



# High-frequency depth changes in Atlantic cod studied with implanted data storage tags

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**ABSTRACT:** The main aim of this study was to investigate high-frequency depth changes in wild adult Atlantic cod *Gadus morhua*. The analysis was based on depth measurements collected with implanted data storage tags. The study was part of a ranching project carried out in an Icelandic fjord. In the project, net bags with frozen fish were regularly provided during the daytime at 4 stations where some cod formed distinct 'herds' ('herd cod') that did not mingle much with the rest of the unconditioned cod in the fjord ('wild cod'). After tagging, some of the cod resumed life in the herds, whereas other cod left the herds immediately. On 20 subsequent Mondays, the electronic tags were programmed to measure at the highest frequency (every 30 s), and these results were used to study high-frequency depth changes in 4 wild cod and 4 herd cod, the latter as a control group. Several times, rapid cyclical depth changes were observed in both groups. This behaviour, which sometimes lasted for hours, was highest during dawn and dusk in wild cod but peaked during daytime in herd cod after deployment of the feed bags. The occurrence and properties of these vertical undulations varied greatly between fish, dates, and time of day. Most commonly, the periods of the cycles varied between 1 and 4 min and the heights between 2 and 4 m, but there were examples of much larger undulations. The results indicate that wild adult cod swim along vertically undulating paths when searching for prey, most likely to optimize foraging.

**KEY WORDS:** *Gadus morhua* · Foraging behaviour · High-frequency depth changes · Data storage tags · DSTs · Spectral analysis · Diel vertical migration

## 1. INTRODUCTION

Evolution has shaped the foraging behaviour of predators towards optimizing the search for prey over the long run (Pyke 1984), but many free-ranging predators are thought to make foraging decisions with little, if any, knowledge of present resource distribution and availability (Stephens & Krebs 1986, Sims et al. 2008). Due to technical difficulties in measuring movements of marine predators, their optimal foraging strategies remain largely unresolved. The development of data loggers attached to fish has allowed depth changes to be recorded with high frequency, but, in most cases, it is not possible to measure accurately the horizontal movement of free-swimming individuals. Data sets in which the depth of a predator was recorded every minute suggested

that several different species of marine predators were adopting Lévy-type foraging behaviour, which is a random short-distance search at a given depth with occasional longer depth changes to continue searching at a new depth (Sims et al. 2008). Optimal search theory predicts that predators should adopt Lévy movements where prey is sparse and distributed unpredictably (Humphries et al. 2010).

Low-frequency depth changes, measured in hours, have been studied extensively for many fish species, such as salmonids (Brett 1971), various species of tuna (e.g. Holland et al. 1990, Furukawa et al. 2014), a benthic shark (Sims et al. 2006), and Atlantic cod *Gadus morhua* (e.g. Hobson et al. 2007, Espeland et al. 2010, Freitas et al. 2015). However, studies of high-frequency depth changes in fish, measured in seconds or a few minutes, are much less common.

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Atlantic cod is a dominant top predator in the North Atlantic (Holt et al. 2019). Its predatory impact and foraging behaviour have been extensively studied with various approaches, e.g. using stomach content analysis (Pálsson 1983, Lilly 1994, Björnsson et al. 2011b), acoustic measurements (Rose 1993, Björnsson & Reynisson 2013), acoustic tags and triangulation (Løkkeborg 1998, Løkkeborg & Fernö 1999), data storage tags (DSTs) (Neat et al. 2006, Sims et al. 2008, Espeland et al. 2010), modelling (Huse et al. 2004), and feeding experiments (Björnsson 1993, Björnsson et al. 2018). Still, relatively little is known about the foraging strategy and the shape of the search path adopted by adult cod.

Cod are opportunistic predators that feed on a variety of prey at different times of the 24 h period depending on prey availability (Mattson 1990). Cod can capture fast-swimming prey and usually catch one prey at a time by individually directed attack (Mattson 1992). Juvenile cod feed mainly on crustaceans and various other invertebrates, but with increasing age and size their diet consists increasingly more of fish, especially capelin *Mallotus villosus* and other pelagic fish species in the North Atlantic (Pálsson 1983). Adult cod spend a large part of their time near the seabed, where they may be resting, digesting, or foraging on benthic animals or demersal fish, but occasionally they ascend into the pelagic zone to feed on energy-rich pelagic prey (Pálsson & Thorsteinsson 2003, Hobson et al. 2007, Strand & Huse 2007). Generally, cod stay deeper during the day than during the night (Espeland et al. 2010).

Peculiar swimming behaviour of Atlantic cod was observed in a ranching study in east Iceland (Björnsson 2011). These wild cod had been conditioned to feed at the sound of a low-frequency signal. On one occasion, several fish followed the feeding boat while it drifted slowly into the fjord with sound emission turned on but no feeding taking place. During a 24 min observational period, several cod were monitored with an echo sounder with pings every 3 s. These 60 cm long fish displayed synchronized horizontal swimming along vertically undulating paths. Each undulation was 40–60 m long with a height of 10–20 m and a period of 2 to 3 min (Björnsson & Reynisson 2013).

This incidental observation of conditioned cod suggested that similar searching behaviour might occur in wild cod undis-

turbed by human activity. The opportunity to answer this question came during a 21 mo ranching experiment in another Icelandic fjord (Björnsson 2011). Several cod were implanted with electronic tags programmed to measure depth every 30 s on 20 consecutive Mondays. About half of the tagged cod joined the cod aggregations ('herds') that remained at the feeding stations in shallow and warm water close to shore ('herd cod'). The remaining cod left the feeding stations immediately after tagging and resumed normal life in deep and cold water ('wild cod'). In the analysis of high-frequency depth changes, records of 4 wild cod and 4 herd cod were studied, with the herd cod used as a control group.

## 2. MATERIALS AND METHODS

The behaviour of adult Atlantic cod was studied in tagged fish that were captured, implanted with electronic tags, and released. Subsequently, data from the tags, returned by commercial fishermen, were downloaded for analysis.

### 2.1. Study site and ranching experiment

The study was part of a ranching project in Arnarfjörður, a 40 km long fjord on the northwest coast of Iceland. Most of the fjord is about 100 m deep with steep subsurface slopes (Fig. 1). In winter, the water column is well mixed with a temperature of 1–2°C and oxygen saturation of 90–100%. During summer

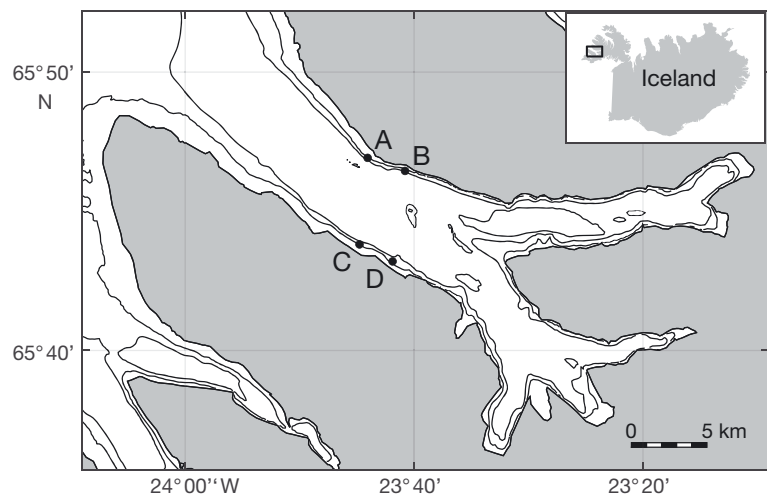


Fig. 1. Arnarfjörður, Iceland, with depth contours of 20, 50, and 100 m and the locations of the 4 feeding stations (A–D) where the herds of cod were formed

and autumn, the water column is stratified with a warmer upper layer, 50–60 m deep, with a maximum temperature of 10–12°C in summer. The bottom layer remains colder, 2–5°C in summer and 4–7°C in autumn, and with oxygen saturation gradually decreasing to 40–60% before the onset of winter mixing in November. There are moderate semi-diurnal tidal currents in the fjord with neap tide about 1.2 m and spring tide about 3.7 m (Macrander et al. 2021).

The purpose of the ranching experiment was to explore the potential for increasing the growth rate of wild cod and developing efficient and environmentally friendly fishing (Björnsson 2011, 2018, Halldórsson et al. 2012). In the experiment, lasting from April 2005 to December 2006, a total of about 260 t of pelagic fish were dispensed at 4 stations located close to shore, 2 on the north side (A and B) and 2 on the south side of the fjord (C and D), at a depth of 20–30 m (Fig. 1). The 4 so-called ‘herds’ were entirely formed by local cod attracted by the feed provided.

The feed, frozen in blocks, was put in bags made of trawl netting. The bags were hung about 15 m from the surface, well above the bottom to avoid benthic scavengers. For the first few months, feed was delivered 5 times  $\text{wk}^{-1}$  and after that usually 2 to 3 times  $\text{wk}^{-1}$ . The time of feeding was variable, both with respect to the day of the week (Monday–Friday) and the time of day (09:00–17:00 h). No specific sound signals were emitted during feeding, but the herd fish clearly associated the noise from the engine and propeller of the feed boat with the arrival of feed. For more details about the ranching study, see Björnsson (2011).

## 2.2. Electronic tags and fish tagging

In the study, 70 cod were tagged with DSTs from Star-Oddi ([www.star-oddi.com](http://www.star-oddi.com)) and 31 of those were also tagged with acoustic transmitter tags from Vemco ([www.vemco.com](http://www.vemco.com)). Similar numbers of tagged cod were released in each herd. Two types of DSTs were used, DST-centi and DST-milli, both for studying hourly changes in depth but only the former type, which was larger and had larger memory, was used to study high-frequency depth changes, which are the focus of this paper.

The DSTs measured and recorded temperature (°C) and pressure, converted to depth (m), whereas the signals from the transmitter tags were recorded by receiver buoys anchored near the feeding sta-

tions. On 2–10 June 2005, 39 cod, captured with a shrimp trawl outside the herds, were surgically implanted abdominally with DSTs, 29 with DST-milli and 10 with DST-centi. The DST fish were immediately released after tagging, but 91% of the retrieved fish left the herds immediately and resumed their wild foraging behaviour in deeper and colder water (Björnsson 2019).

