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Vertical migrations of saithe (*Pollachius virens*) in Icelandic waters as observed with data storage tags

Hlynur Armannsson[1]* and Sigurður Þór Jónsson[2]

[1]*Marine Research Institute and University of Akureyri, Borgir v/Norðurslod, 600 Akureyri*
[2]*Marine Research Institute, Skúlagata 4, PO Box 1390, 121 Reykjavík, Iceland*

**Corresponding Author: tel: +354 4608970; fax: +354 4608998; e-mail: hlynur@unak.is*

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Knowledge of fish behaviour is important for general understanding of fish life history and responses to environmental and biological conditions. Vertical migrations can affect bottom trawl indices of the fish through their availability to the trawl and acoustic indices through changes in target strength. Here we present results based on data sets of hourly recordings of depth from 51 saithe. The data were analysed with respect to diel and seasonal differences in saithe vertical movement. Duration and extent of vertical movements were analysed with 1 min resolution, and the daily vertical range (DVR) was analysed with respect to potential use of the free vertical range (FVR). Our results show diel and seasonal differences in hourly depth changes of saithe, indicating reduced activity during night-time and in winter. Individual saithe are capable of rapid depth changes in <1 min, often of the same order as the maximum observed in movements of longer duration. The DVR often exceeded the FVR, and in some instances exceeded critical limits, indicating that saithe may at times only maintain neutral buoyancy near the upper limit of their daily vertical range.

Keywords: data storage tags, DST, *Pollachius virens*, saithe, vertical migration.

Introduction

Vertical migration of fish is in most cases described as an optimization of predation risk vs. food consumption and/or utilization of energetic refuges having suitable temperatures or currents (Neilson and Perry, 1990; Helfman, 1993; Gauthier and Rose, 2002). Vertical migrations of gadoids are often associated with changes in light intensity, i.e. an active day period and a more passive phase at night (Clark and Green, 1990; Bjordal and Johnstone, 1993; Sarno *et al.*, 1994; Lawson and Rose, 1999; Løkkeborg and Fernö, 1999; Cote *et al.*, 2002), and can have a major influence on fish surveys and interpretation of fisheries data (Michalsen *et al.*, 1996; Aglen *et al.*, 1999; Korsbrekke and Nakken, 1999; Petrakis *et al.*, 2001).

Variations in vertical migrations may affect density estimates commonly used in stock assessment, such as the availability of fish to bottom trawls (Michalsen *et al.*, 1996; Aglen *et al.*, 1999; Petrakis *et al.*, 2001). Acoustic density estimates of semi-demersal fish may also be affected by vertical migrations because a variable proportion of the fish is located in the acoustic bottom dead zone (Ona and Mitson, 1996; Aglen *et al.*, 1999; Lawson and Rose, 1999). Furthermore, vertical migrations are likely to cause changes in the target strength of the fish, through changes in the size of the swimbladder and in the tilt angle (Harden Jones and Scholes, 1985; Arnold and Greer Walker, 1992; McQuinn and Winger, 2003; Hjellvik *et al.*, 2004). The reliability of the indices, therefore, depends on the stability of the bias caused by the vertical distribution (Aglen *et al.*, 1999; Godø and Michalsen, 2000).

Compared with other gadoid species, saithe spend more time in the pelagic habitat and less time at the bottom (Scott and Scott, 1988), and these movements are variable with regards to season and time of day (Schmidt, 1955; Bergstad, 1991; Neilson *et al.*, 2002, 2003). Seasonal changes in depth distribution have also been reported where juvenile fish migrate from shallow to deeper water during the winter and return the following summer (Olsen, 1959, 1961; Jones and Jónsson, 1971; Bergstad *et al.*, 1987; Nedreaas, 1987; Bergstad, 1990, 1991; Armannsson *et al.*, 2007). Neilson *et al.* (2003) reported, based on hydroacoustic information, that saithe become more densely aggregated at night, and diurnal movement patterns of saithe have been observed, with the highest activity and feeding levels occurring during daytime (Bjordal and Johnstone, 1993; Sarno *et al.*, 1994).

Saithe has a closed swimbladder and is thus defined as a physoclist. To maintain neutral buoyancy, physoclists need to fill their swimbladder by gas secretion in downward migration and remove gas by resorption in upward migration, but these processes both take time and cost energy (Blaxter and Tytler, 1978; Harden-Jones and Scholes, 1985). The depth of neutral buoyancy is determined by the gas content of the swimbladder, and the free vertical range (FVR) delimits the depth range within which the fish can deviate from neutral buoyancy through swimming (Blaxter and Tytler, 1978; Harden-Jones and Scholes, 1985; Arnold and Greer Walker, 1992). Blaxter and Tytler (1972) and Tytler and Blaxter (1973) concluded that saithe and cod have a similar FVR based on results from pressure adaptation experiments.

A physoclist risks an uncontrolled rise to the surface or rupture of the swimbladder by ascending too rapidly out of its FVR (Harden Jones, 1951; Tytler and Blaxter, 1973; Harden Jones and Scholes, 1985). On the other hand, descending some distance below the current FVR is probably not a major obstacle to vertical movements (Harden Jones and Scholes, 1985; Arnold and Greer Walker, 1992; Stensholt *et al.*, 2002). Alexander (1971) argued that cod were probably negatively buoyant most of the time, and this was later demonstrated under controlled conditions by Harden Jones and Scholes (1985) and verified in the field by Arnold and Greer Walker (1992). Other studies have described similar results (Godø and Michalsen, 2000; Righton *et al.*, 2001; van der Kooij *et al.*, 2007). Harden-Jones and Scholes (1985) also noted that the extent of diel vertical migrations might be expected to vary with both season and latitude.

