

Herring schooling manoeuvres in response to killer whale attacks

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Abstract: The antipredator behaviour of overwintering Norwegian spring-spawning herring (*Clupea harengus* L.) was investigated during repeated attacks by killer whales (*Orcinus orca* L.) in Tysfjord in northwestern Norway. The observations were made using a high-resolution (455 kHz) multibeam sonar. Ten different types of predator-prey interactions were recorded during 54 observed events (an average of one antipredator event every 3.9 min). Antipredator responses included "split," "hourglass," "vacuole," "bend," "dive," "herd," and "fountain." Large attacked schools demonstrated a different repertoire of antipredator manoeuvres than small ones and were less likely to be attacked. Despite being located in the vicinity of the whales, herring schools with a cross section exceeding 460 m² were not attacked by killer whales. Attacked schools were significantly more circular ($p < 0.0001$) and had higher relative densities ($p < 0.05$) than schools that were not attacked.

Résumé : Nous avons étudié le comportement anti-prédateurs de Harengs (*Clupea harengus* L.) de Norvège soumis aux attaques répétées d'Épaulards (*Orcinus orca* L.) durant la fraye de printemps à Tysfjord, dans le nord-ouest de la Norvège. Nous avons utilisé un sonar à rayons multiples de haute résolution (455 kHz). Dix types différents d'interactions prédateur-proie ont été enregistrés au cours de 54 observations (en moyenne une interaction aux 3,9 min). Parmi les comportements anti-prédateurs observés, il faut mentionner « la division », « le sablier », « la vacuole », « le repliement », « la plongée », « le rassemblement en troupeau » et « la fontaine ». Les grands bancs de harengs avaient un répertoire de manoeuvres anti-prédateurs différent de celui des bancs de petite taille lorsqu'ils étaient attaqués, et ils étaient moins susceptibles de se faire assaillir. Même dans le voisinage immédiat des épaulards, les bancs de plus de 460 m² de coupe transversale ne se faisaient pas attaquer. Les bancs attaqués étaient de forme significativement plus arrondie ($p < 0,0001$) et de densité relative plus élevée ($p < 0,05$) que les bancs non attaqués.

[Traduit par la Rédaction]

Introduction

One of the primary functions of schooling is protection against predators (Pitcher and Parrish 1993), involving rapid changes in school structure and density (Pitcher and Wyche 1983; Hall et al. 1986; Domenici and Batty 1994, 1997). Successful avoidance manoeuvres by schools depend on the ability of individuals to correctly assess the potential danger and respond in a timely, coordinated fashion (Parrish 1992). Experiments indicate that fish antipredator vigilance increases with school size (Magurran et al. 1985; Pitcher and Parrish 1993), although vigilance may be difficult to investigate in large aggregations (Bednekoff and Lima 1998).

Herring schools vary in size from a few hundred to several million individuals (Misund 1993) and can vary greatly in shape (Misund et al. 1995; Nøttestad et al. 1996). Within the same school, density may vary by an order of 100 among areas (Misund 1993; Misund and Floen 1993). Since 1987, Norwegian spring-spawning herring (*Clupea harengus* L.) have wintered in Tysfjord-Ofofjord in northern Norway (Røttingen et al. 1994). Herring enter the fjords in October,

when their principal prey, the copepod *Calanus finmarchicus*, descend to their deep water overwintering habitats (Huse and Ona 1996). The spawning migration starts at the end of January (Røttingen 1990). During the wintering period, from October to January, herring hardly eat (Slotte 1999), and predator avoidance and energy conservation are therefore crucial (Huse and Ona 1996). Herring generally stay deep during the day (150–350 m) in widely distributed layers, probably to avoid predators (Røttingen et al. 1994), but small schools have also been observed in shallow waters less than 100 m deep (Nøttestad 1998; Similä 1997b).

