

How whales influence herring school dynamics in a cold-front area of the Norwegian Sea

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We present the first acoustic observations of predator–prey interactions between fin whales and herring. The school dynamics and predation events of Norwegian spring-spawning herring (*Clupea harengus*) in a cold front area (about 125 km²) in the Norwegian Sea in April were quantified. Data from high-resolution sonar tracking of herring schools combined with echosounder data were integrated with pelagic-trawl samples. A total of 44 herring schools were each observed for an average of 34.8 min. Altogether, 184 behavioural events were recorded, with an event occurring every 8.3 min on average. Intra-school events (compression, reorganization, ring, pseudopodium, elongate, diving, surfacing) were observed every 15.3 min and inter-school events (approach, join, leave, split) every 22.9 min. We observed 17 fin whales (*Balaenoptera physalus*), six Atlantic white-sided dolphins (*Lagenorhynchus acutus*) and five killer whales (*Orcinus orca*) within the experimental area. Predator events occurred every 91 min on average. Of these marine mammals only fin whales swimming alone or in small groups (2–5 ind.) were observed to attack herring. Attacks from fin whales were observed every 170 min. They strongly influenced the density, shape and structure of the herring schools. Large fish such as cod (*Gadus morhua*) and saithe (*Pollachius virens*) preying on herring in coastal areas were not caught in the pelagic trawl or detected by acoustics. Herring schools were on average large (987 m²), dense, swam at depth (148 m) and had a moderate swimming speed (1.1 body lengths per second), reflecting a risk-averse, anti-predator behaviour to marine mammals. We discuss differences in schooling dynamics, anti-predator behaviour, attack frequency and predation risk between herring attacked by fin whales in an offshore area and herring attacked by gadoid predators closer to the coast in a similar study in May.

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Introduction

The large natural variability of school size, density and shape give Norwegian spring-spawning herring (*Clupea harengus*) a dynamic appearance (Misund, 1993; Misund and Floen, 1993; Nøttestad *et al.*, 1996). The plasticity of its shoal dynamics endows herring with a remarkable ability to respond to the local regime of predators and food that is encountered through its life history (Fernö

et al., 1998; Nøttestad, 1999). The herring's vertical migration from 400 m depth to the surface waters and back again (Misund *et al.*, 1997; Mackinson *et al.*, 1999), annual horizontal migrations of more than 5000 km (Røttingen, 1992; Nøttestad *et al.*, 1999) and dynamic school-responses to predator attacks (Nøttestad and Axelsen, 1999) are examples of marked flexibility and adaptation. The herring is embedded ecologically and evolutionary in its ecosystem by its schooling

behaviour (Blaxter, 1985; Fernö *et al.*, 1998), and we aim to compare and understand the adaptive behaviour of herring schools within different areas and life-history stages (Pitcher *et al.*, 1996; Fernö *et al.*, 1998; Nøttestad, 1999).

Marine mammals are key predators on Norwegian spring-spawning herring, particularly during the off-shore summer-feeding period in the Norwegian Sea (Skjoldal *et al.*, 1993). Fin whales (*Balaenoptera physalus*) and minke whales (*Balaenoptera acutorostrata*) exert a major predation pressure on herring (Jonsgård, 1966; Markussen *et al.*, 1992; Haug *et al.*, 1995; Lindström *et al.*, 1997). The abundance of fin whales has been estimated to be about 3000 individuals for the Norwegian Sea and the Barents Sea combined (NAM-MCO, 1998). Fin whales disappear from the coastal waters in April (Jonsgård, 1966), probably moving westwards into the Norwegian Sea to follow the westward feeding migration of herring.