On 24–27 July 2006, 31 cod, captured with a lift net inside the 4 herds, were implanted abdominally, both with a DST tag and a transmitter tag: 17 cod with DST-milli and 14 cod with DST-centi. The fish were released after a 2 d recovery period in subsurface cages placed in the vicinity of the herds (Björnsson et al. 2011a). Most of the retrieved fish (93%) resumed their life in the herds in the shallower (15–35 m) and warmer (6–10°C) water, whereas the rest occupied the deeper (60–90 m) and colder (3–6°C) area of the fjord (Björnsson 2019). In 2006, there were 2 receivers near each feeding station which recorded the presence of the fish with transmitter tags. Surgery was performed in compliance with the rules set by the Committee on Welfare of Experimental Animals established by the Ministry of Agriculture, Reykjavík, Iceland. A detailed description of the electronic tags, receivers, and tagging procedure is given in Björnsson (2019).

To monitor rapid changes in depth, the DSTs were programmed to measure intermittently at a high frequency, in such a way that the memory would last for months. For DST-centi, depth was recorded every 0.5, 1, and 10 min on Mondays, Tuesdays–Wednesdays, and Thursdays–Sundays, respectively, to study not only high-frequency depth changes but also hourly and daily variations which could be used to understand low-frequency depth changes, such as diel changes in depth. In 2005, the DST-centi began to measure on 13 June and the memory was filled on 1 November 2005. In 2006, the DST-centi began to measure on 25 July and the memory was filled on 18 December 2006, and each tag stored a maximum of 130 957 depth records.

For DST-milli, the measuring frequency alternated from week to week between 20 and 10 min, but every 4 wk the measurements were recorded once every minute for 24 h. In 2005, the high-frequency measurements occurred on 20–21 June, 18–19 July, 15–16 August, 12–13 September, and 10–11 October (09:27–09:27 h). In 2005, the DST-milli began to measure on 6 June and the memory was filled on 22 October 2005. In 2006, the high-frequency measurements occurred on 7 August, 4 September, 2 October, 30 October, and 27 November (00:00–00:00 h). In

2006, the DST-milli began to measure on 24 July and the memory was filled on 9 December 2006, as each DST-milli stored maximally 21 724 depth records. The accuracy of the DST clock was  $\pm 1$  min per month (www.star-oddi.com).

### 2.3. Data analysis

A total of 39 DSTs were retrieved, but one-third of those were not used in the analysis mainly due to limited recording time because of either premature capture of the tagged fish or a battery problem. Of the 26 remaining DSTs, 11 and 15 were deployed in 2005 and 2006, respectively, 40% DST-centi and 60% DST-milli. Many of the DSTs showed some deviation from zero depth at sea level (onboard the boat) and thus the respective depth records were corrected with this offset, e.g. if 5 m were measured on average at sea level for a given tag then 5 m were subtracted from every measurement of that tag (see Björnsson 2019).

Both DST-centi and DST-milli were used to estimate the diel change in depth for August, September, and October, the average depth of each hour calculated separately for each day and each fish, to account for different measuring frequencies. Civil dawn and civil dusk (the centre of the sun  $6^\circ$  below the horizon) was calculated from date and the latitude and longitude of the study area. In the spectral analysis (see below), data from hourly windows were assigned according to the average height of the sun during that time period (sun height above  $0^\circ$ : 'day'; sun height between  $0^\circ$  and  $-6^\circ$ : 'dawn/dusk'; sun height below  $-6^\circ$ : 'night').

A total of 8 DST-centi, from 4 wild cod tagged on 8–9 June 2005 and 4 herd cod tagged on 24–25 July

2006, collected high-frequency data during all 20 consecutive Mondays when the DSTs were programmed to measure every 30 s. The analysis of high-frequency depth changes was limited to data from these 8 tags. The 8 fish did have several days to adjust from tagging to the first day of high-frequency recording, namely 11–12 and 6–7 d for the wild and herd cod, respectively, and all 20 consecutive Mondays were included in the analysis. 'Hours of high activity' were defined as those with average depth change  $\geq 1.0$  m per 30 s. Assuming that these depth changes were caused by active swimming, the horizontal distance (h) travelled by fish ascending (or descending) 1.0 m was calculated from an assumed tilt angle ( $\alpha$ ) by the following formula:  $h = \cos \alpha / \sin \alpha$ , since tilt angles were not measured in the present study.

The wild cod used in the analysis were generally smaller than the herd cod (Table 1). Fish sampled and dissected at the time of tagging showed that the herd cod collected with the lift net inside the herds in July 2006 were generally larger and with much larger livers than the wild cod collected with the shrimp trawl in deeper water outside the herds in June 2005; the liver index calculated as a percentage of gutted weight was on average 5 and 20% for wild and herd cod, respectively (Björnsson et al. 2010).

In the spectral analysis, to analyze the vertical movements of the cod in an objective way, short-time Fourier transforms (STFTs) (Oppenheim et al. 1999) were calculated in MATLAB for oscillations with periods between 1 and 4 min to focus on high-frequency depth changes. A comparatively narrow Hamming window of 4 times the period was chosen to study the high-frequency depth changes in the fish. The STFT output was binned in 5 min intervals, and mean amplitude of the oscillations during each

Table 1. Information on the 4 wild (W) and 4 herd cod (H) used for the analysis of high-frequency depth changes: identification number of DSTs (Number), tagging date (Tagging, dates given as d.mo.yr), tagging location (Location 1), tagging length (L1), tagging weight (W1), capture date (Capture), capture length (L2), capture location (Location 2). For tagging, the fish were collected with a shrimp trawl in 2005 and a lift net in 2006. Breidafjörður is a large bay on the west coast of Iceland. Capture date for cod C397 H is missing; nd: no data

Number	Tagging	Location 1	L1 (cm)	W1 (g)	Capture	L2 (cm)	Location 2
C1279 W	8.06.05	Outside herds	54	1527	13.01.06	nd	Arnarfjörður
C1315 W	8.06.05	Outside herds	59	1985	28.06.06	65	Arnarfjörður
C1366 W	8.06.05	Outside herds	59	2075	7.09.06	64	Arnarfjörður
C1455 W	9.06.05	Outside herds	66	2702	16.03.06	70	Breidafjörður
C397 H	25.07.06	Herd D	65	2887	2007	75	Unknown
C417 H	24.07.06	Herd A	79	5136	16.01.07	87	Breidafjörður
C480 H	24.07.06	Herd A	61	2590	16.02.07	67	Breidafjörður
C611 H	24.07.06	Herd A	61	3160	16.01.07	64	Arnarfjörður

Table 2. Depth changes in 8 cod implanted with data storage tags in Arnarfjörður. Depth was recorded every 30 s on 20 consecutive Mondays for 4 wild cod from 20 June to 31 October 2005 and 4 herd cod from 31 July to 11 December 2006. Here, the depth changes ( $\Delta D$  per 30 s), rounded to nearest meter, are tabulated. For each fish, there were 57 580 depth changes

$\Delta D$ (m)	Wild C1279	Wild C1315	Wild C1366	Wild C1455	Herd C397	Herd C417	Herd C480	Herd C611
0	29898	36809	27398	35526	36879	37782	38666	36636
1	20494	16196	20964	18213	15445	15577	14341	15553
2	5703	3436	7209	2726	3705	3001	3109	4187
3	1084	845	1361	772	1038	786	890	809
4	247	218	390	232	285	277	373	267
5	95	60	156	64	157	93	116	93
6	27	7	63	28	39	48	43	20
7	12	6	22	8	14	12	21	9
8	5	1	9	5	8	3	9	3
9	4	1	3	2	6	1	4	2
10	2	1	4	1	2	0	2	0
>10	9	0	1	3	2	0	6	1

interval was calculated. The fish were considered 'active' during each 5 min interval if vertical movements with a period between 1 and 4 min had a mean amplitude of  $\geq 1$  m (or peak-to-peak vertical distance of  $\geq 2$  m). 'Active time' was defined as the sum of active 5 min intervals per hour. 'Active hours' were defined as those with  $\geq 30$  min of active time, 'dominant period' was defined as the most common period during active time, and 'dominant amplitude' was the mean amplitude in the dominant period.

### 3. RESULTS

#### 3.1. Depth changes

For data collected every 30 s for 20 Mondays, depth changes  $< 0.5$  m accounted for 48–64 and 64–67% of all movements of 4 wild and 4 herd cod, respectively (Table 2). Depth changes of 0.5–1.5 m accounted for 28–36 and 25–27% and 1.5–4.5 m accounted for 7–16 and 7–9% of all movements of wild and herd cod, respectively. Larger depth changes within 30 s intervals were much less common (Table 2); changes greater than 10 m were rare events (1:20 938) and greater than 20 m extremely rare events (1:230 320).

A total of 22 depth changes larger than 10 m per 30 s were observed, 13 made by wild and 9 by herd cod (Table 3). Most of the 12 largest depth changes (13–29 m) were sudden dives by 1 of the wild cod (C1279). Two large ascents (18.8 and 15.0 m) by 2 wild cod (C1279, C1455) were immediately followed by large dives (14.8 and 12.4 m). The 22 largest depth

changes occurred equally frequently at night and day, but the 4 largest dives were during the night and the highest ascent during the day (Table 3).

In the study, during summer and early autumn, the wild fish occupied deeper areas (70–90 m) with lower temperatures (3–6°C), whereas the herd fish stayed in shallower areas (15–35 m) with higher temperatures (6–10°C). There was a much greater diel change in depth of wild than herd cod. The wild cod increased their average depth by 8–10 m from night to day, in August (Fig. 2a), September (Fig. 2b), and October (Fig. 2c). In contrast, the herd cod decreased their average depth by about 1 m from night to day during these 3 months (Fig. 2).

