

Pretty patterns but a simple strategy: predator-prey interactions between juvenile herring and Atlantic puffins observed with multibeam sonar

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Abstract: Predator-prey interactions between Atlantic puffins (*Fratercula arctica*) and newly metamorphosed herring (*Clupea harengus*) were studied in the Lofoten-Røst area in northern Norway using a high-resolution multibeam sonar system. Attacks from diving puffins and predatory fish induced massive predator-response patterns at the school level, including bend, vacuole, hourglass, pseudopodium, herd, and split. All patterns have previously been observed, using the same sonar, in schools of adult herring attacked by groups of killer whales. Tight ball, the prevailing response pattern in adult fish under predation, was not observed, but a new pattern, intraschool density propagation, was found and interpreted as an analogue to tight-ball formations moving rapidly within the school. The observed patterns persisted much longer than in schools of adult herring attacked by killer whales, reflecting the different hunting strategies. Traditionally, the repertoire of predator responses observed in schooling fish has been interpreted as a range of cooperative tactics to trick predators, but this has recently been challenged by authors who suggested that fish that behave the same way produce different patterns at group level simply by maintaining a minimum approach distance to predators and hiding behind conspecifics (the "selfish herd"), and that the particular combination of group size and number and behaviour of predators, rather than different individual tactics, determines the outcome at group level. Our findings support the latter hypothesis.

Résumé : Nous avons étudié les interactions prédateurs-proies entre des Macareux moines (*Fratercula arctica*) et des Harengs (*Clupea harengus*) fraîchement métamorphosés dans la région de Lofoten-Røst, dans le nord de la Norvège au moyen d'un sonar de haute résolution à faisceaux multiples. Les attaques des oiseaux en plongée et des poissons prédateurs déclenchent des patterns de réaction massive au sein des bancs de harengs : repliement, vacuole, sablier, pseudopode, troupeau et séparation, types de comportement déjà observés, au moyen du même sonar, dans des bancs de harengs adultes attaqués par des épaulards. La formation d'une boule compacte, la réaction la plus fréquente des poissons adultes face à des prédateurs, n'a pas été observée, mais il s'est produit un nouveau pattern dans les bancs de harengs, la pulsion de densité, interprétée comme analogue à la formation d'une boule compacte, mais se déplaçant rapidement dans le banc. Ces patterns ont duré beaucoup plus longtemps que ceux observés dans les bancs de harengs adultes attaqués par des épaulards, ce qui reflète la diversité des stratégies de chasse. Traditionnellement, le répertoire des réactions aux prédateurs observé au sein des bancs de poissons est considéré comme une série de tactiques de coopération pour tromper les prédateurs, mais cette théorie a été remise en question par les auteurs qui croient que ces poissons qui se comportent de la même façon produisent des patterns différents quand ils sont en groupe en s'approchant tout simplement le moins possible des prédateurs et en se cachant derrière des individus conspécifiques (le « troupeau égoïste »). C'est la combinaison particulière de la taille du groupe, du nombre et du comportement des prédateurs plutôt que l'ensemble des tactiques individuelles qui détermine l'issue de la prédation dans le groupe. Nos résultats supportent cette dernière hypothèse.

[Traduit par la Rédaction]

Introduction

Schooling behaviour is primarily an evolutionary response to predation (Seghers 1974). Escape behaviour in schooling

fish exposed to predators has been documented through numerous laboratory experiments (Pitcher and Wyche 1983; Fuiman and Magurran 1994; Domenici and Batty 1997), but few studies have been carried out under natural conditions

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(Lima and Dill 1990). Laboratory studies of larval and juvenile fish, although regarded as an important component of ecological studies, suffer from crucial limitations such as artificial environments, spatial boundaries, and few specimens. A certain degree of handling is inevitable and may stress the target species (Clark and Mangel 1986; Hilborn and Mangel 1997). To study natural behaviour on a small scale, a controllable environment may be required, but in investigations of meso- and macro-scale schooling dynamics the restrictions of any experimental setting are likely to alter the natural conditions to a critical extent (Schrader-Frechette and McCoy 1992; Hilborn and Mangel 1997).

There is a strong spatiotemporal relationship between herring (*Clupea harengus*) larvae and Atlantic puffins (*Fratercula arctica*) along the west coast of Norway during spring and summer (Anker-Nilssen 1992). The results of studies in the Røst area suggest that puffins breeding along the east coast of the Norwegian Sea are capable of consuming more than 100 billion 0-group herring during the breeding season alone (Anker-Nilssen and Øyan 1995). A better understanding of predator-prey relationships between puffins and herring in their natural environment may greatly improve our ability to predict the growth and survival of puffin chicks as well as 0-group herring, thereby increasing the reliability of models that portray population development in both species.

In this study we observed predator-prey interactions between diving Atlantic puffins (Fig. 1) and schools of newly metamorphosed herring (Fig. 2), using a high-resolution multibeam sonar system (Ridoux et al. 1997; Nøttestad and Axelsen 1999). To the best of our knowledge this is the first time that such an approach has been applied to study interactions between fish and seabirds. Although the sonar system only has been commercially available for a few years (Ridoux et al. 1997), the technology has already been applied to study predator-prey interactions in killer whales (*Orcinus orca*) (Similä 1997; Nøttestad and Axelsen 1999) and bottlenose dolphins (*Tursiops truncatus*) (Ridoux et al. 1997).

