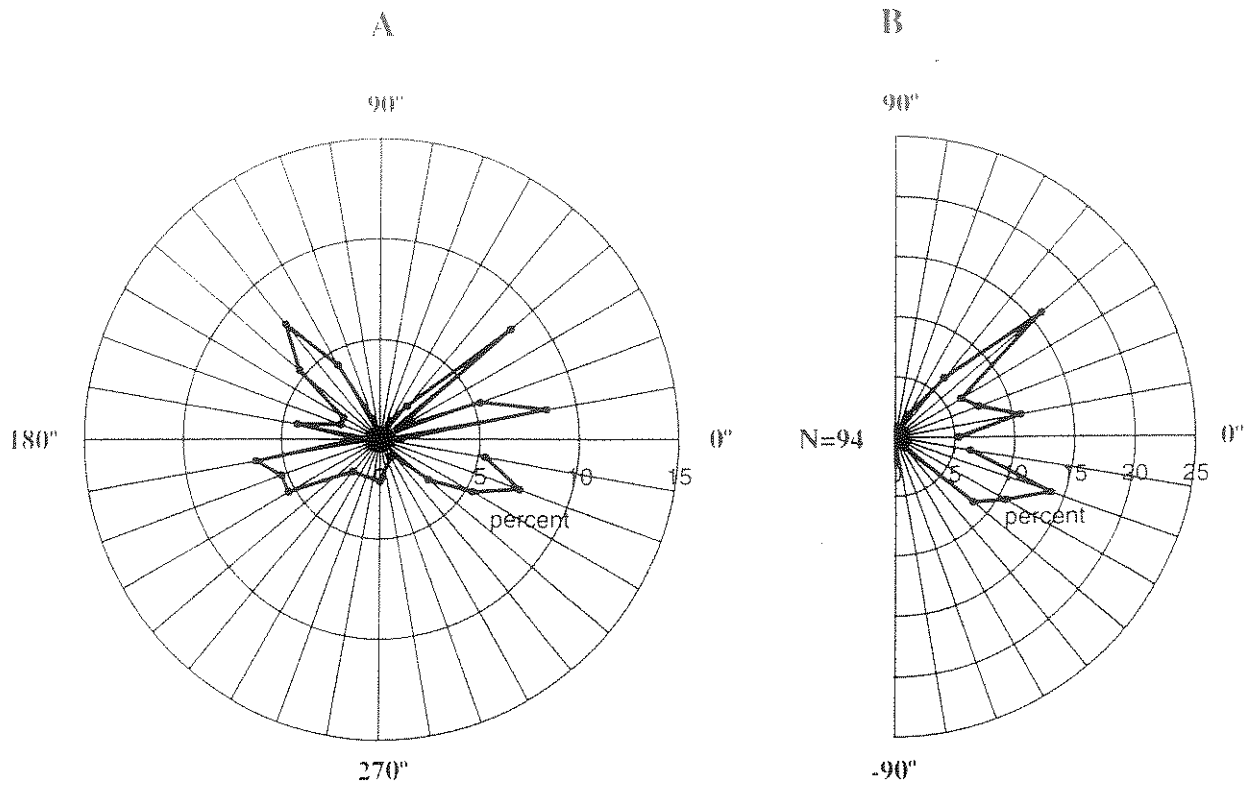


Figure 2. Dive 6 December. 1700-2100 hrs, 150 m depth. Polar diagrams of angular distribution. A) All angles included. $0^{\circ}/180^{\circ}$ is horizontal, 90° is up, 270° is down. B) All angles grouped into two quadrants. 90° is up, -90° is down, 0° is horizontal.