By estimating the hourly activity of the fish as mean depth changes per 30 s, the wild cod were most active at dawn and dusk, and least active during daytime, but the herd cod were most active during the

Table 3. Additional information about the individual depth changes larger than 10 m per 30s ( $\Delta D$ ) displayed in Table 2. Fish number (W: wild, H: herd), date (given as d.mo.yr) and time of measurements, and first and second depth measurement ( $D_1$ ,  $D_2$ ) 30 s apart are shown in chronological order for each fish. Negative and positive depth changes refer to ascending and descending swimming

Fish number	Date	Time (min)	$D_1$ (m)	$D_2$ (m)	$\Delta D$ (m)
C1279 W	27.06.05	15:16	66.0	47.2	-18.8
C1279 W	27.06.05	15:16	47.2	62.0	14.8
C1279 W	15.08.05	23:56	69.6	85.9	16.3
C1279 W	10.10.05	1:08	51.1	65.9	14.8
C1279 W	10.10.05	1:08	65.9	82.6	16.7
C1279 W	10.10.05	1:37	57.9	79.3	21.4
C1279 W	10.10.05	2:05	62.0	75.0	13.0
C1279 W	10.10.05	3:35	56.2	85.3	29.1
C1279 W	10.10.05	23:20	80.6	93.6	13.0
C1366 W	29.08.05	3:46	76.6	87.3	10.7
C1455 W	20.06.05	16:50	72.1	88.0	15.9
C1455 W	11.07.05	4:15	53.8	38.8	-15.0
C1455 W	11.07.05	4:16	38.8	51.2	12.4
C397 H	4.09.06	11:37	16.6	6.1	-10.5
C397 H	4.09.06	11:42	17.3	5.5	-11.8
C480 H	31.07.06	14:52	24.2	12.3	-11.9
C480 H	2.10.06	14:04	19.3	8.1	-11.2
C480 H	2.10.06	14:07	27.2	15.8	-11.4
C480 H	20.11.06	9:47	5.8	17.7	11.9
C480 H	20.11.06	14:19	19.4	32.5	13.1
C480 H	4.12.06	22:48	54.8	66.5	11.7
C611 H	20.11.06	9:48	10.3	21.5	11.2

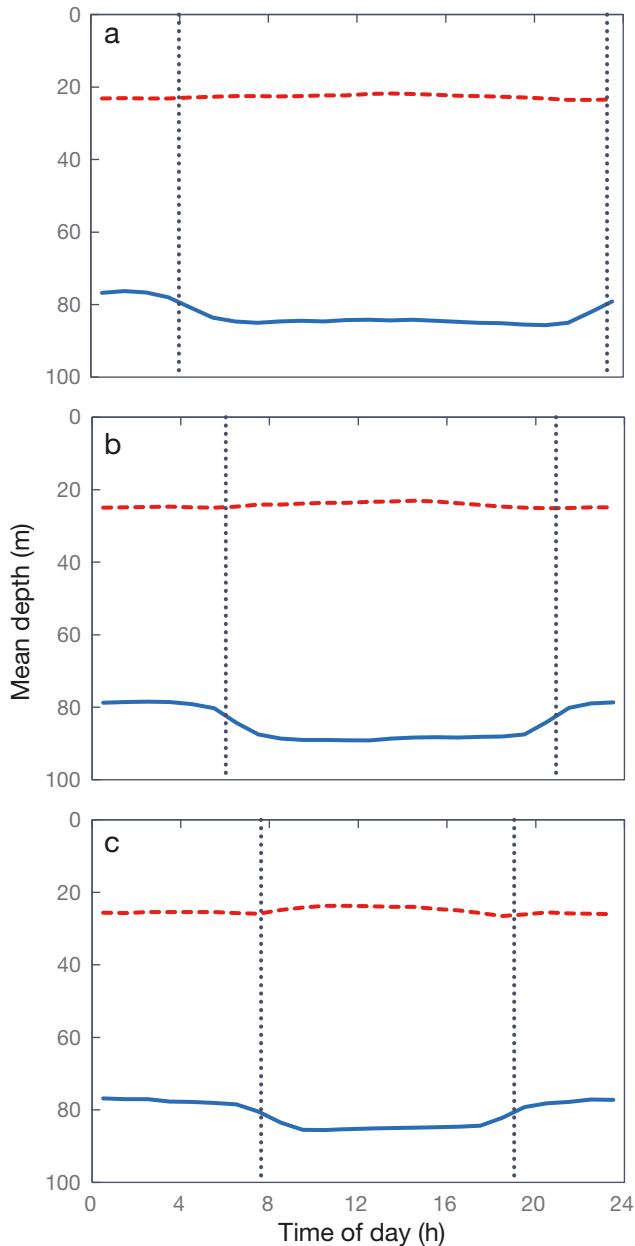


Fig. 2. Diel variation in mean depth of 10 wild cod in 2005 (solid blue lines) and 15 herd cod in 2006 (dashed red lines) in Arnarfjörður, NW Iceland, in (a) August, (b) September, and (c) October, obtained from data storage tags. For each fish, monthly means were calculated for each hour of the day. Vertical dashed lines indicate the time of civil dawn and civil dusk in Arnarfjörður on (a) 15 August, (b) 15 September and (c) 15 October, i.e. when the centre of the sun is  $6^\circ$  below the horizon

middle of the day in August (Fig. 3a), September (Fig. 3b), and October (Fig. 3c). In wild cod, the average nocturnal and crepuscular activity was higher in August and September (0.8–1.0) than in October (0.5–0.7 m per 30 s), whereas their average diurnal

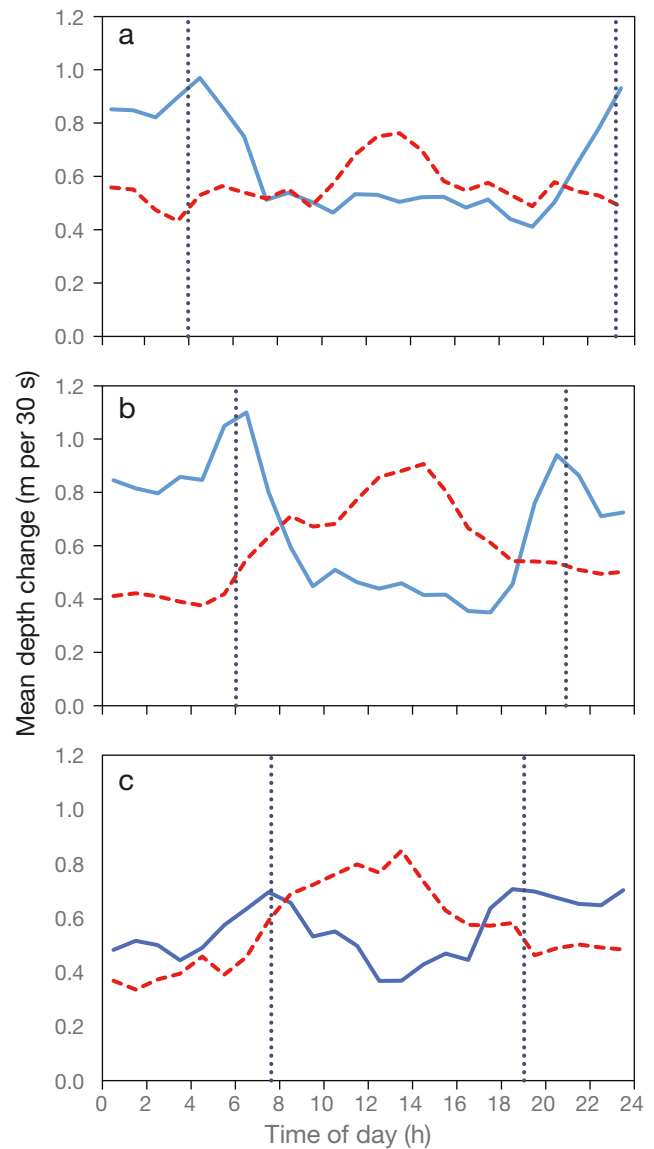


Fig. 3. Diel variation in mean depth change (m per 30 s) of wild cod (solid blue lines) and herd cod (dashed red lines) in Arnarfjörður in (a) August, (b) September, and (c) October in 2005–2006. Dawn and dusk at the middle of each month are indicated with vertical dashed lines. Means were calculated for each hour of the day during Mondays which were the days when depth measurements were made with the highest frequency (every 30 s)

activity was similar in all 3 months (0.4–0.5). In herd cod, the average diurnal activity near noon (0.8–0.9) was about twice as high as the average nocturnal activity (0.4–0.5 m per 30 s, Fig. 3).

Commonly, the herd cod reduced their depth at the time when the feed bags were deployed and started to move up and down for some time, presumably the time it took to empty the feed bag or satiate the fish. This behaviour was used to estimate

the length of the feeding time associated with deployment of feed bags. In 2006, feed bags were deployed on only 7 Mondays (31 July; 28 August; 4, 11, and 25 September; and 2 and 23 October), out of the 20 Mondays being recorded at the highest frequency. For the 4 herd cod, the length of the feeding time was on average 2.2 h in the 13 cases for which the typical feeding activity was observed for individual fish (13 out of 28 cases). As an example, fish C417 at feeding station A, with the largest herd, showed this behaviour on 5 Mondays (Fig. 4). Its average depth was reduced by 8–10 m, and the duration of the feeding activity apparently ranged from 1.2 h on 25 September (Fig. 4d) to 2.8 h on 4 September (Fig. 4b). During feeding, this fish con-

tinuously varied its depth, usually from a minimum depth of about 5 m to a maximum of 15 m, with a periodicity of 3–4 min. Usually, the feeding activity started at the time when the feed bag was deployed, but once, on 28 August, the fish went into this feeding mode about 45 min prior to the deployment of the feed bag (Fig. 4a).

There was a large variation in the number of hours of high activity per day (mean depth changes  $\geq 1.0$  m per 30 s) between individual cod on different Mondays (Fig. 5). The number was highest in the wild cod on 20 June (Fig. 5a) and in the herd cod on 21 August (Fig. 5b). For all 20 Mondays, the average number of hours of high activity per day was larger for the wild fish (3.9 h) than the herd fish (2.9 h).

