

Synchronous and vertically undulating swimming behaviour of Atlantic cod *Gadus morhua*

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ABSTRACT: Predatory fish often forage in schools, but observations of actual schooling behaviour in deep-water ecosystems are scarce. In a ranching study of wild Atlantic cod *Gadus morhua* L. in a fjord in east Iceland, observations of peculiar synchronous and vertically undulating schooling behaviour of the fish were recorded. These fish had been conditioned to feed at the sound of a low-frequency signal. On 23 April 1996, prior to a feeding session, several of these cod followed the feeding boat which drifted slowly (0.35 m s^{-1}) into the fjord. During a 24 min observational period and 500 m drift of the boat, 8 to 12 cod were monitored with an echo sounder. These fish, approximately 60 cm long, showed a striking behaviour of synchronized swimming along vertically undulating paths. Six successive undulations were observed, each 40 to 60 m long, 10 to 20 m high and lasting for 2 to 3 min. The mean angles during ascent and descent were between 50 and 60°. The vertical distances between the paths of single fish decreased as the school approached the bottom and increased as it ascended up into the water column. This undulating swimming behaviour may be a foraging strategy meant to sweep part of the water column in search for the depth where prey with a vertically clumped distribution is located. Additionally, synchronized swimming, where visual contact is maintained, may facilitate the detection and capture of pelagic prey.

KEY WORDS: Atlantic cod · Swimming behaviour · Synchronization · Schooling · Feeding strategies · Echolocation

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INTRODUCTION

According to definition, a group of fish that stay together for social reasons is a shoal, and if they also swim in the same direction in a coordinated manner, the group is a school (Pitcher & Parrish 1993). There are 2 main advantages of schooling: defence against predators and enhanced foraging success (Pitcher et al. 1982, Pitcher & Parrish 1993). The many eyes of a school aid in finding patches of prey. Each fish closely monitors the feeding behaviour of its nearest neighbours, and thus the information of a prey patch which is found can spread as a wave through the school and may direct it towards a good feeding spot (Pitcher & Parrish 1993). Once a school of alert and evasive prey is found, the predator may gain advantage by feeding in groups as opposed to solitarily (Major 1978).

Atlantic cod *Gadus morhua* L. is an example of a large predatory fish that may hunt in schools. It is considered a facultative schooler (Partridge et al. 1980), at times foraging alone or in small schools (Björnsson et al. 2010). Sometimes cod may form huge feeding schools of post-spawning and immature fish which appear to maximize search volumes while maintaining visual contact (Rose 1993, DeBlois & Rose 1995, 1996).

Adult cod spend a large part of their time near the seabed but ascend frequently up into the pelagic zone (Pálsson & Thorsteinsson 2003, Hobson et al. 2007). Possibly the fish are resting, digesting or foraging near the bottom but make excursions up into the water column in search of energy-rich pelagic prey (Strand & Huse 2007). High-frequency recording of depth with data storage tags (DSTs) indicates

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that cod vary their vertical depth more frequently than earlier studies were able to show (Heffernan et al. 2004).

Foraging strategies of cod that facilitate the location of the depth of pelagic prey species may have been shaped by evolutionary processes and social learning (Pyke 1984, Brown & Laland 2006). The genetic basis of fish behaviour has been demonstrated (Danzmann et al. 1993, Norton et al. 2011) and it has been shown that animals make decisions about how to find food, based on information produced by others (Brown & Laland 2006).

Farmed and wild fish can be conditioned to aggregate and initiate feeding at the sound of an audio signal (Abbott 1972, Midling et al. 1987, Zion et al. 2007). During a ranching study with wild cod in an Icelandic fjord, the fish had been conditioned with a low-frequency audio signal to feed on trash fish flushed down a feeding pipe (Björnsson 1999). On a few occasions it had been noticed at the end of a feeding session that the cod moved up and down the water column in a wavelike formation. Therefore, on a day when the feeding boat drifted slowly across and out of the feeding area prior to a feeding session, an attempt was made to record this behaviour. We propose that these observations of synchronous and vertically undulating swimming behaviour may give an insight into the normal foraging strategy of wild cod.