Ground fish trawl survey indices have been used as fishery-independent indices in age-based assessments of saithe in Icelandic waters since 2002 (ICES, 2002, 2010a). Similarly, survey indices, either acoustic or from bottom trawl surveys, are used in all other age-based assessments of saithe in the North Atlantic (Stone *et al.*, 2009; ICES, 2010a, b, c, 2011), although their use has been qualified in some cases because of high coefficients of variations (see, for example, Stone *et al.*, 2009 and stock annexes for Icelandic and Faroe saithe in ICES, 2011). Since vertical migration may affect density measurements from both acoustic and bottom trawl surveys, shedding light on the vertical behaviour of saithe may assist in interpreting the highly variable indices of saithe abundance that are used in stock assessments.

Here, we present data from a major data storage tag (DST) tagging study of saithe vertical migration. Our objective was to analyse diel and seasonal changes in vertical migration, and to explore possible causal factors. Furthermore, we describe the swimming behaviour of saithe in terms of the extent and the duration of upward and downward movements of the fish. We also compare hourly depth change from the DST data with the proportion of saithe in catches from logbook data, in order to evaluate how vertical migration affects commercial catches of saithe. Finally, we analyse vertical profiles of saithe with regards to the 'theoretical' free vertical range available. Such findings are important for understanding of the vertical behaviour of saithe, and in evaluating the reliability of survey estimates of saithe abundance.

Material and methods

Tagging

A total of 184 saithe were tagged in shallow water with DSTs at several locations around Iceland in late summer–early autumn 2002–2004 and 2007 (Figure 1). The timing was chosen to facilitate the capture of saithe in shallow water, thereby enhancing survival, since attempts at tagging adult saithe in offshore waters have been unsuccessful (Schmidt, 1955; Clay *et al.*, 1989; authors' own unpublished data). The DST tagging was conducted alongside tagging with traditional T-bar anchor tags as described by Armannsson *et al.* (2007). The T-bar tagging can contribute to a broad understanding of distribution and migration of the saithe population around Iceland, while the focus of the DST tagging was on individual behaviour. Saithe were captured on small boats using jigging devices, and No. 7 J-hooks with artificial rubber bait and crushed barbs to minimize wounding. Once on board, the fish were kept in 400 litre plastic tanks with flowing seawater until tagging, 1–5 min later. Only saithe in the upper part of the size distribution and judged to be in good condition were selected for DST tagging. Saithe deemed in 'good condition' had no visible or only minimal wounds and showed no swimming

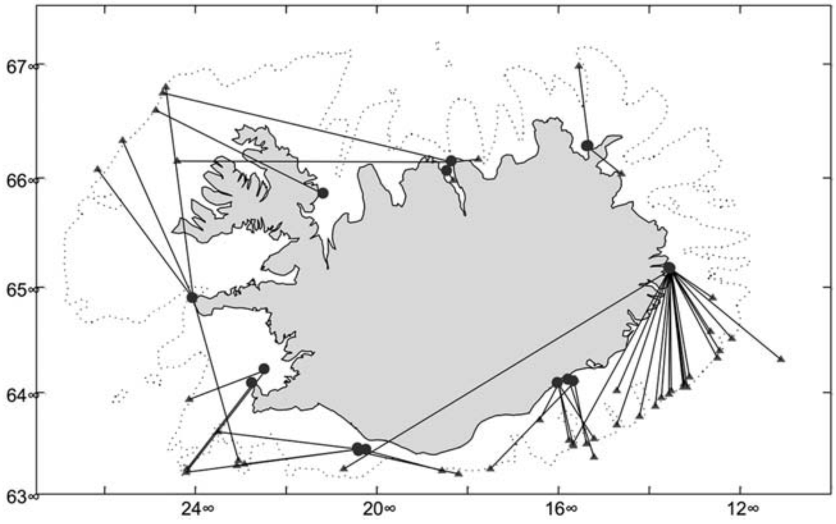

Figure 1. Geographical distribution of tagging sites (circles) and recapture localities (triangles) of 51 recaptured saithe tagged with DSTs. The 200 m isobath is shown with a dotted line.

Table 1. Number of fish at liberty in each month of the year and number of recordings in each month.

	Jan.	Feb.	Mar.	Apr.	May.	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
No. of fish at liberty	31	31	28	28	23	20	26	38	46	41	33	33
No. of recordings	23 808	20 856	21 576	20 214	15 104	12 597	14 512	24 878	32 014	29 889	27 178	25 367

abnormality while in the holding tank prior to tagging. The total lengths of saithe, tagged with DST tags, ranged from 42 to 83 cm (mean length 54 cm).

Data storage tags and implantation

DST-milli data storage tags (size 12.5 × 38.4 mm, weight ~5 g in water) were used in this study (Star Oddi, Marine Device Manufacturing Ltd, Reykjavik, Iceland). To each tag, 8 cm of yellow tubing, with 1 mm diameter (similar to the marker of a T-bar anchor tag), was attached. The data storage capacity was up to 87 000 measurements, and each tag was programmed to record depth and temperature at hourly intervals during the 3 year battery life of the tag. Measurements at 1 min intervals were made in a subset of tags.