We know very little about predator-prey dynamics in the open ocean because it has only recently been possible to quantify school dynamics acoustically using multi-beam sonar technology (Misund *et al.*, 1995, 1997, 1998; Pitcher *et al.*, 1996). Tracking fish schools in the ocean makes it possible to quantify behaviour on various temporal and spatial scales (Fernö *et al.*, 1998; Mackinson *et al.*, 1999) and test hypotheses of predator-prey interactions (Nøttestad and Axelsen, 1999; Axelsen *et al.*, 2001). It is at the small meso-scale, tens to hundreds of metres (Mackinson *et al.*, 1999), that many interactions between predators and pelagic prey takes place (Schneider and Piatt, 1986; Vabø and Nøttestad, 1997), as well as school movements and interaction between schools such as splitting and joining. Previous field herring studies on predator-prey interactions have been concentrated on gadoid predation on herring in fjords and coastal waters (Pitcher *et al.*, 1996; Nøttestad, 1998), and killer whale (*Orcinus orca*) predation on wintering herring in Lofoten (Nøttestad and Axelsen, 1999; Nøttestad and Similä, 2001). The main aim of this study was to quantify the meso-scale dynamics of herring and predator events in a cold-front area offshore and compare the results with a similar study on herring dynamics and predation closer to the coast (Pitcher *et al.*, 1996).

Material and methods

Survey area

Based on knowledge of the migration route of Norwegian spring-spawning herring from surveys in 1993–1995 and the distribution of herring in March 1996 during a previous survey (Misund *et al.*, 1995, 1996), the present investigation was conducted in April 1996 in an area from 67°N to 68°30'N and 5°E to 2°W (Figure 1).

Table 1. Overview of acoustic data collected by sonar and echosounder.

Sonar	Echosounder
Tracking of herring schools	Detection of herring schools
School area (m ²)	Swimming depth (m)
Relative density (colour sum unit)	Vertical extension (m)
Swimming speed (m*s ⁻¹)	
Swimming direction (°)	
Inter-school distance (m)	
Intra- and inter-school events	
Detection and tracking of fin whales	

Initially an exploratory survey was conducted to map the distribution of herring. Tracking of the schools was conducted on a southward transect along 0° starting at circa 68°N and stopping at 67°N, and along a westward transect along circa 67°N starting approximately 0° and stopping at 1°20'W.

Methods

The acoustic data were recorded by sonar and echosounder as specified in Table 1. A calibrated Simrad EK 500 echosounder operating at 38 kHz transducer at 10–500 m connected to a Bergen Echo Integrator (BEI) post-processing system was used to make the acoustic recordings. Selected herring schools were tracked for up to 2 h using a 95 kHz Simrad SA 950 multi-beam sonar operated at 300 m range. The sonar has a beam width of 90° pointed horizontally to either side of the vessel during its operation. The data from the sonar was used to quantify the spatial distribution of schools and to track selected schools continuously for a period of time.

Accurate positions of the vessel were obtained from a Starfix differential global positioning system (dGPS). The migration speed and swimming direction of the schools were calculated using SAS software (SAS Inc., 1988). The behaviour of the schools, observed from the sonar display, was noted continuously by a rapporteur in cooperation with a sonar operator. The sonar data were recorded on a video player and analyzed by a sonar operator who standardized and categorized the acoustic data for further analysis.

The fish species in the acoustic recordings were identified by pelagic trawling. An Åkra-trawl with a vertical opening of about 30 m was used. Usually this trawl is used to catch deep schools but it can be re-rigged to catch fish near the surface (Misund *et al.*, 1997).

Herring behaviour and dynamics

The following school characteristics were recorded: (1) school-area is the horizontal area (m²) of the school