MATERIALS AND METHODS

In Stöðvarfjörður, a 7 km long fjord in east Iceland, the swimming behaviour of wild cod which had been conditioned to feed on trash fish was studied with a Simrad EY500 echo sounder coupled to a 38 kHz 12.4° split beam transducer. The transducer was mounted on the end of a 52 mm wide steel pipe attached to the port side of a small (5 gross register tonnage) boat at a depth of 1.0 m. This boat had also been used for feeding the fish. The depths of the echoes were recorded, but due to wave action causing heaving and rolling of the boat, the echoes were also presented as distances from bottom. Special in-house software was used to view and analyse the data.

Prior to the study on 23 April 1996, the fish had been fed, usually 2 to 3 times wk^{-1} for about 10 mo, from July 1995. Fresh or previously frozen trash fish, mainly capelin *Mallotus villosus*, was flushed down a feeding pipe. The pipe was tugged behind the boat with the end maintained at a depth of 23 m. Above the end of the pipe, an underwater video camera was connected with an onboard monitor to see the out-

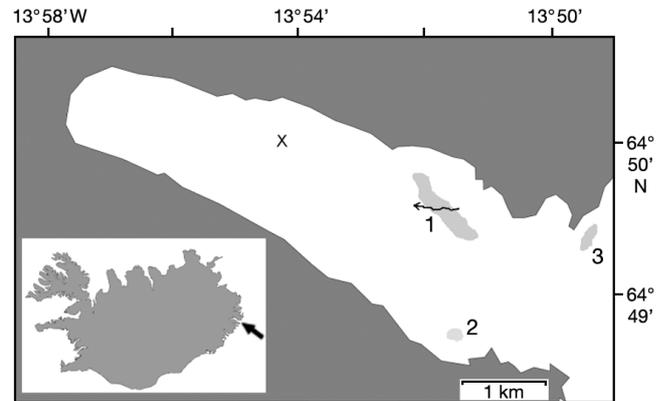


Fig. 1. Study area in Stöðvarfjörður, east Iceland. Land is indicated in grey and the 3 numbered feeding areas in light grey. The arrow in Feeding Area 1 shows the drift of the boat during the observational period (13:57 to 14:21 h), and × marks the location of the temperature recording devices moored at 5 and 30 m depth

coming feed and the fish swimming behind. The feed was deployed in 3 distinct feeding areas near the outer part of Stöðvarfjörður (Fig. 1). During feeding, a 160 Hz audio signal was given in short pulses with an underwater transmitter (Björnsson 1999, 2002).

At the time of the study, the fish had not been fed for 4 d and were thus highly motivated to feed. As the boat approached the innermost feeding area, the audio signal was activated and the boat manoeuvred slowly eastward across the feeding area. Then the propeller was uncoupled to let the boat drift for about 24 min and 500 m with an easterly moderate breeze back across and out of the feeding area, from a depth of about 30 to 45 m. The feeding pipe was not deployed and no feed released, whereas the conditioning sound signals were constantly emitted during the drift. The computer collecting the echo sounder data was also connected to a GPS device used to estimate the location of the boat as it drifted into the fjord (Fig. 1). These measurements were used to calculate the speed of the boat.

RESULTS

Several cod followed the feeding boat as it drifted slowly (0.35 m s^{-1}) into the fjord. On the echo sounder, the fish were seen to swim synchronously up and down the lower part of the water column in an undulating manner for about 15 min and 300 m distance (Fig. 2). At least 6 successive undulations were observed, each lasting for 2 to 3 min, corresponding to a horizontal distance of 40 to 60 m and vertical distance of 10 to 20 m (Fig. 2a). The fish were able to