Nøttestad and Axelsen (1999) studied the schooling dynamics of adult herring during killer whale attacks in Tysfjord, northern Norway, in November 1993. They demonstrated that a variety of previously documented (*split* (separation of school into two or more units), *hourglass* (narrowing of the central part of school), *vacuole* (formation of an empty space inside school), *herd* (school fleeing in front of predator(s)), *fountain* (rapid turn in the direction opposite of a predator) and new (*bend* (inclination of one side of a school), *dive* (rapid downward movement of a school)) predator-response patterns at school level were essentially determined by school size and density, suggesting that the various response patterns at school level were produced by the same behaviour at the individual level. Vabø and Nøttestad (1997) tested this hypothesis by using an individual-based simulation model, demonstrating that complex school dynamic features caused by predators could be explained solely in terms of individuals seeking shelter among conspecifics when exposed to predators, i.e., the behaviour of the "selfish herd" (Hamilton 1971). Our goals were to employ the multibeam sonar methodology to observe and quantify response patterns emerging during predator-prey interactions between puffins and juvenile herring, to compare the results with

those of Nøttestad and Axelsen (1999) on adult herring attacked by killer whales, and to discuss the findings in light of the "cooperative tactics" and selfish herd theories.

Materials and methods

Experimental design

The study was conducted south of the Røst archipelago in the Lofoten Islands in northern Norway, at 67°20'N 12°05'E, on 10–15 July 1996 (Fig. 3). The water depth in the area is about 200 m. The R/V *Michael Sars* (Institute of Marine Research, Bergen, Norway) served as the main platform for the investigation. The weather conditions in the area during data collection were exceptionally good, with moderate winds and waves and good visibility. Samples of herring were obtained using a fine-meshed sampling trawl.

Puffin foraging areas were identified via standard transect surveys of seabirds at sea (e.g., Tasker et al. 1984). The sonar observations were made in two of these areas on 10 July at 13:45–18:05 (local time) and on 14 July at 08:05–08:50. There were thousands of herring schools in the area, and the chance of pseudo-replication was regarded as small. The sonar was installed on board an 18-ft boat that was launched as the vessel entered the feeding areas. The boat had a crew of three: a navigator, a sonar operator, and an ornithologist who visually observed the number, location (distance and bearing from the boat), and behaviour (diving, surfacing, swimming) of the puffins and other birds at the surface within sonar range. The time was indicated on the sonar screen. The sonar image was recorded on a high-quality s-VHS video recorder for later processing. A microphone was fitted to the video recorder for in situ oral recording of bird data and other relevant information.

Seabat 6012 multibeam sonar

A portable 455-kHz multibeam sonar system (Seabat 6012) (Gerlotto et al. 1999; Nøttestad and Axelsen 1999) was utilized. The high sample resolution of the sonar at short ranges enabled acoustic detection of dense schools of juvenile herring and diving puffins. Lung and air-sac systems of birds are strong backscattering targets in water, owing to the high density and sound speed contrasts between water and air (e.g., MacLennan and Simmonds 1992), and air trapped between the feathers and then released as bubbles during diving produced echo traces in the path of the birds. The transducer was mounted on a 3 m long custom-built aluminium rig, and was kept at a depth of about 1 m. The transducer was fixed at an approximately horizontal transmission angle during observations, but was regularly tilted down to check for deeper concentrations of fish.

The transducer consists of 60 elements mounted in a semicircular ceramic array. Transmission occurs uniformly within a 90° (horizontal) × 15° (vertical) sector (−3 dB) at a pulse length of 0.077 ms (35 cycles). During reception, the array forms 60 individual 1.5° × 15° beams (−3 dB) passing the receivers (114 channels), beamformers (60 channels), detectors (60 channels), and the multiplexer, giving a nominal range accuracy of ±5 cm. The angular accuracy in the horizontal plane is 1.5°. The sonar uses a relative colour code in which blue is the lowest density, followed by green, yellow, and red (highest). The sonar operates at ranges adjustable from 5 to 200 m. The sample volume increases exponentially with range, and the target resolution and signal-to-noise ratio drop correspondingly. The operation range was therefore kept as short as possible (usually ≤25 m), while keeping the observed schools within range. The range was occasionally increased in order to obtain an overview of schools in the vicinity and to track diving puffins. The sonar display is illustrated in Fig. 4.

Video observations recorded over a total of 2 h 33 min were analysed. The method of analysis largely followed that of

Fig. 1. Atlantic puffin (*Fratercula arctica*) returning from a successful hunt for juvenile herring (*Clupea harengus*). Photograph by T. Anker-Nilssen.



Nøttestad and Axelsen (1999), to facilitate comparison of results. The s-VHS tapes were converted to digital video format using a Sony DHR-1000 NP video recorder. The footage was analysed frame by frame using an IBM-compatible computer fitted with Image Pro Plus[®] software and an Oculus frame grabber.

Analysis

Schools were readily identified and mapped at ranges up to 100 m. Individual herring could be distinguished (though not in quantitative terms) at the shortest range (5 m). The horizontal cross-sectional area, A (m²), perimeter, P (m), and relative density of each school were measured directly from the sonar images. No corrections were required because of beam-width distortion (Misund 1993) or other distance-induced biases (Axelsen et al. 2000). The schools were grouped into four predetermined categories according to horizontal area: small ($A \leq 50$ m²), medium (50 m² $< A \leq 250$ m²), large (250 m² $< A \leq 500$ m²), and very large ($A > 500$ m²). These categories are those used by Nøttestad and

Axelsen (1999), but because of differences in packing density, the number of individuals represented by each size unit will be several orders of magnitude higher in schools of juvenile herring than in schools of adults. The horizontal shape of each school (round, elliptical, amorphous) was determined manually. The circularity (Gerlotto et al. 1999) was determined as

$$[1] \quad C = \frac{P^2}{4\pi \cdot A}$$

Predator-prey interactions were recorded at ranges up to 50 m. The puffins only dove when schools of juvenile herring were present, and schools displayed obvious response patterns during these events. Acoustic tracks of the birds (air bubbles) could usually be seen as they swam through the schools. Attacks by predatory fish, both solitary (≤ 3 individuals) and schooling (>20 individuals), were observed with the sonar. The attacking fish were not identified, but they were relatively large (apparently >50 cm long), suggesting that they were gadoid species such as cod (*Gadus morhua*),