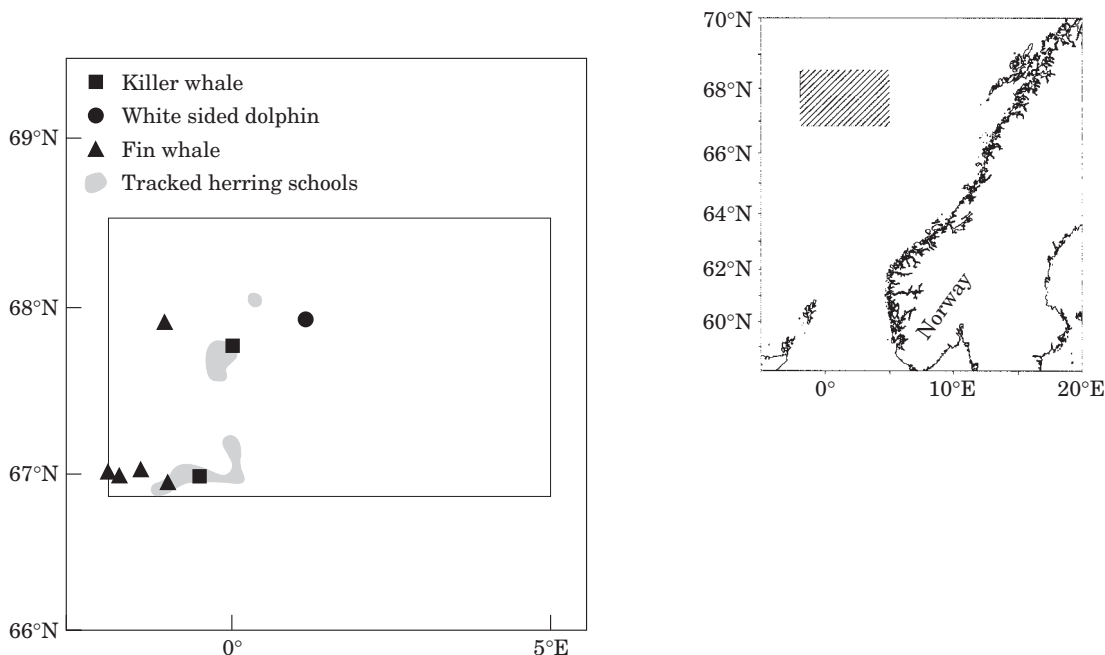


Figure 1. Experimental area (small map) and geographical location of visually-observed marine mammals and tracked herring schools in the period 13–14 April 1996.

detected by the sonar and calculated in a software program developed at the Institute of Marine Research; (2) the vertical extension (m) of the schools is recorded by the echosounder; (3) relative density (colour-sum units) of the recordings is given by a colour code where blue represents low density, yellow shows medium density, and dark red represents high density; (4) horizontal swimming speed ($\text{m}\cdot\text{s}^{-1}$) and direction ($^{\circ}$), given as true heading, are calculated from the horizontal sonar tracking of the schools and information from the differential Global Positioning System (dPGS); (5) vertical swimming depth (m), measured from the top of the school, is recorded when the echosounder is passing over selected schools and (6) inter-school distance (m) is measured as a straight line between two schools observed on the sonar screen.

During school tracking, date, time, duration of tracking, and the exact geographical position were recorded. The school responses and predator events were categorized according to Pitcher *et al.* (1996): (1) intra-school events (compression, reorganization, ring, “pseudo-pod”, elongate, diving, surfacing); (2) inter-school events (approach, join, leave, split) and (3) predator events (present, total attack, fish school attack, herd).

Whale observations

Apart from five fin whales recorded on the multi-beam sonar whale observations were performed visually from

the bridge using binoculars. The observation periods varied from day-to-day during the cruise. During the first part (4–10 April 1996) it was nearly impossible to detect any whales visually because of strong winds up to 45 knots and white caps at the surface. Later when entering the polar front area between the Atlantic current and the Northeast Icelandic current at about $68^{\circ}00'N$, $002^{\circ}00'W$, the prevalent fog resulted in low visibility and again made observing conditions difficult. However, from 12 April the sea was calm and there was a very good visual range (>3000 m). Continuous observations were made when light conditions permitted the detection of whales (from 0600 until 2300 hours). The number and species of marine mammals were recorded in addition to range, heading, group size, diving pattern (time at the surface and underwater) and the breathing frequency (number of “blows” and interval between “blows”) of fin whales.

Whale–herring interactions

Direct interactions between whales and herring were observed using the multi-beam sonar. The behaviour of the whales and herring during an interaction was categorized according to the behavioural scheme adopted from Pitcher *et al.* (1996). The distributions of whales and herring from both visual sightings and acoustic measurements were used to detect potential overlap in spatial and temporal distributions (Figure 1).

