Extensive gas bubble release in Norwegian spring-spawning herring (Clupea harengus) during predator avoidance

L. Nottestad


Events of extensive gas bubble release in over-wintering Norwegian spring-spawning herring (Clupea harengus) were repeatedly observed acoustically and visually in Vestfjorden, northern Norway, during attacks from killer whales (Orcinus orca) and saithe (Pollachius virens). Gas bubbles were visually observed to come from the swimbladder of individual herring swimming very close to the surface and gas bubble production was so extensive that large areas of the sea surface were sometimes covered with white foam after each event. Acoustically, gas bubbles could be identified on the echosounder as strong echoes covering the upper 0-30 m of the water column. It is suggested that herring schools were forced from large depths up to the surface by predatory killer whales and saithe, after which they expelled gas as a consequence of the rapid change in depth. Gas release may confuse and deflect both visually and acoustically oriented predators due to increased scattering of light, reduced range of vision, and confounding effects of the reflection energy of bubbles and fish. Such events may have considerable effect on target strength and estimated stock sizes during acoustic surveys.

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Key words: gas bubbles, herring, killer whales, target strength, saithe.

Received 24 November 1997; accepted 4 June 1998.

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Introduction

Pacific herring (Clupea pallasi) have been observed to release gas bubbles during diel vertical migration (Thorne and Thomas, 1990). Also, gas bubble release has been reported in herring (Clupea harengus) in the Baltic in response to midwater trawling (Suuronen et al., 1997). Although fishermen along the coast of Norway have seen this feature in Norwegian spring-spawning herring (Clupea harengus) and even use the word "mesking" for this type of behaviour, documentation has so far been limited.

Clupeoids are physostomous fish with an open swimbladder, i.e. have a pneumatic duct leading from the posterior end of the stomach to the swimbladder in addition to an anal duct from the swimbladder to the vent (Blaxter et al., 1979). Possessing an open swimbladder is presumably linked to the advantages of making rapid vertical movements in response to predators (Blaxter, 1985), while, according to Blaxter and Hunter (1982), the hydrostatic function in Cupeoids is limited to the near-surface. Herring may swallow air at the surface and pass it into the swimbladder via the pneumatic duct (Brawn, 1962; Blaxter and Batty, 1984).

The volume of gas present is likely to vary in response to changes in ambient pressure (depth) according to Boyle's law (Ona, 1984, 1990). Laboratory studies by Blaxter and Batty (1984) indicate that herring may not be able to secrete gas into the swimbladder like physoclist fish and always be negatively buoyant (Brawn 1962; Blaxter and Batty, 1984; Ona, 1984, 1990).

Overwintering Norwegian spring-spawning herring in northern Norway make diel vertical migration between 400 m depth during daytime up to 50 m depth at night (Huse and Ona, 1996). During this period, they hardly feed (Slotte, 1996) and stay usually in deep water (in schools or dense layers) during daytime, presumably to avoid visually oriented predators (Huse and Ona, 1996). Although herring appear to prefer staying at large depths during daytime, predators are capable of herding schools into dense balls (Simila and Ugarte, 1993; Simila et al., 1996) and forcing them into shallower areas.
sometimes all the way to the surface (Simild and Ugarte, 1993). During such events, release of bubbles has been noticed by fishermen. According to Huse and Ona (1996) and Simild (1997), the main predators in inshore waters are killer whales (Orcinus orca), saithe (Pollachius virens), and cod (Gadus morhua).

The aim of this study was to collect direct observations of gas bubble production in herring and to evaluate the physiological and behavioural significance and implications. Alternative hypotheses to existing theory are presented.

Material and methods

Herring schools in Vestfjorden, Ofotfjorden, and Tysfjorden were observed acoustically by the 16 m long (20 BRT) RV "Fjordfangst" during daylight (0700-1800 h) in the period 7-20 November. Due to its small size, the vessel is appropriate for the study of herring school dynamics within the Vestfjorden system. The research vessel was equipped with a FURUNO CH-12 multi-beam sonar (150 kHz) and a PC based SIMRAD EY-500 echosounder (38 kHz) connected to an echo integrator. The echosounder has similar functions to the SIMRAD EK-500 with the Bergen Echo Integrator system (Knutsen, 1990). Instruments were calibrated according to the standard target method (Foote et al., 1987). Echosounder signals were printed and ping-to-ping data were regularly stored on optical disk. Herring schools were first recorded on the sonar, and lengthwise and crosswise extent of the school projection were measured by a ruler directly on the monitor screen. School area, vertical extent, volume, transect length, fish density, and biomass were calculated using equations from Johannesson and Losse (1977) and Misund (1990, 1991, 1993). Calculations were corrected for beam width and pulse length (Misund, 1993). Horizontal dimensions were corrected by taking into account the school depth and the nominal beam angle of the transducer (McLennan and Simmonds, 1992).