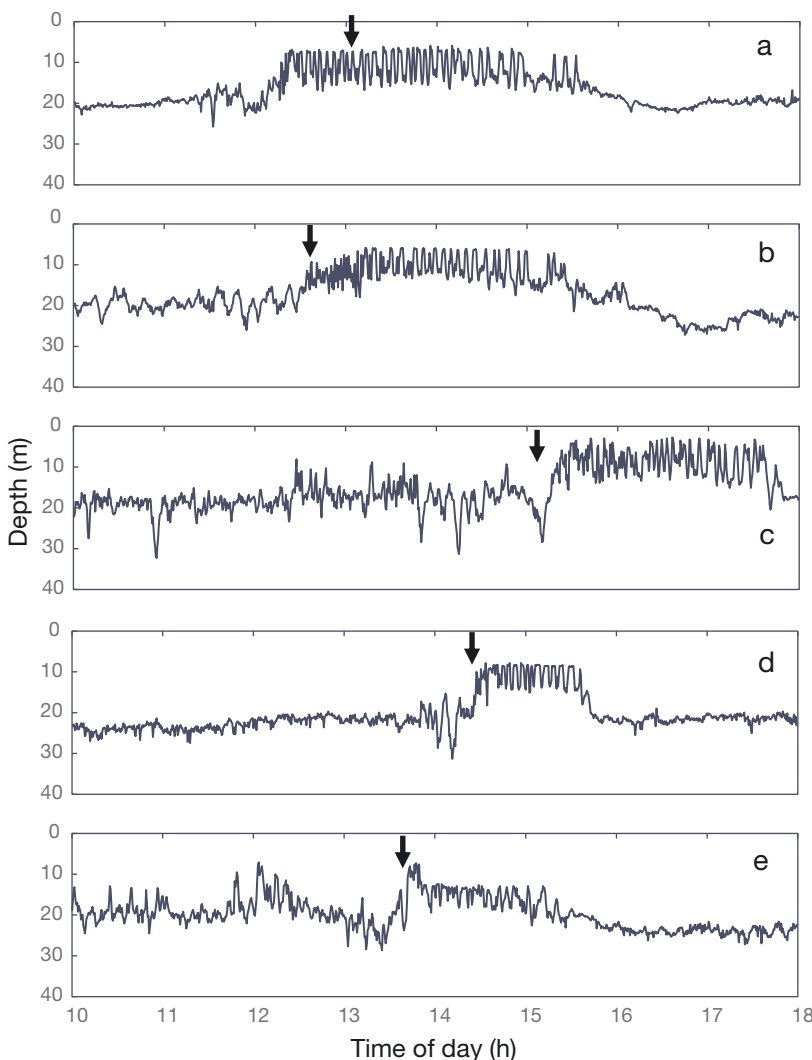


Fig. 4. Depth changes of herd cod C417 at the time when feed bags were deployed (arrows) on (a) 28 August, (b) 4 September, (c) 11 September, (d) 25 September, and (e) 2 October 2006

### 3.2. Cyclical depth changes (CDCs)

Several times during the hours of high activity, rapid CDCs were observed; 8 examples are shown here for both wild (Fig. 6) and herd cod (Fig. 7). Sometimes the peaks and troughs were sharp, indicating quicker turns than can be adequately described with a 30 s measuring interval. In some cases, the fish moved repeatedly up and down every 30 s (e.g. Fig. 6d), indicating cycles with a period of about 1 min and heights 2–5 m. In other cases, the periods and heights were larger (e.g. Figs. 6e & 7c,g; the positive changes lasted for more than 30 s and the negative changes for more than 30 s). In some cases, much larger cycles were observed (e.g. Figs. 6g & 7f). Four of 8 examples shown in Fig. 7 (Fig. 7c,d,g,h) represent high activity of herd fish following deployment of the feed bag (cf. Fig. 4a,c). However, high-frequency depth changes of the herd fish were not only limited to the daytime (Fig. 7).

The number of hours of high activity (mean depth changes  $\geq 1.0$  m per 30 s) was highly variable for the days with these selected examples, i.e. 3–15 and 2–13 h for the wild and herd cod, respectively (Table 4). These prolonged rhythmic depth changes, which were seen both during day and night, were of similar magnitude for both wild cod

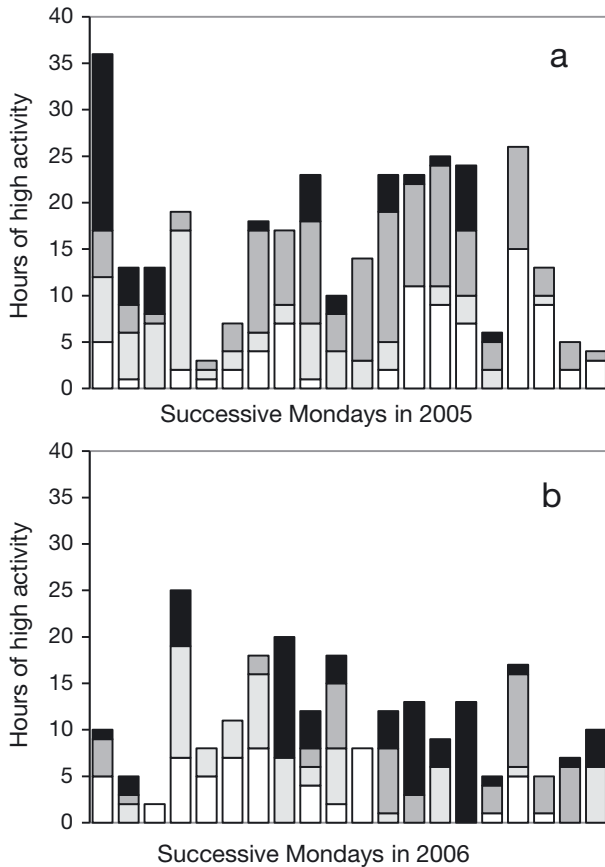


Fig. 5. Number of active hours (mean vertical change  $\geq 1.0$  m per 30 s) in (a) 4 wild cod on successive Mondays in 2005 (C1279  $\square$ , C1315  $\square$ , C1366  $\square$ , C1455  $\blacksquare$ ) and (b) 4 herd cod on successive Mondays in 2006 (C397  $\square$ , C417  $\square$ , C480  $\square$ , C611  $\blacksquare$ ) in Arnarfjörður

(Fig. 6) and herd cod (Fig. 7). The mean depth changes for these selected examples were identical for wild and herd cod: 2.0 and 0.3 m per 30 s for the highest and lowest hourly activity, respectively (Table 4). Commonly at the hour of the highest activity, each depth change was 2–6 m, but on the same day, the hour of the lowest activity usually had heights  $< 1$  m (Table 4, Figs. 6 & 7).

As seen in 5 of the examples from Fig. 6, the undulating search pattern of wild cod was highly variable between individual fish, date, and hour of the day (Fig. 8). For example, during early morning (08:00–09:00 h) on 10 October, fish C1279 searched with large and irregular vertical undulations between depths of 76 and 93 m (Fig. 8a, case b in Fig. 6). At dawn (06:00–07:00 h) on 5 September, fish C1315 searched with high-frequency undulations, gradually increasing the mean depth from about 92 to 102 m (Fig. 8b, case d in Fig. 6). At night (02:00–03:00 h) on 1 August, fish C1366 ascended for the

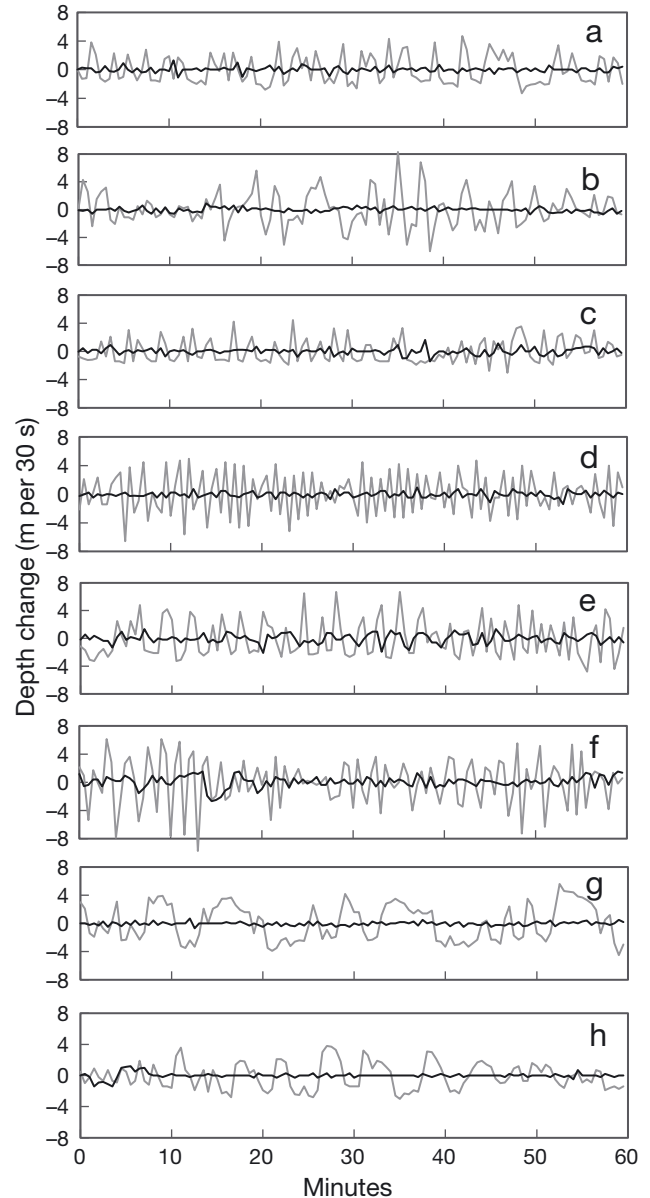


Fig. 6. Eight examples of high-frequency depth changes in 4 wild cod in Arnarfjörður in 2005. For each fish, 2 dates are shown with the lowest (black line) and the highest hourly depth change (grey line). (a) C1279, 1 August (low 17:00–18:00, high 00:00–01:00 h); (b) C1279, 10 October (low 11:00–12:00, high 08:00–09:00 h); (c) C1315, 15 August (low 19:00–20:00, high 03:00–04:00 h); (d) C1315, 5 September (low 01:00–02:00, high 06:00–07:00 h); (e) C1366, 1 August (low 14:00–15:00, high 02:00–03:00 h); (f) C1366, 10 October (low 21:00–22:00, high 15:00–16:00 h); (g) C1455, 15 August (low 06:00–07:00, high 00:00–01:00 h); (h) C1455, 5 September (low 00:00–01:00 h, high 21:00–22:00 h) (see Table 4a)

first 4 min in the water column from 102 to 85 m and then started to search with large undulations for about 30 min. At that time, the fish increased the average depth to about 100 m and initially searched