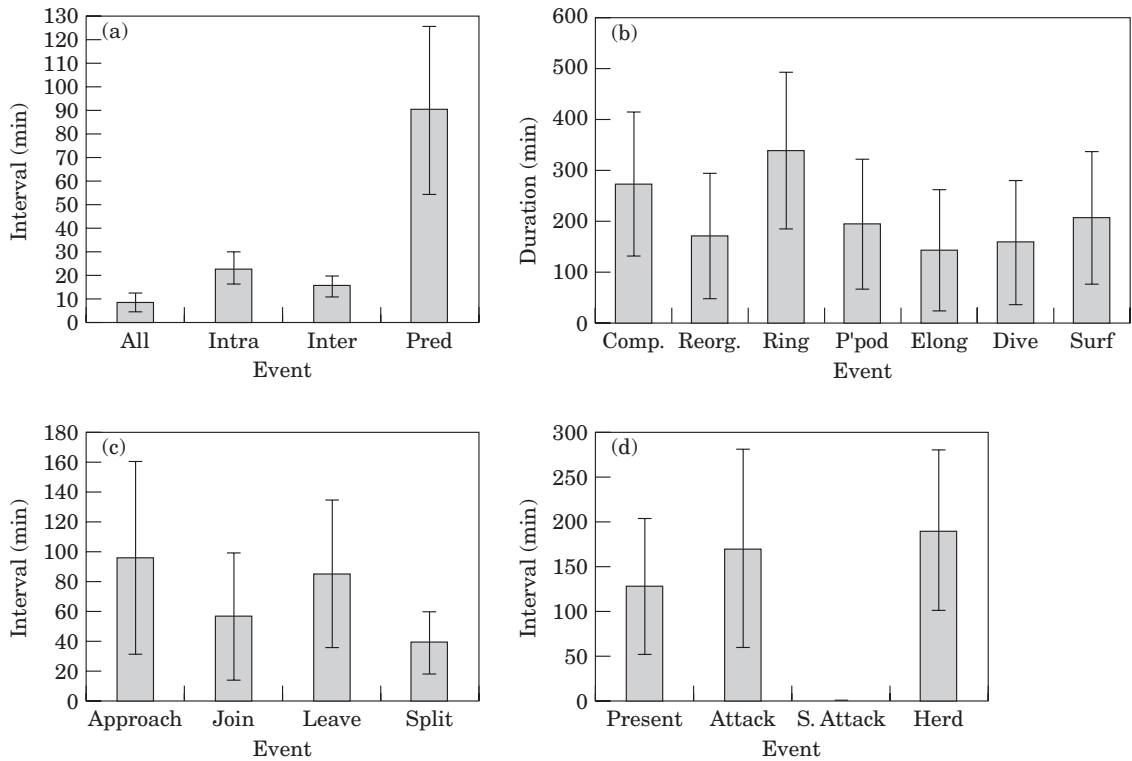


Figure 2. (a) Mean frequency intervals (columns) with 95% confidence limit (bars) for the 15 recorded behavioural events scored for the 44 tracked herring schools. Total of all events and for intra-, inter-school and predator events. (b) The seven intra-school behavioural events. (c) The four inter-school behavioural events. (d) The four putative fin whale interaction behaviours.

Table 2. Individual school data, swimming performance and inter-school distances between schools given as mean values with standard deviation.

School data (n=44)	School area (m ²)	Relative density (colour sum)	Vertical extension (m)	Swim depth (m)	Average heading (°)	Swim speed (m·s ⁻¹)	Inter-distance (m)
Mean	987	2794	33	148	181	0.39	205
St. dev.	936	3038	19	110	46	0.28	145

Results

Herring-school dynamics

All together 184 behavioural events were recorded from 44 herring schools observed for a total of 1531 min (34.8 min per school on average). Figure 2 shows the mean interval between behavioural events with 95% confidence intervals. Events (n=184) occurred every 8.3 min on average (Figure 2(a)). Intra-school events were observed every 22.9 min (Figure 2(b)), and inter-school events every 15.3 min (Figure 2(c)). On average we recorded an event interpreted as involving predators every 91 min. Attacks from fin whales were observed every 170 min (Figure 2(d)).

The school area, relative density, vertical extension, school heading, swimming speed and inter-school distance are given in Table 2. The 44 herring schools were large (987 m²), dense, deep (33 m), had moderate swimming speed (0.39 m per sec=1.1 body lengths per sec) and moved in a southern direction (181°). Inter-school distance was 205 m on average.

Whale behaviour

Seventeen fin whales, six white-sided dolphins and five killer whales were observed (Table 3). Groups of fin whales consisted of one to five individuals (Table 3), mainly swimming 20–100 m apart. Detailed surface

Table 3. Whale observations including date, position, species and number of whales.