Fig. 2. A small, dense school of juvenile herring herded to the surface by one or more predators. Photograph by T. Anker-Nilssen.



haddock (*Melanogrammus aeglefinus*), or saithe (*Pollachius virens*), all known to be important predators on all life stages of Atlantic herring (Toresen 1991; Bergstad and Høines 1998). The numbers of observed avian predators and the duration of the puffin dives (s) were recorded. Horizontal diving speeds ($\text{m}\cdot\text{s}^{-1}$) were calculated from the dive durations and the horizontal distances covered (sonar recordings, Image Pro Plus[®]). Behavioural events were sought in an adaptive manner and hence the estimated puffin attack ratio and response pattern duration ratio may be subject to some bias; nevertheless, they should provide rough indications of the predation level.

Previously documented school-response patterns were observed at ranges up to 50 m, including vacuole, hourglass, *pseudopodium* (formation of a long, slender school appendage), split, *join* (combination of two or more schools into one), herd (Pitcher and Wyche 1983; Nøttestad and Axelsen 1999), and bend (Nøttestad and Axelsen 1999). A new pattern was *density propagation*, defined as rapid shifts (1–5 s) of dense regions within schools. The durations (s) of the response patterns were determined manually.

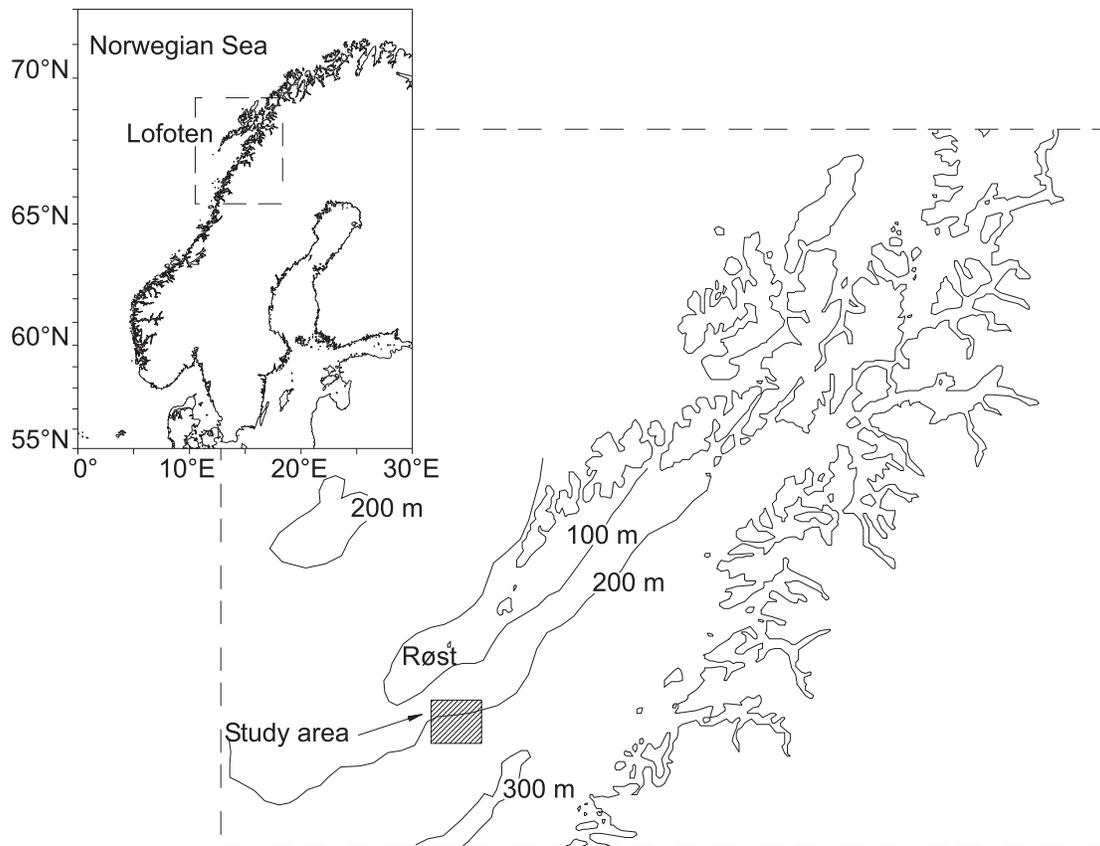
Results

A total of 33 observations of puffin dives covering the full span of the dives were made using the sonar. Dives lasted 25.4 ± 14.7 s (mean \pm SD). In some cases it was possible to confirm visually that the birds had actually preyed on the schools, as their bills were loaded with herring (see Fig. 1). The horizontal diving speed of puffins attacking schools was measured from the sonar recordings as 1.50 ± 0.12 $\text{m}\cdot\text{s}^{-1}$

($n = 5$) over distances of 15–40 m (24 ± 10 m). Although the range of speeds was small (1.36 – 1.67 $\text{m}\cdot\text{s}^{-1}$) and the dives were fairly shallow, the true diving speeds may have been slightly higher, owing to vertical movements of the birds within the beam. Two groups of puffins (about 5 and 10 individuals) that avoided the boat by diving directly away from it were measured at similar speeds (1.47 and 1.43 $\text{m}\cdot\text{s}^{-1}$).