Before implanting a DST, all surgical instruments and the tag were disinfected with betadine alcohol solution. Saithe to be tagged were removed from the holding tank, with a knotless dip net, and placed on a measuring board where the total length was measured to the nearest centimetre. A small incision, ~15 mm long, was made into the abdominal cavity on the left side of the belly, slightly above and behind the anal opening. The tag indicator was threaded into a hollow needle and the needle was then inserted through the incision and poked through the abdominal wall 3–4 cm further back. The needle was then pulled through and the tag pulled into the abdominal cavity, leaving the coloured tubing protruding from the posterior perforation. We decided not to suture the incision since our earlier pilot tagging experiments, performed in the Marine Research Institute (MRI) mariculture laboratory, did not indicate better recovery of fish which were sutured. To increase the likelihood of fishers noticing the tag, a second external tag was attached at the base of the first dorsal fin, with traditional T-bar anchor tag. Floy tags (Floy Manufacturing, Seattle, WA, USA) were used in the years 2000–2004, with Hallprint tags (Hallprint Ltd, Victor Harbour, South Australia) introduced in 2004 and used since then. After surgery, the fish were allowed to recover in a tank filled with fresh seawater for 5–10 min. If the fish sought bottom vigorously and otherwise did not show abnormal behaviour or exhibit difficulty in buoyancy control, the incision was sprayed with disinfectant solution and the fish released overboard. Fish tagging activities were conducted under licence number 0304-1901 issued by the Icelandic Committee for Welfare of Experimental Animals at the Icelandic Food and Veterinary Authority, Reykjavik. Each tag was imprinted with a unique identification number and a return address, printed in Icelandic. On each tagging site, information about position, date and time, depth, and weather was gathered.

Recaptures

Upon recapture, fishers were asked to return tags and otoliths to the MRI along with information about fishing gear, position, depth and date of recapture, length, sex, and sexual maturity of the fish. Fishers were asked to return the fish itself to the MRI, if possible. For each DST tag returned, a reward of 4000 ISK (equivalent to ~€25) was offered. An additional 1000 ISK (€6) reward was paid for the second external T-bar tag if both tags were returned. In addition to the reward, the finder was provided with a summary of release and recapture information for each tag returned and a printout of the data stored in the tag.

By late 2011, the total recaptures of DSTs were 62, or 33.7% of the released tags. Median time at liberty was ~15 months and the maximum almost 8 years. Technical failures or early recaptures led to exclusion of some returned tags, resulting in 51 tags available for this study. Recordings from the first 2 weeks at liberty were omitted since analyses of the data revealed unusual behaviour patterns for some time after tagging which were believed to reflect recovery from the tagging treatment. Cod DST tagging experiments have shown similar post-release behaviour (Godø and Michalsen, 2000; Heffernan *et al.*, 2004; Neat *et al.*, 2006; van der Kooij *et al.*, 2007). The released tags were recording, over variable periods, from July 2002 to June 2005 and from July 2007 to December 2008. The number of fish at liberty with live tags ranged from 20 to 46 per month, and the number of recordings ranged from 14 500 to 32 000 (Table 1).

Analyses of vertical movements

In the analyses of diel and seasonal differences in vertical movements, we used changes in depth (Δz) at hourly intervals. In order to evaluate whether vertical migration could affect commercial catches of saithe, we used data from commercial fishing logbooks. We studied the proportion of saithe in commercial bottom trawl catches, in hauls where saithe were recorded, in the period 1991–2008. Hourly depth change from the DST data, and the proportion of saithe in catches from logbook data, were averaged by month and hour for presentation as contour plots. It should be noted that at Iceland longitudes, the sun is in its highest position from ~13:00 to 14:00 h, on a time axis given in GMT.

For the analysis of depth changes from data with 1 min resolution, the accuracy of the tags was analysed. The tags measured pressure with an accuracy of ~0.4% and a resolution of 0.03% of the selected pressure and depth range. In this pilot DST study, tags were calibrated for different depth ranges, with an upper limit of 1–10 m and a lower limit of 250, 400, and 760 m, and accuracy in depth readings of ~1, 1.5, and 3 m, respectively. Assuming two depth measurements, z_1 and z_2, to be normally and independently distributed with means μ_1 and μ_2 and the same standard deviation, σ:

$$z_1 \sim N(\mu_1, \sigma) \text{ and } z_2 \sim N(\mu_2, \sigma) \tag{1}$$

the difference between the two, Δz, is:

$$\Delta z \sim N(\mu_2 - \mu_1, \sqrt{2}\sigma), \tag{2}$$

i.e. a given reading accuracy multiplied by $\sqrt{2}$ should be the accuracy of the difference between two consecutive readings. However, short-term changes were likely to be measured more accurately, possibly close to the specified resolution, which was an order of magnitude smaller than the accuracy

(S. Guðbjörnsson, Star-Oddi, pers. comm.). This is due to differencing which will remove tag bias and possible drift over time of the pressure sensor. As the accuracies of the DSTs varied, we chose the value of 3 m, *ad hoc*, as the criterion for picking out directed movement, putting emphasis on 'considerable' depth changes. Thus, a run was defined as a series of consecutive measurements, with $|\Delta z| > 3$ m, all increasing or all decreasing in depth. Readings at 1 min intervals were available from 19 recaptured saithe for a total of 78 d in September–October 2003 and 2004 and January 2005. The September–October series started 2 months after tagging, and the January series started 5 months after tagging.