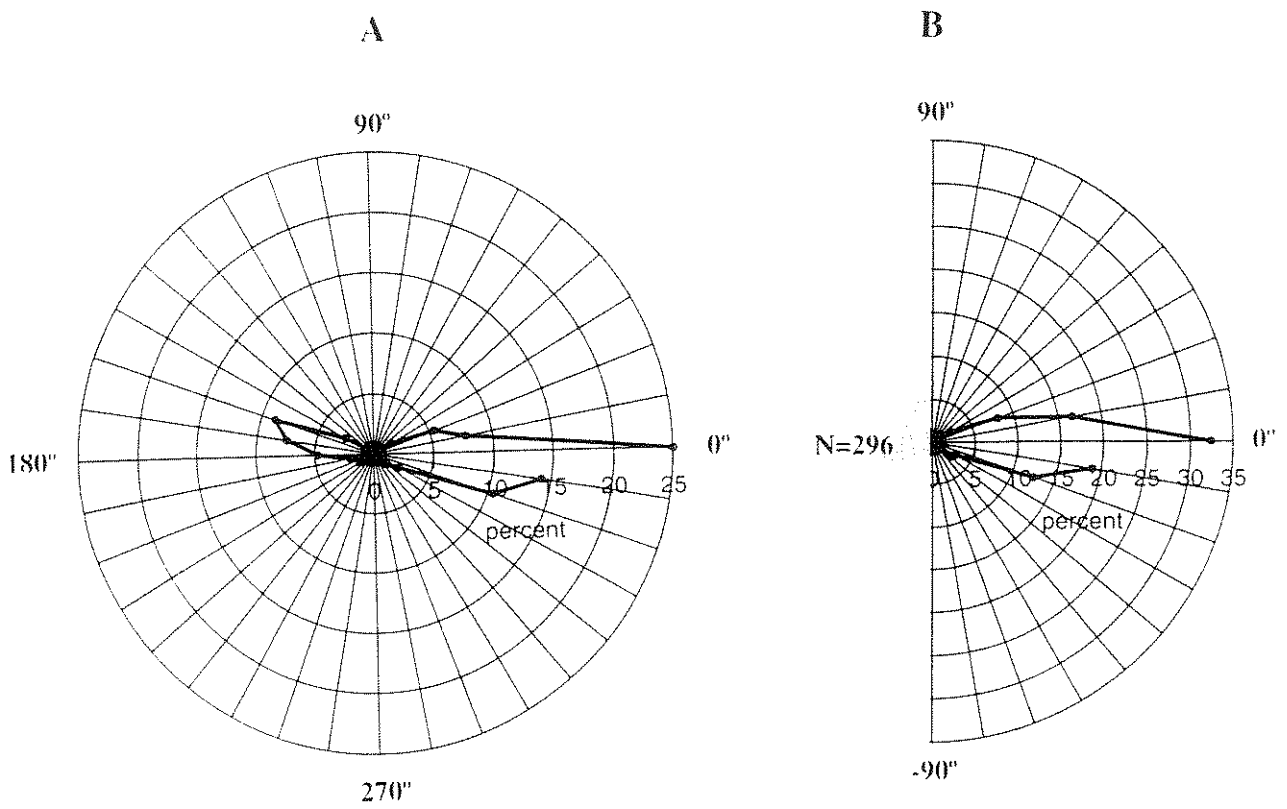


Figure 3. Dive 8 December. 2200-0100 hrs, 62 m depth. For further explanation, see Fig. 2.