About 56 000 herring were caught with the pelagic sampling trawl of R/V *Michael Sars* during the survey. The total length of the sampled herring ranged from 35 to 63 mm (48.8 ± 4.0 mm (mean \pm SD)), and 37.5% were post-metamorphic. Atlantic herring metamorphose at about 30 mm standard length (or after ~2.5 months) (Fuiman 1989; Bolz and Burns 1996), and as most herring do not school until they are past this stage, the schooling herring observed with the sonar were probably mainly post-metamorphic and somewhat larger than the sampled fish (see Anker-Nilssen and Lorentsen 1990). Herring brought to puffin chicks in Røst during our study were predominantly post-metamorphic, with a total length of 51.2 ± 6.3 mm ($n = 91$) (Anker-Nilssen and Brøseth 1998).

A total of 104 schools of juvenile herring were recorded acoustically. The herring remained in the uppermost 15 m of the water column during the study period. Schools at the surface were frequently observed visually from the main vessel at distances of up to several hundred metres. The recorded cross-sectional areas of the schools varied greatly

Fig. 3. Map of the study area (inset: Norway).

(5–2219 m²), and the shape of the school largely depended on its area (χ^2 test, $\chi^2 = 26.5$, $df = 6$, $p < 0.001$): small schools were predominantly round, while most medium-sized schools were elliptical and the largest schools tended to be amorphous (Fig. 5).

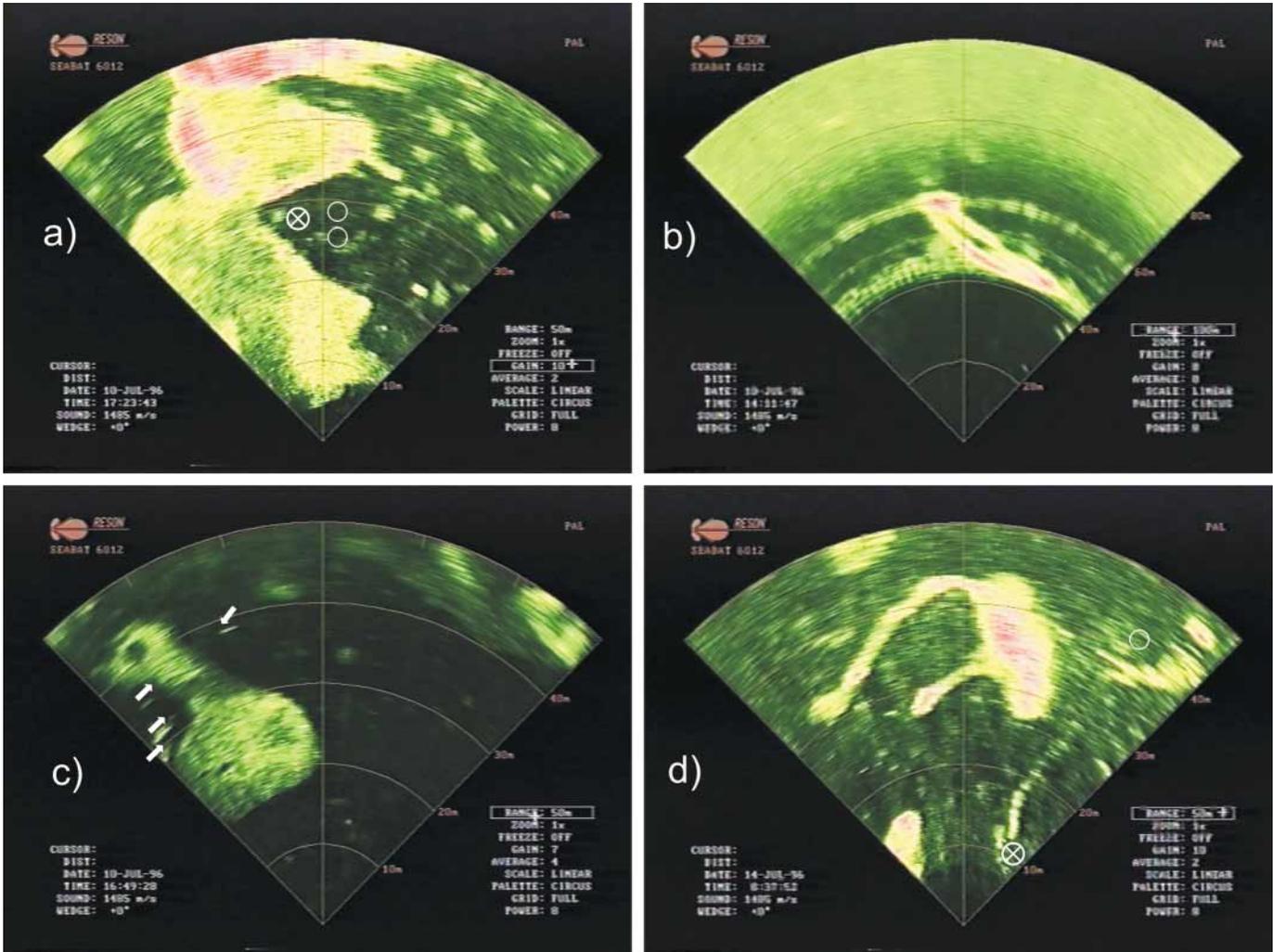
Among the observed schools, 21 were attacked one or more times. Of these, 18 were attacked by puffins, giving an overall school attack ratio of 0.17 for this predator. Four schools were attacked by two types of predators. Table 1 summarizes the measured school areas, relative densities, and circularities for unattacked and attacked schools. There were significant differences in school area between unattacked and attacked schools (Kruskal–Wallis test, $p = 0.000$). Schools attacked by diving puffins were significantly larger (in terms of horizontal cross-sectional area) than unattacked schools (Kruskal–Wallis test with Bonferroni correction, $\alpha = 0.05/10 = 0.005$, $p = 0.000$) (without Bonferroni correction, schools attacked by solitary fish ($n = 4$) were also found to be significantly larger than unattacked schools ($p = 0.020$)). Relative densities did not differ significantly between attacked and unattacked schools (as the distribution of this variable did not deviate from the normal distribution, this conclusion was confirmed using a one-way ANOVA). Attacked schools were significantly less circular than unattacked schools (Kruskal–Wallis test, $\alpha = 0.05$, $p = 0.001$). This effect was most evident among those schools attacked by diving puffins (Kruskal–Wallis test, $\alpha = 0.005$, $p = 0.001$) (without Bonferroni correction, schools attacked by solitary fish were also found to be significantly less circular than either unattacked schools ($p = 0.018$) or schools exposed to puffins at the surface ($p = 0.025$)).