Date	Position	Species	Number	Group size
13 April	N 67°57.0'W01°14.0'	White sided dolphin	6	6
13 April	N 67°01.1'W01°59.9'	Fin whale	3	1+2
13 April	N 67°55.8'W01°14.2'	Fin whale	5	5
13 April	N 67°01.9'W01°45.9'	Fin whale	1	1
13 April	N 66°59.3'W01°79.1'	Fin whale	5	2+3
13 April	N 66°57.7'W01°13.4'	Fin whale	3	3
14 April	N 66°59.1'W00°38.0'	Killer whale	4	4
14 April	N 66°23.0'W00°45.0'	Killer whale	1	1

observations of 10 fin whales observed for 20–50 min revealed that the whales spent on average 2.40 ± 2.09 min ($n=10$) at the surface and 12.73 ± 5.8 min ($n=10$) submerged. The breathing frequency was 3.07 ± 3.34 blows per individual per minute ($n=10$).

Whale–herring interaction

During two sonar-tracking periods of herring schools (the nights of 13–14 April), unique, dense-echo patterns within 300 m of the vessel were interpreted as five fin whales via their size, consistency and pattern of the echo-traces. Sonar printouts of herring schools being attacked by one and two fin whales are shown in Figures 3 and 4. During the day there were no recordings of fin whale attacks on tracked herring schools. The whales were then observed at a considerable distance with no avoidance behaviour to the vessel.

Discussion

To our knowledge this is the first study observing acoustically predator–prey interactions between fin whales and herring in the Norwegian Sea. In these offshore areas no fish predators that might have caused responses such as cod (*Gadus morhua*) and saithe (*Pollachius virens*) were detected acoustically or caught in the trawl samples. This situation contrasts with that in coastal water (Pitcher *et al.*, 1996) where shoaling fish predators were the only predators.

Herring were predominantly at 300–400 m depth in the daytime in very large shoals, and rose to the surface at night. All interactions of herring with fin whales took place at night when the schools were shallower than approximately 200 m, probably reflecting the maximum hunting-depth of fin whales (Watkins *et al.*, 1996). Swimming deep during the day should minimize whale predation. Herring were herded by fin whales towards the surface before the attack, as previously observed in killer whales preying on herring (Nøttestad and Axelsen, 1999; Nøttestad and Similä, 2001). Most fin whales had a short time at the surface, low

breathing frequency and generally a short diving-period, suggesting that the whales were primarily filtering the plankton available in relatively shallow waters during the day.

Predatory events appeared every 91 min in our study, compared to every 27 min in the inshore areas (Pitcher *et al.*, 1996). Differences in predator types and attack frequency between herring in coastal and offshore areas should influence their trade-off between feeding and predation. Adult herring in offshore areas in April performed a risk-averse strategy (see Fernö *et al.*, 1998). Large, dense and deep swimming schools should reflect a precautionary behaviour, where avoiding predation from fin whales and other marine mammals such as killer whales and white-sided dolphins observed in the area is more important than feeding. Close contact between neighbouring schools would also give herring the opportunity of adjusting group size under whale attack (see Fernö *et al.*, 1998; Mackinson *et al.*, 1999). Smaller, less dense and shallow swimming schools dominated in May 1994 in coastal areas (Pitcher *et al.*, 1996), reflecting a risk-prone feeding strategy, where the attack frequency were more than three times higher than offshore.

How herring react to predation should vary depending on the situation, predator type and the individual mortality risk. Lima and Bednekoff (1999) suggested that an animal should exhibit its greatest anti-predator behaviour in high-risk situations that are brief and infrequent. Fin whales could be more dangerous for individual herring in a school than gadoids. Whales tend to force a school to become a very dense aggregation so that they can feed on large portions of the school, or even engulf the whole school in one attempt (Jonsgård, 1966). Gadoids may accompany the schools and perform frequent shoal attacks but probably do not kill as many herring as the whales during a successful school attack. Whether or not attack frequency and mortality risk on herring are correlated to each other needs to be quantified. Putting a video camera on marine mammals (Marshall, 1998) to observe the actual catch of prey is one method of directly testing prey consumption and mortality in predator–prey interactions.