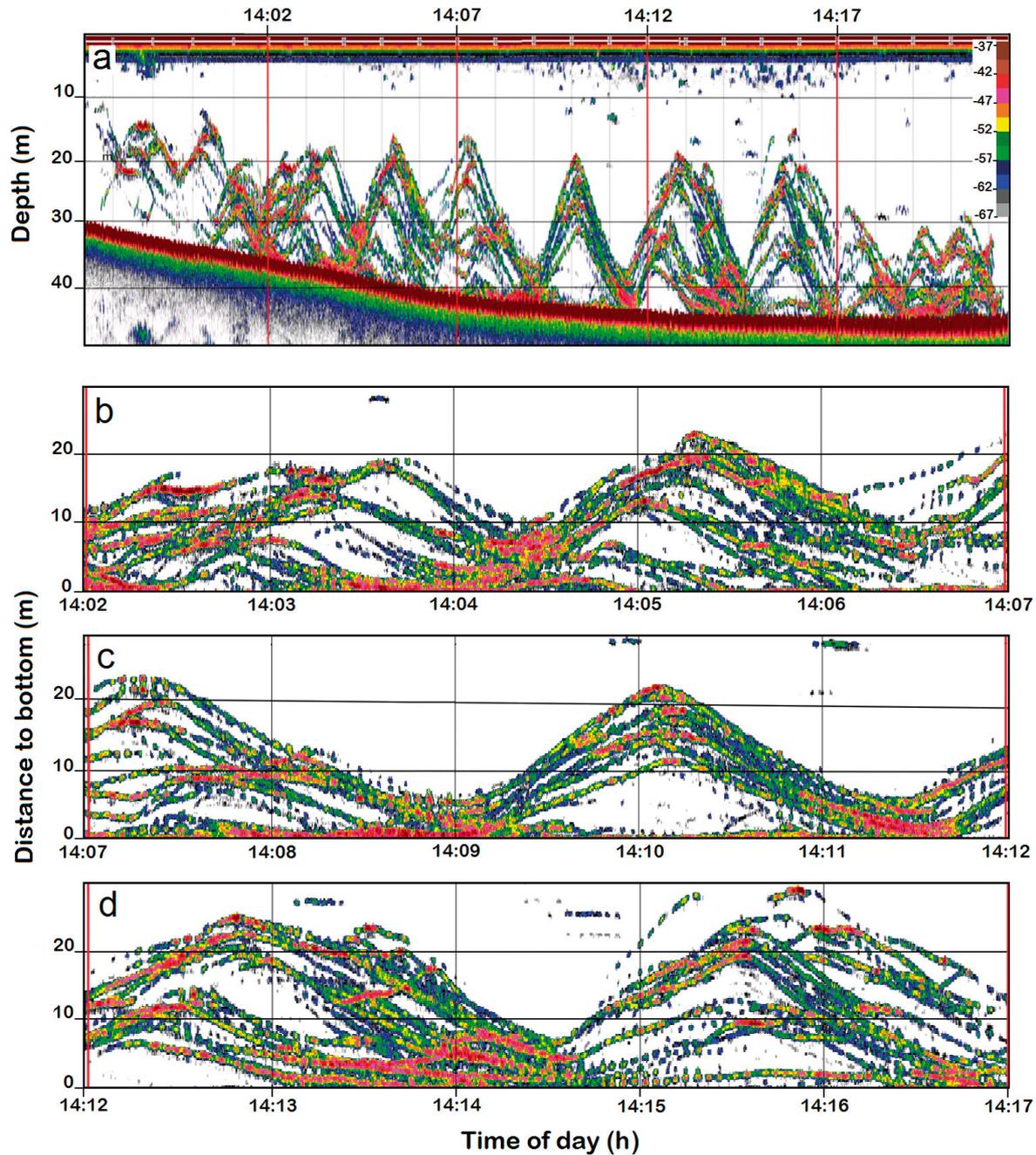


Fig. 2. *Gadus morhua*. Synchronized and vertically undulating swimming behaviour of several cod recorded during a slow drift of the boat (0.35 m s^{-1}). The echo strength S_v dB ref 1 m^{-1} is indicated with the colour bar at the top. (a) Overview of the echoes for the time 13:57–14:21 h, and details of the 5 min intervals starting at (b) 14:02, (c) 14:07, and (d) 14:12 h. Red vertical lines in (a) mark the 3 expanded views in (b–d). Note that in (b–d) the echoes are presented as distances from the bottom

keep up with the boat, as tracks of individual fish could be followed for a considerable length of time (Fig. 2b–d).