A total of 83 school-response patterns were observed, caused mostly by puffins either diving ($n = 31$) or surfacing ($n = 37$) (Fig. 6). Diving puffins triggered all pattern types, while puffins at the surface were associated with all categories except density propagation and herd. Piscine attacks ($n = 8$) were associated with bend, hourglass, vacuole, density propagation, and split. On some occasions, join ($n = 2$), vacuole ($n = 3$), and bend ($n = 1$) were observed in the absence of associated predators. The most frequent response patterns were bend ($n = 27$), vacuole ($n = 18$), and split ($n = 11$). On average, the herring schools displayed 1.48 response patterns per minute during puffin dives and 0.57 per minute while puffins were swimming at the surface.

Behavioural events observed in each size group of herring schools are listed in Table 2. Bend was the most frequent response pattern. Bend and density propagation were observed in all size groups. Vacuole was not observed in small schools, but was common in large and very large schools. Split was not observed in very large schools, while hourglass, pseudopodium, and join were only observed in medium-sized and large schools. The only observation of herd was made on a very large school (it was possibly interpreted incorrectly because of noise or long sonar range).

The response patterns had a duration of 39.2 ± 6.1 s (mean \pm SE). Responses to diving puffins lasted 42.3 ± 10.8 s, to puffins at the surface 46.5 ± 9.9 s, to fish schools 14.2 ± 5.0 s, and to solitary fish 29.7 ± 15.8 s. The longest lasting response pattern was bend, with an average duration of 73 s, followed by pseudopodium (49 s) and vacuole (30 s) (Fig. 7). Disregarding overlapping incidents, the fraction of

Fig. 4. Display from the Seabat 6012 sonar showing various predator-response patterns in schools of herring: bend (a), vacuole (b), hourglass (c), and pseudopodium (d). Observed predators are indicated (× within a circle: a puffin (*Fratercula arctica*) initiating a dive; open circle: puffin surfacing; arrows: solitary fish). The acoustic trace (air bubbles) from a diving puffin can be seen in d (here × within a circle and open circle should be understood as the start and end point of the same dive, respectively). The sonar range is 100 m in b and 50 m in a, c, and d.



total observation time (2 h 33 min) spent in various predator-response patterns was 33 min 35 s, giving a response pattern duration ratio of 0.22.

Discussion

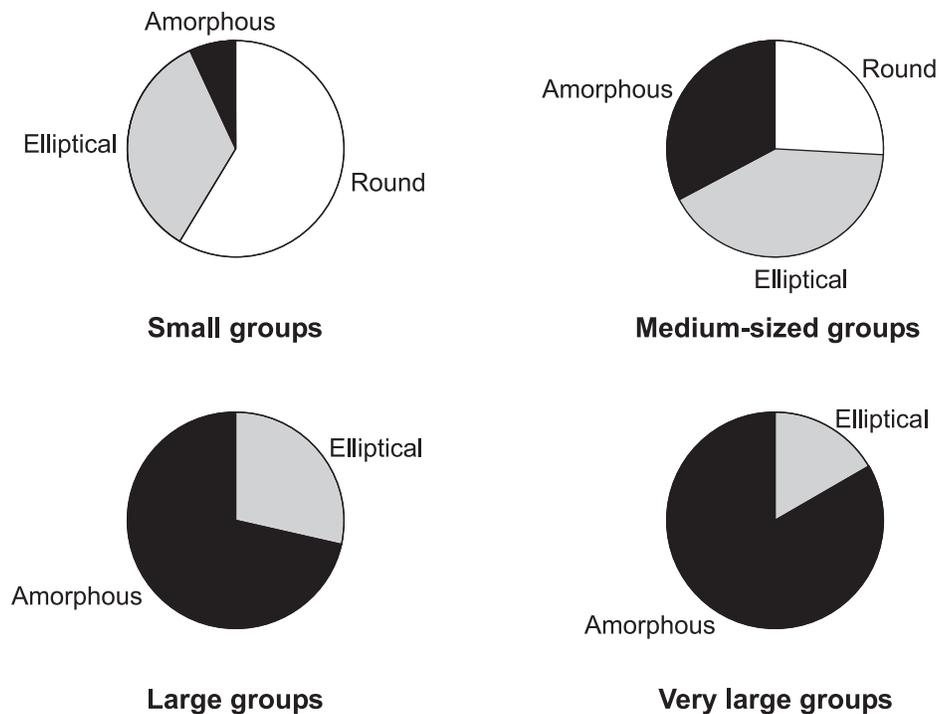
Hunting strategies

Most observed attacks were by puffins. Piscine attacks may, however, be more frequent than is indicated here (Fig. 6), as these observations targeted puffins. Piscine attacks triggered response patterns in most categories, and although the relatively low number of observations makes it hard to evaluate potential differences in types of response caused by puffins and fish, it is evident that the two predator types triggered similar response patterns. The response types caused by puffins and predatory fish in our study largely match those of adult herring attacked by killer whales (Nøttestad and Axelsen 1999).