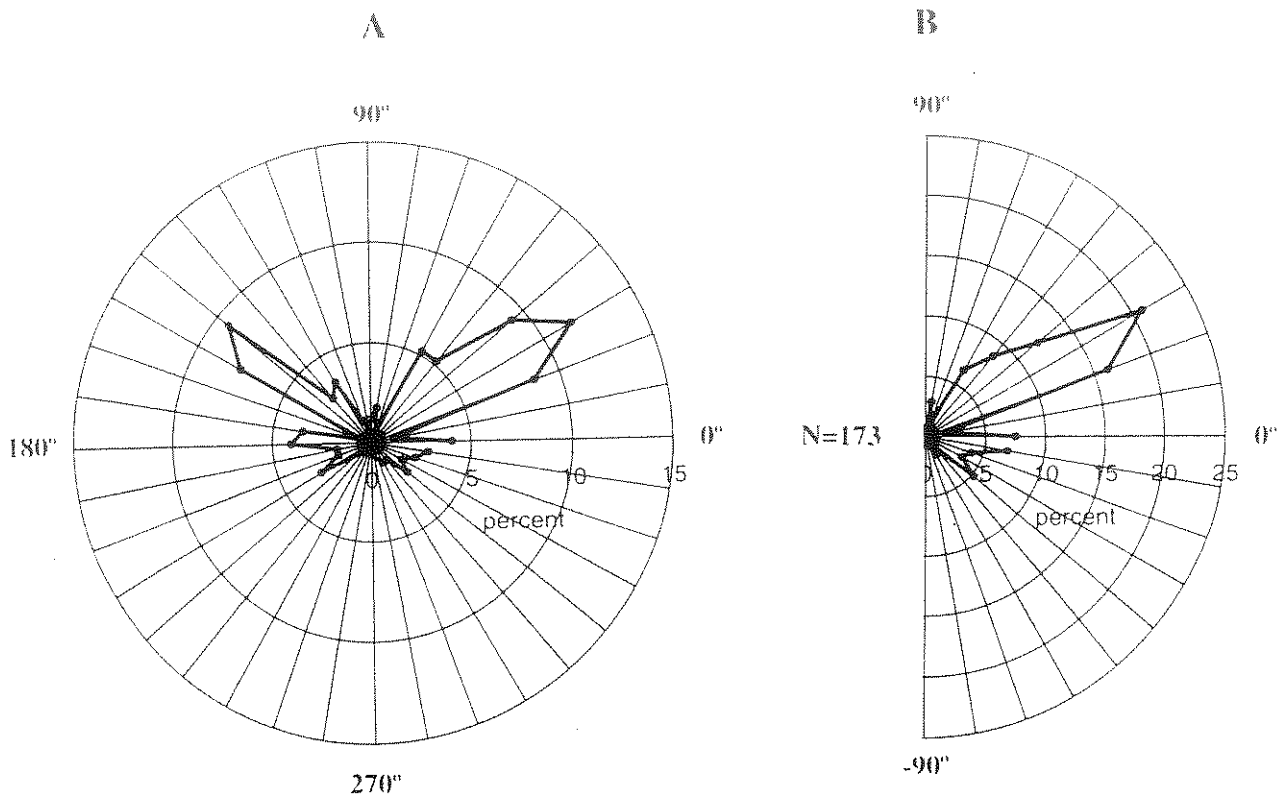


Figure 4. Dive 12 December. 1800-2000 hrs, 120 m dpeth. For further explanation, see Fig. 2.