To some extent killer whales in Norwegian coastal waters follow the migration route of herring (Jonsgård and Lyshoel 1970), which are their main prey (Christensen 1978, 1988). An estimated 560 killer whales are found in the herring wintering areas from October to January (Similä et al. 1996). A certain degree of cooperation is involved when killer whales attack their prey (Baird and Dill 1995), especially when they are feeding on herring (Christensen 1978; Similä and Ugarte 1993). The cooperative strategy is believed to increase hunting success (Similä 1997a). Killer whales exhibit various degrees of cooperative foraging behaviour that may be related to the size and density of prey schools (Felleman et al. 1991).

In the study of interactions between killer whales and herring in nature, acoustic methods may offer a more synoptic view of predator-prey interactions than underwater cameras. Sonars and echo-sounders are widely used, both for assessing fish abundance and for monitoring behaviour during fish-capture situations (Mitson 1983; MacLennan and Simmonds

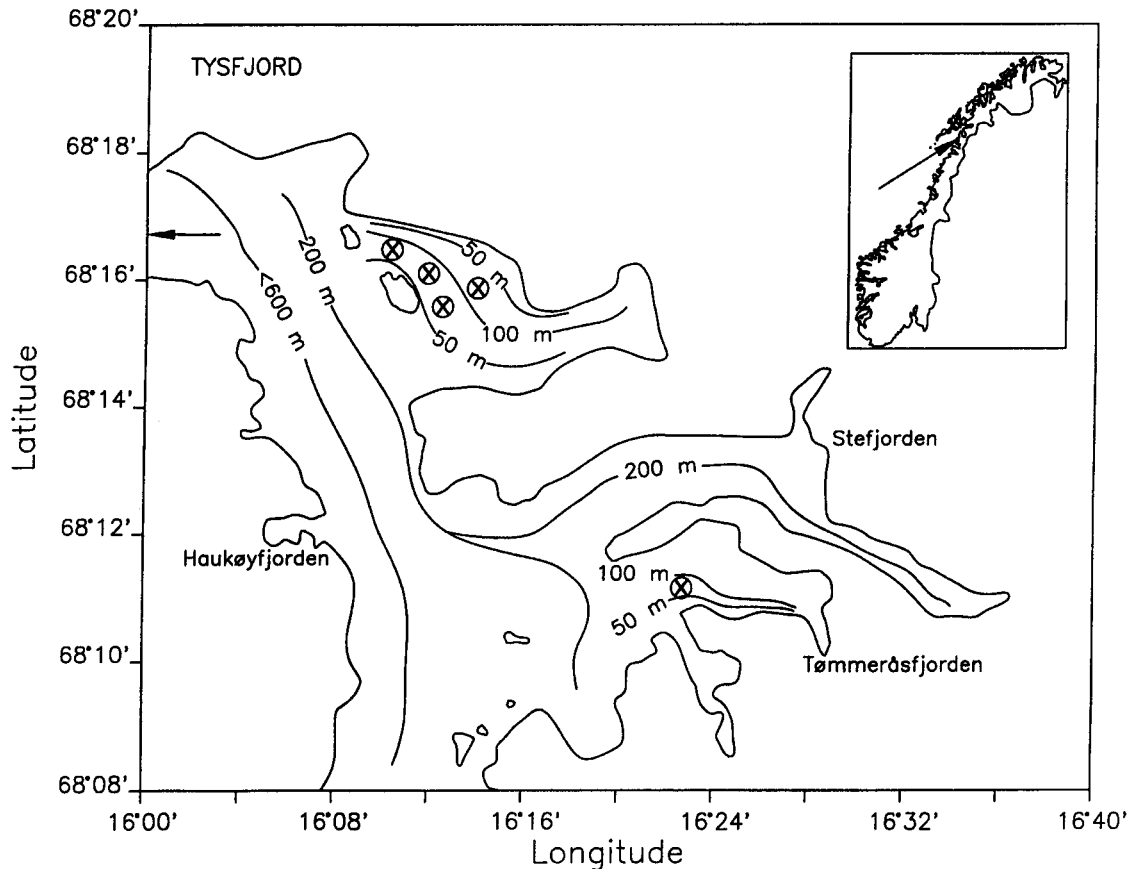
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Fig. 1. A detailed map of the study area in the outer part of Tysfjord (inset, Norway). Depth contours are indicated; crosses indicate those areas where the antipredator behaviour of herring during killer whale attack was recorded using sonar.