The puffins maintained high horizontal diving speeds (equivalent to 31.3 ± 2.5 body lengths/s (mean \pm SD) for a

48-mm herring) for relatively long periods (25 s, on average). Puffins appeared to dive independently of each other, without synchronization between individuals. This attacking behaviour is in contrast to the coordinated hunting strategies found in killer whales (Baird and Dill 1995), particularly when they feed on schools of adult herring (Similä and Ugarte 1993; Nøttestad and Axelsen 1999).

The puffins targeted schools with larger horizontal cross sections (mean = 505 m²) than unattacked schools (87 m²) (Table 1). Puffins locate the herring schools visually from the air during their up to 140 km long offshore migrations (Anker-Nilssen and Lorentsen 1990), and the high prevalence of attacks on larger schools was most likely due to the relatively higher detectability of large than small schools from the air. During the survey, large schools at the surface could sometimes be seen at several hundred metres' distance from the vessel, and such schools must be even more visible to flying puffins. Schools of adult herring attacked by killer whales, on the other hand, were much smaller (180 m²) than unattacked schools (820 m²) (Nøttestad and Axelsen 1999).

Fig. 5. Prevalence of shapes within the different size groups of herring schools (see Table 2 for size ranges and sample sizes).**Table 1.** School areas, relative densities, and circularities of unattacked and attacked herring (*Clupea harengus*) schools.

Predator	<i>n</i>	School area (m ²)			Relative density			Circularity		
		Min.	Max.	Mean ± 2SE	Min.	Max.	Mean ± 2SE	Min.	Max.	Mean ± 2SE
No predators	67	5	287	87 ± 16	44	172	126 ± 6	1.0	9.1	2.5 ± 0.4
Puffins										
Surface	15	27	1132	203 ± 147	97	154	133 ± 8	1.2	6.8	2.9 ± 0.9
Diving	14	40	2219	505 ± 365	112	162	132 ± 7	2.0	9.6	4.5 ± 1.5
Fish										
Solitary	2	266	1455	860 ± 1189	36	141	88 ± 104	7.7	9.6	4.4 ± 2.6
Schooling	4	40	353	185 ± 148	115	153	33 ± 16	2.0	8.1	4.1 ± 2.6
All predators	35	27	2219	359 ± 176	36	162	130 ± 7	1.2	9.6	4.1 ± 0.9

Note: The total number of schools recorded was 104. Schools in the no-predators category that exhibited predator-response patterns ($n = 4$) or join ($n = 2$) are excluded from the table in order to avoid bias. Schools that were attacked consecutively by Atlantic puffins (*Fratercula arctica*) and then by solitary fish (Gadoidae) ($n = 1$), or by puffins and then by fish schools ($n = 3$), are included in both relevant predator groups.

This is, however, likely related to the cooperative hunting techniques of killer whales, as small school sizes mean small volumes to encircle and pack together and hence less handling (Nøttestad and Axelsen 1999; Similä and Ugarte 1993).

No differences in relative density between unattacked and attacked schools were demonstrated. Schools of adult herring attacked by killer whales, on the other hand, were much denser than unattacked schools (Similä and Ugarte 1993; Nøttestad and Axelsen 1999). The volume density of schools of juvenile herring is several orders of magnitude higher (thousands of individuals per cubic metre; Fig. 2) than that of schools of adults (1–2 individuals/m³) (Misund 1993), and the necessity for locating particularly dense schools should therefore be low for puffins. Relatively high densities must, on the other hand, be more important for killer whales (Felleman et al. 1991) that locate their prey acoustically (Nøttestad and Similä 2001) and stun or kill the herring with tailslaps before eating them (Similä and Ugarte 1993; Nøttestad and Axelsen 1999).

Schools attacked by puffins were less circular than unattacked schools. While small schools tended to be round, larger schools were gradually more elliptical and amorphous (Fig. 5). This is consistent with the finding that large schools were attacked more frequently than small schools, since predation from diving birds would be expected to disrupt regular schooling patterns. Schools of adult herring attacked by killer whales, on the other hand, were more circular than unattacked schools (Nøttestad and Axelsen 1999). This difference may also be related to the behaviour of the predators. The puffins did not synchronize their attacks and, hence, have intruded into the schools in a less predictable manner than killer whales, which systematically encircle schools in order to maintain *tight-ball* formations (Nøttestad and Axelsen 1999).

School response patterns

The duration of response patterns caused by puffins were much longer (42 s, on average; Fig. 7) than in adult herring

Fig. 6. Numbers of observed response patterns in the herring schools. Note that the number of observations in the predator groups differs from the numbers in Table 1, as several schools displayed multiple response patterns.