The mean \pm SD angle during ascent and descent, measured for individual continuous tracks, were $53 \pm 14^\circ$ ($n = 140$, mode at 55 to 60°) and $51 \pm 15^\circ$ ($n = 146$, mode at 60 to 65°), respectively. The tracks ranged

from 5 to 68 transmissions from the echo sounder, equivalent to 0.4 to 5.4 m in the horizontal plane. Initially, there was some irregularity in the swimming paths, with some fish descending earlier than others, often those fish that were positioned lower in the school (Fig. 2b). The 4th undulation was the most regularly synchronized, with all fish peaking at a

similar time (Fig. 2c). In the 5th and 6th undulations, there was again some irregularity (Fig. 2d).

Usually the fish maintained their relative vertical position within the school, and the fish in the highest position made the largest undulations. The average vertical distance between the fish increased during the ascending phase and decreased during the descending phase (Fig. 2b–d), becoming about twice as high on the peaks (1–2 m) as in the troughs (0.5–1.0 m). The uppermost fish were 7 to 13 m above bottom in the troughs and 20 to 25 m above bottom on the peaks (Fig. 2b–d). The signal was strongest at the top and bottom of the track where the fish must have been in a near horizontal position.

The width of the acoustic beam increased with depth from 4.3 to 6.5 and 8.6 m at 20, 30 and 40 m depth, respectively. The corresponding cross sectional areas were 14.6, 33.0 and 58.6 m². At and near the peaks, where the acoustic tracks of individual fish could be most easily distinguished, 8 to 12 fish were recorded within the beam. The volume within the acoustic beam from 20 to 35 m depth was about 450 m³ and thus each cod occupied on average ~45 m³ of seawater.

It was assumed that cod of ~60 cm mean length were responsible for the undulating tracks and their ground speed may thus have been ~0.6 body lengths (bl) s⁻¹. Cod was the only species seen with the underwater camera during previous feeding sessions and the only species in 2 fish samples collected in the fjord 10 d prior to the study. In a sample taken with conventional hand lines in feeding areas 1 and 2, the mean ± SD length of cod was 54 ± 9 cm (n = 109, range = 36–82 cm). In a sample taken with gill nets (152 mm mesh size) set at known spawning grounds near the south coast, 2 km from the head of the fjord, the mean length was 67 ± 7 cm (n = 40, range = 57–95 cm). In a larger sample taken with a Danish seine (155 mm mesh size), a less size-selective gear, on the same spawning grounds in April of the following year, the mean length was identical (67 ± 8 cm, n = 196, range = 46–104 cm). Observations with the underwater video camera on feeding days indicated a growing number of large and hungry fish in the schools during the first weeks of April.

The tidal currents inside the fjord were most likely slow at the time of the study, since there was only a 1.2 m height difference between high tide at 6:06 h and low tide at 12:22 h. The undulations were observed 100 to 115 min after low tide when the fjord was beginning to fill, most likely causing a slow current along the swimming path of the fish. The fish that showed the greatest undulations were

swimming about 25% faster and the fish showing the smallest undulations about 10% faster than the ground speed of the boat. Assuming no currents in the study area, the swimming speeds were approximately 0.6 to 0.7 bl s⁻¹, but as the fish most likely had a weak current in their back, the actual speeds through water may have been less. There was no stratification in the fjord, and the temperature was almost the same at 5 m (2.4°C) as at 30 m depth (2.3°C). Visibility, as judged with the underwater camera, was good. Secchi depth was not measured in the study, but in several recent years it has been found to range between 5 and 10 m in Stödvarfjörður in April–May.

DISCUSSION

The free-ranging cod that were conditioned to feed on trash fish 2 to 3 times wk⁻¹ probably remained near the seabed between feeding sessions, apparently in a more or less horizontal position. This was reasoned from observations with the echo sounder of upward moving traces of fish from the bottom every time the feeding boat approached the feeding area. On the day of the study, 23 April 1996, a cod school followed the boat as it drifted through and out of the feeding area. It recognized the conditioning sound and attempted to locate the depth of the presumed feed by swimming synchronously up and down in the water column in an undulating manner. The mean tilt angles during ascent and descent were much higher, 50 to 60°, than previously reported for cod, 1 to 10° (McQuinn & Winger 2003).