1992; Fernö and Olsen 1994), and these have recently also been employed in mesoscale behavioural studies of schools (Nøttestad et al. 1996; Pitcher et al. 1996; Misund et al. 1997; Axelsen et al. 1998). Hydroacoustics have also been used to study marine mammals (1993; Ridoux et al. 1997), including the feeding behaviour of killer whales (Similä 1997a). Using sonar, a larger spatial scale between cetaceans and their prey can be applied than is the case for underwater optics. The objective of this field study was to examine herring antipredator manoeuvres within schools during attacks by killer whales. Measurements of the size, relative density, and shape of attacked and unattacked herring schools were analyzed to investigate how antipredator manoeuvres function in nature.

Materials and methods

The investigation took place from 12 to 17 November 1993 in Tysfjord, a tributary of Vestfjorden in the Lofoten region (Fig. 1). The observations were carried out both day and night within deep (200–600 m) and shallow (<100 m) waters. The observations were conducted using a motorized vessel (9.8 m) equipped with a portable 455 kHz SeaBat 6012 multibeam sonar mounted on an aluminum rig. The transducer consisted of 60 elements transmitting at 1.5° horizontally and 15° vertically (Fig. 2), comprising a full horizontal swathe of 90° for each ping.

The sonar image presents the average density within the vertical cross section for each beam according to a relative colour code in which blue represents the lowest fish density, followed by green,

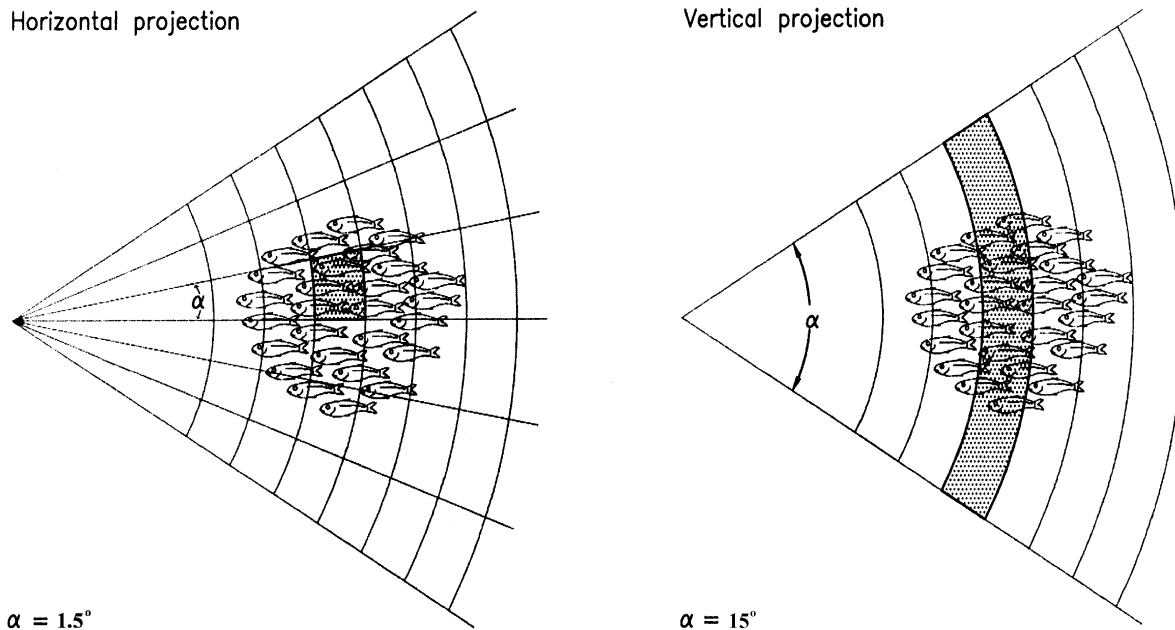
yellow, and then red, which represents the highest fish density. A detailed description of the sonar is given by Ridoux et al. (1997).