The sonar may operate as an omni-sonar sending and receiving acoustic signals over 360°, although ping interval is then quite low. A 90° sector width was applied to the school during observations. The vessel passed over the school with an average speed of 5 knots and the echosounder with echo integrator recorded vertical extension and depth. To record the behaviour and dynamics of a school, an attempt was made to position the vessel directly above, using presence and location of gas bubbles, predators (sea birds, killer whales), and of stunned and dead herring as guidance. During daytime, visual observations were made by several persons and the behaviour of individual herring at the surface was noted. The engine was always put in neutral position during predator-prey interactions once the ship was positioned above the school. The estimated horizontal movement of schools during observations was less than 50 m according to the Global Positioning System. Vessel avoidance, i.e. sudden changes in swimming speed or direction indicating disturbance by the ship (cf. Olsen, 1979), was not observed.

Target strength values were used to distinguish between a school and bottom signals and between herring, saithe, and killer whales. The echo intensity of the extensive gas bubble release was not quantified. Gas bubbles in the surface area may have been partly mixed with herring and therefore difficult to quantify.

Target strength of herring (TS) was calculated from fish length (L) as 
\[ TS = 20 \log L - 71.9 \] (after Foote, 1987), based on subsamples of 400 fish taken from the school. Length and weight were measured and stomach samples from both herring and saithe were analysed.

Detailed information was collected during some events taking place close to surface by day, when it was possible to visually track the wake of frightened herring being herded in schools of considerable size.

Results

Three case studies of rapid vertical migration followed by gas bubble release are reported here. School A (Fig. la) is inseparable from the bottom at 50 m depth and extends up to 27 m depth. Air bubbles are seen as quite strong acoustic signals from the upper left corner at the surface, down to a more scattered and distributed layer at 25 m depth. This situation was recorded when the school had just dived from the surface layers. It was not possible to determine the shoal size and density of saithe because they were too mixed with the herring.

School B (Fig. lb) had dived to deeper waters from approximately 20 m down to 50 m after being attacked simultaneously by six killer whales and by a shoal of saithe. The echogram shows a very dense school extending from very close to the bottom at 65-80 m depth up to 30 m depth. The bottom is irregular but can easily be distinguished from the school on the echogram. Gas bubbles are shown from the surface down to 30 m depth with medium density.

School C was observed at the surface down to approximately 80 m during a predator-prey interaction with a shoal of saithe and eight killer whales (Fig. lc). The bottom at 110 m depth was relatively flat. The echogram shows elongated, strong echoes of variable density, which appear to represent large predators encircling the school. Killer whales are large (3-6 m)
animals and have lungs, which reflect strong echoes. Qualitative evidence obtained from the simultaneous appearance of echo traces and parallel visual observation suggest that the echoes of killer whales are, after some experience, quite easy to distinguish from other echoes and that they have been responsible for the elongated tracks in this particular echogram. Gas bubbles are seen from 0 to 10 m surrounding the school, but were also mixed with herring echoes at the surface in the centre, where they cannot be distinguished. The echogram was taken simultaneously with a photograph of the foam at the surface (Fig. 2). Some minutes later, the school dived to deep water. The killer whales apparently stopped feeding and moved off at high speed.

A common feature of the three cases is that: (1) all schools had been under predator attack either from pods of killer whales and/or shoals of saithe; and (2) gas bubbles were seen in surface waters from the ship, in variable intensity. Hundreds of herring have been seen releasing gas bubbles close to the surface, only a few metres away from the vessel. In one instance, highly visible foam (Fig. 2) covered some 50 m² of water surface around the ship. In contrast, there was no evidence of herring gulping air from the surface. Stunned and dead herring were seen floating at the surface, and some herring had bite marks that appeared to be consistent with the distance between teeth in adult killer whales. The predator-prey interactions attracted hundreds of gulls (Larus spp.) and some white-tailed eagles (Haliaeetus albicilla). Stomach samples of saithe (n=68) showed that 85% had recently been eating one or more herring confirming that predator-prey interactions were actually taking place. Average length of herring was 31.2 cm. Herring caught at the surface during the events (n=24) and subsamples of commercial catches (n=400) had empty stomachs, indicating that their behaviour was not affected by feeding. Table 1 provides relevant data on school dimensions, biomass, and gas bubble release. Although average herring densities were not particularly high, densities up to 20-30 fish m⁻³ were measured in some parts of the schools.