Daily vertical range (DVR) and free vertical range (FVR)

The DVR is calculated as the difference between the greatest depth $z_{\max}$ and the shallowest depth $z_{\min}$ for each day:

$$\mathrm{DVR} = z_{\max} - z_{\min} \tag{3}$$

Based on the assumption that saithe have about the same sensitivity to pressure decrease as cod (Blaxter and Tytler, 1972; Tytler and Blaxter,1973) and that cod tolerate 25% reduction in pressure and 50% increase in pressure without showing abnormal behaviour (Harden-Jones and Scholes, 1985), we calculate the daily FVR from the daily mean residence depth (D_{mean}), based on hourly depth recordings, as:

$$\mathrm{FVR} = D_{\max} - D_{\min} \tag{4}$$

$$D_{\max} = 1.5(D_{\mathrm{mean}} + 10) - 10 \tag{5}$$

$$D_{\min} = 0.75(D_{\mathrm{mean}} + 10) - 10 \tag{6}$$

The value of 10 is added to the equation because depth is used instead of pressure in the calculations, and one atmosphere equals 10 m water pressure. The use of the daily, potential FVR of an individual fish was calculated as the ratio DVR/FVR.

The swimbladder of cod and saithe ruptures if exposed to pressure reduction of 60–70% (Tytler and Blaxter, 1973). To find out if the upper limit of the DVR was within these boundaries, we calculated the critical limit of depth (D_{crit}) from the daily mean residence depth as:

$$D_{\mathrm{crit}} = 0.40(D_{\mathrm{mean}} + 10) - 10 \tag{7}$$

Earlier studies show that depth recordings at hourly intervals for cod underestimate the real vertical movement rate of individual fish (Heffernan *et al.*, 2004). Therefore, we compared the DVR with hourly resolution against DVR with 1 min resolution.

Results

Monthly distributions of depth recordings from the whole data set of 51 DSTs indicated a seasonal trend in the depth preference of the saithe, i.e. a movement from deep to shallow water during summer (May–July) and back to deeper water in winter (November–March; Figure 2). The median depth was largest during March–April (~140 m) but shallowest during summer and autumn (<50 m). The large number of outliers in September and October indicate different times of departure to deeper water in the autumn, while the broad range during summer indicates that some of the saithe remain in deep water.

The hourly depth changes are shown as a contour plot in Figure 3a by time of day and month, pooled over years. The average hourly depth change was highest during daylight hours, and nocturnal activities were much reduced in winter (Figure 3a). It is also noteworthy that the tagged saithe seemed to be more active in the early hours of daylight compared with later in the day. The activity is lowest in July (Figure 3a), which is the month of the year with the shallowest median depth

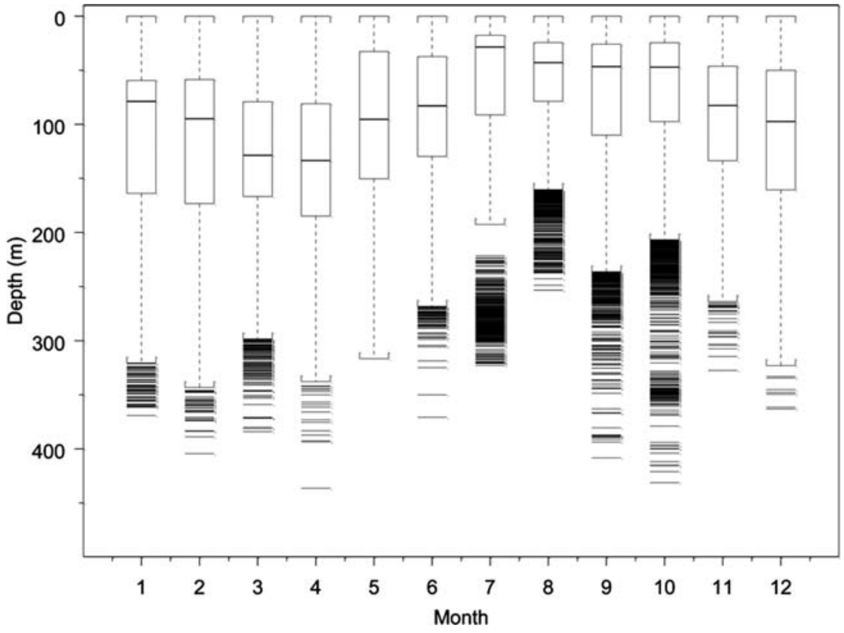

Figure 2. Boxplot of 268 018 hourly depth recordings from 51 DST tags by months, showing median (black middle line), interquartile range (IQR; box), 1.5 × IQR (whiskers), and black lines (outliers). Note that large number of outliers produced a dark bar below July–October whiskers.