The sonar operates at a range that is adjustable between 5 and 200 m, with sample resolution decreasing with range. Schools attacked by killer whales were recorded by setting appropriate sonar ranges from 5 up to 150 m, depending on the situation. The whole school was covered by the beam simply by adjusting the range. The tilt angle was predominantly kept fixed at 0° during a predator-prey interaction, in order to observe and compare changes in interactions over time. Consequently, the transmission direction is interpreted as horizontal. Assuming that the horizontal cross section of a herring school is proportional to its volume (see Misund 1993), this area is an index of school volume.

The sonar image was recorded continuously on super-VHS videotape. Sonar recordings were digitized and analyzed using Image Pro Plus (Microsoft software) on a PC equipped with an Oculus frame-grabber card. Behavioural events were analyzed frame by frame in order to identify behavioural events. Individual fish could be identified at ranges shorter than 25 m, while school shape and area could be identified at medium ranges, from 25 to 100 m. At longer ranges, above 100 m, we obtained an overview of the killer whales in the surrounding area. Behavioural events were recorded at ranges of 50 m and less.

The area, A (m²), perimeter, P (m), relative density, D , and shape, S (circular, elliptical, asymmetric), of the school were measured directly from the sonar images. The whales could be observed on the sonar as relatively large, dense targets and were easily distinguishable from the herring. The presence of killer whales was confirmed visually during surfacing.

Herring-school sizes were allocated to one of four categories according to horizontal cross section: small (0–50 m²), medium (51–250 m²), large (251–460 m²), and very large (>460 m², the

Fig. 2. Top and side views of the sonar image.

maximum size observed). School sizes were corrected for pulse-length and beam-width distortion (Misund 1993). Circularity, C , was calculated as (Gerlotto et al. 1994)

$$C = (P)^2 / (4\pi A)$$

$C > 10$ indicated an asymmetrical shape, $5 < C < 10$ indicated an ellipsoid, while $C < 5$ indicated that the school was fairly circular (ball shape). Herring behaviour was divided into "states" (>10 min) and "events" (<10 s) to distinguish between lasting and spontaneous changes in school-structure responses. The following school states were recognized: "tight ball": $D > 190$, $C < 5$; and "loose ball": $D < 190$, $C < 5$. Following Pitcher and Wyche (1983) and Vabø and Nøttestad (1997), events were recorded as follows: "split": fragmentation of the school; "bend": inflection of the school; "dive": a rapid downward escape movement of the school; "vacuole": an empty space is created in the centre of the school; "hourglass": a constriction in the centre of the school; "herd": herring swim rapidly in front of predator; and "fountain": herring turn rapidly in the direction opposite to the predator. Figure 3 is a composite example of three of the observed antipredator events as seen on the sonar. The duration of each event was calculated as the time elapsed from when a school of herring was acoustically observed to respond to whales that were in physical contact with the school ("strike" and "tail slap") until the school reestablished the initial behaviour.

The behaviour of the killer whales was categorized as follows: "encircle": swimming alongside and around the edge of a school; "chase": swimming immediately behind a fleeing herring school; "strike": penetrating a school; and "tail slap": striking at the edge of a school with the fluke.

Results

Weather conditions during the study period were convenient for making acoustic observations, which is a prerequisite for proper acoustic data collection and analysis. Acoustic observations were made both close to the surface (<20 m) and near the seabed (>60 m), mostly in shallow areas (<100 m) and close to shore. A total of 365 min of footage was analyzed, including 208 min of predator-prey

interactions. We recorded a total of 41 schools, of which 31 were not attacked. The acoustic observations were made in a fairly extended area in Tysfjord, and the possibility of pseudo-replication should be small, although not nonexistent. From visual and acoustic observations, a total of 32 schools were observed while there were killer whales in the area, whereas 9 schools were observed without killer whales being located. There were clear differences in school area, relative density, and circularity between schools that were attacked and those that were not (Table 1).