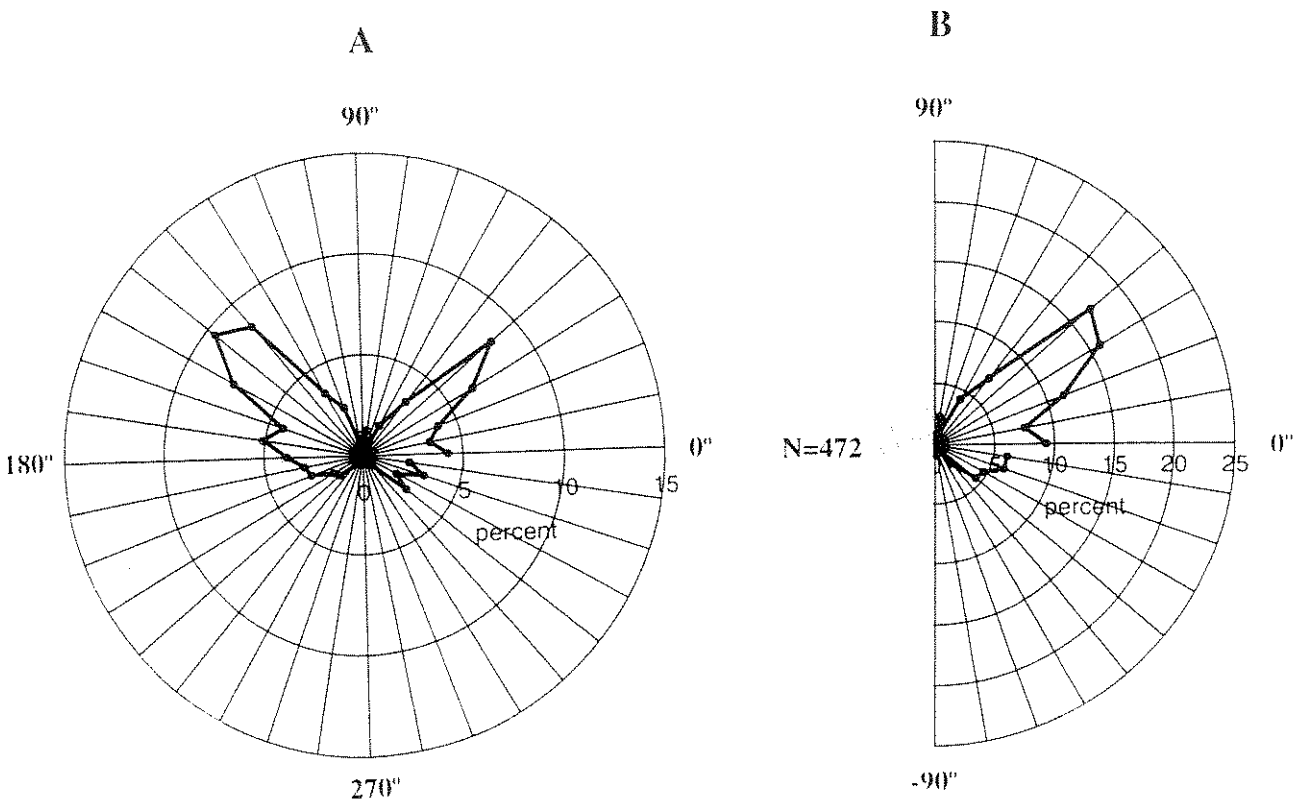


Figure 5. Dive 5 January. 0130-0230 hrs, 337-370 m depth. For further explanation, see Fig. 2.