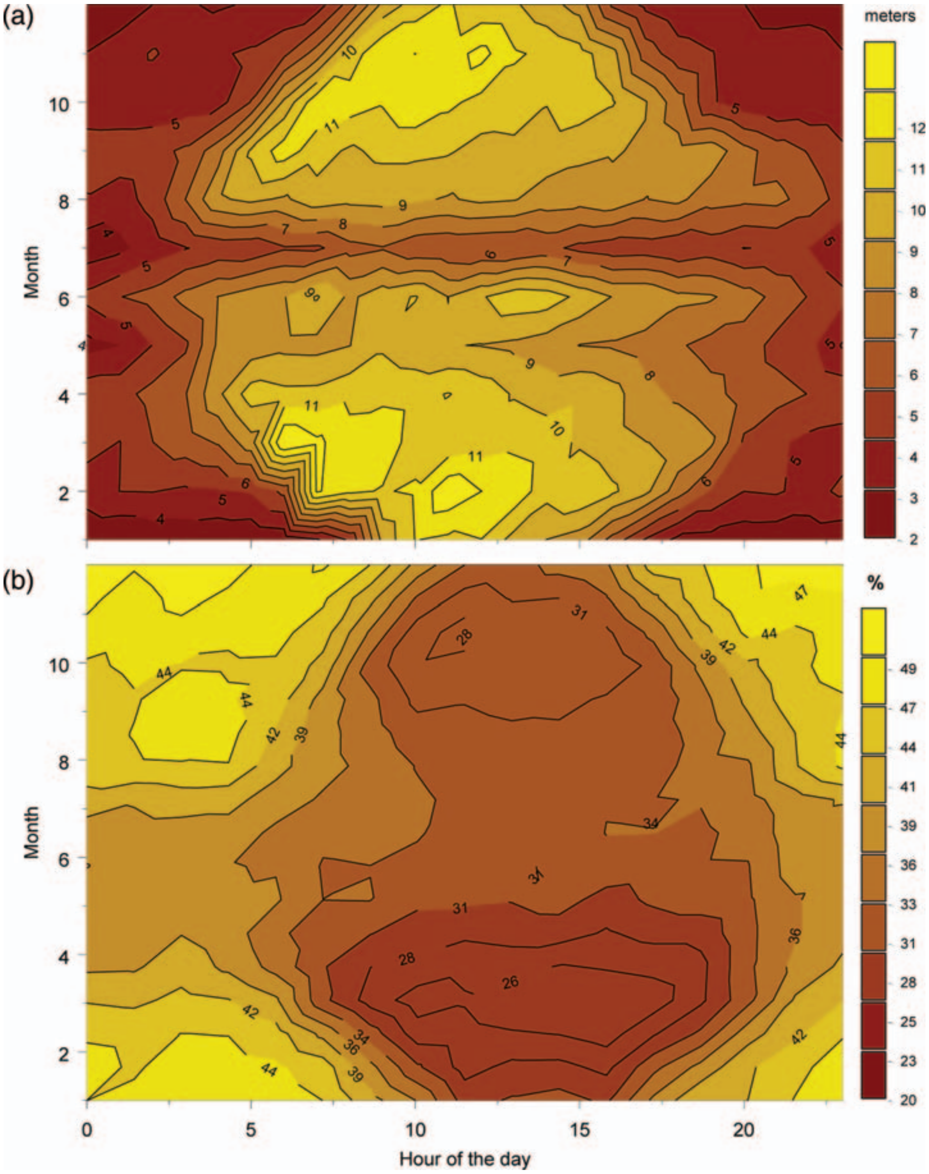

Figure 3. Contour plot of (a) the 'activity pattern' of saithe by time of day and month. Means of absolute hourly depth change ($|\Delta z|$) in metres are shown. (b) Mean proportion of saithe reported in catches (1991–2008) by month of year and time of day.

(Figure 2). The proportion of saithe in trawler catches by month and time of day (Figure 3b) followed a similar but inverted trend. The proportion was highest during the hours of darkness but diminished during the hours of daylight. This pattern was especially evident in the first 2 months of the year.

The maximum upward or downward movement (Δz) for run lengths from 1 to 8 min for each of the 19 tags is given in Table 2. No runs of >8 min duration that met the set criteria were found in the data set. The behaviour of individual saithe was highly variable; some travelled great distances up and down the water column in a relatively short space of time (i.e. 6009, 919, 6002, and 734), while others were more passive (i.e. 909, 914, and 6012). Time spent moving rapidly (moving at >3 m min^{-1}) up or down varied between individuals and ranged from 0.2% to 33% (average ~15%) (Figure 4).

The DVR was positively related to median residence depth of individual saithe (Figure 5a). The DVR/FVR ratio declined as the median residence depth increased (Figure 5b). This means that individual saithe exceeded the limits of FVR more frequently when residing at shallower depth.

Individual saithe remained within their FVR, as calculated from the mean residence depth, on the majority of days (63%; Figure 6). On 22% and 2% of the days, individuals travelled above or below the FVR limit, respectively, and on 13% of days the saithe crossed both the upper and lower limits. In 197 instances (1.8%), the saithe travelled above the D_{crit} level, as calculated from the daily mean depth. The DVR/FVR ratio differed between months, and was highest during August–September and lowest in December–January (Figure 7). DVRs calculated with 1 min intervals were in most cases considerably higher than DVRs calculated with hourly intervals (Figure 8). On average, DVRs calculated with hourly intervals underestimated the DVR by 70% as compared with DVRs calculated with 1 min intervals.

Table 2. Maximum extent of upwards (↑) and downwards (↓) movements (runs) for each DST where |Δz| >3 m between consecutive 1 min depth recordings, either all increasing or all decreasing in depth.