The question arises whether these records of undulating movements are artificial due to the anthropogenic feeding and conditioning of the fish or whether they represent the normal behavioural repertoire of wild cod. Although our study cannot answer this question, it can point out the adaptive advantage of such behaviour and refer to studies that support its existence. Furthermore, if wild cod undertake these oscillating vertical movements in nature, why have they not been reported before? The main reason may be the difficulty in measuring this phenomenon.

In most acoustic studies, the research vessel travels at a much faster speed than the fish (Rose et al. 1995) and therefore such undulating tracks of individual fish will not be picked up. If a research vessel could be manoeuvred accurately enough to follow a single target, there is the danger that the sound from the engine would disturb the natural foraging behaviour

of the fish (Misund et al. 1992, Rosen et al. 2012). Also it is quite probable that undulating foraging behaviour of cod may only occur under certain conditions, e.g. depending on type of prey, time of year or time of day.

Cod fitted with acoustic tags have been tracked in the southern North Sea for periods up to 52 h from the time of release (Arnold et al. 1994), but the positioning errors with this method are too large to study high-frequency undulations such as those observed in our study. Potentially, DSTs could measure such vertically undulating behaviour, if depth was recorded with sufficient frequency (Heffernan et al. 2004). However, most published studies with DSTs have used measuring frequencies that are too low to detect high-frequency vertical changes (2 h: Godø & Michalsen 2000; ≥ 40 min: Pálsson & Thorsteinsson 2003; ≥ 10 min: Thorsteinsson et al. 2012). Yet, DSTs would not be suitable for detecting synchronization in swimming, as their horizontal location is usually unknown.

Cod with DSTs often perform fast vertically undulating swimming behaviour with no systematic pattern, which has been suggested to represent food searching activity (Godø & Michalsen 2000). Estimated rates of vertical movements of cod are highly dependent on the frequency at which depth is recorded. For Barents Sea cod, the mean ascent rate was 174, 90 and 41 m h⁻¹ for recording frequency of 15, 30 and 60 min, respectively (Heffernan et al. 2004). These results support the suggestion that vertically undulating searching behaviour is a natural foraging strategy of wild cod. Fish have been found to undertake oscillating vertical migrations in accordance with internal waves (Kaartvedt et al. 2012), but this cannot explain the undulating movements of cod in the present study, as the seawater in this relatively short, shallow and open fjord was vertically mixed at the time of the study and thus no internal waves were present.

Atlantic cod of the size in the present study (50 to 70 cm) feed mainly on pelagic prey, especially capelin, euphausiids and northern shrimp *Pandalus borealis* (Lilly 1994, Worm & Myers 2003, Björnsson et al. 2011, Pálsson & Björnsson 2011). This requires 3-dimensional searching. During a large-scale feeding migration of Atlantic cod along the bottom of the 350 m deep Newfoundland shelf, fish in 50 to 150 m thick schools appeared to maintain visual contact (Rose 1993). During these feeding migrations at relatively low light levels, each cod occupied on average 66 to 83 m³ of seawater (Rose 1993). In our study, conducted in shallow and clear water, the cod clearly

maintained visual contact as each cod occupied only about 45 m³ of seawater in midwater and less than that near the bottom.

The adaptive advantage of vertically undulating swimming behaviour may be to facilitate the location of the depth where prey aggregate. Usually, the pelagic prey of cod form aggregations that have dimensions that are orders of magnitude larger in the horizontal than vertical plane (Ressler et al. 2005, Olafsdottir & Rose 2012). Therefore, vertical searching may be an important strategy in locating these prey patches. For the largest cod stocks in the North Atlantic, capelin is the most important prey (Taggart et al. 1994, Dolgov 2002, Pálsson & Björnsson 2011) and therefore cod may have evolved a foraging strategy to facilitate detection of capelin schools.

Commonly, the horizontal diameter of conglomerated migratory schools of capelin is measured in hundreds of km (Vilhjálmsson 1994, 2002, Huse et al. 2004), whereas their vertical diameter usually ranges from 50 to 150 m (Mowbray 2002, Davoren et al. 2006). Therefore, it may be an effective foraging strategy for cod to swim up and down in the water column to search for pelagic prey, such as capelin and euphausiids, that are spread out in a relatively thin layer. We conclude that synchronous and vertically undulating swimming may be part of the normal behavioural repertoire of wild cod.

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