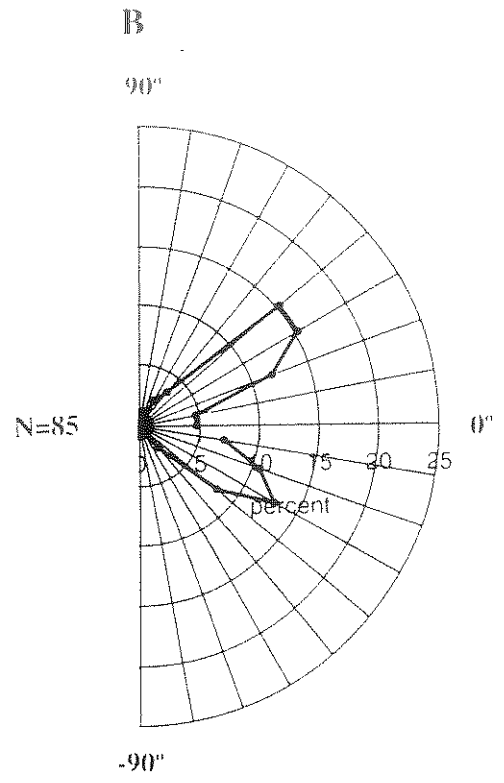
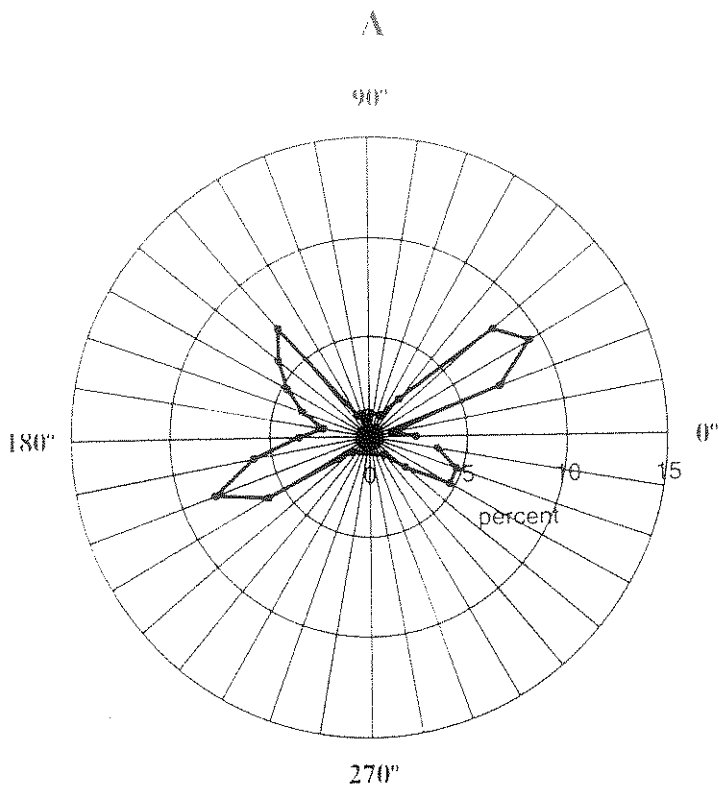


Figure 6. Dive 6 January. 1600-1715 hrs, 330-360 