DST no.	Length (cm)	Run length (min)															
		1		2		3		4		5		6		7		8	
		↓	↑	↓	↑	↓	↑	↓	↑	↓	↑	↓	↑	↓	↑	↓	↑
715	62	−51.0	35.5	−54.3	37.4	−43.7	34.2	−38.5	34.7								
723	42	−23.3	33.5	−31.5	37.8	−32.5	23.7	−22.1	25.3	−20.0							
725	57	−18.2	20.7	−22.9	23.8	−24.3	21.0	−29.0	20.6	−26.2							
727	68	−24.1	19.8	−40.0	22.8	−44.8	27.0	−54.6	30.8		34.4						
734	50	−33.5	21.4	−43.7	32.7	−51.7	40.2	−55.6	48.4	−58.4	47.2	−63.0					
737	49	−34.4	29.0	−43.8	32.3	−32.7	39.5	−36.2	32.1		30.3						
908	49	−27.7	17.8	−26.5	23.6	−29.6	26.6	−16.5									
914	49	−8.9	7.7	−9.8	10.5												
918	50	−86.1	76.7	−76.2	83.9	−69.2	86.9	−72.4	87.3	−40.4	75.2	−26.2	52.4				
919	58	−51.2	42.1	−35.3	52.9	−42.7	57.8	−49.4	68.7	−54.7	46.9	−62.2	44.7	−61.3	48.7	−54.5	
6002	77	−30.6	20.1	−36.5	35.7	−39.2	45.5	−44.1	42.4	−45.5	46.6	−48.5	43.3				
6009	57	−29.8	27.2	−47.1	44.7	−61.3	58.9	−78.6	66.3	−89.9	83.4	−96.7	88.2	−104.4		−110.9	
6012	78	−7.6	6.6														
6017	79	−28.8	18.3	−31.6	23.4	−32.8	27.8	−29.9	32.1	−29.4							
728	50	−9.9	11.0	−17.0	13.6	−15.3	19.7										
739	47	−18.4	13.5	−11.5	8.0												
907	46	−14.7	20.0	−12.9	19.4												
909	62	−4.1	4.8														
853	51	−33.9	20.2	−37.0	25.4	−31.1	26.8	−35.5	30.8								

Lengths represent length at tagging.

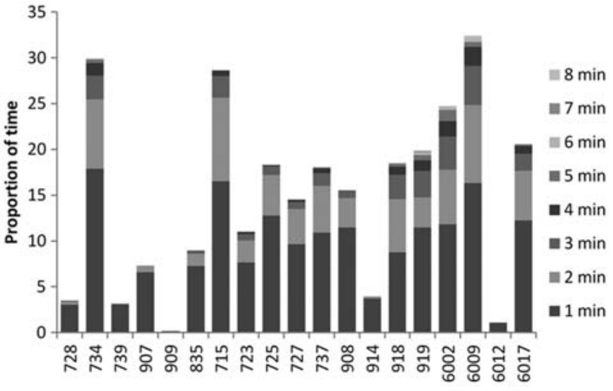

Figure 4. Proportion of time devoted to runs (|Δz| >3 m between consecutive 1 min depth measurements) of different duration by individual tagged fish. Numbers represent tag numbers.

Discussion

The DST data showed seasonal changes in depth distribution when saithe moved from deep to shallow waters in summer, then back to deeper waters in late autumn. This is in accordance with the results from Armannsson *et al.* (2007) on the depth distribution of recaptured saithe with traditional T-bar anchor tags. The tagged fish were on average in deeper waters during winter (Figure 2) with greater scope for vertical movement, since the deeper a fish travels the greater its FVR will be (Blaxter and Tytler, 1978; Harden-Jones and Scholes, 1985; Arnold and Greer Walker, 1992). Diel and seasonal patterns in hourly depth changes indicated reduced vertical activity during night-time and in winter, consistent with the findings of Johnstone *et al.* (1991), Glass *et al.* (1992), Bjordal and Johnstone (1993), and Sarno *et al.* (1994), all of whom reported reduced night-time activity in their studies of saithe.

Saithe have been described as voracious predators (Du Buit, 1991), and adult saithe around Iceland prey mostly on pelagic fish and krill (Pálsson, 1983; Jónsson, 1996). Reduced activity during the hours of darkness could be attributed to the fact that saithe are visual feeders that forage in the daylight hours. It is thus likely that night-time behaviour is more relaxed and less directed. Bjordal and Johnstone (1993) and Sarno *et al.* (1994) both reported a higher activity and feeding level of saithe during daytime in their studies. Cod, who are also visual feeders, have been shown to exhibit a similar activity rhythm, with higher swimming speeds and a larger activity range during the day than at night (Lawson and Rose, 1999; Løkkeborg and Fernö, 1999). Diel patterns in activity and catch proportions suggest a connection between catchability and diel activity. The reduced activity of saithe during night-time is reflected in logbook data on saithe catches, where the proportion of saithe in the catches was higher during the night (Figure 3b). An alternative explanation could be that during daylight the fish can see the gear at a greater distance, and a larger proportion may thus escape (Petrakis *et al.*, 2001). Neilson *et al.* (2003) reported, based on hydroacoustic information, that saithe become more densely aggregated at night, which could explain a night-time increase in the proportions of saithe in commercial catches.

As shown in Figure 5a, the DVR is positively related to the median depth during the day. Since the FVR increases with depth (Harden-Jones and Scholes, 1985), this outcome is in accordance with expectations. This could explain the maxima in diel depth changes observed in daytime in winter, as seen in Figure 3a, since saithe were on average in deeper water during the winter. Harden-Jones and Scholes (1985) also noted that the extent of diurnal vertical migration