Schools that were not attacked were significantly larger in area (Student's t test, $t = 4.09$, $df = 40$, $p < 0.0001$) than schools that were attacked. The relative density of unattacked schools was significantly lower than that of attacked schools ($t = 1.68$, $df = 40$, $p < 0.05$). Schools that were attacked had significantly higher circularity than those that were not ($t = 4.09$, $df = 40$, $p < 0.0001$). The 10 observed whale-herring interactions lasted 2–80 min. A total of 54 antipredator responses were observed on the sonar. About 10 herring seen floating on the surface were collected. They did not appear to have suffered any physical damage other than some scale loss, and had probably been attacked by the whales. Isolated herring scales were also frequently observed visually over a considerable area on the surface. We can divide events into two categories: shape-changing events (split, bend, vacuole, and fountain) and movement events (dive and herd). On eight occasions, killer whales initiated "encircling," while we observed two cases of strike through schools. In 80% of the cases when killer whales (2–12 individuals) were close (<5 m) to a school, the herring rapidly organized into a tight-ball state from a loose-ball state; in only 20% of the cases when strike was observed did the herring remain in a loose-ball state. Most of the time (97%) the herring remained in a tight-ball state throughout an attack, but 3% of the time was spent on other defined antipredator events (Fig. 4).

Depending on the size and relative density of the school and whether the killer whales displayed encircle or strike,

Fig. 3. Print of sonar picture showing killer whales and herring schools. A small school (<math><50\text{ m}^2</math>) is seen in a “tight-ball” state, while five killer whales “encircle.” “Vacuole,” “bend,” and “split” events taken from various predator-prey interactions are seen in the inset smaller boxes.