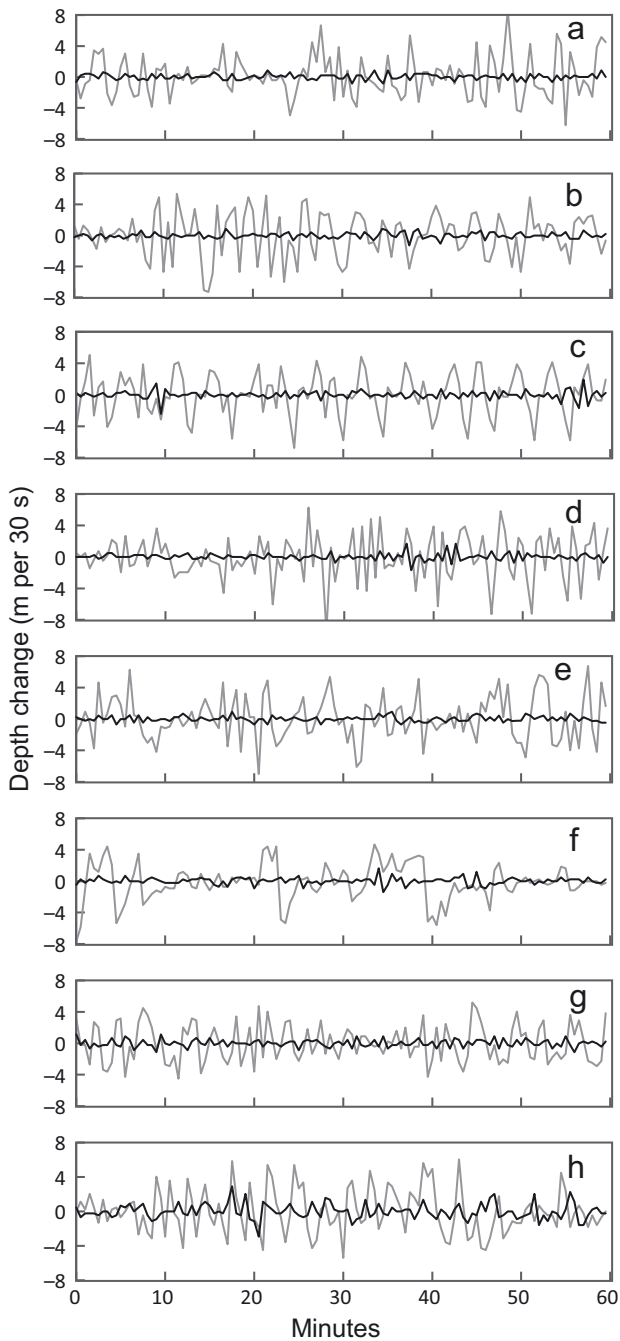


Fig. 7. Eight examples of high-frequency depth changes in 4 herd cod in Arnarfjörður in 2006. For each fish, 2 dates are shown with the lowest (black line) and the highest mean hourly depth change (grey line). (a) C397, 28 August (low 03:00–04:00, high 11:00–12:00 h); (b) C397, 2 October (low 02:00–03:00, high 13:00–14:00 h); (c) C417, 28 August (low 09:00–10:00, high 13:00–14:00 h); (d) C417, 11 September (low 18:00–19:00, high 15:00–16:00 h); (e) C480, 2 October (low 22:00–23:00, high 12:00–13:00 h); (f) C480, 27 November (low 07:00–08:00, high 18:00–19:00 h); (g) C611, 18 September (low 03:00–04:00, high 17:00–18:00 h); (h) C611, 6 November (low 12:00–13:00, high 05:00–06:00 h) (see Table 4b)

with small undulations for about 15 min and then finally resumed the search at a lower depth (Fig. 8c, case e in Fig. 6). In the afternoon (15:00–16:00 h) on 10 October, fish C1366 searched with large undulations at an average depth of about 103 m (Fig. 8d, case f in Fig. 6). In the final example occurring during the night (00:00–01:00 h) on 15 August, fish C1455 searched with very large and irregular undulations at depths between 53 and 93 m (Fig. 8e, case g in Fig. 6). The maximum heights of the vertical undulations in these examples were approximately 12, 6, 10, 10, and 30 m (Fig. 8a–e, respectively). However, the dominant heights in these examples according to spectral analysis were 3.2, 3.4, 2.5, 3.7, and 4.0 m, respectively (see Table 4a, dominant height = dominant amplitude  $\times$  2).

### 3.3. Spectral analysis

Using spectral analysis to compare the examples in Figs. 6 & 7 showed that the CDCs were more commonly of higher frequency and lower amplitude for the wild cod (Table 4a) compared with the herd cod (Table 4b); on average during active hours, the dominant period was 2.2 and 3.4 min, amplitude in the dominant period was 1.6 and 2.0 m, and number of cycles in the dominant period was 26 and 13  $\text{h}^{-1}$  for wild and herd cod, respectively (Table 4). Using spectral analysis to study the activity of every hour in the entire data set indicates that days of inactivity were more common in the herd cod than in the wild cod (Table 5). Enumerating the active hours shows that although single active hours were most common, there were numerous examples of active hours lasting for 2 to 7 h and even 2 examples of active hours lasting continuously for 12 h (Table 5).

Spectral analysis confirmed that wild cod were most active during dawn and dusk, and least active during daytime, and that herd cod were most active during daytime. Wild cod were active during 25.5% of the hours at dawn and dusk, but herd cod were active during 13.4% of the hours during daytime (Table 6). During active hours of both wild and herd cod, the most common dominant amplitude was 1.0–1.4 m, and amplitudes  $\geq 1.6$  m ranged between 5 and 12% of all active hours, highest for herd cod during the day. The average amplitude of active hours was similar for all 6 groups, 1.2–1.3 m (Table 7), corresponding to about 2.5 m heights of the sinusoidal depth cycles assumed in the STFTs.

Table 4. Additional information about the 8 examples of high-frequency depth changes of (a) 4 wild cod (see Fig. 6) and (b) 4 herd cod (see Fig. 7). Results are shown for both the hour of the highest (High) and lowest (Low) average depth change. Hours of high activity are those with mean depth changes  $\geq 1.0$  m per 30 s. The hours of the day during darkness are shown in **bold**. The mean depths and the mean depth changes (m per 30 s) are also shown. The estimated dominant period (min), active time in the dominant period (min), dominant amplitude (m), and the number of cycles in the dominant period are based on spectral analysis. Dates are given as d.mo.yr

Fish number	Date	Activity level	No. of hours of high activity	Hour of the day	Mean depth (m)	Mean depth change (m)	Dominant period (min)	Active time (min)	Dominant amplitude (m)	No. of cycles
<b>(a) Wild cod</b>										
C1279	1.08.05	High	4	<b>0–1</b>	84.5	1.76	1.8	35	1.15	20
C1279	1.08.05	Low	0	17–18	92.4	0.26		0		0
C1279	10.10.05	High	15	8–9	82.7	1.92	2.0	40	1.61	20
C1279	10.10.05	Low	0	11–12	93.6	0.24		0		0
C1315	15.08.05	High	6	<b>3–4</b>	69.1	1.46	2.0	25	1.11	12.5
C1315	15.08.05	Low	0	19–20	69.5	0.32		0		0
C1315	5.09.05	High	3	6–7	95.8	2.52	1.2	60	1.70	48
C1315	5.09.05	Low	0	<b>1–2</b>	81.8	0.31		0		0
C1366	1.08.05	High	11	<b>2–3</b>	94.6	2.36	1.2	50	1.25	40
C1366	1.08.05	Low	0	14–15	95.4	0.52	2.5	5	1.10	2
C1366	10.10.05	High	11	15–16	103.2	2.62	1.5	60	1.85	40
C1366	10.10.05	Low	0	<b>21–22</b>	90.8	0.60	4.0	15	1.43	3.8
C1455	15.08.05	High	5	<b>0–1</b>	73.1	2.29	4.0	40	1.98	10
C1455	15.08.05	Low	0	6–7	86.4	0.19		0		0
C1455	5.09.05	High	4	21–22	89.2	1.42	4.0	40	1.92	10
C1455	5.09.05	Low	0	<b>0–1</b>	91.6	0.18		0		0
Mean high			7.4		86.5	2.04	2.21	44	1.57	25.7
Mean low					87.7	0.33	1.56	2		0.7
<b>(b) Herd cod</b>										
C397	28.08.06	High	5	11–12	18.1	2.11	2.2	35	1.72	15.6
C397	28.08.06	Low	0	<b>3–4</b>	20.4	0.29		0		0
C397	2.10.06	High	2	13–14	15.5	2.25	3.5	45	2.00	12.9
C397	2.10.06	Low	0	<b>2–3</b>	27.4	0.27		0		0
C417	28.08.06	High	3	13–14	8.8	2.10	3.5	60	2.44	17.1
C417	28.08.06	Low	0	9–10	19.4	0.34		0		0
C417	11.09.06	High	8	15–16	10.1	2.18	3.5	35	1.59	10.0
C417	11.09.06	Low	0	18–19	18.4	0.28		0		0
C480	2.10.06	High	7	12–13	33.5	2.22	4.0	50	2.27	12.5
C480	2.10.06	Low	0	<b>22–23</b>	25.2	0.26		0		0
C480	27.11.06	High	4	<b>18–19</b>	31.2	1.69	4.0	45	2.62	11.2
C480	27.11.06	Low	0	<b>7–8</b>	22.0	0.30		0		0
C611	18.09.06	High	13	17–18	11.6	2.02	3.0	45	1.79	15.0
C611	18.09.06	Low	0	<b>3–4</b>	18.7	0.38		0		0
C611	6.11.06	High	13	<b>5–6</b>	29.3	2.00	3.5	45	1.95	12.9
C611	6.11.06	Low	0	12–13	18.7	0.64	4.0	5	1.08	1.2
Mean high			6.9		19.8	2.07	3.40	45	2.05	13.4
Mean low					21.3	0.34	1.38	0.6		0.2