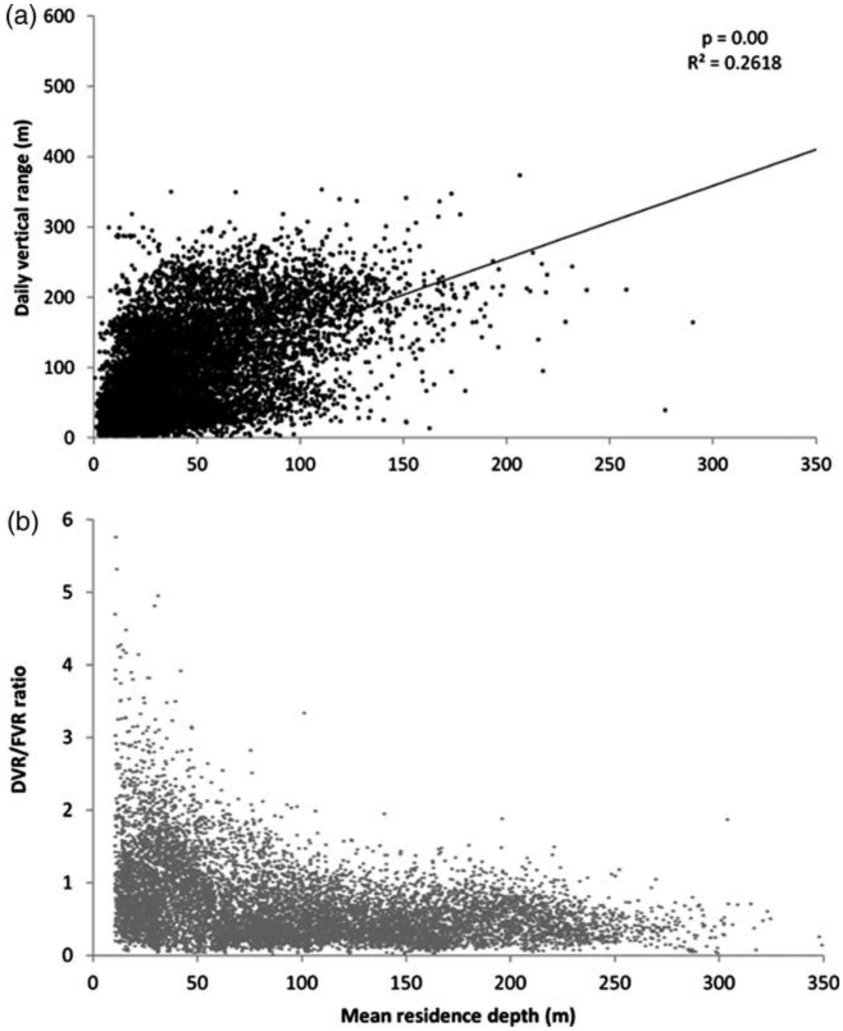

Figure 5. (a) Observed daily vertical range (DVR) and (b) the DVR/FVR ratio, against the mean residence depth of individual saithe.

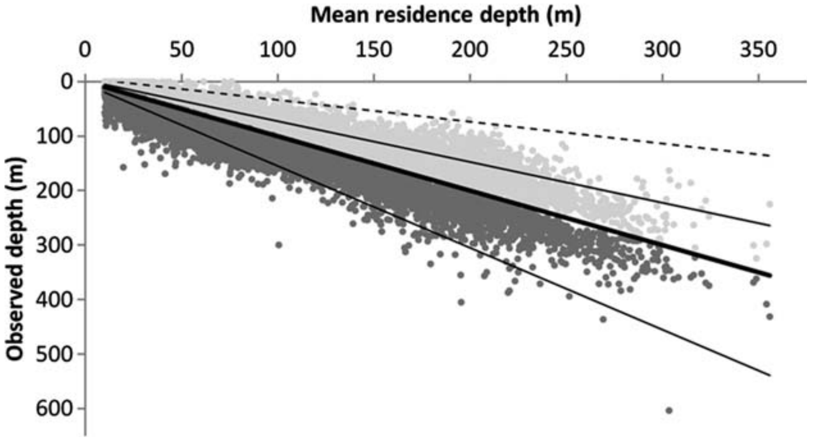

Figure 6. Upper (D_{max}) and lower (D_{min}) depth limit of the FVR shown by narrow black lines, as calculated from the daily mean residence depth shown by a broad black line. The critical depth (D_{crit}) is shown as a dashed line. The daily maximum and minimum depths are shown in dark grey and light grey, respectively.

might be expected to vary with both season and latitude, since, if neutral buoyancy is to be maintained throughout a diurnal vertical migration, the height that a fish (cod in their example) could be expected to rise above the daytime depth in midwater should not exceed, in meters, the hours of darkness available for descent.

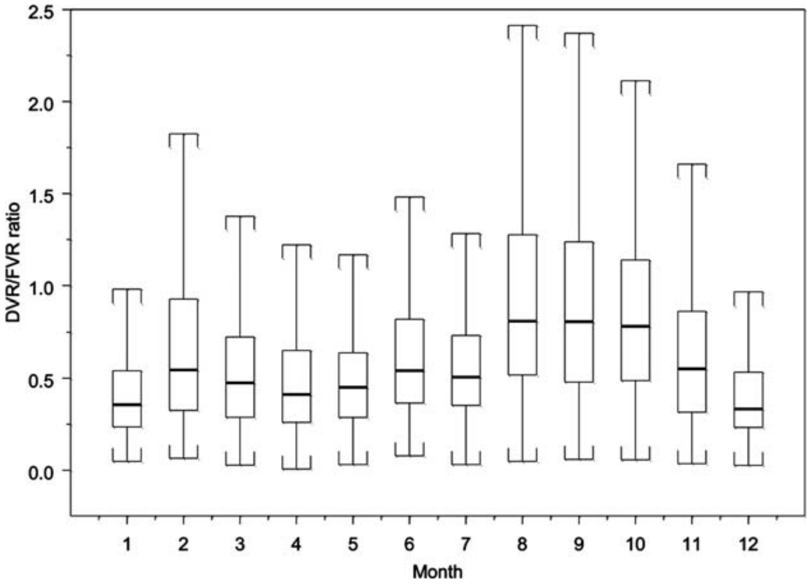

Figure 7. Boxplot of the DVR/FVR ratio by months, showing median (black middle line), interquartile range (IQR; box), and 1.5 × IQR (whiskers). Outliers are not shown.