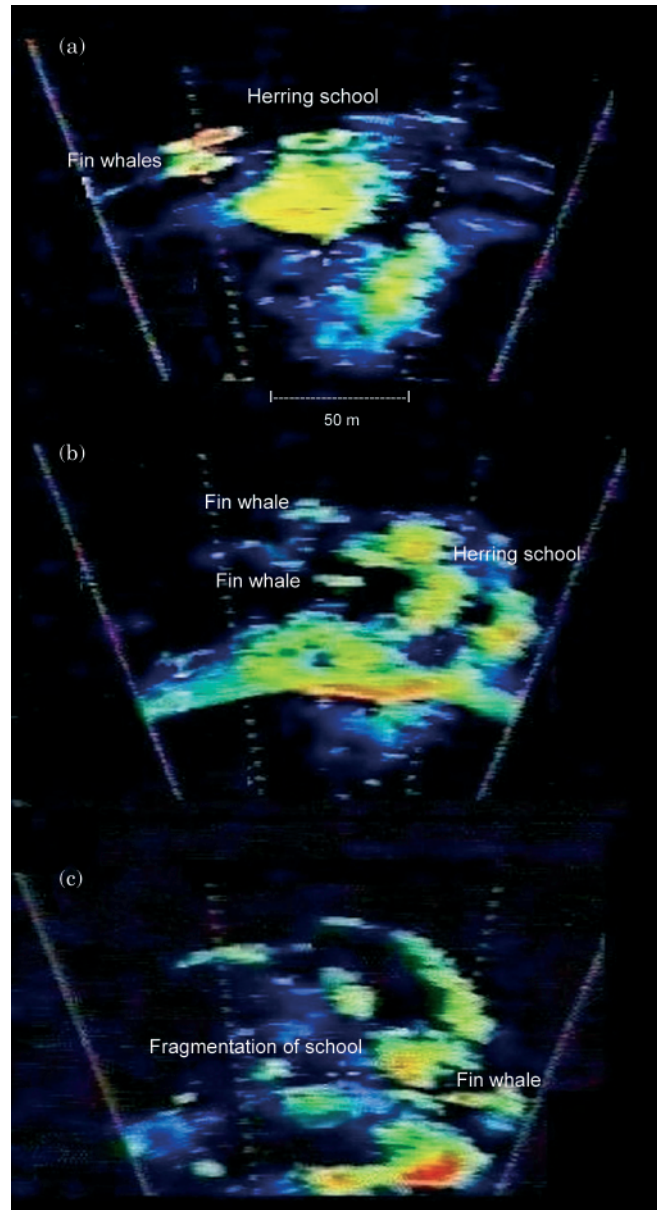


Figure 3. Sonar sequences of two fin whales attacking a herring school on 13 April 1996 22:19–22:22 UTC. Position: 66.891°N, 01.176°W. depth=19 m, area=115 m², relative density=6740. (a) Fin whales approaching the school from upper-left corner of the sonar printout. Herring closest to the predator were seen aggregating from a dispersed and loose layer of herring (blue) into a dense school (red). (b) Fin whales are penetrating the school and the herring split into several smaller aggregations of varying size, shape and density. (c) Fin whales remain within the school. The high density of herring (red) in the lower-right corner is interpreted as a strong predatory response (“tight ball”). Note that the co-ordinated school manoeuvres take place in the middle of the night.

In the offshore area herring stayed in large and dense schools, swam at depth and close to neighbouring schools. This suggests that they spent most of their time avoiding high-risk predation. Lima and Beddheoff (1999) suggest that the need to feed forces an animal to decrease its allocation of anti-predator effort to high-risk situations as they become more frequent or lengthy. Our

results support the view that herring should exhibit its highest antipredator behaviour to fin whale predation that is brief and relatively infrequent for individual herring in offshore areas.