Discussion
Visual observations confirmed that gas bubbles may be released by herring on particular occasions and the available evidence suggests that this behaviour is strongly related to predator-prey interactions. However, the first question to be addressed must be whether the herring is solely responsible for the extensive foam seen on the surface. Saithe, as members of the gadoid family, are physoclist (Gunderson, 1993). Therefore, they are not able to release gas and cannot be held responsible for any gas bubbles observed. Another possibility would be that killer whales released air from their blowhole.
during the encounter with a herring school. However, the type of bubbles produced by killer whales - large bubbles with low frequency - are quite different from those coming from herring (Simila and Ugarte, 1993) and can easily be recognized. In contrast, bubbles produced by herring are small (< 1 cm) and may be released more or less continuously as long as individuals in the school have some gas left in their swimbladder. Thus, although no effort was undertaken to analyse the foam observed at the surface chemically, the only plausible explanation appears to be that it originated from gas released by herring, possibly with a minor contribution of air exhaled by killer whales.

Since herring are considered not to have the physiological mechanisms to secrete gas (Brawn, 1962; Blaxter and Batty, 1984; Ona, 1984, 1990), Thorne and Thomas (1990) put forward two alternative hypotheses to explain its source: (1) gas is formed during fermentation in the gut; and (2) herring may gulp air at the surface prior to descent. Neither of these hypotheses is supported by the present observations. Since herring do not feed during the over-wintering period (Dommasnes
Figure 1(c).

Figure 1. Echogram showing vertical position of herring schools under attack from predators in relation to the location of gas bubbles in the water column. Note that the surface is drawn as a thick line at the top. The line below indicates the start of the echo integration process. Integration values by layer are indicated at the right; water depth at the left. (a) School A: 15 November 1997 at 1129 UTC (68°23'27"N, 15°58'65"E), under attack of saithe. Gas bubble concentrations range from approximately 5 m down to 30 m depth. Duration echogram is 95 s; vessel stationary. (b) School B: 17 November 1996 at 1032 UTC (68°22'11"N, 15°51'01"E), under attack of saithe. Gas bubble concentrations close to the surface down to approximately 25 m depth. Duration echogram 120 s; vessel slightly moving (<50 m) in NE direction. (c) School C: 17 November 1997 at 1348 UTC (68°22'05"N, 15°48'40"E), under attack of killer whales. Gas bubble concentrations visible at the surface and down to approximately 10 m depth. Note that gas bubbles and herring are inseparable in some regions. Also, difficulties were encountered in detecting the bottom below part of the school, indicating that registrations in the region >80 m probably represent false echoes. Duration echogram 120 s; vessel stationary.
Figure 2. Photograph of foam at the surface caused by massive gas bubble release by herring school C (Fig. lc), covering an area of up to 50 m².

et al., 1994; Huse and Ona, 1996; Slotte, 1996), fermentation in the gut can be rejected as a possible explanation in this case, while, according to our visual observations, herring did not come right up to the surface to gulp air. Although herring have been observed swallowing air under experimental conditions (Blaxter and Batty, 1984), the Norwegian spring spawners would normally have little opportunity to do so during the over-

wintering period, because they stay in deep water (>50 m) most of the time (Huse and Ona, 1996). Also, such behaviour would cause serious risk because of predation by the numerous seabirds in the area. Therefore, an alternative hypothesis is required to explain the present observations. I suggest that herring may secrete gas from the blood system into the swimbladder. Although gas secretion for physostome swimbladder inflation or deflation is generally considered to be insignificant (Moyle and Cech, 1988), rapid upward swimming may result in an increase in partial pressure of gas in the blood which would then create a more favourable situation.

In practice, it is impossible to study the initial part of school formation without a good deal of luck, because it is unpredictable where predators will start to stir up the dense layer of herring present in deep water. It is only when a school has been formed that it may be picked up by sonar and tracked. Thus, we cannot be sure that the fish in a school had been staying in surface waters for an extended period of time or that they had just arrived after having been chased from the deeper layers.

Table 1. Estimated dimensions and other characteristics of the three herring schools reported. Note that vertical swimming distance has been derived from the position of the centre of mass.