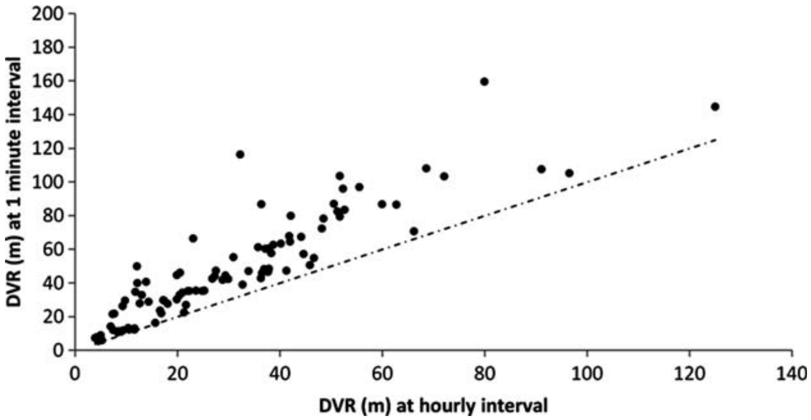

Figure 8. Comparison of the DVR calculated with hourly resolution against DVR calculated with 1 min resolution. The broken line represents values if there was no difference.

Judging from depth recordings at 1 min intervals, saithe are capable of depth changes in less than a minute of the same order as the maximum achieved in runs of longer duration. These maximum rates of vertical movement were in most cases inconsistent with the maintenance of neutral buoyancy. In comparison, Heffernan *et al.* (2004) reported that high-frequency depth data in their study provided evidence that cod routinely and frequently make vertical movements with maxima inconsistent with the maintenance of neutral buoyancy, and Arnold and Greer Walker (1992), Godø and Michalsen (2000), and Righton *et al.* (2001) have all reported vertical movements of cod which are inconsistent with the maintenance of neutral buoyancy at all depths.

Assuming that the theoretical physiological limits for pressure changes are similar for saithe and cod, saithe seem to remain inside its FVR for the majority of days. Compared with results regarding cod described by Righton *et al.* (2001), saithe more often exceed the limits of the FVR, especially if we consider higher recording frequency in their study (10 min intervals vs. hourly intervals). When we look at the DVR/FVR ratio (Figure 5b), individuals travel relatively more frequently outside their FVR when dwelling in shallow water than in deep water, which is in accordance with results on cod from Righton *et al.* (2001), although their ratio was never as high as that presented here for saithe. The reason could be that the FVR is relatively large in deeper water and more likely to meet the foraging requirements of saithe. In shallower water, the FVR will, on the other hand, be relatively short and, therefore, a greater foraging range will be available if individuals are negatively buoyant at their mean daily depth. An inspection of the highest DVR/FVR ratios revealed that most of the time they resulted from a large descent during the day rather than a large ascent, which indicates that these individuals are strongly negatively buoyant during these deep dives.

Vertical migration of fish poses challenges for abundance estimation. Bottom trawl surveys only capture fish relatively close to the bottom, and thus become biased if the availability of the fish to the trawl changes from year to year (Michalsen *et al.*, 1996; Aglen, *et al.*, 1999; Korsbrekke and Nakken, 1999; Petrakis, *et al.*, 2001). Acoustic measurements may also be affected by the vertical migration, e.g. when fish are inaccessible in the acoustic dead zone near the bottom (Ona and Mitson, 1996; Aglen *et al.*, 1999; Lawson and Rose, 1999) or when vertical migrations are affecting the target strength of the fish (Harden Jones and Scholes, 1985; Arnold and Greer Walker, 1992; McQuinn and Winger, 2003; Hjellvik *et al.*, 2004). Based on our results, it is clear that saithe are often negatively or positively buoyant; the resulting size differences in swimbladder would therefore contribute to variability in target strength. Individual saithe also continually change their tilt angle in the water column because of frequent ascent and descent. Heffernan *et al.* (2004) came to the same conclusion regarding acoustic returns from cod in the Barents Sea, the North Sea, and the Irish Sea.

Our research has demonstrated that vertical migrations of saithe vary between seasons and time of the day. The reduced vertical activity during the hours of darkness will influence abundance indices from both surveys and fisheries, and should be considered when interpreting the results. The results show that saithe can be negatively buoyant at their mean daily depth in order to increase their foraging range. It is obvious, by comparing DVRs from hourly intervals with DVRs from 1 min intervals, that the former greatly underestimate the real DVR (Figure 8), and the same will also be the case with the activity pattern. Therefore, we classify the results presented here as minimum values, useful for comparison, but not as the 'true values'. Our results agree with those of Heffernan *et al.* (2004) stating that low-frequency sampling (e.g. 1 h resolution) can underestimate the real maximum rate of vertical movement of fish. Furthermore, saithe seem to spend a relatively high proportion of the time on directed runs, which will influence tilt angle and therefore the acoustic target strength of individual fish.

Our tagging experiment shows that it is feasible to tag saithe caught in shallow waters intraperitoneally with DSTs and that the saithe can carry the DSTs for many years. The resulting data add to information on factors affecting saithe abundance measurements and will also aid in our general understanding of saithe biology. Future work should focus on increasing the length distribution of tagged fish and expanding the study area, possibly by co-operation in saithe tagging between fishing nations in the North East Atlantic. DSTs with higher memory capacity have become available since our tagging, and could be deployed to give both more frequent and longer time-series of depth and temperature for the fish. Comparing saithe and cod DST results would also be of interest.

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