Less overall herring-school movements (inter-, intra- and predation events combined) were observed offshore (0.12 events min⁻¹) compared to the coastal study (0.18

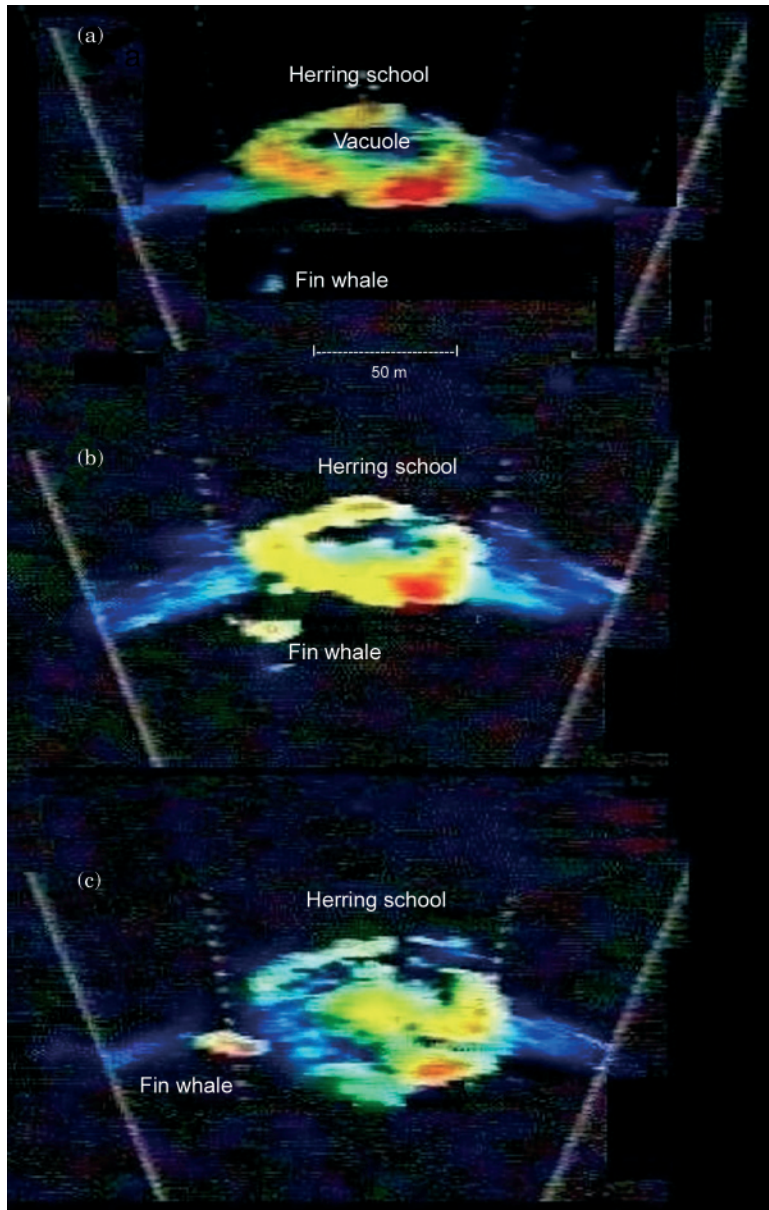


Figure 4. Sonar sequences of one fin whale attacking a herring school on 14 April 1996, 03:32–03:36 UTC. Position: 66.894°N, 01.218°W. depth=66 m, area=442 m², relative density=962. (a) Fin whale approaching the school from lower-left corner of the sonar printout. The herring were seen aggregating from a dispersed and loose layer to form a circular and dense school thus creating an empty space in the middle of the school (vacuole). (b) Fin whale herding and attacking the school from the left-hand side. The herring are responding by turning away from the whale-maintaining a safe distance from the predator and thus influencing both school shape and density. (c) Fin whale seen on the left-hand side after penetrating the school, which has now been split in the area of attack.

events min⁻¹) (Pitcher *et al.*, 1996). Intra-school events also appeared significantly less frequently than in coastal water. Higher dynamics in coastal areas probably reflects the high number of predatory attacks and higher feeding activity compared to offshore areas (see Mackinson *et al.*, 1999). Predation could all the same strongly shape offshore behaviour of herring. Even

though the recent number of fin whales in the Norwegian Sea has been low compared with historical trends (NAMMCO, 1998), only one encounter of a herring with a group of whales during its 14 years of life is sufficient to remove its genes from the population. The selection pressure of even one group of whales cruising the offshore portions of the Norwegian Sea at the same

time of year as migrating herring may be sufficient to strongly select for the predator avoidance and schooling dynamics that we observed (Pitcher, 1995).

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