## 4. DISCUSSION

### 4.1. Diel depth changes

In the present study, the wild cod primarily occupied deeper and colder areas of the fjord, whereas the herd cod stayed mainly in shallower and warmer areas close to shore. It is preferable for wild cod, obtaining limited amounts of wild prey, to stay mainly

in the cold water to conserve energy and for the amply-fed herd cod to stay mainly in the warm water to maximize food intake and growth rate (Björnsson 2019). The wild cod undertook classical diel vertical migrations, ascending several meters at dusk and descending back at dawn similar as that found for juvenile and adult cod (30–80 cm) in small inlets on the Norwegian Skagerrak coast (Espeland et al. 2010, Freitas et al. 2015). The diet of wild cod in Arnarfjör-

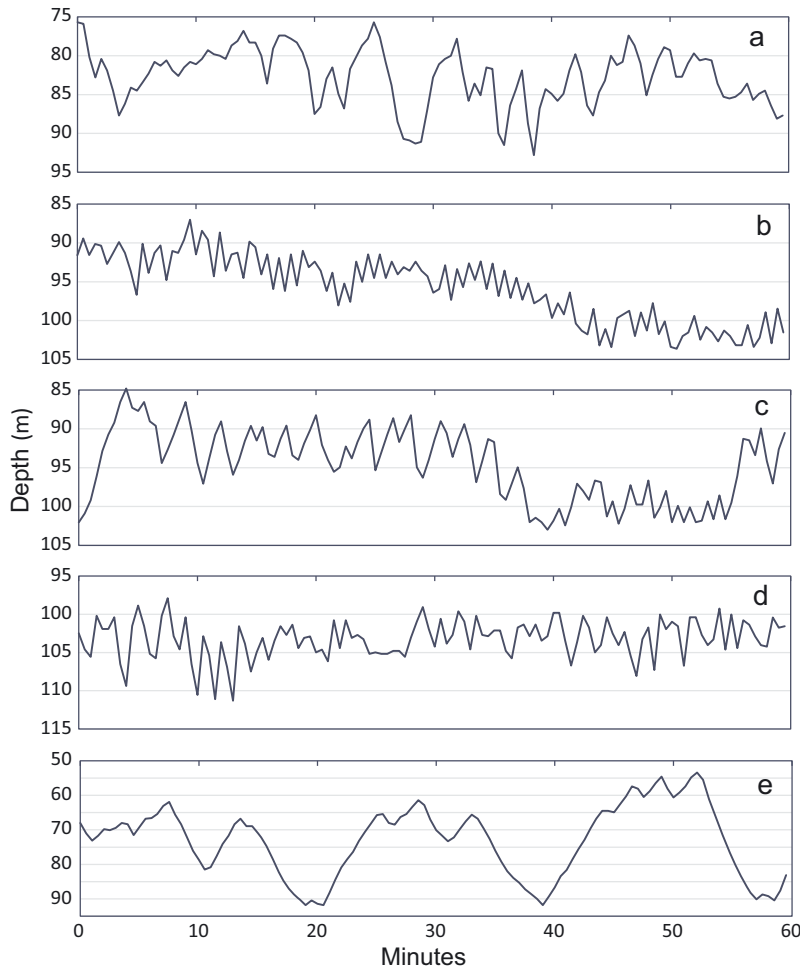


Fig. 8. Search pattern of wild cod for 5 of the examples in Fig. 6b,d–g: (a) C1279, 10 October, 08:00–09:00 h; (b) C1315, 5 September, 06:00–07:00 h; (c) C1366, 1 August, 02:00–03:00 h; (d) C1366, 10 October, 15:00–16:00 h; (e) C1455, 15 August, 00:00–01:00 h

dur in June 2005 and 2006 and October 2005 and 2006 consisted mainly of euphausiids, northern shrimp, and demersal fish (Björnsson et al. 2011b). Both euphausiids and northern shrimp remain near the bottom during daylight hours and undertake vertical migration during the night to feed on plankton (Bergström & Strömberg 1997, Bergström 2000). Cod feed both during night and day (Løkkeborg 1998), but the night-time is thought to be the main foraging period (Espeland et al. 2010).

In comparison, the herd cod, conditioned to feed on frozen forage fish kept in net bags at 10–20 m depth, showed on average only minor diel changes in depth, although they moved closer to the surface by about 10 m for 2 h on approximately half of the days when feed bags were deployed. The minimum and maximum depths during each feeding were constant but somewhat different between individual

feedings, most likely because the feed bag was lifted according to the strength of the tidal current. The observed undulating behaviour by the herd cod during the day may represent searches for an opening to approach the highly crowded feed bag. However, the high-frequency depth changes of the herd cod sometimes found during twilight and darkness may be due to searches for wild prey, indicating that the well-fed herd cod likely supplemented their diet of frozen capelin with some live prey.

Herd fish C417 showed no feeding reaction on 31 July, possibly because it had not fully recovered from tagging, and no reaction on 23 October, probably because it had lost appetite. According to the signals from the acoustic tag, this fish remained in the herd until November. Previous studies indicate that herd cod lose appetite in autumn when they have developed large livers (Björnsson 2011). Cod are lean fish that accumulate fat reserves in the liver, and this energy can later be used for various activities, such as gonad development and migration (Lambert & Dutil 1997). In the herds, the fish were amply fed with capelin, their preferred food, and thus grew fast and developed large livers (Björnsson 2019).

#### 4.2. Internal waves

It is imperative to ensure that the observed CDCs of the fish were due to active swimming and not due to wave action. Sea surface waves can be ruled out as they have heights which are usually only a small fraction of the 3–10 m heights commonly found in the DST records. Orbital motions from surface gravity waves decay rapidly with depth (Pond & Pickard 1983) and will be near zero at the depths where the herd and wild cod were generally swimming, i.e. 15–35 and 60–90 m, respectively.

Internal waves have larger heights and longer periods than surface waves, but no attempts were made to measure internal waves during the study. However, internal waves can only form when the water column is stratified with a layer of low-density water above a layer of high-density water,

Table 5. Total occurrence of single and multiple active hours (N) based on spectral analysis for 2 data sets (4 wild cod and 4 herd cod) on 20 consecutive Mondays. Active hours are defined as those with active time  $\geq 30 \text{ min h}^{-1}$ , and active time is defined as each 5 min interval with an amplitude of  $\geq 1.0 \text{ m}$ . Days of inactivity are those with no active hours

N	Occurrence of active hours	
	Wild cod	Herd cod
1	79	48
2	20	11
3	16	9
4	10	4
5	3	4
6	2	1
7	3	2
8	1	0
9	1	0
10	0	0
11	0	0
12	1	1
Days of inactivity	22 (27.5%)	32 (40.0%)

Table 6. Percent of hours with various length of active time at night, dawn and dusk, and day according to spectral analysis of 4 wild cod and 4 herd cod during 20 consecutive Mondays. For each hour, activity was calculated for every 5 min interval which was defined as active if the amplitude was  $\geq 1.0 \text{ m}$ . The total number of hours in each group was 1920 (= 20 × 24 × 4). Active time was binned in 5 min intervals

Minutes	Wild cod			Herd cod		
	Night	Dawn and dusk	Day	Night	Dawn and dusk	Day
0	35.1	19.3	50.8	66.9	65.0	51.8
5	13.0	11.5	12.4	11.1	13.0	13.1
10	10.7	14.6	9.0	8.6	6.0	8.9
15	7.6	12.0	6.9	3.4	4.0	5.6
20	8.3	10.9	5.3	2.9	5.0	4.1
25	6.2	6.3	4.1	2.5	1.5	3.2
30	4.8	5.2	3.2	1.4	2.5	3.2
35	2.5	3.1	1.6	1.3	0.0	2.9
40	3.7	3.6	1.6	0.9	1.0	1.6
45	2.1	3.6	1.5	0.6	1.5	1.1
50	2.5	1.6	0.9	0.2	0.5	1.9
55	1.9	4.7	1.2	0.2	0.0	1.6
60	1.7	3.6	1.4	0.0	0.0	1.2
Total N	484	192	1244	864	200	856
$\geq 30 \text{ min}$	19.0	25.5	11.5	4.6	5.5	13.4

but strong winds or tidal currents are required to initiate these waves. Many density profiles have been recorded in Arnarfjörður at different times of the year (Macrander et al. 2021), and from them the nature of potential internal waves can be estimated.

Table 7. Percent of dominant amplitudes during active hours in 4 wild and 4 herd cod on 20 consecutive Mondays based on spectral analysis. Dominant amplitudes were defined as mean amplitudes during active time (minutes in each hour when amplitude  $\geq 1.0 \text{ m}$ ), and active hours are defined as those with undulations with mean amplitudes  $\geq 1.0 \text{ m}$  for at least 5 min. Also shown are percent of active hours with amplitudes  $\geq 1.6 \text{ m}$  and mean amplitude of all active hours

Amplitude (m)	Wild cod			Herd cod		
	Night	Dawn and dusk	Day	Night	Dawn and dusk	Day
1.0–1.19	55.1	61.3	67.6	59.1	60.0	44.6
1.2–1.39	25.8	25.2	19.6	25.9	20.0	27.6
1.4–1.59	12.7	7.7	7.8	9.4	15.7	15.7
1.6–1.79	2.9	2.6	3.1	4.2	2.9	7.0
1.8–1.99	1.3	2.6	1.1	0.7	0.0	0.7
2.0–2.19	1.0	0.6	0.5	0.3	1.4	2.2
2.2–2.39	0.3	0.0	0.0	0.0	0.0	1.2
2.4–2.59	0.6	0.0	0.2	0.0	0.0	0.7
2.6–2.79	0.0	0.0	0.0	0.3	0.0	0.0
2.8–2.99	0.3	0.0	0.0	0.0	0.0	0.2
3.0–3.19	0.0	0.0	0.0	0.0	0.0	0.0
Active hours	314	155	612	286	70	413
Total hours	484	192	1244	864	200	856
Active hours (%)	64.9	80.7	49.2	33.1	35.0	48.2
Active hours $\geq 1.6 \text{ m}$	6.4	5.8	4.9	5.6	4.3	12.1
Mean	1.25	1.20	1.18	1.22	1.23	1.30

Usually there is little or no stratification in this fjord from late autumn to early spring (November–April) and thus internal waves are not possible during that time. During summer and fall (May–October), however, the fjord becomes increasingly stratified because of seasonal warming of the upper layer, and the available density profiles confirm a pycnocline forming at 60 m depth. Based on the buoyancy frequency (Brunt-Väisälä frequency), the minimum period of internal waves would be 4, 6, 7, and 15 min in August, September, October, and November, respectively (Pond & Pickard 1983, Macrander et al. 2021), much longer than the most common periods of CDCs.