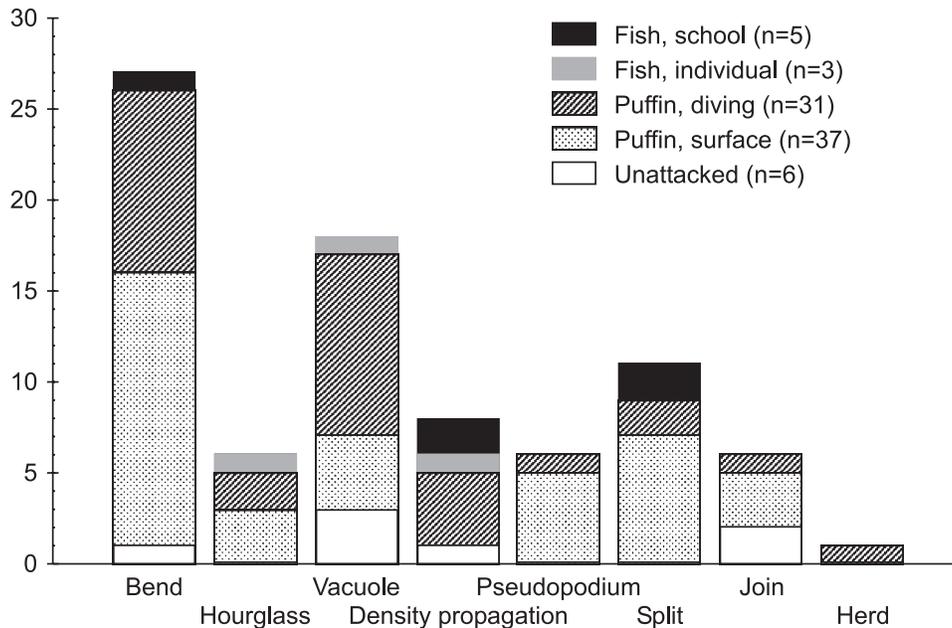


Table 2. Numbers of behavioural events observed for each size group of herring schools.

School size ^a	Bend	Hour-glass	Vacuole	Density propagation	Pseudo-podium	Split	Join	Herd	Total no. of events	Total no. of schools
Small ($A \leq 50 \text{ m}^2$)	1			1		2			4	2
Medium ($50 \text{ m}^2 < A \leq 250 \text{ m}^2$)	8	2	2	3	4	3	4		26	11
Large ($250 \text{ m}^2 < A \leq 500 \text{ m}^2$)	8	4	7	1	2	6	2		30	9
Very large ($A > 500 \text{ m}^2$)	10		9	3				1	23	5
Total	27	6	18	8	6	11	6	1	83	27

^aA is the horizontal school area measured from sonar recordings.

attacked by killer whales (<5 s) (Nøttestad and Axelsen 1999). This probably reflects longer attacks by puffins and piscine predators than by killer whales, but may, at least in part, also be related to the greater anti-predator vigilance of juveniles than adults. Puffins induced response patterns both during dives (1.48 responses/min) and at the surface (0.58 responses/min), strongly suggesting that juvenile herring perceive puffins at the surface as a potential threat and behave in a precautionary manner (Blaxter and Batty 1985; see also Fernö et al. 1998).

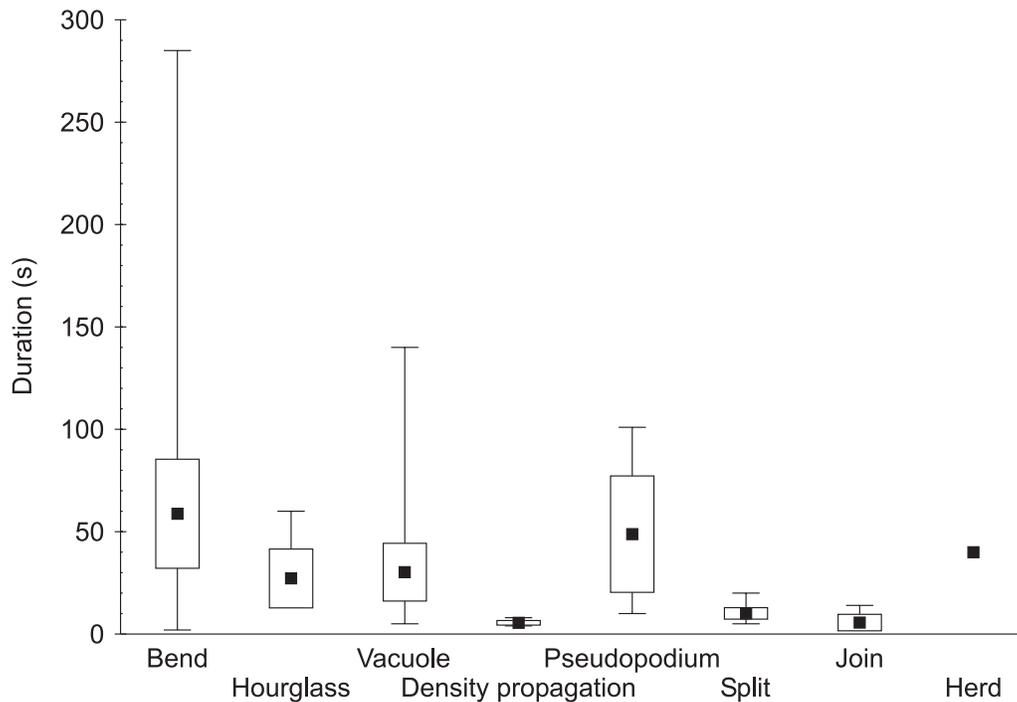
A new observation was intraschool density propagation. Godin and Morgan (1985) showed that the reactions of individuals to a model predator can spread across a fish school faster than the swimming speed of the predator. Such rapid transfer of information about the presence of a predator across an animal aggregation has been termed the Trafalgar effect (Webb 1980; Treherne and Foster 1981) and it can occur in fish schools with high fish densities, as in the present study. Tight ball (see also Breder 1951; Pitcher and Wyche 1983), the dominant response pattern in adult herring attacked by killer whales (Nøttestad and Axelsen 1999), was not observed in our study. This may have been due to the much smaller size of puffins than killer whales and the high fish densities in juvenile herring schools. Density propagation involves a (local) compaction of a part of a school and,

hence, may be viewed as an analogue to a tight-ball formation moving rapidly within a school.