m depth. For further explanation, see Fig. 2.

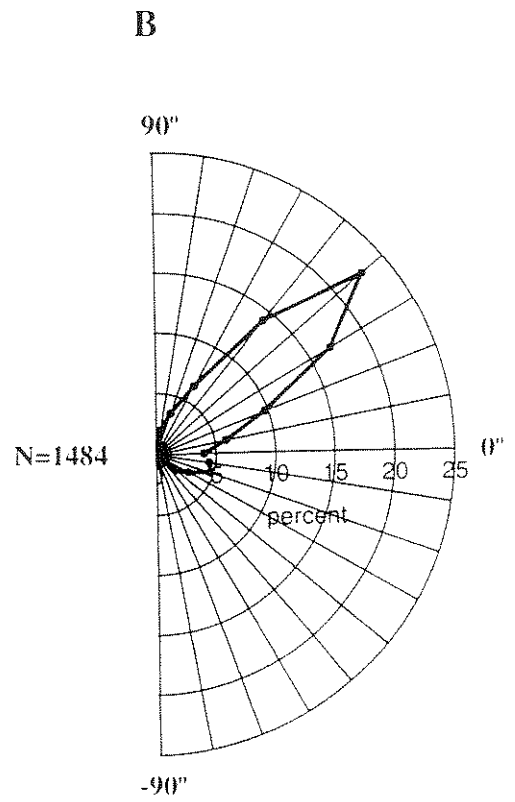
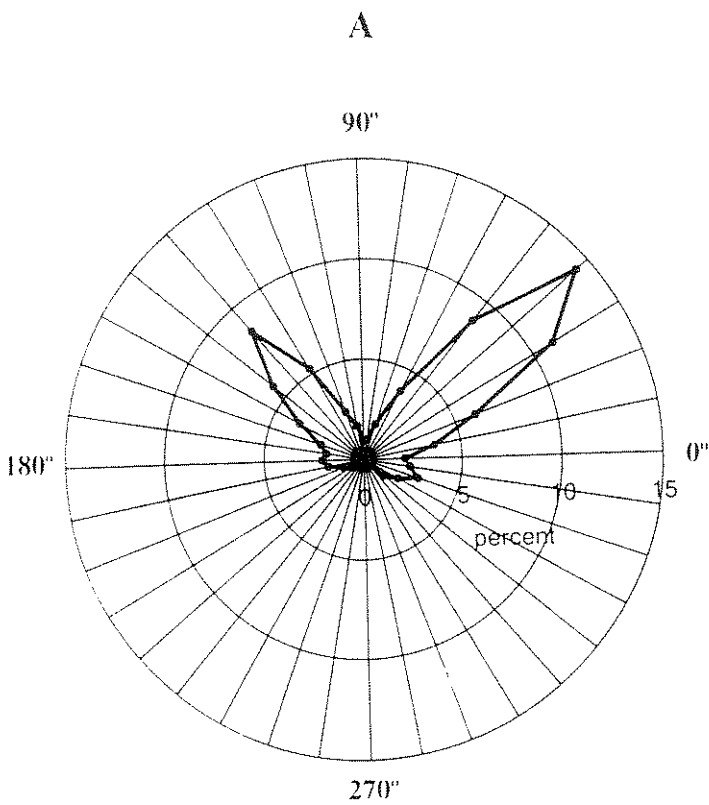