Exploratory analysis of the data showed that for each of the 4 wild cod and 4 herd cod, there was never a positive correlation between (1) active time ( $\text{min h}^{-1}$ ) vs. mean hourly tidal current and (2) dominant amplitude during active time vs. mean hourly tidal current, as would be expected if internal waves were involved. Thus, internal waves can be ruled out as the explanation for the observed high-frequency depth changes of cod in the study.

### 4.3. CDCs

Vertically undulating swimming behaviour has been reported for both freshwater and marine fishes. In a reservoir 170 km south of Prague, individual targets of pelagic fish were monitored with an echosounder fixed on the bottom and sending signals towards the surface. During daytime in summer, the majority of the larger individual fish (14–36 cm) displayed sinusoidal swimming patterns in the epilimnion close to the surface (Cech & Kubecka 2002). The cycles, usually with a frequency of 3–4 min<sup>-1</sup> and a height of 2 m, were repeated several times while the fish moved across the ultrasonic beam. Most likely these fish were common bream *Abramis brama* and roach *Rutilus rutilus* searching visually for large zooplankton, whose density was thought to be low and patchy (Jarolim et al. 2010).

Vertically undulating swimming behaviour has been recorded with DSTs for tunas, large marine fish known for their fast swimming, e.g. 44–75 cm yellowfin tuna *Thunnus albacares* with 2–5 undulations per hour, each 30–100 m high; 57–75 cm bigeye tuna *T. obesus* with 1–15 undulations per hour, each 40–200 m high (Holland et al. 1990); and immature Pacific bluefin tuna *T. orientalis* with several undulations per hour, each 20–80 m high (Furukawa et al. 2014). The average diving frequency of 180–220 cm Atlantic bluefin tuna *T. thynnus* was about 1 per hour, and the mean diving depth was significantly correlated with the depth of the thermocline, varying seasonally from 20 to 150 m (Walli et al. 2009). The density gradient at the thermocline (pycnocline) provides physical means to aggregate food for prey species (Gray & Kingsford 2003, Furukawa et al. 2014). By intermittently diving through the thermocline, the tuna were thought to maximize the probability of encountering prey.

However, the vertical undulations by adult cod were usually of much lower heights (2–4 m) and higher frequency (15–60 cycles h<sup>-1</sup>) than that found for tuna. In Arnarfjörður, there is a well established thermocline in summer and early autumn at a depth of 40–60 m (Björnsson 2019, Macrander et al. 2021), but the present study did not indicate that cod repeatedly dove through the thermocline, as the wild cod remained below it and the herd cod above it. On the other hand, the vertical undulations by adult cod (70 cm) were substantially larger than those displayed by the relatively small freshwater species (23 cm) in a reservoir in the Czech Republic (Cech & Kubecka 2002).

The heights of the CDCs recorded with DSTs were usually of smaller magnitude (2–4 m) than the 10–20 m observed with an echo sounder for several cod following a feeding boat in an Icelandic fjord (Björnsson & Reynisson 2013). The sharp spikes on many of the depth records during high-frequency depth changes indicate that the measuring frequency of 30 s was insufficient to measure the heights accurately. Thus, in our study, the actual heights of the sinusoidal trajectories may have been underestimated to some degree. Usually, the period of each cycle was 1–4 min, similar to the 2–3 min found by Björnsson & Reynisson (2013). In that study, the boat was drifting slowly (0.35 m s<sup>-1</sup>), and as the fish were keeping up with the boat, it was possible to estimate the horizontal speed of the fish and depth of individual fish every 3 s. The trajectories were relatively smooth and sinusoidal with a length of about 50 m. However, in the present study using DSTs, it was not possible to measure the horizontal speed of the fish and thus the length of the undulations. Commonly, the DST-tagged cod showed large CDCs for a few hours during the 24 h period, but for the rest of the time the depth changes every 30 s were small. The CDCs occurred at different times of the 24 h period, although more often during night-time and dawn and dusk for wild cod and during daytime for herd cod.

The high-frequency depth changes of cod imply simultaneous forward propulsion, since there is a limit to the tilt angle of the fish during ascent or descent. The maximum tilt angle during vertically undulating swimming of cod, as observed by Björnsson & Reynisson (2013), was 50–60°. Assuming this high tilt angle, a depth change of 1.0 m during a 30 s interval corresponds to 0.58–0.84 m horizontal movement. However, on average, the tilt angles may have been much lower and thus the horizontal movements much greater (McQuinn & Winger 2003). Heffernan et al. (2004) used depth changes in DST-tagged cod in the northern North Sea to calculate tilt angles assuming realistic swimming speeds of 0.3, 0.5, 0.7, and 0.9 body lengths s<sup>-1</sup>. Their estimate was that tilt angles above 15° were relatively rare. Assuming an average tilt angle of 30° during the ascending and descending phase of the cycle, as found for freshwater fish displaying sinusoidal swimming (Cech & Kubecka 2002), would give horizontal movement of 1.73 m for a cycle with a height of 1.0 m. Thus, the cycle heights of 2–4 m, commonly found for adult cod in Arnarfjörður, would correspond to cycle lengths of 3.5–6.9 m. It seems unlikely that the swim bladder

plays a big role in the high-frequency undulating swimming because of the relatively slow process involved in adding gas to the swim bladder of cod (Korsøen et al. 2010).

The present study indicates that spectral analysis using STFT is a useful tool in analysing high-frequency depth changes in cod. Previously, spectral analysis has been used to study depth measurements in pelagic shark *Cetorhinus maximus* (Shepard et al. 2006), Pacific halibut *Hippoglossus stenolepis* (Scott et al. 2016), and European seabass *Dicentrarchus labrax* (Heerah et al. 2017). In these studies, depth was recorded every 0.5 to 2.0 min and STFT was used in the analysis. However, the focus in their analyses was on relatively long-term cyclical changes with a period of several hours, e.g. to detect tidal rhythms and diurnal behaviour, but no attempts were made to detect high-frequency CDCs. For example, Heerah et al. (2017) applied 7 d Hamming windows shifting by 1 d increments, and Scott et al. (2016) applied 10 d Hamming windows, sliding the 10 d sample in 60 min increments through the tag data. These wide windows do not allow fine-scale cyclical changes to be studied. However, in the present study, a much narrower Hamming window (4 times the period of 1–4 min) shifting by 30 s was selected for studying the high-frequency depth changes.

It seems likely that the observed CDCs of wild cod are caused by vertically undulating swimming during food searches, most likely for either demersal fish, euphausiids, or northern shrimp, which were the main prey items of cod in Arnarfjörður during the study (Björnsson et al. 2011b). According to optimal foraging theory, animals adopt behaviour that maximizes the net energy gain from foraging, behaviour which is shaped by natural selection. There are 2 possible reasons why it may be optimal for cod to search in an undulating way: (1) it may facilitate finding suitable prey, which at a given time may be located most often at a given depth (Sims et al. 2003, Ressler et al. 2005, Olafsdottir & Rose 2012); (2) it may facilitate the capture of a suitable prey by approaching it at different angles (McHenry et al. 2019).

Cod select food patches according to food density and hunting success (van Duren & Glass 1992), and the CDCs allow cod to pass repeatedly through patches of prey found at a certain depth. The results also indicate that, if cod do not find food for some time with CDCs, it may be worth taking the odd deep dive or high ascent to explore the entire water column. As this undulating feeding behaviour

of wild cod occurs both during day and night, it seems unlikely that cod rely only on visual detection of prey and possibly use tactile senses to detect immobile prey and the lateral line system to detect vortices produced by rapidly moving prey (Bond 1979).

The present results suggest that DSTs are a useful tool in studying high-frequency depth changes adopted by fish searching for prey. In future studies, the tags should be programmed to measure at a much higher frequency than was done in the present study. Currently, there are commercially available DSTs with memory for as many as 525 068 depth measurements ([www.star-oddi.com](http://www.star-oddi.com)), which would be sufficient to record 6 full 24 h periods with a measuring frequency of 1 s. The tags should be programmed to start measuring after a sufficiently long adaptation period following the surgery required to implant the tags. Implants are preferred because tags attached externally may adversely affect fish behaviour (Broell et al. 2016). To avoid premature recapture of the tagged fish, closure of the relevant fishing grounds should be arranged to make best use of the valuable tags.

The greatest advantage of using DSTs to study depth changes in marine fish is that the measurements can be carried out without disturbing the natural behaviour of the fish, unlike when underwater filming is carried out with the presence of a noisy boat, cameras, and artificial lights. It is also advantageous that DSTs can collect information on the same fish for an extended period, unlike when echosounders are used. Using DSTs, there are no uncertainties about the species of fish and their sizes, contrasting with the use of echosounders for this purpose. In future studies of the foraging behaviour of cod, it would be of great interest to record the search pattern of cod feeding on capelin, their most important prey. The study area and season must be carefully selected to represent predation on both immature capelin during summer and autumn and mature capelin during the spawning migration in winter and spring.