<table>
<thead>
<tr>
<th>School number</th>
<th>A</th>
<th>B</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density (N m⁻³)</td>
<td>2.6</td>
<td>5.2</td>
<td>3.1</td>
</tr>
<tr>
<td>Biomass (tonnes)</td>
<td>4.3</td>
<td>23</td>
<td>18.6</td>
</tr>
<tr>
<td>Height of school (m)</td>
<td>23</td>
<td>58</td>
<td>44</td>
</tr>
<tr>
<td>Vertical swimming distance (m)</td>
<td>10-40</td>
<td>25-60</td>
<td>30-70</td>
</tr>
<tr>
<td>Gas bubble depth (m)</td>
<td>0-20</td>
<td>5-30</td>
<td>0-10</td>
</tr>
<tr>
<td>Bottom depth (m)</td>
<td>50</td>
<td>65-90</td>
<td>110</td>
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However, after being spotted, we were not able to track a school for much longer than half an hour (25, 32, and 39 min, for schools A, B, and C, respectively), before it dived to deeper water. This, together with the observation that (1) the formation of a surface school is a relatively rare event, (2) schools appear suddenly where they had not been before, and (3) that there were always predators around each school, suggests that it is not unlikely that the herring were driven by predators from deeper water to the surface and that the vertical migration is fast. Killer whales are known to herd herring from deep water to the surface as part of their hunting strategy (Simila and Ugarte, 1993; Simila, 1997).

The depth range over which gas bubbles were seen differed between cases (<30, <20, and <10 m, respectively), which may reflect the original depth from which the schools originated. More importantly, releases of gas preceded rapid downward movements and an end to the predator-prey interaction event in all cases. Rapid downward swimming appears to be a common and efficient anti-predator reaction in herring schools (Blaxter, 1985). In addition, active release of gas bubbles may effectively contribute to predator avoidance by scattering the light and thereby reduce the visual range of predators, especially near the surface during daytime. It has also been suggested that gas bubbles may confuse the biological sonar of killer whales (Barrett-Lennard et al., 1997) by dispersion and scattering of the sound. Although marine mammals are reported to use air bubbles to increase hunting efficiency on schooling fish (Sharpe and Dill, 1997), our results indicate that pelagic physostomous species release gas as part of a tactical anti-predator repertoire. The opposite effect of the proposed mechanisms may be related to size and concentration of the bubbles.

There were no opportunities to examine stomach samples from killer whales, and individuals actually catching fish were not seen. Direct evidence of feeding was only provided by damaged herring with appropriately spaced tooth marks. Also, herring is considered the main prey for the killer whale population in northern Norway all year around (Simila et al., 1996). Therefore, it seems unlikely that their presence was just a coincidence. The normal density in fish schools is approximately one fish per cube of body length for herring schools (Simila and Ugarte, 1993; Simila, 1997). The depth range over which gas bubbles were seen differed between cases (<30, <20, and <10 m, respectively), which may reflect the original depth from which the schools originated. More importantly, releases of gas preceded rapid downward movements and an end to the predator-prey interaction event in all cases. Rapid downward swimming appears to be a common and efficient anti-predator reaction in herring schools (Blaxter, 1985). In addition, active release of gas bubbles may effectively contribute to predator avoidance by scattering the light and thereby reduce the visual range of predators, especially near the surface during daytime. It has also been suggested that gas bubbles may confuse the biological sonar of killer whales (Barrett-Lennard et al., 1997) by dispersion and scattering of the sound. Although marine mammals are reported to use air bubbles to increase hunting efficiency on schooling fish (Sharpe and Dill, 1997), our results indicate that pelagic physostomous species release gas as part of a tactical anti-predator repertoire. The opposite effect of the proposed mechanisms may be related to size and concentration of the bubbles.

The dimensions of the herring schools attacked were relatively small (4.5-18 tonnes) schools compared to the huge areas up to several kilometres long in the deep layers inhabited during overwintering (Vabo and Nottestad, 1997), and in shallow water (50-110 m) compared to the normal bottom depths within most of the Vestfjorden system, which range largely between 300 down to 700 m depth (Rottingen et al., 1994). Thus, it would seem that only a relatively small component of the stock have been observed undergoing this anti-predator response.

If herring are able to build up gas in and expel gas from the swimbladder over short time intervals then abrupt changes in target strength might be expected. Due to the low specific acoustic impedance of gas compared to fish flesh and bones, the swimbladder is the primary organ responsible for the reflected energy from a fish (Foote, 1980, 1985; Furusawa, 1988). Therefore, any change in its size should affect target strength. Moreover, rapid vertical swimming has a significant effect on the tilt angle and reduces the dorsal aspect target strength of recorded fish (Huse and Ona, 1996). When acoustic population estimates of herring are made in these wintering areas, ecological interactions as shown may affect in situ acoustic measurements, and should be taken into account during the surveys.

Acknowledgements

The author would like to thank skipper Paul Jorgensen for excellent manoeuvring on board RV "Fjordfangst" and invaluable technical assistance from Bjorn Tolland and Roger Larsen. Geir Huse, Anders Fernø, Ole Arve Misund, Egil Ona, Mike Breen, and Tony Pitcher are thanked for valuable criticism and suggestions to the manuscript. Comments by two reviewers greatly improved the quality. The Research Council in Norway are thanked for financial support.

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