Figure 7. Dive 7 January. 0530-0740 hrs, 300-350 m depth. For further explanation, see Fig. 2.

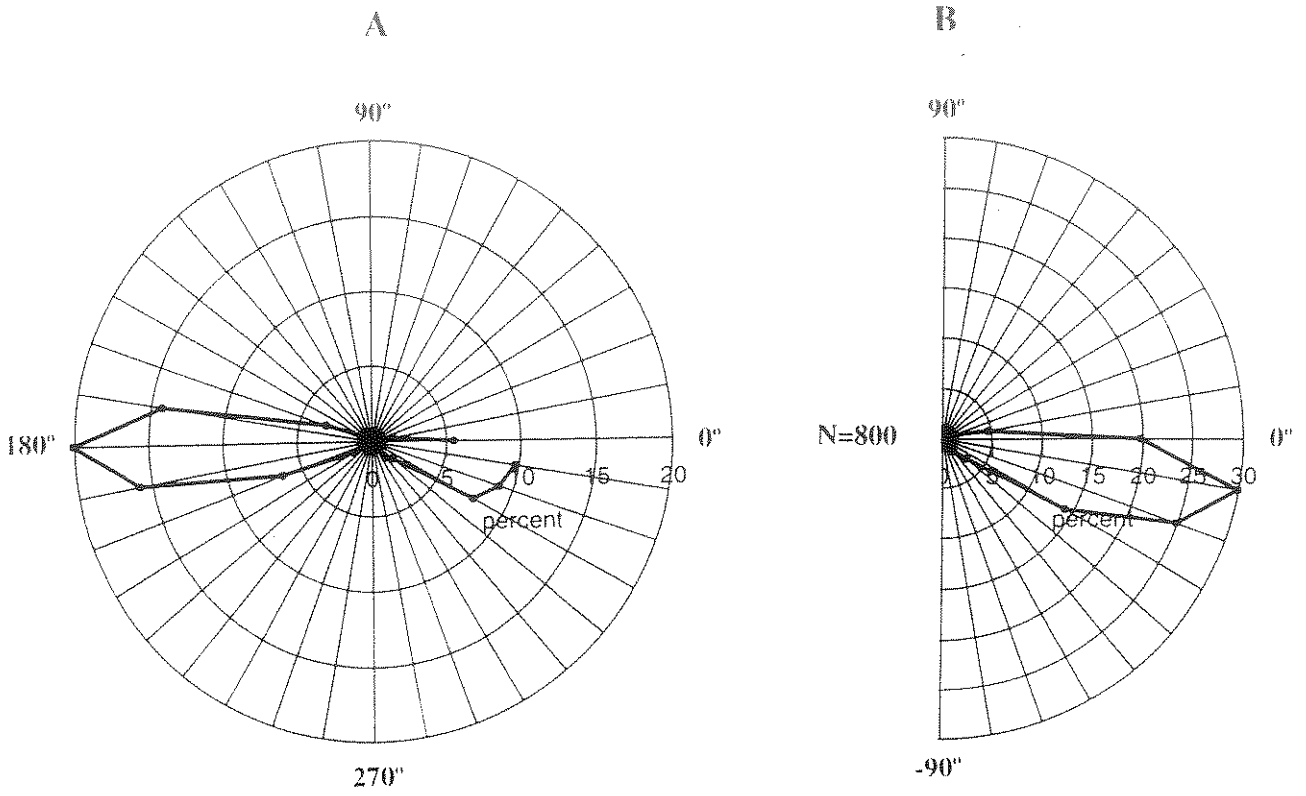


Figure 8. Dive 8 January. 1230-1430 hrs, 200-260 m depth. For further explanation, see Fig. 2.

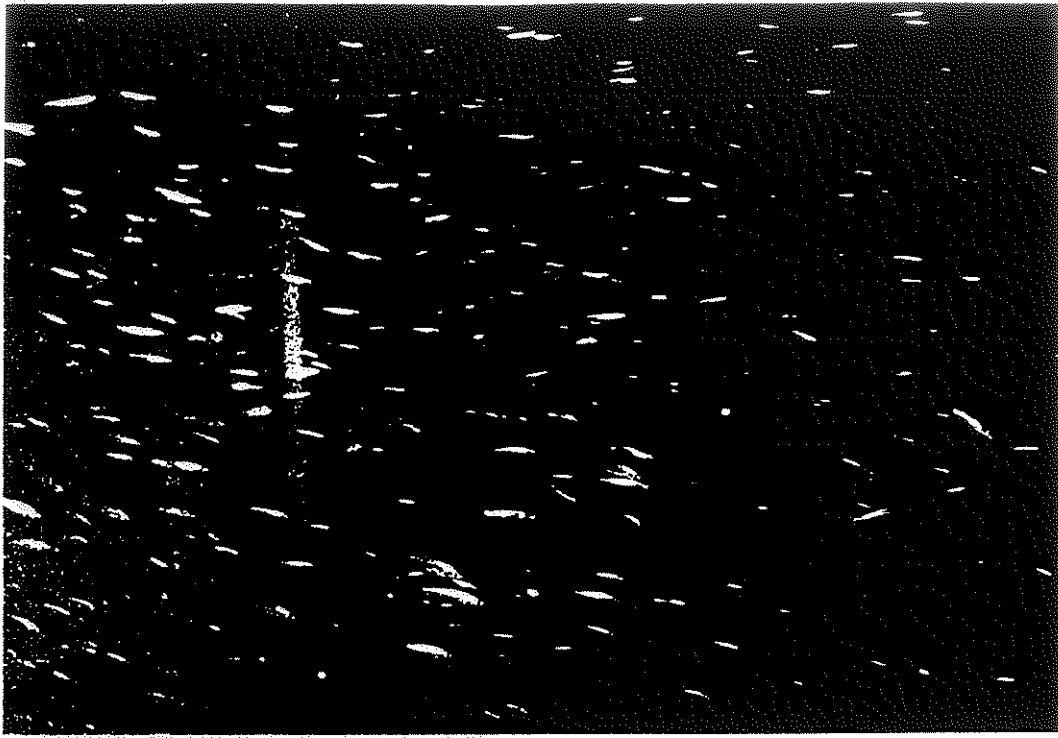


Figure 9. Daytime orientation. Dive 8, January.



Figure 10. Night-time deep water orientation. Dive 7, January.