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## LITERATURE CITED

- Bergström B (2000) The biology of *Pandalus*. *Adv Mar Biol* 38:55–245
- ✦ Bergström B, Strömberg JO (1997) Behavioural differences in relation to pycnoclines during vertical migration of the euphausiids *Meganyctiphanes norvegica* (M. Sars) and *Thysanoessa raschii* (M. Sars). *J Plankton Res* 19: 255–261
- ✦ Björnsson B (1993) Swimming speed and swimming metabolism of Atlantic cod (*Gadus morhua*) in relation to available food: a laboratory study. *Can J Fish Aquat Sci* 50: 2542–2551
- ✦ Björnsson B (2011) Ranching of wild cod in ‘herds’ formed with anthropogenic feeding. *Aquaculture* 312:43–51
- ✦ Björnsson B (2018) Fish Aggregating Sound Technique (FAST): How low frequency sound could be used in fishing and ranching of cod. *ICES J Mar Sci* 75:1258–1268
- Björnsson B (2019) Thermoregulatory behaviour in cod: Is the thermal preference in free-ranging adult Atlantic cod affected by food abundance? *Can J Fish Aquat Sci* 76: 1515–1527
- ✦ Björnsson B, Reynisson P (2013) Synchronous and vertically undulating swimming behaviour of Atlantic cod *Gadus morhua*. *Aquat Biol* 19:13–18
- ✦ Björnsson B, Karlsson H, Thorsteinsson V (2010) Effects of anthropogenic feeding on the migratory behaviour of coastal cod (*Gadus morhua*) in Northwest Iceland. *Fish Res* 106:81–92
- ✦ Björnsson B, Karlsson H, Thorsteinsson V, Sólmundsson J (2011a) Should all fish in mark-recapture experiments be double tagged? Lessons learned from tagging coastal cod (*Gadus morhua*). *ICES J Mar Sci* 68:603–610
- ✦ Björnsson B, Reynisson P, Solmundsson J, Valdimarsson H (2011b) Seasonal changes in migratory and predatory activity of two species of gadoid preying on inshore northern shrimp *Pandalus borealis*. *J Fish Biol* 78: 1110–1131
- ✦ Björnsson B, Karlsson H, Macrander A (2018) Food searching behaviour in adult Atlantic cod *Gadus morhua* during acoustic training: social learning and leadership within a school. *J Fish Biol* 93:814–829
- Bond CE (1979) *Biology of fishes*. WB Saunders Company, Philadelphia, PA
- ✦ Brett JR (1971) Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *Am Zool* 11:99–113
- ✦ Broell F, Burnell C, Taggart CT (2016) Measuring abnormal movements in free-swimming fish with accelerometers: implications for quantifying tag and parasite load. *J Exp Biol* 219:695–705
- ✦ Cech M, Kubecka J (2002) Sinusoidal cycling swimming pattern of reservoir fishes. *J Fish Biol* 61:456–471
- ✦ Espeland SH, Thoresen AG, Olsen EM, Stige LC, Knutsen H, Gjøsæter J, Stenseth NC (2010) Diel vertical migration patterns in juvenile cod from the Skagerrak coast. *Mar Ecol Prog Ser* 405:29–37
- ✦ Freitas C, Olsen EM, Moland E, Ciannelli L, Knutsen H (2015) Behavioral responses of Atlantic cod to sea temperature changes. *Ecol Evol* 5:2070–2083
- ✦ Furukawa S, Tsuda Y, Nishihara GN, Fujioka K and others (2014) Vertical movements of Pacific bluefin tuna (*Thunnus orientalis*) and dolphinfish (*Coryphaena hippurus*) relative to the thermocline in the northern East China Sea. *Fish Res* 149:86–91
- ✦ Gray CA, Kingsford MJ (2003) Variability in thermocline depth and strength, and relationships with vertical distributions of fish larvae and mesozooplankton in dynamic coastal waters. *Mar Ecol Prog Ser* 247:211–224
- ✦ Halldórsson JE, Björnsson B, Gunnlaugsson SB (2012) Feasibility of ranching coastal cod (*Gadus morhua*) compared with on-growing, full-cycle farming and fishing. *Mar Policy* 36:11–17
- ✦ Heerah K, Woillez M, Fablet R, Garren F, Martin S, De Pontual H (2017) Coupling spectral analysis and hidden Markov models for the segmentation of behavioural patterns. *Mov Ecol* 5:20
- ✦ Heffernan O, Righton D, Michalsen K (2004) Use of data storage tags to quantify vertical movements of cod: effects on acoustic measures. *ICES J Mar Sci* 61: 1062–1070
- ✦ Hobson VJ, Righton D, Metcalfe JD, Hays GC (2007) Vertical movements of North Sea cod. *Mar Ecol Prog Ser* 347: 101–110
- Holland KN, Brill RW, Chang RKC (1990) Horizontal and vertical movements of yellowfin and bigeye tuna associated with fish aggregating devices. *Fish Bull* 88:493–507
- ✦ Holt RE, Bogstad B, Durant JM, Dolgov AV, Ottersen G (2019) Barents Sea cod (*Gadus morhua*) diet composition: long-term interannual, seasonal, and ontogenetic patterns. *ICES J Mar Sci* 76:1641–1652
- ✦ Humphries NE, Queiroz N, Dyer JRM, Pade NG and others (2010) Environmental context explains Lévy and Brownian movement patterns of marine predators. *Nature* 465: 1066–1069
- ✦ Huse G, Johansen GO, Bogstad B, Gjøsæter H (2004) Studying spatial and trophic interactions between capelin and cod using individual-based modelling. *ICES J Mar Sci* 61:1201–1213
- ✦ Jarolim O, Kubecka J, Cech M, Vasek M, Peterka J, Matena J (2010) Sinusoidal swimming in fishes: the role of season, density of large zooplankton, fish length, time of the day, weather condition and solar radiation. *Hydrobiologia* 654:253–265
- ✦ Korsøen ØJ, Dempster T, Fosseidengen JE, Fernö A (2010) Behavioural responses to pressure changes in cultured Atlantic cod (*Gadus morhua*): defining practical limits for submerging and lifting sea-cages. *Aquaculture* 308: 106–115
- Lambert Y, Dutil JD (1997) Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of Atlantic cod (*Gadus morhua*)? *Can J Fish Aquat Sci* 54(Suppl 1):104–112
- Lilly GR (1994) Predation by Atlantic cod on capelin on the southern Labrador and Northeast Newfoundland shelves during a period of changing spatial distributions. *ICES Mar Sci Symp* 198:600–611
- ✦ Løkkeborg S (1998) Feeding behaviour of cod, *Gadus morhua*: activity rhythm and chemically mediated food search. *Anim Behav* 56:371–378
- ✦ Løkkeborg S, Fernö A (1999) Diel activity pattern and food search behaviour in cod, *Gadus morhua*. *Environ Biol Fishes* 54:345–353
- ✦ Macrander A, Ólafsdóttir SR, Danielsen M, Karlsson H, Kristjánsson AB, Sliwinski J (2021) Arnarfjörður: hydrographic conditions, currents, and renewal of bottom layer. *Marine and Freshwater Research in Iceland*, HV 2021-38, Reykjavík (in Icelandic with English abstract). <https://www.hafogvatn.is/static/research/files/hv2021-38.pdf>

- ✦ Mattson S (1990) Food and feeding habits of fish species over a soft sublittoral bottom in the Northeast Atlantic. 1. Cod (*Gadus morhua* L.) (Gadidae). *Sarsia* 75:247–260
- ✦ Mattson S (1992) Food and feeding habits of fish species over a soft sublittoral bottom in the Northeast Atlantic. 3. Haddock (*Melanogrammus aeglefinus* (L.)) (Gadidae). *Sarsia* 77:33–45
- ✦ McHenry MJ, Johansen JL, Soto AP, Free BA, Paley DA, Liao JC (2019) The pursuit strategy of predatory bluefish (*Pomatomus saltatrix*). *Proc R Soc B* 286:20182934
- ✦ McQuinn IH, Winger PD (2003) Tilt angle and target strength: target tracking of Atlantic cod (*Gadus morhua*) during trawling. *ICES J Mar Sci* 60:575–583
- ✦ Neat FC, Wright PJ, Zuur AF, Gibb IM and others (2006) Residency and depth movements of a coastal group of Atlantic cod (*Gadus morhua* L.). *Mar Biol* 148:643–654
- ✦ Olafsdottir AH, Rose GA (2012) Influences of temperature, bathymetry and fronts on spawning migration routes of Icelandic capelin (*Mallotus villosus*). *Fish Oceanogr* 21: 182–198
- Oppenheim AV, Schafer RW, Buck JR (1999) Discrete-time signal processing, 2nd edn. Prentice Hall, Upper Saddle River, NJ
- Pálsson ÓK (1983) The feeding habits of demersal fish species in Icelandic waters. *Rit Fiskid* 7:1–60
- ✦ Pálsson ÓK, Thorsteinsson V (2003) Migration patterns, ambient temperature, and growth of Icelandic cod (*Gadus morhua*): evidence from storage tag data. *Can J Fish Aquat Sci* 60:1409–1423
- Pond S, Pickard GL (1983) Introductory dynamical oceanography. Pergamon Press, Oxford
- ✦ Pyke GH (1984) Optimal foraging theory: a critical review. *Annu Rev Ecol Syst* 15:523–575
- ✦ Ressler PH, Brodeur RD, Peterson WT, Pierce SD, Vance PM, Røstad A, Barth JA (2005) The spatial distribution of euphausiid aggregations in the Northern California Current during August 2000. *Deep Sea Res II* 52:89–108
- ✦ Rose GA (1993) Cod spawning on a migration highway in the north-west Atlantic. *Nature* 366:458–461
- ✦ Scott JD, Courtney MB, Farrugia TJ, Nielsen JK, Seitz AC (2016) An approach to describe depth-specific periodic behaviour in Pacific halibut (*Hippoglossus stenolepis*). *J Sea Res* 107:6–13
- ✦ Shepard ELC, Ahmed MZ, Southall EJ, Witt MJ, Metcalfe JD, Sims DW (2006) Diel and tidal rhythms in diving behaviour of pelagic sharks identified by signal processing of archival tagging data. *Mar Ecol Prog Ser* 328: 205–213
- ✦ Sims DW, Southall EJ, Richardson AJ, Reid PC, Metcalfe JD (2003) Seasonal movements and behaviour of basking sharks from archival tagging: no evidence of winter hibernation. *Mar Ecol Prog Ser* 248:187–196
- ✦ Sims DW, Wearmouth VJ, Southall EJ, Hill JM and others (2006) Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. *J Anim Ecol* 75:176–190
- ✦ Sims DW, Southall EJ, Humphries NE, Hays GC and others (2008) Scaling laws of marine predator search behaviour. *Nature* 451:1098–1102
- Stephens DW, Krebs JR (1986) Foraging theory. The Princeton University Press, Princeton, NJ
- ✦ Strand E, Huse G (2007) Vertical migration in adult Atlantic cod (*Gadus morhua*). *Can J Fish Aquat Sci* 64:1747–1760
- ✦ van Duren LA, Glass CW (1992) Choosing where to feed: the influence of competition on feeding behaviour of cod, *Gadus morhua* L. *J Fish Biol* 41:463–471
- Walli A, Teo SLH, Boustany A, Farwell CJ and others (2009) Seasonal movements, aggregations and diving behavior of Atlantic bluefin tuna (*Thunnus thynnus*) revealed with archival tags. *PLOS ONE* 4:e6151

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