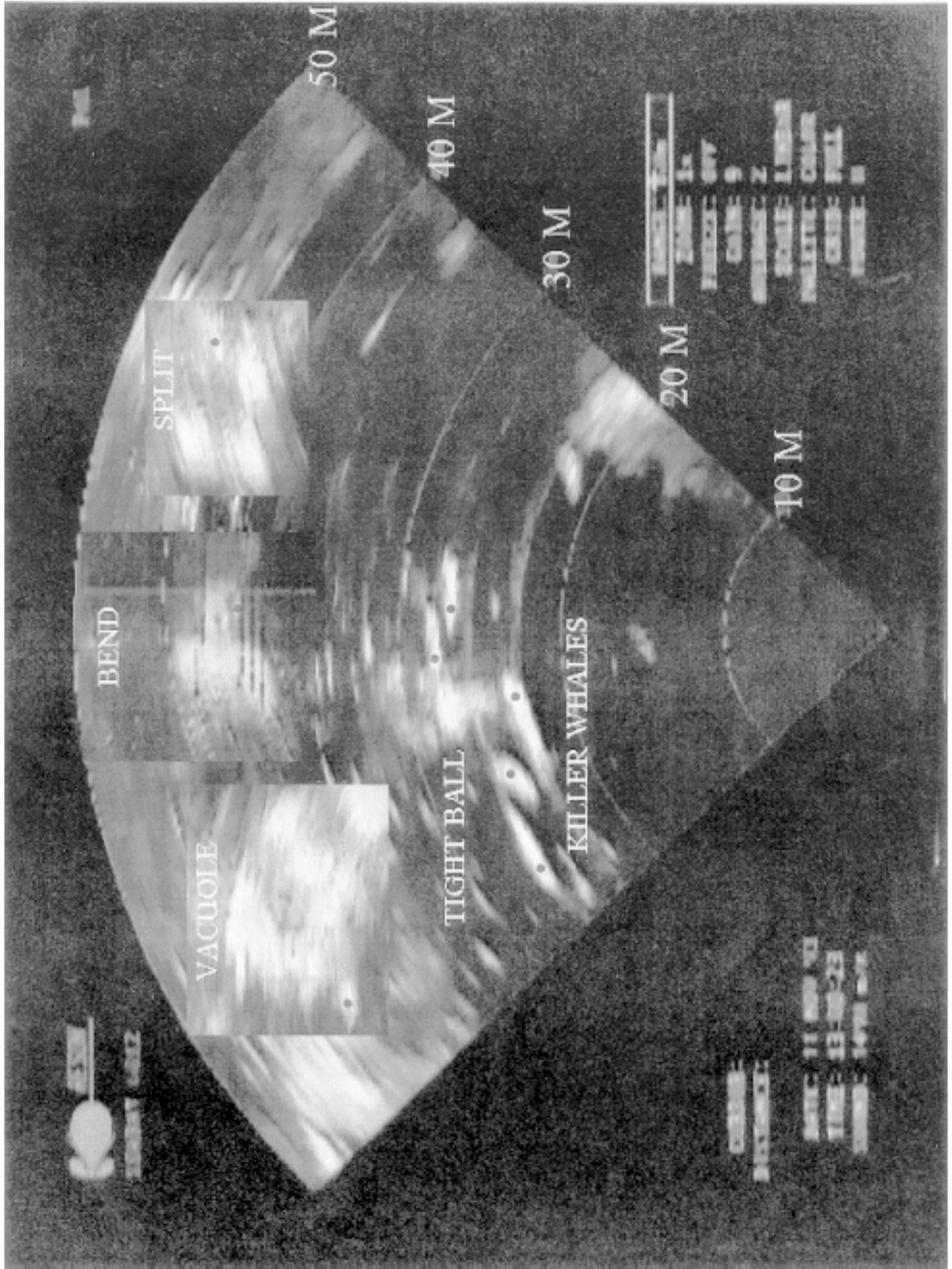


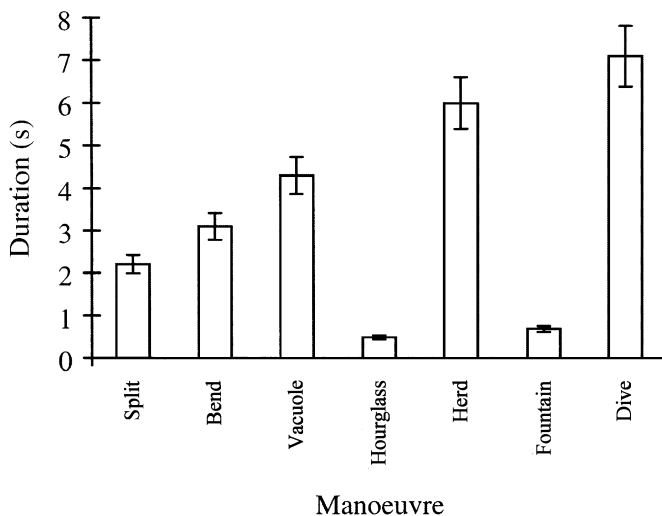
Table 1. School area, relative density, and circularity of unattacked and attacked herring schools.

	<i>n</i>	Area (m ²)			Relative density			Circularity		
		Min.	Max.	Mean ± SD	Min.	Max.	Mean ± SD	Min.	Max.	Mean ± SD
Unattacked	31	540	1610	830±215	130	210	160±30	6.2	17	8.9±3.8
Attacked	10	20	460	180±135	190	240	210±21	1.7	5.8	3.1±1.2

Note: Significance level of two-sample *t* test with unequal *n* (Zar 1996): area, $p < 0.001$; relative density, $p < 0.05$; circularity, $p < 0.0001$.

Table 2. Number of behavioural events observed for each size category of herring school.