Bend (Fig. 4a) was the most common predator response pattern. The bend shape may be explained by fish at the boundary of a school avoiding predators that are located only on one side of the school. Surprisingly, most bend events were triggered by puffins at the surface, signifying the precautionary behaviour of juvenile herring (Blaxter and Batty 1985). Bend was also a common response pattern in adult herring attacked by killer whales, reflecting the encircling and tailslapping behaviour of the killer whales at the school boundaries (Similä and Ugarte 1993; Nøttestad and Axelsen 1999).

Vacuole (Fig. 4b) was prevalent in large schools. In most cases, diving puffins were detected acoustically within vacuoles. Split, on the other hand, was not very common and was not observed in the largest school category. School fragmentation reduces dilution, one of the main forces behind the evolution of schooling behaviour (Pitcher and Parrish 1993), and is not a desirable outcome for the prey. Conversely, vacuole was rare (5 of 54) and split the most commonly observed pattern (21 of 54) in adult herring attacked by killer whales (Nøttestad and Axelsen 1999). The difference is likely related to the size of the predator relative to the school. The fish should tend to stick together whenever pos-

Fig. 7. Mean durations of recorded response patterns in the herring schools, indicated by ± 2 standard errors (boxes) and minimum/maximum values (whiskers). Note that herd was observed only once.



sible, and the probability of succeeding should be higher in schools attacked by puffins (leading to vacuole) than in similar sized schools attacked by killer whales (split). Additionally, killer whales target smaller schools, encircling them before attacking (Nøttestad and Axelsen 1999; Nøttestad and Similä 2001), while puffins more frequently dive into the schools.

Join was only observed in intermediate-sized schools. Join events lead to bigger schools and therefore beneficial for prey in terms of dilution effect. This may well occur in the absence of predators (e.g., Fernö et al. 1998). Hourglass and pseudopodium were also associated with medium-sized schools, but only when several predators were present outside the school. These response patterns are interpreted as variants of bend, but with predators simultaneously intruding into the school from different angles.

Pretty patterns: complex strategies or the selfish herd?

Predator-response patterns have previously been interpreted as antipredator tactics at the school level (Pitcher and Wyche 1983; Pitcher and Parrish 1993; Pitcher et al. 1996). Pitcher and Parrish (1993) stress the evolution of behaviour that preserves group integrity: "A major reason for compaction (i.e., shoaling fish adhering more closely to conspecifics when alarmed) is to enable the fish to take advantage of cooperative escape tactics. ... Individuals cooperate because these behaviours only work when fish behave as a coordinated group." "Tactics" included response patterns observed in the present study except *bend* (Nøttestad and Axelsen 1999) and density propagation, with the addition of *cruise* and *flash expansion* (Pitcher and Wyche 1983). Pitcher et al. (1996) further conclude that the antipredator behaviour of the herring is adapted to the type of attack, the different patterns hence reflecting a range of tactics.

An alternative explanation is that the different response patterns are different overall outcomes of individual fish avoiding predators in the same way (Vabø and Nøttestad 1997; Nøttestad and Axelsen 1999). Isolation from the school reduces dilution and hence increases predation risk (Pitcher and Parrish 1993). Indiscriminate fast swimming away from predators, with anaerobic exhaustion as a consequence (Videler and Wardle 1991), further endangers fish (Hall et al. 1986). Fish should therefore be expected to stay with the group (Axelsen et al. 2000) and to flee from predators only when facing an immediate threat, i.e., during targeted attack or when one or more predators trespass within the minimum approach distance (MAD) of ~ 15 body lengths (e.g., Jakobsson and Järvi 1978; Pitcher and Wyche 1983). Vabø and Nøttestad (1997) tested this hypothesis using an individual-based simulation model. School patterns, such as bend, split, vacuole, herd, and fountain, were induced by attacking predators, and could hence be explained solely in terms of the selfish herd theory. The model also predicted that split would be more common in small schools, while vacuole would be associated with larger schools. This is in agreement with the results of both the present study and that of Nøttestad and Axelsen (1999), although vacuole was more commonly observed in the former. Consequently, vacuole in large schools may correspond to split (Fig. 3 in Nøttestad and Axelsen 1999) in small schools and hourglass (Fig. 4c) or pseudopodium (Fig. 4d) in medium-sized schools. This is supported by our observations on juvenile herring (Table 2). "Pretty patterns" (see Rohani et al. 1997) observed and modelled in schooling fish and many other flocking animals may, in other words, be produced simply through selfish herd behaviour (Hamilton 1971) without involving any cunning strategies aimed at distracting the predators.

If herring always respond in the same way, why would the

emerging school-response patterns differ with school size? In retrospect, this is exactly what we would expect. Assuming that the prey tend to maintain MAD, all predators will have a “ploughing” effect on schools (Vabø and Nøttestad 1997), and schools that are large compared with the predators will form empty spaces, or vacuoles, around the predators. In smaller schools, predators may suppress too many individuals for group integrity to be maintained (Pitcher and Parrish 1993). Consequently such schools will split, an event that killer whales are believed to exploit (Nøttestad and Axelsen 1999). Hence, school size and the number and behaviour of the predator(s) will determine school-response patterns. Large schools have more potential response patterns, and the increase in complexity with school size may well have a confusing effect on predators. Despite the fact that the large schools in the present study appeared to be more susceptible to predation than the small schools (in contrast to adult herring attacked by killer whales), fish in large schools may have a selective advantage other than the dilution effect that follows sheer numbers, and this constitutes another argument for the evolution of the selfish herd.

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