School size	Event						
	Vacuole	Split	Bend	Hourglass	Herd	Fountain	Dive
Not attacked							
Very large	0	0	0	0	0	0	0
Attacked							
Large	5	2	4	0	0	0	1
Medium	0	0	14	4	0	0	1
Small	0	19	0	0	2	2	0

Fig. 4. Duration of antipredator events. Values are given as the mean ± SE.

the behavioural outcome within the school unit changed. Very large schools were never attacked by killer whales (Table 1). Vacuole appeared only within large schools, while splitting occurred after two, sometimes three, successive strikes in large schools and when individual whales attacked small schools. Hourglass was observed after whale attacks on medium-sized schools. Herd was observed to follow killer whale chase within small schools. Fountain was observed twice and was preceded by herd. Twice we observed dive, where herring escaped vertically to deeper waters (Table 2). Because of limited vertical sonar resolution, dive may sometimes be difficult to observe. Nevertheless, wintering herring may dive rapidly from the surface to a depth of 100–150 m during or after an attack (Nøttestad 1998).

Unattacked schools were elliptical, whereas during an attack, 60% of the schools were circular. Asymmetric or amorphous schools were observed after massive attacks by 6–12 whales; this led to the school splitting into smaller units.

Discussion

School size

Norwegian spring-spawning herring hardly feed in winter (Slotte 1999). Thus, decreased intraspecific competition enhances large schools (Nøttestad 1998). School size has also been identified as a key factor in defence against predators, owing to the increased dilution and confusion effects provided by large schools (Pitcher and Parrish 1993). However, a predator can reduce the potential perceptual confusion effect of a large group by attacking stragglers or individuals at the periphery of the group (Milinski 1977) or by dividing the group into smaller units. Vacuole formation was only performed by large schools during a whale attack, while small schools always split. A split will divide herring into smaller groups, which may lead to isolation of individuals, making them more vulnerable to predator attack (Parrish 1992). This tendency has also been demonstrated and visualized by using individual-based models (Vabø and Nøttestad 1997).

School density

Unattacked schools had significantly lower relative densities than schools that were attacked (Table 1). The tight-ball state, which dominated the organization of attacked schools in the present study, is thought to be an individual response to predation (Pitcher and Wyche 1983; Pitcher and Parrish 1993). High density is normally considered to be anti-predator behaviour, where individuals seek shelter in the centre of the group (Breder 1951; Hamilton 1971; Pitcher and Wyche 1983). This individual hiding tactic may also influence the shape of a herring school, as it becomes more circular during predator attacks (Table 1). Since an attacked school was horizontally stationary, herring were forced to swim in a circular pattern, as was also observed by Similä and Ugarte (1993). The high density of attacked schools suggests that the whales “packed” the herring to a certain density before starting to feed. Gas-bubble release by whales (Similä and Ugarte 1993) may also contribute to packing herring, since herring are known to exhibit strong avoidance of bubbles (Sharpe and Dill 1997).

Antipredator strategies versus manoeuvres

Similar types of individual fish behaviour may give rise to apparently different school manoeuvres (Vabø and Nøttestad 1997). A behavioural continuum may link at least some of the different antipredator manoeuvres. Herd, fountain, split, and vacuole events should not be considered alternative tactics, but rather as different total outcomes based on the same individual antipredator behaviour. For instance, herd can lead to fountain. Similarly, vacuole in a large school may correspond to split in a small school.

Conclusions

Spatial and temporal aspects of antipredator behaviour of wintering herring were investigated using a high-resolution sonar during repeated killer whale attacks in Lofoten, northern Norway. Observed antipredator responses observed included split, hourglass, vacuole, bend, dive, herd, and fountain. Schools that were attacked were significantly smaller, more circular, and of higher relative density than those that were not attacked. An average of one antipredator event was observed every 3.9 min. All antipredator events lasted less than 10 s, reflecting the highly dynamic and coordinated movements within attacked schools. In the near future, modern high-resolution acoustics, in combination with underwater cameras, ought to provide new and promising quantitative knowledge of the interactions between marine mammals and their prey.

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